Functional neuroimaging of autobiographical memory

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Autobiographical memory (AM) refers to memory for events from our own personal past. In the last decade there has been an explosion in the number of functional neuroimaging studies of AM, which is best exemplified in the number of reviews on this topic, varying from those focusing on the core regions involved in AM retrieval and methodological challenges (Maguire, 2001; Svoboda, McKinnon, and Levine, 2006), to emphasizing task-related differences in AM versus laboratory memory studies (Gilboa, 2004; McDermott, Szpunar, and Christ, 2009) or highlighting task-invariant patterns of activations common to AM and other similar tasks, such as imagining the future (e.g., Buckner and Carroll, 2007; Hassabis and Maguire, 2007; Schacter, Addis, and Buckner, 2007; Spreng and Grady, 2010). Functional neuroimaging studies of AM are important because they can investigate the neural correlates of processes that are difficult to study in laboratory stimuli (Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, 2012). An AM researcher, however, may still question what exactly such studies contribute to our theoretical understanding of personal memory. The present chapter considers three integral aspects of AM where functional neuroimaging data provide us with important insights. First, functional neuroimaging studies can inform our understanding of the complex retrieval processes in AM by allowing the examination of separable phases of memory retrieval. Second, such studies can distinguish the specific role of self-reference in AM and how it potentially directs memory construction. Third, functional neuroimaging studies of AM offer compelling ideas regarding the role of recollection in the timing and interaction of multiple component processes during retrieval, as well as the potential contribution of familiarity processes in recognizing autobiographical experiences. Before turning to these aspects, I first briefly review the main functional neuroimaging methods for investigating AM and the core brain regions typically involved in AM retrieval, which will be relevant to the studies discussed here.
Overview of functional neuroimaging of AM

Eliciting AMs in the scanning environment

Several methods have been used to investigate AM with functional neuroimaging (for review, see Cabeza and St. Jacques, 2007). The primary challenge of these methods is balancing the ability to exert control over the phenomenological properties of memory retrieval while also maintaining ecological validity (for review, see Cabeza and St. Jacques, 2007; Maguire, 2001; Svoboda, et al., 2006). For example, it is particularly 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 subsequent interpretations of brain activation (Cabeza and St. Jacques, 2007). Here I discuss two of the main methods, relevant to the studies reviewed below, which represent the extremes of control.

In the generic cues method (e.g., Daselaar, Rice, Greenberg, et al., 2008; St. Jacques, Botzung, Miles et al., 2011) AMs are generated from novel retrieval cues (e.g., table; Crovitz and Schiffman, 1974) and there is less experimental control over the type and properties of the retrieved memories. Memories elicited by generic cues are not necessarily emotional or significant, but they are unrehearsed such that retrieval in the scanner tends to be protracted and is not contaminated by recent retrieval attempts. These aspects result in two primary advantages for interpreting functional neuroimaging data. First, online ratings of reliving, the senses of re-experiencing, and other phenomenological properties associated with memory retrieval during scanning 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 by parametric analysis. Second, memory construction processes can be investigated more easily. Combined with a self-paced design, the protracted construction processes associated with the generic cue method make it possible to disentangle the functional activations associated with separable retrieval phases by using functional magnetic resonance imaging (fMRI). In these studies, participants search for a memory, press a button once a memory is formed, and then maintain and elaborate upon the memory. The self-paced button press is then used to segregate the search and maintenance/elaboration phases (see also Rubin, this volume, Figure 2.2).

In the prospective method, participants are asked to keep a record of events in their lives to be used as retrieval cues in the scanner (e.g.,
Cabeza, Prince, Daselaar, et al., 2004; St. Jacques, Rubin, Labar, et al., 2008). One of the main advantages of the prospective method is that it allows the greatest amount of control over the properties of retrieved memories. For example, it allows accuracy to be assessed, and this is important given that brain activity tends to vary as a function of retrieval accuracy (e.g., Daselaar, Fleck, Prince, et al., 2006). Until recently, however, the main disadvantage of the prospective method was that it interfered with the natural encoding of AMs. With 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 autobiographical memories in the laboratory (e.g., St. Jacques, Conway, and Cabeza, 2010; St. Jacques, Conway, Lowder, et al., 2011a). For example, SenseCam (also known as ViconRevue) is a small wearable digital camera that has electronic sensors (e.g., light, heat) that can automatically trigger thousands of photographs in a single day. This differs considerably from typical use of a digital camera to generate retrieval cues to elicit AMs during scanning (e.g., Cabeza et al., 2004; St. Jacques et al., 2008), because it does not disrupt the experience of events through the act of taking a photograph. Also, several photographs from a particular event (e.g., eating ice cream) can be consecutively viewed to create a dynamic retrieval cue (www.youtube.com/watch?v=sr1i-sICafs). The SenseCam lens also maximizes the field of view to better capture the perspective of the wearer by incorporating a wide-angle (fish-eye) lens. An additional advantage of these sensor-based camera technologies is that they are easier to implement in special populations (e.g., Berry, Kapur, Williams, et al., 2007; Pauly-Takacs, Moulin, and Estlin, 2010) because they require minimal input from the user.

Core regions involved in AM

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 (for review, see Svoboda et al., 2006), which has been referred to as the AM retrieval network (see Figure 7.1). AM retrieval depends upon control processes mediated by the lateral prefrontal cortex (PFC) (Petrides, 2005; also see Miller and Cohen, 2001) and top-down attention mediated by the dorsal parietal cortex (DPC) (for reviews, see Cabeza, 2008; Cabeza, Ciaramelli, Olson, et al., 2008), which guide the search and construction of spatiotemporally specific AMs supported by semantic information about oneself and the world. Because the
The final target of AM construction is a personal memory, it is critically dependent on self-referential processing involving the recruitment of the medial PFC (e.g., Craik, Moroz, Moscovitch, et al., 1999; Kelley, Macrae, Wyland, et al., 2002; Macrae, Moran, Heatherton, et al., 2004). The ability to retrieve a rich episodic AM also depends upon recollection processes, mediated by the hippocampus and retrosplenial cortex (for review, see Diana, Yonelinas, and Ranganath, 2007; e.g., Valenstein, Bowers, VerFaellie, et al., 1987) and is enhanced by emotional processing in the amygdala (for review, see LaBar and Cabeza, 2006) and visual imagery in occipital and cuneus/precuneus regions (Greenberg and Rubin, 2003). As memory details are retrieved, there is greater bottom-up attention mediated by the ventral parietal cortex (e.g., Berryhill, Phuong, Picasso, et al., 2007; for reviews, see Cabeza, 2008; Cabeza et al., 2008). There is interaction among these and other brain regions during AM retrieval, but for simplicity I discuss in isolation only the most important regions relevant to the present discussion.
Contribution of functional neuroimaging to theoretical perspectives of AM

Below I consider how functional neuroimaging studies have provided insight into three integral components of AM: (1) complex retrieval, (2) self-reference, and (3) recollection.

Complex retrieval

Previous functional neuroimaging studies have emphasized that AM retrieval involves controlled search processes associated with the recruitment of the PFC. The link between memory search and controlled retrieval processes in AM was first detected by an early positron emission tomography study that found activation in lateral PFC regions when comparing AM to semantic memory (Conway, Turk, Miller, et al., 1999). Although activation differences between these tasks may reflect many different factors (e.g., Cabeza et al., 2004) the link between AM and activations in the lateral PFC and other brain regions was supported by subsequent reviews (Maguire, 2001; Svoboda et al., 2006). The lateral PFC activity elicited by AM retrieval is predominantly left-lateralized (Maguire, 2001; Svoboda et al., 2006), and this is thought to reflect the contribution of semantic information to AM. Consistent with this suggestion, the left-lateralized pattern of activation in the PFC during AM is observed irrespective of the nature of the eliciting cue (Denkova, Botzung, Scheiber, et al., 2006). These findings provide empirical support for the model proposed by Conway and colleagues (Conway, 2001, 2005; Conway and Pleydell-Pearce, 2000), which suggests that AM construction typically involves generative retrieval associated with effortful and protracted search processes supported by semantic knowledge.

The protracted retrieval length of AMs combined with the generic cue method and a self-paced design during fMRI scanning enables the segregation of brain regions involved in different phases of memory retrieval (Daselaar et al., 2008; St. Jacques, Botzung, et al., 2011; St. Jacques, Kragel, and Rubin, 2011; St. Jacques, Rubin, and Cabeza, 2010). For example, Daselaar et al. (2008) compared activity related to the search period of AM with 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. Other research groups using different methods have largely found consistent results (e.g., Botzung, Denkova, Ciuciu, et al., 2008; Conway, Pleydell-Pearce, Whitecross, et al., 2003; Steinvorth, Corkin, and Halgren, 2006). The engagement of multiple frontal and posterior regions across the separable phases of retrieval demonstrates additional complexity regarding the generative nature of AM retrieval. These findings inform current models of AM (e.g., Conway, 2005) by suggesting that the iterative retrieval process consisting of multiple memory-construction mappings continues even after a spatiotemporally AM is accessed.

Understanding the separable phases of memory retrieval can also provide important insights into AM across the life span and in clinical populations. First, turning to research in life-span development, fMRI was employed to examine the effects of age during the search and elaboration phases of AM retrieval (St. Jacques, Rubin, et al., 2010). The main effect of healthy aging on AM retrieval is attenuation in episodic richness (Levine, Svoboda, Hay, et al., 2002; Piolino, Desgranges, Benali, et al., 2002; St. Jacques and Levine, 2007), but when during retrieval the age effect occurs is largely unknown. The results of this study suggest that the age-related attenuation in the episodic richness of AMs is associated with specific difficulty during elaboration, involving strategic retrieval processes underlying recovery of details. Age effects on AM activity were more pronounced during elaboration than search, with older adults showing less sustained recruitment of the hippocampus and lateral PFC (see Figure 7.2A). In linking the fMRI results to the age-related reductions in episodic richness observed behaviorally, it was found that functional activity in these regions was attenuated for AMs that were more episodically detailed. Further, there was an age-related decrease in the top-down modulation of the PFC on the hippocampus by episodic richness, possibly reflecting fewer controlled processes operating on the recovery of memory details in the hippocampus during elaboration. The present study shows that changes in the sustained response and coupling of the hippocampus and PFC underlie age-related reductions in episodic richness of the personal past. These results underscore the importance of decomposing the time course of retrieval processes when examining age-related effects by showing a differential pattern of functional activation across search versus elaboration processes in AM retrieval, and they provide greater understanding of the age-related reduction in episodic richness. For example, they suggest novel interventions to attenuate age-related...
Figure 7.2. Complex retrieval of autobiographical memory (AM). A) Interrogating the search and elaboration phases of AM reveals age-invariant activity in the right hippocampus and left ventrolateral prefrontal cortex (PFC) during search, but age-related differences in these same regions during elaboration. Dotted line represents the peak of the average motor cortex response for the button press. B) Simplified
differences in episodic richness by providing retrieval support at separable
time points during AM construction.

Second, turning to its use in clinical populations, we examined the
neural mechanisms affected by post-traumatic stress disorder (PTSD)
symptoms during the retrieval of emotionally intense AMs (St. Jacques,
Botzung, et al., 2011). PTSD affects a number of brain regions involved
in AM (Etkin and Wager, 2007; Shin, Rauch, and Pitman, 2006), and the
effects of emotional reactions extend beyond traumatic memories to non-
trauma-related AMs (Rubin, Boals, and Berntsen, 2008). However, little
is known regarding how PTSD would affect the neural basis of retrieval
across a sample of emotionally intense AMs. We used the generic cue
method and employed emotional words to elicit spontaneously generated
memories during scanning, and then combined this with online ratings of
emotional experience. This method allowed us to examine brain activity
during search and elaboration that parametrically varied with the emo-
tional intensity associated with retrieved memories on each trial. The
fMRI results showed that there was greater recruitment of the MTL and
other memory-related brain regions during the initial search versus elabo-
ration of negatively intense AMs in PTSD when compared to controls.
Thus, by segregating the time course of AM retrieval, using fMRI, we
revealed that PTSD affects the initial reactivity of brain regions supporting
emotion and memory. Understanding why PTSD leads to a boost in the
initial recruitment of the memory network during retrieval of emotionally
intense memories may provide novel insight into the alteration of AM in
this disorder.

The findings reviewed thus far suggest that the complex retrieval of AM
retrieval is supported by a distributed set of brain regions (Conway and
Pleydell-Pearce, 2000; Norman and Bobrow, 1976); however, they do not
consider the functional connections among these regions nor the potential
influence of memory accessibility. AM retrieval encompasses multiple

Caption for Figure 7.2. (cont.)
version of a dynamic causal model showing the integration among
networks contributing to AM retrieval and the influence of memory
accessibility and recollection. The medial PFC network drives the
construction and elaboration of AMs. Memory accessibility increases
the bottom-up influence of the medial temporal lobe (MTL) and
frontoparietal networks on the medial prefrontal cortex (PFC) network
during the construction of AMs. In contrast, recollection influences the
top-down influence of the medial PFC on the frontoparietal network
(during construction; rectangle) and MTL network (during elaboration;
circle).
neural systems that interact and are influenced by the properties of the retrieval process (Greenberg and Rubin, 2003; Rubin, 2005; 2006; also see Rubin, this volume). For example, the ease with which memories are accessed potentially influences whether generative or direct retrieval mechanisms are engaged (Conway and Pleydell-Pearce, 2000; Uzer, Lee, and Brown, in press; also see Moscovitch, 1992). To investigate these issues, we (St. Jacques, Kragel, et al., 2011) identified neural networks contributing to AM retrieval by independent-components analysis (ICA) (Calhoun, Adali, Pearlson, et al., 2001), and then examined whether memory accessibility (i.e., greater ease of retrieval) influenced the interaction among these networks in a dynamic causal model (DCM) (Friston, Harrison, and Penny, 2003; for a similar approach, see Stevens, Kiehl, Pearlson, et al., 2007). The fMRI results revealed several large-scale brain networks contributing to AM retrieval, including the following: (1) a left-lateralized frontoparietal network, including frontal and parietal cortices (primarily DPC extending into ventral parietal cortex [VPC]), which is linked to adaptive cognitive control processes (Dosenbach, Fair, Miezin, et al., 2007; Seeley, Menon, Schatzberg, et al., 2007; Vincent, Kahn, Snyder, et al., 2008); (2) the medial PFC network, involving anterior and posterior midline regions along with the bilateral VPC, which is a network associated with self-referential processes (Andrews-Hanna, Reidler, Sepulcre, et al., 2010; for a review, see Buckner, Andrews-Hanna, and Schacter, 2008); and (3) the MTL network, including the MTL and retrosplenial cortex, ventromedial PFC, and bilateral VPC, which is a network involved in declarative memory and the construction of mental scenes (Andrews-Hanna et al., 2010; Kahn, Andrews-Hanna, Vincent, et al., 2008; Vincent et al., 2006). These networks were differentially engaged across the separable phases of AM retrieval, such that the frontoparietal network was recruited only during the initial construction of AM, whereas the medial PFC and MTL networks were recruited across both phases. One interpretation of these results is that the initial construction of AM involves greater top-down control over memory, whereas recovery of memory details can occur throughout AM retrieval (also see Daselaar et al., 2008). These findings are potentially consistent with the attention to memory (AToM) model (for reviews, see Cabeza, 2008; Cabeza et al., 2008), which postulates that the DPC, observed here in the frontoparietal network, is associated with greater top-down attentional control during memory search, whereas the VPC, observed here in both the medial PFC and MTL networks, is linked to bottom-up attention processes as memory details are detected. Additionally, we also found that memory accessibility, defined as the fastest retrieval times within each participant, modulated the connectivity
among the neural networks supporting AM. During construction, memory accessibility increased the influence of the MTL and frontoparietal networks (see Figure 7.2B) on the medial PFC network. There was no effect of memory accessibility during elaboration. Thus, the ease of retrieval influenced both the bottom-up networks associated with the recovery of the memory trace and the top-down control network, which impinged on a network linked to self-referential processes. These results suggest that memory accessibility increases the integration among the neural networks supporting AM retrieval, and potentially contributes to direct retrieval processes.

Self-reference

Self-reference is a critical and defining feature of AM (e.g., Brewer, 1986; Conway, 2005). Functional neuroimaging studies have shown that AM retrieval typically involves greater self-referential processes when compared to memory retrieval for stimuli encoded in the laboratory (for review, see Gilboa, 2004). For example, Cabeza et al. (2004) conducted an fMRI study in which participants were asked to recognize photographs of familiar locations taken by themselves compared to photographs encoded in the laboratory. Using the prospective method allowed control over most of the factors that could potentially differ between the conditions, such as the type of test (recognition in both), emotional content (minimal in both), memories’ age (recent in both), retrieval success (measured and similar in both), semantic memory (similar in both), and internal structure (simple, disconnected events in both). With these six factors controlled, the AM and laboratory condition yielded very similar activations in several brain regions. Self-referential processing, however, was not controlled and likely accounted for the greater activity in the AM condition in the medial PFC based on previous functional neuroimaging evidence regarding the role of this region in self-reference (see Figure 7.3A; Kelley et al., 2002; Raichle et al., 2001). Others using different methods have also found greater involvement of the medial PFC in AM versus control tasks (Denkova et al., 2006), as well as when self-referential processes were manipulated within the AM condition (Levine et al., 2004; Maguire, Henson, Mummery, et al., 2001; Muscatell, Addis, and Kensinger, 2010).

Self-referential processes in AM allow for the awareness of the self in time, or autonoetic awareness (Tulving, 1983; Wheeler, Stuss, and Tulving, 1997). The ability to self-project to the personal past is closely related to the ability to understand another person’s perspective (Buckner and Carroll, 2007; Mitchell, 2009; Suddendorf and Corballis, 2007),
such that there is overlap in the neural correlates supporting these processes (for meta-analysis, see Spreng, Mar, and Kim, 2009). Thus, in order to fully understand the specificity of self-referential processes in AM, it is important to determine the differential aspects involved in the ability step into one’s own personal past versus another individual’s
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In order to address this issue, we conducted an fMRI study that employed the first-person perspective cues generated by the SenseCam to examine neural differences in projection of self versus other (St. Jacques, Conway, et al., 2011a). During functional scanning, participants were shown short event “movies” composed of 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. Our results showed that projection of self versus other differentially recruited distinct regions of the medial PFC. Projection to the personal past recruited the ventral medial PFC, whereas observing another person’s perspective recruited the dorsal medial PFC (see Figure 7.3B). These results are consistent with studies linking ventral medial PFC to inferences about one’s own self and dorsal medial PFC to mentalizing about another individual, such as during theory-of-mind tasks (Krueger, Barbey, and Grafman, 2009; Mitchell, 2009; Van Overwalle, 2009; also see Spreng and Grady, 2010). Further, parametric analyses linked the recruitment of each of these medial PFC subregions to online ratings tracking the ability to project. In order to gain further insight into the contribution of subregions of the medial PFC to projection of self versus other, we examined the functional connectivity of ventral versus dorsal medial PFC. These results revealed that the ventral medial PFC showed greater functional connectivity with the MTL network supporting memory (Kahn et al., 2008; Vincent et al., 2006), whereas dorsal medial PFC showed greater functional connectivity with the frontoparietal network supporting controlled processes (Vincent et al., 2008). Our fMRI results suggest 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, and this is similar to findings observed by other research groups (Rabin, Gilboa, Stuss, Mar, et al., 2010; Spreng and Grady, 2010; also see D’Argembeau, Ruby, Collette, et al., 2007; Rosenbaum, Stuss, Levine, et al., 2007).

The recruitment of the medial PFC is usually described for simplicity as activations; however, these differences typically occur because this region is less deactivated in the condition involving self-referential processing than in the control condition, as was also found in the aforementioned AM studies (see Figure 7.3; Cabeza et al., 2004; St. Jacques, Conway, et al., 2011a). That is, the AM condition does not elicit more activation in the medial PFC when compared to an implicit baseline condition where participants are asked to passively view a fixation. One explanation of this phenomenon is that self-referential processing, such as occurs during AM retrieval, is part of a default state of the brain (Gusnard and Raichle, 2001; Raichle et al., 2001). Consistent with this suggestion, the pattern of activation observed during
passive rest referred to as the default network overlaps with the regions supporting AM retrieval (for reviews, see Buckner et al., 2008; Spreng et al., 2009). Additionally, the content of thought during passive resting states appears to be largely composed of personally relevant events (e.g., Klinger and Cox, 1987). The fMRI findings reviewed here suggest that the number of personal memories that come to mind effortlessly may be much more prevalent than previously considered in the domain of AM, which has largely focused on voluntary and generative retrieval processes (but see Berntsen, 1996; also see Berntsen, 2007, this volume).

Not only are self-referential processes an important feature of AM, but they may also contribute to the construction of memory. The idea that the self modulates AM retrieval is consistent with theories of AM proposed by Conway (Conway, 2005; Conway and Pleydell-Pearce, 2000), but has been difficult to demonstrate behaviorally. Functional neuroimaging studies of AM provide direct evidence to support the widely accepted role of the self in memory construction. For example, in a previous fMRI study, Daselaar et al. (2008) found that the medial PFC was recruited to a greater extent during the initial search of AM than during the later maintenance or elaboration phase. This boost in the initial engagement of the medial PFC may help to initiate the construction of AM. Consistent with this idea, in another study, we found that the medial PFC network, rather than other candidate networks associated with memory (MTL network) or controlled processes (e.g., frontoparietal network), drove neuronal activation within the interacting neural networks supporting AM construction (see Figure 7.2B; St. Jacques, Kragel, et al., 2011). Similarly, Muscatell et al. (2010), in an fMRI study that directly modulated the extent of self-involvement, found increased connectivity with the medial PFC within the network supporting AM retrieval. In sum, the results of these fMRI studies suggest that self-reference does not simply reflect the contents of AM, but actually helps to initiate and maintain AM construction, thereby providing support for current models of AM (Conway, 2005; Conway and Pleydell-Pearce, 2000) that emphasize the role of the self in modulating memory construction.

Recollection

Recollection, the ability to retrieve contextual details and to re-experience or relive a past event, is an integral feature of AM (e.g., Baddeley, 1992; Brewer, 1996). Functional neuroimaging studies have linked recollection processes in AM to regions such as the hippocampus, left PFC, and visual cortex (Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, 2012; Svoboda et al., 2006). For example, we found hippocampal activity
associated with successful retrieval of both temporal and spatial context in AM (St. Jacques, Rubin, Lowder, et al., 2009). However, the functional connectivity of the hippocampus differed according to source memory demands. There was greater co-activation between the hippocampus and visual cortex for spatial context, whereas the temporal context increased the connectivity between the hippocampus and left PFC. Because AMs are encoded in the rich multisensory environment of the real world, they often involve the recall of numerous contextual details, and thus recollection may tend to be more graded when it occurs (e.g., Mitchell and Johnson, 2009; Parks and Yonelinas, 2007) versus memory for simple laboratory stimuli (for review, see St. Jacques and Cabeza, 2012). For example, in the aforementioned photo study, Cabeza et al. (2004) found greater recruitment in the hippocampus for AM versus laboratory memory retrieval. This finding may be explained by the fact that the amount of visual detail was one of the additional factors not controlled in this study and contributed to the recruitment of additional contextual details, as is consistent with the observation that the AM condition also elicited greater activity in the visual cortex.

Visual imagery is an important component of the rich recovery of contextual information in AM (Rubin, Burt, and Fifield, 2003; Rubin, Schrauf, and Greenberg, 2003; for a review, see Greenberg and Rubin, 2003). Visual imagery impairment can disrupt the entire retrieval process, potentially because AM depends upon the interconnection and activation of many separate systems, of which the visual system plays an integral role (Greenberg and Rubin, 2003; Rubin and Greenberg, 1998; also see Rubin, 2006). In order to better understand the mechanisms by which visual imagery enhances recollection, we conducted an fMRI study in which we compared the functional connections among the regions supporting AM retrieval elicited via verbal descriptions or visual images (St. Jacques, Conway, Lowder, et al., 2011b). We used the SenseCam to generate personal photographs to elicit AMs (visual) and compared this to memories retrieved via event descriptions (verbal) taken from logs of daily events that participants recorded. Following a week delay, participants were asked to recall the events depicted in short SenseCam clips or event descriptions, and then to rate the amount of reliving. We identified a common functional region of interest in the hippocampus based on parametric modulation analysis using the reliving ratings, which was then used in subsequent functional connectivity analysis. Given the central importance of visual imagery in AM, we predicted that visual images would foster integration among the brain regions supporting memory retrieval. Consistent with this prediction, the results indicated that AMs elicited using visual versus verbal cues involved greater co-activation among the
hippocampus and critical regions of the retrieval network, including the lateral PFC involved in retrieval control, the medial PFC associated with self-referential processing, and the ventral parietal cortex linked to bottom-up attention processes (see Figure 7.4A). The fMRI results

Figure 7.4. Recollection and familiarity processes in autobiographical memory (AM). A) Visual images augment AM recollection by increasing the functional connectivity of the hippocampus with the ventral parietal cortex (VPC) and medial prefrontal cortex (PFC). B) Left prefrontal cortex (PFC) was recruited to a greater extent when temporal-order judgments for AM events relied on recollection processes (shorter time lags), whereas right PFC showed a preferential recruitment when temporal-order judgments relied on familiarity (longer time lags).
suggest that visual images augment the recollection of autobiographical experiences by strengthening the functional connections among the retrieval network.

Providing visual cues to elicit AMs could also potentially attenuate reported gender differences in recollection. Several studies document superior AMs in females compared to males. For example, compared to males, females recall longer and more detailed AMs (e.g., A. Friedman and Pines, 1991; Pillemer, Wink, DiDonato, et al., 2003; Pohl, Bender, and Lachmann, 2005; Ross and Holmberg, 1992; Seidlitz and Diener, 1998), are more accurate at dating their AMs (e.g., Skowronski and Thompson, 1990), and are faster to recall AMs (e.g., Davis, 1999). However, previous studies examining gender differences in AM have relied upon verbal cues to elicit AMs and verbal processing strategies to determine the quality of retrieval, in which males might be at a disadvantage (for a review, see Andreano and Cahill, 2009). One means to examine gender differences in AM retrieval in a more unbiased way is to use functional neuroimaging to examine covert retrieval and also to manipulate the cue modality. We examined the interaction between gender and the type of cue (visual, verbal) on brain activity sensitive to reliving in a study using the SenseCam (St. Jacques, Conway, et al., 2010). Based on reported gender differences in the reliance on spatial versus verbal processing (for a review, see Andreano and Cahill, 2009), we predicted that males would retrieve more richly experienced AMs when cued via the photographs versus the verbal descriptors, whereas females would show an equal benefit for both types of cues. The behavioral results indicated that there were no gender differences in subjective ratings of reliving, importance, vividness, emotion, and uniqueness, suggesting that gender differences in brain activity were not due to differences in these measures of phenomenological experience. Consistent with our predictions, the fMRI results revealed that, compared to females, males showed a greater difference in functional activity sensitive to reliving for AMs elicited by visual versus verbal cues in the hippocampus, retrosplenial cortex, and visual cortex. Other functional neuroimaging studies of AM have suggested that gender differences may be due to differences in retrieval strategy (Piefke, Weiss, Markowitsch, et al., 2005), which may preferentially benefit some retrieval cues. The fMRI results emphasize the importance of using unbiased measures to elicit and evaluate AMs when examining gender differences, and they suggest that the female advantage in AM retrieval might be less robust once potential gender differences in cognitive strategies are controlled.
Emotion is an additional component of AM that contributes importantly to recollection during retrieval (e.g., Reisberg, Heuer, McLean, et al., 1988; Talarico, LaBar, and Rubin, 2004). AMs infused with emotion are associated with greater recruitment of the amygdala and the hippocampus (Cabeza and St. Jacques, 2007; St. Jacques and Cabeza, 2012; Svoboda et al., 2006). For example, Botzung, Rubin, Miles, Cabeza, et al. (2010) observed emotional modulation in the amygdala and hippocampus during retrieval of real-world memories for an emotionally charged college basketball game. Emotion may enhance AM recollection via the modulatory influence of the amygdala on the hippocampus (LaBar and Cabeza, 2006). For example, Greenberg et al. (2005) found greater amygdala–hippocampal interactions during AM compared to a neutral control task. In this study, activity in the amygdala was also correlated with activity in lateral PFC, suggesting a potential interaction between the emotional response and memory construction.

Given that both visual imagery and emotion contribute to AMs, an interesting question is whether their contributions occur simultaneously or at different points during AM construction. To investigate this issue, 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. Whereas emotion ratings were correlated with early amygdala activity, reliving ratings were correlated with late visual cortex activity. This finding indicates that emotion contributes to AM even before event-specific memories are completely formed, whereas vividness develops late, as reflexive processes turn to recovered visual images. Similarly, in other studies using the generic cue method, we have observed that the effects of emotion tend to occur earlier (St. Jacques, Botzung, et al., 2011), whereas the effects associated with vividness occur later (St. Jacques, Kragel, et al., 2011; St. Jacques, Rubin, et al., 2010). The fMRI results suggest that even though emotion and vividness ratings are positively correlated (e.g., Talarico et al., 2004), the time course of the underlying processes is different.

In contrast with recollection, familiarity, the sense of knowing without being able to retrieve contextual information or to re-experience the past, is not typically considered to be an integral aspect of AM (e.g., Conway, 2001). This may be the result of the greater emphasis on recall versus recognition in AM research. In order to investigate the potential contribution of both recollection and familiarity processes in AM retrieval, we conducted an fMRI study that relied on a recognition memory paradigm involving temporal-order decisions (St. Jacques et al., 2008). We used a prospective method employing a photo-paradigm in which participants took photos of many familiar campus locations in a particular order over a
period of several hours. On the following day, they were scanned while making temporal-order judgments to pairs of photographs from different locations. We manipulated the extent to which temporal order of autobiographical events relied on recollection versus familiarity processes by varying the time lag between pairs of photographs. For example, differences in memory strength can be used to temporally parse photographs separated by longer distances (e.g., photo taken in morning vs. afternoon), but contextual information would need to be reconstructed in order to distinguish two photographs with similar memory strength (Friedman, 1993, 2004). Thus, we predicted that familiarity processes would be engaged to discriminate events farther away in time, whereas recollection processes would be required to discriminate events closer in time. Consistent with our hypotheses, parametric fMRI analyses linked shorter time lags to activations in regions previously associated with recollection (left PFC, parahippocampal, precuneus, and visual cortices) and longer time lags with regions previously associated with familiarity (right PFC; see Figure 7.4B). We also observed sub-threshold activity in the hippocampus proper for shorter time lags, consistent with the role of this region in memory in parsing temporal information (Kesner, Gilbert, and Barua, 2002). The current findings suggest that one factor explaining the predominantly left-lateralized recruitment of lateral PFC within AM is the bias toward retrieval tasks that emphasize recollection processes. Future studies of AM retrieval that incorporate retrieval tasks that rely on familiarity, such as recognition memory, may find greater involvement of the right lateral PFC and potentially lead to novel understanding of both recollection and familiarity processes in AM.

Conclusions

The evidence reviewed here suggests that functional neuroimaging studies of AM potentially provide novel insight by contributing to our understanding of the complex retrieval, self-referential, and recollective properties of the personal past. I focused on three critical components of AM retrieval, but this is certainly not an exhaustive list of the potential contributions of functional neuroimaging to our theoretical understanding of personal memory. Functional neuroimaging evidence contributes to issues of memory remoteness/consolidation (Moscovitch, this volume), future simulation (D’Argembeau, this volume), child (Bauer, this volume) and life-span development (Fitzgerald and Broadbridge, this volume), and the contribution and interaction among separable systems underlying AM retrieval (Rubin, this volume). Further, although direct empirical studies are currently lacking, one could also
foresee future areas where functional neuroimaging studies could provide important insight, such as understanding the retrieval mechanisms of involuntary AM (Berntsen, Hansen, Lee, et al., this volume) or the organizational structure of AM (Brown, this volume). Understanding the neural correlates that orchestrate the recovery and conscious experience of our personal past is critical for a comprehensive theoretical understanding of autobiographical memory.

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