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Factors affecting medial temporal lobe engagement for past and future episodic events: An ALE meta-analysis of neuroimaging studies

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ABSTRACT

Remembering the past and envisioning the future are at the core of one's sense of identity. Neuroimaging studies investigating the neural substrates underlying past and future episodic events have been growing in number. However, the experimental paradigms used to select and elicit episodic events vary greatly, leading to disparate results, especially with respect to the laterality and antero-posterior localization of hippocampal and adjacent medial temporal activations (i.e., parahippocampal, entorhinal and perirhinal cortices, amygdala). Although a central concern in today's literature, the issue of hippocampal and medial temporal lobe laterality and antero-posterior segregation in past and future episodic events has not yet been addressed extensively.

Using the activation likelihood estimation (ALE) procedure (Turkeltaub, Eden, Jones, & Zeffiro, 2002), we performed a meta-analysis of hippocampal and adjacent medial temporal coordinates extracted from neuroimaging studies examining past remembering and future envisioning. We questioned whether methodological choices could influence the laterality of activations, namely (1) the type of cue used (generic vs. specific), (2) the type of task performed (recognition vs. recall/imagine), (3) the nature of the information retrieved (episodic vs. "strictly" episodic events) and (4) the age of participants. We consider "strictly" episodic events as events which are not only spatio-temporally unique and personal like episodic events, but are also associated with contextual and phenomenological details. These four factors were compared two-by-two, generating eight whole-brain statistical maps. Results indicate that (1) specific cues tend to activate more the right anterior hippocampus compared to the use of generic cues, (2) recall/imagine tasks tend to recruit more the left posterior parahippocampal gyrus compared to recognition tasks, (3) (re/pre)experiencing strictly episodic events tends to activate more the bilateral posterior hippocampus compared to episodic events and (4) older subjects tend to activate more the right anterior hippocampus compared to younger subjects. Importantly, our results stress that strictly episodic events triggered by specific cues elicit greater left posterior hippocampal activation than episodic events triggered by specific cues. These findings suggest that such basic methodological choices have an impact on the conclusions reached regarding past and future (re/pre)experiencing and their neural substrates.

1. Introduction

In its current definition, episodic memory is closely related to episodic autobiographical memory (Wheeler, Stuss, & Tulving, 1997; Tulving, 2002). Autobiographical memory (AM) is composed of different types of self-representations, from general knowledge about oneself (semantic AM, also referred to as "personal semantics") to very specific personal events (episodic AM) (Conway, 2001; Tulving, 1985; Tulving, Schacter, McLachlan, & Moscovitch, 1988). Episodic AM is characterized by a particular self-reflective mental state, termed autonoetic consciousness, which implies that the person recollects or imagines his/her personal events with a sense of (re/pre)experiencing, by mentally "travelling in time" whether in the past or in the future (Tulving, 2001; Wheeler et al., 1997). A further distinction can be made between episodic and strictly episodic AMs (Viard et al., 2007, 2010; for reviews, Moscovitch et al., 2005; Piolino, Desgranges, & Eustache, 2009).

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Strictly episodic events are not only spatio-temporally unique and personal like episodic events, but are also accompanied by subjective (re/pre)experiencing (autonoetic consciousness) associated with recall/imagination of phenomenological details, i.e., sensory, perceptual, cognitive, affective internal contextual details (Brewer, 1996; Conway, 2001; Conway & Pleydell-Pearce, 2000; Conway, Singer, & Tagini, 2004; Moscovitch, 1995, 2000; Tulving, 2001; Tulving & Markowitsch, 1998).

Autobiographical investigations generally concern the retrieval of the personal past. They can be subdivided between those dealing with the more general aspects of AM (semantic AM), in which participants retrieve the general facts about a personal event without re-experiencing it (e.g., recall familiar self-relevant faces or places), and those which focus on the specific aspects of AM (episodic AM) in which participants have to consciously recollect a personal past event, in its original encoding context (e.g., recall a specific event, in a unique spatio-temporal context). Concerning episodic future thinking (Atance & O'Neill, 2001), studies have required participants to either imagine future specific events which are not necessarily going to happen (Addis, Wong, & Schacter, 2007; D'Argembeau et al., 2008; Hassabis, Kumaran, & Maguire, 2007) or future specific events which are actually planned or are reasonably going to happen in the future (Botzung, Denkova, & Manning, 2008; Okuda et al., 2003; Peters & Büchel, 2010; Szpunar, Watson, & McDermott, 2007; Viard, Chételat, et al., 2011; Weiler, Suchan, & Daum, 2010a).

Findings from neuroimaging studies in healthy adults have brought new insights on the cerebral organization of episodic events, completing findings from neuropsychology (for autobiographical memory: Andelman, Hoofien, Goldberg, Aizenstein, & Neufeld, 2010; Eustache et al., 2004; Noulhiane, Piolino, Hasboun, Baulac, & Samson, 2007; Piolino et al., 2003; Rosenbaum, Gilboa, Levine, Winocur, & Moscovitch, 2009; Rosenbaum, Winocur, & Moscovitch, 2001; Spiers, Maguire, & Burgess, 2001; St-Laurent, Moscovitch, Levine, & McAndrews, 2009; for episodic future thinking: Hassabis et al., 2007; Klein, Loftus, & Kihlstrom, 2002; Tulving, 1985). Previous reviews have shown that episodic AM retrieval involves a circumscribed cerebral network comprising both anterior and posterior regions, including prefrontal and medial temporal cortices, medial parietal (posterior cingulate and retrosplenial cortices), posterior parietal (precuneus and temporo-parietal junction), occipital regions and the cerebellum (Cabeza & St Jacques, 2007; Conway, Pleydell-Pearce, Whitecross, & Sharpe, 2002; Maguire, 2001; Moscovitch, Nadel, Winocur, Gilboa, & Rosenbaum, 2006; Moscovitch et al., 2005; Svoboda, McKinnon, & Levine, 2006). This neural pattern has striking similarities with the one recruited during episodic future thinking (for reviews, Buckner & Carroll, 2007; Hassabis & Maguire, 2007, 2009; Schacter & Addis, 2007).

Neuroimaging studies of past remembering and future thinking have shown many consistencies, but some aspects remain unclear or obscure, especially concerning hippocampal and adjacent medial temporal lobe (MTL) laterality and antero-posterior activity. Within the MTL, the hippocampus is particularly important in episodic memory. Concerning its laterality, results are discrepant: several episodic AM studies have shown preferentially left-sided hippocampal activations (Daselaar et al., 2008; Maguire, Henson, Mummery, & Frith, 2001; Maguire & Mummery, 1999; Maguire, Mummery, & Buchel, 2000; Markowitsch, Vandekerckhove, Lanfermann, & Russ, 2003; Oddo et al., 2010; Piefke, Weiss, Zilles, Markowitsch, & Fink, 2003; St Jacques, Conway, Lowder, & Cabeza, 2011; Svoboda & Levine, 2009), while others have detected predominantly right hippocampal activations (Fink et al., 1996; Okuda et al., 2003; Steinvorth, Corkin, & Halgren, 2006). Furthermore, an increasing number of studies have shown bilateral hippocampal recruitment during episodic AM retrieval (Addis, Moscovitch, Crawley, & McAndrews, 2004; Cabeza et al., 2004; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Greenberg et al., 2005; Hoscheidt, Nadel, Payne, & Ryan, 2010; Maguire & Frith, 2003a; Maguire & Frith, 2003b; Mayes, Montaldi, Spencer, & Roberts, 2004; Mendelsohn, Furman, Navon, & Dudai, 2009; Nadel, Campbell, & Ryan, 2007; Piolino et al., 2004, 2008; Rabin, Gilboa, Stuss, Mar, & Rosenbaum, 2010; Rekkas & Constable, 2005; Ryan et al., 2001; Trinkler, King, Doeller, Rugg, & Burgess, 2009; Viard et al., 2007, 2010). Concerning episodic future thinking, results are also inconsistent since some studies detect left hippocampal (Addis, Wong, & Schacter, 2008; Addis et al., 2007; Spreng & Grady, 2010), right hippocampal (Addis, Cheng, Roberts, & Schacter, 2011; Okuda et al., 2003; Weiler et al., 2010a) or bilateral activation (Abraham, Schubotz, & von Cramon, 2008; Addis, Sacchetti, Ally, Budson, & Schacter, 2009; Hassabis et al., 2007; Viard, Chételat, et al., 2011; Weiler, Suchan, & Daum, 2010b).

Hypotheses have been formulated concerning the differential contribution of each hippocampus in episodic AM retrieval. It has been suggested that the left hippocampus is more involved in context-dependent episodic memory and is triggered by retrieval details (Addis, Moscovitch, et al., 2004) or vividness of remote AMs (Gilboa et al., 2004), whereas the right hippocampus is more linked to the emotional nature of AMs (Fink et al., 1996) or more engaged by spatial memory (for reviews, Burgess, Maguire, & O'Keefe, 2002; Svoboda et al., 2006), sense of remembering and richness of mental visual imagery (Viard et al., 2007, 2010). Personal importance of AMs was shown to correlate with activation in the hippocampus bilaterally (Addis, Moscovitch, et al., 2004). The age of the participants can also affect hippocampal laterality as several studies have shown greater right hippocampal activation in older compared to younger adults (Maguire & Frith, 2003b; St Jacques, Rubin, & Cabeza, 2012). However, inconsistencies remain, for example, in several context-dependent episodic memory tasks which do not detect left-hippocampal activation, but right activation instead (Okuda et al., 2003; Steinvorth et al., 2006) or in tasks with a strong spatial component which do not recruit the right hippocampus (Niki & Luo, 2002). A further point concerns studies reporting no hippocampal activations during personal episodic AM retrieval (see methods; Andreasen et al., 1995, 1999; Conway et al., 1999; D'Argembeau et al., 2010; Denkova, Botzung, Scheiber, & Manning, 2006a; Gardini, Cornoldi, De Beni, & Venneri, 2006; Graham, Lee, Brett, & Patterson, 2003; Levine et al., 2004; Markowitsch et al., 2000; Niki & Luo, 2002; Nyberg, Forkstam, Petersson, Cabeza, & Ingvar, 2002; Tsukiura et al., 2002).

Furthermore, the antero-posterior hippocampal differentiation has been shown to depend on a variety of different processes. The anterior hippocampus has been associated with processing environmental context (Bannerman et al., 2004; Kjelstrup et al., 2008), stimulus novelty (Daselaar, Fleck, Prince, & Cabeza, 2006; Doeller, King, & Burgess, 2008; Dudukovic & Wagner, 2007; Poppenk, McIntosh, Craik, & Moscovitch, 2010; Strange, Fletcher, Henson, Friston, & Dolan, 1999), arousal, emotion, reward and goal proximity (Fanselow & Dong, 2010; Moser & Moser, 1998; Royer, Sirota, Patel, & Buzsáki, 2010; Viard, Doeller, Hartley, Bird, & Burgess, 2011). The posterior hippocampus is thought to support spatial navigation (Burgess, Maguire, & O'Keefe, 2002; Doeller et al., 2008; Ekstrom et al., 2003; Hartley, Maguire, Spiers, & Burgess, 2003; Maguire et al., 1998; Moser, Kropff, & Moser, 2008; Moser & Moser, 1998; O'Keefe & Nadel, 1978). Various claims have been advanced regarding the locus of activation along the antero-posterior axis of the hippocampus during encoding vs. retrieval. Its anterior portion would support episodic encoding (Lepage, Habib, & Tulving, 1998; Schacter & Wagner, 1999; Spaniol et al., 2009), while its posterior portion, and adjacent parahippocampal structures, would support episodic retrieval (Greicius et al., 2003; Henson, Hornberger, & Rugg, 2005; Lepage et al., 1998; Ludowig et al., 2008; Schacter & Wagner, 1999; Spaniol et al., 2009).