

Review

The functional neuroanatomy of autobiographical memory: A meta-analysis

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Abstract

Autobiographical memory (AM) entails a complex set of operations, including episodic memory, self-reflection, emotion, visual imagery, attention, executive functions, and semantic processes. The heterogeneous nature of AM poses significant challenges in capturing its behavioral and neuroanatomical correlates. Investigators have recently turned their attention to the functional neuroanatomy of AM. We used the effect-location method of meta-analysis to analyze data from 24 functional imaging studies of AM. The results indicated a core neural network of left-lateralized regions, including the medial and ventrolateral prefrontal, medial and lateral temporal and retrosplenial/posterior cingulate cortices, the temporoparietal junction and the cerebellum. Secondary and tertiary regions, less frequently reported in imaging studies of AM, are also identified. We examined the neural correlates of putative component processes in AM, including, executive functions, self-reflection, episodic remembering and visuospatial processing. We also separately analyzed the effect of select variables on the AM network across individual studies, including memory age, qualitative factors (personal significance, level of detail and vividness), semantic and emotional content, and the effect of reference conditions. We found that memory age effects on medial temporal lobe structures may be modulated by qualitative aspects of memory. Studies using rest as a control task masked process-specific components of the AM neural network. Our findings support a neural distinction between episodic and semantic memory in AM. Finally, emotional events produced a shift in lateralization of the AM network with activation observed in emotion-centered regions and deactivation (or lack of activation) observed in regions associated with cognitive processes.

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Contents

1. Introduction	2190
2. Methods	2191
2.1. Inclusion and exclusion criteria	2191
2.2. Analysis and structure of figure and tables	2191
2.2.1. Analysis	2191
2.2.2. Figure	2191
2.2.3. Tables	2191
3. Results and discussion	2192
3.1. An overview of regional activation during autobiographical remembering	2192
3.2. The prefrontal cortex	2195
3.2.1. The reconstruction of autobiographical memories	2195

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3.2.2.	Self-referential processing: the medial prefrontal cortex	2196
3.3.	The temporal lobes	2196
3.3.1.	Event retrieval: the hippocampus and functional associations	2196
3.3.2.	Age of memory and activation in the medial temporal lobe	2197
3.3.3.	Semantic memory processes in autobiographical memory: the lateral temporal cortex and related regions	2199
3.4.	Dissociating episodic from semantic autobiographical memory	2200
3.4.1.	Direct comparison of episodic to semantic autobiographical memory	2200
3.4.2.	Contrasting short and long retrieval times: implications for episodic and semantic autobiographical memory	2200
3.5.	Visuospatial imagery in autobiographical memory	2201
3.6.	Emotion and autobiographical re-experiencing	2201
3.7.	Network approaches to the study of autobiographical remembering	2202
4.	Summary and conclusions	2203
	Acknowledgements	2204
	References	2205

1. Introduction

Ecologically valid paradigms have become increasingly popular in the study of cognitive processes, both at the behavioral and at the neural levels. A growing number of studies, for example, have investigated real-life autobiographical memory (AM). AM paradigms are different from typical laboratory memory tasks that require the encoding and retrieval of experimenter-generated stimuli. In studies of AM, participants instead recall events from their own history that are more distinct and of greater personal significance than are laboratory stimuli, promoting the subjective re-experiencing of emotions, sensory characteristics and temporal, spatial and perceptual context of events. Recent advances in neuroimaging technology have added to our understanding of memory and cognitive processes and the neural correlates engaged both by traditional laboratory and ecologically valid paradigms. In the present meta-analysis, we review functional neuroimaging studies of AM, examining several key variables that influence brain activation patterns in AM retrieval and the functional processes that underlie AM recollection.

Due to the multi-modal nature of AM retrieval, several functional domains are engaged during recollection, such that no single imaging study can capture the entire network involved in autobiographical recollection. Moreover, interpretation is affected by the heterogeneity of target and reference tasks across AM studies. Nonetheless, the number of AM imaging studies has grown to the point where it is possible, through meta-analysis, to identify shared patterns of brain activation engaged by AM as well as to examine the influence of task variables on this pattern.

Interpretation of AM functional neuroimaging data is affected by the specificity of AM retrieval cues and information about the quality of recollective experience. There is a continuum of specificity of retrieval cues for eliciting AM across imaging studies, ranging from very low specificity, where participants are simply instructed to retrieve an AM (Andreasen et al., 1995, 1999; Gemar, Kapur, Segal, Brown, & Houle, 1996)¹ to arbitrary word cues (Conway et al., 1999; Graham,

Lee, Brett, & Patterson, 2003; Lars Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002)¹ to very high specificity, where cues are culled from interviews conducted prior to scanning, the most common method (e.g., Addis, Moscovitch, Crawley, & McAndrews, 2004; Maguire & Mummery, 1999)¹. Although the pre-scan interview technique has been criticized due to the effect of re-encoding the episode (Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2002), similar results are obtained when this effect is experimentally controlled (Maguire, Vargha-Khadem, & Mishkin, 2001; Ryan et al., 2001)¹. A small number of studies have further increased the specificity of retrieval cues via audio or photographic records of naturalistically occurring events (Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Levine et al., 2004)¹ or manufactured life-like events (Burgess, Maguire, Spiers, & O'Keefe, 2001; Cabeza et al., 2004¹; Fujii et al., 2004). Qualitative ratings can be used to probe the effect of personal importance, amount of detail recalled, and vividness on activation patterns (e.g., Addis, Moscovitch et al., 2004; Gilboa et al., 2004; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; Ryan et al., 2001)¹.

The present analysis builds on two earlier review papers examining neuroimaging studies of AM (Conway et al., 2002; Maguire, 2001). In an initial review of the first 11 studies of AM conducted using hemodynamic imaging methods (PET, fMRI), Maguire (2001) reported a predominantly left lateralized and medial pattern of brain activation, including the retrosplenial/posterior cingulate cortex, medial temporal regions, temporoparietal junction, medial prefrontal cortex, temporopolar cortex and cerebellum. Conway et al. (2002) examined the relationship between patterns of hemispheric activation and AM task requirements. This review included electrophysiological as well as hemodynamic studies, allowing for greater specification of the temporal and spatial aspects of AM. Conway concluded that the left lateralized pattern of activation may reflect the initial search process of general autobiographical knowledge. By contrast, on-line re-experiencing of the event, which occurs later in the retrieval process, was thought to engage the right cerebral hemisphere, especially the posterior cortical regions, a finding that has since been replicated (see section on visuospatial processing below).

In the present study, meta-analysis was used to investigate the current corpus of AM PET and fMRI studies, which has

¹ See Appendix A for cross-reference.

doubled in size since the publication of Maguire and Conway's initial review articles. We examine the influence of emotion on AM retrieval, as well as variables that may influence differences in neural activation in response to recent and remote events, such as importance of the event, level of detail, and the vividness of the recollection. We also examine the impact of different types of reference conditions (e.g., rest, memory conditions) and information processing (semantic memory) on neural activation observed in response to autobiographical remembering. Although our findings are largely consistent with those reported in earlier reviews, our analysis reveals novel findings and insights made possible by the large scale efforts applied to the examination of AM in recent years.

2. Methods

We used the "effect-location" method of meta-analysis (see, Fox, Parsons, & Lancaster, 1998) where the parameter of interest is the location rather than the magnitude of the effect. We included published studies using hemodynamic methods, such as PET and fMRI ($n=24$). Electrophysiological studies ($n=3$) were not included in the figure and tables but are reviewed in the text.

2.1. Inclusion and exclusion criteria

English-language articles published prior to January 2004 were garnered from searches using *Medline*, *PsycINFO*, and *Science Citation Index*. The reference section of each article was examined for further studies. Several authors of published studies or relevant conference presentations were contacted to obtain data from unpublished work that was in press. The following criteria were used to select studies for inclusion in the AM meta-analysis:

- (1) Scanning occurred at the stage of memory retrieval, and was assumed to capture the brain activation associated with these retrieval processes.
- (2) Retrieval involved the recollection of episodic AMs that were personally experienced, relatively remote (i.e., occurring at least several weeks before the scanning session), and specific in time and in place (for exception, see Maddock, Garrett, & Buonocore, 2001)¹.
- (3) Each study included at least one contrast in which a reference task was compared with the AM condition. Our definition of a statistical contrast was broad and encompassed a range of statistical comparisons. The majority of the studies contrasted activation patterns associated with a target task (i.e., AM retrieval) to those associated with a reference or control task (e.g., rest, semantic memory). Brain-behavior correlations and multivariate analyses were also acceptable, although reported in a few studies only (Addis, Moscovitch et al., 2004; Levine et al., 2004; Maguire, Mummery, & Büchel, 2000; Maguire, Vargha-Khadem & Mishkin, 2001)¹.

Our analysis of AM imaging studies is based on 243 participants (excluding repeat analyses of the same group of participants across published studies). The studies included in our analysis involved healthy adults with no pre-existing psychiatric or medical illnesses known to affect memory or cognitive functioning. Studies that compared patient and healthy control groups were included only if they reported experimental effects exclusive to control participants that met our other inclusion criteria.

2.2. Analysis and structure of figure and tables

2.2.1. Analysis

Our analysis was based on examination of patterns of activation as represented in a figure and several tables. Only statistically significant activations or deactivations were included. Region of interest analyses or studies that did not report coordinates for the entire brain were included, although there

were only two such studies (Conway et al., 1999; Gilboa et al., 2004)¹. Coordinates in the figure and tables are reported in standard stereotaxic space, as defined by Talairach and Tournoux (1988). For studies reporting findings in MNI space, we used a publicly available non-linear algorithm to transform the coordinates to Talairach space (for details see <http://www.mrc-cbu.cam.ac.uk/Imaging/Common/mnispace.shtml>).

All AM studies included one target condition of event recollection and usually multiple reference conditions involving different cognitive processes. For the purpose of avoiding over-representation of any one study in the AM neural network (seen in Fig. 1), we depicted only one contrast per study. Contrasts were selected on the basis of having a reference condition that revealed the widest pattern of activation, hence revealing as much of the AM network as possible. Although AM studies that manipulated the remoteness of the event or emotional content were the most likely to use a closely matched comparison condition, they were nonetheless depicted in the omnibus AM figure. When multiple studies used the same group of participants, only one contrast, depicting the widest activation pattern (usually the earlier study), was selected for the figure.

In contrast to Fig. 1, all AM retrieval contrasts per study were depicted or considered in the tables (see Tables 1–5) as each contrast provided additional information and allowed for examination of the contribution of individual variables to the overall AM network (e.g., different reference conditions, remoteness of the event, and emotional content, depicted in Tables 3–5, respectively). In emotion AM studies that included more than one emotional event involving different valences (e.g., happy memory and sad memory) as the target conditions, the contrast for each emotion type (valence) is shown. The coordinates represented in Fig. 1 were used to calculate ratios in order to quantify laterality of activation patterns (see Section 3 for detailed explanation).

2.2.2. Figure

Fig. 1 summarizes AM retrieval activation patterns. The first row (see a and b) shows right and left lateral views of the whole brain. Lateral activations were defined as coordinates that were greater than +20 mms (right-lateralized) and less than –20 mms (left-lateralized) on the x -axis. Regions shown in this plane include lateral frontal, parietal, temporal, insular and occipital cortices, and the cerebellum. The second row (see c and d) shows right and left medial views. Coordinates were shown in the right medial view if they were between 0 and +20 mms and left medial view if they were between 0 and –20 mms on the x -axis, inclusive. Coordinates that represented bilateral activation and fell directly on the $x=0$ plane were represented in both medial views. Regions shown in the medial plane include those in the frontal, parietal, and occipital lobes, cerebellum, thalamus and brainstem. The third row of Fig. 1 (see e and f) shows right and left lateral-subcortical views in the $x=\pm 28$ mms plane. These views were chosen in order to depict activation of structures within the medial temporal lobes, the amygdala and basal ganglia.

2.2.3. Tables

Tables 2 through 5 are modeled on those used in a review paper of neuroimaging studies of cognition (Cabeza & Nyberg, 2000). In each table, the first column lists the studies, followed by a general abbreviated description of the contrast in the second column. For studies where activation for the same participants was published more than once, additional contrasts from more recent studies provided incremental information and were included on this basis (see above). In this regard, the tables are more inclusive than is the figure. The remaining columns show all the statistically significant activations reported in response to the contrasts. Brodmann areas (BA) were used as headings to represent regional activation. For studies that did not provide BAs, coordinates were plotted in the Talairach and Tournoux (1988) atlas to attain this information.

Table 1 provides an overview of the number of AM studies (all contrasts were considered per study) reporting activation for each brain region (shown in first column). It illustrates the core AM network as well as other regions less frequently activated but nonetheless supporting AM. The BAs representing each of these regions are listed in the second column followed by the number of studies that reported left, right and medial patterns of activation, and the total number of studies per brain region. The studies are listed in the last column,

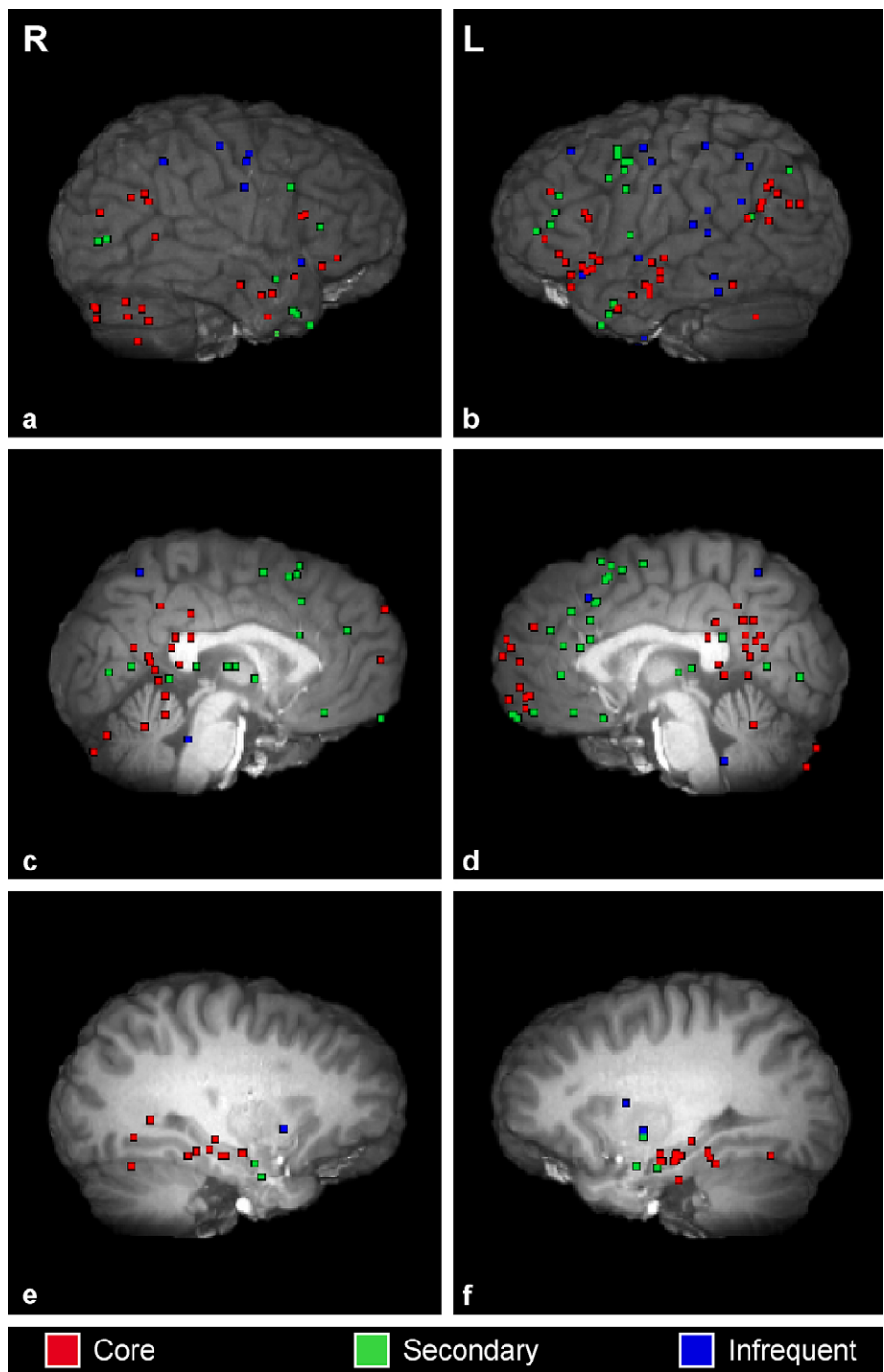


Fig. 1. Significant peaks of activation reported across imaging studies of AM. Activations in core, secondary and infrequently reported regions are depicted across right (left column) and left (right column) lateral, medial and lateral subcortical planes.

each represented by a number (see Appendix A for the references associated with each number). The remaining tables depict regional activation in response to individual contrasts. Table 2 shows regional activation reported across all AM retrieval studies with the exception of those that manipulated either emotional content, shown in Table 5, or remoteness of the event, shown in Table 4, in the target condition. All contrasts are represented only once across tables with the exception of Table 3, which depicts all contrasts involving rest as the reference condition regardless of target condition.

3. Results and discussion

3.1. An overview of regional activation during autobiographical remembering

As illustrated in Fig. 1 and Tables 1 and 2, AM engages a network of predominately left-lateralized and medial brain regions.

Table 1
Brain regions activated across imaging studies of autobiographical memory

Brain regions	BA	Left	Right	Medial ($x=0$)	Total	Studies
Frontal						
DL PFC	9, 46, 9/46	4	2	~	6*	[5,6,11,12,20,24]
VL PFC	45, 44, 47	11	6	~	13**	[3,5,6,11,12,13,15,19,20,22,23,24]
Sup. DM PFC	Medial 6	5	4	1	8*	[6,7,11,12,19,22,23,24]
Sup. DL PFC	Lateral 6	6	0	~	6*	[3,6,12,19,23,24]
Med. PFC	9, 10	12	2	2	15**	[2,5,6,9,10,11,13,14,16,17,18,21,22,23,24]
OFC	11, 13	2	4	~	6*	[3,12,20,21,22,23]
Eye fields	8	2	0	~	2	[12,13]
Motor	4	4	3	~	4	[3,9,12,24]
Cingulate/retrosplenial						
Anterior cingulate	25, 32, 24	7	2	2	8*	[3,4,5,8,9,10,19,20]
Retrospl./post-cing.	29, 30, 23, 31	10	6	4	17**	[2,3,5,7,9,10,11,12,13,14,16,17,19,20,21,23,24]
Parietal/temporal						
Precuneus	Medial 7	2	1	1	3	[9,19,21]
Lateral parietal	Lateral 7, 40	4	1	~	4	[4,12,24,23]
Temporoparietal junc.	39	10	4	~	10**	[2,5,6,9,10,11,13,16,17,22]
Temporal						
MTL	HC, 34, 27, 28, 35, 36/37	13	9	~	14**	[2,5,9,11,13,14,15,16,17,18,20,21,23,24]
Fusiform	37	3	3	~	4	[9,20,23,24]
Mid. lateral temporal	21	11	5	~	14**	[2,3,6,7,9,10,12,13,16,17,19,20,23,24]
Sup. lateral temporal	22, 41	2	3	~	3	[3,9,19]
Inf. lateral temporal	20	3	1	~	4	[3,9,11,13]
Temporal pole	38	4	5	~	7*	[3,7,13,16,17,23]
Insula	~	1	2	~	3	[7,9,19]
Occipital						
Occipital lobe	19, 18, 17	5	4	1	8*	[2,5,6,8,9,12,20,23]
Other						
Amygdala	~	4	2	~	5*	[7,14,19,20,23]
Basal ganglia	~	2	2	~	4	[3,9,12,20]
Thalamus	~	3	5	1	8*	[2,3,4,11,12,19,24]
Brain stem	~	1	1	0	2	[2,11]
Cerebellum	~	7	11	0	13**	[3,4,7,9,11,12,13,17,19,20,22,23,24]

Abbreviations: (DL) dorsolateral; (DM) dorsomedial; (Inf.) inferior; (junc.) junction; (Med.) medial; (Mid.) middle; (MTL) medial temporal lobe; (OFC) orbitofrontal cortex; (PFC) prefrontal cortex; (Retrospl./post-cing.) retrosplenial/posterior cingulate; (Sup.) superior; (VL) ventrolateral.

Note: **Core AM regions; *secondary AM regions; & remaining regions that were infrequently activated across studies.

In order to quantify the degree of laterality across imaging studies of AM, we calculated a left-relative-to-right lateral ratio across lateral cortical, medial and lateral subcortical coordinates that are depicted, respectively, in the panels (a–f) of Fig. 1 (a ratio of 1 represents equal left and right hemispheric representation). Medial coordinates falling on the $x=0$ axis were excluded from this calculation. The lateral cortical activation ratio was 1.81, indicating that nearly twice as many coordinates were located in the left hemisphere as in the right hemisphere. The medial ratio was 1.73 and the lateral subcortical ratio was 1.46. These ratios suggest that left lateral activation was greatest in the cortex, followed by the medial regions and lateral subcortical structures, such as the amygdala, hippocampal complex and basal ganglia. Cerebellar activation was predominantly right-lateralized. Given the crossed connectivity between the cerebral and cerebellar cortices (Schmahmann & Pandya, 1997), we recalculated the left relative to right index with cerebellar activations coded opposite to those of the cerebral cortex (i.e., left cerebellar activation was coded as right cortical activation and vice versa). The resulting index was 1.92. AM imaging paradigms to date rely predominantly on the verbal presentation of stimuli (auditory or text

cues) which, along with other factors (e.g., semantic memory processes, retrieval effort), may have contributed to the left-lateralized pattern of activation, a point to which we return to below in our discussion of regional activation patterns.

A consistent network of regions activated across AM imaging studies included the medial and ventrolateral prefrontal cortices, medial and lateral temporal cortices, temporoparietal junction, retrosplenial/posterior cingulate cortex, and the cerebellum (see Table 1). These regions were activated in at least 10 (or approximately half) of the studies (shown in red in Fig. 1) and are identified here as belonging to a “core” AM network. This pattern of brain activation is similar to the one reported in an earlier review of AM retrieval by Maguire (2001), except that we found the temporopolar cortex to be less consistently activated and the ventrolateral prefrontal and lateral temporal cortices to be part of the core AM network (see Table 1).

Activation was also observed in several additional brain regions across studies but on a less consistent basis. Because these regions were activated in approximately a quarter to a third (in five or more) of the reviewed studies, we define them as “secondary” to the core AM network. These regions included the

Table 2
Brain regions activated in response to assorted contrasts across standard autobiographical memory studies

AM studies		Frontal												Cingulate								Temporal								Parietal				Occipital			Subcortical				
Study	Contrast	10	9	46	44	6	45	47	11	25	8	4	25	32	24	23	31	29	30	ins	38	20	21	22	41	37	mtl	123	7	40	39	19	18	17	Ag	bg	th	cb	bst		
Andreasen 95-1	am-sem					◁			●			◇					∞							◇																	
Andreasen 95-2	am-rest							▷				◇			∞						▶	▷	▶	▷											◁	●	∞				
Andreasen 99-1	am-rest									○				○	∞																					○	●				
Andreasen 99-1	am-rest																													◁							◇				
Gemar 96-3	am neut-rest														∞																		●								
Conway 99-1	am-am emot		◁			○	◇	▷															▷								▷		▷								
Conway 99-1	am-am emot		○			▷																																			
Maguire 99	am-pronoun/1 syllable	○															○				▷		▷				▷				◇										
Maguire 00	am-pronoun/1 syllable	○															∞				◇		▷				▷				▷								▶		
Maguire 01a	am-am gen	∞																									▷														
Ryan 01-1	am-sem/rest		▷	▷		▷	▶	▷				◇					∞						▷				▷	◇			▷						●	▶			
Ryan 01-1	am-sem/rest		●			∞																																			
Maddock 01-1	am		▷	▷		▷	▷	▷	∞		▷	◇					∞	∞					▷								◇		∞		▷	●	◇				
Maddock 01-1	sem-fictitious																																								
Maddock 01-1	am					∞																																	●		
Maddock 01-1	sem-fictitious																																								
Nyberg 02	am-am emot		○			●		▷	○																							▷							▶		
Maguire 03a-1	am-pronoun/1 syllable	○			▶												○				▶	▷	▷				◇				▷	▷							▶		
Maguire 03b-1	am-sem	∞																	○							◇															
Graham 03-1	am-sem	○	●												∞		○						◇									▷									
Levine 04	am-sem/am gen/other	○	▶			○		▷										∞									▶				◇					∞	○		●		
Gilboa 04-1	am-fictitious		○					▷												○	▷						◇	◇		∞		◇					○	▷			
Gilboa 04-2	am-am gen											▷			○	○				▷				▷			◇		●				▷			▶		▷			
Gilboa 04-2	am-am gen																										◇							●							
Addis 04-1	am-sem	○															∞		●				▷				◇				▷	▷				●			○		
Cabeza 04-1	am/emot			▶				◇								○											◇				◇		∞								
Cabeza 04-1	(common coord)																									◇															
Cabeza 04-2	am-am emot	○															●										◇						○								

Symbols and abbreviations in Tables 2–5: (◁) left lateral; (▷) right lateral; (◇) bilateral lateral; (○) left medial; (●) right medial; (∞) bilateral medial; (Ag) amygdala; (am) autobiographical memory; (bg) basal ganglia; (bst) brainstem; (cb) cerebellum; (coord) coordinates; (covar.) covariance; (emot) emotion; (gen) general; (ins) insula; (mtl) medial temporal lobe; (neg) negative; (neut) neutral; (pos) positive; (sem) semantic; (th) thalamus. *Note:* Anterior cingulate: BA 25, 32, 24; retrosplenial/posterior cingulate: BA 23, 31, 29, 30.

dorsolateral prefrontal cortex (BA 9, 9/46, 46), superior medial and superior lateral cortex (BA 6), anterior cingulate (BA 25, 32, 24), medial orbitofrontal, temporopolar and occipital cortices, thalamus and amygdala (shown in green in Fig. 1; see also Table 1). Regions that were reported infrequently (in less than five) across AM studies included the frontal eye fields, motor cortex, medial (precuneus) and lateral parietal cortices, fusiform gyrus, superior and inferior lateral temporal cortices, insula, basal ganglia and brain stem (shown in blue in Fig. 1; see also Table 1). For the present analysis, we refer to these regions as tertiary to the core AM network. Although the frequency with which specific regions are reported across studies attests to their importance in the AM network, other factors such as those unique to experimental paradigms or the neuroimaging milieu, can modulate regional activation as well.

The widespread activation patterns observed across AM studies suggests the recruitment of regions involved in domain-specific processes unique to phenomenal re-experiencing, such as perceptual and emotional processes, as well as domain-general processes required for successful memory retrieval, such as working memory, attention, and basic mnemonic processes. In the sections that follow, we examine the contribution of these processes to AM by highlighting key differences in activation and methodology across studies in an attempt to better understand the core and extended pattern of regional activation. We also contrast studies that have manipulated a particular cognitive construct (e.g., remoteness of event recalled, emotional or semantic content), to reveal an AM network that engages both central memory processes and sub-networks of cognitive and emotional processing, as well as accounting for some of the inconsistencies in regional activation across studies. For ease of presentation, our review is organized according to brain region. This is not, however, meant to endorse a modular approach to AM. On the contrary, we regard these regions as part of an interactive network, a point which will be elaborated later in this paper.

3.2. *The prefrontal cortex*

In line with previous reviews of AM imaging studies (Conway et al., 2002; Maguire, 2001), nearly all studies of AM retrieval reported activation of the prefrontal cortex. In one of the earliest published functional neuroimaging studies of memory, using PET with an *N* of 2, Tulving (1989) reported increased cerebral blood flow in the frontal lobes in response to thinking about events that were personally experienced. His hypothesis that this activation was important to the conscious experience of re-experiencing, explored in depth using laboratory materials (Tulving, Kapur, Craik, Moscovitch, & Houle, 1994), now receives strong support from the AM functional neuroimaging literature. The prefrontal cortex is involved in numerous functions related to AM retrieval, chiefly reconstructive mnemonic processes and self-referential processes.

3.2.1. *The reconstruction of autobiographical memories*

The majority of AM studies that reported frontal lobe activation showed predominantly left-lateralized activation, with

some activation evident in the right hemisphere (see Fig. 1; Tables 1 and 2). Activation in the ventrolateral prefrontal cortex, a core region in the AM network, was more frequently reported in the left hemisphere (see Table 1). Ventrolateral prefrontal activity has been associated with strategic retrieval, verification, and selection of information from posterior cortical association areas (Fletcher & Henson, 2001; Henson, Shallice, & Dolan, 1999; Petrides, 2002), processes relevant to AM retrieval. It is also observed when participants are required to maintain search results online (D'Esposito, Postle, Ballard, & Lease, 1999; Wagner, Maril, Bjork, & Schacter, 2001). Activity in this region may be material specific, with the left hemisphere engaged by verbal retrieval (a region also activated in generative retrieval processes during semantic tasks) and the right hemisphere engaged by the retrieval of images (see Petrides, 2002).

In addition to the ventrolateral prefrontal cortex, studies using standard laboratory stimuli implicate the dorsolateral prefrontal cortices, the superior medial and lateral prefrontal cortex, and the dorsal component of anterior cingulate, and the frontopolar cortex in memory reconstruction (Cabeza & Nyberg, 2000; Duncan & Owen, 2000; Fletcher & Henson, 2001). These regions, however, were classified as secondary in the AM network (see Table 1). In a systematic review of prefrontal activations in autobiographical versus laboratory-based studies, Gilboa (2004) suggested that these dorsal regions, particularly in the right hemisphere, were more likely to be activated by laboratory stimuli because these require more monitoring relative to self-relevant and unique autobiographical experiences (see also King, Hartley, Spiers, Maguire, & Burgess, 2005). Accordingly, studies of more mundane, laboratory-like autobiographical events show dorsal prefrontal activation (Burgess et al., 2001; Cabeza et al., 2004¹; Levine et al., 2004¹). In a similar vein, well-rehearsed events that are readily accessible during AM experiments may not place high demands on monitoring processes. Familiarity and repeated exposure are known to affect activation patterns in episodic memory paradigms and to reduce activation in the dorsolateral prefrontal region during retrieval (Andreasen, 1995a, 1995b; Jansma, Ramsey, Slagter, & Kahn, 2001; Jessen et al., 2001).

The orbitofrontal cortex, strongly interconnected with the medial temporal lobes (Aggleton & Brown, 1999; Suzuki, 1996; Suzuki & Amaral, 1994) was identified as secondary to the core neural network (see Table 1), with activation reported bilaterally, right greater than left. Animal work suggests that damage to the orbitofrontal cortex impairs recognition memory (for review, see Petrides, 2000).

Numerous studies also reported medial and right lateralized activation in the cerebellum (see Table 1), another key region in the core neural signature of AM. The cerebellum is connected to the dorsolateral prefrontal cortex via the cerebello-thalamocortical pathway (Middleton & Strick, 1994, 2001). Neuroimaging and patient studies have implicated the cerebellum in a host of cognitive tasks; particularly in executive functions (see Cabeza & Nyberg, 2000; Grafman et al., 1992; Schmahmann & Sherman, 1998; Vokaer et al., 2002).

3.2.2. Self-referential processing: the medial prefrontal cortex

Self-referential processing, considered a key element of AM, provides a basis for the development of AM over time (Howe & Courage, 1997) and is central to the social and directive function of AM (Conway, 2003). Indeed, Conway and Pleydell-Pearce (2000) describe the role of the “self-memory system” in AM as the organising force of other lower level memory systems and processes.

Recent studies of self-referential processing have reported activation in medial frontal regions (BA 9, 10) when self-referential or internally orientated processing is manipulated (e.g., Craik et al., 1999; Gusnard, Akbudak, Shulman, & Raichle, 2001; Kelley et al., 2002). In a similar vein, imaging studies examining theory of mind have consistently reported medial prefrontal activation (Fletcher et al., 1995; Gallagher & Frith, 2003). This locus of activation has been attributed to the act of inferring other people’s mental states by their actions while recognizing that their mental states are different from our own (Frith & Frith, 1999). Activation in the medial prefrontal region was also reliably observed in the vast majority of AM studies, making this region an obvious component of the core AM neural network, with a striking degree of left-lateralization (see Table 1). Indeed, activation in this region distinguished AM from laboratory-based episodic memory imaging studies (Cabeza et al., 2004¹; Gilboa, 2004).

Studies of self-referential processing typically rely on judgments of self-knowledge or personal semantic information (e.g., personality traits), although these tasks do not exclude episodic recollection. AM paradigms, in contrast, emphasize episodic recollection, with personal semantic processing almost certainly present, but not primary, raising the question as to whether the medial prefrontal activation is due to episodic memory, personal semantic memory, or both. This question can be addressed by studies that included both semantic AM and episodic AM conditions (Addis, McIntosh, Moscovitch, Crawley, & McAndrews, 2004; Addis, Moscovitch et al., 2004; Gilboa et al., 2004; Levine et al., 2004; Maguire & Frith, 2003a; Maguire & Mummery, 1999)¹. In these studies, medial prefrontal activation was significantly greater in the episodic AM condition relative to the personal semantic condition (although the personal semantic condition also showed significant medial prefrontal activation relative to the control condition), suggesting that, at the very least, medial prefrontal activation is enhanced by autobiographical recollection. A stronger hypothesis would state that medial prefrontal activation in self-referential processing is due to contamination from autobiographical recollection. Support for the relation of autobiographical recollection to the medial prefrontal cortex can be drawn from this region’s connectivity to medial temporal and diencephalic regions (critically involved in recollection) via the cingulum bundle (Petrides & Pandya, 2002).

Lesion studies in humans would not have predicted the robust left medial prefrontal activation. Unilateral damage along the medial prefrontal wall is rare, and bilateral damage here causes severe deficits in arousal and initiation of behavior, possibly obscuring more subtle lesion effects. On the other hand, the functional neuroimaging findings, while reliable across stud-

ies, do not indicate the left medial frontal region’s necessity for AM. It is possible that this finding may signal co-activation with connected posteromedial temporal lobe regions engaged by mnemonic stimuli, coincidental to but not *necessary* for the task. An examination of differential directional influence between medial prefrontal and medial temporal structures using multivariate analyses may clarify this issue.

Finally, studies that have contrasted AM retrieval exclusively with rest have been less successful in capturing medial prefrontal activation (see Table 3). Participants who have been debriefed after a resting state have reported re-experiencing past events and planning future activities during this baseline condition (Andreasen et al., 1995¹; Binder et al., 1999; Gusnard et al., 2001; Mazoyer et al., 2001). As the resting state has been shown to activate regions similar to those observed during autobiographical remembering (Andreasen et al., 1995¹; Binder et al., 1999; Mazoyer et al., 2001; McGuire, Paulesu, Frackowiak, & Frith, 1996; Newman, Twieg, & Carpenter, 2001; Stark & Squire, 2000) caution is warranted in attributing activations, deactivations or the absence of activation to the AM task when rest is used as a comparison condition.

3.3. The temporal lobes

3.3.1. Event retrieval: the hippocampus and functional associations

More than half of the AM imaging studies reported activation in the medial temporal lobe region (MTL; see Tables 1 and 2), a region we identified as a core contributor to the AM network. In the present analysis, MTL refers to the hippocampus, parahippocampus, perirhinal and entorhinal cortices, whereas reference to the hippocampus is exclusive. All but two of the AM retrieval studies reporting MTL activation, in which only the parahippocampus was activated (Levine et al., 2004; Niki & Luo, 2002)¹, showed hippocampal activity. For the most part, related MTL structures were activated only in conjunction with the hippocampus (Addis, Moscovitch et al., 2004; Cabeza et al., 2004; Gilboa et al., 2004; Maguire & Mummery, 1999; Maguire et al., 2000; Maguire, Henson et al., 2001; Maguire, Vargha-Khadem et al., 2001; Piefke et al., 2003)¹. We therefore consider MTL and hippocampal activation together, followed by interpretation of thalamic, retrosplenial/posterior cingulate, and temporopolar activation.

It is well established in the patient literature that the hippocampus plays an important role in episodic memory, particularly during the encoding phase (for review, see Spiers, Maguire, & Burgess, 2001). What remains controversial is the role of the hippocampus in episodic memory retrieval, particularly long-term retrieval (see below). This issue appears to also be reflected in the imaging literature, as it is unclear why activation in the hippocampus is not more consistently observed in the AM imaging studies as well as in laboratory based studies of memory retrieval. Moreover, within the context of neuroimaging, technical difficulties inherent in the ability of hemodynamic methods to image the hippocampus may have a role to play in the inconsistent pattern of activation reported across studies (Brewer & Moghekar, 2002).

We identified several additional key variables that may have contributed to the inconsistent pattern of MTL activation observed during AM retrieval. For example, AM studies that used rest as the reference condition reported no MTL activation for these contrasts (see Table 3). Rest itself may activate the MTL (Binder et al., 1999; Stark & Squire, 2001), altering or masking activation of this region within the target condition as a result (Stark & Squire, 2001). Comparison conditions that involved memory recall (e.g., semantic memory, episodic memory or AM), used frequently in AM imaging studies may also have masked patterns of MTL involvement, although this was not always the case (Maguire & Frith, 2003a; Maguire, Henson et al., 2001; Maguire & Mummery, 1999; Maguire, Vargha-Khadem et al., 2001)¹. Interestingly, when non-memory reference conditions were used instead, clear patterns of MTL activation were revealed (Addis, Moscovitch et al., 2004; Maguire & Frith, 2003a; Maguire, Henson et al., 2001; Maguire & Mummery, 1999; Piefke et al., 2003)¹.

MTL activation in studies of AM is typically left-lateralized or bilateral (for exception, see Levine et al., 2004; Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003)¹. Lesion studies show that left lateralized damage to the MTL region is more often associated with severe episodic memory impairment than is right lateralized damage (for review, see Spiers, Maguire, & Burgess, 2001). However patients with right lateralized MTL lesions tend to perform worse on tasks of spatial memory than those with left lateralized lesions (Abrahams et al., 1999; Abrahams, Pickering, Polkey, & Morris, 1997; Spiers et al., 2001; for review, see also Morris, Nunn, Abrahams, Feigenbaum, & Recce, 1999). Similarly, neuroimaging studies of spatial memory have also found task-related activity in the right MTL (Ghaem et al., 1997; Maguire et al., 1998; Owen, Milner, Petrides, & Evans, 1996). Maguire (2001) reasoned that the asymmetry observed in MTL activation across AM studies may relate to stimulus modality, with the left hippocampus engaged by retrieval of contextual details and the right by spatial memory and navigation.

Damage to the thalamus, for instance from thalamic infarction (Gentilini, de Renzi, & Crisi, 1987; Graff-Radford, 1990; Hodges & McCarthy, 1993; Stuss, Guberman, Nelson, & Larochelle, 1988; Von Cramon, Hebel, & Schuri, 1985) or alcoholic Korsakoff syndrome (Butters, 1984; Kopelman et al., 2001; Kopelman, Stanhope, & Kingsley, 1999; Mair, Warrington, & Weiskrantz, 1979; Zola-Morgan, Cohen, & Squire, 1983), has been associated with amnesia. The thalamus, specifically the anterior region, receives both direct (via the fornix) and indirect (via the mamillary bodies and mamillothalamic tract) projections from the hippocampus (for review, see Aggleton & Brown, 1999). Eight AM imaging studies (see Table 1) reported significant activation in the thalamic region, with one additional study reporting activation in this region that fell short of significance (Maguire & Mummery, 1999)¹, suggesting a secondary role to the AM network within the context of neuroimaging. It is possible that several cognitive and mnemonic conditions engage the thalamus and hence mask its activation.

The retrosplenial cortex and posterior cingulate (combined in our analysis due to inconsistent reporting of location in imag-

ing studies; Vogt, Absher, & Bush, 2000), is a core area in the AM network (see Table 1; at least in combined form). The retrosplenial cortex and posterior cingulate are bidirectionally connected to each other, and to the anterior cingulate via association pathways with thalamic and medial limbic regions in the temporal lobes (Morris, Petrides, & Pandya, 1999; Petrides & Pandya, 2002). The position of the retrosplenial/posterior cingulate cortex corroborates clinical evidence suggesting that damage to this area can result in memory deficits due to a disconnection syndrome (Aggleton & Pearce, 2001; Gainotti, Almonti, Di Betta, & Silveri, 1998; Heilman et al., 1990; Rudge & Warrington, 1991; Valenstein et al., 1987). The posterior cingulate is implicated in visuospatial processing, with material-specific effects paralleling those of the MTL (Gainotti et al., 1998; Takahashi, Kawamura, Shiota, Kasahata, & Hirayama, 1997; Valenstein et al., 1987; see also Rosenbaum, McKinnon, Levine, & Moscovitch, 2004, for similar neuroimaging findings).

Finally, a number of AM imaging studies reported activation in the temporopolar cortex (see Table 1), although activity in this region fell short of meeting core network criteria. The high number of published AM imaging studies (three-quarters) to date using fMRI may have resulted in this region playing a less prominent role in our analysis, possibly due to susceptibility artifact (Binder & Price, 2001; Devlin et al., 2000), than in a previous review by Maguire (2001), where fMRI methods were less pervasive. Several case studies have reported focal retrograde amnesia for episodic AM in association with damage to the temporopolar cortices, regardless of laterality (for review, see Wheeler & McMillan, 2001). The temporopolar cortices likely act as convergence zones that integrate diverse streams of information into unique entities, receiving afferent fibers from anterior and posterior association cortices as well as from limbic structures (Markowitsch, Emmans, Irle, Streicher, & Preilowski, 1985). Damage to the temporopolar cortices may interfere with information transfer, particularly when white matter tracks are involved (Levine et al., 1998; Markowitsch, 1995).

3.3.2. Age of memory and activation in the medial temporal lobe

Numerous theories of memory suggest that the hippocampus and related MTL structures contribute to episodic remembering by binding the pattern of activity present at the time of encoding into a memory trace that is sustained across time and reinstated during retrieval (Buckner & Wheeler, 2001; Eichenbaum, 2000; McClelland, McNaughton, & O'Reilly, 1995; Squire, 1992). Much debate in the memory literature has focused on the contribution of these MTL structures (particularly the hippocampus) to the retention and retrieval of memory traces over time.

The standard model of memory consolidation suggests that following temporary dependency on hippocampal structures, long-term remote memories can be accessed directly via the neocortex, such that the hippocampus is no longer required for retrieval of these memories (Squire & Alvarez, 1995; Squire, Cohen, & Nadel, 1984). By contrast, multiple-trace theory holds that neocortical representations are bound by MTL structures (referred to as the hippocampal complex) into a memory trace.

Table 3
Brain regions activated in response to autobiographical remembering when a resting state is used as the reference condition

AM studies		Frontal												Cingulate								Temporal								Parietal				Occipital			Subcortical				
Study	Contrast	10	9	46	44	6	45	47	11	25	8	4	25	32	24	23	31	29	30	ins	38	20	21	22	41	37	mtl	123	7	40	39	19	18	17	Ag	bg	th	cb	bst		
AM (vs. rest)																																									
Andreasen 95-2	am-rest							◁				◇			∞						▶	◁	▶	◁										◁	●	∞					
Fink 96-1	am emot-rest					▶										●					▶		▶														○				
Gemar 96-1	am sad-rest																																								
Gemar 96-2	am neut-rest																																								
Andreasen 99-1	am-rest														∞																◁							●			
Andreasen 99-1	am-rest																																					●			
Markowitsch 00	am emot-rest					○		◁							○	○	○	○					◁	◇						◁							○	◇	●		
Markowitsch 03-1	am sad-rest							◁								○			○																	∞	●	●			
Markowitsch 03-2	am happy-rest											○				●											▶						◁		◁						

Table 4
Brain regions activated in response to recent relative to remote autobiographical events

AM studies		Frontal												Cingulate								Temporal								Parietal				Occipital			Subcortical				
Study	Contrast	10	9	46	44	6	45	47	11	25	8	4	25	32	24	23	31	29	30	ins	38	20	21	22	41	37	mtl	123	7	40	39	19	18	17	Ag	bg	th	cb	bst		
AM (time since event)																																									
Conway 99-2 ^a	am recent–am remote																																								
Maguire 01b	am recent–am remote							▶																																	
Ryan 01-2	am recent–am remote																																								
Niki 02	am recent–am remote	○							○							●											◁			∞											
Piefke 03-1	am recent–am remote															●											◇														
Maguire 03b-2	am recent–am remote																										▶														
Graham 03-2	am recent–am remote																																								
Gilboa 03-3	am recent–am remote																																								
Addis 04-2	am (covar. recency)																																								

^a Note: No information regarding lateralization of activation was provided.

Here, the hippocampal complex is thought necessary for recovery of an episodic memory for as long as it exists, serving as a pointer or index to more detailed information stored in parts of the neocortex (Moscovitch & Nadel, 1998; Nadel & Moscovitch, 1997; Nadel, Samsonovich, Ryan, & Moscovitch, 2000). Re-instatement of each memory leads to the creation of multiple and widely distributed memory traces, rendering older memories less vulnerable to disruption than recent memories.

This controversy has been addressed in numerous studies of patients with MTL damage and dementia (e.g., Bayley, 2003; Rosenbaum et al., 2004; Steinvorth, Levine, & Corkin, 2005; for review, see Moscovitch et al., 2005). Functional neuroimaging studies of AM contribute to this debate by contrasting age of AMs across target conditions and interrogating the hippocampus as a region-of-interest. In these experiments, participants are typically asked to retrieve events from their recent and from their remote past, forming two conditions that undergo statistical comparison. The findings to date appear equivocal, in that some studies have found the hippocampal area to be activated in response to both recent and remote episodic events (Addis, Moscovitch et al., 2004; Conway et al., 1999; Gilboa et al., 2004; Graham et al., 2003; Maguire, Henson et al., 2001; Maguire, Vargha-Khadem et al., 2001; Ryan et al., 2001)¹, and other studies have found this region, or related MTL structures, to be more active for recent than for remote events (Niki & Luo, 2002; Piefke et al., 2003)¹. A separate study (Maguire & Frith, 2003b)¹ found left hippocampal activation in relation to both recent and remote events, and right hippocampal activation in relation to recent, but not remote events (see Table 4).

Although the patterns of hippocampal involvement reported in these studies have been putatively linked to the age of the memory retrieved, additional factors related to memory age may account for differences observed across studies. For example, Johnson, Foley, Suengas, & Raye (1988) found that recent events received higher ratings than did remote events across numerous phenomenal characteristics including vividness, amount of detail and emotionality of the event recalled. These findings raise the possibility that such variables may impact on patterns of brain activity in age-of-memory studies, independent of or in combination with, time of encoding of the memory retrieved.

Indeed, several recent imaging studies have examined the impact of these factors on patterns of activation for old and for new AMs. When factors such as personal significance and vividness were accounted for, memory age no longer modulated activity in the hippocampal region (Addis, Moscovitch et al., 2004; Gilboa et al., 2004; Ryan et al., 2001)¹. In studies in which differential hippocampal activation was reported, qualitative factors received higher ratings for recent relative to remote events (perception, re-experiencing, amount of detail recalled) but were not analyzed in conjunction with hippocampal activation (Piefke et al., 2003)¹; further analysis of these variables would be useful in determining the effect of age of memory on hippocampal activation. In one additional study, qualitative ratings did not differ with memory age (amount of detail recalled; Niki & Luo, 2002)¹, but these were too coarse to be confirmatory (Gilboa et al., 2004)¹.

Although qualitative aspects of new and old memories appear to modulate hippocampal activation, there is nonetheless evidence for an effect of memory age. Two studies suggest that modulation of hippocampal activity by memory age may be specific to the right hippocampus, even when qualitative factors are accounted for (e.g., amount of detail, emotionality; Addis, Moscovitch et al., 2004; Maguire & Frith, 2003b)¹. In a region of interest analysis examining hippocampal activation, Gilboa (2004) observed that recent events engaged the anterior aspect of the hippocampus whereas remote events showed a broader activation pattern along the anterior–posterior axis regardless of activation laterality. Three studies in our sample reporting hippocampal activation in response to new relative to old memories also showed activation in the anterior to mid-portion of the hippocampus (Maguire & Frith, 2003b; Niki & Luo, 2002; Piefke et al., 2003)¹. Because hippocampal activation across memory conditions is masked in statistical contrasts, further within-study region of interest analyses may shed light on hippocampal engagement across the continuum of memory age.

The results of these studies suggest that several factors including personal significance, vividness, amount of detail, and emotionality of the event recalled affect hippocampal involvement in the recall of old and of new memories. Moreover, age of memory may differentially influence the left and right sides of the hippocampus as well as the pattern of activation along the anterior–posterior axis. Future investigations of hippocampal involvement in retrieval of old and of new memories will need to consider these variables in order to understand patterns of activation in MTL regions.

3.3.3. *Semantic memory processes in autobiographical memory: the lateral temporal cortex and related regions*

Semantic memory and general autobiographical knowledge permeate much of our autobiographical recollections (Barsalou, 1998; Levine, Svoboda, Hay, Winocur, & Moscovitch, 2002). Overarching autobiographical life periods and themes form the backdrop of recollective experience and provide avenues (or cues) to more specific incidents (Conway & Bekerian, 1987; Conway & Pleydell-Pearce, 2000). Most episodic events are accessed by sifting through these broad themes and general autobiographical knowledge, especially at the early stages of recollection. Moreover, specific incidents contain numerous personal or general semantic representations related to the recollected environment (e.g., people, friends, buildings, objects, broader public events, etc.), that, in combination with other factors (e.g., personal relevance, physical features, emotional relevance), allow the rememberer to form an episodic AM.

Accordingly, most imaging studies of AM reported activation in the middle (predominantly left) temporal gyrus (BA 21), a core region in the AM signature, with fewer studies reporting activity in the superior and inferior temporal gyri of both hemispheres (BA 22, 20; see Table 1; Fig. 1). Neuropsychological case studies of patients who have sustained damage to the lateral temporal cortex (right or left) report selective deficits in semantic memory (e.g., public events, famous people, technical terminology; De Renzi, Liotti, & Nichelli, 1987; Kitchener & Hodges, 1999; Yasuda, Watanabe, & Ono, 1997). Consistent

with these reports, the neuroimaging literature reveals activation in the middle temporal gyrus (mostly in the left hemisphere) and, to a lesser extent, in the inferior and superior temporal gyri in response to a variety of semantic tasks including semantic fluency or generation tasks (Lee et al., 2002; Mummery, Patterson, Hodges, & Wise, 1996) and semantic decision making tasks (Binder et al., 1997; Chee, O'Craven, Bergida, Rosen, & Savoy, 1999). Moreover in an imaging study of AM using multivariate analyses, Maguire et al. (2000)¹ reported increased effective connectivity between the lateral temporal and temporopolar cortices in response to the retrieval of semantic AM information, as well as memory for public events, further implicating the middle temporal gyrus in semantic processing.

Behavioral studies of older adults show an age-related bias towards semantic relative to episodic details (Levine et al., 2002; Piolino, Desgranges, Benali, & Eustache, 2002). Interestingly, older adults engage the middle temporal gyrus more than younger adults when scanned during episodic AM retrieval (Maguire & Frith, 2003a)¹, possibly reflecting greater engagement of semantic processing.

3.4. Dissociating episodic from semantic autobiographical memory

3.4.1. Direct comparison of episodic to semantic autobiographical memory

As noted above, the episodic/semantic distinction has been influential to conceptualizations of AM. According to Tulving (2002), episodic memory entails mental time travel and the sense of the subjective self in time, processes that are not required for semantic memory. In comparison to laboratory studies that use stimuli of limited personal significance, studies of AM are well suited to test this hypothesis. A number of AM imaging studies have reported differences in neural activation in core AM network regions when contrasting episodic with semantic memory conditions, including the anterior prefrontal cortex and hippocampus (Addis, McIntosh et al., 2004; Levine et al., 2004; Maguire & Frith, 2003a; Maguire & Mummery, 1999; see also Maguire, Vargha-Khadem, & Mishkin, 2001, for confirmation with an MTL amnesic patient and Maguire et al., 2000, for effective connectivity analysis)¹. Differences between semantic and episodic AM also differ according to the paradigm used, with the greatest differences revealed when single-instance, prospectively collected AMs were contrasted to various semantic conditions, including personal semantic AM (Levine et al., 2004)¹, supporting the hypothesis that semantic memory, regardless of type, is different relative to episodic AM, with the latter uniquely engaging mental time travel (Tulving, 2002; see also Kapur, 1999; Wheeler, Stuss, & Tulving, 1997). There is also substantial overlap in neural activation in response to episodic and general semantic tasks (e.g., in the lateral temporal cortex, as well as the extended semantic memory network including the ventrolateral prefrontal cortex, temporoparietal junction, anterior cingulate and cerebellum; for review, see Martin, 2001) that may reflect both substantial semantic representation within the AMs retrieved and the contribution of domain-general processes (e.g., executive functions) that serve diverse cognitive and mem-

ory functions (see, Cabeza & Nyberg, 2000; Duncan & Owen, 2000).

The capacity of mental time travel allows people to mentally project into the future as well as the past (Atance & O'Neill, 2001). Evidence from behavioral studies supports a correspondence between past and future autobiographical thought (D'Argembeau & Van der Linden, 2004; Spreng & Levine, *in press*). This correspondence has also been observed in a functional neuroimaging study directly investigating past and future autobiographical thought, where both conditions engaged anteromedial prefrontal and medial temporal regions (Okuda et al., 1998).

3.4.2. Contrasting short and long retrieval times: implications for episodic and semantic autobiographical memory

The specificity of information retrieved during autobiographical recollection is related to the amount of time provided for recall. Addis, Moscovitch et al. (2004)¹ and Addis, McIntosh et al. (2004)¹ found that retrieval of single-instance AMs was associated with activation in regions concerned with visual processing (left precuneus, left superior parietal lobule, and right cuneus), peaking 6–8 s after stimulus onset. Retrieval of repeated events (semantic AM) evoked right-lateralized activity (inferior temporal, medial frontal, as well as the left thalamus) peaking 2–6 s after stimulus onset. These findings were interpreted as consistent with Conway's (1992) hypothesis that episodic AMs are accessed through personal semantic AMs.

In a series of PET experiments, Graham et al. (2003)¹ found that when participants were allotted longer retrieval times, the contents of their recollections (which were audio recorded) were rated as proportionately more specific than when less time was provided. Short AM retrieval times were associated with left middle temporal activation, suggesting a link between this region and initial semantic retrieval operations. Interestingly, studies using prospective collection of everyday events are distinguished by a lack of lateral temporal activation, suggesting reduced semantic processing, possibly because events are more directly accessed (Cabeza et al., 2004; Levine et al., 2004)¹. Indeed, Levine et al. (2004)¹ reported left lateral temporal *deactivation* in association with highly vivid episodic AM in contrast to semantic AM conditions.

Additional evidence suggesting retrieval stage-specific regional engagement can be drawn from contrasting studies with varying amounts of time allotted to memory retrieval, which in our sample ranged from 2 s (Maddock et al., 2001)¹ to 2 min (Andreasen et al., 1995)¹. Of the 22 AM imaging studies surveyed, together containing a total of 40 contrasts (one study did not publish time-related data, and another study re-analyzed already published contrasts using multivariate analyses), approximately half of the contrasts (21) included a memory retrieval interval of 10 or fewer seconds (mean, 6.48 s; S.D., 2.73 s) whereas the other half (19) included a retrieval interval of 20 or more seconds (mean, 45.79 s; S.D., 32.80 s). When groups with brief and extended retrieval intervals were compared (10 or fewer seconds versus 20 or more seconds), using ratios to equate for differences in number of contrasts, we found that the brief

interval group had approximately double the ratio of contrasts showing activation in the medial prefrontal cortex (BA 9, 10), ventrolateral prefrontal cortex (BA 45, 47), superior dorsolateral cortex (BA 6), middle temporal gyrus (BA 21), temporoparietal junction (BA 39) and MTL than the longer interval group. These findings possibly reflect initial processes including cue-driven associative remembering (Moscovitch, 1992), working-self-guided retrieval (Conway et al., 2002), maintenance and monitoring of retrieved contents, and semantic processes.

The longer interval group had a five-fold greater proportion of contrasts showing right-sided activation in the medial prefrontal cortex and middle temporal gyrus than the shorter retrieval interval group, although activation in the left hemisphere predominated in both interval groups. Given the iterative nature of AM retrieval (Burgess & Shallice, 1996; Conway & Pleydell-Pearce, 2000), it is possible that left-sided activation remains tonic as retrieved information cues further search processes. Although the above findings are preliminary and are based on hemodynamic methods that are low in temporal specificity, they are consistent with findings derived from temporally sensitive electrophysiological methods, which indicate a shift from left to right hemispheric engagement over the course of remembering (Conway, Pleydell-Pearce, & Whitecross, 2001; Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2003, but see Ranganath & Paller, 1999).

3.5. Visuospatial imagery in autobiographical memory

An accumulating number of lesion studies suggest that visuospatial processes may be crucial to autobiographical recall. Rubin and Greenberg (1998) recently coined the term “visual–memory–deficit–amnesia” to refer to cases in which amnesia is reported in conjunction with damage to the visual cortices. Although additional temporal damage is reported in the bulk of these cases (for reviews, see Greenberg & Rubin, 2003; Rubin & Greenberg, 1998; Wheeler & McMillan, 2001), a few studies show amnesia in association with relatively isolated damage to the striate and extrastriate cortices as indicated by MRI (Brown & Chobor, 1995; Hunkin et al., 1995; Ogden, 1993). Researchers have suggested that AM retrieval requires the ability to recall through imagery detailed visual features present at encoding of the event in memory; these long-term visual representations then in turn reactivate non-visual percepts, conceptual knowledge, and emotions related to the event as they are placed within a spatial and temporal context (Brewer, 1986; Conway, 1992, 1996; Greenberg & Rubin, 2003; Rubin & Greenberg, 1998). According to this analysis one would expect regions involved in visuospatial processing and visual imagery to be prominently engaged across imaging studies of AM.

Only eight AM imaging studies reported activation in the occipital regions (see Table 1), suggesting a secondary role in the AM network. Of the two studies that used photographs to access AMs (Cabeza et al., 2004; Gilboa et al., 2004)¹, both reported occipital activation. In an electrophysiological study of AM, Conway et al. (2003) found that activity in the occipital region was greater for events that actually occurred relative to those that were imagined. Interestingly, Levine et al. (2004)¹

observed occipital deactivation during episodic and semantic AM, a finding these authors attributed to greater processing of the visual fixation during control conditions.

Prominent activation was observed in the temporoparietal junction (BA 39), with greater activation apparent in the left than in the right hemisphere (see Table 1). Activation in this core AM region has been reported in response to observing goal-directed actions (Frith & Frith, 1999). The temporoparietal junction has also been implicated in retrieval of the spatial context of events, specifically in translating allocentric spatial information into egocentric space and vice versa (Burgess et al., 2001). In the left hemisphere, this region is involved in manipulating visuospatial representations of body schema (Gerstmann, 1957).

3.6. Emotion and autobiographical re-experiencing

Autobiographical remembering is inherently personal and is characterized by varying gradients of emotional content. Most imaging studies of AM to date have not separately accounted for feeling states, such as joy or sadness, associated with the retrieval of emotional events from memory. Several studies demonstrate that emotional characteristics of episodic stimuli enhance recollection and alter patterns of brain activity (Cahill et al., 1996; Canli, Zhao, Brewer, Gabrieli, & Cahill, 2000; Hamann, Cahill, McGaugh, & Squire, 1997; Hamann, Ely, Grafton, & Kilts, 1999). Despite a large body of behavioral research examining the impact of emotion on AM retrieval (Brown & Kulik, 1977; Christianson, 1989; D’Argembeau, Comblain, & Van der Linden, 2003), of the 24 published AM imaging studies reviewed here, only 5 have examined specifically the retrieval of emotional AM events (see Table 5). Nonetheless, these studies reveal intriguing findings with respect to the neural substrates of emotional retrieval and lay the groundwork for future research in this area. In this section, we compare the findings of studies without instructions to retrieve emotional memories (i.e., “standard AM”) to those that specifically elicited recall of emotional memories (i.e., “emotion AM”), with the assumption that the former scanned on average fewer and less intense emotional memories than the latter.

Studies of emotion AM were more likely to report patterns of deactivation than were standard AM studies, consistent with reporting styles in the emotion and psychiatric literature. This deactivation may be due to emotion-related suppression of activity in regions mediating cognition (Drevets & Raichle, 1998; Mayberg et al., 1999) or to the use of non-emotional AM reference conditions sharing cognitive processes with the emotion AM conditions, cancelling out activations related to retrieval and attention. These factors cannot be dissociated in the current collection of studies.

The results of the five emotion AM imaging studies (Fink et al., 1996; Gemar et al., 1996; Markowitsch et al., 2000; Markowitsch et al., 2003; Piefke et al., 2003)¹ reported to date revealed a network consistent with that of the standard AM studies described above (see Fig. 1 and Tables 1 and 2). This pattern, however, included additional activation in emotion-specific regions. Furthermore, in contrast to the left-lateralized find-

Table 5
Brain regions activated and deactivated in response to emotion autobiographical memory studies

AM studies	Contrast	Frontal					Cingulate					Temporal					Parietal					Occipital					Subcortical														
		10	9	46	44	6	45	47	11	25	8	4	25	32	24	23	31	29	30	ins	38	20	21	22	41	37	mtl	123	7	40	39	19	18	17	Ag	bg	th	cb	bst		
AM (emotion: activations)																																									
Fink 96-1	am emot-rest																																								
Fink 96-2	am emot-am other																																								
Gemar 96-1	am sad-am neut																																								
Gemar 96-2	am sad-rest																																								
Piefke 03-2	am emot-read text																																								
Piefke 03-2	am emot-read text																																								
Piefke 03-3	am happy-am neg																																								
Piefke 03-4	am sad-am pos																																								
Markowitsch 00-1	am-rest																																								
Markowitsch 00-2	am-fictitious																																								
Markowitsch 03-1	am sad-rest																																								
Markowitsch 03-2	am happy-rest																																								
Markowitsch 03-3	am sad-am happy																																								
Markowitsch 03-4	am happy-am sad																																								
Markowitsch 03-4	am happy-am sad																																								
AM (emotion: deactivations)																																									
Fink 96-1	am emot-rest																																								
Fink 96-2	am emot-am other																																								
Gemar 96-1	am sad-am neut																																								
Gemar 96-2	am sad-rest																																								

ings from standard AM studies, emotion AM paradigms evoked largely bilateral activation, with one early study reporting right-lateralized activation (Fink et al., 1996)¹. This bilateral pattern of activation is consistent with findings from mood-induction studies in the psychiatry literature that rely on AM scripts to induce the desired emotional state (Svoboda, McKinnon, & Levine, *in preparation*, for review of the mood-induction literature see also, Phan, Wager, Taylor, & Liberzon, 2002). The additional recruitment of right hemisphere brain regions in emotional re-experiencing is consistent with other findings across numerous domains suggesting preferential right-hemisphere involvement in emotional processing and in social cognitive processes (e.g., Shammi & Stuss, 1999; Stuss, Gallup, & Alexander, 2001; Winner, Brownell, Happe, Blum, & Pincus, 1998; Winston, Strange, O'Doherty, & Dolan, 2002).

Regional activation patterns attributed to emotional processing included the amygdala, which is engaged during encoding and retrieval of emotional events (Hamann, 2001; Maratos, Dolan, Morris, Henson, & Rugg, 2001; McGaugh, 2002), the insular cortex, which is sensitive to a diverse range of emotional stimuli, particularly those involving visceral representations (Critchley, Wiens, Rotshtein, Ohman, & Dolan, 2004; Davidson & Irwin, 1999), and the orbitofrontal cortex, which is implicated in representations of reward and punishment (Rolls, 2002). Areas of visual processing and imagery were also noted, possibly reflecting enhanced visual processing for highly emotional arousing events stemming from feed-forward amygdala connectivity (Anderson & Phelps, 2001). Deactivation in regions associated with cognitive processing may be related to the relatively automatic and less resource-demanding nature of recollecting emotional AMs, or, as discussed previously, cognitive activity in the reference condition (e.g., neutral AM retrieval, rest).

3.7. Network approaches to the study of autobiographical remembering

The foregoing analysis focused on areas of regional activation revealed across studies of AM. Although this may suggest a modular approach to the analysis of the functional neuroanatomy of AM, such a conclusion would merely reflect the predominant application of univariate image analysis methods within the AM functional neuroimaging literature (not to mention the functional neuroimaging literature in general), rather than the actual mechanism of the mind, which is interactive and networked (Damasio, 1989; Geschwind, 1965; Lashley, 1929; Mesulam, 1998). This issue is of particular relevance to higher cognitive functions, especially AM, which by definition draws upon multiple processes and modalities. Although it is clear that memory is enabled by the functional interaction of regions within a network rather than brain areas acting in isolation (e.g., the hippocampus), at this stage it is not clear how these regions actually *interact* to support remembering. Similarly, discerning which regions are functionally related to the behavior of interest is also a challenge as univariate methods of analysis, the standard method of analyzing functional imaging data, emphasize differences between target and reference tasks such that

regional activation shared by both tasks is masked and possibly not considered important in supporting the target behavior. Conversely, regions found to differentiate the target from the reference task may not be relevant to the functional network that supports the target behavior (Nyberg & McIntosh, 2001).

Multivariate approaches to functional image analysis address some of these challenges by providing a means to investigate the functional and effective connectivity of regions related to task performance (Friston, 1994; McIntosh, Bookstein, Haxby, & Grady, 1996; McIntosh & Gonzalez-Lima, 1994). Functional connectivity refers to which regions function collectively as a network to support the behavior of interest. The partial least squares (PLS) approach to image analysis operates on the covariance between the percentage signal change within voxels and the experimental design, identifying latent variables that express relationships between task effects and the brain activation networks (McIntosh & Gonzalez-Lima, 1994). An ancillary advantage to this approach is that, unlike univariate approaches, task contrasts are not forced by the experimenter but rather determined statistically in relation to patterns of brain activation. Using univariate statistics, Addis, Moscovitch et al. (2004)¹ and Addis, McIntosh et al. (2004)¹ documented a general AM network (similar to the core network described herein) in which singular and repeated AM events were differentiated from control conditions, but not from each other. However, differences emerged in a subsequent PLS analysis that incorporated time-lag as an additional independent variable, with the pattern of brain activity associated with repeated events peaking earlier than that associated with singular events, suggesting more semantic content earlier in the recollection process (Addis, McIntosh et al., 2004)¹. Levine et al. (2004)¹ used PLS to assess the hypothesis that multiple types of semantic memory stimuli, including semantic AM, could be dissociated from singular episodic AMs, yet the special status of semantic relative to other forms of AM was confirmed by a second latent variable. Effective connectivity refers to how brain regions interact or influence each other to support the behavior, requiring a model of brain connectivity that is derived from known anatomical connections as described in the primate literature. Maguire et al. (2000)¹ examined effective connectivity between left temporal lobe regions activated across several memory conditions including episodic AM using structural equation modeling (SEM). They found increased interconnected activity between the parahippocampus and both the hippocampus and the temporopolar cortex for autobiographical incidents, whereas memory for public events and general knowledge was associated with increased left lateral temporal and temporopolar interconnectivity. Analysis of temporopolar activity alone using the more standard univariate method indicated a similar degree of activity across all conditions, when in fact this region's interactions with other temporal regions as revealed by SEM was highly specific in relation to task demands. In contrast to controls, a patient with bilateral hippocampal damage resulting in autobiographical amnesia showed increased activity between retrosplenial cortex and both the hippocampus and the medial frontal cortex, indicating the use of an alter-

nate (albeit less effective) medial temporal pathway involved in retrieval of specific memories (Maguire, Henson et al., 2001; Maguire, Vargha-Khadem et al., 2001)¹. Univariate analyses of this patient's hippocampal activity did not differ from controls; SEM analyses were necessary to reveal the connectivity changes. Although SEM is necessarily limited to a select number of regions and connections, these results demonstrate that it can provide significant data unavailable from standard univariate methods.

4. Summary and conclusions

AM is the product of a number of component processes that together enable the re-experiencing of a phenomenologically rich and textured past. The large number of AM imaging studies published to date provided us with the opportunity to examine the AM neural network as a whole, along with the impact of several variables on this network. We found a left-lateralized AM network, including select regions in the frontal, temporal and posterior cortices, as well as the cerebellum and a number of subcortical structures. These findings are broadly consistent with those of two earlier reviews of AM (Conway et al., 2002; Maguire, 2001). We further examined several variables modulating the AM network, accounting for some of the discrepancies observed across studies and providing insight into the neural underpinnings of AM.

Preliminary evidence suggests that the passage of time may both directly and indirectly modulate MTL involvement in AM event retrieval. Qualitative aspects of memory appear to have a significant modulating effect on MTL activation, such as personal significance, amount of detail recalled and vividness, which under some circumstances may change with the passage of time and subjective perspective. We also found that reference conditions engaging memory processes tended to mask hippocampal activation in the target AM task. Similarly, resting state reference conditions masked neural correlates of self-referential processes, particularly activation in the medial prefrontal cortex.

Autobiographical events are embedded within a semantic context that situates them within larger personal and public spheres. Unique fragments of new episodes are bound to established semantic representations (e.g., familiar people, objects, locations), increasing the efficiency of memory retrieval as well as the redundancy of neural representation across episodes (Conway, 2001; Damasio, 1989). Episodic and semantic AM showed both overlapping and distinct patterns of activation, the latter supporting the notion that episodic AM has special status relative to semantic AM (Tulving, 2002; Wheeler et al., 1997). The pattern of brain activation observed when short and extended intervals for AM retrieval were contrasted across studies further support postulations that initial stages of retrieval are proportionately higher in semantic content than are later stages.

Emotional content was manipulated across several imaging studies of AM. In contrast to the left-lateralized pattern of activation observed in most standard AM studies, emotion AM studies were associated with a bilateral pattern of activation. In addi-

tion to the typical neural network observed for standard AM, prominent activation was observed in regions associated typically with emotional processes. Corresponding deactivations were observed in regions associated typically with cognitive processing.

Further study is needed to understand the nature of executive processes in AM, such as the neural correlates of spontaneous retrieval relative to generative or effortful retrieval. To date the executive demands of autobiographical remembering have only been addressed by a few electrophysiological studies (Conway et al., 2001, 2003; Ranganath & Paller, 1999). Existing theories of memory (Burgess & Shallice, 1996; Conway & Pleydell-Pearce, 2000; Moscovitch, 1992; Norman & Bobrow, 1979) as well as findings from patient studies (Della Sala, Laiacina, Spinnler, & Trivelli, 1993; Kopelman et al., 1999; Levine, 2004; Svoboda et al., 2002) suggest a significant role of the frontal system in AM recollection. Continued examination of the effects of qualitative factors on neural activation may further contribute to the theoretical debate concerning the nature of hippocampal involvement in memory consolidation and retrieval (McClelland et al., 1995; Nadel & Moscovitch, 1997; Squire, 1992). In a similar vein, other brain regions are likely modulated by qualitative factors, as seen in a handful of studies that investigated the impact of emotional content on AM retrieval. Finally, AM is a prime exemplar of integrated brain activity giving rise to conscious experience, yet most functional neuroimaging studies of AM employ univariate analysis techniques that foster interpretation of activations within a modular framework. Multivariate connectivity analyses provide a richer understanding of how various component processes and qualitative factors influence regional interaction within the AM network.

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Appendix A

Autobiographical memory studies in the meta-analysis and listed numerically in Table 1.

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