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Neural Correlates of Autobiographical Memory

Methodological Considerations

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Introduction

Autobiographical memory (AM) refers to the retrieval of memories from the personal past. It encompasses multiple processes and neural systems (Conway and Pleydell-Pearce, 2000; Rubin, 2006) often difficult to capture in a single study. AM retrieval typically involves complex retrieval processes, semantic content, personal significance, subjective re-experience, spatiotemporal context, emotion, social interactions, and varying levels of specificity, remoteness, and rehearsal. These qualities make personal memories important and relevant for the future, but also difficult to investigate with traditional laboratory materials (Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, 2012). Neuroimaging studies of AM were much slower to develop compared to similar studies on laboratory memory. For example, an early review of neuroimaging studies of AM reported 11 studies (Maguire, 2001), whereas another review of 275 studies of imaging of cognition included over 50 studies on laboratory memory (Cabeza and Nyberg, 2000). One reason for the relatively slower development of neuroimaging studies of AM is that their inherent complexity can be challenging within the controlled and rigorous scanning environment, and such studies were often criticized by other cognitive neuroscientists as a "waste of time" (see Maguire, 2012). Fortunately, the development of novel techniques and methodologies that capture this inherent complexity, along with the increasing viewpoint that such studies can offer valuable insight into memory and other related processes (Cabeza and St. Jacques, 2007; Gilboa, 2004; Maguire, 2001, 2012; McDermott, Szpunar, and Christ, 2009; Spreng, Mar, and Kim, 2009), has led to a rise in the number of functional neuroimaging studies of AM. Such studies are important because they are generally more ecologically valid (Neisser, 1978), they contribute to the understanding of neural correlates of processes that are difficult to study using laboratory memory stimuli (Cabeza and St. Jacques, 2007; Gilboa *et al.*, 2004; St. Jacques and Cabeza, 2012), and they can inform theories of AM (St. Jacques, 2012).

In this chapter we review innovative methods and analysis techniques that have allowed neuroscientists to overcome some of the challenges of AM research, as well as

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how the findings from such studies can provide a unique perspective on cognitive neuroscience. The primary focus of the current chapter is on functional MRI (fMRI), the methodology of choice for the majority of neuroimaging studies in AM, but positron emission tomography (PET) and event-related potential (ERP) studies are mentioned where relevant. Additionally, we focus on neuroimaging studies of primarily healthy young adults. Topics will include an overview of the neural correlates supporting AM retrieval, the methods of eliciting AMs within the rigorous scanning environment, analysis methods, and future methodological directions in this field. Throughout the chapter we will discuss some of the challenges of functional neuroimaging methods that are particularly relevant to AM.

Neural Correlates Supporting Autobiographical Memory Retrieval

Recalling memories from our personal past involves a distributed set of primarily left-lateralized brain regions (Maguire, 2001), although not all studies show this pattern (Addis *et al.*, 2012; for review see Svoboda, McKinnon, and Levine, 2006). Functional neuroimaging studies have identified a number of regions that are frequently involved during AM retrieval, including the medial and lateral prefrontal cortices (PFC), lateral and medial temporal lobes (MTL; hippocampus, parahippocampal gyrus), ventral parietal cortex, and posterior cingulate cortex (Cabeza and St. Jacques, 2007; McDermott, Szpunar, and Christ, 2009; Spreng, Mar, and Kim, 2009; Svoboda, McKinnon, and Levine, 2006). The typical neural regions involved during AM are sometimes referred to as the "AM retrieval network" or even the "core network" because of their frequency and evidence for interactions among many of these regions. However, it would be more appropriate to consider AM retrieval as involving the interaction among multiple neural networks or systems (Fuster, 2009; Rubin, 2006; also see Svoboda, McKinnon, and Levine, 2006), and some functional neuroimaging studies have employed analysis techniques that allow the examination of the co-activation and interaction among these large-scale networks during AM retrieval (Andrews-Hanna *et al.*, 2010; Spreng *et al.*, 2010; St. Jacques, Kragel, and Rubin, 2011; see Figure 13.1).

One of the primary networks recruited during AM retrieval overlaps with the default network (Figure 13.1), a set of brain regions that are co-active during passive resting states (Raichle *et al.*, 2001). The default network is composed of two subnetworks: (1) a medial PFC network that includes dorsal medial PFC, posterior cingulate, and ventral parietal cortices (Andrews-Hanna *et al.*, 2010; Buckner, Andrews-Hanna, and Schacter, 2008), and (2) an MTL network that comprises hippocampal, ventral medial PFC, retrosplenial, and ventral parietal cortices (Andrews-Hanna *et al.*, 2010; Kahn *et al.*, 2008; Vincent *et al.*, 2006). The medial PFC network is recruited to a greater extent when making decisions that are self-referential versus decisions that are not (Andrews-Hanna *et al.*, 2010), and anterior midline regions overlapping with this network are associated with self-referential processes during AM retrieval (Muscatell, Addis, and Kensinger, 2010; Rabin *et al.*, 2010; Spreng and Grady, 2010; St. Jacques *et al.*, 2011b). In contrast, the MTL network has been linked to constructing a scene based on memory (Andrews-Hanna *et al.*, 2010). Regions within the MTL network, such as

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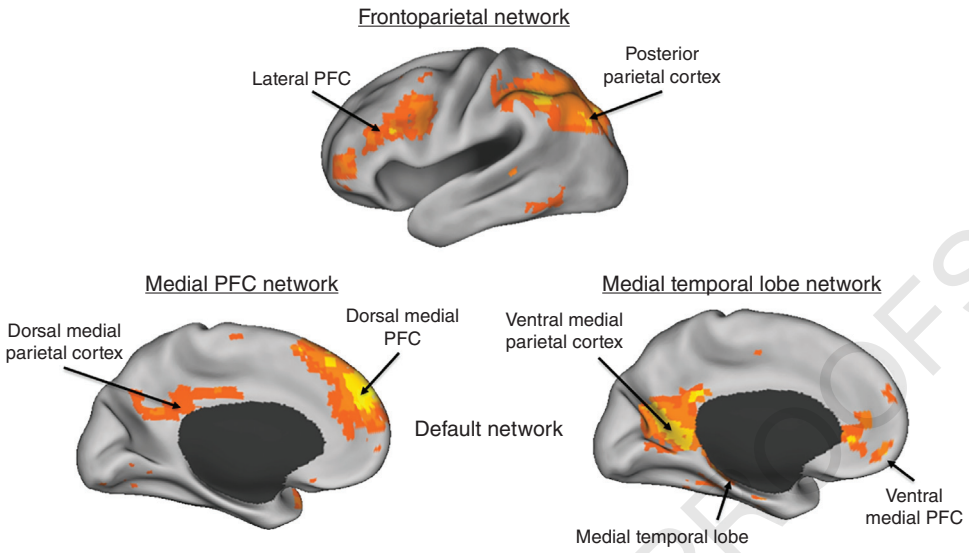

Figure 13.1 Large-scale networks contributing to autobiographical memory (AM). PFC, prefrontal cortex.

the hippocampus, are associated with recollection processes during memory retrieval (Diana, Yonelinas, and Ranganath, 2007), and activity within many of the regions comprising the MTL network is frequently correlated with detailed recall and subjective recollection during AM retrieval (Addis *et al.*, 2004b; Daselaar *et al.*, 2008).

The frontoparietal or central executive network (Figure 13.1) is another important neural network involved in AM retrieval. It includes lateral PFC, anterior cingulate, and inferior parietal cortices and is associated with adapative cognitive control processes (Dosenbach *et al.*, 2007; Seeley *et al.*, 2007; Vincent *et al.*, 2008). Frontal and parietal components of this network are engaged during controlled operations that act on memory (Cabeza *et al.*, 2008; Moscovitch and Winocur, 2002). The link between memory search and controlled retrieval processes in AM was based on evidence from an early PET study that found activation in lateral PFC regions when comparing AM to semantic memory (Conway *et al.*, 1999) and has since been supported by subsequent studies (Maguire, 2001; Svoboda, McKinnon, and Levine, 2006). The lateral PFC activity elicited during AM retrieval is predominantly left-lateralized (Maguire, 2001; Svoboda, McKinnon, and Levine, 2006), which is thought to reflect the contribution of complex strategic retrieval processes and the contribution of semantic information during retrieval (Conway, Pleydell-Pearce, and Whitecross, 2001; Conway *et al.*, 1999; Denkova *et al.*, 2006; for review see Svoboda, McKinnon, and Levine, 2006). Consistent with these early observations, St. Jacques, Kragel, and Rubin (2011) found that AM retrieval involved recruitment of a left-lateralized frontoparietal network, suggesting that engagement of this network during AM retrieval is less bilateral than that observed during resting state or in other cognitive tasks.

The neural networks that contribute to AM retrieval may also support tasks relying on similar processes, such as episodic future and counterfactual thinking,

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perspective taking, and mental navigation. In a meta-analysis of neuroimaging studies including AM, Spreng, Mar, and Kim (2009) observed overlap among neural regions supporting AM, prospection, theory of mind, and the default network (Spreng and Grady, 2010). The remarkable similarity between the neural correlates supporting AM and simulation has led many researchers to suggest that there are common mechanisms underlying both abilities, such as self-projection (Buckner and Carroll, 2007), scene construction (Hassabis and Maguire, 2007), and recombination of episodic components of memory (Schacter, Addis, and Buckner, 2007; see also Chapter 14). Additionally, the frontoparietal network recruited during AM retrieval is also frequently engaged during tasks that involve cognitive control and decision making (e.g., Dosenbach *et al.*, 2007). Subtle differences in these networks may emerge depending on context. For example, St. Jacques, Kragel, and Rubin (2011) observed that recruitment of the frontoparietal network was isolated to the initial search and construction of AM retrieval, whereas default network activation extended into the elaboration period. Using dynamic causal modeling (Friston, Harrison, and Penny, 2003), St. Jacques, Kragel, and Rubin found that the medial PFC network was integral to driving the interaction among these networks. Additionally, memory accessibility and recollection uniquely altered connectivity between these neural networks. Recollection modulated the influence of the medial PFC on the MTL network during elaboration, suggesting that greater connectivity among subsystems of the default network supports greater re-experience. In contrast, memory accessibility modulated the influence of frontoparietal and MTL networks on the medial PFC network, suggesting that the ease of retrieval involves greater fluency among the multiple networks contributing to AM. Examination of the recruitment of particular neural networks, their interaction, and modulation by behavior may help to further distinguish AM retrieval from other similar tasks (e.g., Spreng *et al.*, 2010).

Eliciting Autobiographical Memories in the Scanning Environment

There are multiple ways to elicit AM in the scanning environment, which differ according to how well control is exerted over the phenomenological properties of memory retrieval while also maintaining ecological validity (Cabeza and St. Jacques, 2007; Maguire, 2001; Svoboda, McKinnon, and Levine, 2006). It is difficult to determine the retrieval cues that will be effective in eliciting AMs without also interfering with the properties of the retrieved memory during scanning and, consequently, subsequent interpretations of brain activations (Cabeza and St. Jacques, 2007). Here we discuss the four main methods that have been used to query AM in the scanning environment: generic cues, pre-scan interview, independent sources, and prospective (Figure 13.2).

Generic cues

In the *generic cues* method (Crovitz and Schiffman, 1974), participants are provided with a novel retrieval cue and are asked to retrieve an AM associated with the cue (Figure 13.2a). The generic cues method has generally used verbal cues such as nouns

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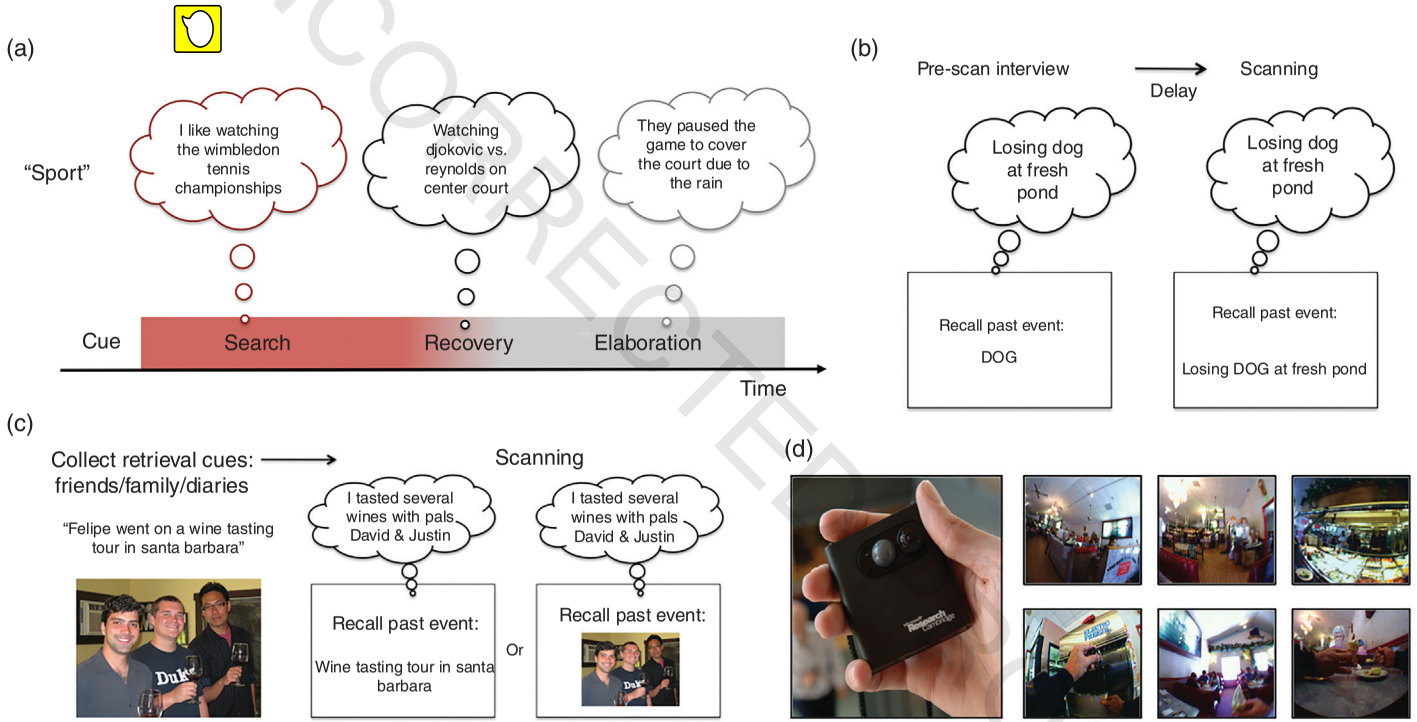

Figure 13.2 Different methods for eliciting autobiographical memories during functional scanning: (a) generic cues, (b) pre-scan interview, (c) independent sources method, and (d) prospective collection using sensor-based camera.

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(e.g., "teapot"; Conway *et al.*, 1999; Graham *et al.*, 2003), emotional words (e.g., "kiss"; Markowitsch *et al.*, 2003; St. Jacques *et al.*, 2011a), or other specialized words (e.g., hockey words; Muscatell, Addis, and Kensinger, 2010). Some studies have also employed odors (Masaoka *et al.*, 2012), pictures (Burianova and Grady, 2007; Burianova, McIntosh, and Grady, 2010; Fitzgerald *et al.*, 2004; Spreng and Grady, 2010; St-Laurent *et al.*, 2011), or musical clips (Ford, Addis, and Giovanello, 2011) as effective cues for eliciting AMs. For example, Ford, Addis, and Giovanello (2011) used musical excerpts to investigate the neural correlates supporting different levels of AM specificity in an unbiased way. During fMRI scanning, participants listened to musical clips and were instructed to press a button indicating the level of specificity of recall from lifetime period (e.g., "when I was in graduate school"), to more general event knowledge for repeated or extended events (e.g., "Christmas day"), and specific events (e.g., "the day I defended my PhD"). They found that more specific events elicited activity in bilateral MTL and medial PFC, whereas less specific events elicited activity in dorsolateral PFC. Thus, the neural correlates supporting AM retrieval differed according to the level of specificity (Addis *et al.*, 2012; Holland, Addis, and Kensinger, 2011).

AMs elicited by generic cues may not always be emotional or significant. However, they are unprepared and can involve a protracted period of retrieval (Figure 13.2a). These features result in two primary advantages of the generic cue method. First, the neural regions supporting memory construction can be investigated (Addis, Wong and Schacter, 2007; Conway, Pleydell-Pearce, and Whitecross, 2001; Daselaar *et al.*, 2008; St. Jacques, Kragel, and Rubin, 2011). For example, Daselaar *et al.* (2008) compared activity related to the search period of AM versus the maintenance/elaboration period. The initial search period was found to engage frontal regions involved in retrieval effort (right lateral PFC) and self-referential processes (medial PFC) but also posterior regions involved in accessing the memory trace (hippocampus, retrosplenial cortex), whereas the later period recruited posterior regions involved in the retrieval of contextual details (visual cortex, precuneus) and frontal regions linked to working memory (left lateral PFC). By segregating the search and elaboration phases of memory construction, the fMRI results show that AM retrieval relies upon separable component processes that come online at different points in time, and which can vary across the lifespan (Addis, Roberts, and Schacter, 2011; St. Jacques, Rubin, and Cabeza, 2012) and in clinical populations (St. Jacques *et al.*, 2011a).

A second advantage of the generic cue method is that online subjective ratings of AM retrieval are more accurate. This is important because phenomenological ratings and other properties of the retrieved memory can be used to examine trial-to-trial fluctuations in behavior as a function of brain activity using parametric analysis (see below). For example, in the aforementioned study using the generic cue method, Daselaar *et al.* (2008) examined activity during search and elaboration phases of AM retrieval that was associated with online ratings of emotion and reliving. They observed that emotion ratings were correlated with early amygdala activity, whereas reliving ratings were correlated with late visual cortex activity. This finding indicates that emotion contributes to AM retrieval even before event-specific memories are completely formed, whereas vividness develops late, as attention is directed to recovered visual images. Similarly, other studies using the generic cue method have observed that the effects of emotion tend to occur earlier (St. Jacques *et al.*, 2011a), whereas

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the effects associated with vividness occur later (St. Jacques, Kragel, and Rubin, 2011; St. Jacques, Rubin, and Cabeza, 2012).

Pre-scan interview

In the *pre-scan interview* method (Figure 13.2b), AMs are elicited by cues that refer to specific events (e.g., visiting the London Eye) collected prior to the scanning session (e.g., Addis *et al.*, 2004b; Denkova *et al.*, 2011; Maguire *et al.*, 2001). An advantage of this method is that the memories retrieved in the scanner can be controlled using pre-scan ratings (e.g., age of the memory, emotion, vividness, etc.). For example, Söderlund *et al.* (2012) used this method to pre-select memories of varying remoteness to examine how the connectivity of the hippocampus varied with memory age. Two days before the scanning session, participants were asked to generate, date, and provide titles for events that had occurred in the last week, month, year, and 10 years. During the fMRI scan, participants were presented with the event titles and instructed to retrieve the AM indicated. Similar to previous studies (Cabeza and St. Jacques, 2007; Moscovitch *et al.*, 2005), the hippocampus was active irrespective of the age of the memory. However, the pattern of functional connectivity with the hippocampus and other brain regions differed for AMs that were more recent (1 week to 1 year) versus those that were more remote (10 years). The hippocampus was functionally connected with anterior and posterior midline regions for recent AMs, but not for remote AMs.

Another advantage of the pre-scan interview is that the pre-selected retrieval cues can result in highly specific and accessible memories during scanning. Addis *et al.* (2012) took advantage of this aspect of the pre-scan interview to investigate the neural substrates supporting the two routes to AM retrieval: (1) direct, involving immediate access to a memory via a retrieval cue, and (2) generative retrieval, involving additional strategic retrieval processes to select a specific memory (for review see Conway and Pleydell-Pearce, 2000). One month prior to scanning, participants were asked to retrieve AMs cued using generic cue words (e.g., "dog"). Later, during scanning, participants retrieved an AM elicited by personalized cues from the pre-scan interview ("losing DOG at fresh pond") or generic cues ("event DRESS reminds me of"). Addis and colleagues reasoned that personalized cues should provide more direct access to a specific memory, whereas generic cues would involve more generative retrieval to select a specific memory. There were many similarities in the neural correlates supporting AMs retrieved more directly versus generatively. However, generative retrieval was associated with early recruitment of the lateral PFC, and direct retrieval generally involved stronger activations among regions involved in AM retrieval, such as the posterior and anterior midline.

There are some potential disadvantages to using the pre-scan interview method. During scanning participants may recall the interview session instead of the AM they had originally recalled. Further, retrieving the AM during the interview session could alter its subsequent retrieval during scanning (St. Jacques and Schacter, 2013), and, consequently, the AM actually retrieved during scanning may differ in its content and phenomenological properties. These issues could potentially be

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attenuated by interposing a substantial time interval between the pre-scan and scanning sessions (e.g., Maguire and Mummery, 1999). In sum, the neural properties supporting AM can differ due to previous retrieval attempts during the pre-scan interview.

Independent sources method

In the *independent sources* method (Figure 13.2c), cues to elicit AMs are generated by external sources such as friends and family (Gilboa *et al.*, 2004; Rabin *et al.*, 2010; Rabin and Rosenbaum, 2012; Steinvorth, Corkin, and Halgren, 2006). The independent sources method combines some of the advantages of the foregoing two methods, because memories are unrehearsed and can be constrained by gathering additional information from the sources. Additionally, it can provide greater variability in the vividness of memory retrieval, although this could be a disadvantage if participants are unable to remember a large number of events provided by the sources. Gilboa and colleagues (2004) used the independent sources method to investigate the role of the hippocampus in the recall of recent and remote memories that varied in vividness. AMs were elicited by personal photographs that depicted events ranging from childhood to the present collected from friends and relatives of the participants. Participants were asked to recall the event depicted in the photograph during fMRI. Gilboa and colleagues found that the hippocampus was recruited to a greater extent when memories were vividly recalled compared to when they were less vividly recalled, but the extent to which the hippocampus was recruited was not strongly associated with the particular age of the memory.

Similarly, Steinvorth, Corkin, and Halgren (2006) employed the independent sources method to investigate the retrieval processes involved in remembering recent and remote AMs. In this study, personal diaries were also used, and retrieval cues during fMRI scanning consisted of sentences describing personally experienced events. During scanning, participants were asked to search for the described memory and to press a button as soon as they could recall the memory, and then to elaborate upon it. They found that search and elaboration recruited a similar pattern of activation, with involvement of the hippocampus across both retrieval phases irrespective of the age of the memory.

Prospective method

In the *prospective* method (Figure 13.2d), participants are asked to keep a record of events in their lives to be used as retrieval cues in the scanner (e.g., Cabeza *et al.*, 2004; Levine *et al.*, 2004; St. Jacques *et al.*, 2008). The main advantage of the prospective method is that it allows for the greatest amount of control over the encoding of retrieved memories and can allow verification of retrieval accuracy. For example, St. Jacques *et al.* (2008) used the prospective method to investigate accurate temporal-order memory. Using a digital camera, participants took photos of familiar campus locations in a particular order over a period of several hours, just as a tourist might take photos of landmarks while on vacation. On the following day participants were

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scanned while making temporal-order judgments concerning pairs of photographs from different locations that varied in the number of photos between them. It was found that accurate temporal-order decisions on pairs of photos with shorter time-lags recruited regions previously associated with recollection (left PFC, parahippocampal gyrus), whereas longer time-lags recruited regions linked to familiarity (right PFC). Use of the prospective method allowed for control over the temporal order of encoding and verification of accuracy, making this study one of the first to examine the neural correlates of temporal order for autobiographical events. Greater control over the properties of memory encoding and accuracy can also allow for careful assessment of impairment in individuals with memory complaints (e.g., Levine *et al.*, 2009).

Until recently, a disadvantage of the prospective method was that recording experiences interfered with the natural encoding of AMs. By using innovative camera technologies that employ sensors and timers to automatically capture hundreds of photographs when worn, it is now possible to prospectively generate idiosyncratic and visually rich retrieval cues which may be more effective in eliciting AMs in the laboratory (e.g., St. Jacques, Conway, and Cabeza, 2010; St. Jacques *et al.*, 2011b). One example of such technology is the SenseCam (also known as ViconRevue), a small wearable digital camera that can automatically trigger thousands of photos in a single day without disrupting the ongoing experience, which differs from other methods using digital cameras to elicit AMs (Cabeza *et al.*, 2004; St. Jacques *et al.*, 2008). Several photographs from a particular event (e.g., eating ice cream) can be consecutively viewed to create a dynamic retrieval cue from the field of view of the wearer (http://www.youtube.com/watch?v=sr1i-sICafs). For example, St. Jacques *et al.* (2011b) used the SenseCam to examine neural differences in self-projection of self versus other perspectives. During functional scanning, participants were shown short event "movies" composed of SenseCam photographs from their own life (self) or another individual's life (other) and were asked to re-experience or understand the self versus other perspectives, respectively. The results showed that projection of self versus other differentially recruited distinct regions of the medial PFC. Projection to the personal past recruited ventral medial PFC, whereas observing another person's perspective recruited dorsal medial PFC, suggesting that the rich sense of re-experience of the personal past is functionally dissociable from similar shifts in perspective that contribute to inference of another person's mental state (also see Rabin *et al.*, 2010; Spreng and Grady, 2010).

Analysis Methods Relevant to Autobiographical Memory

Most fMRI studies on AM employ a general linear modeling (GLM) approach, as it can be used for several kinds of statistical analysis such as correlations, one- and two-sample *t*-tests, analysis of variance, etc. It is thus frequently utilized to identify brain regions preferentially recruited by a particular task, condition, and/or group – as compared to a contrasting task, condition, and/or group (i.e., subtraction method) – as well as brain regions commonly activated during two or more tasks, conditions

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and/or groups (i.e., conjunction method). Additionally, researchers capitalize on the fact that AMs vary across subjective (e.g., vividness, valence, etc.) and objective dimensions (e.g., recency/remoteness), which can be analyzed parametrically as predictors shown to modulate activity in different brain regions. Finally, the very complexity of AM has motivated researchers to start employing multivariate approaches in an attempt to understand the relationship between functional brain networks underlying AM. These methods include, but may not be limited to, functional and effective connectivity analyses. These analysis approaches are discussed in turn.

General linear model

The general linear model (GLM) is a univariate analysis technique that fits a continuous dependent variable – that is, the proxy of neural signal measured by fMRI known as blood-oxygen-level-dependent (BOLD) signal – onto a linear model relating it to one or more continuous or categorical variables, such as reaction times or experimental conditions. Most fMRI researchers in AM use the GLM to determine statistically significant differences in BOLD responses between two or more experimental conditions. More simply, each fMRI dataset could be seen as a matrix of voxels coding for varying levels of BOLD activation for a set time-course. The GLM computes whether the average activation per voxel correlates with the time-course of a particular experimental condition, and whether or not this average statistically differs from the average activation in another condition. Thus, *t*-tests are usually employed to find out whether such differences in activation are statistically significant – a process commonly known as *contrast*. The GLM can also analyze commonalities between conditions, by way of using contrasts in an additive rather than a subtractive manner. Essentially, these *conjunction* analyses examine whether two or more tasks (or groups) engage the same brain regions, by determining whether the same voxels are activated during both tasks (or for both groups) in the absence of any interaction effects (Friston *et al.*, 1999; Nichols *et al.*, 2005).

The first functional neuroimaging studies of AM contrasted autobiographical retrieval tasks with either a resting baseline or a control condition, using the *subtraction* method: the direct comparison of two conditions that are assumed to differ in only the aspect or process being manipulated (i.e., the independent variable). It is thus assumed that the activated voxels that survive this comparison reflect the underlying neural activity of the process of interest. Some of the earliest functional neuroimaging studies actually contrasted AM retrieval against a resting baseline (Andreasen *et al.*, 1995, 1999). For example, Andreasen *et al.* (1995) used PET to examine the neural correlates of AM retrieval versus resting baseline, thought to be an "unfocused" recall of past experiences. The results showed similar activation in the medial PFC and precuneus during focused AM and unfocused memory retrieval occurring during resting baseline. However, it is important to keep in mind the significant overlap between the neural regions associated with AM retrieval and the default network when using resting baseline as a control task. Indeed, in a review of functional neuroimaging studies of AM, Svoboda and colleagues (2006) observed that studies that had employed baseline as a control task were less successful in reporting some of the brain regions that support AM retrieval, such as the medial PFC (Stark and Squire, 2001).

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Another strategy is to use a semantic memory task as control (e.g., Conway *et al.*, 1999; Denkova *et al.*, 2006; Graham *et al.*, 2003; Ryan *et al.*, 2001). Following this logic, in an early PET study Conway and collaborators (1999) intended to subtract out the non-autobiographical components of memory retrieval to isolate activations uniquely related to AM (see also Graham *et al.*, 2003). Unfortunately, the use of semantic memory tasks as a control condition for AM could subtract away brain activity that actually supports AM retrieval. For example, an influential theory of AM suggests that semantic memory gates access to autobiographical details (Conway and Pleydell-Pearce, 2000), and there is evidence that AM retrieval involves the integration of both episodic and semantic components in memory (Levine *et al.*, 2002; St. Jacques and Levine, 2007). Moreover, brain regions involved in semantic memory are frequently observed in AM retrieval (for review see Svoboda, McKinnon, and Levine, 2006).

Other studies have attempted to control for visual imagery processes (e.g., Addis *et al.*, 2004b; Gardini *et al.*, 2006) and episodic memory processes (e.g., Cabeza *et al.*, 2004), among other factors. Unfortunately, for complex processes such as those involved in AM, there is really no perfect control condition. Use of the GLM in functional neuroimaging studies of AM is probably most effective when contrasts compare variations within AM, such as recent versus remote AMs (for review see Cabeza and St. Jacques, 2007), episodic AM versus semantic AM (for review see St. Jacques and Cabeza, 2012), direct versus generative retrieval (e.g., Addis *et al.*, 2012; Holland, Addis, and Kensinger, 2011), specific versus general AMs (Ford, Addis, and Giovanello, 2011; Levine *et al.*, 2004; Maguire and Mummery, 1999), etc.

Parametric approach

Similar to directly contrasting AMs that categorically vary on certain dimensions, the parametric approach examines how AMs vary according to continuous dimensions of AM experience by including additional regressors on variables within the GLM. Parametric modulators can include subjective ratings and other dimensions that are captured online or in a post-scan interview. For example, using a parametric modulation analysis, Addis *et al.* (2004b) observed that activation of the left hippocampus is positively correlated with the level of detail and personal significance, as well as valence, when recency is controlled for. A subsequent study showed that the right frontopolar cortex also co-varies with the amount of detail during both AM and future projection tasks (Addis and Schacter, 2008).

However, the parametric approach should be used with caution. One major issue is that the effects of two phenomenological characteristics that we take to be psychologically distinct may actually be correlated, which means that it may be difficult to interpret whether a parametric effect is unique to a particular regressor. For example, AMs that are more arousing (e.g., Reisberg *et al.*, 1988; Talarico, LaBar, and Rubin, 2004) or positively valenced (e.g., D'Argembeau, Comblain, and Van der Linden, 2003; Destun and Kuiper, 1999; Schaefer and Philippot, 2005) also tend to be more richly recollected. Although it is possible to "control" for the effects of another dimension by including it as a different regressor, a GLM will still have difficultly assigning variance to each regressor when they are highly correlated.

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Multivariate approaches

Multivariate techniques allow for the simultaneous analysis of patterns of co-activation across voxels. One of the most utilized multivariate statistical techniques in neuroimaging research of AM is *partial least squares* analysis (PLS). First introduced to fMRI by McIntosh *et al.* (1996), PLS allows the identification of commonalities or "patterns" of whole-brain activity that correlate with either behaviors or specific aspects of the experimental design (e.g., groups, tasks, conditions). Although several variants of PLS can be used in neuroimaging research (Krishnan *et al.*, 2011), functional neuroimaging studies of AM have used spatiotemporal PLS (ST-PLS) because it permits ~~to identify~~ cross-correlations between brain activity across multiple time-points ~~(i.e., TRs)~~ and some factor of interest from the experimental design. This temporal dimension of ST-PLS proves advantageous when it comes to studying the neural structures underlying complex cognitive processes that take time, such as those involved in AM. Essentially, ST-PLS takes each participant's fMRI data into a data matrix (or "datamat") and cross-correlates it with a matrix of vectors coding for some factor of the experimental design ("design matrix"). Next, singular value decomposition is used to reveal orthogonal latent variables (LVs) that best account for the covariance. Repeated permutations and bootstrapping are then utilized to calculate the statistical significance of each LV. As such, when a~~n~~ LV reaches statistical significance, it indicates ~~statistically significant~~ similarities and differences between brain areas underlying two or more design features.

One of the first ST-PLS studies in AM was conducted by Addis and collaborators (2004a). In this study, participants were asked to recall either general or specific AMs, as characterized in Conway's hierarchical AM model (Conway, 1992; Conway and Pleydell-Pearce, 2000). LVs differentiated brain regions preferentially involved during specific (e.g., left precuneus and superior parietal lobe) versus general AM retrieval (e.g., right inferior temporal gyrus and right medial PFC). Importantly, by using ST-PLS analysis, Addis *et al.* (2004a) found that this differential pattern of activity emerged at different times in the trial, with activity in regions associated with general AM peaking earlier (~ 4 seconds after stimulus onset) than those associated with specific AM retrieval (~ 7 seconds). The authors interpreted this finding as lending credence to Conway's model, according to which general AM gates access to information about specific autobiographical events. Levine *et al.* (2004) also employed a PLS analysis in a prospective memory study examining neural regions associated with episodic and semantic components of AM retrieval. This study revealed a~~n~~ LV that differentiated regions uniquely associated with personal episodic information (e.g., medial temporal and posterior cingulate cortices) from general semantic information included in autobiographical remembering (e.g., left temporal and parietal cortices; see also Rajah and McIntosh, 2005).

More recently, PLS analysis in AM research has been employed to explore commonalities and differences between neural processes unique to AM and those engaged during other cognitive tasks, such as prospection, mentalizing, and counterfactual thinking. In addition to the Spreng and Grady (2010) study mentioned above, in which common patterns of brain activity for AM, prospection, and theory of mind were identified, other studies have explored similarities and differences in brain patterns during AM and episodic counterfactual thinking tasks, i.e., in which participants generate alternative ways in which one's past personal events could have occurred but

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did not (De Brigard and Giovanello, 2012). These studies have shown that episodic counterfactual thinking and AM share a common brain pattern of activation, and that the commonalities between the two vary as a function of how likely participants think it is that the counterfactual event could have occurred (Addis *et al.*, 2009; De Brigard *et al.*, 2013).

Another statistical approach used in AM research is known as *independent component analysis* (ICA; Calhoun *et al.*, 2001). ICA is a data-driven approach that decomposes neural networks via their time-course, and, unlike PLS, the components extracted are not limited to those related to task. While the overlap between components is minimized by ICA, the networks are not necessarily orthogonal as in PLS. Few studies have employed ICA to investigate AM (St. Jacques, Kragel, and Rubin, 2011; also see Botzung *et al.*, 2010). For example, St. Jacques, Kragel, and Rubin (2011) used ICA to examine the large-scale networks contributing to the construction and elaboration of AM. They found that AM retrieval involved functionally dissociable networks including the frontoparietal network, the MTL network and medial PFC network.

Another common approach is to explore functional connectivity, that is, functional relationships among different brain areas engaged during a particular task (Friston *et al.*, 1993; Friston, 1994). As mentioned, AM retrieval involves co-activation of different brain regions. However, mere co-activation does not mean that such regions are functionally, let alone causally, connected. To investigate how different regions cooperate with one another during a particular task, statistical models incorporate information about the time-course and intensity of activations. As such, functional connectivity analyses enable researchers to determine activation synchronicity through time across cross-correlated voxels or regions of interest (ROIs). The resultant pattern of cross-correlations provides an idea of the different brain regions that functionally cooperate during a particular task.

An example of this approach is a study conducted by Greenberg *et al.* (2005), in which, prior to scanning, participants were asked to generate cue words for a number of AMs. During scanning, participants were presented with self-generated word-cues and unrelated words, and they were asked either to retrieve the corresponding AM or else to perform a semantic memory task. Correlational analysis between a-priori regions of interest revealed functional connectivity among the amygdala, hippocampus, and right inferior frontal gyrus for the AM task but not for the semantic memory task. In another study, Viard *et al.* (2007) employed targeted correlational analyses to explore patterns of functional connectivity between different brain regions during retrieval of AMs from five lifetime periods in older adults. The analysis revealed strong functional connectivity among left hippocampus, left superior frontal gyrus, bilateral precuneus, and posterior cingulate gyrus across all lifetime periods. More recently, Viard *et al.* (2010) used this same approach to explore the interaction between this network and different retention intervals, revealing that it contributes equally to AM retrieval regardless of the age of the remembered episode – a result that lends credence to the view that the MTL is permanently required to recover episodic AMs irrespective of their remoteness (Nadel and Moscovitch, 1997; Nadel, Campbell, and Ryan, 2007; see also St. Jacques *et al.*, 2011b). Seed-PLS analyses have also been used to study functional connectivity between specific nodes and voxels across the rest of the brain throughout the duration of the event (Addis *et al.*, 2004a; Burianova, McIntosh and Grady, 2010; Söderlund *et al.*, 2012).

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One of the limitations of functional connectivity is that it does not provide information about the specific directionality of the functional connections, because it does not make reference to the causal contribution of the neural structures underlying the model. For that reason, researchers have incorporated statistical techniques that allow inference about causal influences among functionally connected neural regions – an approach known as *effective connectivity*. One such technique is structural equation modeling (SEM; Büchel and Friston, 1997; McIntosh and Gonzalez-Lima, 1994), which takes single nodes from the dataset revealed by the connectivity analysis and fits known neuroanatomical constraints onto the correlational model to reveal specific paths that best account for the interregional covariance in the BOLD signal.

Muscatell, Addis, and Kensinger (2010) used this methodology in a study examining differences in effective connectivity depending on the level of self-involvement participants felt toward the remembered AM. Among other findings, their SEM analysis revealed that left hippocampus exerts a positive influence on the medial PFC, which in turn positively influences the amygdala–hippocampal complex, during high self-involvement recollections. However, during low self-involvement recollections, the influence of the medial PFC on the amygdala–hippocampal complex is negative, suggesting that medial PFC and the amygdala–hippocampal complex work together during the retrieval of AMs with high levels of self-involvement, but independently when the level of self-involvement is low. SEM has also been used to examine how the effective connectivity network underlying AM retrieval is altered in patients with hippocampal damage (e.g., Addis, Moscovitch, and McAndrews, 2007; Maguire, Vargha-Khadem, and Mishkin, 2001).

Although we have almost exclusively limited our discussion to PET and fMRI studies, it is worth noting that other techniques have been employed by cognitive neuroscientists studying AM. One such technique is transcranial magnetic stimulation (TMS), whose repetitive use is often employed as a treatment for major depression, typically causing disruption in AM recollection (Burt, Lisanby, and Sackeim, 2002). With the advent of safer and more controlled ways of employing TMS in experimental settings, researchers are starting to use it to examine specific aspects of AM (for a review see Guse, Falkai, and Wobrock, 2010). Intracranial electroencephalography (EEG) has also been employed to explore variations in electrophysiological oscillations during AM. For instance, Steinvorth and colleagues (2010) used intracranial EEG to identify theta, gamma, and delta oscillatory signatures in hippocampal and entorhinal cortex for remote autobiographical recollection, which differed from those evoked by visual imagery and semantic retrieval. No doubt, future research will start incorporating different techniques as they become available.

Conclusions and Future Directions

Since the mid-1990s, research on functional neuroimaging of AM has come a long way. As Maguire (2012) reminds us, conducting functional neuroimaging studies on AM was initially viewed with skepticism, even disdain. Many thought that such an endeavor would produce essentially uninterpretable data, as it was

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thought that the complexity of the processes underlying autobiographical recollection would render them unwieldy. Nowadays, however, the consistency and reliability of a growing number of experimental results strongly suggest that functional neuroimaging of AM is a fecund area of investigation, and that its results helps us understand the neural mechanisms responsible for our ordinary experience of remembering the past. Functional neuroimaging evidence has revealed, for instance, that autobiographical recollection involves the interaction of different neural networks, which may depend on the nature of the retrieved memory (Andrews-Hanna *et al.*, 2010; Muscatell, Addis, and Kensinger, 2011; St. Jacques, Kragel, and Rubin, 2011). Additionally, it has also revealed that such networks overlap with the default network (Buckner, Andrews-Hanna, and Schacter, 2008), that they contribute to other cognitive processes such as mentalizing, future and counterfactual thinking (De Brigard *et al.*, 2013), and that, contrary to the classical model of memory consolidation, the hippocampus – and, in general, the MTL – appears to be involved in the retrieval of episodic autobiographical memory regardless of the remoteness of the remembered episode (Söderlund *et al.*, 2012). Additionally, functional neuroimaging studies of AM have also helped to expand the methodological reach and experimental design in research in neuroimaging in general. For instance, many of the studies reviewed above provide evidence demonstrating that it is possible to conduct experiments using ecologically valid stimuli, and that there are several alternatives to manipulate personally relevant stimulus in the scanner without sacrificing experimental control (e.g., St. Jacques *et al.*, 2011b).

Among the most exciting areas of ongoing and future research in functional neuroimaging of AM are studies on involuntary recollection (Berntsen, 1998, 2009). Most of the time, when we remember our personal past, we tend to do so involuntarily, which often results in a vivid recollective experience. However, it is still an open question to what extent the mechanisms of voluntary and involuntary AM retrieval overlap. Using the techniques for functional neuroimaging reviewed above, researchers may be able to shed light on these issues. Equally interesting is the question of the effect of reactivation on the original autobiographical memory (St. Jacques and Schacter, 2013). In one study, Mendelsohn *et al.* (2009) filmed a person during two days. Four months, and then two and a half years later, they tested this person's memory while undergoing fMRI. Their results showed, among other things, that even though the participant tended to incorporate more false details into her recollections as time went by, the AM network tended to correlate more strongly with memory confidence rather than with accuracy (Nadel, Campbell, and Ryan, 2007; Svoboda and Levine, 2009). Given the frequency with which AMs are reactivated in ordinary life, understanding the effects of reactivation on AM and its neural correlates constitutes an exciting avenue for future research. Finally, another research line that promises important developments in cognitive neuroscience of AM pertains to studies with special populations. The extent to which the neural correlates of AM are altered in pathological aging (see Chapter 20), in individuals with developmental or mood disorders, or in individuals with superior AM (Ally, Hussey, and Donahue, 2012; LePort *et al.*, 2012), to name a few, is still unknown. As a result, functional neuroimaging of autobiographical memory promises to be at the forefront of research in the cognitive neuroscience of memory.

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