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The precuneus and hippocampus contribute to individual differences in the unfolding of spatial representations during episodic autobiographical memory

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ABSTRACT

Spatial information is a central aspect of episodic autobiographical memory (EAM). Space-based theories of memory, including cognitive map and scene construction models, posit that spatial reinstatement is a required process during early event recall. Spatial information can be represented from both allocentric (third-person) and egocentric (first-person) perspectives during EAM, with egocentric perspectives being important for mental imagery and supported by the precuneus. Individuals differ in their tendency to rely on allocentric or egocentric information, and in general, the subjective experience of remembering in EAM differs greatly across individuals. Here we examined individual differences in spatial aspects of EAM, how such differences influence the vividness and temporal order of recollection, and their anatomical correlates. We cued healthy young participants (n = 63) with personally familiar locations and non-locations. We examined how cue type affects (i) retrieval dynamics and (ii) phenomenological aspects of remembering, and related behavioural performance to regional brain volumes (n = 42). Participants tended to spontaneously recall spatial information early during recollection, even in the absence of spatial cues, and individuals with a stronger tendency to recall space first also displayed faster reaction times. Across participants, place-cued memories were re-experienced more vividly and were richer in detail than those cued by objects, but not more than those cued by familiar persons. Volumetric differences were associated with behavioural performance such that egocentric remembering was positively associated with precuneus volume. Hippocampal CA2/CA3 volumes were associated with the tendency to recall place-cued memories less effortfully. Consistent with scene construction theories, this study suggests that spatial information is reinstated early and contributes to the efficiency and phenomenology of EAM. However, early recall of spatial information is not universal and other routes to recall exist, challenging some aspects of these models. Variability among participants highlights the importance of an individual differences approach to studying EAM.

1. Introduction

Episodic autobiographical memory (EAM) enables reliving personally experienced past events, recalling the sensory information associated with that event (Greenberg and Rubin, 2003). Spatial information is a central aspect of EAM and may be represented from both allocentric (third-person, viewpoint independent) and egocentric perspectives (first-person, viewer centered). An extensive network of cortical and subcortical structures allows for flexible transformations across different viewpoints. Two key structures according to influential theories are the hippocampus, supporting allocentric spatial processing (O'Keefe and Nadel, 1978; Nadel and Hardt, 2004; Zaehle et al., 2007), and the posterior parietal neocortex, supporting egocentric processing during spatial memory and navigation (Committeri et al., 2004; Galati et al., 2000; Zaehle et al., 2007), and also during EAM (Freton et al., 2014).

Scene construction, the ability to mentally generate a coherent spatial context, is considered fundamental to the vivid recollection of memories (Hassabis and Maguire, 2007; Robin et al., 2015; cf. Burgess et al., 2001a for a related view). The hippocampus facilitates scene construction, allowing the details of a memory, represented in various regions throughout the neocortex (Wheeler et al., 2000) to be reconstructed into a coherent spatial context (Hassabis and Maguire, 2007). Scene construction accounts view spatial context as a scaffold for EAM

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(Hassabis and Maguire, 2007; Robin et al., 2015), implying that spatial context is reinstated before other information. Consistent with scene construction theories as well as with cognitive map interpretations of memory and the hippocampus (e.g. Burgess et al., 2001a; Nadel and Hardt, 2004), a recent study found that spatial context during encoding in a navigational task is reinstated by the hippocampus very early during memory recall (Miller et al., 2013) suggesting similar dynamics could exist in EAM. Thus, according to these theories, spatial context reinstatement is believed to be an early, crucial process associated with the hippocampus.

Individuals can use both allocentric and egocentric strategies during navigation and spatial memory and may favour one strategy over the other (Bohbot et al., 2004; Iglói et al., 2009). Similarly, individuals differ in their perspective-taking tendencies during autobiographical remembering (Rice and Rubin, 2011), with egocentric strategies being used more commonly than allocentric (Freton et al., 2014; Sutin and Robins, 2008). The ability to experience events from an egocentric perspective is fundamental to our ability to vividly re-experience EAMs (Bergouignan et al., 2014; Vogeley et al., 2004). Similarly, the type of perspective taken during recall can influence the conscious experience during remembering. Memories re-experienced from egocentric perspectives tend to include greater affective and sensory details compared to those recalled from allocentric perspectives (McIsaac and Eich, 2002; Robinson and Swanson, 1993; Berntsen and Rubin, 2006). The relationship between egocentric perspective and vivid recall may be mediated by the precuneus, a region involved in mental imagery (Gardini et al., 2006). The tendency to recall EAMs from an egocentric perspective has been associated with greater precuneus gray matter volume (Freton et al., 2014).

Beyond differences in perspective-taking, individuals vary greatly in their overall ability to recall EAMs. Cases of highly superior and severely deficient EAM have been identified in healthy individuals with otherwise normal cognitive functions. In highly superior autobiographical memory (HSAM; LePort et al., 2012), individuals are able to recall in great detail even the most mundane events from their past given a randomly selected date. Individuals with Severely Deficient Autobiographical Memory (SDAM), on the other hand, are unable to vividly recollect personally experienced events and notably, report difficulty remembering events from an egocentric perspective (Palombo et al., 2015). Even among individuals within the normal range of EAM, there is variability in subjective ratings of vividness and the use of different memory strategies (D'Argembeau and Van der Linden, 2006; Palombo et al., 2013). Trait-like differences in episodic and semantic remembering, as measured by self-reported ratings, are further related to intrinsic functional connectivity patterns (Sheldon et al., 2015). Endorsement of EAM ability is associated with connectivity between the MTL and posterior occipital/parietal regions (Sheldon et al., 2015), suggesting that accessing visual-perceptual information may allow individuals to re-experience memories more vividly (Greenberg and Rubin, 2003). On the other hand, endorsement of semantic memory ability is related to MTL– middle prefrontal connectivity (Sheldon et al., 2015), suggesting that higher-order control and organization are involved in a semantic memory style.

Previous studies have further related differences in autobiographical and episodic memory ability to differences in hippocampal volumes in patients (Gilboa et al., 2005; Herold et al., 2013) and healthy individuals (Chadwick et al., 2014). The nature of the relationship between episodic memory and hippocampal volume is unclear, with the strength and direction of this relationship depending on factors such as the age of participants (Van Petten, 2004). The relationship between spatial memory and hippocampal volume is clearer, with larger hippocampi predicting greater spatial memory in healthy individuals (Maguire et al., 2000, 2006; Erickson et al., 2009). Hippocampal volume is further related to scene construction of fictitious events in healthy older adults (Irish et al., 2015). Thus, structural differences in the hippocampus appear to be related to spatial memory and scene construction, and possibly to autobiographical and episodic memory abilities.

These studies demonstrate that the subjective experience of remembering in EAM varies across healthy individuals, that these differences pertain to spatial representations (Rice and Rubin, 2011; Bohbot et al., 2004), and that they may be represented in the brain structurally (Freton et al., 2014; Chadwick et al., 2014) and functionally (Sheldon et al., 2015). Structural differences may reflect more stable recollection tendencies and consistent reliance on certain strategies (Kanai and Rees, 2011).

In the present study we cued participants with familiar locations and non-locations and related behavioural performance to regional brain volumes. We hypothesized that cueing participants with familiar locations would serve as a shortcut to scene construction, allowing them to access memories more easily and recollect them more vividly (Hassabis and Maguire, 2007; Burgess et al., 2001a; Robin et al., 2015). This ability to benefit from spatial cues may vary depending on hippocampal volume, in line with the established relationship between hippocampal volume and spatial memory (Maguire et al., 2000, 2006; Erickson et al., 2009) and scene construction (Irish et al., 2015). Based on scene construction models, we expected that participants would demonstrate a tendency to report a location as the first thing that came to mind when not cued with a location, and that this may also vary depending on hippocampal volume. Finally, we predicted that egocentric over allocentric remembering would be associated with greater vividness and re-experiencing of memories (McIsaac and Eich, 2002; Robinson and Swanson, 1993; Berntsen and Rubin, 2006), and that the tendency to recall events from an egocentric perspective would be associated with precuneus volume.

2. Materials and methods

2.1. Participants

63 healthy young adults (21 males, mean age = 24.3, SD = 3.5, range = 19–35) participated in the experiment. Participants were recruited from the Rotman Research Institute's healthy volunteer pool. Participants had completed an average of 16.7 years of formal education (SD = 2.0), were all native or fluent English speakers, had normal or corrected-to-normal vision, and were free from a history of neurological illness or injury, psychiatric condition, substance abuse, or serious medical conditions. All participants provided informed consent prior to participating in the experiment in accordance with the Rotman Research Institute/Baycrest Hospital ethical guidelines.

2.2. Episodic autobiographical memory task

2.2.1. Pre-study stimulus collection interview

At least 48 h prior to the study, participants provided the names of familiar places, objects, people, and fruits and/or vegetables in a telephone interview. Locations, people and objects were used as cues because they are elements that commonly make up an event (Addis et al., 2009; Burgess et al., 2001b). Fruits and vegetables were used as a comparison as they are less commonly a central element of events. Participants were instructed to name the first fifteen items that came to mind and to limit items to those encountered within the past year. For the places category, participants were allowed to name multiple locations in the same building (i.e. my office, the cafeteria), so long as these were distinct enough to serve as independent cues for personal memories. Participants could also name public places, but could not name places tied exclusively to a particular person (e.g. could not use "my friend's house"). For objects, participants were told to provide objects that were unique and personally meaningful, but that were not tied exclusively to a particular location (e.g. could not use "my TV chair"). To disguise the purpose of this interview, participants were led to believe that this was a study aimed at collecting norms of familiar