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Alice Yang April 9, 2021

Neural correlates of Recollection and Familiarity responses in episodic memory:

A Seed-based d Mapping Meta-Analysis

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An abstract of
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Abstract

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By Alice Yang

According to the dual process theory of episodic memory retrieval, successful memory retrieval for specific events can be obtained through two distinct processes known as recollection and familiarity (Tulving, 1985). The two processes are distinguishable at a neurological level based on neuropsychiatric and neuroimaging evidence, which suggested that different subregions of the frontal, parietal and medial temporal lobe were involved differentially for recollection and familiarity (Eichenbaum, Yonelinas, & Ranganath, 2007; Ranganath, 2010; Spaniol et al., 2009). However, huge variance resides in results from past neuroimaging studies, possibly due to the small sample size and methodological difference between them (Skinner & Fernandes, 2007; Spaniol et al., 2009). Here we provide a quantitative summarization of neural correlates for recollection and familiarity by employing the meta-analytic method seed-based d-mapping (SDM) to summarize findings across studies that reported contrasts including recollection > familiarity and familiarity > miss/correct rejection (Tulving & Craik, 2005). Consistent with our hypothesis, we found unique subregions that activate more for recollection including the parahippocampal cortex and default mode network regions. We also found significant activations of ventral salience network regions associated with familiarity responses. Sub-analyses based on different retrieval paradigms were also conducted in order to assess the influence of methodological difference upon the results. We found distinctive results between analyses based on the remember-know and source memory paradigms. Results also favored the use of remember-know paradigm over source memory to distinguish recollection from familiarity. The current findings illustrate the involvement of parahippocampal and default mode network regions associated with contextual details and self-referential content in recollection and the involvement of salience processing related ventral network regions in familiarity responses. In addition, our results provide guidance in task selection and design for relevant future research.

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Neural correlates of Recollection and Familiarity responses in episodic memory: A Seed-based *d* Mapping Meta-Analysis

1. Introduction

Episodic memory is a type of declarative memory that involves conscious recall for personally experienced events that occurred at a specific time and place, as distinct from semantic memory (Tulving, 1985). Episodic memory is crucial to our normal daily life and such importance is evidenced by patients with severe memory impairments such as amnesia (Eichenbaum et al., 2007; Hamann & Squire, 1995; Squire, 2004; Squire et al., 2007). Studies on episodic memories utilizing psychophysiological assessments, electrophysiological procedures such as event-related potentials (ERP), and neuroimaging methods such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI) have revealed distinct neuronal basis for episodic memory and helped refine the definition and features of this unique memory system. (Addis et al., 2015; Moscovitch et al., 2016; Tulving, 2002; Tulving & Craik, 2005).

1.1 The dual-process model of episodic memory

The most widely accepted model of episodic memory retrieval is the dual process model. This model proposes two distinct processes for episodic memory retrieval: recollection and familiarity (Greve et al., 2010; Jacoby, 1991; Mandler, 1980; Yonelinas, 1994). Recollection refers to retrieval of items or events that include additional contextual information such as sounds, scents, colors, or memories of thoughts or experiences during the encoding of the target while familiarity refers to retrieval in the absence of being able to recollect contextual details of a target's prior occurrence (Daselaar et al., 2006; Squire et al., 2007; Yonelinas, 1994). An item's level of familiarity can range continuously from low to high, whereas recollection is typically proposed to be an all-or-none threshold-based process (Yonelinas et al., 1996). Although high familiarity is often associated with items that can also be recollected, these two processes are dissociable in the sense that items can be highly familiar even in the absence of recollection (Knowlton & Squire, 1995).

Evidence supporting the idea that recollection and familiarity are distinct functional processes in episodic memory comes from multiple behavioral, neuroimaging, and lesion studies in humans, monkeys and rodents (Diana et al., 2007; Eichenbaum et al., 2007; Yonelinas et al., 2002). The primary region that a majority of studies focused on is the medial temporal lobe (MTL), which includes many subregions essential to learning and memory (Daselaar et al., 2006; Diana et al., 2007; Eichenbaum et al., 2007; Ranganath, 2010; Squire & Wixted, 2011). Within the MTL, the perirhinal cortex is proposed to process visual attributes and familiarity of encoded items whereas the parahippocampal cortex is proposed to process contextual information; both types of information then project to the entorhinal cortex and converge within the hippocampus where the item and contextual information are bound together (Diana et al., 2007; Ranganath, 2010). Support for these hypotheses can be found in past reviews of neuropsychological and neuroimaging data that showed increased hippocampal and posterior parahippocampal activation relating to recollection as compared to familiarity, and activations in the perirhinal cortex relating to familiarity (Eichenbaum et al., 2007; Skinner & Fernandes, 2007).

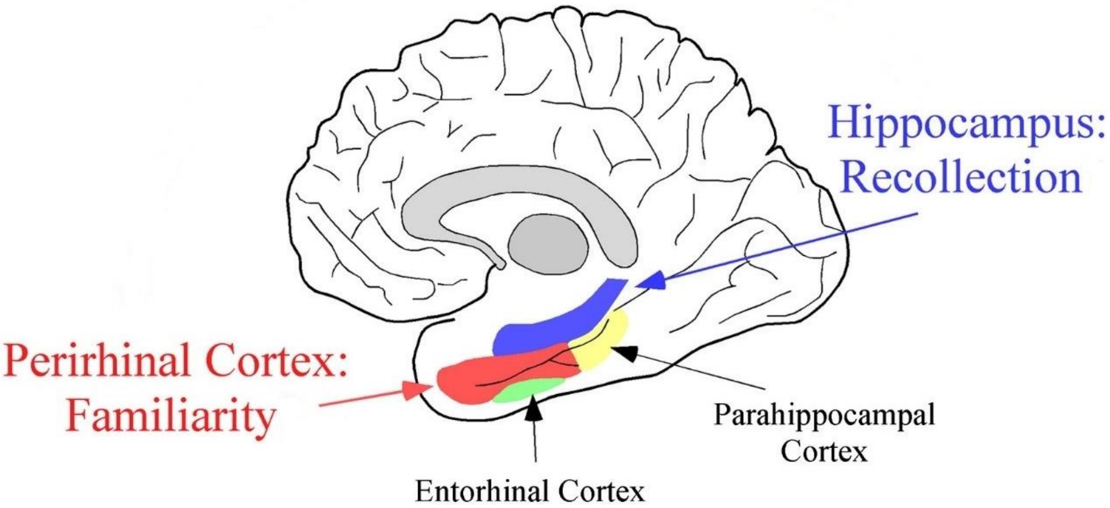

Figure 1. The dual process theory of recognition memory in the medial temporal lobe (figure adapted from Burwell and Furtak (2008).

Although the functional division between the medial temporal lobe regions including parahippocampal cortex, perirhinal cortex and hippocampus has been widely proposed, evidence for this division is absent in many experimental results. For example, several human neuroimaging studies and reviews did not find perirhinal activations associated with familiarity (Eickhoff et al., 2012; Henson et al., 1999; Mayes et al., 2019; Montaldi et al., 2006; Ranganath, 2010; Rugg & Yonelinas, 2003; Smith et al., 2011; Spaniol et al., 2009; Yonelinas, 2001). One review article summarizing results from neuroimaging, single unit-recording and hippocampal lesion studies in humans, monkeys and rodents also pointed out that neurons in perirhinal cortex encodes for recall whereas hippocampal neurons encode for familiarity (Squire et al., 2007). It is possible that some of these discrepancies may be a result of variance brought by different types of retrieval tasks used to assess the neural correlates of recollection and familiarity across episodic memory studies (Horn et al., 2016; Spaniol et al., 2009; Squire et al., 2007).

Although most research examining the neural correlates of recollection and familiarity focus on the functional dissociations within the MTL, important functional differences have also been found in the prefrontal cortex and parietal lobe (Cabeza, 2008; Scalici et al., 2017; Vilberg & Rugg, 2008). Past meta-analyses on fMRI studies by Kim (2010), for example, proposed that recollection primarily engages areas in the default mode network including the anterior medial prefrontal cortex, the anterior and posterior cingulate and the angular gyrus. These regions are highly relevant for self-referential processing, introspective cognitive control and navigation, which matches the assumption that recollection involves more self-relevant components than familiarity (Kim, 2010, 2016). Familiarity responses, on the other hand, have been proposed to engage areas in the ventral attention network （MacDonald et al., 2000; Corbetta and Shulman, 2002; Wager and Smith, 2003; Nee et al., 2007). The ventral network includes ventral prefrontal and parietal regions as well as the insula and other subcortical regions which are highly relevant for salience processing (Phillips et al.,1998; Corbetta and Shulman, 2002; Peyron et al., 2002; Seeley et al., 2007; Sridharan et al., 2007). Although there are still many controversies regarding the exact functional significance of each region within the proposed networks (Kim, 2010), this summary of past neuroimaging data provides preliminary support that established neural networks covering the frontal and parietal regions are involved differentially for recollection and familiarity during episodic memory retrieval.

1.2 fMRI study design for recollection and familiarity

As a non-invasive neuroimaging technique with increasingly improved spatial and temporal resolution, fMRI has been increasingly employed in studies of recollection and familiarity (Cabeza & Nyberg, 2000; Spaniol et al., 2009). These studies generally use an event-related design with an encoding period and retrieval period. During encoding, a series of stimuli such as words, faces or pictures of objects and scenes would be shown to the participants. At retrieval, participants would be asked to perform a recognition memory task where they need to characterize the stimuli as something that is presented during encoding (old) or as something novel (new). For the purpose of dissociating recollection and familiarity responses, there are three major retrieval paradigms employed in the literature (Horn et al., 2016; Squire et al., 2007). The first one is termed the “remember-know” paradigm, which requires participants to make a subjective judgement on their responses in a recognition memory task (Diana et al., 2007; Guillaume et al., 2007; Yonelinas & Levy, 2002). During retrieval, participants would be instructed to give a “remember” response to an item recognized as “old” if they can recollect additional details associated with the encoding period for that item; if they cannot remember additional details, they would give a “familiar” response. The second type of paradigm involves the use of a confidence rating scale after a classic “old/new” judgement. Based on the theory that familiarity is a signal detection process, “old” items that elicit the highest confidence would be classified as recollected, and all other responses with lower confidence levels would be classified as familiar (Kim & Cabeza, 2009; Montaldi et al., 2006; Yonelinas et al., 1996). The third type of paradigm is the source/associative memory paradigm. In this paradigm, additional contextual details (such as font size or color difference) or paired stimuli would be presented during encoding and later tested at retrieval. Recollection is assumed to reflect correct retrieval for both the stimuli and contextual information while familiarity reflects correct retrieval for just the stimuli but not the additional associated context or stimuli.

Although all three types of episodic memory retrieval paradigms have been widely employed, there has been substantial debate in the literature regarding their reliability. For example, a review by Squire et al. (2007) proposed that tasks such as source memory judgement or confidence ratings instead measure “strong” versus “weak” memory as opposed to recollection and familiarity (Smith et al., 2011). Former meta-analysis also pointed out that the use of source memory tasks to dissociate recollection from familiarity might weaken the “familiarity” effect (Spaniol et al., 2009). In circumstances where people recollected additional contextual details not tested in the source memory task but did not recollect the correct source, the recollection response would be wrongly classified as familiarity. Such circumstance, termed as “non-critical recollection”, would contaminate the baseline familiarity condition (incorrect source retrieval for correct item recognition) and undermines the purpose of dissociating the two responses. Therefore, the inherent differences between different retrieval paradigms, as well as nuances between each study, impose great difficulty in summarizing past neuroimaging findings to delineate neural correlates of recollection and familiarity.

1.3 Previous Meta-analyses

The difficulty in integrating past neuroimaging findings can be addressed by quantitative meta-analyses, which help reduce the influence of inter-study heterogeneity upon the synthesized results. Compared to a qualitative review, quantitative meta-analysis of fMRI data integrates results from multiple studies using rigid statistical testing to identify brain regions that consistently activate for a specific construct such as episodic memory (Albajes-Eizagirre & Radua, 2018; Radua et al., 2012). One of the commonly used meta-analytic methods is the coordinate based meta-analysis (CBMA) method, which pools activation foci coordinates from individual neuroimaging studies to yield a whole-brain summary of activations associated with contrasts of interests via rigid statistical test. Previous CMBA meta-analyses done by Spaniol et al. (2009) and Kim (2010) for example, pooled results relating to recollection and familiarity from multiple studies and utilized the Activation Likelihood Estimation (ALE) method to identify commonly activated regions.

Spaniol et al. (2009) conducted separate ALE meta-analyses to find the neural correlates of recollection responses based on remember-know paradigms (termed as subjective recollection) and source memory paradigms (termed as objective recollection). Analysis on remember-know paradigms revealed left hippocampal activations relating to recollection while analysis on source memory studies revealed unexpected activation in the left amygdala but no hippocampal or parahippocampal activations. Differences between the results for remember-know and source memory paradigms were also found in prefrontal and parietal areas such as the superior lateral parietal lobe. The differences between objective and subjective recollection highlight the risk of employing source memory tasks to successfully differentiate recollection and familiarity. However, because there were an insufficient number of studies to examine familiarity specific contrasts (e.g. familiarity > miss) this study shed little light on potential differences in neural substrates between recollection and familiarity.

Correspondingly, ALE meta-analysis by Kim (2010) summarized neural correlates for both recollection and familiarity by basing their analysis on remember-know and confidence rating studies only. They reported results from analyses on three separate contrasts: remember > know (equivalent to recollection > familiarity or R > F), know > remember (equivalent to familiarity > recollection or F > R) and increasing familiarity. R > F contrast revealed regions primarily engaged in the default mode network as well as the hippocampus; F > R contrast revealed regions in the dorsal network while increasing familiarity contrast revealed regions in the ventral network. However, there exists some limitations in these analyses. First, results for the F > R and increasing familiarity contrasts were statistically underpowered as they only included 6 and 4 studies respectively. Secondly, the increasing familiarity analysis also included inappropriate contrasts that show increase from the lowest to highest confidence ratings. Since the highest confidence ratings are generally associated with recollection responses, inclusion of this level in the familiarity contrast could bias the results.

Although these previous quantitative meta-analysis have begun to shed light on the neural basis of recollection and familiarity, some concerns have also been raised regarding the use of ALE methodologies in fMRI meta-analysis (Albajes-Eizagirre & Radua, 2018; Laird et al., 2005). The first concern is that ALE tests for convergence of findings by using random permutations of activation peaks across the brain, which essentially relies on an assumption of spatial independence for voxel-wise activation. Such assumption is violated by the fact that activations in the brain are spatially dependent according to tissue type or functions (e.g. More activation peaks in gray matter than white matter) (Albajes-Eizagirre & Radua, 2018; Albajes-Eizagirre et al., 2019). The second concern is the use of false discovery rate (FDR) method to correct for multiple comparisons in ALE, which also contradicts the spatially correlated features of fMRI data (Chumbley & Friston, 2009; Eickhoff et al., 2012; 2016). Newer meta-analytic methods, such as Seed-based *d* Mapping Permutation of Subject Image (SDM), have since been developed to help resolve these issues.

1.4 Seed-based d Mapping meta-analysis

Seed-based *d* Mapping Permutation of Subject Images (SDM) (https://www.sdmproject.com/) (Albajes-Eizagirre et al., 2019) addresses the limitations of previous meta-analytic methods by incorporating effect sizes as well as spatial correlations between different brain tissue, and conducting permutation testing at the subject level contrasting against the null-condition on a voxel-wise basis. SDM also uses threshold-free cluster enhancement (TFCE) rather than FDR to control for multiple comparisons, which avoids the limit of selecting an arbitrary minimum cluster size in ALE and thus allows smaller clusters of activation to be detected. Collectively, these approaches help decrease false positives and increase reliability of a meta-analysis.

1.5 Current Study

Given the limitations of the previous meta-analyses and the significant growth and developments in fMRI studies on episodic memory over the last decade, we would like to update the current knowledge of the neural correlates of recollection and familiarity via SDM meta-analyses. To dissociate regions associated with recollection, we conducted a meta-analysis on the contrast of recollection > familiarity (R > F). To dissociate regions associated with familiarity, we conducted a meta-analysis on the contrasts that compared familiarity responses to either misses or correct rejections (F > M, F > CR) or contrasts of increasing familiarity. Since the specific contrasts we examined are consistent with those reported in the Kim (2010) meta-analysis, we expected to replicate some of the findings from this previous meta-analyses. Specifically, we hypothesized that recollection would mostly reveal hippocampal and parahippocampal activations, as well as regions common to the default mode network such as anteromedial PFC, cingulate gyrus and the angular gyrus. For familiarity, we hypothesized that activations would be found in regions such as the perirhinal cortex, as well as more ventral network associated regions such as the ventral medial and lateral PFC, middle frontal gyrus, inferior parietal lobe and other subcortical regions such as the insula, thalamus and caudate. However, we also expect that the addition of more than 10 years of new research, a more inclusive selection of recollection contrasts, a more appropriate selection of familiarity contrasts, and the use of the SDM method might result in novel consistently activated regions as well as regions that do not remain when more studies are considered.

Considering the variance across the three major retrieval paradigms employed in these studies, we also hypothesized that methodological differences between studies would impact the results. To test this hypothesis, we conducted meta-analyses based on only remember-know studies for the R > F and familiarity associated contrasts

(F > M/CR, increasing familiarity), as well as a meta-analysis based on only source memory studies for the R > F contrast. Since the source memory paradigm tend to underestimate recollection responses (“recollection” classified as “familiar” when participants recollected information not tested in the source memory task), the specific contrasts “correct > incorrect source” included in our analyses might not capture all activations that important for recollection as opposed to familiarity. Therefore, we hypothesized that sub-analysis based on remember-know studies should reveal increased number of activations or activations that are more consistent with the predicted neural correlates for recollection as compared to source memory studies.

2. Methods

Since the aim of our study partially overlaps with previous meta-analyses, we first examined studies included in past meta-analysis to determine if they met our inclusion criteria (Kim, 2010, 2016; Spaniol et al., 2009). Of all studies included in Spaniol et al. (2009) (Table 3 & 4), 3 studies employing source memory paradigm were excluded. All studies from Kim (2010) were included while 2 studies from Kim (2016) (Table S1) were excluded from our analyses. These studies were excluded as they failed to meet at least one of our inclusion criteria.

To identify additional studies as well as new studies published after the previous meta-analyses, we conducted a PubMed (www.pubmed.org) search using the following search terms "(fMRI) AND ((Recollection) OR(Remember)) AND

((Familiar) OR (Know))" prior to September 2020, which yielded 956 results. In order to ensure that we examined all contrasts sufficing our inclusion criteria, especially those reported in source memory studies, an additional search using the search terms "fMRI AND (source OR confidence) AND memory AND recognition" was also conducted in March 2021 and this gave 390 results. Results from the two searches were compared and 119 duplicate studies were removed. In total, 1227 studies were identified from the literature search.

For completeness, we also compared our literature search results to the lists of studies that were included in a previous meta-analysis focusing on source memories (Kim, 2020). Studies from Kim (2020) that did not show up in the database search then went through the selection process. We excluded 36 studies that did not report the target contrasts as detailed in our criteria. In the end, 17 additional studies from Kim (2020) were included in the final analysis. After final evaluations using the detailed inclusion and exclusion criteria listed below, 63 studies were included in the final analysis.

2.1 Inclusion and exclusion criteria

All papers identified from the online database and previous meta-analyses were next screened based on our inclusion and exclusion criteria. Our criteria were specified in regards to the neuroimaging methods and the retrieval tasks employed, the participants, the type of stimuli and whether whole brain coordinates for our contrasts of interests were reported in these studies.

2.1.1 Neuroimaging method

We included studies that tested retrieval success of episodic memory in an event-related fMRI design. For these studies, because SDM requires the coordinates of whole-brain activation maxima from voxel-wise univariate neuroimaging activation analyses, the inclusion of such data was a prerequisite for inclusion in the meta-analysis. For one study that reported results from regions-of-interests (ROI) analysis in the MTL separately, the resulting coordinates were included because the maximal activation statistic surpassed the whole-brain threshold for correction for multiple comparisons. We excluded studies that exclusively reported results from ROI analyses, multivariate pattern analyses, and functional connectivity analyses as these results either measure localized activities or correlation between regional activations and are thus inherently different from univariate voxel-wise activations required in the SDM analyses.

2.1.2 Participants

We included studies that reported results from healthy adults. For comparative studies between adults of different age group, contrasts reporting effects common to all age groups were included. For comparative studies between patients and healthy, unimpaired control subjects, results were only included if contrasts of interest were reported separately for control subjects.

To avoid statistical bias stemming from repeated sampling from the same population (so-called “within-group-effects”), we also combined contrasts that are based on same sample population as recommended by current meta-analysis guidelines (Alegria et al., 2016; Muller et al., 2018; Norman et al., 2016). This process ensures that no over-influence from any specific group of participants would occur for the results.

2.1.3 Stimuli

Included studies employed stimuli consisting of words, scenes, faces, locations, pictures, or line drawings of objects. For studies that reported mapped contrasts based on multiple types of stimuli, the most general mapped contrasts are included. For studies that reported appropriate contrasts separately for emotional and neutral stimuli, we combined all appropriate contrasts into one.

2.1.4 Retrieval tasks

We included studies that reported whole-brain activation maxima for our contrasts of interests from the retrieval scanning session. Studies that only reported activations from encoding scanning sessions.

Upon systematic review, all included studies were sorted into 3 different groups based on what types of retrieval tasks that they employed: studies that employed a remember-know paradigm, studies that employed a confidence rating paradigm, and studies that employed a source memory task. Studies that employed more than one types of retrieval tasks were grouped based on specific type of each included contrast (see below). For studies that reported more than one appropriate contrast based on different retrieval tasks, all contrasts were combined for the main analysis that included all papers and retrieval tasks, and the coordinates for each separate retrieval task were used instead for the supplemental analyses that were divided based on retrieval task type.

2.1.5 Contrasts of interests

In order to dissociate the neural correlates specific to recollection and familiarity, included studies were required to report at least one of the following types of contrasts: Recollection > Familiarity (R>F), Familiarity > Miss (F>M), Familiarity > Correct Rejection (F>CR), or increasing levels of familiarity (^F). The main analysis consisted of two meta-analyses: Analysis for recollection including the R>F contrasts and analysis for familiarity including all three of the remaining contrasts (F>M, F>CR, and ^F). Due to the theoretical concerns that recollection can occur along with familiarity and thus cause areas unique to familiarity to also activate in recollection responses, we predicted that this would decrease activations in the contrast “familiarity versus recollection” (Knowlton & Squire, 1995; Spaniol et al., 2009). As a result, we excluded this contrast from the analysis (Knowlton & Squire, 1995; Squire et al., 2007). More specific definitions of included contrasts based on retrieval task types are detailed below:

Remember know: Recollection (R>F) contrasts included “remember hits > know hits”. Familiarity contrasts included “know hits > miss” and “know hits > correct rejection”.

Confidence: Recollection (R>F) contrasts included “highest confidence hits > all other ratings hits” and “high confidence hits > low confidence hits”. Familiarity contrasts included parametric analysis on increasing confidence levels for familiar hit responses (^F), “familiarity hits with highest confidence > miss” and “familiarity hits with highest confidence > correct rejection”.

Source Memory: Recollection contrasts included “correct source hit > incorrect source hit”. Familiarity contrasts included “incorrect source>miss" and “F>CR” “incorrect source > correct rejection”.

2.1.6 Description of included studies

The selection process returned 63 studies to be included in the analysis. For the recollection analysis, a total of 59 studies, 1329 participants and 678 foci were included. For the familiarity analysis, a total of 28 studies, 547 participants and 232 foci were included. Upon summarization of different retrieval paradigms employed, 22 studies employed remember know paradigm, 7 studies employed confidence ratings, 25 studies employed source memory paradigm, and 9 studies employed a combination of remember know and either one of the other two tasks. For detailed descriptions of each study see Table 1.

Table 1

Studies included in the SDM meta-analysis

1st Author	Year	N(f)	Stimuli	Retrieval Task	Recollection		Familiarity	
					Contrast	Foci	Contrast	Foci
Angel	2012	40(?)	objects	Remember/Know	R > K	20	K > CR	19
Bowman	2016	18(12)	objects	Remember/Know	R > K	6		
Cansino	2014	24(13)	objects	Source memory	SH > IH	4		
Cansino	2002	17(15)	objects	Source memory	SH > IH	17		
Cansino	2015	36(?)	objects	Source memory	SH > IH across age groups	9		
Cohn	2009	13(6)	words	Remember/Know + confidence ratings	R > F4*	12		
Daselaar	2006	14(6)	words	Confidence ratings	nonlinear oldness (R) > linear oldness (K) masked with nonlinear oldness	9	Linear increase for familiarity ratings (1-4)	15
DennIH	2011	17(11)	objects	Remember/Know	R > K	17		

Diana	2017	21(?)	words	Source memory	SH > IH	14		
Dobbins	2002	14(?)	words	Source memory	SH > IH	21		
Dörfel	2009	30(19)	words	Remember/Know			K > M	4
Duarte	2007	44(?)	objects	Remember/Know	R > K	16		
Duarte	2008	33(?)	objects	Remember/Know	R > K	1	K > CR	11
Duarte	2011	15(9)	objects & scenes	Source memory	SH > IH	15		
Duarte	2008	33(?)	objects	Source memory	R > FH	1	FH > CR	11
Dulas	2016	44(?)	face & objects	Source memory	AC > AI across age groups	5		
Ekstrom	2011	16(13)	scenes	Source memory	SH > IH	5		
Eldridge	2000	11(?)	words	Remember/Know	R > K	15		
Elward	2015	20(?)	objects	Source memory	SH > IH	10		
Fenker	2005	20(14)	words & faces	Remember/Know	R > K (neutral/emotional)	30/36		
Frithsen	2014	25(7)	words	Remember/Know + source judgements	R > K/SH > IH	15/14	K > CR/IH > CR	11/9
Gimbel	2017	13(?)	faces & names	Remember/Know	R > K	12	K > CR	10

Hayes	2011	16(7)	words	Source memory	Source Hit (HC > LC) > Item Hit (HC > LC)	6		
Henson	1999	9(?)	words	Remember/Know	R > K	4	Linear increase K > CR	7
Herweg	2016	19(?)	scenes	Remember/Know	R > K	5	K > CR	14
Hutchinson	2014	19(11)	words	Source memory	SH > IH masked with IH > CR	22	IH > CR	14
Johnson	2013	16(10)	words & scenes	Remember/Know + confidence ratings	R > K1/2/3/4 masked with 1-4 linear increase*	16	1-4 linear increase masked with R > K1/2/3/4	6
Johnson	2007	16(6)	words & scenes	Remember/Know + confidence ratings	R > K	24		
Kafkas	2012	15(8)	objects	Remember/Know + confidence ratings	R > F3*	5	F3 > CR*	5
Kafkas	2014	17(10)	objects	Confidence ratings			Linear increase for familiarity ratings (1-3)	11
Kensinger	2007	19(10)	objects	Remember/Know	R > K (negative & neutral)	1		

Kim	2009	12(6)	words	Confidence ratings	HC > LC masked with HC > CR	5		
Kirwan	2009	13(4)	words	Confidence ratings	6,1,1,1,1,1 weighted pos	7		
Kragel	2015	20(12)	words & objects	Source memory	SH > IH	11	IH > CR	14
Kuchinke	2013	20(14)	words	Confidence ratings	Old > New + confidence interaction	13		
Kukolja	2010	50(23)	objects	Source memory	SH > IH	22		
Leshikar	2014	38(18)	objects & scenes	Source memory	SH > IH task invariant	3		
Lundstrom	2005	16	words	Source memory			IH > CR	7
Mayes	2018	17(7)	words	Remember/Know + confidence ratings	R3>F3*	15	Linear increase for familiarity ratings (1-3)	5
McDonough	2014	40(?)	words	Confidence ratings	Confidence 3 > confidence (2-1)	21		
Milton	2011a	10(4)	scenes	Remember/Know	R > K	8	K > CR	20
Milton	2011b	12(?)	scenes	Remember/Know	R > K	3		

Montaldi	2006	13(6)	scenes	Remember/Know + confidence ratings	R > F3*	6	Linear increase for familiarity ratings (1-3)*	12
Mugikura	2015	24(10)	faces & facts	Source memory	LC SH > LC IH	4	LC IH > CR	10
Nah	2018	22(22)	words	Remember/Know	R > K (control)	107		
Park	2014	20(10)	objects	Source memory	SH > IH & AC > AI	1/12		
Ragland	2006	13(1)	words	Source memory	SH > IH	8	K > CR	9
Sharot	2004	13(8)	scenes	Remember/Know	R > K (neutral/emotional)	2/5	K > CR (neutral/emotional)	10/9
Smith	2011	16(7)	words	Remember/Know + confidence ratings	HC R > HC K	8		
Smith	2006	16(8)	objects	Source memory	SH > IH	9		
Staresina	2012	20(14)	words	Source memory	SH > IH	6	IH > CR	7
Stephen-Otto	2017	24(?)	words	Source memory	SH > IH	6		
Taylor	2012	18(?)	words	Remember/Know	R > K	7	K > CR	5
Uncapher	2005	18(?)	words	Remember/Know			Familiarity delay-invariant	2
van Dongen	2016	72(?)	objects	Source memory	SH > IH	7		

Ventura	2020	23(21)	objects & scenes	Source memory	SH > IH	3		
Vilberg	2007	28(?)	objects	Remember/Know	R > K masked with K > M	13	K > M masked with R > K	16
Vilberg	2008	18(?)	objects	Remember/Know	R > K masked with K > M	9	K > M masked with R > K	19
Vinogradov	2006	8(4)	words	Source memory	SH > IH	1		
Wang	2013	20(8)	words	Confidence ratings	R(6) > K(1-5)*	26	Linear increase for familiarity ratings (1-5)	7
Wang	2016	48(26)	objects & words	Remember/Know	R > K masked with Rpic > K and Rword > K	16		
Wang	2015	48(26)	words & scenes	Remember/Know	R > K across age groups	16		
Yonelinas	2005	16(7)	words	Remember/Know + confidence ratings	R > F4*	26	Linear increase for familiarity ratings (1-4)*	11

Note. Table shows the studies that are included in the main analysis. (N) = total number of subjects, (f) = number of female subjects, (?) indicates that the number of female participants is unknown because participants were dropped from subsequent analyses without mentioning the genders of dropped participants, R = Remember, K = Know, F = Familiarity, M = MIHs, CR = Correct Rejection/New, HC = high confidence, LC = low confidence, SH = correct source/source hit, IH = incorrect source/item hit

*Indicates contrasts from studies that employed more than one type of retrieval tasks, e.g. both RK and confidence ratings / both RK and source. The numbers indicate specific levels of confidence, e.g. F3/F4 = highest level of familiarity

2.2 Seed-based d Mapping meta-analysis

For the SDM analyses, we first obtained activation foci, t-statistics, whole-brain thresholds, and sample sizes for each study. Statistical analyses were run using the SDM-PSI software (Albajes-Eizagirre et al., 2019). In cases where z-statistics are reported instead of t-statistics, the z-values were converted via the SDM online converter (www.sdmproject.com). All coordinates entered into the software were either reported in standard Montreal Neurological Institute (MNI) space (Evans et al., 1993) or otherwise converted via the SDM software. For coordinates that required conversion the appropriate conversion method was determined based on information detailed on the BrainMap webpage (http://brainmap.org/icbm2tal/). Preprocessing was conducted according to the standard SDM guidelines using a 20 mm full width half maximum (FWHM) anisotropic Gaussian kernel and 2 mm voxel size. In this step SDM used the reported coordinates and t-statistics as well as knowledge of spatial correlations based on brain tissue type to estimate effect sizes for every voxel in the brain. Voxel-wise permutation testing was then conducted at the subject level. The number of imputations was set to 50 and permutations was set to 1000. Next, we conducted family-wise error correction for multiple comparisons using threshold-free cluster enhancement (TFCE). Lastly, effect sizes were recalculated at the group level and a random mixed effects model was run where each study was weighted by its variance and between-study heterogeneity. The results were reported at a TFCE threshold of p < .05 with a minimum cluster size of 10 voxels. All regions reported in the result tables were labeled using the Harvard-Oxford neuroanatomical atlas (http://www.cma.mgh.harvard.edu). Additional reference was used to rename activations in certain medial temporal lobe subregions (parahippocampal gyrus to parahippocampal cortex) for more specific identifications (Bouyeure et al., 2018).

2.2.1 Supplemental analyses

To determine whether retrieval task type differentially impacts the neural correlates of recollection, we ran separate sub-analyses with only studies that employed remember know and source memory paradigms. There were not enough studies using the confidence ratings to run a supplemental analysis based on the minimum recommendation of at least ten studies (Radua, 2016). To determine whether retrieval task type differentially impacts the neural correlates of familiarity, we ran separate sub-analyses with only studies that employed remember know paradigms. There were not enough studies using the source memory task or confidence ratings to run a supplemental analysis based on these methods.

2.2.2 GLM analysis for remember-know studies vs. source memory studies

To identify regions that show statistically significant differential activations for studies that employed the remember-know paradigm and studies that employed the source memory task, we conducted a general linear model (GLM) analysis on the recollection contrast in SDM. This function subtracted two groups from each other and compared their results using statistical method (Albajes-Eizagirre et al., 2019). There were 27 papers, 547 participants, and 388 foci included for remember-know studies and 23 papers, 555 participants and 209 foci included for source memory studies, which satisfies the equal sample sizes criteria for conducting a GLM analysis. Since the analysis is a 2-tailed comparison instead of 1-tailed, the images are reported using a corrected threshold of $p<0.025$.

3. Results

3.1 Neural correlates for recollection

The SDM meta-analysis revealed 5 clusters that show significant greater activations for recollection compared to familiarity (Table 2, Figure 2). Cluster one included 18707 voxels in the frontal regions (bilateral paracingulate, left medial anterior cingulate, bilateral superior frontal gyrus, left frontal orbital cortex), parietal regions (bilateral posterior cingulate, left supplementary motor regions), medial temporal lobe (left hippocampus, left amygdala) as well as subcortical regions such as the left thalamus, caudate and pallidum. Cluster two included 3257 voxels in the frontal regions (right orbital frontal cortex, inferior frontal gyrus, right precentral gyrus) and temporal regions (right insula, right putamen, right central opercular cortex and right amygdala). Cluster three included 1875 voxels in the temporal lobe (middle temporal gyrus and inferior temporal gyrus), parietal lobe (left angular gyrus) and left lateral occipital cortex. Cluster four included 92 voxels in the right parahippocampal cortex. Cluster five included 26 voxels in the right precentral gyrus.

Consistent with our hypothesis, neural correlates of recollection responses mostly included default mode network regions such as the orbital frontal cortex, paracingulate and cingulate gyrus (Raichle, 2015) as well as MTL regions such as the hippocampus and parahippocampal cortex. Activations in the lateral frontal, superior parietal and medial temporal lobe were left lateralized while activations in the middle frontal, ventral parietal and subcortical regions in the temporal lobe were right lateralized.

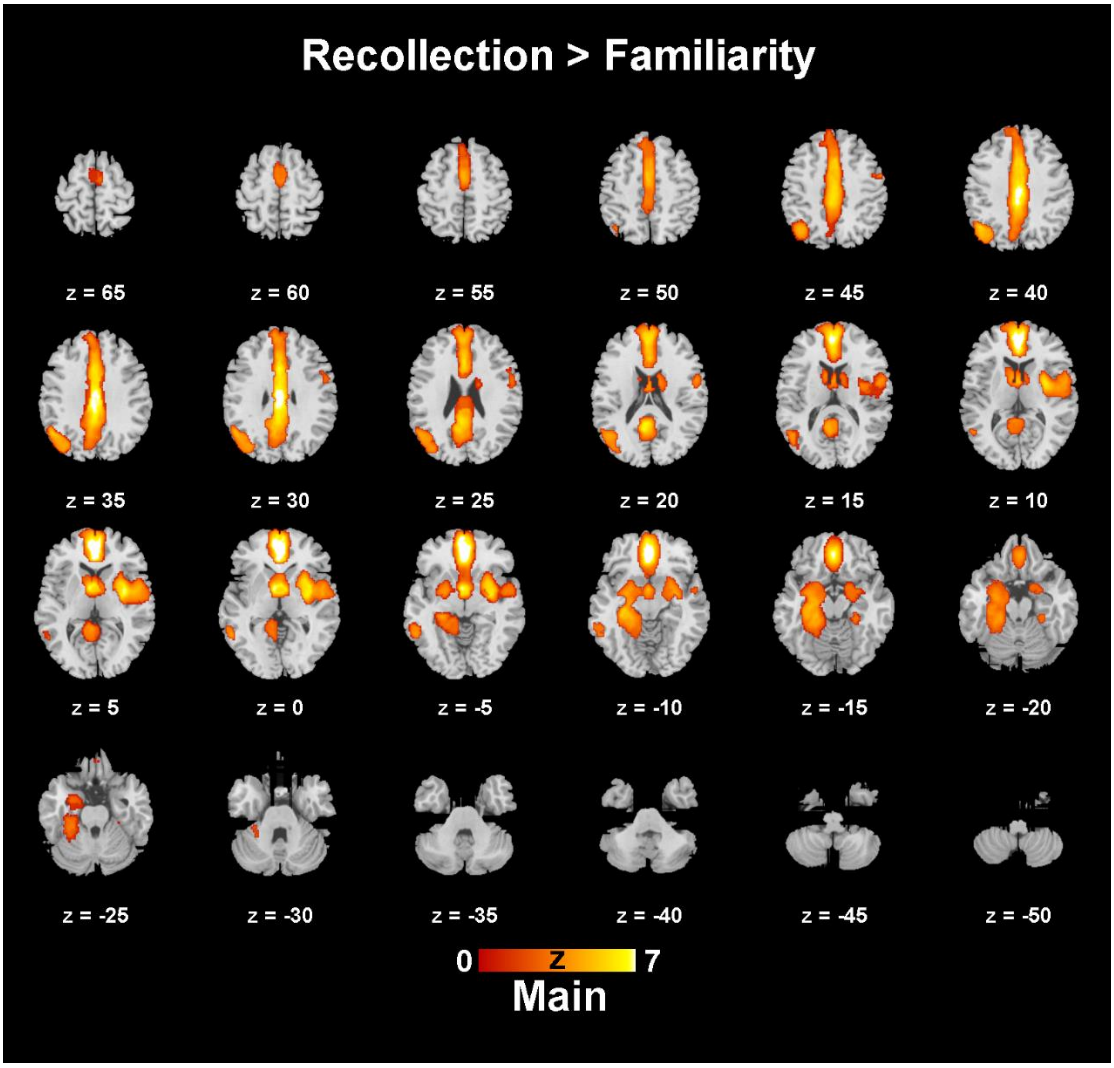

Figure 2. Figure shows regions that are more active for recollection vs. familiarity responses. Panel shows axial slices every 5 mm from 65 to -50

Table 2

Abbreviated regions showing significant activations for recollection responses

					Peak		
Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Paracingulate Gyrus**	**L**	**18707**	**-4**	**50**	**8**	**9.86**

		-2	26	36	5.54
Paracingulate Gyrus	R	2	46	-6	9.11
		4	10	44	6.07
Anterior Cingulate Gyrus	L	-2	36	0	8.01
		-2	16	38	6.35
Posterior Cingulate Gyrus	L	-2	-16	32	7.82
		-2	-30	42	7.35
		-4	-46	6	4.36
Frontal Pole	L	-4	58	-6	7.77
Thalamus	L	-6	2	0	7.47
Posterior Cingulate Gyrus	R	6	-24	34	6.91
		2	-50	22	6.25
Precuneus	L	-6	-56	20	6.88
		-6	-70	36	3.81
Anterior Cingulate Gyrus	Medial	0	18	28	6.83
		0	-6	30	6.70
		0	4	32	6.43

	Posterior Cingulate Gyrus	Medial		0	-42	34	6.71
	Hippocampus	L		-30	-28	-8	6.08
	Supplementary Motor Cortex	L		-2	-2	52	5.63
				-24	-18	-14	5.45
	Parahippocampal cortex	L		-20	-30	-14	5.33
				-24	-42	-12	4.58
	Amygdala	L		-28	-4	-12	4.98
	Supplementary Motor Cortex	R		6	0	62	3.64
	Caudate	R		14	0	20	3.61
	Pallidum	L		-14	-2	-8	3.60
	Superior Frontal Gyrus	L		-6	38	48	3.43
	Lingual Gyrus	L		-12	-44	-10	3.29
	Frontal Orbital Cortex	L		-30	8	-18	2.62
	Subcallosal Cortex	L		-2	16	-10	2.51
	Superior Frontal Gyrus	R		2	26	56	2.55
2	**Insula**	**R**	**3257**	**36**	**0**	**4**	**7.07**

	Putamen	R		32	-6	-6	6.41
				28	8	-4	6.16
				30	8	6	6.01
	Central Opercular Cortex	R		48	0	4	5.28
	Precentral Gyrus	R		56	2	20	4.15
				56	4	30	2.92
	Amygdala	R		20	-6	-12	3.70
	Planum Polare	R		60	-6	4	3.62
	Frontal Orbital Cortex	R		18	4	-16	3.30
	Inferior Frontal Gyrus	R		54	14	22	2.82
3	**Lateral Occipital Cortex**	**L**	**1875**	**-44**	**-62**	**40**	**6.02**
				-38	-72	38	4.83
				-48	-64	18	4.79
	Angular Gyrus	L		-52	-58	32	5.19
	Middle Temporal Gyrus	L		-60	-52	-2	4.36
				-54	-60	10	3.78
				-64	-44	-10	3.42

	Inferior Temporal Gyrus	L		-56	-54	-12	3.49
4	**Parahippocampal Cortex**	**R**	**92**	**26**	**-30**	**-16**	**3.38**
5	**Precentral Gyrus**	**R**	**26**	**56**	**-2**	**46**	**3.60**

3.2 Neural correlates for familiarity

The SDM meta-analysis revealed 7 clusters that significantly activate more for familiarity as opposed to miss or correct rejection responses (Figure 3, Table 3). Cluster one included 12607 voxels in the frontal regions (bilateral superior frontal gyrus, paracingulate gyrus, right medial anterior cingulate gyrus), parietal regions (bilateral posterior cingulate gyrus, left supplementary motor areas, left posterior parietal lobule, left angular gyrus), occipital lobe (left lateral occipital cortex) and other temporal regions such as the left precuneus. Cluster two included 1130 voxels in subcortical regions (right insula and putamen). Cluster three also included 717 voxels in subcortical regions (bilateral thalamus and caudate). Custer four included 544 voxels in left middle frontal gyrus while cluster five includes 358 voxels in right middle frontal gyrus. Cluster six included 191 voxels in the right frontal pole. Cluster seven included 164 voxels in the right superior parietal lobule and supramarginal gyrus.

Consistent with our hypothesis, neural correlates for familiarity responses included dorsal and ventral attention network regions such as the frontal pole, superior frontal gyrus, posterior parietal lobule, angular gyrus and salience processing areas such as the insula, the thalamus, the caudate and putamen (Kim, 2010)..

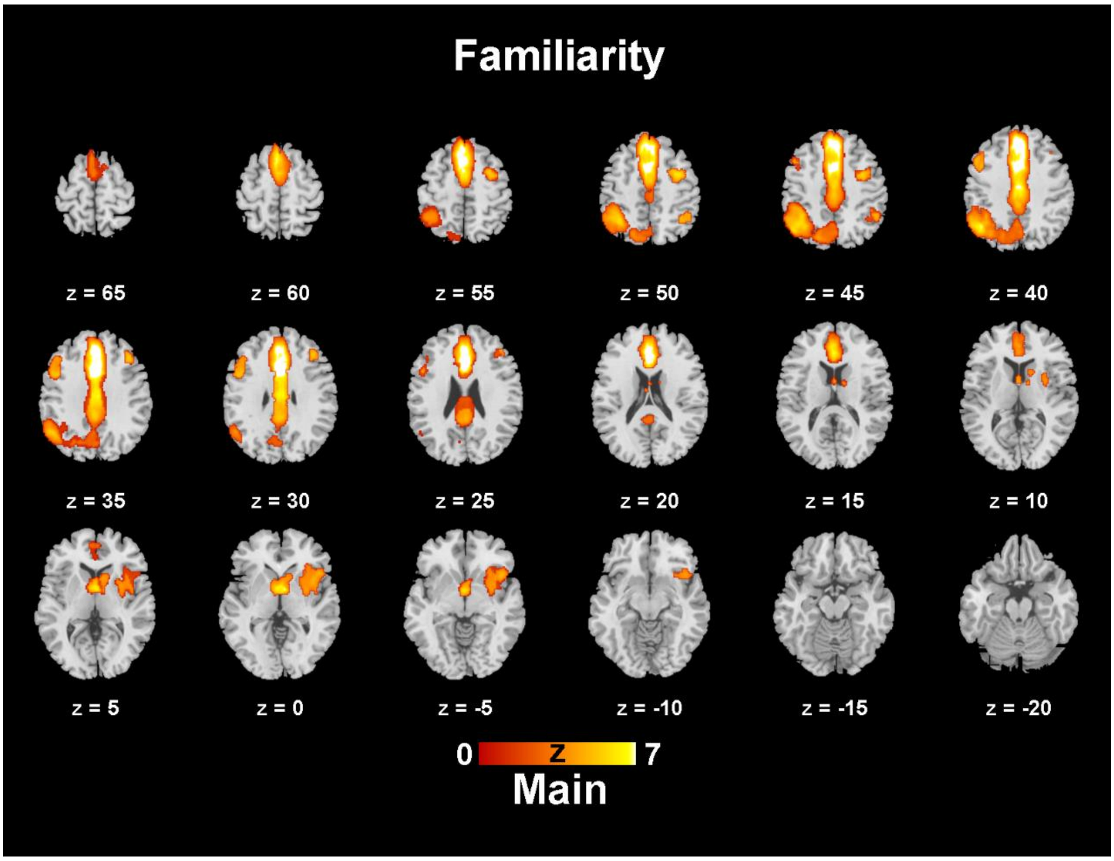

Figure 3. Figure shows regions that activate in relation to familiarity responses. Panel shows axial slices every 5 mm from 65 to -20

Table 3

Abbreviated regions showing significant activations for familiarity responses

				Peak			
Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Paracingulate Gyrus**	**R**	**12607**	**2**	**38**	**36**	**9.55**
				6	28	40	8.05
	Anterior Cingulate Gyrus	Medial		0	16	30	9.17
		R		2	10	42	9.02
				2	32	20	8.48
	Superior Frontal Gyrus	L		-4	14	56	8.48
				-2	26	56	7.78
				-8	36	48	7.35
	Superior Frontal Gyrus	R		4	34	48	8.45
				12	8	64	2.71
	Posterior Cingulate Gyrus	L		-2	-16	38	7.63
				-4	-26	40	6.16
	Lateral Occipital Cortex	L		-44	-62	40	7.14
				-18	-74	46	4.66
				-26	-72	36	3.22

	Superior Parietal Lobule	L		-38	-50	46	6.10
	Posterior Cingulate Gyrus	R		6	-24	34	6.01
	Angular Gyrus	L		-54	-58	38	5.94
	Posterior Cingulate Gyrus	Medial		0	-38	32	5.75
	Supramarginal Gyrus	L		-44	-42	48	5.18
				-52	-46	38	4.33
	Precuneus	L		-2	-58	42	3.60
				2	-68	42	3.52
				-10	-70	38	2.92
2	**Insula**	**R**	**1130**	**42**	**16**	**-6**	**5.07**
				36	8	-2	4.94
				34	26	0	3.74
	Putamen	R		30	6	8	4.49
3	**Thalamus**	**Right**	**717**	**6**	**0**	**0**	**7.08**
	Thalamus	Left		-4	2	2	6.60
	Caudate	R		8	14	2	4.41
				12	-2	14	4.34

				18	12	10	3.95
	Caudate	L		-6	14	2	3.92
4	**Middle Frontal Gyrus**	**Left**	**544**	**-48**	**8**	**34**	**5.58**
				-44	16	44	5.21
				-50	18	36	4.88
5	**Middle Frontal Gyrus**	**Right**	**358**	**32**	**0**	**50**	**6.37**
6	**Frontal Pole**	**Right**	**191**	**42**	**38**	**26**	**4.59**
	Middle Frontal Gyrus	Right		40	28	36	5.73
7	**Superior Parietal Lobule**	**Right**	**164**	**38**	**-52**	**50**	**4.88**
	Supramarginal Gyrus	Right		48	-46	48	4.87

3.3 Supplementary analyses results

The supplementary analysis examining recollection subdivided based on only studies using the remember know paradigm (R > K), SDM revealed 5 clusters that are generally in line with the main analysis (Figure 4A, Table 4). While there were some changes in the cluster size, nearly all activated regions in the main analysis were retained. Cluster one, which included the medial frontal and parietal regions such as the paracingulate gyrus, cingulate gyrus, and supplementary motor regions, shrank from 18707 voxels to 11477 voxels. Cluster two, which included the right temporal lobe regions such as the insula, putamen and central opercular cortex, increased from 3257 to 4270 voxels. The remaining three clusters differed from those reported in the main analysis. Cluster three, which included 1150 voxels, revealed novel activations in the bilateral thalamus, right caudate and left accumbens. Cluster four included 1021 voxels in the left lateral occipital cortex, left middle temporal gyrus and left supramarginal gyrus that were reported in cluster three in the main analysis. Cluster five included 534 voxels in the left hippocampus and parahippocampal cortex that were originally reported in cluster one of the main analysis. However, the decreased size of cluster one has resulted in this cluster breaking away from the original cluster in the main analysis. Regions reported in the main analysis results but not present when only papers using a remember know paradigm were considered, included the bilateral amygdala, bilateral orbital frontal cortex, left superior frontal gyrus, left angular gyrus and right parahippocampal cortex.

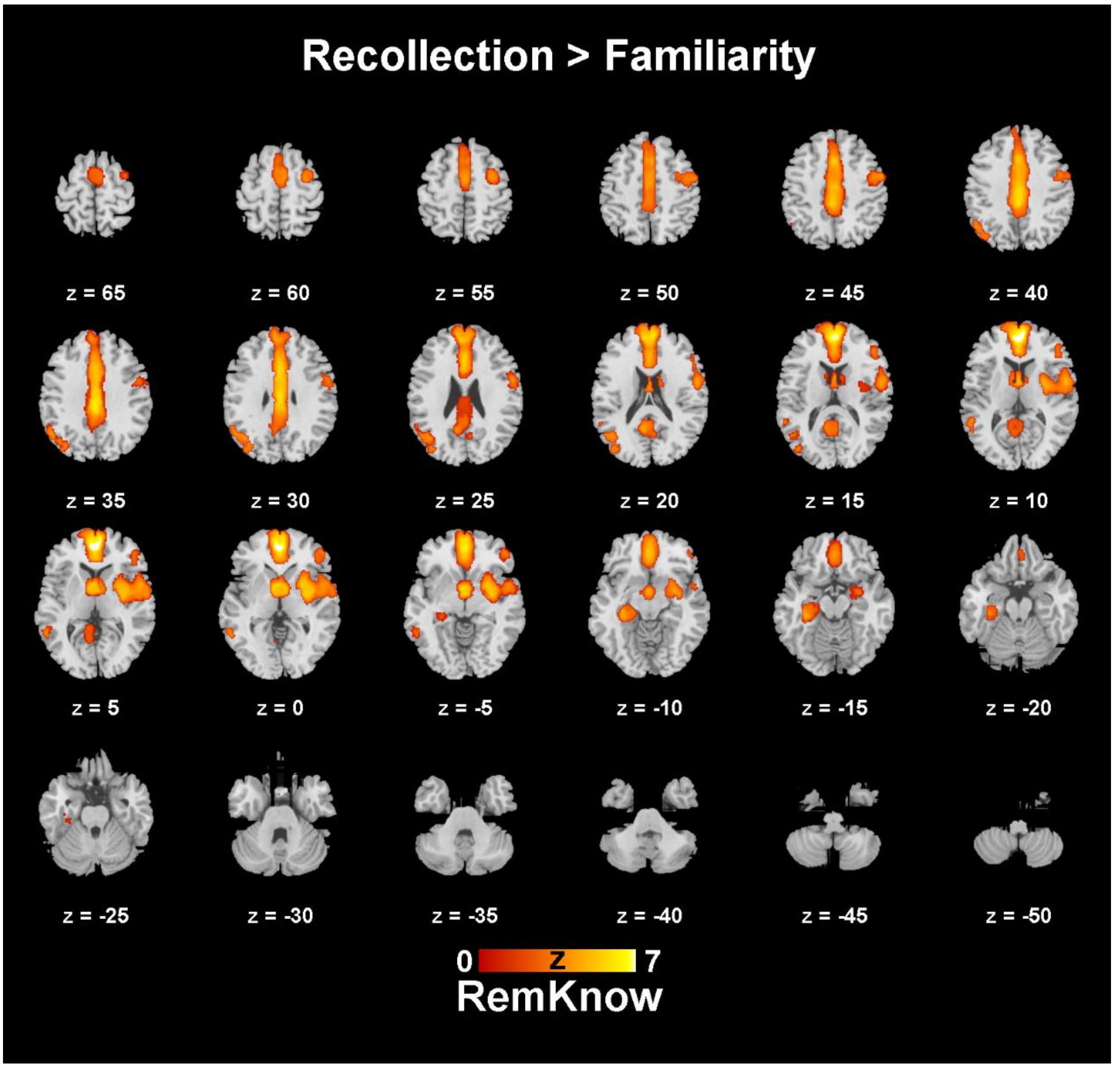

Figure 4A. Figure shows regions that are more active for recollection vs. familiarity responses in remember know studies.

Panel shows axial slices every 5 mm from 65 to -50

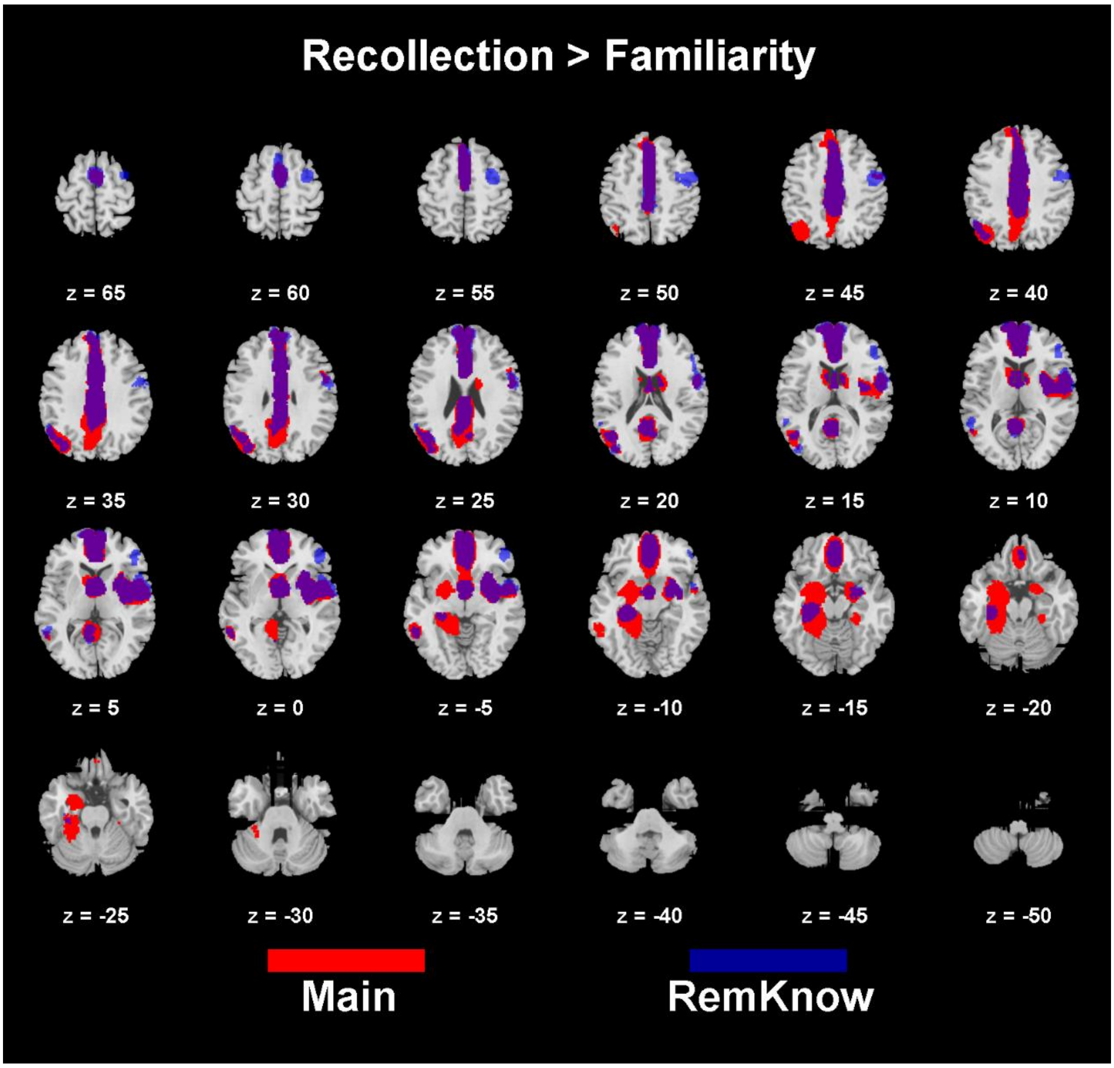

Figure 4B. Figure shows regions that are more active for recollection vs. familiarity responses. Red = results from main analysis; Blue = results from sub-analysis on remember know studies; Purple = overlap. Panel shows axial slices every 5 mm from 65 to -50

Table 4

Abbreviated regions showing significant activations for recollection responses in remember-know studies

	Peak

Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Paracingulate Gyrus**	**Medial**	**11477**	**0**	**50**	**6**	**8.14**
				0	16	44	5.71
	Frontal Pole	R		6	58	8	7.78
	Posterior Cingulate Gyrus	Medial		0	-26	34	6.86
	Frontal Pole	L		-4	62	-2	6.42
				-8	62	26	
	Posterior Cingulate Gyrus	L		-2	-16	32	6.26
				-6	-44	8	2.83
	Posterior Cingulate Gyrus	R		2	-32	42	6.15
	Anterior Cingulate Gyrus	Medial		0	18	28	6.10
				0	4	40	5.03
	Anterior Cingulate Gyrus	L		-2	38	8	6.02
				-4	-4	30	5.20

	Anterior Cingulate Gyrus	R		2	30	26	5.53
				6	-2	46	4.05
	Paracingulate Gyrus	L		-4	48	22	5.87
	Precuneus	L		-6	-56	20	4.63
	Supplementary Motor Cortex	Medial		0	-4	54	4.54
	Supplementary Motor Cortex	R		6	4	60	4.05
	Paracingulate Gyrus	R		2	26	46	3.95
	Supplementary Motor Cortex	L		-4	6	60	3.64
	Precuneus	R		6	-62	22	3.14
	Lingual Gyrus	L		-8	-60	4	2.59
2	**Putamen**	**R**	**4270**	**30**	**-6**	**-2**	**5.79**
				28	6	0	5.47
	Insula	R		38	0	0	5.35
	Precentral Gyrus	R		56	4	8	5.10
				56	-2	46	4.62
				56	2	20	4.51
	Superior Frontal Gyrus	R		30	-6	60	4.41

	Central Opercular Cortex	R		52	6	-2	4.34
	Middle Frontal Gyrus	R		30	4	56	4.30
	Planum Polare	R		52	-4	2	4.09
	Frontal Pole	R		48	44	-2	3.73
				46	36	14	3.61
	Inferior Frontal Gyrus	R		54	20	18	3.05
3	**Thalamus**	**L**	**1150**	**-4**	**4**	**-2**	**6.34**
	Thalamus	R		6	2	0	5.61
				2	0	10	5.23
	Caudate	R		12	0	18	2.85
	Accumbens	L		-10	-4	-10	2.56
4	**Lateral Occipital Cortex**	**L**	**1021**	**-42**	**-64**	**30**	**4.29**
				-50	-60	38	4.23
				-46	-64	18	4.08
	Middle Temporal Gyrus	L		-58	-52	-2	4.17
				-54	-58	10	3.16

	Supramarginal Gyrus	L		-58	-46	12	3.82
5	**Hippocampus**	**L**	**534**	**-32**	**-32**	**-12**	**5.11**
	Parahippocampal Cortex	L		-18	-26	-12	3.49

The supplementary analysis examining familiarity subdivided based on only studies using the remember know paradigm (K > M/CR), reveals only 4 as opposed to 7 clusters in the main analysis (Figure 5A, Table 5). Additionally, all clusters decreased in size and number of peak activations. Cluster one including the bilateral paracingulate gyrus, anterior and posterior cingulate and superior frontal gyrus shrinks from 12607 to 8015 voxels. Cluster two included 1374 voxels in the left superior parietal lobule, left lateral occipital cortex and left supramarginal gyrus. Cluster three included 805 voxels in the left middle frontal gyrus. Cluster four included 477 voxels in the right angular gyrus and right superior parietal lobule. The cluster covering subcortical salience processing regions such as the right thalamus and insula from the main analysis results was no longer present (Figure 5B).

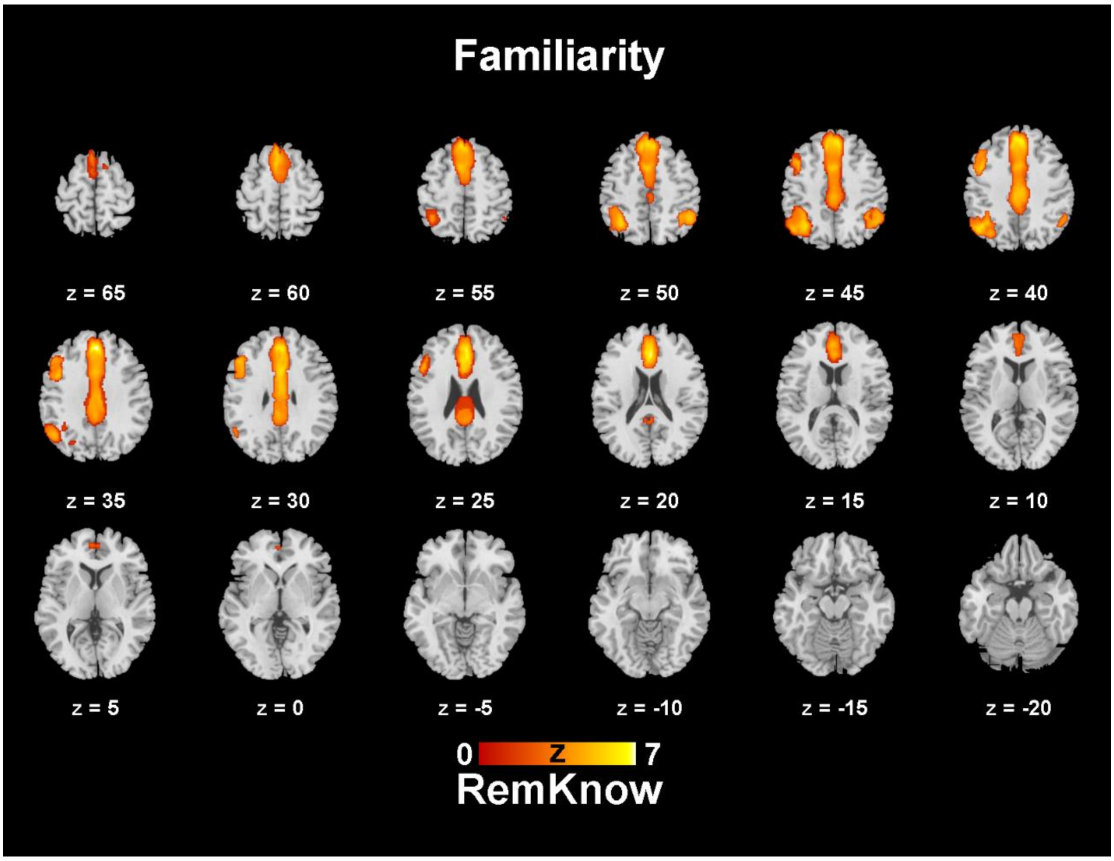

Figure 5A. Figure shows regions that are more active for familiarity vs. miss or correct rejection responses in remember know studies. Panel shows axial slices every 5 mm from 65 to -20

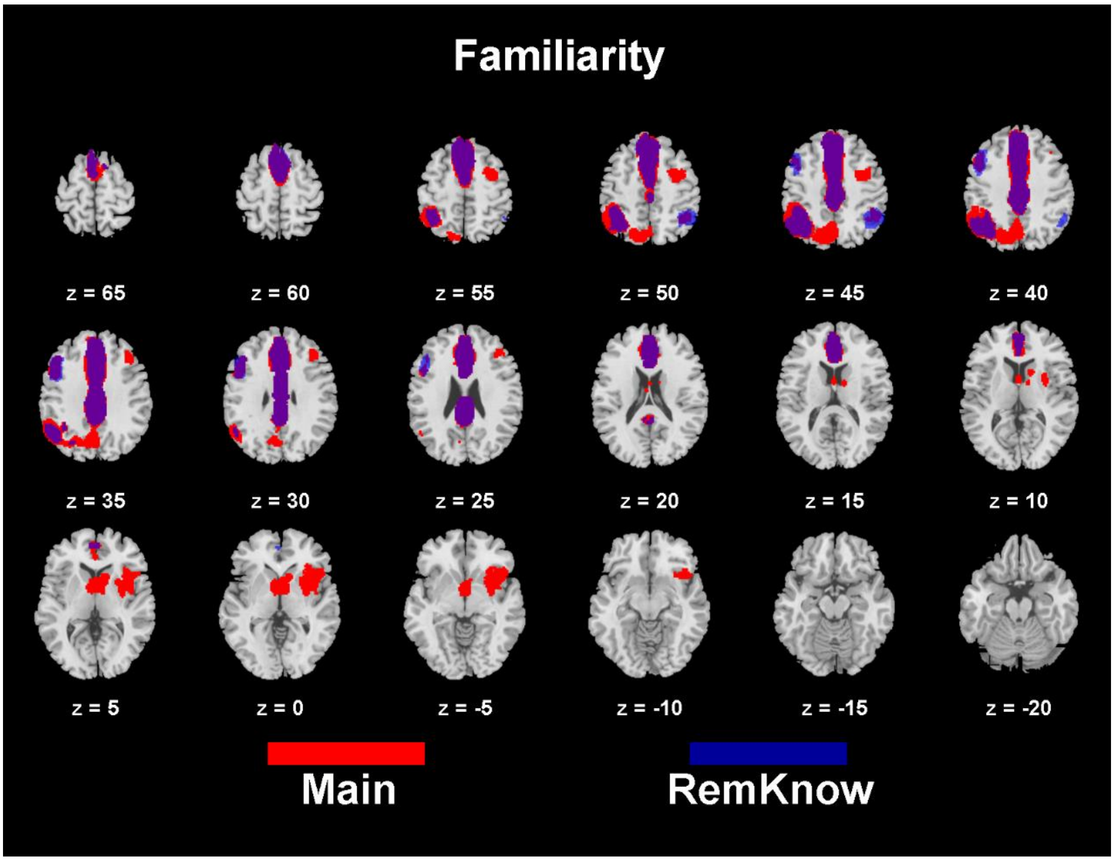

Figure 5B. Figure shows regions that activate in relation to familiarity responses. Red = results from main analysis; Blue = results from sub-analysis on remember know studies; Purple = overlap. Panel shows axial slices every 5 mm from 65 to -50

Table 5

Abbreviated regions showing significant activations for familiarity in remember know studies

					Peak		
Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Paracingulate Gyrus**	**R**	**8015**	**2**	**40**	**34**	**7.88**
	Anterior Cingulate Gyrus	R		2	30	22	7.35

				2	16	28	5.97
				2	-8	46	4.21
	Superior Frontal Gyrus	R		4	34	48	6.62
				10	10	64	2.70
	Superior Frontal Gyrus	L		-4	34	56	6.33
				-4	42	44	5.83
				-4	10	56	5.75
	Paracingulate Gyrus	L		-2	42	24	5.94
				-2	50	2	2.62
	Anterior Cingulate Gyrus	L		-2	8	42	5.73
	Anterior Cingulate Gyrus	Medial		0	-4	30	5.57
	Posterior Cingulate Gyrus	R		2	-24	42	5.57
	Posterior Cingulate Gyrus	L		-2	-38	30	4.88
2	**Superior Parietal Lobule**	**L**	**1374**	**-32**	**-58**	**48**	**6.37**
	Lateral Occipital Cortex	L		-48	-64	42	6.09

				-26	-72	36	3.24
	Supramarginal Gyrus	L		-58	-50	32	3.08
3	**Middle Frontal Gyrus**	**L**	**805**	**-44**	**8**	**38**	**5.78**
				-46	22	28	5.71
				-44	22	42	4.58
4	**Angular Gyrus**	**R**	**477**	**50**	**-52**	**48**	**5.51**
	Superior Parietal Lobule	R		38	-50	50	4.80

The supplementary analysis examining familiarity subdivided based on only studies using the source memory task, revealed 5 clusters (Figure 6A, Table 6). Cluster one included 3271 voxels in the ventral frontal and parietal lobe (right and medial posterior cingulate gyrus, left anterior cingulate gyrus and bilateral precuneus). Cluster two included 2260 voxels in the frontal lobe (right and medial anterior cingulate gyrus, left frontal medial cortex and left paracingulate gyrus). Cluster three included 651 voxels in the left medial temporal lobe (left amygdala, left hippocampus, left lingual gyrus, left parahippocampal cortex). Cluster four included 161 voxels in the left lateral occipital cortex. Cluster five included 24 voxels in the parietal lobe (left posterior cingulate gyrus). Compared to the main analysis results, a number of regions and clusters in the frontal and parietal regions were absent from results based on source memory studies only. These included the frontal pole, superior frontal gyrus, orbital frontal gyrus, right central opercular cortex, and left angular gyrus activations. There was also a general decrease in extent of activations (cluster sizes) (Figure 6B). Compared to results based on remember-know studies, a similar set of activations were also absent in these results. The remember-know analysis also yielded unique additional activations in the right middle frontal gyrus (Figure 6C).

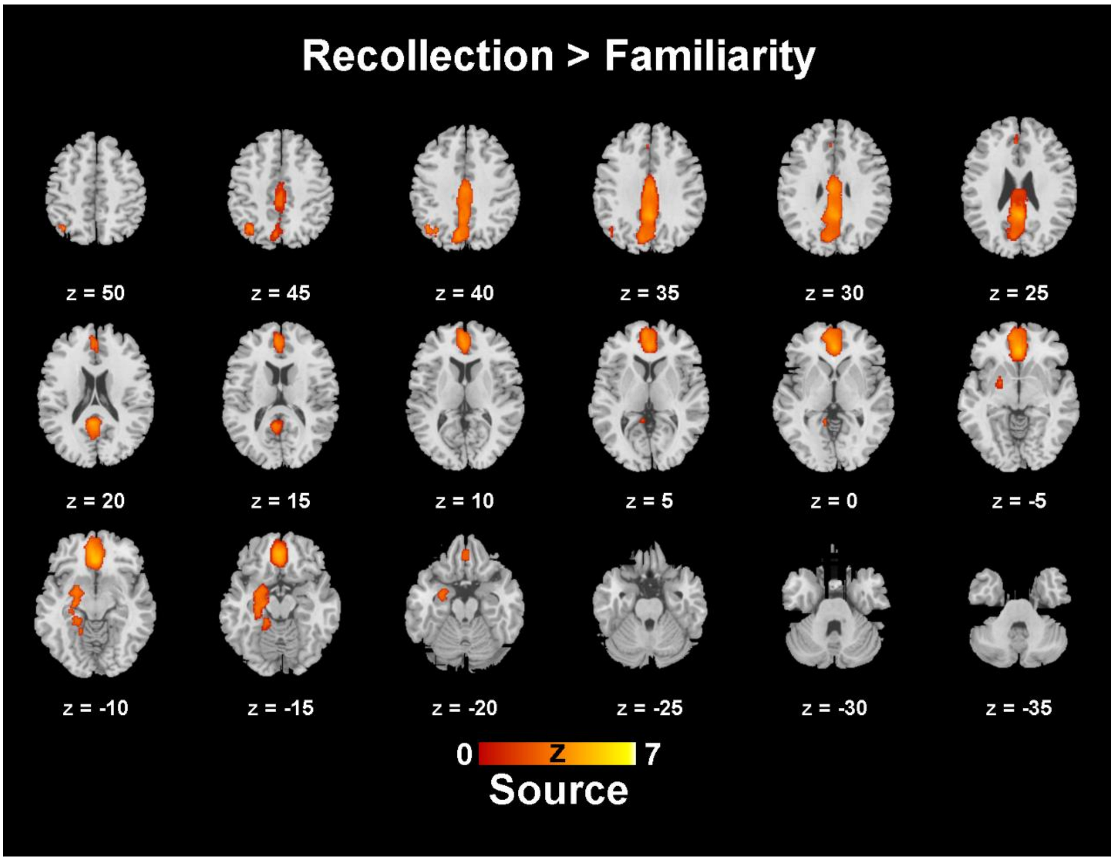

Figure 6A. Figure shows regions that are more active for recollection vs. familiarity responses in source memory studies. Panel shows axial slices every 5 mm from 50 to -35

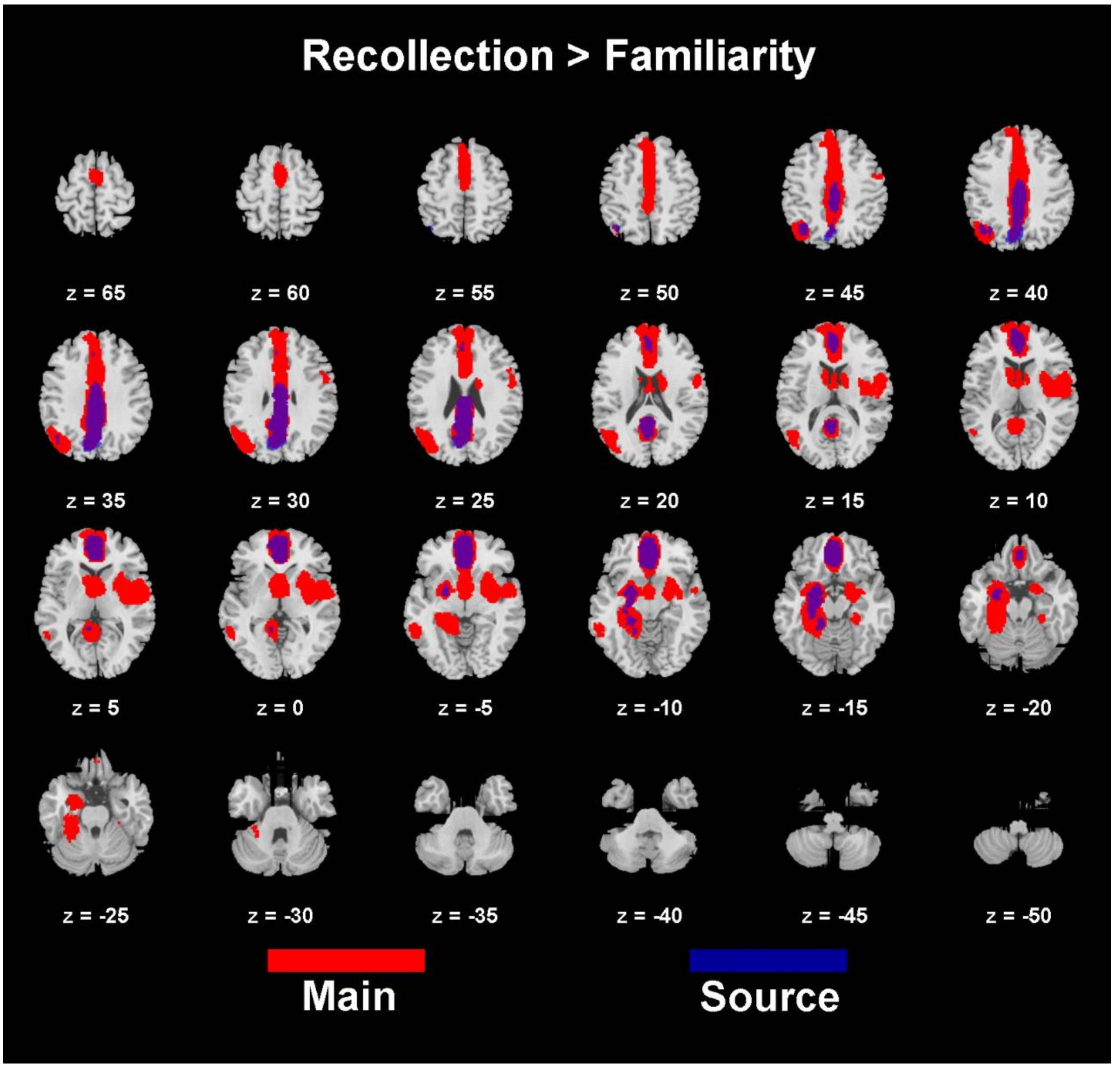

Figure 6B. Figure shows regions that activate in relation to familiarity responses. Red = results from main analysis; Blue = results from sub-analysis on remember know studies; Purple = overlap. Panel shows axial slices every 4 mm from 65 to

-50

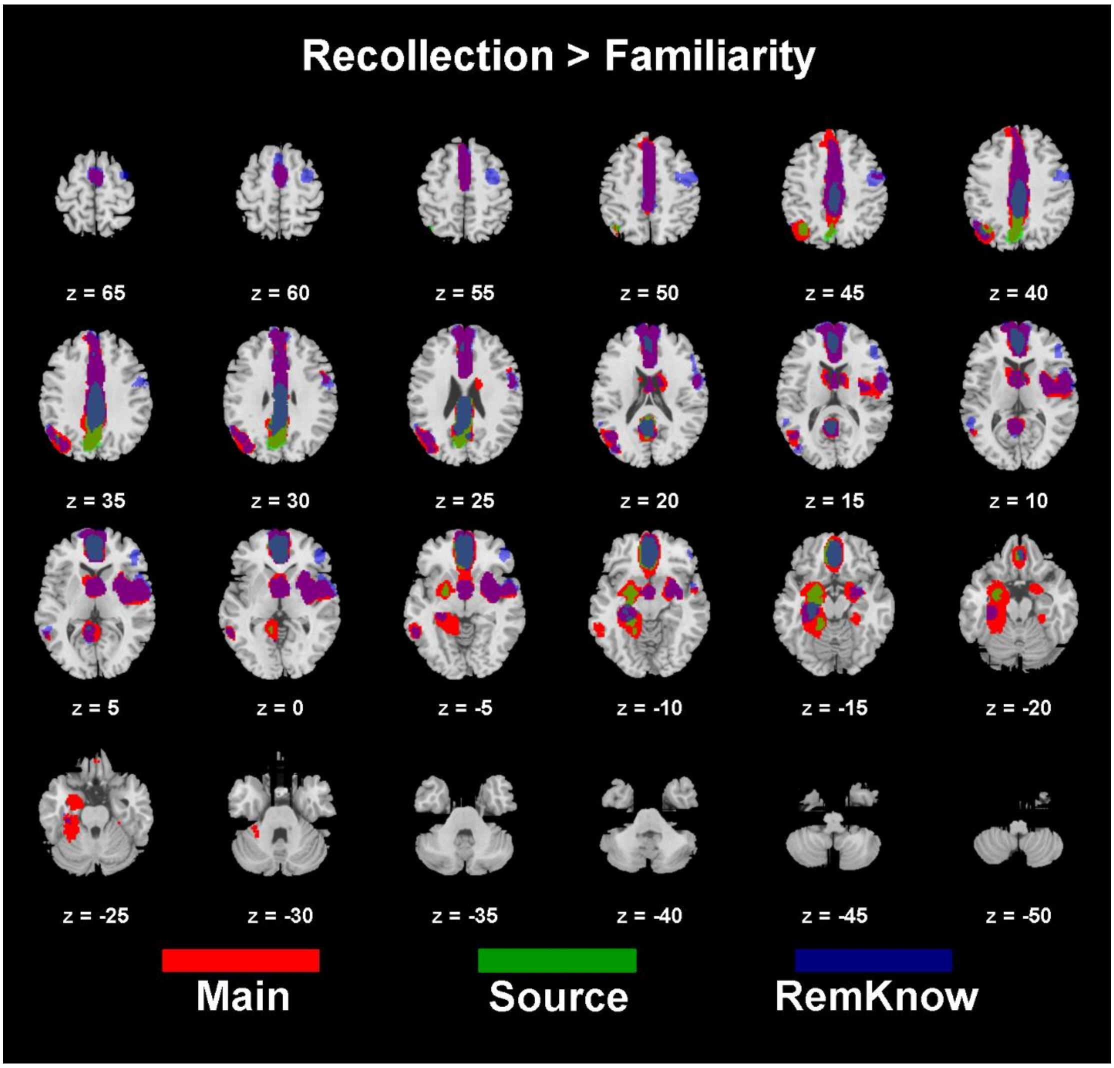

Figure 6C. Figure shows regions that activate in relation to familiarity responses. Red = results from main analysis; Blue = results from sub-analysis on remember know studies; Green = results from sub-analysis on source studies. Panel shows axial slices every 5 mm from 65 to -50

Table 6

Abbreviated regions showing significant activations for recollection in source memory studies

	Peak

Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Posterior Cingulate Gyrus**	**Right**	**3271**	**2**	**-48**	**24**	**4.94**
				2	-18	40	3.71
				4	-30	32	3.21
	Anterior Cingulate Gyrus	Left		-2	-14	30	4.13
	Precuneus	Left		-8	-70	40	4.04
	Posterior Cingulate Gyrus	Medial		0	-34	42	3.35
	Precuneus	Right		6	-62	32	2.68
2	**Anterior Cingulate Gyrus**	**Right**	**2260**	**2**	**36**	**-8**	**5.39**
	Frontal Medial Cortex	Left		-4	46	-14	5.05
	Anterior Cingulate Gyrus	Medial		0	42	4	4.64
	Paracingulate Gyrus	Left		-4	50	12	4.32
				-4	48	-4	4.17
				-2	32	36	2.58

3	**Amygdala**	**Left**	**651**	**-24**	**-16**	**-12**	**3.99**
				-22	-2	-10	3.54
	Hippocampus	Left		-26	-30	-14	3.17
	Lingual Gyrus	Left		-20	-48	-12	2.68
				-26	-40	-8	2.65
	Parahippocampal cortex	Left		-16	-36	-14	2.86
4	**Lateral Occipital Cortex**	**Left**	**161**	**-38**	**-62**	**50**	**3.64**
				-44	-62	40	3.58
5	**Posterior Cingulate Gyrus**	**Left**	**24**	**-10**	**-48**	**0**	**2.86**

3.4 GLM analysis results

The general linear model analysis statistically compared results from remember know studies to results from source memory studies for the recollection (R > F) contrasts. Results demonstrated recollection based neural correlates that are reported with higher activities in remember know studies but not source memory. The analysis outputted 5 clusters of significant activations (Figure 7, Table 7). Cluster one included 1208 voxels in the right frontal pole. Cluster two included 410 voxels in the left and medial anterior cingulate gyrus as well as right paracingulate gyrus. Cluster three included 400 voxels in the right superior frontal gyrus and precentral gyrus. Cluster four included 321 voxels in the right thalamus. Cluster five included 78 voxels in the bilateral supplementary motor cortex. The results demonstrate clear distinction between the two different methodologies, with the remember know paradigms generating more significant activations in the frontal, parietal and subcortical regions.

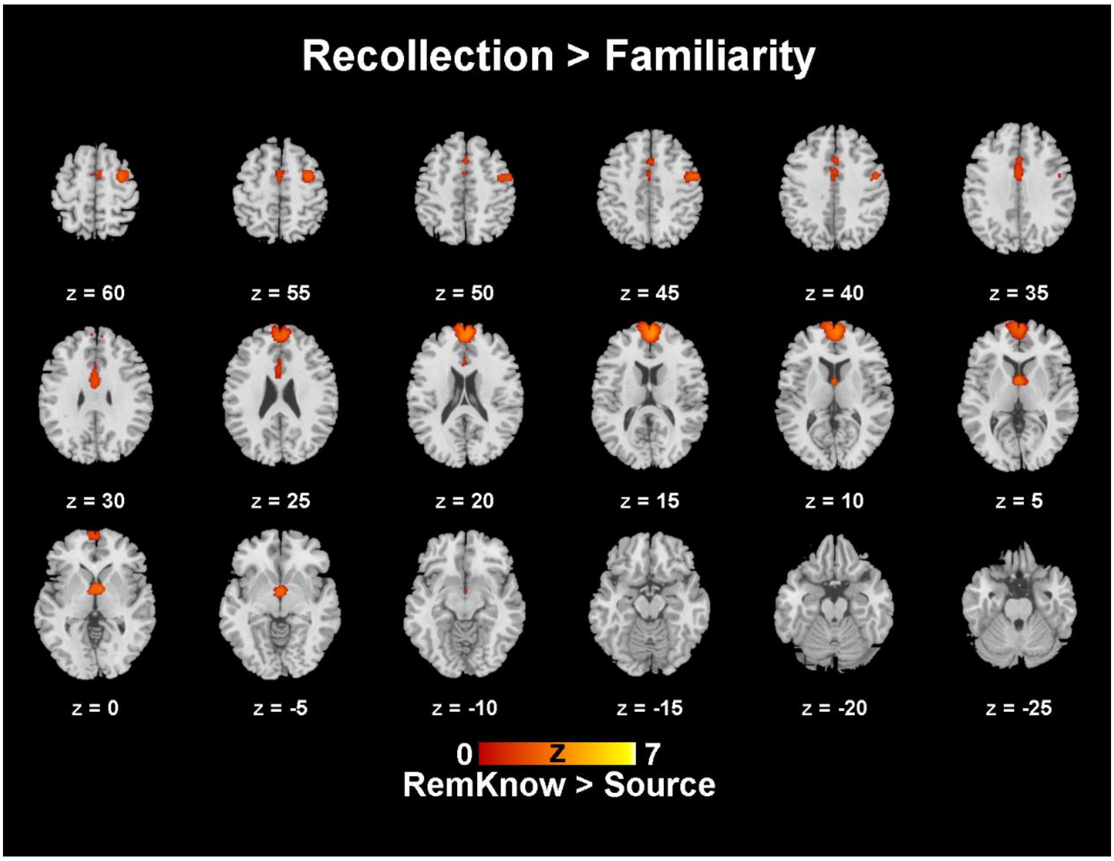

Figure 7. Figure shows recollection > familiarity contrast results that are more active in the remember-know studies vs. source memory studies. Panel shows axial slices every 5 mm from 60 to -25

Table 7

Abbreviated recollection related regions that are more significantly activated for remember know vs. source memory studies

				Peak			
Cluster	Anatomical Regions	L/R	Voxels	x	y	z	Z Value
1	**Frontal Pole**	**R**	**1208**	**4**	**56**	**14**	**4.23**
2	**Anterior Cingulate Gyrus**	**L**	**410**	**-2**	**4**	**28**	**2.27**
				-2	2	42	1.93
	Paracingulate Gyrus	R		2	16	48	2.07
	Anterior Cingulate Gyrus	Medial		0	26	20	1.87
				0	14	34	1.87
3	**Superior Frontal Gyrus**	**R**	**400**	**30**	**-4**	**58**	**3.03**
	Precentral Gyrus	**R**		**54**	**-2**	**46**	**2.95**

				48	-2	36	1.99
4	**Thalamus**	**R**	**321**	**6**	**2**	**0**	**3.26**
	Thalamus	Medial		0	0	8	2.83
5	**Supplementary Motor Cortex**	**R**	**78**	**6**	**2**	**60**	**2.07**
	Supplementary Motor Cortex	L		-2	-4	56	1.82

4. Discussion

The present study primarily focused on finding neural correlates of recollection and familiarity responses in episodic memory retrieval. To achieve this end, we conducted a coordinate based SDM meta-analysis on the following two types of contrasts reported in fMRI studies: recollection > familiarity contrasts and familiarity > miss or correct rejections or increasing levels of familiarity. Consistent with our hypotheses, our results demonstrated that there were distinct regions activated in association with these two types of contrasts.

4.1 Activations different for recollection and familiarity

Consistent with our hypothesis, we observed distinct differences between recollection and familiarity in the frontal, parietal, medial frontal regions as well as subcortical regions. Specific patterns of differences also shared some similarities to past meta-analyses (Kim, 2010), with generally greater extent of activations brought on by employment of the SDM methods. Detailed distinctions were discussed by subdivisions below.

4.1.1 Differences in the MTL memory system

The SDM analysis reported regions within the MTL that activated significantly more for recollection as opposed to familiarity. These included the left hippocampus, bilateral parahippocampal cortex and bilateral amygdala. The hippocampal and parahippocampal activations were consistent with our predictions based on the literature (Eichenbaum et al., 2007; Kim, 2010, 2013, 2016; Ranganath, 2010; Squire & Wixted, 2011). During recollection responses, retrieval processes would be mediated primarily via the hippocampus while parahippocampal regions facilitate retrieval of additional contextual and spatial information, which accounted for their activations in a contrast of recollection > familiarity.

We did not observe perirhinal activations in relation to familiarity, in line with the results of previous meta-analyses (Horn et al., 2016; Kim, 2010). However, this does not necessarily negate previous theoretical predictions as it may be explained by the fact that perirhinal cortex activations were primarily reported in studies that focused on the MTL or directly measured via ROI analyses (which would be excluded from the whole brain wise meta-analysis).

4.1.2 Recollection involves the default mode network

Consistent with our hypothesis, the recollection versus familiarity contrast reported frontal and parietal regions commonly associated with the default mode network. This mainly included the superior frontal areas, the paracingulate and cingulate gyrus and the angular gyrus. These regions were commonly found to be associated with self-reference heavy processes such as autobiographical memory retrieval (Spreng et al., 2009; Svoboda et al., 2006). These processes were also relevant for recollection probably due to reason that a majority of contextual information involves self-referencing content. For example, recollection involves memory of personal experiences or thought during the encoding period. This finding was therefore consistent with the idea that self-related content is an important component in recollection (Kim, 2010).

Compared to familiarity, recollection also recruited additional activations in the frontal pole, inferior frontal and temporal gyrus, orbital frontal cortex and left middle temporal gyrus. These regions were commonly found to be associated with executive control processing, which was highly required in the selection and maintenance of contextual details during recollection (Blumenfeld & Ranganath, 2007; Lepage et al., 2000). This assumption was corroborated by studies involving attention manipulations such as levels of processing manipulations (Gregg & Gardiner, 1994; Rajaram, 1993) or division of attention (Gardiner & Parkin, 1990; Yonelinas, 2001), which found recollection performance to be more affected than familiarity.

4.1.3 Familiarity involves the ventral network

Results of increasing familiarity contrasts from past meta-analysis included ventral network regions associated with salience processing (Kim, 2010). On that basis, we hypothesized that familiarity mainly recruits the ventral medial and lateral frontal lobe, ventral parietal lobe, the insula as well as other subcortical regions. Consistent with our hypothesis, we found familiarity associated activations in the ventral frontal (anterior medial cingulate, bilateral middle temporal lobe) and ventral parietal regions (left supramarginal gyrus, left angular gyrus) as well as subcortical regions including the right insula, bilateral thalamus and bilateral caudate. These regions may collectively represent salience signals downstream of retrieval, with each sub-region representing different aspects of salience processing. The involvement of ventral frontal region in salience processing is supported by evidence in prior studies that demonstrated increased ventral frontal activities for old/new effects when number of new items decreased; in other words, ventral frontal activities correlated with increasing salience for new items (Herron et al., 2004; Vilberg and Rugg, 2009b). The ventral frontal regions may thus play a role in initiating bottom-up salience signals based on cognitive control while the insula is responsible for processing salience awareness (Craig, 2009; Kim, 2010). Further downstream, the caudate could be mediating the reward effects associated with successful detection of “old” item (Kim, 2010); Haruno et al., 2004; Delgado et al., 2004).

As distinct from Kim (2010), we also obtained novel activations in bilateral thalamus unique for familiarity. Since prior studies have revealed that neurons in paraventricular thalamus responds to dynamic salience signals (Zhu et al., 2018), our finding would gap the discrepancy in the network described above, connecting the salience signal from the ventral frontal regions to the caudate. Regions within the ventral network could thus collaborate together to process salience quality for the stimuli during retrieval.

4.1.4 Parietal dissociations between recollection and familiarity

We observed dissociative activations for recollection and familiarity in the parietal region consistent with results from previous meta-analyses on neuroimaging results as well as electrophysiological studies (Kim, 2010; Spaniol et al., 2009). Specifically, ventral lateral parietal regions such as the angular gyrus were more active for recollection versus familiarity whereas familiarity recruited superior parietal regions compared to miss or correct rejection responses (Figure 2 & 3). This dissociation was consistent with the Attention to Memory (AtoM) model, which proposed that dorsal parietal cortex (superior parietal activations) mediates top–down attention processes guided by retrieval goals, whereas ventral parietal cortex (angular gyrus activations) mediates bottom–up attention processes captured by the retrieval output or the retrieval cue (Cabeza, 2008; Cabeza et al., 2011).

4.2 Comparisons between different retrieval paradigms

To explore the influence that different retrieval paradigms could have upon the results, we conducted supplemental analysis based on only remember-know studies for R > F and the familiarity related contrasts, as well as supplemental analysis based on source studies only for R > F. Sizes of clusters reported in supplemental analysis generally decreased compared to those reported in main analysis, most likely due to decreased number of studies, foci and participants included in the analysis.

Consistent with our hypothesis, R > F results revealed by the remember-know studies analysis generally overlapped with findings from the main analysis. Apart from retaining all frontal, parietal and medial temporal lobe activations found in the main analysis, the remember-know sub-analysis for R > F revealed additional right lateral prefrontal activations and bilateral subcortical activations including the thalamus and caudate (Figure 4B). These additional activities relating to cognitive control (Badre & Wagner, 2007) and processing of sensory and contextual information (Carlesimo et al., 2015; Hsieh & Ranganath, 2015) were in line with definition of recollection responses. The reliance on subjective answers to distinguish recollection and familiarity responses may have also contributed to activations in additional prefrontal and subcortical regions, as these findings were associated with mental load and salience processing and were absent from R > F results based on source memory studies (Blumenfeld & Ranganath, 2007; Spaniol et al., 2009).

Likewise, familiarity related activations revealed by the remember-know studies were also generally in line with results from the main analysis as well as our hypotheses. A major distinction between the present sub-analysis and the main analysis was that subcortical salience processing regions previously reported were no longer present for remember-know studies. Although this finding was seemingly at odds with our core predictions, it should be noted that the smaller number of studies (18) and foci (166) included in this analysis likely contributed to the decrease in extent of activations as well as absence of certain regions. Thus, the sub-analysis results for familiarity have lower statistical power due to smaller sample size compared to the results of the main-analysis.

Consistent with our hypothesis, R > F results revealed by the source memory studies demonstrated significantly lesser extent of activations (Table 5 & 6; Figure 6C) compared to results from the remember-know analysis. Most notably, predicted activations within the default mode network regions for recollection only included posterior midline cortex activations in source memory studies (Figure 6B). In addition, critical self-referencing and attention modulatory regions such as the left angular gyrus and right lateral prefrontal cortex were now absent from these results.

The GLM analysis comparing results from the remember-know and source R > F sub-analysis revealed a series of significant activations ($p < 0.025$) including the dorsal and medial prefrontal regions as well as ventral medial parietal regions. These results demonstrated that R > F analysis based on remember-know studies yielded significantly greater activations compared to source memory studies in most key recollection associated regions. This provided statistical corroborations to our observations that source memory studies provided less results compared to remember know studies. This is in line with our hypothesis based on the speculation that source memory task may invoke the so-called “non-critical recollection”, when the source memory task misses out recollection responses based on information not tested and wrongly classify those responses as familiarity (Spaniol et al., 2009). This would therefore reduce the number of activations we see in a recollection > familiarity contrast for source memory paradigms.

Again, we took note that the difference between foci number of recollection responses for remember-know studies (388) and source memory (209) may have contributed to the phenomenon that fewer regions or lesser extent of activations were reported in the source memory sub-analysis. However, this limitation cannot overthrow the fact that remember know studies yielded results that are more consistent with the hypothesized results for recollection. We thus concluded that the remember know paradigm might be the better paradigm to dissociate recollection and familiarity responses in the context of the dual-process model.

5. Conclusion

The present study has two primary goals. First, to update the current meta-analytic knowledge on neural correlates of recollection and familiarity. Second, to examine potential influence of different retrieval paradigms used to distinguish recollection and familiarity upon the results. To achieve our first goal, we conducted SDM meta-analyses on past fMRI studies of episodic memory retrieval. Consistent with our hypothesis, we found that the hippocampus, parahippocampal cortex as well as prefrontal and parietal regions associated with the default mode network were more activated for recollection versus familiarity and that prefrontal, parietal and subcortical regions associated with the ventral network were more activated for familiarity related contrasts (F > CR/M and increasing familiarity). These findings implicate the significance of contextual memory, detail maintenance, executive control and self-referential processing related regions in recollection responses and the significance of salience-processing and attention modulation related regions in familiarity responses. To achieve our second goal, we also conducted supplementary SDM meta-analyses as well as GLM analysis based on different retrieval paradigms. Our results suggested that the remember know paradigm yielded results that were more in line with our theoretical predictions. Consistent with our hypothesis, the source memory paradigm yielded less activations for recollection versus familiarity compared to remember-know studies. This finding may therefore serve as a guidance in selection of retrieval paradigms for future research that wish to study recollection and familiarity responses within the context of the dual-process model.

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