



## Research Report

# Neural correlates of autobiographical memory retrieval: An SDM neuroimaging meta-analysis



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## ABSTRACT

Autobiographical memory (AM) is a type of episodic memory that involves the recollection and re-experiencing of personal life events. AM retrieval is a complex process requiring the coordination of multiple memory processes across the brain. Important questions remain regarding the degree to which specific brain regions are consistently recruited during AM retrieval and the influence of methodological factors such as type of AM retrieval task and control task. Neuroimaging meta-analyses can summarize the brain regions associated with AM retrieval, addressing these questions by revealing consistent findings across multiple studies. We used a coordinate-based neuroimaging meta-analysis method, seed-based  $d$  mapping (SDM), to assess the largest set of neuroimaging studies of AM retrieval to date. An important advantage of SDM over other methods is that it factors in the effect sizes of the activation coordinates from studies, yielding a more representative summary of activations. Studies were selected if they elicited AM retrieval in the scanner, contrasted AM retrieval with a matched control task, and used univariate whole-brain analyses, yielding a set of 50 papers with 963 participants and 891 foci. The findings confirmed the recruitment of many previously identified core AM retrieval regions including the prefrontal cortex (PFC), hippocampus and parahippocampal cortex, retrosplenial cortex and posterior cingulate, and angular gyrus, and revealed additional regions, including bilateral inferior parietal lobule and greater activation extent through the PFC, including lateral PFC activation. Results were robust across different types of AM retrieval tasks (previously rehearsed cues vs. novel cues), and robust across different control tasks (visual/attention vs. semantic retrieval). To maximize the utility of the meta-analysis, all results image files are available online. In summary, the current meta-analysis provides an updated and more representative characterization of the neural correlates of autobiographical memory retrieval and how these neural correlates are affected by important experimental factors.

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## 1. Introduction

Episodic memory is a form of memory defined by consciously accessible memory for specific events (Tulving, 1983). Episodic memory is a fundamental type of memory that allows us to “time travel” back through subjective time to remember and re-experience past events (Tulving, 2002). Through retrieval of relevant information from past events, episodic memory can guide behavior in service of our current and future goals (Conway & Pleydell-Pearce, 2000). Episodic memory and semantic memory (factual knowledge) together comprise declarative memory, consciously accessible memory for events and facts (Squire, 2004). A wealth of experimental evidence indicates that declarative memory function is supported by the structures in the medial temporal lobe, including the hippocampus, entorhinal cortex, perirhinal cortex, and parahippocampal cortex (Moscovitch et al., 2016; Squire, 2004).

Autobiographical memory (AM), defined as memory for specific events from one's own past, combines both episodic and semantic memory content (Cabeza & St Jacques, 2007; Piolino et al., 2009; Rubin, 2005). For example, an AM of a trip to a café might include vivid episodic recollection of a social interaction, together with semantic knowledge about the café and new people who were met there. Autobiographical memories are fundamentally important to one's sense of self and play important roles in a wide variety of domains ranging from social behavior, problem solving, and emotion regulation (Bluck, 2003; Cabeza & St Jacques, 2007; Nelson & Fivush, 2020).

A large and growing literature of neuroimaging studies has investigated the neural basis of AM retrieval (for reviews see Cabeza & St Jacques, 2007; Daselaar et al., 2008; Rugg & Vilberg, 2013; Moscovitch et al., 2016). The brain regions reported to be active during AM retrieval differ considerably across studies, reflecting a wide range of factors such as differences in the tasks used to elicit retrieval, differences in control tasks, and the relatively limited statistical power of many fMRI studies. As with many cognitive domains, the findings from multiple studies need to be combined and synthesized to yield a comprehensive view of the regions that are consistently involved in AM retrieval. Although narrative reviews that are qualitative in nature can be informative, quantitative meta-analyses have several advantages over qualitative reviews (Albajes-Eizagirre & Radua, 2018; Laird et al., 2005; Müller et al., 2018; Radua & Mataix-Cols, 2012).

Quantitative meta-analysis methods such as Activation Likelihood Estimation (ALE) and Seed-based  $d$  Mapping (SDM) are coordinate based meta-analysis (CBMA) methods that identify regions of the brain that are consistently activated across numerous studies (Addis et al., 2016; Albajes-Eizagirre & Radua, 2018; Boccia et al., 2019; Laird et al., 2005; Witteman et al., 2019). Because the original neuroimaging data from individual studies are typically not available, CBMA methods use the peak coordinates of activations reported in each published study to estimate the original functional activation maps. These estimated activation maps are then pooled and analyzed at the voxel level to yield meta-analytic summaries of regions that are consistently activated across studies.

Previous quantitative meta-analyses have been conducted to identify the common regions associated with AM retrieval (Addis et al., 2016; Boccia et al., 2019; Spreng et al., 2009). However, these previous studies have limitations in terms of sample size, study selection criteria, and analytic method (see Discussion for a detailed discussion). To address these issues, we examined the neuroimaging correlates of AM retrieval in the current study, using the largest sample of neuroimaging studies to date (50 studies), improved study selection criteria, and a different analysis method, Seed-based  $d$  Mapping with Permutation of Subject Images (SDM-PSI) (<https://www.sdmproject.com>).

A key advantage of SDM over other CBMA methods such as ALE is that SDM takes into account variations in the effect size of each reported activation maximum (based on their maximum  $t$  values), better representing the original neuroimaging results, whereas ALE does not explicitly factor in effects sizes and treats all statistically significant maxima equivalently. Other advantages of SDM include its sophisticated random-effect modeling of subject-level data (which increases reliability and performance of the analysis) and the use of threshold-free cluster enhancement (TFCE) to control for multiple comparisons, a method that has advantages relative to cluster-based thresholding methods (Albajes-Eizagirre et al., 2019). Finally, because the results of neuroimaging meta-analyses are frequently used for many purposes such as providing regions of interest for fMRI or brain stimulation studies, or to interpret new neuroimaging findings, our goal was to make the meta-analysis results maximally useful by making all the SDM meta-analysis results images freely available online (on the Mendeley repository <https://data.mendeley.com/datasets/w9p86fndr7>), in contrast to previous meta-analyses of AM retrieval, which have not provided public open access to their results images.

In addition to characterizing the neuroimaging correlates of AM retrieval, we also addressed how two important methodological variables may affect these neuroimaging correlates. One of these differences concerns whether the memories being retrieved have been pre-rehearsed prior to neuroimaging scanning or alternately, are retrieved via a specific cue for the first time during scanning. Most AM retrieval studies cue memory retrieval with a method where single word cues are presented and participants are instructed to retrieve an AM that is related either directly or indirectly to the cue (the Galton-Crovitz cueing method; Crovitz & Schiffman, 1974; Galton, 1879). In some neuroimaging studies, these cues are presented to participants prior to scanning and participants retrieve AM memories. This *cue-rehearsed retrieval* method is advantageous because experimenters know in advance which memories will likely be retrieved to the cues during scanning, affording greater experimental control. However, due to concerns over the possible effects of prior rehearsal on subsequent memory retrieval processes, other neuroimaging studies have presented participants with retrieval cues for the first time in the scanner, with no prior rehearsal (Cabeza & St Jacques, 2007). We will refer to studies in which AM retrieval is cued with no prior rehearsal as studies that use the *cue-novel retrieval* method. Prior rehearsal has been suggested to have a particularly prominent effect on the initial memory search processes involved in AM retrieval (Nadel et al., 2007). One previous study

found that activation in areas supporting episodic and semantic memory retrieval decreased with increasing amounts of memory rehearsal (Svoboda & Levine, 2009). However, the impact of this key methodological factor has yet to be systematically examined in a meta-analytic study. Accordingly, we examined this question by comparing the activations from neuroimaging studies using cue-rehearsed retrieval to those from studies using cue-novel retrieval.

A second important methodological variable we examined is the type of control task used to compare with the primary AM retrieval task. As with any neuroimaging study, the type of control task used can have a considerable influence on the activation results. A particularly important consideration is the degree to which the chosen control task recruits cognitive processes that overlap with those involved in AM retrieval. A key difference in the control tasks used in neuroimaging studies examined in this study is the extent to which perceptual/attentional vs. semantic processing is engaged during the control task. Several studies have used visuo-attention tasks such as pressing a button in the direction of an arrow or performing a simple arithmetic task, whereas another large set of studies have used semantic memory retrieval tasks such as generating category exemplars. We predicted that AM retrieval studies that used semantic retrieval tasks as control conditions would be associated with decreased activation in regions associated with semantic memory retrieval (due to subtraction of semantic memory retrieval activations associated with the semantic control task), relative to studies that used visuo-attention control tasks (which involved minimal or no semantic memory retrieval). To examine this issue, we compared the meta-analysis results between studies that used visuo-attention tasks vs. semantic control tasks.

In summary, the goal of the current study was to update the current understanding of the neural basis of AM retrieval using the largest set of neuroimaging studies of AM retrieval to date and a powerful meta-analytic approach (SDM), to provide an updated, more representative summary of the regions involved in AM retrieval. While we expected our results to have broad similarities with prior neuroimaging meta-analysis studies and qualitative reviews of AM retrieval (e.g., medial temporal regions such as the hippocampus, prefrontal and parietal regions, among several other regions), given the differences in approach and the studies included, we expected our meta-analysis to potentially yield different results from prior meta-analytic studies. Finally, we addressed two novel questions about how two important methodological factors (type of retrieval task and type of control task) influence these meta-analysis results.

## 2. Methods

We report here how we determined our sample size, all data exclusions, all inclusion/exclusion criteria, whether inclusion/exclusion criteria were established prior to data analysis, all manipulations, and all measures in the study. Materials and data for the study are available at <https://data.mendeley.com/datasets/w9p86fndr7>. No part of the study procedures or analyses was preregistered prior to the research being conducted.

We conducted a literature search on PubMed in October 2020. The PubMed search for autobiographical memory retrieval used the following search term: autobiographical AND memory AND (fMRI OR PET OR neuroimaging). This search yielded 624 papers. We also conducted additional searches in Neurosynth and Scopus, but they did not identify additional relevant papers. Fig. 1 outlines the process of identifying the papers utilized in the meta-analysis.

### 2.1. Inclusion and exclusion criteria

All papers were examined to determine whether they met the criteria for inclusion in our meta-analysis. Our criteria specified the neuroimaging method used, the sample population included, the type of task used, the contrasts of interest, and whether whole brain coordinates for activation maxima were reported. Detailed descriptions of these criteria are described below.

#### 2.1.1. Neuroimaging method

To be included, a study was required to use either fMRI or PET. In addition, studies needed to use univariate neuroimaging activation analyses. Functional connectivity and multivariate results (e.g., partial least-squares analyses, principal component analyses) were excluded because their results are qualitatively different from univariate activation analyses and therefore should not be combined in the same meta-analysis (Müller et al., 2018; Radua, 2020).

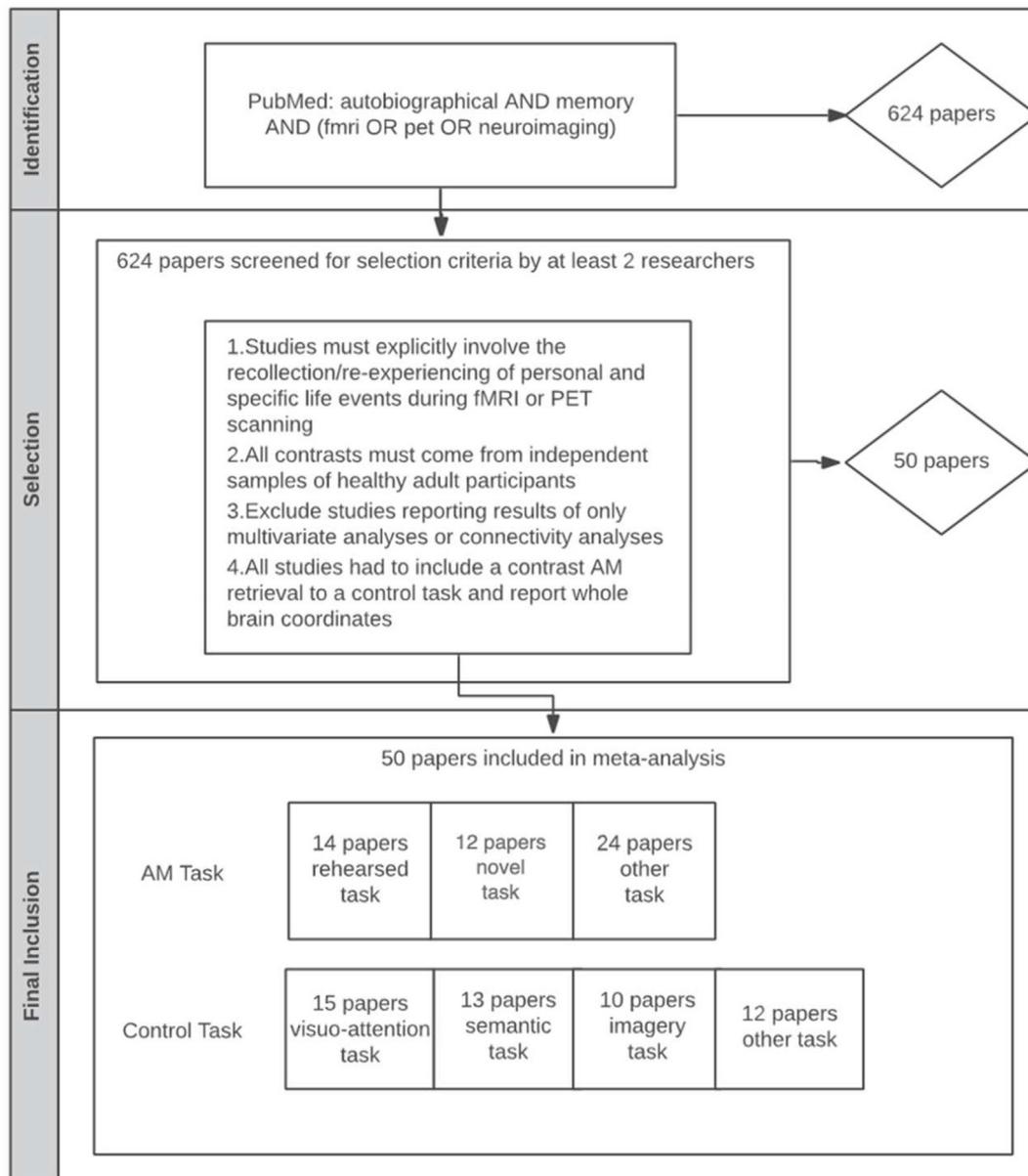
#### 2.1.2. Sample population

Only studies reporting data from healthy young adults were included. Studies that compared healthy young adult populations to other populations were included if the data for the young adults were reported separately. Also, if the studies manipulated any clinical factor (i.e., hormonal, pharmacological manipulations, or sleep deprivation), they could be included if they separately reported the placebo or control condition group results.

In order to minimize the chances of a single study influencing the results of the meta-analysis, we followed the current guidelines on the inclusion of multiple contrast originating from the same sample (Alegria et al., 2016; Müller et al., 2018; Norman et al., 2016). If a study reported two contrasts of interest from the same sample (e.g., positive AM retrieval > control and negative AM retrieval > control), then the two contrasts were combined into a single contrast through the *combine images* function of SDM. This combination allows for the data to be pooled, minimizing over-representation of data from a single subject group. However, if a more general combined contrast was also available, then that contrast would be used instead.

#### 2.1.3. AM task criteria

Studies were only included if they involved the recollection of autobiographical memories while subjects were being scanned. Studies were excluded if they did not use neuroimaging during active retrieval (i.e., turning off the scanner while participants retrieved an AM aloud), used mood induction before retrieval, included future, prospective planning, collapsed across real and fictitious AM retrieval, or instructed



**Fig. 1 – Workflow chart illustrating the processes from identification to final inclusion of papers in the meta-analysis.**

participants to manipulate their memories in any specific way. Real-time fMRI neurofeedback studies were excluded because the addition of neurofeedback during scanning may alter the nature of the AM retrieval process.

#### 2.1.4. Contrasts of interest

To be included, studies were required to contrast successful AM retrieval to a valid control task. Valid control tasks were defined as rest (but see section 2.1.6 below for issues regarding rest as a control condition), motor movements, visual tasks, semantic memory tasks, or imagery tasks. Studies were also excluded if their control task involved autobiographical memory retrieval such as such as contrasting positive or negative AM retrieval to neutral AM retrieval, because such contrasts explicitly subtract out activation involved in AM retrieval.

#### 2.1.5. Whole-brain coordinates

Studies were included only if they reported whole brain activations. Studies were excluded if they only reported coordinates of regional activations such as from ROI analyses. For studies reporting whole brain coordinates that included coordinates identified using more lenient thresholds in a-priori regions of interest (small volume corrections), only the coordinates that also met the whole brain threshold were included.

#### 2.1.6. Included papers

After each paper was screened using these criteria, 58 papers remained. Next, we excluded studies that used rest as a control condition, in line with [Boccia et al. \(2019\)](#) who also excluded such studies. The resting state elicits activation of

the default mode network (DMN), a network that is strongly associated with AM retrieval (Spreng & Grady, 2010). Thus, studies that use the resting state as a control task would be expected to yield significantly biased AM retrieval activation results, with reduced activation in the DMN due to DMN activation in the rest condition being subtracted out. To avoid this potential bias, we excluded the 8 studies that used rest as a control condition from our main meta-analysis, leaving 50 papers which formed the basis of our meta-analysis. As a supplemental analysis, to determine whether including studies using rest as a control condition would have yielded substantially different results, for all relevant analyses we conducted the analyses a second time including the 8 papers that included rest control conditions (see Supplementary Materials). In the selected 50 papers in the main meta-analysis, there were 963 participants, 891 foci, and 62 contrasts (11 were pooled and one paper (Compere et al., 2016) had two contrasts from separate samples). A complete list of these studies and their design characteristics are included in Table 1.

## 2.2. Selection of AM retrieval and AM control tasks

For all 50 selected papers, the retrieval task (task used to elicit autobiographical memory retrieval) and the corresponding control task were examined. There were two common types of retrieval tasks: cue-rehearsed and cue-novel. Cue-rehearsed AM tasks were defined as tasks in which autobiographical memories had been retrieved within 1 week before scanning (in order to develop verbal retrieval cues that would be presented during scanning). Cue-novel AM tasks were defined as tasks using novel word and phrase retrieval cues in the scanner. 14 papers were identified that used cue-rehearsed AM tasks, 12 papers used cue-novel tasks, and 24 papers used different retrieval tasks (see Table 1 for descriptions of each study's tasks). For control tasks, there were three common types of tasks: visuo-attention, semantic, and imagery. Visuo-attention control tasks were defined as low level tasks such as simple math, visual search, or arrow tasks (or other simple motor control tasks). Semantic control tasks included tasks such as sentence completion, category exemplar retrieval, or semantic fact retrieval questions. Imagery control tasks included tasks such as imagining a scene from a sentence, imagining fictitious scenes from books/novels, or viewing AM retrieval cues generated by other individuals and imagining a scenario based on those cues. There were 15 papers that used a visuo-attention control task, 13 papers used a semantic control task, 10 papers used an imagery control task, and 12 papers used other types of control tasks (see Table 1 for descriptions of each study's tasks). The set of papers that used an imagery control task was associated with substantially fewer participants and foci than the visuo-attention and semantic control task papers, and this number of participants and foci was insufficient to conduct a valid meta-analytic comparison between the imagery control task studies and other types of studies. Therefore, in the current study, only the studies using visuo-attention and semantic control tasks were directly compared to each other.

## 2.3. Meta-analysis method

### 2.3.1. Meta-analysis of AM retrieval

Seed-based  $d$  mapping with permutation of subject images (SDM-PSI; referred to as SDM hereafter) is a method that conducts statistical inferences on results from multiple studies, with varying tasks and sample sizes, to identify significant areas of activation across subject groups (for a complete description of SDM-PSI, see Albajes-Eizagirre et al., 2019). To identify the brain regions that were consistently activated during autobiographical memory retrieval, we used SDM-PSI version 6.21 ([www.sdmproject.com](http://www.sdmproject.com); Albajes-Eizagirre et al., 2019). For each contrast, coordinates of the activated peaks and their  $t$ -values, the whole-brain threshold, sample size, active task type, and control task type were collected and entered into the SDM program. All statistical values were converted to  $t$ -values before being entered. If a study only reported cluster size rather than  $t$ -values, the whole-brain threshold was entered instead. Preprocessing was performed according to SDM guidelines, using a 20 mm full width half maximum (FWHM) anisotropic Gaussian kernel and 2 mm voxel size. After preprocessing, for the studies reporting more than one contrast, the upper and lower maps for each contrast were combined using SDM's *combine image* function. This function creates a map that is the mean of the effect sizes and variance of the different contrasts (for details, see Supplemental Material for Alegria et al., 2016; Norman et al., 2016). For the main analysis, the number of imputations was set to 50, and the permutations was set to 1000. Voxel-wise results are reported using threshold-free cluster enhancement (TFCE) using a family wise error rate (FWE) of  $p < .05$ .

### 2.3.2. Analyses of the effects of retrieval task and control task

For the retrieval task and control task analyses, our goal was to identify activations that differed between studies that used cue-rehearsed vs. cue-novel AM retrieval paradigms. The *linear model* function in SDM allows two sets of activation to be statistically compared (Albajes-Eizagirre et al., 2019). The first linear model contrasted cue-rehearsed AM retrieval and cue-novel AM retrieval. We used the linear model function to contrast activations related to cue-rehearsed AM retrieval with the corresponding activations associated with cue-novel AM retrieval. The same procedure was conducted for the second linear model, which contrasted AM retrieval for studies that used a semantic control task to studies that used a visuo-attention control task. The *linear model* function is mathematically very similar to the traditional SDM meta-analysis, with two differences: permutations can only be conducted at the study level and the linear model comparison is two tailed (for full information on the linear model method see Albajes-Eizagirre et al., 2019). The SDM results were thresholded using TFCE with an FWE of  $p < .025$ .

To complement these supplementary analyses of the differences between studies that used a cue-rehearsed vs. cue-novel retrieval tasks and the differences between studies that used a semantic control task vs. a visuo-attention control task, we used SDM to create separate maps of regions showing significant SDM activations associated with AM retrieval using

**Table 1 – Studies included in the AM retrieval meta-analysis.**

1st Author and Date	N	Foci	Contrast	Control Task	Active Task
Addis et al., 2004	14	16	AM retrieval > Control	Semantic (sentence completion and size judgement)	Cue-Rehearsed (pre-scan interview within 1 week)
Andreasen et al., 1995	13	7	Focused episodic memory > semantic memory	Semantic (word production beginning with a specified letter)	Other (retrieved 15 min prior then un-cued retrieval)
Arshamian et al., 2013	15	16	Odor cued OEAM > control odors; word cued OEAM > control words	Other (smelling/reading a cue that would not elicit a memory)	Other (rehearsed odor cues)
Bauer et al., 2016	14	7	Adult AM retrieval > semantic	Semantic (word presentation and elaboration)	Cue-Rehearsed (previously presented cue words)
Botzung et al., 2008a	10	11	AM retrieval > control	Semantic (associated word pair judgement)	Cue-Rehearsed (pre-scan interview within 1 week)
Botzung et al., 2008b	10	34	Past event evocation	Semantic (associated word pair judgement)	Cue-Rehearsed (pre-scan interview within 1 week)
Cabeza et al., 2004	13	6	CA > CL	Other (controlled laboratory memory retrieval)	Other (controlled AM retrieval)
Chen et al., 2017	27	18	Life memory test > picture memory test	Other (picture recognition memory task)	Other (picture presentation)
Compère et al., 2016	20 M 16 F	4 11	EAM > control	Imagery (impersonal scene imagery task)	Other (cues for scanner were created without retrieving the memory)
Conway et al., 1999	6	11	Recent + remote AM > cued recall	Other (paired associate recall task)	Cue-Novel (novel cue presentation)
Denkova et al., 2006a	10	26	Autobiographical > control	Semantic (famous faces recognition task)	Other (picture cues)
Denkova et al., 2006b	20	38	Verbal AM > control; Nonverbal AM > control	Semantic (associated word pair judgement)	Other (word and picture cues)
Denkova et al., 2015	17	19	Emotion vs SM; Context vs SM	Semantic (generation of exemplars)	Other (pre-scan interview over 1 week before scan)
Detour et al., 2011	7	5	Memory Effect	Visuo-Attention (passively viewing a photo)	Other (picture cues)
Donix et al., 2010	15	17	AM > semantic (irrespective of remoteness) (young subjects)	Other (recall of public events)	Other (pre-scan interview over 1 week before scan)
Eich et al., 2009	16	38	Field memories > control; Observer memories > control	Visuo-Attention (visual search task)	Other (controlled laboratory memory retrieval)
Fink et al., 1996	7	5	Personal > impersonal	Imagery (visualizing someone else's autobiographic memory)	Other (pre-scan interview over 1 week before scan)
Fleischer et al., 2018	33	9	Recall > calculate	Visuo-Attention (simple arithmetic)	Cue-Novel (novel cue presentation)
Fuentes-Claramonte et al., 2019	34	12	Memory > control	Visuo-Attention (view three random words)	Rehearsed (pre-scan interview within 1 week)
Gardini et al., 2006	14	14	Episodic autobiographical > baseline	Visuo-Attention (read a pseudo-word)	Cue-Novel (novel cue presentation)
Graham et al., 2003	24	8	Autobiographical > semantic	Semantic (producing semantic facts about a word)	Cue-Novel (novel cue presentation)
Greenberg et al., 2005	11	18	Autobiographic > semantic	Semantic (think of exemplars of a category)	Other (pre-scan interview over 1 week before scan)
Grol et al., 2016	27	77	Positive field perspective > control; Neutral field > control; Positive observer > control; Neutral observer > control	Visuo-Attention (visual search task)	Other (verbally instructed cues)
Holland et al., 2011	25	16	Specific and General AM construction; Specific and General AM elaboration	Imagery (sentence construction and elaboration)	Cue-Novel (novel cue presentation)
Hoscheidt et al., 2010	17	27	Main effect of memory type (episodic)	Semantic (true/false judgements to semantic facts)	Cue-Rehearsed (pre-scan interview within 1 week)
Lempert et al., 2017	35	12	Memory recall > control cue	Other (interroception questions)	Cue-Rehearsed (pre-scan interview within 1 week)
Maguire et al., 2003a	12	11	AE > control	Visuo-Attention (syllable decision task)	Other (pre-scan interview over 1 week before scan)
Maguire et al., 2003b	24	4	Autobiographical > public events	Other (memories of public events)	Other (auditorily presented cues)
Markowitsch et al., 2000	8	8	Autobiographic > fictitious	Imagery (fictitious event construction)	Rehearsed (pre-scan interview within 1 week)
Martinelli et al., 2013	20	25	Young EAM; Young SAM	Imagery (sentence completion then imagining the scene)	Cue-Novel (novel cue presentation)
Martin-Subero et al., 2019	30	11	Autobiographical recall > non-memory-evoking condition	Visuo-Attention (read 3 random words)	Cue-Rehearsed (pre-scan interview within 1 week)

McCormick et al., 2017	12	21	AM retrieval (healthy controls)	Visuo-Attention (math task)	Cue-Novel (novel cue presentation)
Metz et al., 2019	37	9	Recall > calculate	Visuo-Attention (math task)	Cue-Novel (novel cue presentation)
Miró et al., 2019	18	35	Autobiographic memory (healthy controls)	Other (left/right arrow task)	Cue-Novel (novel cue presentation)
Muscattell et al., 2009	13	14	AM > control	Imagery (read and visualize a sentence)	Cue-Novel (novel cue presentation)
Noreen et al., 2016	22	39	Think > no-think (local maxima from major clusters and minor clusters)	Other (no-think)	Other (pre-scan interview over 1 week before scan)
Oddo et al., 2008	15	6	AM > SM	Other (remember public events)	Other (auditorily presented cues)
Parlar et al., 2017	20	3	HC: positive memory > number task; HC: negative memory > number task	Visuo-Attention (odd number detection task)	Cue-Rehearsed (pre-scan interview within 1 week)
Piefke et al., 2003	20	18	CP/CN/RP/RN > baseline	Other (subordinate reaction time task)	Other (pre-scan interview over 1 week before scan)
Rabin et al., 2009	18	9	AM > ToM	Imagery (theory of mind – image a novel event/scenario)	Other (photo cues)
(Rekkas et al., 2005)	12	44	Retrieval of recent > semantic; Retrieval of remote > semantic	Semantic (semantic memory task)	Cue-Rehearsed (pre-scan interview within 1 week)
St. Jacques et al., 2013	26	9	True memories (target > lure) > False memories (target > lure)	Visuo-Attention (target is presented but not recognized)	Other (SenseCam images were used as cues)
St Jacques et al., 2017	29	7	AM retrieval > episodic counterfactual simulation	Imagery (creation of counterfactual AMs)	Cue-Rehearsed (pre-scan interview within 1 week)
St-Laurent et al., 2016	14	9	AM > narratives (healthy controls)	Other (recalling previously encoded narratives from pre-scan)	Other (pre-scan interview over 1 week before scan)
Summerfield et al., 2008	18	12	Recall of real autobiographical events > recall of imagined autobiographical events	Imagery (recalling imagined autobiographical events created pre-scan)	Cue-Rehearsed (pre-scan interview within 1 week)
Svoboda et al., 2009	11	46	Episodic AM > control; Episodic AM > general semantic	Other (listening to themselves read a book and recalling semantic information from the book)	Other (pre-scan interview over 1 week before scan)
Wilbers et al., 2012	30	13	AM > non-AM	Imagery (fictitious memories originating from books/movies)	Cue-Rehearsed (pre-scan interview within 1 week)
Xu et al., 2018	25	26	Positive AM > baseline; Negative AM > baseline	Visuo-Attention (detecting pseudo-Chinese characters)	Other (pre-scan interview over 1 week before scan)
Young et al., 2011	14	10	Specific memories > subtraction	Visuo-Attention (subtraction task)	Cue-Novel (novel cues presented in scanner)
Young et al., 2012	40	18	AM recall > example generation	Semantic (semantic example generation)	Cue-Novel (novel cues presentation)

Note. The names of the contrasts in this table are the same as the names of the contrasts in the corresponding original papers. AM (autobiographical memory); OEAM (odor evoked autobiographical memory); EAM (episodic autobiographical memory); CA (controlled autobiographical); CL (controlled laboratory); SM (semantic memory); HC (healthy control); CP (childhood positive); CN (childhood negative); RN (recent negative); RP (recent positive); ToM (theory of mind).

cue-rehearsed retrieval task (results shown in [Supplementary Figure 2](#)), AM retrieval using a cue-novel retrieval task (results shown in [Supplementary Figure 3](#)), AM retrieval using a visuo-attention control task (results shown in [Supplementary Figure 4](#)) and AM retrieval using a semantic control task (results shown in [Supplementary Figure 5](#)). We used the same analysis parameters and thresholds as the main SDM analysis of AM retrieval. The dataset including the SDM. nii format output for the overall analysis, overall analysis including rest, cue-rehearsed retrieval analysis, cue-novel retrieval analysis, semantic control task analysis, and visuo-attention control task analysis is available at Mendeley Data (<https://data.mendeley.com/datasets/w9p86fndr7>).

**2.3.3. Comparison of overlap with the default mode network**  
The default mode network (DMN) is a large-scale brain network implicated in several cognitive processes involving self-generated thought, including autobiographical memory, planning for the future, and mind-wandering ([Andrews-Hanna et al., 2014](#)). Given current interest in the role of the DMN in AM retrieval, we determined the degree of overlap between the DMN and our main SDM meta-analytic map of AM retrieval-related regions by determining the spatial overlap between our main SDM map and a voxel-based map of the DMN. The DMN map was generated from a widely used dataset derived from the resting state fMRI scans of 1,000 healthy subjects ([Yeo et al., 2011](#)) that is included with the Neurosynth online tools (<https://neurosynth.org/>). A standard approach to generating a map of the DMN is to calculate the resting-state connectivity between a seed region in either the anterior or posterior node of the DMN and every voxel in the rest of the brain. We selected a voxel in the posterior cingulate cortex (MNI coordinates:  $-4, -52, 22$ ) which was identified in [Laird et al. \(2009\)](#) as a major focus of task-independent deactivations in the BrainMap database and used Neurosynth to create a whole-brain voxel-based map of the DMN. Although the spatial distribution of the DMN can vary depending on the specific location of the seed region, the regions encompassed by this DMN map closely matches other functional-connectivity based DMN maps in the literature, and overlaps almost completely with (and contains as a subset) a DMN map created using the Neurosynth meta-analytic association analysis tool using the term “default mode” to query 777 neuroimaging studies using that term (comparing these with the studies in the database that are not associated with that term).

#### 2.3.4. Analysis of the effects of excluding studies that used rest as a control condition

As a supplementary analysis, to determine whether including studies using rest as a control condition in the meta-analysis would have yielded substantially different results, for all relevant analyses we conducted the analyses a second time including the 8 papers that included rest control conditions (see [Supplementary Materials](#)).

#### 2.3.5. Comparison of overlap with AM retrieval SDM analysis that excluded studies that explicitly elicited emotional AMs

We assessed whether the extent to which including vs. excluding studies that explicitly elicited emotional AM retrieval (6 studies) affected the meta-analysis results, by

conducting the main AM retrieval SDM analysis a second time, excluding the studies that explicitly involved emotional AM retrieval, and assessing the spatial overlap between the two SDM maps (see [Supplementary Materials](#)).

#### 2.3.6. Comparison with overlap with the anterior vs. posterior hippocampus

Given the key role of the hippocampus in AM retrieval and proposals regarding functional differences between the anterior vs. posterior hippocampus, we examined the relative degree of overlap between the main AM retrieval SDM map and the anterior vs. posterior hippocampus bilaterally. We created the bilateral anterior and posterior hippocampal regions of interest (ROI) by segmenting the AAL3 anatomical atlas ([Rolls et al., 2020](#)) bilateral hippocampus ROI into anterior and posterior sections by dividing it at the approximate location of the uncus apex (at MNI  $y = -21$ ) ([Poppenk et al., 2013](#)), a landmark often used to divide the anterior and posterior hippocampus. The spatial overlap between each of these ROIs and the main AM retrieval SDM map was then assessed.

## 3. Results

### 3.1. Autobiographical memory retrieval

The SDM meta-analysis of AM retrieval revealed two large clusters of significant activation ([Table 2, Fig. 2](#)). Cluster one included 48,006 voxels in the prefrontal cortex (including ventrolateral PFC), the parietal lobe (including bilateral angular gyrus and bilateral inferior parietal lobule), bilateral medial temporal lobe (including parahippocampal gyrus, hippocampus, and amygdala), left temporal lobe, bilateral cerebellum, and additional regions listed in [Table 2](#). Cluster two included 8,313 voxels in the right angular gyrus, inferior parietal lobule, the right temporal lobe, and additional regions listed in [Table 2](#).

To assess whether excluding studies that used rest as the control task affected these results, the SDM analysis was repeated, this time including the 8 studies that had been excluded because they used rest as the control task. This follow-up SDM meta-analysis revealed largely similar results to the original analysis with the exception of slightly greater activation extent in some regions within cluster one, and one small additional cluster in right caudate ([Supplementary Figure 1; Supplementary Table 3](#)).

The results of the supplementary analysis that assessed the degree of overlap between the default mode network (DMN) and our main SDM meta-analytic map of AM retrieval-related regions are shown in [Supplementary Figure 6](#). The DMN map is almost completely contained as a subset of the SDM map and the largest regions of overlap between the maps correspond to the “core DMN” regions (most consistently activated regions within the DMN; [Andrews-Hanna et al., 2014](#)) including the anterior mPFC, posterior cingulate/pre-cuneus, and bilateral angular gyrus. The largest regions where AM-related activations extend outside the DMN map are in the medial and lateral PFC (especially left ventrolateral PFC), bilateral parietal cortex, the medial temporal lobe, and right cerebellum.

**Table 2 – Regions showing significant activations during retrieval of autobiographical memories.**

Cluster	Anatomical Regions(s)	L/R	Voxels	Peak			Z Value
				x	y	z	
1	<b>Anterior Cingulate Cortex</b>	R	<b>48,006</b>	<b>4</b>	<b>40</b>	<b>–2</b>	<b>11.96</b>
	Paracingulate Gyrus	L		–4	52	20	11.54
	Posterior Cingulate Cortex	R		2	–50	22	11.34
	Frontal Pole	L		–8	60	10	11.02
	Lateral Occipital Cortex	L		–44	–72	22	10.92
	Posterior Cingulate Cortex	L		–8	–50	20	10.91
	Precuneus Cortex	R		4	–64	18	10.57
	Paracingulate Gyrus	R		4	46	16	10.39
	Precuneus Cortex	L		–6	–64	20	9.92
	Angular Gyrus	L		–42	–60	26	9.04
	Superior Frontal Gyrus	L		–6	22	58	7.24
	Parahippocampal Gyrus	L		–24	–32	–16	7.23
	Angular Gyrus <sup>b</sup>	L		–46	–56	42	6.92
	Frontal Orbital Cortex	L		–38	26	–8	6.74
	Temporal Pole	L		–48	8	–18	6.73
	Right Hippocampus	R		24	–16	–24	6.31
	Middle Temporal Gyrus	L		–58	–26	–8	6.15
	Left Hippocampus	L		–26	–26	–16	6.10
	Temporal Fusiform Cortex	L		–30	–36	–28	5.50
	Inferior Temporal Gyrus	L		–54	–14	–30	5.34
	Middle Frontal Gyrus	L		–32	14	48	5.22
	Superior Temporal Gyrus	L		–48	–18	–8	5.16
	Superior Frontal Gyrus	R		8	12	56	5.03
	Left Amygdala	L		–14	–10	–14	5.01
	Inferior Frontal Gyrus, pars triangularis	L		–50	26	2	4.75
	Cerebellum	R		46	–72	–32	4.72
	Inferior Frontal Gyrus, pars opercularis	L		–54	16	16	4.58
	Occipital Fusiform Gyrus	R		24	–72	–22	4.37
	Parahippocampal Gyrus	R		20	–34	–12	4.19
	Cerebellum	L		–26	–48	–26	4.16
Subcallosal cortex	R		12	28	–14	3.25	
2	<b>Lateral Occipital Cortex/Angular Gyrus<sup>a</sup></b>	R	<b>8,313</b>	<b>48</b>	<b>–72</b>	<b>20</b>	<b>9.13</b>
	Middle Temporal Gyrus	R		60	–18	–8	6.23
	Superior Temporal Gyrus	R		50	4	–16	5.77
	Inferior Frontal Gyrus, pars triangularis	R		50	20	0	5.24
	Angular Gyrus <sup>b</sup>	R		44	–58	44	4.71
	Temporal Pole	R		40	12	–24	4.58
	Frontal Orbital Cortex	R		50	32	–8	3.19
	Heschl's gyrus	R		46	–22	4	2.53

Note. Table shows local maxima separated by more than 10 mm. The family-wise error (FWE) threshold was  $p < .05$  and used threshold-free cluster enhancement (TFCE). The maximal peak for each cluster is in bold font. Due to a large number of local maxima, this table has been abbreviated by including only the peak with the highest z-value if there were multiple local maxima in the same labeled region and hemisphere (a complete table with all peaks can be found in [Supplementary Table 2](#)). Coordinates are reported in Montreal Neurological Institute (MNI) space with x, y, and z in the left-right, anterior-posterior, and inferior-superior dimensions, respectively.

<sup>a</sup> Also labeled as angular gyrus in AAL3.

<sup>b</sup> Also labeled as inferior parietal lobule in AAL3.

The results of the supplementary analysis that assessed the extent to which including vs. excluding studies that explicitly elicited emotional AM retrieval (6 studies) affected the meta-analysis result are shown in [Supplementary Figure 7](#). The figure shows the original analysis results in red, the results of the analysis excluding the 6 emotional AM retrieval studies in green, and the overlap between the two SDM maps is shown in yellow. When emotion AM retrieval studies were excluded, this resulted in a slight decrease in the total SDM map activations in 5 separate activation clusters, in contrast to the original analysis that contained 2 separate activation clusters. The greater number of clusters in the map with emotion AM studies omitted appears to be due to separation of the original 2

activation clusters into smaller clusters due to reduced activation in connecting regions. Although the two SDM maps overlapped closely in most regions, the exclusion of emotional AM retrieval studies reduced activation most prominently in the bilateral ventrolateral prefrontal cortex, part of the right amygdala, right middle temporal gyrus, the bilateral temporal pole, and the right cerebellum.

### 3.2. Cue-rehearsed vs cue-novel autobiographical memory retrieval

We contrasted activations associated with cue-rehearsed vs. cue-novel AM retrieval, first conducting separate SDM meta-

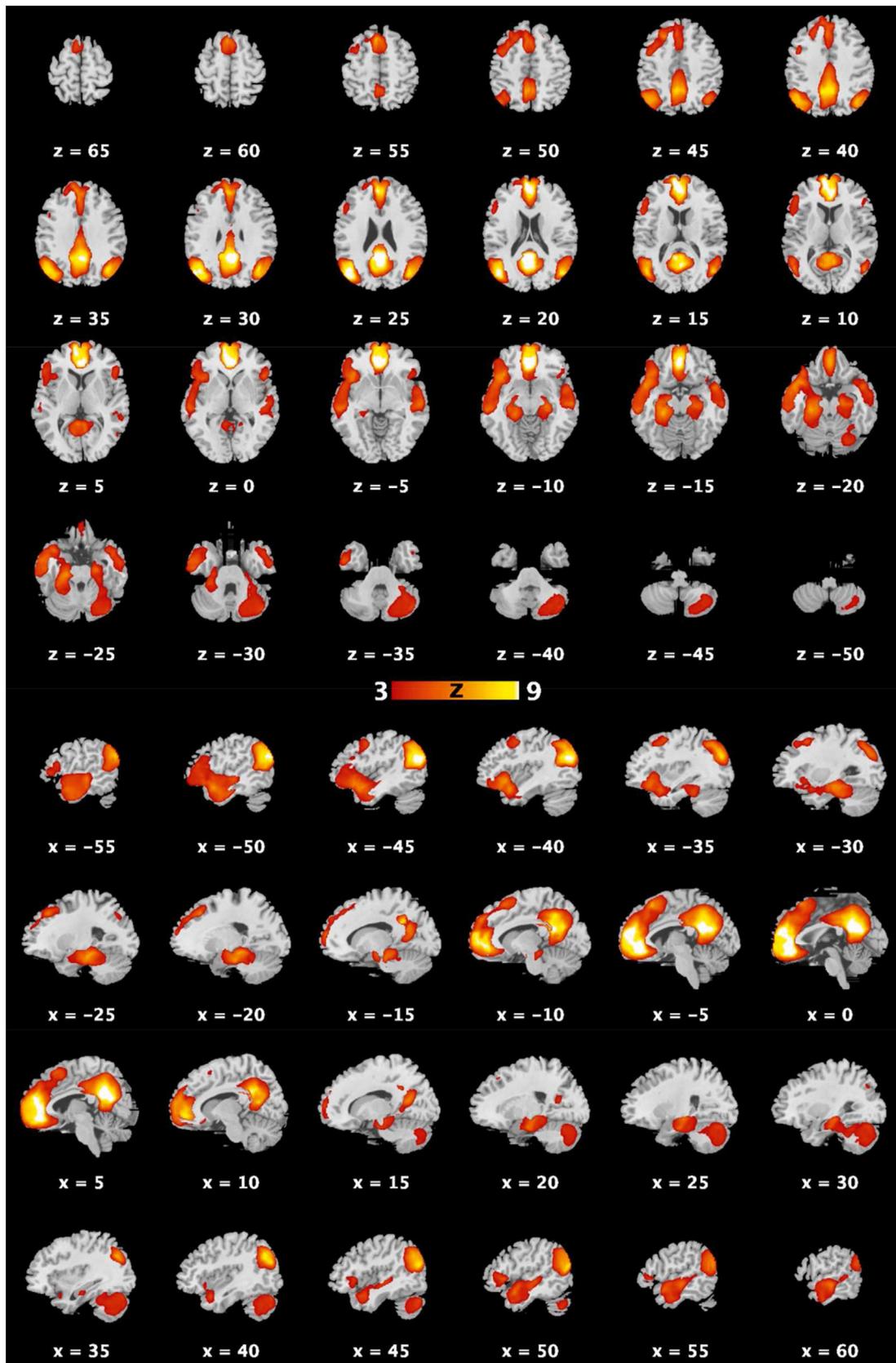


Fig. 2 – Regions showing significant SDM activations associated with autobiographical memory retrieval (voxel-wise threshold free cluster enhancement family wise error corrected  $p < .05$ ) are overlaid on a standard single-subject anatomical MRI image from SPM12 (Holmes et al., 1998). Intensity color scale indicates Z score value. Coordinates are in MNI space.

**Table 3 – Regions showing significant activations in the subtraction of cue-rehearsed and cue-novel AM retrieval.**

Cluster	Anatomical Regions(s)	L/R	Voxels	Peak			Z Value
				x	y	z	
1	<b>Frontal Pole</b>	L	63	–8	50	34	4.06
2	<b>Angular Gyrus<sup>b</sup></b>	R	276	48	–52	42	3.35
	Lateral Occipital Cortex <sup>a</sup>	R		40	–60	46	3.14
	Angular Gyrus <sup>b</sup>	R		58	–54	42	3.01

Note. Table shows local maxima separated by more than 10 mm. The family-wise error (FWE) threshold was  $p < .025$  and used threshold-free cluster enhancement (TFCE). The maximal peak for each cluster is in bold font. Coordinates are reported in Montreal Neurological Institute (MNI) space with x, y, and z in the left-right, anterior-posterior, and inferior-superior dimensions, respectively.

<sup>a</sup> Also labeled as angular gyrus in AAL3.

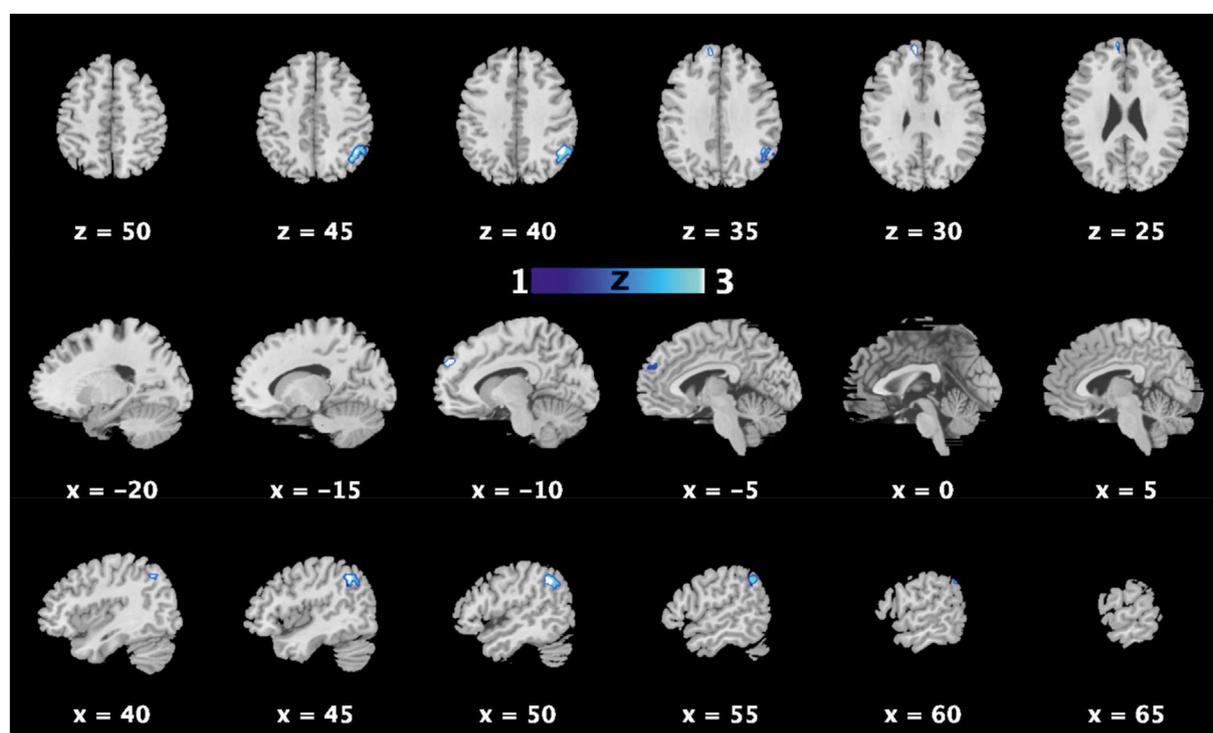
<sup>b</sup> Also labeled as inferior parietal lobule in AAL3.

analyses on the subset of papers associated with each type of task and then conducting a linear model analysis in SDM to identify regions that were significantly more activated for either type of retrieval task. The results from the separate SDM meta-analyses for cue-rehearsed AM retrieval and cue-novel AM retrieval are reported in [Supplementary Figure 2](#), [Supplementary Table 4](#), [Supplementary Figure 3](#), and [Supplementary Table 5](#). For the contrast between the two types of retrieval task, there were 2 clusters that were activated significantly more for cue-novel AM retrieval than for cue-rehearsed AM retrieval ([Table 3](#), [Fig. 3](#)). The first cluster included 63 voxels in the left medial frontal pole, and the second cluster included 276 voxels in the right angular gyrus and inferior parietal lobule. As with the main AM retrieval analysis, to assess the potential effects of excluding papers

that used rest as a control task, these analyses were conducted a second time, now including the papers that used rest as a control task ([Supplementary Tables 6 and 7](#)). This supplementary analysis yielded results that were highly similar to those obtained in the analysis that excluded papers using rest as a control task.

### 3.3. Effects of control tasks

To determine the effect of different control tasks on the neural correlates of autobiographical memory retrieval, additional SDM meta-analyses were conducted on the subset of papers that used a visuo-attention control task and on the subset of papers utilizing a semantic control task. Additional types of control tasks were also considered for comparison (imagery



**Fig. 3 – Regions showing significant SDM activations from the subtraction of cue-novel from cue-rehearsed autobiographical memory retrieval (voxel-wise threshold free cluster enhancement family wise error corrected  $p < .025$ ) are overlaid on a standard single-subject anatomical MRI image from SPM12 (Holmes et al., 1998). Intensity color scale indicates Z score value. Coordinates are in MNI space.**

**Table 4 – Regions showing significantly greater activations for AM retrieval studies using a semantic control task vs. those using a visuo-attention control task.**

Cluster	Anatomical Regions(s)	L/R	Voxels	Peak			Z Value
				x	y	z	
1	<b>Cerebellum</b>	R	721	<b>18</b>	<b>-28</b>	<b>-22</b>	<b>3.98</b>
	Lingual Gyrus	R	721	14	-30	-12	3.90
	Parahippocampal Cortex	R	721	20	-36	-16	3.01

Note. Table shows local maxima separated by more than 5 mm. The family-wise error (FWE) threshold was  $p < .025$  and used threshold-free cluster enhancement (TFCE). The maximal peak for each cluster is in bold font. Coordinates are reported in Montreal Neurological Institute (MNI) space with x, y, and z in the left-right, anterior-posterior, and inferior-superior dimensions, respectively.

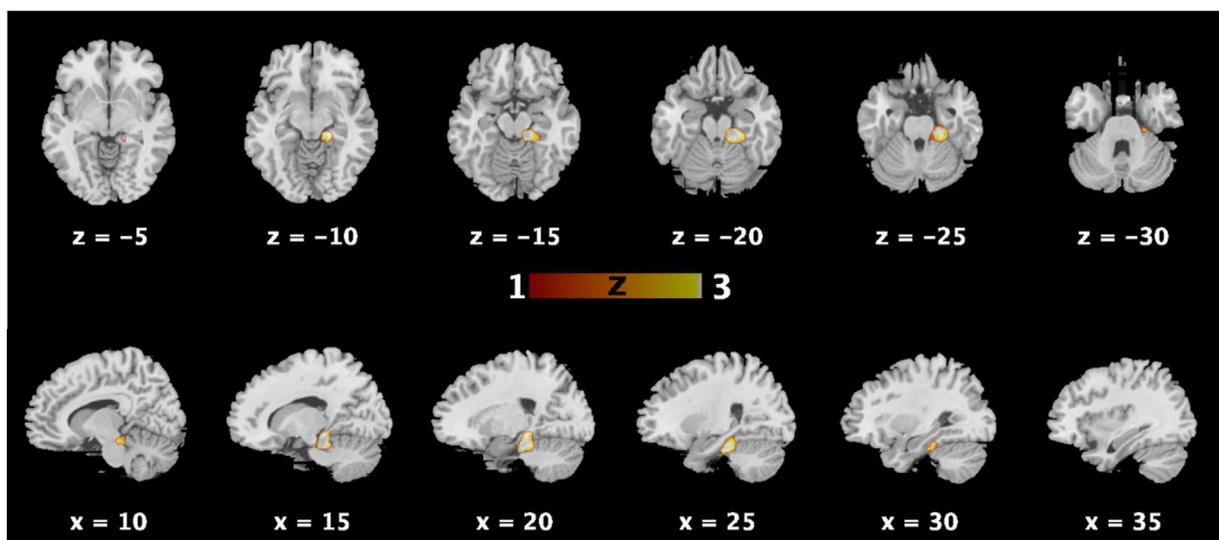
and rest), but there were an insufficient number of associated papers, participants, and foci to conduct a valid comparison with the other task types using SDM. We contrasted activations associated with studies using a visuo-attention control task vs. those using a semantic control task, first conducting separate SDM meta-analyses on the subset of papers associated with each type of control task and then conducting a linear model analysis in SDM to identify regions that were significantly more activated for either type of control task. The results from the separate SDM meta-analyses including only the papers using each control task condition are reported in [Supplementary Figure 4](#) and [Supplementary Table 8](#) (AM vs visuo-attention) and [Supplementary Figure 5](#) and [Supplementary Table 9](#) (AM vs semantic). For the contrast between studies using a visuo-attention control task and studies using a semantic control task, studies using a semantic control task were associated with significantly greater activation than studies using a visuo-attention control task in one cluster that included 721 voxels in the right parahippocampal gyrus that extended to the cerebellum, lingual gyrus, and parahippocampal cortex ([Table 4](#), [Fig. 4](#)).

### 3.4. Overlap between main AM retrieval map and the anterior vs. posterior hippocampus

The results of the supplementary analysis that assessed the extent to which the main SDM AM retrieval map and the anterior vs. posterior hippocampus is shown in [Supplementary Figure 8](#), displayed in coronal sections (ranging from  $y = 0$  to  $y = -46$  in MNI space). The bilateral anterior hippocampal ROI overlaps almost completely with the main SDM map, whereas the overlap with the bilateral posterior hippocampus ROI is primarily with the more anterior aspect of this structure, with relatively little overlap from  $y = -34$  to the most posterior part of the bilateral posterior hippocampus.

## 4. Discussion

This study had two primary goals. The first goal was to provide an updated and more representative characterization of the regional brain activations elicited by autobiographical memory (AM) retrieval, by analyzing the largest set of



**Fig. 4 – Regions showing significant SDM activations from the subtraction of AM retrieval with a visuo-attention control task from AM retrieval with a semantic control task (voxel-wise threshold free cluster enhancement family wise error corrected  $p < .025$ ) are overlaid on a standard single-subject anatomical MRI image from SPM12 (Holmes et al., 1998). Intensity color scale indicates Z score value. Coordinates are in MNI space.**

neuroimaging papers to date and using improved selection criteria and methods compared to prior meta-analyses. The second goal was to assess the extent to which AM retrieval activations are affected by key experimental factors that frequently vary across studies: different types of retrieval cues (novel vs. rehearsed), and different types of control tasks (visuo-attention vs. semantic control tasks). In the following sections, we summarize the main relevant meta-analysis results, relate them to the relevant AM neuroimaging literature, discuss these findings in relation to the findings of previous related meta-analyses, discuss the broader implications of the current findings, and outline future directions.

Three previous coordinate-based neuroimaging meta-analyses of AM retrieval have been reported (Spreng et al., 2009; Addis et al., 2016; and Boccia et al., 2019). Although the Spreng et al. (2009) and Addis et al. (2016) meta-analyses each summarized some aspects of the AM retrieval neuroimaging literature, these meta-analyses had important limitations relative to both Boccia et al. (2019) and the current study. First, the two older meta-analyses analyzed substantially fewer neuroimaging studies, because of the smaller contemporaneous literature and the narrower focus of each study on specific questions such as the role of the cerebellum in AM retrieval (Addis et al., 2016). As previewed in the Introduction, of these three studies, Boccia et al.'s (2019) study is the most recent neuroimaging meta-analysis and included the largest set of neuroimaging studies. Thus, in relating our findings to previous meta-analysis findings we focus here primarily on comparisons with Boccia et al. (2019), noting connections to the earlier studies where relevant.

#### 4.1. Summary of main findings

Consistent with previous reviews, the current meta-analysis identified the regions most frequently associated with AM retrieval: prefrontal cortex (PFC), hippocampus and parahippocampal cortex, retrosplenial cortex and posterior cingulate, and angular gyrus (Addis et al., 2016; Boccia et al., 2019; Moscovitch et al., 2016; Rugg & Vilberg, 2013; Spreng et al., 2009; Svoboda et al., 2006). Specifically, this analysis identified regions associated with distinct aspects of AM retrieval: left lateral PFC (memory search and controlled retrieval), medial PFC (self-referential processes), ventromedial PFC (monitoring), hippocampus (successful recollection), amygdala (recollection of emotional attributes), and occipital/precuneus (visual imagery) (Cabeza & St Jacques, 2007). In comparison with (Boccia et al., 2019), we identified activity in all the same regions they reported and also found additional areas of activation not reported in that study. We found that AM retrieval activated a considerably greater extent of activation throughout the PFC compared to Boccia et al. (2019), including the bilateral dorsolateral PFC, bilateral ventrolateral PFC, and bilateral inferior frontal gyrus (see Table 1, Fig. 1). In addition, although bilateral activation of the angular gyrus has been consistently identified previously in association with AM retrieval, our meta-analysis found that bilateral activation of the angular gyrus extended further into the inferior parietal lobule than reported by Boccia et al. (2019). Other additional areas of activation included the bilateral middle temporal

gyrus and the bilateral cerebellum (see Table 1, Fig. 1), regions which were only identified in the right hemisphere by Boccia et al. (2019).

Regarding the activations in PFC, medial PFC areas have been consistently reported in previous meta-analyses and qualitative reviews (Cabeza & St Jacques, 2007; Moscovitch et al., 2016; Rugg & Vilberg, 2013), however, lateral PFC activation was not identified by Boccia et al. (2019). Consistent with their established roles in episodic memory retrieval (e.g., memory search and controlled retrieval processes), we found activation in the bilateral dorsolateral PFC, bilateral ventrolateral PFC, and bilateral inferior frontal gyrus (Cabeza & St Jacques, 2007). The ventrolateral PFC is involved with controlled retrieval of information relative to a given cue (Cabeza & St Jacques, 2007; Petrides, 2005). The dorsolateral PFC maintains retrieved autobiographical memory content in working memory and is involved in manipulating and organizing that content (Cabeza & St Jacques, 2007; Petrides, 2005). The inferior frontal gyrus has been associated with several aspects of memory retrieval that are relevant to AM retrieval: retrieval of emotional autobiographical information (Denkova et al., 2013), cognitive control of memory retrieval (Badre, 2008), and semantic retrieval (Bookheimer, 2002; Greenberg et al., 2005; Markowitsch, 1995). All three of these regions have been previously identified as key regions important for autobiographical memory function.

We also found bilateral activation in the inferior parietal lobule (IPL) associated with AM retrieval. The previous meta-analysis (Boccia et al., 2019) also identified parietal activation, in the precuneus and the angular gyrus (a subregion of the IPL). However, whereas the activation in the angular gyrus that we observed extended anteriorly into the IPL (Table 2, Fig. 2), the corresponding activation reported by Boccia et al. did not extend into the IPL. The IPL, also referred to as the ventral parietal cortex (Cabeza et al., 2012), has been noted to play an important role in AM retrieval, and has been associated with successful recollection, source monitoring, and high-confidence responses (Moscovitch et al., 2016). The left and right lateral occipital cortex and right fusiform gyrus activations are consistent with the role of these regions in memory for objects and faces, which are both commonly recalled elements of autobiographical memories (Barbieri et al., 2016; Kuskowski & Pardo, 1999).

Prior research interest has focused most strongly on the role of the hippocampus in AM retrieval. However, the hippocampus is a heterogeneous structure and the anterior and posterior hippocampus have different patterns of connectivity with other regions involved in autobiographical memory as well as different proposed functional roles. One important proposed functional distinction between the anterior and posterior hippocampus is that the anterior hippocampus processes relatively global, coarse, gist-based memory information whereas the posterior hippocampus processes local, fine-grained representations (Poppenk et al., 2013). Another proposed functional difference between these subregions is that the posterior hippocampus exhibits temporally graded activation, with greater activation during retrieval of recent vs. remote events, whereas the anterior hippocampus's activity is not temporally graded, being similarly active for both

recent and remote events and reflecting in part an active construction process that is required for retrieval of all AM memories regardless of age of the memory (Audrain et al., 2022). These two proposals are related in the sense that the retrieval of more remote events is typically more gist-based due to the more rapid forgetting of event details vs. gist-based schematic information, and this in turn would be expected to result in relatively greater anterior vs. posterior hippocampal activation.

To explore this issue, we examined the relative overlap between our meta-analysis results and the anterior and posterior hippocampus (see Supplementary Figure 8). Whereas the bilateral anterior hippocampal ROI overlaps almost completely with the main AM retrieval map, the overlap with the bilateral posterior hippocampus ROI is primarily with the more anterior aspect of this structure, with relatively little overlap from  $y = -34$  to the most posterior part of the bilateral posterior hippocampus. Since many of the studies included in the SDM meta-analysis examined AM retrieval from both recent and remote time periods, the relatively greater meta-analytic activation in the anterior hippocampus vs. the posterior hippocampus may reflect relatively lower posterior hippocampal activation due to decreased activation in this subregion during remote AM retrieval.

As noted above, the default mode network (DMN) is a large-scale brain network implicated in a wide range of cognitive processes involving self-generated thoughts, including AM retrieval (Andrews-Hanna et al., 2014). The DMN is functionally heterogeneous, and studies of the functional organization of the DMN have produced different proposed subdivisions of the DMN into functional subsystems. One highly influential subdivision of the DMN separates it into three interacting subsystems: A “core” subsystem including the anterior medial PFC (amPFC) and the posterior cingulate cortex (PCC), a medial temporal subsystem including the hippocampus, parahippocampal cortex, retrosplenial cortex, posterior inferior parietal lobule/angular gyrus, and ventromedial PFC, and a dorsal medial subsystem including the dorsomedial PFC, temporal pole, lateral temporal cortex and the tempo-parietal junction (Andrews-Hanna et al., 2014). With respect to autobiographical memory, regions in each of these three subsystems play important roles and this tripartite organization of the DMN can help to clarify the functional organization of the multiple regions involved in AM retrieval. For example, the medial temporal subsystem is proposed to mediate episodic memory retrieval and scene construction, both during autobiographical memory retrieval and when individuals are engaged in episodic future thought about potential future events. In the core subsystem, in relation to autobiographical memory, the amPFC has been proposed to mediate self-related processing and emotional salience and the PCC is involved in a variety of types of self-generated thought and integration of information drawn from memory with ongoing memory processing (Andrews-Hanna et al., 2014). In contrast, the dorsal medial subsystem is proposed to mediate self-reflective processes (including evaluation of retrieved memory content), processing of social information, and recollection of context; each of these processes play important roles in AM retrieval (Andrews-Hanna et al., 2014).

To what extent does the AM retrieval network overlap spatially and functionally with the DMN? To help clarify the relationship between our AM retrieval meta-analysis results and the DMN, we determined the spatial overlap between our main SDM map and a voxel-based map of the DMN (see Methods for details). Supplementary Figure 6 shows the overlap between our AM retrieval SDM map and a map of the DMN derived from a separate study of resting state connectivity (Yeo et al., 2011). Notably, the AM retrieval map almost completely contains the DMN map as a subset and extends substantially outside the DMN in several areas. As expected, the largest regions of overlap between the maps correspond to the “core DMN” regions (the most consistently activated regions within the DMN) including the anterior mPFC, posterior cingulate/precuneus, and bilateral angular gyrus. Although the spatial distribution of the DMN varies depending on the method used to define it, our DMN map closely resembles other functional-connectivity based DMN maps in the literature (Alves et al., 2019; Buckner & DiNicola, 2019). For example, this DMN map overlaps almost completely with a DMN map created using the Neurosynth meta-analytic association analysis tool (<https://neurosynth.org>), using the term “default mode” to query 777 associated neuroimaging studies, with the Neurosynth-derived map almost completely contained within our DMN map.

The largest regions where AM-related activations extend outside the DMN map are in the medial and lateral PFC (especially left ventrolateral PFC), bilateral parietal cortex, the medial temporal lobe, and right cerebellum. According to the tripartite division of the DMN, these additional medial temporal lobe and bilateral parietal regional activations correspond to the medial temporal subsystem and the medial and lateral PFC (including the left ventrolateral PFC) correspond to the dorsal medial subsystem. The cerebellum is part of the DMN but is not explicitly included in the three subsystems.

The relationship between the DMN and the variety of different cognitive processes that are associated with it (including AM retrieval) can be viewed as variations on theme, with the core network consistently present, augmented to varying degrees by regions in the dorsal medial and medial temporal subsystems as well as additional regions not closely associated with the DMN, depending on the particular cognitive processes involved, with memory retrieval related regions prominently recruited during AM retrieval. In line with this view, Spreng et al. (2009) proposed that an extended core default mode network contributes to multiple cognitive domains, ranging from autobiographical memory, theory of mind, and future thinking (prospection), with the specific regions in the extended network varying according to task demands.

Within the medial temporal lobe, whereas the DMN map is spatially limited primarily to the hippocampus, the AM retrieval map has a much greater spatial extent and additionally encompasses the amygdala, perirhinal cortex, parahippocampal cortex, and entorhinal cortex. The greater involvement of the medial temporal lobe in AM retrieval is consistent with the roles of each of these regions in memory retrieval, and the recruitment of the amygdala is consistent with the strong emotional content of many autobiographical

memories (Dahlgren et al., 2020). Similarly, the greater involvement of parietal cortex, particularly the angular gyrus, is consistent with the role of this region in recollection (Bonnici et al., 2018), and the greater involvement of the medial and lateral PFC is in line with the roles of these regions in memory search, self-related processing, and monitoring of memory accuracy.

A limitation of neuroimaging studies is that they can only identify correlations between regional activation and AM retrieval and cannot determine whether those activated regions are essential for that cognitive function. Neuropsychological studies of the effects of brain lesions can complement neuroimaging studies by providing evidence that AM retrieval is impaired following lesions to specific regions. There is a remarkable degree of overlap between the regions identified in the current meta-analysis and regions where brain lesions have been reported to impair AM retrieval. The default mode network has been proposed to play a central role in AM retrieval and thus lesions to this network would be predicted to lead to impairments in AM retrieval. Consistent with this prediction, Philippini et al. (2015) examined the relationship between regional brain damage and AM retrieval performance in a large group of patients with a wide variety of lesions distributed across the entire brain, using voxelwise lesion-deficit analysis, and found that lesions to any part of the DMN impaired AM retrieval, with different types of impairment associated with specific regions within the DMN.

Within the DMN, lesions to the hippocampus and its related neocortical structures that comprise the medial temporal lobe memory system (Squire & Zola-Morgan, 1991) have long been known to impair the encoding and retrieval of episodic memory, including retrieval of autobiographical memories (Bayley et al., 2006). Whereas patients with bilateral hippocampal lesions are substantially impaired in the number of autobiographical memories they can recall, patients with ventromedial prefrontal (VMPFC) lesions are specifically impaired in their use of retrieval strategies to retrieve past events (McCormick et al., 2017). The hippocampus and VMPFC have been proposed to work together during AM retrieval with the VMPFC initiating the strategic construction of a mental scene via recruitment of other neocortical areas such as parietal cortex, which are then assembled into a coherent, retrieved scene in the hippocampus (McCormick et al., 2017). Lesions to the VMPFC also have been shown to impair the monitoring of the accuracy of episodic memory retrieval, with such lesions sometimes resulting in a tendency to confabulate (unintentionally generate false memories and fail to realize they are inaccurate) (Gilboa et al., 2009). Although lesions to the parietal lobe are less commonly associated with episodic memory deficits, bilateral lesions to parietal lobe (including the angular gyrus, a core DMN region) have been reported to impair recall of autobiographical memories and impair the amount of retrieved detail and the sense of subjective vivid recollection (Berryhill et al., 2007).

In summary, using the largest sample of neuroimaging studies to date (50 studies), improved study selection criteria, and a new meta-analysis method, the current study found

new regions associated with AM retrieval not previously identified in previous meta-analyses, greater activation extent in other regions previously implicated in AM retrieval, and confirmed the recruitment of several regions previously associated with AM retrieval.

#### 4.2. Effects of AM retrieval tasks

The comparison of studies that used cue-novel vs. cue-rehearsed autobiographical memory retrieval tasks revealed that all the regions of greater activation were regions where cue-novel AM retrieval elicited greater activation (Table 3; Fig. 3), and there were no regions where cue-rehearsed AM retrieval was associated with greater activations than cue-novel AM retrieval. This finding suggests that cue-novel AM retrieval requires additional cognitive processes compared to rehearsed AM retrieval, consistent with findings from Svoboda and Levine (2009). Svoboda and Levine (2009) found suppression of neural activity when AMs had been repeated multiple times compared to when they were retrieved for the first time. Although we observed some differences in regional activation between studies that used cue-rehearsed vs. cue-novel retrieval, these differences were limited in number and in spatial extent, suggesting considerable similarity in the AM retrieval activations elicited across these different retrieval tasks.

The regions more active for cue-novel retrieval included the right angular gyrus (extending into the IPL) and the bilateral frontal pole. As discussed above, the IPL and the angular gyrus have important roles in episodic recollection. Thus, greater activation of the angular gyrus and IPL for cue-novel retrieval may reflect a greater subjective experience of recollection for unrehearsed AMs relative to those that have been recently rehearsed. Transient disruption (via transcranial magnetic stimulation; TMS) and lesions to the angular gyrus have been shown to impair free recall of autobiographical memories but not cued recall (memories cued with specific information from the event) (Berryhill et al., 2007; Bonnici et al., 2018). This finding could indicate that the angular gyrus is more involved with search processes, which may be less engaged when memories are more accessible due to recent prior rehearsal.

Regarding the greater activation we observed in the bilateral frontal pole during cue-novel retrieval, the frontal pole has been suggested to be a key region involved in the episodic retrieval mode, a brain state required for remembering past experiences (LePage et al., 2000). The frontal pole has also been linked with activation of the concept of the self and with self-appraisal. Ochsner et al. (2005) found increased activation of the frontal pole when participants were asked to judge the extent to which various positive and negative adjectives described themselves vs. another person. Cue-novel retrieval of autobiographical memories may require more activation of retrieval-mode regions vs. recently retrieved AMs and may also engage self-referential processes to a greater extent during retrieval (Cabeza & St Jacques, 2007).

### 4.3. Effects of AM control tasks

The current meta-analysis found broadly similar regional activations regardless of whether the control task was visuo-attention or semantic in nature (Table 4, Fig. 4), indicating that the findings of AM retrieval studies are relatively robust to one of the most common variations in control tasks. The only difference associated with differences in control task was observed in a small cluster located in right parahippocampal cortex (extending into the cerebellum and lingual gyrus), representing greater activation for studies using semantic control tasks vs. studies using visuo-attention control tasks. The right parahippocampal cortex has been shown to have an important role in spatial memory (Bohbot et al., 1998). Given that some of the visuo-attention control tasks involved visual search tasks and visual search can elicit increased parahippocampal activation (Mavritsaki et al., 2010), it is possible that the right parahippocampal cortex was more active during these visuo-attention control tasks, which in turn would have been subtracted out from AM retrieval activations.

Although we had predicted that AM retrieval studies that used semantic retrieval tasks as control conditions would be associated with decreased activation in regions associated with semantic memory retrieval (relative to studies that used visuo-attention control tasks), we did not find any regions in which activation was relatively decreased for studies that used semantic tasks vs. visuo-attention tasks. AM retrieval prominently involves the retrieval of semantic memory in addition to episodic memory. Thus, it is possible that the levels of AM retrieval activation in regions involved in semantic memory retrieval were sufficiently strong and robust such that the resulting pattern of activations was affected to a relatively minor degree by subtraction of semantic retrieval control task activation.

### 4.4. Comparison with methods of previous studies

As discussed in the Introduction, the current meta-analysis included several methodological and other improvements relative to previous neuroimaging meta-analyses of AM retrieval. These included the analysis of the largest set of relevant studies to date, use of more rigorous study selection criteria, and the SDM meta-analytic method.

While ALE and SDM are both widely used, valid meta-analysis methods, SDM has some important advantages relative to ALE. An important advantage of SDM over ALE is that it takes into account the effect sizes of the activation coordinates from studies, whereas ALE treats all above-threshold activation coordinates equivalently. SDM uses threshold-free cluster enhancement (TFCE, a method which simulates cluster-wise effects by enhancing voxel-wise statistical values for voxels which are close together) which controls for multiple comparisons without the need for arbitrary cluster size thresholds (Albajes-Eizaguirre et al., 2019; Smith & Nichols, 2009). An additional advantage of the TFCE method used in SDM is that the activation maxima in the resulting activation maps are more interpretable than the activation maps created using cluster-based thresholding methods such as ALE used by Boccia et al. (2019). The spatial

location of local maxima of an activation cluster created by cluster-based thresholding in ALE are more difficult to interpret because they do not directly correspond to locations of maximum activation in the original activation images. In contrast, the local activation maxima in SDM maps do correspond to the location of maximal activation in the summary activation statistic image, retaining more spatial information than cluster-based thresholding methods (Smith & Nichols, 2009). These features of SDM allowed the current meta-analysis to create a more spatially representative summary of activations across studies, taking into account variations in effect sizes and greater ability to detect arbitrarily small regions of activations.

The validity of neuroimaging meta-analyses depends on the use of appropriate inclusion and exclusion criteria, to avoid potential biases and other problems. Comparing the inclusion and exclusion criteria we used in the current study (see Section 2.1 for detailed criteria) to those used by Boccia et al. (2019), of the original 37 papers used by Boccia et al. (2019), we excluded 11 papers due to the issues noted above. We included the remaining 26 papers from Boccia et al. (2019) in the current study, and we included 24 new papers that were not included in the previous meta-analysis. Thus, 48% of the 50 papers in the meta-analysis were new.

Two aspects of the study inclusion criteria used by Boccia et al. (2019) are potentially problematic: the inclusion of studies that reported qualitatively different types of neuroimaging results and the inclusion of multiple contrasts from the same study in a manner that would tend to over-represent the results of individual studies in the analysis results. Regarding the first issue, Boccia et al. (2019) included the results of both univariate analyses and multivariate analyses (partial-least squares analyses; PLS) in their meta-analysis. When using coordinate-based neuroimaging methods, it is considered inappropriate to combine results obtained from qualitatively different types of analyses (e.g., univariate and multivariate analyses) in the same analysis (Müller et al., 2018; Radua, 2020). Multivariate analyses such as PLS produce latent variables which express patterns of brain activity. These patterns of brain activity associated with latent variables are qualitatively different from the voxel-wise activation maps produced by univariate analyses and thus are not appropriate to combine in the same meta-analysis.

Regarding the second issue, Boccia et al. (2019) included multiple contrasts from the same sample such as the results from each latent variable identified in the PLS analysis and similar contrasts within one study (e.g., the inclusion of three extremely similar contrasts from the paper Rabin et al. (2009): episodic autobiographical memory (EAM) > theory of mind (ToM), EAM > ToM construction, and EAM > ToM elaboration) which overrepresents the findings from these studies. Entering additional contrasts from the same sample into a meta-analytic program such as ALE implies to the program that the coordinates of activation identified in each of these contrasts was identified three times, by three separate samples, when it was in fact only identified once by one sample (Müller et al., 2018). Therefore, these coordinates of activation were overrepresented in the analysis, raising the possibility of

statistical dependence and consequent over-representation of these results in the meta-analysis.

A third selection issue concerned the exclusion of papers. [Boccia et al. \(2019\)](#) excluded papers from analysis that specifically elicited emotional autobiographical memories. However, emotional valence is a very common characteristic attribute of autobiographical memories ([Cabeza & St Jacques, 2007](#)) and no specific rationale was provided by [Boccia et al. \(2019\)](#) for excluding studies that explicitly elicited emotional memories. Given the lack of a clear rationale to exclude such studies, we did not exclude them in the current meta-analysis.

Regarding the role of emotion, because the number of studies that explicitly elicited emotional AM retrieval and contrasted this with retrieval of neutral AMs (6 studies) was below the generally advised SDM benchmark of a minimum of 10 studies, we did not directly compare those 6 studies to the other 44 studies that did not explicitly elicit emotional AMs. However, we addressed this issue in a different way, by comparing the main AM retrieval SDM analysis with those of the same analysis conducted again, this time omitting the 6 studies that explicitly involved emotional AM retrieval, allowing the overlap between the two meta-analysis maps to be examined. Excluding the emotional AM retrieval studies slightly reduced the total number of voxels in the SDM map and the original SDM map separated into more clusters (5 vs. 2 for the original SDM map). The increase in the number of clusters was due to the separation of the SDM map into smaller clusters because of the loss of activated voxels in connecting regions, rather than the inclusion of new activated regions.

As can be seen in [Supplementary Figure 7](#), in addition to large areas where the two maps overlapped (in yellow), excluding the emotional AM retrieval studies reduced SDM activation in the bilateral ventrolateral prefrontal cortex, part of the right amygdala, right middle temporal gyrus, the bilateral temporal pole, and the right cerebellum. Of these regions, the amygdala is a key structure involved in emotional responses and emotional memory ([Davis & Whalen, 2001](#)), the temporal pole has roles in both emotional responses and memory for social stimuli ([Olson et al., 2007](#)), and the ventrolateral prefrontal cortex is a key region involved in the regulation and inhibition of emotional responses ([Andrewes & Jenkins, 2019](#)). The specific reductions in SDM activation in these regions may reflect a more prominent role of these regions in the emotional AM retrieval studies that were omitted in this secondary analysis. Alternately, these regional changes in the SDM map may also reflect in part the lower number of total studies contributing to the analysis. Thus, it would be worthwhile to revisit this issue using SDM once a sufficient number of new neuroimaging studies are published on the neural correlates of emotional AM retrieval, which would permit more readily interpretable direct SDM comparisons to be conducted.

An important function of neuroimaging meta-analyses is to provide information used to compare and interpret results from fMRI studies or to create regions of interest to focus fMRI analyses to specific regions with particular functional attributes such as AM memory. Previous meta-analyses such as [Boccia et al. \(2019\)](#) provided lists of the MNI coordinates of the global and local activation maxima of ALE clusters. However,

as discussed above, the TFCE thresholding method used in SDM improves the interpretability of the local activation maxima relative to cluster-based thresholding methods used in ALE. To maximize the usefulness of the current findings, we have made the neuroimaging image SDM output files for all the main analyses publicly available on an online data sharing archive. This will allow any of the SDM maps to be used to create regions of interest for future fMRI studies or to be compared with the findings of other studies or meta-analyses.

#### 4.5. Limitations

Because the SDM method identifies activations that are consistent across many studies, the current meta-analysis necessarily omitted regions active during autobiographical memory retrieval that may be active less frequently or that are active only in particular experimental contexts. In addition, AM retrieval activations change dynamically across time as memory processes shift from initial memory search and access to retrieval of perceptual content, emotion, elaborative processing, memory monitoring, and strategic processes ([Inman, James, Vytal, & Hamann, 2018](#)). The studies summarized here all reported activations across the entire time course of AM memory retrieval rather than reporting separate retrieval phases from different time windows during retrieval. As more neuroimaging studies report temporally specific (or memory-phase specific) brain activations during AM retrieval, these temporally dependent brain activations should be summarized.

Previous meta-analyses of AM retrieval have reported analyses on the difference in neural activations between remote (more than 5 years) and recent (less than 1 year) AM retrieval ([Boccia et al., 2019](#)). The present analysis did not report an updated account of these analyses because, after updating the selection criteria to be more methodologically rigorous, there were too few studies in each category to conduct an SDM analysis. After excluding analyses using multivariate techniques such as PLS, there were only 4 remote studies, which is too few to analyze with current CBMA techniques.

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## 5. Conclusions

In conclusion, the current study provides an updated and improved characterization of the neural correlates of autobiographical memory retrieval. We confirmed the recruitment of multiple regions previously identified as core AM retrieval regions, including the prefrontal cortex (PFC), hippocampus and parahippocampal cortex, retrosplenial cortex and posterior cingulate, and angular gyrus, and also identified additional regions including the bilateral inferior parietal lobule and a greater extent of PFC involvement, including lateral PFC activation. There were few differences between cue-rehearsed and cue-novel retrieval, suggesting considerable similarity in the AM retrieval activations elicited across these different retrieval tasks. Similarly, AM retrieval activations were broadly similar regardless of whether the control task was visuo-attention or semantic in nature suggesting that the findings of AM retrieval studies are relatively robust to some

commonly used variations in control tasks. Future research should expand upon these findings to characterize AM retrieval dynamics across the time course of retrieval and the role of other factors such as emotional valence and memory remoteness.

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### CRedit author statement

**Susie Shepardson:** Conceptualization, Methodology, Formal analysis, Investigation, Writing–Original Draft, Review & Editing **Kristina Dahlgren:** Conceptualization, Methodology, Formal analysis, Investigation, Writing–Original Draft, Review & Editing **Stephan Hamann:** Conceptualization, Investigation, Methodology, Writing–Original Draft, Review & Editing, Supervision.

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### Open practices section

The study in this article earned Open Data badge for transparent practices. The data for the study are available at: <https://data.mendeley.com/datasets/w9p86fndr7>.

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### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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### Supplementary data

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