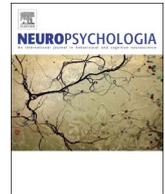


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Editorial

Autobiographical memory: From experiences to brain representations

Autobiographical memory (AM) refers to representations of one's personal history that integrate self-related knowledge with experienced events (including their interpretation and evaluation) across the extended self (Conway and Pleydell-Pearce, 2000; Levine, 2004; Rubin, 2006). AM is shaped by a multitude of factors, including self-schema, goals, emotion, culture, age, gender, and genetics. The vastness and diversity of past personal experiences captured in our AMs define who we are (Conway and Pleydell-Pearce, 2000; Fitzgerald, 1996; Levine, 2004; Libby and Eibach, 2002), help us relate to other people (Fivush, 2011; Nelson and Fivush, 2004), and enable future planning (Klein et al., 2002; Rosenbaum et al., 2005; Schacter et al., 2007; Tulving, 1985). The same processes that allow for its flexibility can also lead to inaccuracies and distortions (Schacter et al., 1998).

The dynamics of AM across development, and the disorders that disturb it, remind us of its intricacies and fragility, and the complex network of brain regions on which it depends. AM continues to be of widespread interest, studied with a range of methods from a variety of disciplines. To a large extent, psychological and neuropsychological studies of memory that treat the encoding and recollection of discrete stimuli in the lab as 'mini-events' aim to model the processes that allow for AMs to be retained and retrieved. While the rigorous study of mini-events serves to illuminate important aspects of fundamental memory mechanisms, it does not necessarily capture the processes that enable the representation and retention of real-life AM. A deeper understanding of AM and the neural systems and processes that support it is therefore critical to the field of memory research more broadly. This special issue should be of interest to a broad audience that includes those interested in memory theory, brain function, clinical populations, and methodological approaches to the study of the human mind. Below we provide an overview of some of the themes that cut across the twenty papers that comprise this issue.

1. Competing theoretical frameworks

In the past four decades, models of AM have been greatly influenced by conceptual advances and theoretical discussions of episodic and semantic memory (Tulving, 1972, 1983) and of declarative memory more generally (Squire, 1992). These models focus on diverse forms of conscious experiences that are associated with retrieval of different kinds of autobiographical knowledge (Levine et al., 2002; Tulving, 2002). The present volume demonstrates that this conceptual framework still stimulates discussion and continues to yield valuable insights to the field. For example, using magnetoencephalography (MEG) techniques in healthy individuals, episodic AMs were distinguished from semantic ones by large-scale neural synchrony in the gamma range (Fuentemilla et al., 2017). Patient studies suggest that processes of semanticization or schematization may account for apparent preservation of autobiographical details with advancing neurodegeneration (Irish et al., 2017) and for the phenomenology of gist-based AMs in patients with temporal lobe epilepsy (McCormick et al., 2017b). Furthermore, AM was found to be more semantic in nature in older adults compared with younger adults (Spreng et al., 2017 cf. Levine et al., 2002). The interpretation of AM characteristics in these studies is consistent with the broad memory systems framework that considers declarative memory as consisting of two memory types: episodic and semantic (regardless of continued discussion as to the extent to which these are dissociable systems).

There are, however, competing theories of AM. One prominent theory considers the Self as a separate system around which AMs are constructed, and emphasizes the hierarchical structure of the autobiographical knowledge base (Conway and Pleydell-Pearce, 2000; for other influential models see Rubin and Umanath (2015), and Maguire and Hassabis, (2007). The Self memory system model considers episodic memory and AM as distinct entities, generating different predictions as to the neural mechanisms of laboratory-tests of episodic memory and AM. According to meta-analyses of neuroimaging studies, there are indeed significant differences in the functional neuroanatomy of AM and episodic memory (McDermott et al., 2009). A notable problem with meta-analytic studies is that they survey episodic and AM tasks that differ on many confounding dimensions, thus questioning the validity of the detected activity patterns. In this issue, Monge and colleagues attempted to overcome this challenge by employing tasks that induced comparable reaction times for retrieval from episodic memory of 4-word chains previously studied in a laboratory setting and retrieval of AMs using cue words. They found that these tasks generated similar activation patterns during memory search (or construction), but significantly different patterns during memory recovery (or elaboration) (Monge et al., 2017). AMs were associated with greater activation in brain regions that comprise the default mode network, including posterior and prefrontal midline cortices, angular gyrus, hippocampus, and parahippocampal gyri, whereas lab-based episodic memory was associated with greater superior parietal lobule activation. Interestingly, network functional connectivity (regardless of retrieval stage) also differed between AM and lab-based episodic memory, with AM showing stronger network connectivity between the DMN and the ventral attentional network (Monge et al., 2017).

In a separate study, Zeman and colleagues found dissociations between episodic memory as measured by neuropsychological tests and AM in two

patients with temporal lobe epilepsy (TLE). The two suffer from severe AM deficits in the face of normal performance on neuropsychological tests (although there is suggestion of accelerated long-term forgetting over a week). Consistent with theories that place the self memory system and personal goals at the heart of AM, this study highlights the impact of AM deficits on participants' coherent sense of self, place in interpersonal relationships, and ability to imagine different future scenarios. These findings are consistent with the idea that the self is a critical component for the long-term survival of episodic memories that can be briefly formed, but cannot be integrated into very long-term autobiographical representations (Zeman et al., 2017).

Tanguay and colleagues propose that self knowledge differs from both semantic and episodic memory. Participants rated adjectives either in relation to the self or to a semantic category, and were later tested on recognition of the adjectives (episodic memory) while EEGs were recorded (Tanguay et al., 2017). Self-related processing was associated with a unique P200 and a late positive component, which was modulated by its temporal orientation (past, present or future).

Another tenet of the Self memory system model (Conway and Pleydell-Pearce, 2000), the hierarchical nature of AMs, is also reflected in the present volume (Grilli et al., 2017). The life stories of amnesic individuals with damage to the medial temporal lobe (MTL) were segmented into chapters that could span months or even years based on shared themes, such as education, career, relationships, etc., and were further scored for the quality (complexity and richness) of their descriptions. One fascinating finding from this study is that event-specific or experience-near representations may be critical for more complex representation of higher-level life "chapters". This is reflected in the tendency of MTL patients to report life chapters in a more linear fashion, with little temporal overlap between them, even though their life chapters were thematically connected to each other in a way that was similar to those of control participants.

2. Disorders of autobiographical memory

Much of what we have learned about memory generally, and AM in particular, has been inspired by studies of patients with memory disorders, and such studies continue to lead to new discoveries (Rosenbaum et al., 2014). In addition to allowing inference of causation, patient studies also impose constraints on the interpretation of findings from neuroimaging, often forcing a more nuanced approach to neurocognitive theories. For example, two patient studies reported in the present special issue demonstrate these constraints in the realm of the hippocampal role in AM, future-oriented cognition, and narrative construction, all of which have been argued to draw on similar processes and functional neuroanatomy (further discussed below). Patient SG, with focal autobiographical retrograde amnesia due to hypoxia, is described with deficits in episodic future thinking, but intact future-oriented cognition outside of subjective time (De Luca et al., 2017), suggesting that subtle differences in types of future-related thought need to be addressed cf. Craver et al. (2014). Moreover, amnesic patients with hippocampal damage were found to be able to generate coherent narratives when provided with external structure in the form of a picture book (Keven et al., 2017), placing constraints on theoretical models advocating that the ability to form a coherent narrative is one of the common underlying features of memory and imagination.

Patient studies also allow insight into the long-term dynamics of AM formation, which are difficult to observe using neuroimaging techniques. For example, early-onset amnesia was found to impair retrieval of retrograde life chapters compared with later-life amnesia, suggesting the MTL supports a protracted process of binding and organizing autobiographical knowledge into abstract life themes, but that once organized, this knowledge is independent of the MTL (Grilli et al., 2017). The current issue also showcases how longitudinal studies of patients with neurodegenerative disorders are of great value in shedding light on the neural architecture of AM by tracking changes in the expression of remote and recently acquired memories (Irish et al., 2017). Patients with Alzheimer's disease displayed flat retrograde gradients for detailed AMs, with little change over a year; however, because only on follow-up did AM details correlate with semantic cognition, the authors suggest that a process of gist extraction and semanticization may be at play (Irish et al., 2017). This is consistent with the observation that performance was associated with cortical thinning of regions traditionally thought to support semantics (lateral and anterior temporal cortices). This study also highlights inherent difficulties associated with studying memory in the context of brain damage. Specifically, some of the findings, such as the association between deterioration of recent memories and progressive cortical thinning in posterior parietal regions in frontotemporal dementia could reflect either encoding or retrieval deficits as more recent memories are also acquired by a more impaired system (Irish et al., 2017). Studies with patients with neurodegenerative disorders also offers the opportunity to examine how AMs are accessed. Kirk and Berntsen cued patients with Alzheimer's disease and matched controls with everyday objects presented either as words or as actual objects that were appropriate for participants' early lives. Concrete objects facilitated memory recall for all subjects, but disproportionately so for the Alzheimer's disease patients (Kirk and Berntsen, 2017). Notably, cueing with real objects not only enhanced the initial access to a memory, but also the quality of recalled events as reflected by the number and nature of details recalled. It is interesting that in another study reported here, personal object names were found to be inferior to personal location names in cueing memories for a majority of participants (Hebscher et al., 2017). It is possible that photos of familiar places could enhance patients' memories even further, unless the multimodal nature of the cue was a critical component of the observed facilitation in Kirk and Bensten's study.

Studies of neuropsychiatric disorders are also highly instructive in understanding pathological AMs and their functional neuroanatomy to such an extent that AM disturbances are considered core symptoms for some disorders. Psychogenic (dissociative) amnesia and major depressive disorder (MDD) traditionally differ in the treatment of AM impairment as a defining feature of the disorder, although AM impairment is often viewed as more central to psychogenic amnesia than to MDD (but see Dalgleish and Werner-Seidler, 2014 for a view of AM as instigating depression). Moreover, dissociative symptoms - the hallmark of psychogenic amnesia - can also co-occur in individuals with MDD who were exposed to trauma. In one of the largest formal surveys of cases of psychogenic (dissociative) amnesia to date, Staniloiu and colleagues highlight the functional quality of retrograde AM impairment in helping patients to cope with traumatic life events for which they are amnesic but also point to individual differences in the nature of AM deficits, particularly as they apply to the anterograde domain and the co-occurrence of other cognitive and somatic changes (Staniloiu et al., 2017). While no clear or consistent structural brain abnormalities emerged in this population, the study by Parlar and colleagues demonstrates functional differences in brain activity during AM retrieval in MDD patients with co-morbid history of trauma, which might help to explain the neural basis of dissociative symptoms. Activity within left anterior insula and left parahippocampal cortex was lower in patients compared to controls during retrieval of positive AMs, suggestive of reduced embodiment and vividness of the patients' memories. Interestingly, reduced insula activity correlated with low episodic specificity of positive events, whereas increases in parahippocampal activity during retrieval of negative events correlated with level of parental support (Parlar et al., 2017). Impaired recollection of AMs is a central symptom in both of these disorders, and in both it may serve as a protective mechanism against intense emotional reactions.

3. Neuroimaging and indirect approaches

Functional neuroimaging techniques revolutionized cognitive neuroscience starting in the 1980's; AM, however, was a relative latecomer to the scene, with only a handful of studies published before the mid 2000's (Fink et al., 1996; Nadel et al., 2000). Methodological advances in scanning and analytical approaches as well as in how AM is tested have led to a dramatic increase in research on the topic, and many of the studies presented here reflect these advances. Bonnici and Maguire address a critical question about the dynamics of memory representations of AM over time by scanning the same participants retrieving the same memories in two scan sessions two years apart (Bonnici and Maguire, 2017). Using multivoxel pattern analysis (MVPA) to 'decode' the same memories, they demonstrate that as memories age from two weeks to two years, they can be better decoded from activity in voxels within the ventromedial prefrontal cortex (vmPFC). Moreover, within the hippocampus, informational maps of the same memories over time have little overlap and tend to be more posteriorly distributed two years later. The final informational maps were almost identical to those of memories studied at ages 10 and 12, suggesting 'systems consolidation' may be completed within 2 years at most, much shorter than suggested by standard consolidation theories (Squire, 2004). This is consistent with memory transformation accounts that suggest vmPFC is involved in extracting the gist from episodic memories (Winocur and Moscovitch, 2011) and models of vmPFC emphasizing its role in schematic representations generally (Gilboa and Marlatte, 2017; van Kesteren et al., 2012) and self-related schema in particular (Gilboa and Moscovitch, 2017; Rameson et al., 2010). The intriguing shift in hippocampal informational maps may, in addition, suggest that rather than 're-activating' the same hippocampal-neocortical ensembles that were active during encoding, the vmPFC (and/or other cortical regions) provide the hippocampus with informational units which it uses to construct a coherent representation 'on the fly' rather than re-construct a previously activated pattern (McCormick et al., 2017a).

While the dynamics of episodic AM have mostly been investigated by examining representational changes over time, St Jacques and colleagues take a different approach to examine this question. Participants generated personal event cues and then before scanning were asked to retrieve the event or generate a counterfactual for that cue either from an egocentric perspective or from an observer's perspective (St Jacques et al., 2017). During scanning, the same event cues were presented with the same instruction (repetition), or with the instruction to adopt a novel visual perspective or episodic counterfactual simulation (flexible repetition). Using fMRI adaptation, the authors demonstrate that adopting alternative perspectives for a memory renders its neural signature more similar to counterfactual simulation. Interestingly, however, this shift in memory representation does not involve vmPFC or the hippocampus, and, instead, appears to recruit left posterior inferior parietal and ventrolateral frontal cortices. Assuming these differences in neuroanatomy do not reflect methodological differences (e.g. fMRI adaptation vs. MVPA, use of region of interest/ROI etc.), they could reflect the explicitly spatial manipulation as well as the fact that it is likely that the same basic event details were retrieved on both occasions. A central issue that is not addressed directly by the studies in the present issue and that could affect the apparent dynamics of AM is accuracy. For example, the representational mismatch across time could reflect schema-consistent distortions of the original event that begin at encoding (Gilboa and Marlatte, 2017) and are exacerbated over time leading to overconfidence in erroneous memories of one's life (Barclay and Wellman, 1986; Mendelsohn et al., 2009). Indeed, follow-up studies on verifiable AMs demonstrate increased acceptance of false details and activity in the AM network that tracks confidence rather than accuracy, primarily in anterior temporal cortical regions (Mendelsohn et al., 2009), similar to models that implicated vmPFC in subjective confidence rather than knowledge per se (Lebreton et al., 2015; Hebscher et al., 2016).

There is a clear overlap between the core network supporting AM, prospection, and the so-called default mode network that is apparent in fMRI during resting state (Buckner and Carroll, 2007; Spreng et al., 2009). While broadly similar, it is important to also understand what distinguishes these functional networks to allow different cognitive functions (Rabin et al., 2010). One fruitful approach described in this issue is the use of resting state functional connectivity together with task-based analysis of autobiographical retrieval and prospection (Gilmore et al., 2017). By seeding ROIs from task-related activity of AM and future episodic thinking, different resting-state correlational maps could be more directly related to either of these functions using hierarchical clustering. It was reported that episodic future thinking corresponded more to default mode network regions and autobiographical remembering to the contextual association network, possibly reflecting the more constrained context in which AMs occur (Gilmore et al., 2017). The finding that AM retrieval is associated with regions outside the DMN at the network level (Gilmore et al., 2017) or to DMN's unique interactions with other networks (Monge et al., 2017) begins to elucidate how similar activation patterns may give rise to different phenomenological experiences. The different patterns reported by the different studies (contextual association network vs. ventral attentional network) need to be further investigated and could be the result of different analytical approaches, different ways of probing AMs, or a combination of these and other factors.

4. Individual differences and lifespan changes

Subjective experiences of remembering past events as well as objective measures of memory quantity and accuracy are significantly influenced by individual differences (D'Argembeau and Van der Linden, 2006; Palombo et al., 2013; Sheldon et al., 2016). In the present issue, individual differences in AM and their structural and functional brain correlates were demonstrated within healthy younger controls, across personality dimensions, based on gender and based on age. One study in the present issue demonstrated substantial individual differences in the dynamics of retrieval of AMs among healthy young adults (Hebscher et al., 2017). In this study, many but not all participants reported spatial context as a preferable point of access into their memories, and differences in the tendency to benefit from spatial memory cues was related to hippocampal CA1 volume; conversely, re-experiencing events from a first person's perspective was associated with precuneus volume. In another study, an interesting relationship was found between individual differences on personality dimensions and the influence of negative AMs on corticospinal excitability (Mineo et al., 2017). TMS-induced sensorimotor neurophysiological responses were influenced by concurrent retrieval of a negative affect AM compared with a neutral memory. Modulation of motor excitability in response to affective states may reflect preparatory 'fight or flight' reaction when a memory cue evokes a negative memory. Interestingly, higher scores on the Neuroticism personality trait predicted greater influence of memories on neurophysiological responses, suggesting those individuals who tend to respond negatively to threat and frustration show greater modulation of the excitability of motor areas. This is consistent with research showing that high neuroticism is associated with a tendency to report more intense emotional reactions to negative AMs (Ogle et al., 2017).

New insights into known gender differences in AM are provided by Manns and colleagues. They recorded EEGs while participants retrieved AMs, tracking changes in the time-frequency domain as memories unfolded over 3 s of retrieval (Manns et al., 2017). Alpha power was consistently reduced during cued retrieval, whereas alpha power synchrony demonstrated complex patterns of reduction and enhancement across time and across electrodes. There were early frontal alpha coherence reductions followed by later increases in parietal alpha coherence. Interestingly, in women, the

parietal alpha coherence was sustained throughout the retrieval period, whereas in men, it returned to baseline. This was interpreted as possibly reflecting more sustained elaboration processes in women or alternatively memory evaluation processes (Manns et al., 2017). While gender differences in AM recall are well-documented (Nelson and Fivush, 2004; Piefke et al., 2005), in this study, males and females did not differ on any of the rating scales used to assess memory. It remains to be clarified whether this reflects an insensitivity of the behavioural tools compared with neurophysiology or whether some aspect of the task (e.g., the short duration) did not allow for such differences to develop and the physiological changes are the precursors for subjective differences in recollection.

Finally, one study in the present volume investigated changes in AM as people age and linked these changes to age-related alterations in resting state connectivity (Spreng et al., 2017). Specifically, resting state connectivity in aging is associated with greater coupling between the default mode network and executive control regions in left prefrontal cortex, and the present study sought to investigate the relationship between the neuro-functional signature and characteristics of AM as people age. A common finding with aging is that older adults tend to produce fewer internal (or episodic) details and more external (or semantic) ones when recalling personal memories (Levine et al., 2002). As expected, older age was associated with stronger default to executive coupling during rest, and only in older adults the strength of this coupling predicted more semantic retrieval of AMs. Because the association was specific to the older adult sample, the authors suggest that it is the gradual accrual of life experiences and build-up of semantic knowledge that drives greater cross-network coupling and the age-related shift to reliance on more semantic processing. One interesting question that arises both from findings on gender differences and age differences in AM and the neural substrate that support it is the extent to which these reflect qualitative differences between groups or end states of continua within naturally occurring individual differences.

5. Relationship to future thinking and other cognitive abilities

A close relationship between remembering the past and imagining the future has long been identified (Klein et al., 2002; Okuda et al., 2003; Tulving, 1985). It has recently become a popular area of research boosted by the accumulation of neuroimaging data demonstrating similar patterns of activation during AM and future imagination (Addis et al., 2007; Schacter et al., 2007), the development of clear theoretical frameworks accounting for these similarities (Schacter et al., 2007, 2012), and the identification of commonalities across these functions and resting-state fMRI (Andrews-Hanna et al., 2010; Spreng et al., 2009). While commonalities have been the focus of much of this vast literature, researchers have also been interested in identifying differences between remembering and imagining. The typical finding is that imagining tends to recruit the core AM network more strongly as well as more distributed regions outside that network (Benoit and Schacter, 2015). This pattern is replicated in this issue (Gilmore et al., 2017), but in addition to the differential association with resting-state networks described above, the authors also found greater activity in parahippocampal and retrosplenial regions associated with AM compared to imagining future events.

A central theory of hippocampal function in memory and imagination suggests that the hippocampus is critical for construction of available details into a representation that places events within coherent (spatial) scenes (Hassabis and Maguire, 2007; Rubin and Umanath, 2015). One difficulty in testing this hypothesis is that most tasks that require construction also require the generation of the details that form the scene or the narrative. In this issue, Keven et al. use a picture book to show that when provided with details of an event, individuals with deficits in autobiographical remembering and in future imagining are nonetheless able to construct coherent narratives. The narratives constructed by these individuals were as detailed and coherent as healthy controls', and the patients were able to relate events to those that preceded them (Keven et al., 2017). It is therefore suggested that the hippocampal system is required for remembering and imagining not because it helps bind details into coherent wholes, but because it is needed to generate these details in the first place. If this is indeed the case, an alternate interpretation can be suggested regarding fMRI reports of stronger activation of the core AM network, including the hippocampus, during imagining than during remembering. At least for the hippocampus, this greater activation may not reflect the greater demands on constructive processes, as suggested in various forms elsewhere in this volume (Gilmore et al., 2017; St Jacques et al., 2017), but rather greater demands on detail generation.

This brief overview of the studies that appear in this special issue demonstrates how far we have come in research on AM as well as the extent to which this research has implications for other domains of human cognition. The great advances in behavioural and neuroimaging methodologies allow for a much more detailed account of how this unique human ability is made possible by the brain. The vibrant community that studies these functions put forward clear competing theoretical accounts that can be tested in new and creative ways using multiple methodologies including patient methods, neurophysiology and fMRI, each providing its unique strength. Many of the leading researchers in the field showcase their latest research into the inner workings of this critical human capacity in an attempt to answer long-standing questions, generate new ones and point to future directions.

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