

## Review article

## Event-related fMRI studies of false memory: An Activation Likelihood Estimation meta-analysis



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## ABSTRACT

Over the last two decades, a wealth of research in the domain of episodic memory has focused on understanding the neural correlates mediating false memories, or memories for events that never happened. While several recent qualitative reviews have attempted to synthesize this literature, methodological differences amongst the empirical studies and a focus on only a sub-set of the findings has limited broader conclusions regarding the neural mechanisms underlying false memories. The current study performed a voxel-wise quantitative meta-analysis using activation likelihood estimation to investigate commonalities within the functional magnetic resonance imaging (fMRI) literature studying false memory. The results were broken down by memory phase (encoding, retrieval), as well as sub-analyses looking at differences in baseline (hit, correct rejection), memoranda (verbal, semantic), and experimental paradigm (e.g., semantic relatedness and perceptual relatedness) within retrieval. Concordance maps identified significant overlap across studies for each analysis. Several regions were identified in the general false retrieval analysis as well as multiple sub-analyses, indicating their ubiquitous, yet critical role in false retrieval (medial superior frontal gyrus, left precentral gyrus, left inferior parietal cortex). Additionally, several regions showed baseline- and paradigm-specific effects (hit/perceptual relatedness: inferior and middle occipital gyrus; CRs: bilateral inferior parietal cortex, precuneus, left caudate). With respect to encoding, analyses showed common activity in the left middle temporal gyrus and anterior cingulate cortex. No analysis identified a common cluster of activation in the medial temporal lobe.

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## Contents

1. Introduction	150
1.1. Memory phases	150
1.1.1. Retrieval	150
1.1.2. Encoding	151
1.2. Experimental design considerations	151
1.2.1. Experimental paradigm	151
1.2.2. Memoranda type	151
1.2.3. Baseline contrast	152
1.3. Neural correlates mediating false memories	152
1.4. The present study	153
2. Methods	153
2.1. Systematic searches and inclusions criteria	153
2.2. Contrast selection and analyses	154
2.3. Activation Likelihood Estimation	157
3. Results	159
3.1. General false retrieval	159
3.2. Hit baseline	159

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3.3.	CR baseline. ....	159
3.4.	Verbal stimuli ....	159
3.5.	Pictorial stimuli ....	159
3.6.	Semantic relatedness. ....	159
3.7.	Perceptual relatedness. ....	159
3.8.	Encoding ....	159
4.	Discussion ....	160
4.1.	General false retrieval ....	161
4.2.	Examining hit and CR baselines at retrieval. ....	163
4.3.	Verbal and pictorial memoranda at retrieval ....	164
4.4.	Encoding studies ....	164
5.	Conclusions ....	165
5.1.	Limitations and future directions ....	165
	Acknowledgments. ....	165
	Appendix A. Supplementary material. ....	165
	References ....	165

## 1. Introduction

Human memory is inherently prone to distortion. For years, researchers have sought to characterize the fallibility of memory (for review see [Schacter \(1999\)](#)). While traditionally research into memory errors has investigated the subjective experience of forgetting, more recently research has explored false memories, or memory for facts, items, or events that never happened ([Brainerd and Reyna, 2005](#)). Examples include remembering you drafted and sent an email, when in fact you did not; remembering that lettuce and celery were on a grocery list, when in fact tomatoes and cucumbers were the to-be-purchased vegetables; and remembering that the new co-worker's name was 'Rick' when in fact it was 'Steve'. Key to the study of false memories is that when making such an error of commission, an individual sincerely believes that the misremembered event actually occurred in the past. As such, a false memory has been suggested to represent faulty memory reconstruction, an overreliance on gist and familiarity in the absence of detailed retrieval, as well as a failure of retrieval monitoring (see [Brainerd and Reyna \(2005\)](#)).

In the last two decades, many studies have investigated the neural basis of false memories, taking into account the foregoing behavioral theories. In addition, several qualitative reviews have sought to summarize the neuroimaging literature on false memories ([Abe, 2012](#); [Dennis et al., 2015](#); [Schacter et al., 2012](#); [Schacter and Slotnick, 2004](#); [Straube, 2012](#)). While informative, these qualitative reviews have often based their conclusions on only a subset of false memory studies and conclusions have tended to focus on only a few neural patterns that appear ubiquitous across studies. While such reviews are helpful in consolidating the findings across an ever growing number of false memory studies, they have failed to pinpoint the precise overlap in neural activity shared across studies of false memories. The current study sought to expand upon previous qualitative reviews and take a quantitative approach to elucidating the shared neural correlates across studies by performing the first meta-analysis of the fMRI studies investigating false memories. In doing so, we aim to elucidate the common neural correlates mediating false memories, at both the encoding and retrieval phase of memory. Further, given the range of paradigms as well as the different analytical approaches used to study false memories, we also sought to identify how such differences inform our understanding of false memories.

### 1.1. Memory phases

#### 1.1.1. Retrieval

The majority of studies that examine false memories have

focused on neural activity underlying the identification of a false alarm (FA) during retrieval. In signal detection theory, a FA is a positive ('yes') response to a novel distractor, or lure, trial. Within the context of neuroimaging, retrieval studies are able to isolate neural activity associated with the incorrect endorsement of the lure item. As such, they allow for the identification of a specific instance of making a false memory which, in turn, is a powerful component to understand the cognitive processes mediating false memories. Despite the relative clarity in the neuroimaging process for isolating FAs, there are multiple factors involved in fMRI design and analysis that can contribute to our understanding of false memories. As alluded to above, multiple paradigms have been utilized in the investigation of the neural basis of false memories. Across each type of paradigm, false memories are operationalized in a slightly different manner. This can create significant variability in the neural signature. (For a lengthier discussion regarding paradigm design, see below). Furthermore, while the identification and isolation of the false memory trial is a relatively clear process, experimenters must choose an appropriate contrast or baseline in which to probe the neural correlates specific to the false memory trial. Often times this has taken the form of correct rejections (CRs) or hits. In some cases, studies have looked at differences in confidence ratings or simply used a passive baseline. Like the issue with paradigm design, this can introduced significant differences in how the neural activity supporting false memories is ultimately defined. (For a lengthier discussion regarding baseline issues, see below). Finally, related to the issue of paradigm design is that of basic stimuli properties. The use of words compared to pictures for example, has been shown to activate discrete neural regions (e.g., [Starrfelt and Gerlach, 2007](#); [Vandenberghe et al., 1996](#)). This difference, in turn, has been shown to alter the network underscoring retrieval processing and thus could have a significant impact on false retrieval as well.

As such, in understanding the neural basis of false memories it may be valuable to consider both activity that is ubiquitous across all types of false memory retrieval as well as each design/analysis choice separately. The former analysis allows for the identification of the cognitive and neural mechanisms that are fundamental to the process of false memory retrieval, irrespective of differences in the exact manner in which it is studied. Whereas the latter allows for a more nuanced investigation into the component processes that mediate false memories, both from a general perspective as well as with respect to specific design properties. With respect to a more generalized investigation of the neural mechanism supporting false memory retrieval, one of our main analyses will be to examine the neural mechanisms supporting false memory retrieval, irrespective of differences in paradigm design, memoranda

type, or differences in baseline. This will be a powerful analysis as it will reduce the bias in reporting that can exist in qualitative reviews as well as overcome power issues that are often inherent in individual studies (Spaniol et al., 2009). The ultimate goal is to identify concordant activity across a large number of false memory retrieval studies that differ with respect to aspects of experimental design and methodology. This finding will represent the most critical and ubiquitous neural regions that support false memory retrieval.

### 1.1.2. Encoding

While most studies examining the neural correlates of false memories have focused on retrieval-based processes, it has been well argued that processes at encoding also contribute to false memories. For several reasons, however, it is relatively difficult to design a study that isolates the neural processes that contribute to the formation of a false memory. First, lures are, by definition, not present during encoding. Second, in relatedness paradigms, for example, it is suggested that false memories arise from gist that is built up across many trials (see Brainerd and Reyna (2002)). Therefore, activity on any given trial may only partially contribute to a subsequent false memory. Similarly, in misinformation paradigms false memories may arise due to processing during either the original encoding phase or misinformation phase. Thus, the practice of isolating a single time point during encoding that would create a false memory is particularly difficult. Nevertheless, it has been attempted across a handful of studies. For example, relatedness paradigms will often examine subsequent false memory activity by assessing activity associated with the encoding of an item that later leads to a false memory of its associated critical lure (Dennis et al., 2007; Kim and Cabeza, 2007a). Analogously, source misattribution paradigms have taken advantage of the subsequent memory paradigm, whereby they analyze neural activity associated with an item whose source was later misattributed (e.g., a word that was imagined was later claimed to have been visualized) (see Gonsalves et al. (2004) and Kensinger and Schacter (2005)). Thus, while the methods have varied, encoding studies have focused their analyses on discrete time points which can be directly associated with producing subsequent false memory. As such, the present study will investigate whether there is concordance in the neural processes underlying this process across different types of paradigms.

## 1.2. Experimental design considerations

### 1.2.1. Experimental paradigm

False memory research differs greatly with respect to the methods used to induce and test false memories. The foundational false memory studies focused on *semantic relatedness* and the extent to which semantic associations amongst stimuli produce false memories for semantically related lure words. One of the most widely utilized of these experimental paradigms is the Deese–Roediger–McDermott (DRM) paradigm (Deese, 1959; Roediger and McDermott, 1995). The DRM paradigm presents participants with lists of semantically related words (e.g., pillow, mattress, sheet, and blanket), which all converge on a single critical lure (e.g., sleep). Participants are later given a recognition memory test which elicits high rates of false recognition of the critical lure. Neuroimaging researchers have since modified this paradigm to present many semantically related lures at retrieval, instead of a single critical lure, allowing for the many observations of false recognition needed to perform statistical tests using neuroimaging data (e.g., Cabeza et al., 2001; von Zerssen et al., 2001).

Similar to studies using semantic relatedness amongst stimuli to elicit FAs, many studies also manipulate the *perceptual relatedness* between targets and lures to elicit and examine false

memories. Specifically, at encoding, participants study one or more pictorial exemplars from a given category (e.g., chairs, dogs, and abstract shapes) then at retrieval, participants are presented with lures that are perceptually related to, but different from, the originally presented stimuli. This perceptual relatedness paradigm relies on a similar mechanism to the DRM paradigm, focusing on similarities in the perceptual characteristics of lures in order to induce false memories for what was presented at encoding. Like the DRM paradigm, perceptual relatedness paradigms reliably produce high levels of false recognition, allowing for robust neuroimaging analyses (e.g., Gutchess and Schacter, 2012; Lidaka et al., 2014; Slotnick and Schacter, 2004).

Another category of paradigms often used to induce and examine false memories can be labeled as *source misattribution* paradigms. In the *classic source memory paradigm*, a subject must identify the origin of a given item, such as the speaker of a word or color of the text in which an item was presented (Johnson et al., 1993). One specific offshoot of this paradigm is the *reality-monitoring paradigm*, in which participants are either presented with an item or asked to imagine an item during encoding. At retrieval the subject is asked to determine in which encoding context the item was encountered, requiring participants to differentiate imagined items from encountered items (e.g., Gonsalves et al., 2004; Kensinger and Schacter, 2005, 2006). Another misattribution paradigm, the *misinformation paradigm*, asks participants to encode information and subsequently provides them with some incorrect information with respect to the original encoding episode. A later memory test examines an individual's ability to retrieve the original information, ignoring the misinformation (see Loftus (2005) for review; Okado and Stark, (2005)). Finally, in *associative memory paradigms* (e.g., Dennis et al., 2014a; Giovanello et al., 2009) participants are asked to encode a pair of items (e.g., face and names), then later remember the specific association from encoding. False memories arose when participants misremember the association.

In addition to identifying common neural activity supporting false memory across all paradigms, there may be processes that are unique to a given set of stimuli or specific experimental approach. For example, false memories in semantic relatedness paradigms may arise from semantic elaboration processes, whereas those in perceptual relatedness paradigms may arise from failed perceptual reconstruction. False memories in source memory paradigms may, in turn, result from a failure to bind information together in memory. Consequently, each paradigm may utilize different cognitive and neural mechanisms to support false memories. Thus, in addition to investigating overarching mechanisms that may be at play across all types of false memories, it may be critical to examine the methods by which false memories are elicited.

### 1.2.2. Memoranda type

Related to the issue of paradigm design, is the issue of differences in memoranda used across false memory studies. The most common memoranda types used in the study of false memory are verbal stimuli (e.g., visually or auditory presented words or misinformation) followed by classes of pictorial stimuli (e.g., abstract shapes, pictures, vignettes). [While other memoranda types have also been studied (e.g., odors; see Royet et al. (2011)), their presence in the literature occurs is far less frequent]. To date, while qualitative reviews of false memory have acknowledged differences in memoranda across studies, they have not focused on the potential issue of how differences in memoranda across studies may contribute to our understanding of how false memories arise. With respect to general information processing, evidence from patient and neuroimaging studies has shown that verbal and pictorial information is processed in discrete brain regions and

thus involve different processing networks (see Binder et al. (2009), Cabeza and Nyberg (2000) and Vandenberghe et al. (1996)). Likewise, retrieval studies have shown that while there exists common retrieval process, irrespective of the stimulus material, the retrieval network is influenced by the specific stimuli (Kim, 2011; McDermott et al., 1999). Thus, while there may exist common processes underlying false memories, irrespective of stimuli type, the choice of memoranda could be influential in mediating false memories. One of the purposes of this meta-analysis was to break down retrieval studies by memoranda type in order to investigate its influence on false memory retrieval.

### 1.2.3. Baseline contrast

In addition to paradigm choices and memoranda, another important factor when designing and conducting an fMRI study on false memory is the choice of baseline. In order to isolate activity supporting false memories, studies have typically contrasted FAs with either CRs or hits (although other cognitive baselines have been used). While both are appropriate baselines within a recognition paradigm, each controls for different environmental and cognitive variables and, as a result, highlights different neural correlates and component processes underlying false retrieval. Specifically, with respect to FAs, a CR baseline controls for the presentation history of the items (i.e., both are responses to lures which, by definition, were not previously presented) and allows for the identification of neural activity that contributes to the incorrect recognition process. As such, false memory contrasts using a CR baseline identify processes contributing to a general (false) retrieval network as opposed to a novelty detection network. On the other hand, use of a hit baseline controls for the memory decision (an “old” response) and identifies retrieval activity that is unique to the veracity of the memory decision. Thus, while the neural activity underlying false alarms remains constant in both cases, the use of one baseline over another may introduce a bias in the identification of the cognitive processes and corresponding neural correlates mediating false memories. Because both false memory and true memory retrieval are believed to incur similar reconstruction processes, the distinction between the two cognitive states is more limiting than that of false memories and CR. As such, false memory studies often find little, if any, neural activity unique to false alarms, when contrasted to hits (e.g., Dennis et al., 2012). When activity is identified in this contrast, it has been relatively limited in scope, occurring in medial prefrontal and inferior parietal regions, reflective of the more difficult memory decision (i.e., that of ‘old’ in the absence of a prior sensory signal) (e.g., Kim and Cabeza, 2007b; Nessler and Mecklinger, 2003; Schacter et al., 1996). Studies using a CR baseline on the other hand have often found activity throughout the general retrieval network including multiple regions in frontal, parietal, and visual cortices as well as the medial temporal lobe (MTL) (e.g., Abe et al., 2008; Dennis et al., 2014a). Prior qualitative reviews have largely fell silent on issues with regards to baseline, simply discussing regions that are commonly reported across studies. One of the goals of the present meta-analysis is to perform a quantitative review separately for each of these types of contrasts in order to gain a complete picture regarding the cognitive operations underlying, and unique to, false memory retrieval.

### 1.3. Neural correlates mediating false memories

Recently, several qualitative reviews have attempted to consolidate the false memory findings stemming from the use of the paradigms described above (Abe, 2012; Dennis et al., 2015; Schacter et al., 2012; Schacter and Slotnick, 2004; Straube, 2012). The reviews have tended to separate their conclusions on the basis of retrieval and encoding findings, as well as have focused on

differences across multiple methodological approaches. Across all findings, qualitative reviews have pointed to the prefrontal cortex (PFC) as by far the most widely found neural correlate underlying false memories. Although there seems to be consistency with respect to the engagement of the PFC during false memory retrieval, prior reviews have been unable to identify a single region within the PFC that exhibits consistent activation supporting false memories. For example, several neuroimaging studies have identified the right anterior/dorsal lateral PFC as mediating the retrieval of false memories, with the interpretation that this region is responsible for increased retrieval monitoring associated with the strong sense of familiarity evoked by lures (see Schacter and Slotnick (2004)). The anterior cingulate cortex (ACC) has also been observed across many studies and has been interpreted as supporting a large array of functions, including top-down retrieval verification, general task difficulty, internal and external monitoring, general decision making, and visual imagery at encoding (e.g., Cabeza et al., 2001; Dennis et al., 2012, 2014a, 2014b; Duarte et al., 2010; Gonsalves et al., 2004; Iidaka et al., 2012). Still, other studies have identified the left dorsal lateral prefrontal cortex (dlPFC) in supporting false memories at encoding and retrieval, citing its role in general semantic and general language processing, as well as semantic elaboration (Cabeza et al., 2001; Dennis et al., 2008; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; Kubota et al., 2006; von Zerssen et al., 2001). Taken together, it appears that the PFC plays a large role in mediating false memories, but which specific areas of the PFC most consistently support false memories and under what methodological conditions this occurs, remain unanswered questions.

In addition to the PFC, several parietal regions, including the inferior parietal lobe (IPL), the posterior cingulate cortex (PCC), and the precuneus have been found to support false retrieval (Abe et al., 2008; Atkins and Reuter-Lorenz, 2011; Cabeza et al., 2001; Duarte et al., 2010; Heun et al., 2004; Kim and Cabeza, 2007b; Slotnick and Schacter, 2004). Given the role of frontoparietal regions in mediating familiarity (Cansino et al., 2002; Yonelinas et al., 2005), researchers have suggested that parietal activity reflects an overall sense of familiarity associated with the critical lure, supporting the false memory response at retrieval (Duarte et al., 2010; Kim and Cabeza, 2007b). Others have attributed parietal activation to part of a top-down fronto-parietal control network (Dennis et al., 2014a, 2014b; Kim and Cabeza, 2007b), memory reconstruction (Dennis et al., 2012), or a general labeling of oldness, regardless of veracity (Slotnick and Schacter, 2004). While there is some common consensus regarding the role of the parietal cortex in mediating false memories, it is unclear whether quantitative methods would also identify common activity in parietal cortex and if so, what specific region(s) would be evident.

Despite a wealth of studies finding false memory activity in the prefrontal and parietal cortices, other regions that have been shown to support false memories are often more paradigm specific. For example, several studies that utilize visual stimuli have found occipital cortex activity supporting false memories at both retrieval (Dennis et al., 2012; Garoff-Eaton et al., 2006; Iidaka et al., 2012; Schacter et al., 1997; Slotnick and Schacter, 2004; Stark et al., 2010; von Zerssen et al., 2001) and encoding (e.g., Dennis et al., 2007; Garoff et al., 2005; Kim and Cabeza, 2007a). Much of this work has also pointed to a dissociation in visual cortex with respect to true and false memories, such that early (BA 17/18) visual cortex has been shown to support true memories whereas late (BA 19/37) visual cortex is associated with both true and false retrieval (e.g., Dennis et al., 2012; Slotnick and Schacter, 2004). Given that early visual cortex is associated with object perception and identification and late visual regions with general object identity and meaning (Buckner and Wheeler, 2001; Rugg and Wilding, 2000; Vaidya et al., 2002a, 2002b, Wheeler and Buckner, 2003; Wheeler



et al., 2000), false memory studies have suggested that the foregoing differences in activation reflect sensory reactivation associated with true memories (Vaidya et al., 2002a, 2002b; Wheeler and Buckner, 2003; Wheeler et al., 2000) and retrieval of general object properties which supports both true and false memories (e.g., Dennis et al., 2012; Slotnick and Schacter, 2004). While this theoretical distinction has been discussed in recent qualitative reviews, it remains unclear the specific regions in visual cortex that might support this process or whether there is true consistency across false memory studies.

Similarly, many false memory studies utilize semantic stimuli and have exploited semantic relatedness amongst studied items and lures to invoke false memories (e.g., DRM paradigm). Thus, regions involved in semantic processing and semantic gist processing, such as the left inferior and middle frontal gyri (see Binder et al. (2009) for a meta-analysis of semantic processing) and superior and middle temporal gyri (Noppeney et al., 2007; Price, 2000; Simons et al., 2005; Wise and Price, 2006) have been posited to be critical to generating semantic false memories at both encoding (Dennis et al., 2007; Kim and Cabeza, 2007a) and retrieval (Cabeza et al., 2001; Dennis et al., 2014a, 2014b, 2008; Duarte et al., 2010; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; Kubota et al., 2006).

Finally, given its central role in supporting both encoding and retrieval phases of memory (see Kim (2011) and Spaniol et al. (2009) for a meta-analysis of episodic memory), the medial temporal lobe (MTL) is another region that is often investigated in false memory studies, however, results have been mixed. While some studies have found the MTL to be active for both true and false retrieval (Cabeza et al., 2001; Dennis et al., 2012; Garoff-Eaton et al., 2006; Kahn et al., 2004; Schacter et al., 1997, 1996; Stark et al., 2010), others cite MTL activity only associated with true, but not false, memories (Dennis et al., 2008; Giovanello et al., 2009; Kim and Cabeza, 2007b; Paz-Alonso et al., 2008). While no studies find MTL activity for false greater than true memories (but see Abe et al. (2013), Karanian and Slotnick (2014) and Kim and Cabeza (2007b) for MTL activity support false familiarity), the fact that it does appear often for both true and false retrieval begets the question of whether it is a consistent component of false memory during either encoding or retrieval, or specific to false memory in only specific instances. It is our aim that the current meta-analysis will help elucidate whether these findings are systematic within the false memory literature and under what, if any specific circumstances, do they appear.

#### 1.4. The present study

As noted, several reviews have provided an excellent *qualitative* review of the false memory literature (Abe, 2012; Dennis et al., 2015; Schacter et al., 2012; Schacter and Slotnick, 2004; Straube, 2012). Qualitative reviews are, by their nature, selective, and can depend on the biases of the author(s). A quantitative review is often better equipped to objectively review a given literature, especially in the face of concerns of methodological variability and high false positive rates (see Carp (2012) and Lieberman and Cunningham (2009)). For example, qualitative reviews frequently make generalizations about brain regions that underlie false memories (e.g., “the PFC underlies false memories”), but often fail to be specific with localization within these brain areas. A quantitative meta-analysis can identify the specific foci within these general brain regions where numerous studies report activation. To this end, the main goal of this study is to provide the first quantitative review of the fMRI false memory literature. We hope to answer several questions that we believe remain unanswered. These questions include:

- Are there *specific* brain regions that are *consistently* activated across the different types of experimental paradigms and contrasts used to study (a) false retrieval and (b) the encoding of subsequent false memories?
- Within retrieval, does the *type of experimental paradigm* serve to mediate common activity supporting false memories?

To answer these questions, the present study performed a systematic search of two widely used databases and performed an Activation Likelihood Estimation (ALE) meta-analysis on these false memory studies. We performed 8 analyses to accomplish our objectives: (1) a general false retrieval analysis to find consistent brain activation across all retrieval-based experimental paradigms, and 6 sub-analyses within retrieval in order to identify activity that is unique to the use of (2) correct rejections and (3) hits as a baseline; those that examine false memories using (4) verbal stimuli and those using (5) pictorial stimuli; and within the previous sub-analysis, those that specifically utilize (6) perceptual and (7) semantic relatedness paradigms.<sup>1</sup> Finally we identified neural processes that contribute to the (8) encoding of subsequent false memories.

## 2. Methods

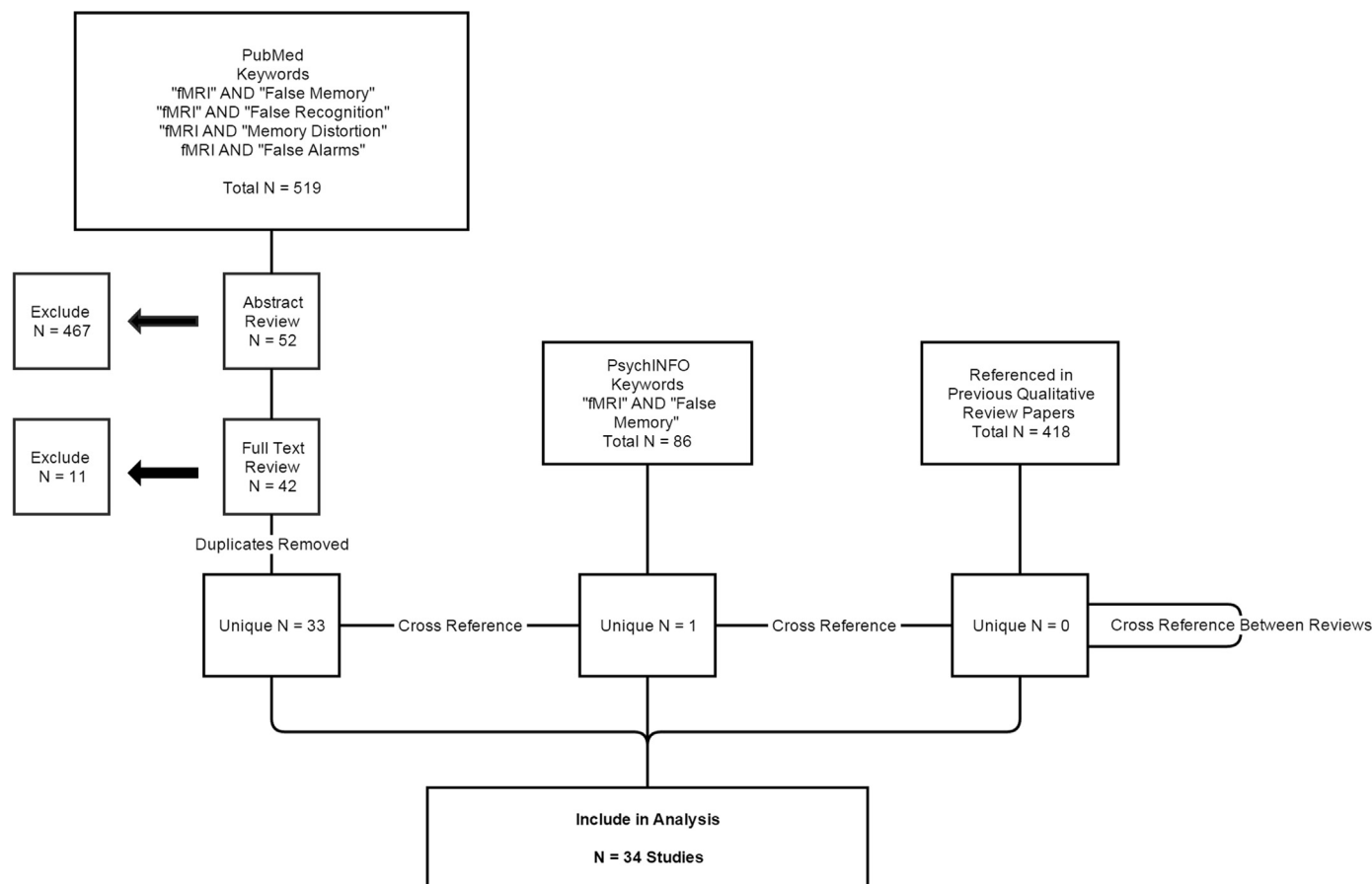
### 2.1. Systematic searches and inclusions criteria

To identify studies for inclusion in the meta-analysis, five separate systematic searches of two scientific databases were performed (see Fig. 1) and cross-referenced with the citations from several reviews of false memory and neuroimaging (Abe, 2012; Dennis et al., 2015; Schacter et al., 2012; Schacter and Slotnick, 2004; Straube, 2012). Empirical studies that were published prior to January 2015 were included in our analyses if, and only if, they met all of the following inclusion criteria:

- Experiments studied false memory, false alarms, or false recognition at either encoding or retrieval using any aforementioned behavioral paradigm (i.e. DRM lists, perceptual similarity, source memory, etc.)
- Primary methodology used was functional magnetic resonance imaging (fMRI)
- Included only healthy participants with no signs of mental illness or neurological disease and participants were not under the influence of pharmaceuticals that could affect brain function
- Performed at least one whole brain analysis
- Reported coordinate-based data for their whole-brain analyses

A total of four systematic searches of the PubMed database were performed, using combinations of the keywords “fMRI” AND “false memory”, “false recognition”, “memory distortion”, and “false alarms” (see Fig. 1). These searches yielded 519 total hits, of which 467 studies were excluded based on abstract review and an additional 11 were excluded based on a full text review, leaving a total of 33 unique studies to be included in the present meta-analysis. To ensure completeness, a fifth and final systematic search was performed using a different database (PsychInfo) and using the original keywords “fMRI” AND “false memory”. This search yielded 86 hits, of which 61 studies were excluded based on review of the abstracts, and 4 were excluded based on a full text review, leaving a single unique additional study included in later

<sup>1</sup> There was insufficient power with respect to the number of studies utilizing other paradigms to constitute additional retrieval sub-analyses based on experimental design.



**Fig. 1.** Systematic searches. Flowchart of the systematic searches undertaken for the present study. Our main searches of the PubMed database consisted of combinations of the keywords “fMRI” AND “False Memory”, “False Recognition”, “Memory Distortion”, and “False Alarms”. Two follow-up searches of the PsychINFO database and of the references sections of several fMRI false memory qualitative reviews were performed to ensure completeness. *N*=number of studies.

analyses.

To further supplement our systematic searches and to make sure that all eligible studies were included, the references of several reviews of false memory and neuroimaging (Abe, 2012; Dennis et al., 2015; Schacter et al., 2012; Schacter and Slotnick, 2004; Straube, 2012) were checked for inclusion. These reviews resulted in no additional unique studies being included in our analysis, leaving us with a total of 34 studies, incorporating a total of 604 unique participants and some 293 unique foci of activation in our later analyses (see Table 1 for Retrieval Studies and Table 2 for Encoding Studies).

## 2.2. Contrast selection and analyses

The 34 studies that qualified for inclusion into our study were further reviewed for contrasts of interest. Contrasts of interests included any full brain contrasts reported in each study that sought to identify the neural correlates of false memories, distorted memories, or false alarms. In the context of Activation Likelihood Estimation (ALE) using GingerALE, contrasts are often referred to as experiments. Both terms will be used interchangeably for the remainder of the report.

The pool of false memory experiments was first broken up into two subsets of analyses based on memory phase: an analysis of false memory retrieval and an analysis of encoding that led to subsequent false memories (Table 1 and Table 2, respectively). In the main retrieval analysis, we included all experiments that investigated the neural correlates supporting FAs during memory retrieval. In doing so, our goal was to elucidate the critical and

universal neural correlates that supported false memory retrieval. While this analysis includes different paradigms, stimuli, and baselines we feel that these differences across studies are the inherent strength of the analysis, such that regions that are found to be significant in this retrieval analysis represent the most robust regions supporting false memory retrieval. As a follow-up to this robust general false retrieval analysis, we next aimed to break down false memory retrieval by experimental factors including baseline contrast, memoranda type, and experimental paradigm type (see below). Furthermore, we anticipated that the combined results stemming from the subsequent sub-analyses would help us in our interpretation of results not only across sub-analyses, but within the general false retrieval analysis as well.

With respect to the general false retrieval analysis, a handful of studies report multiple false memory contrasts, utilizing either different baseline contrasts (e.g., hits and CRs) or different types of FAs (e.g., emotional FAs and neutral FAs). When considering multiple contrasts reported in a single fMRI study, contrasts can either be independent of one another or share common variance. In line with previous ALE meta-analyses (see Fox et al. (2015) and Keuken et al. (2014) for examples) we included multiple contrasts from the same study in our retrieval analyses if, based upon the nature of the experimental design, the contrast contributed unique observations to the analysis. For example, Garoff-Eaton et al. (2007) report results for both “conceptual” and “perceptual” false memories, wherein each contrast of interest identified neural correlates from unique sets of observations (“conceptual” stimuli and “perceptual” stimuli, see text). When multiple, non-independent contrasts were reported (for example, Dennis et al.

**Table 1**  
Summary of false memory retrieval experiments.

First author	Year	Experimental paradigm type	Stimuli description	Retrieval response options	n	Foci	Contrast(s) of interest description	Meta analysis
Heun	2000	Semantic	Lengthy (240) visually presented word list	Yes/no	14	3	FA > Hits	Ret, Verbal, Hit
Cabeza	2001	Related-semantic	Auditory words at Enc, visual words at Ret	Old/new	12	3	[FA > Rest] > [Hits > Rest]	Ret, Verbal, Hit, Rel Sem
von Zerssen	2001	Related-semantic	Auditory words at Enc, visual words at Ret	Old/new with confidence	10	10	[FA > Rest] > [CR > Rest]	Ret, Verbal, CR, Rel Sem
Heun	2004	Semantic	Lengthy (400) visual word list	Yes/no	15	1	FA > CR	Ret, Verbal, CR
Slotnick	2004	Related-perceptual	Abstract shapes	Old/new with confidence	12	2	FA > Hit	Hit
Kensinger	2006	Reality monitoring	Words with or without accompanying pictures	Word-picture/word-only/new	16	11	FA > Hits	Ret, Pictoral, Hit, Rel Percep
Garoff-Eaton	2006	Related-perceptual	Abstract shapes	Same/similar/new	11	9	"Word-Picture" FA > "Word-Picture" Hits	Ret, Hit
Moritz	2006	Related-semantic	Visual words	Old/new with confidence	17	12	"Word-Only" FA > "Word-Only" Hits	Ret, Pictoral
Hofer	2007	Perceptual	Faces	Old/new/scrambled	21	4	Unrelated FA > [Hit + Related FA]	Ret, Verbal, Hit, Rel Sem
Kensinger	2007	Related-perceptual	Emotional/neutral pictures of objects	Same/similar/new	19	1	FA > Hits	Ret, Pictoral
	2007					3	FA > Rest	Ret, Pictoral, Hit, Rel Percep
	2007					1	FA > Hit, negative valence	Ret, Pictoral, Hit, Rel Percep
Garoff-Eaton	2007	Related-semantic	Conceptually vs. perceptually related words lists	R/K/N	14	14	FA > Hit, Neutral Valence	Ret, Pictoral, Hit, Rel Percep
	2007					1	"Conceptual" FA > "Conceptual" Hits	Ret, Verbal, Hit, Rel Sem
Kim	2007	Related-semantic	Visual words	Old/new with confidence	11	1	"Perceptual" FA > "Perceptual" Hits	Ret, Verbal, Hit, Rel Percep
Marchewka	2008	Perceptual	Unrelated emotional and neutral pictures of objects	Old/new	16	6	High confidence FA > high confidence Hit	Ret, Verbal, Hit, Rel Sem
	2008					4	FA > CR, LVF, Negative pictures	Ret, Pictoral, CR
Kuehnel	2008	Related perceptual; episodic memory	Film at Enc, pictures of scenes at Ret	Known/unknown	12	2	FA > CR, LVF, Neutral pictures	Ret, Pictoral, CR
	2008					1	FA > CR, RVF, Negative pictures	Ret, Pictoral, CR
Abe	2008	Related-semantic	Auditory words at Enc, visual words at Ret	Old/New	20	6	"Similar" FA > Rest	Ret, Pictoral, Rel Percep
Giovanello	2009	False associative memory	Visually presented compound words	Old/new	15	11	"Unknown" FA > Rest	Ret, Pictoral
Duarte	2010	Perceptual	Line drawings of objects	R/K/N	33	10	FA > CR	Ret, Verbal, CR, Rel Sem
Royet	2011	Perceptual	Odorants	Yes/no	16	1	"Feature" FA > Hit	Ret, Verbal, Hit
	2011				22	11	Familiar FA > CR, common to OA and YA	Ret, Pictoral, CR
Atkins	2011	Related-semantic; short term memory	Visual words	Yes/no	19	1	YA FA > CR	Ret, CR
Gutches	2012	Related perceptual	Categorical images in small, medium, large sets	Yes/no	9	1	OA FA > CR	Ret, CR
Iidaka	2012	Related-perceptual	Morphed faces	Old/new	19	1	YA FA > Hit	Hit
Dennis	2012	Related perceptual	Images presented in categories	R/K/N	17	9	Related lure FA > unrelated lure CR	Ret, Verbal, CR, Rel Sem
Risius	2013	Episodic memory	Film at Enc, True/false statements about film at Ret	Yes/No	29	11	FA (positive modulation) > Hits (negative modulation)	Ret, Pictoral, Hit, Rel Percep
Dennis	2014	False associative memory	Faces and scenes	R/K/N	18	2	FA to a related lure > CR of a related lure	Ret, Pictoral, CR, Rel Percep
						4	FA to an Unrelated Lure > CR of a Unrelated Lure	Ret, Pictoral, CR
						14	False recollection > false familiarity	Ret, Pictoral, Rel Percep
						5	"Volunteering an Incorrect Answer" > "Withholding an Incorrect Answer"	Ret, Verbal
						12	FA > CR	Ret, Pictoral, CR
						10	FA > Hit	Hit

**Table 1** (continued)

First author	Year	Experimental paradigm type	Stimuli description	Retrieval response options	n	Foci	Contrast(s) of interest description	Meta analysis
Karanian	2014	Source memory	Moving abstract shapes	Moving/stationary	12	7	FA > Hit	Ret, Pictorial, Hit
Iidaka	2014	Related-perceptual; short term memory	Morphed faces	Old/new	19	3	[Related FA > Related CR] > [Hit > Miss]	Ret, Pictorial, Rel Percep
<b>Total</b>					<b>464</b>	<b>225</b>		

Notes: This table reports details of each study and experiment included in the false memory retrieval analyses. R/K/N=Remember/Know/New. Enc=Encoding. Ret=Retrieval. FA=False Alarms. CR=Correct Rejections. LVF=Left Visual Field. RVF=Right Visual Field. YA=Young Adults. OA=Older Adults. Rel Sem=Related Semantic. Rel Percep=Related Perceptual. n=Number of Subjects. Description of contrasts reflects a common nomenclature for ease of comparison across studies, with study specific nomenclature in quotation marks.

**Table 2**

Summary of false memory encoding experiments.

First author	Year	Experimental paradigm	Stimuli	Retrieval options	n	Foci	Contrast(s) of interest description
Gonsalves	2004	Reality monitoring	Words with pictures, words with mental imagery	With picture/without picture	11	3	Subsequent FA > subsequent hit
Garoff-Eaton	2005	Related perceptual	Pictures of objects	Same/similar/new	13	29	Subsequent "Non-Specific" FA > subsequent miss
Kensinger	2005	Reality monitoring	Words with pictures, words with mental imagery	With picture/without picture	19	1	[Neutral word subsequent FA > neutral word subsequent hit] > [emotional word subsequent FA > emotional word subsequent hit]
Okado	2005	Misinformation	Vignettes made of 50 still pictures	Three-alternative forced choice (original episode, misinformation episode, or foil)	20	12	Subsequent FAs > subsequent hits
Kim	2006	Related semantic	Visually presented categorical word lists	Old/new with confidence	16	9	Subsequent FAs to critical lures PM by FA rate
Dennis	2007	Related semantic	Visually presented categorical word lists	Old/new with confidence	17	4	Conjunction between OAs and YAs, FA PM by "False DM Scores"
Straube	2010	Source memory	Film of an actor speaking	Recognition: yes/no with confidence; Source: yes/no with confidence	18	8	Subsequent FA > misses
St Jacques	2013	Misinformation	Photographs of a museum tour	Yes/no	26	2	Subsequent FAs > subsequent hits
<b>Total</b>					<b>140</b>	<b>68</b>	

Notes: This table reports a detailed description of each false encoding experiment included in the present report. PM=Parametrically Modulated. FA=False Alarm. OAs=Older Adults. YAs=Younger Adults. DM=Difference in Memory. Contrast descriptions reflect a common nomenclature for ease of comparison across studies, with study specific nomenclature in quotations.



(2014a) report both FAs greater than hits and FAs greater than CRs), we choose a single contrast to represent the neural basis of false memories.

In choosing which of the non-independent contrasts to include, we chose to prioritize contrasts that examined FAs compared to CRs over all other types of baselines (i.e., Hits, confidence levels within false memories, other non-retrieval baselines, parametric analyses), as we felt that this best reflected the cognitive processes underlying false memory retrieval.<sup>2</sup> While there are always issues surrounding the pure insertion assumption in fMRI analysis, as a baseline CRs control for the history of the stimuli while elucidating the retrieval processes supporting the erroneous recognition of the lure. While a comparison between FAs and hits is also informative, we note that this contrast controls for the basic retrieval processes that may be common to both false and veridical retrieval, while elucidating activity that is unique to false compared to veridical retrieval. As such, we felt that this removed basic retrieval processes that we felt were critical to the understanding of the 'retrieval' aspect of the task. (As noted in the Introduction, based on these issues concerning baseline, we chose to look at each baseline in its own sub-analysis; see below). In the absence of a contrast using a CR baseline, we prioritized contrasts that utilized Hits, as again we felt that this next best isolated neural cognitive processes related false memories by identifying processes related to the veracity of the memoranda, holding the endorsement decision constant. If neither CR nor Hit baseline contrasts were reported, then a contrast using a passive baseline was included. Finally, if none of these common baseline contrasts were reported, then other contrasts examining false memories were considered (e.g., confidence in false memories, parametric modulations, interaction analyses; see Tables 1 and 2). Similar considerations were undertaken for the encoding analysis and various retrieval sub-analyses.

In addition to the independence of multiple contrasts reported within the same study, there is also a concern that a single sample of participants (e.g., Garoff-Eaton et al., 2007) may contribute disproportionately to the results. We note this potential bias and include the percentage of experiments that contribute to each analysis in our results tables (see Table 3) with footnotes on results that may represent a single sample bias.

In addition to the main general false retrieval analysis, retrieval studies were separated into 6 sub-analyses, based on common differences in experimental designs. The first two sub-analyses examined the role of baseline differences. As noted, false memories can be compared to a variety of different cognitive states depending on the nature of the experimental design, with the two most common baselines being CRs and Hits. In order to examine how each baseline differentially contributes to our understanding of the neural basis of false memories, we sub-divided the main retrieval analysis into sub-analyses examining FAs with respect to the specific baseline contrast used in the experiment. Those contrasts that utilized hit and CR baselines were included in the respective analyses, with contrasts utilizing other baselines (e.g., fixation, parametric modulations, interaction contrasts) were excluded from these sub-analyses. Second, we examined the role stimulus properties play in mediating false memories. As noted, false memory studies typically utilize either verbal or pictorial stimuli and each may contribute to stimulus-specific activity supporting false memories. To investigate this possibility, we performed two sub-analyses examining false retrieval studies that used either verbal or pictorial stimuli. The verbal sub-analysis included experiments that used exclusively words as memoranda, whereas the pictorial sub-analysis included experiments that

exclusively used visual images as memoranda. Experiments using an alternative stimulus type (i.e., odorants: Royet et al. (2011)) or used a mixture of verbal and pictorial stimuli (Kensinger and Schacter, 2006) were excluded from these sub-analyses.

Finally, we investigated the role of the experimental paradigm in contributing to false memories. Unfortunately there was insufficient power to look beyond relatedness paradigms (i.e., too few studies examining source, misinformation, and associative false memories). Thus, we performed retrieval sub-analyses separating out studies that used perceptual similarity and semantic relatedness to elicit false memories. These analyses are similar, yet unique from the foregoing verbal and pictorial sub-analyses as they focus not only on the stimulus properties, but on a specific experimental manipulation designed to elicit false memories. Contrasts were included in these sub-analyses if the study manipulated relatedness of lures to targets (along either a perceptual or semantic scale) and the contrast looked specifically at false memories to these related lures.

With respect to power, we note that the general false retrieval analysis included contributions from 34 independent experiments, contributing a total of 212 foci from 561 subjects and the encoding analysis included 8 experiments contributing a total of 69 foci from 140 subjects. With respect to the retrieval sub-analyses, the hit baseline sub-analysis included 17 experiments contributing a total of 111 foci comprising data from 250 subjects, the CR baseline sub-analysis included 13 experiments contributing a total of 68 foci from 240 subjects, the verbal sub-analysis included 12 experiments contributing a total of 68 foci from 190 subjects, the pictorial sub-analysis included 18 experiments contributing a total of 121 foci from 301 subjects, the semantic relatedness sub-analysis included 7 experiments contributing a total of 57 foci from 103 subjects, and the perceptual relatedness sub-analysis included 8 experiments contributing a total of 68 foci from 126 participants (see Table 1). Finally, the encoding analysis included 8 experiments, contributing a total of 68 foci from 140 participants (see Table 2). Consistent with recent meta-analyses (Belyk and Brown, 2014; Cona et al., 2015; Feng et al., 2015), we recognize that the encoding analysis as well as semantic and perceptual relatedness sub-analyses are considered relatively underpowered compared to the general false retrieval analysis. However, while results should be interpreted with caution, we note that there is utility in performing said sub-analyses as they will inform the interpretation of findings from the more powered retrieval analyses (see also Belyk and Brown (2014)).

### 2.3. Activation Likelihood Estimation

The meta-analysis technique used was a coordinate based technique using an algorithm originally developed by Turkeltaub et al. (2002), later refined on three separate occasions by Eickhoff et al. (2009, 2012) and Turkeltaub et al. (2012) and implemented in GingerALE 2.3.4 ([www.brainmap.org](http://www.brainmap.org)). In brief, this algorithm takes the foci reported in whole brain analyses and estimates activation likelihood by first placing a 3-D Gaussian distribution of probability around each reported foci. The union of these 3-D Gaussian distributions of probability is calculated to obtain Modeled Activation (MA) maps for each included experiment. The union of these individual experiment MA maps is then calculated to create an analysis ALE map, which importantly take into account sample size and replication by giving additional weight to experiments with larger samples (Eickhoff et al., 2009) and by giving additional weight to foci that converge across experiments (versus within the same experiment; see Turkeltaub et al. (2012)).

This analysis level ALE map was then tested against a null hypothesis activation map generated using a non-linear histogram integration method (Eickhoff et al., 2012). This method tallies the

<sup>2</sup> This decision was necessitated by only three studies: Royet et al. (2011), Dennis et al. (2014a, 2014b) and Heun et al. (2004).

**Table 3**  
Results summary.

Analysis	Lobe	Brain region	Approximate BA	Hemisphere	T&T coordinates			ALE ( $10^{-2}$ )	Cluster Size (mm <sup>3</sup> )	Contributing experiments ( <sup>a</sup> %)
					x	y	z			
All retrieval studies	Frontal	Medial superior frontal gyrus	32/8	M	−6	14	48	2.1	3016	10/29
		vmPFC/ACC	11	M	2	32	−12	2	800	<sup>b</sup> 5/15
		Precentral gyrus	6/44	L	−42	0	40	1.4	760	4/12
		Inferior frontal gyrus	45/47	L	−34	22	8	1.6	424	3/9
		Inferior frontal gyrus	44/45	R	54	24	20	1.6	386	<sup>a</sup> 3/9
	Parietal	Inferior parietal lobe	40	L	−32	−42	40	1.8	672	4/12
Hit baseline studies	Frontal	vmPFC/ACC	24	M	2	32	−12	2	1008	<sup>b</sup> 4/24
		Medial superior frontal gyrus	32	M	0	22	42	1.2	608	3/18
		Precentral gyrus	6/44	L	−46	8	34	1.4	600	3/18
		dACC	32/24	M	6	26	28	1.2	552	3/18
	Parietal	Inferior parietal lobe	40	L	−30	−40	40	1	536	3/18
	Occipital	Inferior occipital gyrus	18/19	L	−30	−82	−2	1.3	856	3/18
	Sub cortical	Brainstem		M	−4	−18	−4	1.2	560	3/18
CR baseline studies	Frontal	Precentral gyrus	6/44	L	−44	2	38	1.2	560	3/23
		Medial superior frontal gyrus	32	L	−10	22	38	1.3	392	2/15
		Middle frontal gyrus	46/47	R	44	44	−6	1	272	2/15
	Parietal	Inferior parietal lobe	40	L	−34	−46	40	1.3	344	2/15
		Precuneus	7	M	−4	−70	40	1.1	328	2/15
		Inferior parietal lobe	40	R	48	−48	38	1.1	304	2/15
	Sub Cortical	Caudate		L	−14	6	8	1	312	2/15
		Caudate		L	−14	22	10	1	224	2/15
Verbal studies	Frontal	Medial superior frontal gyrus	32/8	M	−8	22	38	1.4	2416	5/42
		Inferior frontal gyrus	45/47	L	−34	22	8	1.6	848	3/25
		Precentral gyrus	6/44	L	−40	8	32	1.3	768	3/25
		Middle frontal gyrus	6/8	L	−24	12	42	1.2	384	2/17
		dACC	32	R	12	40	20	1	296	2/17
	Parietal	Inferior parietal lobe	40/7	L	−32	−66	34	1	472	3/25
Semantic relatedness studies	Frontal	Medial superior frontal gyrus	32/8	M	−8	22	38	1.4	1576	4/57
		Precentral gyrus	6/44	L	−40	8	32	1.3	824	3/43
		Middle frontal gyrus	6/8	L	−24	12	42	1.2	448	2/29
		dACC	32	R	12	40	20	1	336	2/29
		Inferior frontal gyrus	45/47	L	−38	24	6	0.9	280	2/29
	Parietal	Inferior parietal lobe	40/7	L	−28	−66	46	0.8	176	2/29
Pictorial studies	Frontal	Inferior frontal gyrus	44/45	R	54	24	20	1.6	568	<sup>a</sup> 3/17
		vmPFC/ACC	11	M	2	32	−12	1.4	432	<sup>b</sup> 2/11
		Medial superior frontal gyrus	32/6	M	−6	16	48	1.3	376	2/11
Perceptual relatedness studies	Frontal	vmPFC/ACC	11	M	2	32	−12	1.4	664	<sup>b</sup> 3/33
		vmPFC/ACC	10/11	M	2	44	−6	1.3	448	2/22
	Occipital	Inferior occipital gyrus	18/19	L	−28	−82	−2	1.3	448	2/22
		Middle occipital gyrus	19/37	L	−44	−72	10	1.1	336	2/22
All encoding studies	Frontal	ACC	32	M	−4	46	8	1	304	2/29
	Temporal	MTG	21	L	−60	−44	−8	1.4	464	2/29

Notes: This table reports results of all of the current meta-analyses. Each resulting cluster is organized by lobe, then by Activation Likelihood Estimation (ALE) statistic, and finally by cluster size. T&T=Talairach & Tournoux. BA=Brodman's Area. ALE=Activation Likelihood Estimation. vmPFC=ventral medial Prefrontal Cortex. ACC=Anterior Cingulate Cortex; d=dorsal. M=Medial. L=Left. R=Right. mm=millimeters.

<sup>a</sup> Two Kuehnel et al. (2008) contrasts contribute to this cluster.

<sup>b</sup> Two Kensinger and Schacter (2007) contrasts contribute to this cluster.

values in each experiments MA map to make histograms. These histograms are then divided by the total number of voxels in each MA map to create tables of probabilities of finding each value in a MA map. Combining these tables of probability across included experiments yields a table of  $p$  values for the analysis level ALE image. The ALE image and the  $p$  value table are combined to create a 3-D  $p$  value image, which is then thresholded for multiple comparisons. The present study controlled for multiple statistical tests using a Family Wise Error (FWE) cluster level correction as implemented in GingerALE 2.3.4 and suggested by Eickhoff et al. (2012). The present report thresholded ALE maps for all analyses at a cluster forming threshold of  $p < .001$  and a cluster level threshold of  $p < .05$  after 1000 permutations (see Eickhoff et al. (2012)). Finally, we only report results for clusters that listed two or more contributing experiments.

Prior to performing analyses, foci were collected and classified based on the normalized template space [either MNI space (Montreal Neurological Institute) or Talairach space (Talairach and Tournoux, 1988)]. In order to properly interpret the activation likelihood maps, all studies that reported foci in MNI space were transformed into Talairach space using a Lancaster Transformation (Laird et al., 2010; Lancaster et al., 2007) as implemented in GingerALE 2.3.4.

Across all eight of our analyses, eight foci appeared to be located outside of the Talairach mask implemented in GingerALE 2.3.4. In order to avoid a potential loss of data, we performed a minimum linear translation of these foci to incorporate them into GingerALE's Talairach mask (Fox et al., 2015). Note that none of the foci were translated into brain regions that were outside of where they were originally reported. A table of the original foci and the translated foci are reported in supplementary material (see Supplemental Table S1).

Results images were created using the Colin-152 template in MRIcron ([www.mricron.com](http://www.mricron.com)). Anatomical labels were given to clusters using a combination of the Talairach Daemon ([www.talairach.org/daemon](http://www.talairach.org/daemon)) and visual inspection of the results. We note that in several instances, particular with regard to frontal clusters, labeling of regions was hampered by the fact that there exists no single nomenclature for activation labeling. For example, what was labeled as medial PFC in one study was labeled as anterior cingulate cortex (ACC) in another – yet both studies contributed to a common focus of activation in our analysis. As such, we labeled the region as we saw appropriate with respect to its anatomical/Talairach coordinates.

### 3. Results

#### 3.1. General false retrieval

Cluster maxima were found in a variety of regions across all false retrieval studies, irrespective of the experimental paradigm. The most highly replicated clusters included the medial superior

frontal gyrus, the ventral medial prefrontal cortex (vmPFC)/ventral ACC, the left precentral gyrus, and the left inferior parietal lobe (IPL). Other cluster maxima include the bilateral inferior frontal gyri (see Table 3, Fig. 2).

#### 3.2. Hit baseline

False retrieval analyses utilizing a hit baseline identified cluster maxima in the vmPFC/ventral ACC, inferior occipital gyrus, medial superior frontal gyrus, precentral gyrus, the brainstem, dorsal ACC, and the left IPL (see Table 3, Fig. 3).

#### 3.3. CR baseline

False retrieval analyses utilizing a CR baseline identified cluster maxima in a variety of cortical and sub cortical areas, including the precentral gyrus, medial superior frontal gyrus, the right middle frontal gyrus, the bilateral IPLs, the Precuneus, and two clusters in the caudate (see Table 3, Fig. 3).

#### 3.4. Verbal stimuli

The verbal sub-analysis identified cluster maxima in several frontal regions including the medial superior frontal gyrus, precentral gyrus, the dorsal ACC, and the left middle and inferior frontal gyri. An additional cluster was found left IPL (see Table 3).

#### 3.5. Pictorial stimuli

The pictorial sub-analysis identified three cluster maxima in the PFC, including maxima in the right inferior frontal gyrus, the vmPFC/ventral ACC, and medial superior frontal gyrus (see Table 3).

#### 3.6. Semantic relatedness

Identical to the verbal sub-analysis, the semantic relatedness sub-analysis identified several frontal regions including medial superior frontal gyrus, the precentral gyrus, the dorsal ACC, the left middle and inferior frontal gyri as well as a cluster in the left IPL (see Table 3, Fig. 4).

#### 3.7. Perceptual relatedness

The perceptual relatedness sub-analysis identified two clusters in vmPFC/ventral ACC and two in left inferior and middle occipital gyri (see Table 3, Fig. 4).

#### 3.8. Encoding

False encoding studies showed cluster maxima in the middle temporal gyrus (MTG) and ACC (see Table 3, Fig. 5).

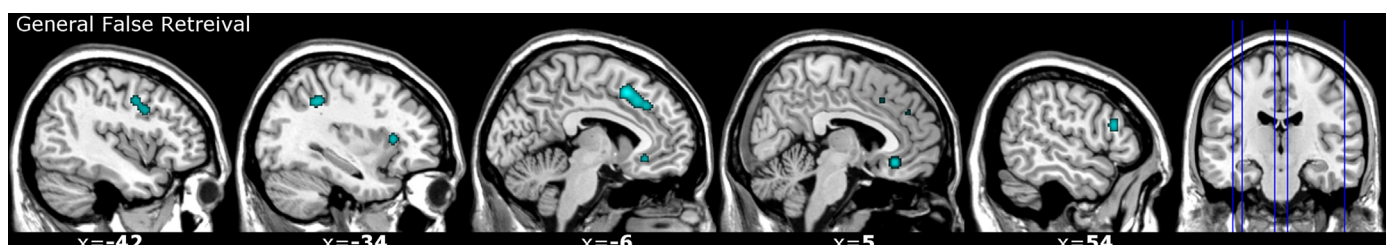
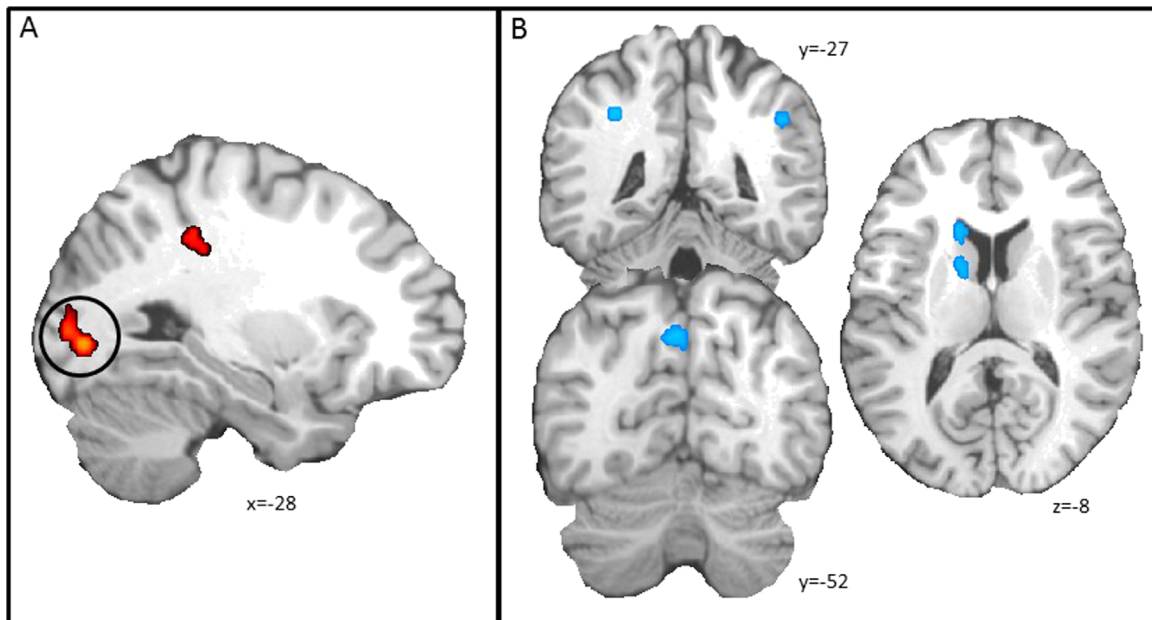


Fig. 2. General false memory retrieval. Regions showing consistency across false memory retrieval studies, irrespective of paradigm, memoranda type, and baseline contrast.

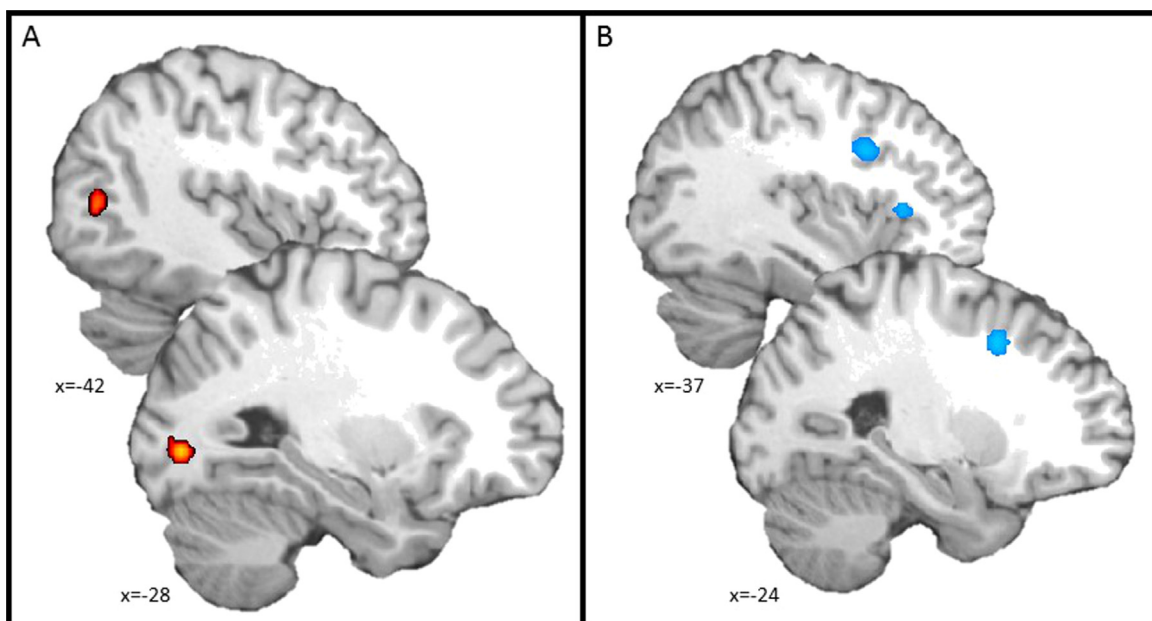


**Fig. 3.** Hit and CR baselines at retrieval. Highlighting unique foci of activity in the retrieval sub-analyses using (a) hits and (b) correct rejects as a baseline for examining false memories. Regions showing consistency included left inferior occipital gyrus for Hits and bilateral inferior parietal cortex and precuneus as well as left caudate for CRs.

#### 4. Discussion

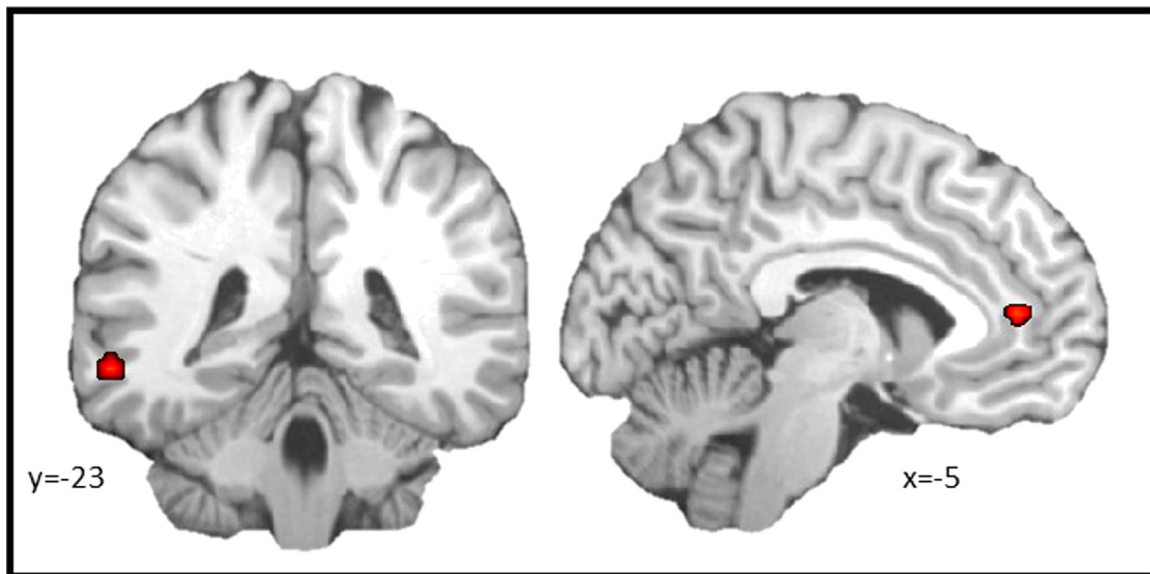
The present study sought to quantitatively summarize the false memory neuroimaging literature through eight separate meta-analyses. The first meta-analysis examined all fMRI studies that included an investigation of false memory at retrieval, collapsing across differences in stimuli, baseline, and experimental paradigm. Next, in order to examine consistencies that may differ across types of experiments, 3 pairs of sub-analyses were performed. The first pair of sub-analysis sought to identify results that were specific to the baseline used to examine false memories. Specifically, while one sub-analysis examined the neural basis of false

memories contrasted against a CR baseline, the other examined false memories when compared to Hits. The second pair of sub-analyses sought to identify memoranda specific neural correlates by selecting studies utilizing verbal stimuli and pictorial stimuli as memoranda. A third and final pair of sub-analyses sought to identify consistent neural correlates that differ based on experimental manipulation, specifically examining both semantic relatedness paradigms and perceptual relatedness paradigms. The final analysis focused on studies that examined subsequent false memories, quantifying encoding related activity that leads to subsequent false memory. The results of the eight meta-analyses can be found in [Table 3](#) and are discussed in turn below.



**Fig. 4.** Semantic and perceptual relatedness paradigms at retrieval. Highlighting unique foci of activity in the retrieval sub-analyses examining false memories arising from the use of (a) semantic and (b) perceptual relatedness paradigms. Regions showing consistency included left inferior and middle frontal gyrus for semantic relatedness and left inferior and middle temporal gyrus for perceptual relatedness.





**Fig. 5.** False memory encoding. Regions showing consistency across false memory encoding studies, including left middle temporal gyrus and the anterior cingulate cortex.

#### 4.1. General false retrieval

The results of our general false retrieval analysis identified several clusters of consistency across all studies irrespective of differences in experimental design and analysis, the majority of which were localized within the PFC, including clusters in the medial superior frontal gyrus, vmPFC/ventral ACC, left precentral gyrus, as well as bilateral inferior frontal gyri. An additional cluster of activation was identified in the left IPL (see Fig. 2, Table 3).

The most prominent of the frontal regions, the medial superior frontal gyrus was found active across multiple types of experimental paradigms including reality monitoring (Kensinger and Schacter, 2006), semantic relatedness (Atkins and Reuter-Lorenz, 2011; Garoff-Eaton et al., 2007; Kim and Cabeza, 2007b; von Zerssen et al., 2001), perceptual relatedness (Hofer et al., 2007; Iidaka et al., 2012), associative memory (Dennis et al., 2014a, 2014b), and general episodic memory paradigms (Kuehnel et al., 2008; Risius et al., 2013).

Across false retrieval studies, the most common interpretation of the medial superior frontal gyrus (and other midline frontal) activations has been that it is part of a frontal-parietal, cognitive control network that is responsible for the evaluation and monitoring of critical lures (Atkins and Reuter-Lorenz, 2011; Dennis et al., 2012, 2014a, 2014b; Garoff-Eaton et al., 2007; Hofer et al., 2007; Iidaka et al., 2012; Kensinger and Schacter, 2006; Slotnick and Schacter, 2004; von Zerssen et al., 2001). For example, midline prefrontal activity has been associated with top-down retrieval monitoring and verification processes, particularly in the absence of a strong sensory signal (Dennis et al., 2014a), as well as during tasks eliciting competing representations (Iidaka et al., 2012), and in tasks that involve the presence of strong conceptual similarity and semantic interference between targets and lures (Garoff-Eaton et al., 2007). Other studies interpret medial PFC regions as acting in a similar vein, suggesting that this activation supports monitoring when making demanding decisions, such as those required when presented with related lures at retrieval (Hofer et al., 2007; von Zerssen et al., 2001). Similar to the medial superior frontal gyrus, a second foci in the medial PFC, the vmPFC/ventral ACC was active across several different types of paradigms, including related perceptual (Kensinger et al., 2007; Slotnick and Schacter, 2004), source monitoring (Kensinger and Schacter, 2006), and semantic relatedness (Abe et al., 2008) paradigms.

Support for this cognitive control interpretation of medial PFC activation is found across general memory retrieval studies (e.g., Iidaka et al., 2006; Jacques et al., 2011; Johnson et al., 1993; Kim, 2010, 2013), as well as decision making studies (see Krain et al. (2006)), which have particularly identified the medial superior frontal gyrus, as well as the vmPFC/ventral ACC, as critical regions underlying one's ability to decide between multiple response options. Moreover, research has found that activation in these regions increases as the difficulty or uncertainty of a decision increases (e.g., Volz et al., 2005; Zysset et al., 2006) and has attributed increased midline PFC activity to the need for greater monitoring when memory judgments are less certain (Henson et al., 1999a, 199b), as is the case for false compared to true memories which are posited to be a relatively easier memory decision as targets are accompanied by greater sensory signals and reinstatement of the studies item (Dennis et al., 2014a, 2014b; Slotnick and Schacter, 2004).

Interestingly, activity in the medial superior frontal gyrus was identified in the general false memory analysis as well as the majority of our sub-analysis (all but the perceptual relatedness sub-analysis). As such, results speak to the ubiquitous nature of this region with respect to false memory retrieval, suggesting that, irrespective of differences in baseline or stimuli type, the medial superior frontal gyrus is a critical component of the false memory network. Interestingly, the vmPFC/ventral ACC was also identified within the general false retrieval analysis as well as the hit, but not CR baseline sub-analysis and the pictorial/perceptual, but not verbal/semantic sub-analyses. In addition to its role in cognitive control, the vmPFC/ventral ACC is often identified as part of a larger "saliency network", which has been linked to emotional processing (Lindquist et al., 2012) and processing of highly salient items more generally (Seeley et al., 2007). A closer look at the studies contributing to this cluster shows several experiments utilizing emotional stimuli (Kensinger et al., 2007; Kensinger and Schacter, 2006). Thus, it is likely that the vmPFC/ventral ACC mediates emotional false memories through its role in salience processing and may not be critical to false memory retrieval in the absence of an emotion component to the task. With respect to the experiments contributing to the vmPFC/ventral ACC cluster that did not appear to include an emotional component to the task (e.g., Slotnick and Schacter, 2004), it may be that the task demand and/or encoding task evoked more emotional processing. Future



research is needed to verify this interpretation.

The left precentral gyrus activation was also observed not only in the general false retrieval analysis but also all retrieval sub-analyses except for those focusing on perceptual stimuli and relatedness. While the ventrolateral PFC has been implicated in cognitive control processing (e.g., [Badre and Wagner, 2004](#)), the region identified in the current meta-analysis is more superior than that which is typically reported. Furthermore the cluster sits at the border of the premotor cortex, an area involved in the planning, coordination, and learning of motor movements (e.g., [Hardwick et al., 2013](#); [Rizzolatti et al., 2002](#)). Given that all memory outcomes in the involved paradigms include motor responses it is not clear why those reflecting false memories would require any greater involvement of the precentral gyrus. Furthermore, if planning and execution of a motor response for a false memory does involve greater effort, it is not clear why those involving perceptual stimuli would be less affected. Perhaps a closer look at repose time differences could shed light on this issue (unfortunately, the reported data for studies in the current analysis was insufficient to full explore this possibility).

Finally, foci of activity in bilateral inferior frontal gyrus were observed in the general false retrieval analysis, with the left cluster also presented in both the verbal and semantically related sub-analyses. Given the role of this region in semantic processing ([Noppeney et al., 2007](#); [Price, 2000](#); [Simons et al., 2005](#); [Wise and Price, 2006](#)), it is likely that the region is mediating false memories by activating the semantic relatedness and or semantic gist that links target items with lures. Further discussion of this finding can be found below (see verbal studies/semantic relatedness sub-analysis). With respect to the function of the right cluster, several language studies have suggested that language processing is not simply left lateralized, but engages contralateral processing regions as well ([Beeman and Chiarello, 1998](#); [Bright et al., 2004](#); [Pilgrim et al., 2002](#); [Rossell et al., 2001](#)). However, the fact that the right focus is not present in the verbal sub-analyses, but rather the pictorial sub-analysis argues against this possibility. Furthermore, given that 2 of the 3 experiments contributing to this cluster derive from the same study ([Kuehnel et al., 2008](#)), we do not feel we have strong evidence to speculate on the independent function of this cluster with respect to general false memory retrieval.

In addition to the foregoing PFC clusters, the general false memory analysis also revealed a common cluster of activity in the left IPL, which, like several PFC regions, was also active across multiple sub-analyses. Also, like the frontal findings, this cluster stemmed from several different false memory paradigms, including source monitoring ([Kensinger and Schacter, 2006](#)), DRM ([Kim and Cabeza, 2007b](#)) and perceptual unrelated ([Duarte et al., 2010](#); [Iidaka et al., 2012](#)) studies. The most common interpretation of parietal activation in the false memory literature has been that it serves to track familiarity associated with a lure. For example, [Kim and Cabeza \(2007b\)](#) attribute their inferior parietal findings to strong gist traces created by the semantic similarity shared between related lures and targets in their DRM paradigm. In that same vein, several studies ([Dennis et al., 2014a, 2014b](#); [Duarte et al., 2010](#); [Iidaka et al., 2012](#)) propose that inferior parietal activation in their experiments also reflects familiarity processing, with a possible role in guiding attention.

While the notion that familiarity or gist-based processing supports false memories is well supported in the behavioral literature (see [Brainerd and Reyna \(2002\)](#), [Jacoby \(1991\)](#) and [Yonelinas et al. \(1996\)](#)), the interpretation that inferior parietal activation supports familiarity processing is not consistent with findings from the general memory retrieval literature. That is, in studies examining both recollection and familiarity, it is the superior parietal cortex that is associated with familiarity, whereas the inferior parietal cortex is associated with recollection-related

retrieval ([Vilberg and Rugg, 2008](#); [Yonelinas et al., 2005](#)). Specifically, during memory retrieval, the inferior parietal cortex has been linked to the bottom-up capture of attention that supports the reinstatement of encoding-related details supporting a recollection memory decision ([Cabeza et al., 2012](#)) as well as processes supporting the representation of recollected information, akin to Baddeley's theoretical 'episodic buffer' ([Vilberg and Rugg, 2008](#)). Due to a lack of recollection/familiarity specificity in the response options involved in the contributing studies it is difficult to say if the identified cluster in IPL reflects such strong memory responses.

However, parietal activity is not solely associated with differences in veridical memory decisions, but has been found to be active during retrieve attempt, regardless of the success of the memory decision (i.e., recollective orienting effects) ([Dobbins et al., 2002, 2003](#); [Dobbins and Wagner, 2005](#); [Henson et al. 1999a, 1999b](#)). Taken together with the foregoing theories of inferior parietal function, it is possible that, with respect to false memories, ILP activity reflects the capture of attention and recollection of the original study episode, evoked by the lure item. Together, with monitoring processing in the PFC, the parietal may support false memory decisions by keeping active the encoding episode and evaluating the retrieved details within the context of the lure item (e.g., content borrowing; content-borrowing; [Lampinen et al., 2005](#)) – and ultimately leading to an incorrect endorsement of the lure based on this evidence. That is, when presented with a lure item, individuals are recollecting encoding items associated with that lure or the encoding context in which the lure would readily be associated. This recollection may, in turn, support the endorsement of the lure as 'old', thereby leading to a false memory. Future work should not only continue to interrogate the role of the IPL within false memories, but also the connectivity between the IPL and PFC regions.

Interestingly, no common retrieval cluster was identified within either the occipital or temporal cortex (either medial or lateral). With respect to the absence of occipital activity, results suggest that visual processing is not a fundamental process supporting false retrieval. We did, however, find that occipital activity supports false retrieval when using hits as baseline and also when studies exploit the perceptual relatedness between targets and lures (see discussion of the hit and perceptual relatedness sub-analysis below). Thus, results suggest that potential reconstructive processes in occipital cortex which have been identified in supporting false memories in past studies ([Dennis et al., 2012](#); [Slotnick and Schacter, 2004](#)) and qualitative reviews (i.e., [Dennis et al., 2015](#)) are specific to not only the type of stimuli, but the paradigm utilized to investigate false memories.

With respect to the absence of temporal activity, the false memory literature has long debated over the role of the medial and lateral temporal cortices during false retrieval, with some studies finding evidence for MTL and lateral temporal activation during false retrieval and others not (see [Dennis et al. \(2015\)](#) for a qualitative review). With regard to the MTL in particular, there is strong evidence supporting its role in encoding and episodic memory retrieval ([Kim, 2011](#); [Spaniol et al., 2009](#)). The results of the present meta-analysis, however, suggest that there is not strong fMRI evidence for consistent MTL involvement in false memory retrieval. This may be due to several factors. For one, it may be that previously observed MTL activation for false retrieval is widespread and not localized to a common MTL sub-region. While the ALE method detects spatial consistency of reported foci across studies, the MTL is unlikely to be detected as a consistent neural correlate if foci are located in spatially diffuse sub-regions of the MTL (e.g., anterior versus posterior). Second, despite the observation of MTL activity for false memories, a common finding across several studies is that of greater MTL activity for true

compared to false memories (with studies rarely observing greater MTL activity for false compared with true memories; but see Abe et al. (2013) and Karanian and Slotnick (2014)). As such, the choice and inclusion of contrasts that compared false to true memories as well as false to other types of baseline activity may have hindered our ability to detect MTL activity. However, if this was the case, then we would have expected our CR baseline sub-analysis to detect MTL activation, yet it did not. A third possibility is that the MTL is particularly responsible for false recollection versus false familiarity or that different MTL regions support false memory of different strengths (Abe et al., 2013; Kim and Cabeza, 2007b). Thus, given that the vast majority of studies have collapsed across recollection and familiarity or other measures of memory strength (i.e., confidence judgements), false retrieval studies to date may simply be failing to detect MTL contributions to false memories. Further work is necessary to better understand the conditions and/or paradigms under which the MTL supports false memory retrieval.

In addition to the MTL, the lateral temporal lobes are also regions that are commonly reported in false memory studies (Cabeza et al., 2001; Dennis et al., 2014a, 2014b, 2008; Garoff-Eaton et al., 2006; Schacter et al., 1996; Stark et al., 2010). However, we did not find evidence of common lateral temporal engagement in the general false retrieval analysis. Lateral temporal cortices, in particular the middle and superior temporal gyri, have been shown to be critical to semantic processing, semantic elaboration and the processing of semantic gist (Noppeney et al., 2007; Price, 2000; Simons et al., 2005; Wise and Price, 2006). As such, they are posited to support false memories by means of the semantic similarities amongst stimuli typically utilized in false memories studies. The results of the present meta-analysis suggest, however, that the foci in the lateral temporal cortex are not consistent across studies (or at the very least not consistent enough to be picked up by our quantitative method).

#### 4.2. Examining hit and CR baselines at retrieval

In addition to the general false retrieval analysis, the present study sought to highlight differences in the neural correlates supporting false retrieval that are attributable to the use of differing baselines in false memory studies. To that end, the CR baseline analysis identified foci of consistency in areas previously highlighted in the general false retrieval analysis, including medial superior frontal gyrus, left IPL, and precentral gyrus, as well as additional clusters in the right middle frontal gyrus, precuneus, right IPL, and caudate. The Hit baseline analysis also identified clusters of consistency that were previously identified in the general false retrieval analysis including the medial superior frontal gyrus, precentral gyrus, vmPFC/ventral ACC, and left IPL, as well as additional clusters in the dorsal ACC, inferior occipital gyrus, and the brainstem.

As noted previously, the utility in using CRs as a baseline for which to identify false memory activity stems from the fact that CRs hold constant the novelty of the item (i.e., lure) while parceling out activity associated with (erroneous) retrieval. A comparison of false memories to CRs identified additional parietal regions (i.e., right IPL and precuneus) to that which was identified in the general false retrieval analysis, and which was absent in the hit baseline analysis. Taken together, results support the foregoing interpretation that inferior parietal activity reflects retrieval of the prior episode of which the lure item is related. That is, compared to CRs which are mediated by novelty detection, the current results highlight the importance of memory retrieval and memory search underlying false memories. Such search and retrieval of past episodic details are critical to the memory retrieval process (Kim, 2013; Spaniol et al., 2009). The fact that multiple parietal regions

were identified in the current sub-analysis supports the view that such processes are ubiquitous to the retrieval process itself and not solely involved in retrieval success. A similar interpretation can be made for the right middle frontal gyrus foci. Within the context of memory retrieval, the right middle frontal gyrus has been associated with retrieval monitoring and evaluation (Henson et al., 1999a, 1999b; Schacter and Slotnick, 2004). The fact that activity in this region is present only in the CR sub-analysis, which is the only analysis that does not also include experiments including true hits as a comparison baseline, highlights the retrieval component inherent in false memory decisions.

Finally, the CR baseline sub-analysis identified foci of consistent activity in bilateral caudate. Interestingly, caudate activity is thought to be dependent on task demands, with past research suggesting that it is engaged depending on the complexity and difficulty of the retrieval task (Le Bras et al., 1998). To this end, false memory studies are typically designed to be highly difficult, encouraging FAs through various experimental manipulations (e.g., manipulation of the relatedness of lures, introduction of misinformation). Thus, the caudate could be active in response to the difficult retrieval task and the difficulty involved in making the false memory decision compared to a relatively easier novelty decision. However, recent work in our lab has suggested that the caudate is more active when making correct recall-to-reject memory decisions compared to false recognition (Bowman and Dennis, 2015). Consequently, additional research is needed to resolve these conflicting results.

Compared to the CR baseline sub-analysis, the use of a hit baseline highlights neural activity that is unique to the veracity of the memory retrieval decision. As such, hit baseline contrasts reveal neural regions that are recruited above and beyond what is required for true retrieval, a process that shares the subjective experiencing of recognition. In addition to that discussed in the general false retrieval analysis, the hit baseline analysis revealed two additional clusters of neural activity that were unique to hit baseline contrasts: a more dorsal ACC region and a cluster in the occipital cortex. Within the context of retrieval, the dorsal ACC has been associated with conflict monitoring, particularly in the context of response competition (for a review see Botvinick et al. (2001)). To this end, dorsal ACC activity may reflect the heightened monitoring and difficulty of decisions inherent in false memory retrieval compared to veridical retrieval.

Finally, the hit baseline sub-analysis identified a single foci of activity in the inferior occipital gyrus. Recent studies utilizing visual memoranda as well as qualitative reviews have focused on the role of early visual cortex in supporting true (but not false) memories through the process of sensory reactivation (Dennis et al., 2015; Schacter and Slotnick, 2004). The foregoing studies further suggest that false memories are associated with processing in late visual regions which support object/item identity. In other words, by virtue of having been presented previously, targets are posited to elicit sensory reinstatement of the original encoding episode in early visual processing regions, whereas lures, which by definition, were not seen previously would not be accompanied by stored sensory signals. However, the current result argues against this view and suggests that processing in early visual cortex may lead to erroneously endorsing a lure as old. Given that the experiments contributing to the foci in early visual cortex utilized relatedness paradigms and that a subset of these experiments also contributed to the same finding in the perceptual relatedness sub-analysis (see Supplemental Table 2), it may be that the contribution of early visual cortex to false memories occurs is specific for lures that share common perceptual features with target items. More research comparing the role of the visual cortex across different types of false memories is needed to confirm this distinction.

#### 4.3. Verbal and pictorial memoranda at retrieval

Additional retrieval sub-analyses sought to identify patterns of consistency that were unique to both the use of verbal as well as pictorial stimuli, further focusing on the use of the relatedness paradigm using each type of stimuli. The verbal sub-analysis and the semantic relatedness sub-analysis yielded the exact same results. In addition to common activity in the medial superior frontal gyrus, precentral gyrus, left IPL, and left inferior frontal gyrus (discussed above), the analysis of verbal stimuli identified foci of common neural activity in the dorsal ACC (more superior to that identified in the hit baseline sub-analysis) and left middle frontal gyrus. As mentioned previously, the left lateral prefrontal areas have been shown to support general language and semantic processing (see [Binder et al. \(2009\)](#) and [Price \(2010, 2012\)](#) for qualitative and quantitative reviews of semantic processing). Given the strong semantic component underlying the false memory tasks in this sub-analysis (e.g., the DRM task), false memory studies have interpreted left lateral PFC activation as evidence for semantic elaboration ([Cabeza et al., 2001](#); [Dennis et al., 2007](#); [Garoff-Eaton et al., 2007](#); [Kim and Cabeza, 2007a](#); [Kubota et al., 2006](#); [von Zerssen et al., 2001](#)). The semantic elaboration account presumes that when presented with a typical DRM list (e.g., nap, rest, wake, pillow, etc.) the presentation of the semantically related lure (e.g., sleep) elicits retrieval of the semantic associates encountered during encoding, as well as any previous activation of the lure ([Deese, 1959](#); [Roediger and McDermott, 1995](#)). At retrieval, this activation leads individuals to endorse these lures as having been seen previously. The meta-analytic finding of consistent activation in the foregoing left lateralized frontal language and semantic processing regions supports this account from past semantic relatedness studies of false memories.

The dorsal ACC foci identified in the verbal sub-analysis sits superior to that which was identified in the hit sub-analysis, with different experiments contributing to each finding. In light of these differences, we maintain the prior interpretation of this finding regarding the role of the dorsal ACC in conflict monitoring and resolving response competition ([Botvinick et al., 2001](#)). However, results suggest that stimulus and response properties may influence the exact region within the ACC that supports these processes.

With respect to pictorial stimuli, results of the sub-analysis identified only common foci of activity that were also seen in the general false retrieval analysis, including the medial superior frontal gyrus, vmPFC/ventral ACC and the right inferior frontal gyrus. On the other hand, the perceptual relatedness sub-analysis identified a second cluster of activity in vmPFC/ACC (to that which was observed in the general false retrieval analysis), as well as two foci of activity in left visual cortex, specifically inferior and middle occipital gyrus. Interestingly, the occipital activity was only identified in the perceptual relatedness sub-analysis, whereas the pictorial analysis failed to find visual activity. Taken together, the results suggests that visual processing may be particularly important to the retrieval of false memories when lures are highly perceptually related to targets – and not a component of false memory retrieval simply as a function of the inclusion of visual stimuli. Past research has attributed occipital activation to visual reconstructive processes that underscore false memories when lures are perceptually similar to targets ([Dennis et al., 2012](#); [Garoff-Eaton et al., 2006](#); [Gutchess and Schacter, 2012](#); [Slotnick and Schacter, 2004](#)). That is, the general properties associated with a target item, such as its shape, size, orientation, or identity is posited to form the basis of a false memory decision. As such, our results suggest that faulty perceptual reconstruction in the late visual cortices may be a characteristic of false retrieval of visual stimuli when the lures sharing similar perceptual characteristics to

the targets. Furthermore, as noted above, this explanation has largely been linked to activity in later visual cortex (e.g., the middle occipital gyrus foci), whereas activity in early visual cortex has been more often associated with sensory reinstatement of true memories ([Abe, 2012](#); [Dennis et al., 2015](#); [Schacter et al., 2012](#)). As noted above, the current results argue against this dissociation, suggesting that the role of early visual cortex in supporting false memories be re-evaluated.

#### 4.4. Encoding studies

While the majority of research examining the neural correlates of false memories has focused on retrieval, it has been argued that encoding processes also contribute to false memories. However, it is relatively difficult to design a study that isolates the neural processes that contribute to the formation of a false memory. As such, only a handful of studies have examined the influence of encoding processes on false memories (8 included in the current analysis). Yet, despite this small number the current analysis identified several foci of consistent activation across studies including the ACC, left middle temporal gyrus (MTG).

While both true retrieval studies and false memory retrieval studies have interpreted ACC activity within the context of monitoring and decision making, the same interpretation has not been applied to encoding results. For example, in the context of their reality monitoring paradigm, [Gonsalves et al. \(2004\)](#) attributed ACC activity to vivid visual imagery at encoding that led participants to mistakenly believe that they actually perceived (and not imagined) the lure. A second study utilizing the misinformation effect did not offer an explanation of its ACC finding ([Okado and Stark, 2005](#)). Interestingly, while two recent meta-analyses examining veridical encoding have not found ACC activity to support successful subsequent memories ([Kim, 2011](#); [Spaniol et al., 2009](#)), medial PFC activity was found to support subsequent forgetting ([Kim, 2011](#)). That is, medial prefrontal activity during encoding was found to be detrimental to subsequent memory success and was associated with subsequent forgetting. Given that this activation was associated with activity in other regions that comprise the default mode network, the meta-analysis attributes this activity to mind wandering and lapses of attention that lead to forgetting and failures of memory. Given that false memories are also failures of memory, a similar interpretation might be offered in the current analysis. At this time, however, there is not enough replication to support a definitive conclusion of the ACC's specific role in false encoding.

In addition to the ACC, our encoding analysis identified foci of consistency in the left MTG. Semantic processing and language research has shown that, in addition to left PFC, the left lateral temporal cortex is critical in mediating semantic processing, including processing of semantic gist ([Noppeney et al., 2007](#); [Price, 2000](#); [Simons et al., 2005](#); [Wise and Price, 2006](#)). Additionally, two behavioral theories of semantic false memories, the activation monitoring theory and the fuzzy trace theory, posit that false memories are linked to semantic processing during encoding. According to the activation monitoring theory, during encoding, activation spreads between closely related semantic associates (e.g., list items to lures) such that at retrieval internal activation of the lure is misattributed to an external presentation source ([Roediger et al., 2001](#); [Underwood, 1965](#)). Alternatively, according to the fuzzy trace theory, two types of memory traces are created during encoding: item-specific traces, which retain the distinctive features of the individual items, and gist traces, which retain only the general meaning of the event ([Brainerd and Reyna, 1990](#)). False memories arise when the gist trace is retrieved in absence of the item-specific trace. Based on these literatures, false memory studies have posited that activation in lateral temporal cortices is a



significant factor contributing to false memory of lures that are semantically related to encoded information (Dennis et al., 2007; Garoff et al., 2005; Kim and Cabeza, 2007a).

## 5. Conclusions

The current meta-analysis aimed to synthesize results from previous studies examining the neural basis of false memories. It further aimed to identify neuroanatomical similarities supporting retrieval, as well as encoding processes supporting false memories. In doing so, our results support several conclusions from previous individual studies and qualitative reviews. First, irrespective of the variability in testing paradigms, results showed that false retrieval is supported by top-down cognitive control mechanisms mediated by the prefrontal cortices and parietal cortex. Our results provide greater specificity to the earlier qualitative reviews by identifying specific foci of activation in each region. Specifically, the current set of analyses identify a critical role of medial superior frontal gyrus and left inferior parietal cortex in supporting false memory retrieval. Second, our sub-analyses focusing on the different contributions of baselines to the identification of false memory suggest that, compared to CRs, false memories elicit greater activity in right middle frontal gyrus and throughout parietal cortex as well as the left caudate. As this activity was absent in the hit baseline sub-analysis, results suggest that false memory retrieval evokes activity in the typical retrieval network and that activity in the foregoing regions, which are often identified in retrieval analyses (Kim, 2013; Spaniol et al., 2009), are not unique to veridical retrieval. Finally, results identify a role for stimulus specific processing supporting false memories such that activity in verbal processing regions including left middle and inferior frontal gyrus support semantic false memories whereas activity in visual processing regions support false memories in a perceptual relatedness paradigms. Furthermore, our results challenge the notion that activity in early visual cortex mediates true retrieval whereas activity in late visual cortex mediates both true and false retrieval, finding a focus of activity in left inferior occipital gyrus associated with false memories in the hit and perceptual-related sub-analyses. Finally, results of the encoding analysis find that activation supporting false memory formation is mediated by general stimulus and gist processing within left lateral temporal cortex as well as control processes within the medial frontal cortex.

In addition to the contributions described above, neither the encoding or retrieval analyses (nor sub-analyses) found any consistent basis for a role of the MTL in mediating false memories. As noted above, evidence for the role of the MTL in mediating false memories has been mixed. We note that the absence of MTL activity may stem from the inclusion of contrasts that pair false memories with true memories, such that while the MTL may serve a role in mediating false memory retrieval, it may be that it does not exceed that exhibited for true retrieval (e.g., Dennis et al., 2012). Additionally, methodological differences, such as collapsing across memory strength (e.g., confidence; recollection/familiarity) may have also contributed to the absence of MTL activity in the current analyses (see Abe et al. (2013) and Karanian and Slotnick (2014)). Future studies should both attempt to break up false memories by memory strength and should utilize a baseline other than hits in order to examine the role of the MTL in mediating false memories.

### 5.1. Limitations and future directions

While several limitations and areas of future research were identified in Section 4, we would like to highlight the following: First, because the power in a handful of the false retrieval sub-

analyses was low ( $N$ s of 7–18) a direct statistical comparison (often called a subtraction analysis) could not be computed (a minimum of 15 studies is typically suggested for such a test). As such, the qualitative comparisons between sub-analyses should be interpreted with caution. Additionally, there was not enough power to conduct even a cursory analysis into other paradigm designs (e.g., source monitoring, associative memory) or to investigate differences in the strength of the false memory (e.g., confidence, Recollection/Familiarity). Similarly, the encoding analysis included a limited number of studies ( $N=8$ ), which range widely in several qualitative ways (see Table 2). More experiments looking at encoding processing leading to subsequent false memories is needed before more definitive conclusions can be drawn. As such, as future studies continue to contribute to this emerging literature, follow-up analyses to those presented here should be performed. Second, future false memory studies should continue to consider the baseline which they use to define false memories. While a correct rejection baseline may overestimate neural processes specific to false memories (and identify processes reflecting general retrieval mechanisms), using a baseline of true memories may likewise underestimate these processes as well. Third, given recent evidence that memory strength may be critical to identifying a role of the MTL in mediating false memories, analyses should attempt to examine the separate contribution of recollection and familiarity to false memory retrieval. A fourth and final limitation of our study is shared among other ALE meta-analyses. Namely, that our analysis quantitatively calculated spatial concordance of foci, without regard to magnitude of activation. Future studies should address this issue while further investigating the current conclusions. One avenue for future research would be to examine differences in false retrieval among memoranda types within the same study as well as that of different paradigm manipulations.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2015.12.006>.

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