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Theta oscillations orchestrate medial temporal lobe and neocortex in remembering autobiographical memories

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ABSTRACT

Remembering autobiographical events can be associated with detailed visual imagery. The medial temporal lobe (MTL), precuneus and prefrontal cortex are held to jointly enable such vivid retrieval, but how these regions are orchestrated remains unclear. An influential prediction from animal physiology is that neural oscillations in theta frequency may be important. In this experiment, participants prospectively collected audio recordings describing personal autobiographical episodes or semantic knowledge over 2 to 7 months. These were replayed as memory retrieval cues while recording brain activity with magnetoencephalography (MEG). We identified a peak of theta power within a left MTL region of interest during both autobiographical and General Semantic retrieval. This MTL region was selectively phase-synchronized with theta oscillations in precuneus and medial prefrontal cortex, and this synchrony was higher during autobiographical as compared to General Semantic knowledge retrieval. Higher synchrony also predicted more detailed visual imagery during retrieval. Thus, theta phase-synchrony orchestrates in humans the MTL with a distributed neocortical memory network when vividly remembering autobiographical experiences.

Introduction

Humans have the ability to vividly recollect previous autobiographical experiences. Neuroimaging studies have shown that a distributed network of brain regions is associated with the retrieval of autobiographical memories (AM), comprising prefrontal, medial (including the hippocampus) temporal lobe (MTL), and posterior regions, such as precuneus and posterior cingulate cortex (Cabeza and St-Jacques, 2007; Maguire, 2001; Svoboda et al., 2006). The sense of recollection brought by the act of recalling unique personal memory episodes is thought to be mediated by the effective coordination of this set of regions (Maguire, 2001). In fact, influential models of memory organization hold that recollecting personal episodes require the coordination of neocortical areas and the MTL, thereby implementing reinstatement of retrieved information in distributed neocortical assemblies (Marr, 1971; McClelland et al., 1995; Rolls, 2000; Treves and Rolls, 1994). Yet, little is known about the mechanisms governing such neural interactions.

A putative mechanism by which functional neural integration could take place is through brain oscillations. Oscillatory rhythms are thought to coordinate the precise timing of neurons in large-scale neural networks and thereby influence representation and long-term coding of information (Buzsaki and Draguhn, 2004; Huxter et al., 2003; Lisman and Otmakhova, 2001; Steriade, 2000). A special emphasis has been given to theta (4–8 Hz) oscillations in learning and memory tasks in animal (Huxter et al., 2003; O'Keefe and Recce, 1993) and human research (Caplan et al., 2003; Ekstrom et al., 2005; Guderian and Duzel, 2005; Kahana et al., 1999; Osipova et al., 2006; Raghavachari et al., 2001; see for a recent review Duzel et al., 2010). These findings support the view that cortical theta oscillations are crucial to memory-related processes, consistent with computational models of memory postulating that theta mediates a dynamic MTL–neocortical orchestration, allowing a functional implementation of cortical reinstatement during recollection.

Formal assessment of this prediction is hampered by the methodological complexity of testing AM. The typical retrospective sampling of

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AMs for laboratory assessment lacks experimental control over prior rehearsal, personal significance, emotionality, and retrieval effort. Prospective collection of autobiographical stimuli enhances experimental control and can provide highly specific retrieval cues, akin to revisiting a particular scene where a unique or important event occurred (Conway et al., 2002; Heisz et al., in press). Such cues promote vivid recollection of everyday episodes (Brewer, 1988; Sheldon and Levine, 2013), engaging episodic memory and its accompanying state of autonoetic consciousness (Wheeler et al., 1997).

Furthermore, despite evidence from animal and human intracranial recordings (e.g., Anderson et al., 2010; Colgin, 2011; Foster et al., 2013; Watrous et al., 2013) and human functional neuroimaging studies (Tambini et al., 2010), investigating the neurophysiological mechanisms sustaining MTL–neocortical interactions in memory has been affected by limited access to simultaneous acquisition of distributed neural activity together with anatomically targeted recordings. However, a number of recent studies (Cornwell et al., 2010; Guitart-Masip et al., 2013; Kaplan et al., 2012; Poch et al., 2011; Riggs et al., 2009) have shown that it is possible to record simultaneously and non-invasively from the MTL and cortex using whole-head magnetoencephalography (MEG), and that such sensitivity might be incremented when using a realistic anatomical and electrophysiological model of deep brain activity (Attal and Schwartz, 2013). In fact, it has been observed that there could be zero-phase lag correlation between hippocampal activity and MEG (Buzsaki et al., 2012). It should be noted that, albeit some initial available empirical evidence that theta emanating from the MTL (specifically from the hippocampus) could be observed in correspondence with MEG activity (Dalal et al., in press), it is possible that not all hippocampal activity patterns can be measured from the scalp. One reason for this could be that some circuits within the hippocampus form closed loops (see Nunez and Silberstein (2000) for a theoretical discussion on this topic).

Here, we investigated whether and how MTL–neocortical orchestration takes place during the retrieval of unique episodic elements of AM through the recording of MEG data during stimulation with prospectively collected AM cues. We sought to test the hypothesis that neocortical activity linked to the retrieval of AMs was coordinated by dynamic interactions with the MTL through the phase of the ongoing theta.

Material and methods

Participants

Eight healthy adults (3 males; mean age = 30; STD = 5.34; mean education = 18 years; STD = 2.5 years) participated in the study. None of the participants reported a history of neurological, psychiatric or any other serious medical problems. All participants gave written informed consent for the study, which was approved by the hospital research ethics board.

Collection of autobiographical stimuli

Participants collected stimuli prospectively over 2–7 months using a portable digital recorder (ICD-BP100 V-O-R; Sony) following the methods specified by Levine et al. (2004) and Svoboda and Levine (2009). Extensive training on recording methodology was provided along with a detailed instruction manual and feedback on several practice recordings. A cue-card was attached to each recorder for guidance.

There were two recording conditions, Personal Episodic and General Semantic memory. Personal Episodic recordings comprised a 1–2 min description of a unique autobiographical episode, defined according to theoretical works on this topic (Wheeler et al., 1997), including the story line, location, perceptions, thoughts, and emotional reactions. Very significant emotional events were excluded. Participants were instructed to make Personal Episodic recordings during or soon after the event occurred and within the same day (mean time elapsed since the event = 131 min; STD = 91 min). General Semantic recordings comprised a 1–2 min reading from a book about neighborhoods in Toronto, Canada (excluding those evoking a specific autobiographical event), and were yoked in time to the Personal Episodic recordings (for PE: M = 159d, range: 55–199; for GS: M = 206d, range: 19–226; not significantly different, $t = 0.61$, $p = 0.52$). Participants included a title in each recording (e.g., "Michael and Erika's wedding", "Bloor West Village"). Following Personal Episodic recordings, participants indicated time elapsed since the event and ratings for event uniqueness (1, routine; 4, completely novel), personal importance (1, not important; 4, highly important), and emotional change as a result of the event (1, no change; 4, major change). The average of these three ratings across the eight participants was 2.32 (STD = 0.59), indicating a moderate level of novelty and significance, confirming that, as instructed, participants recorded daily events that were unique, although not of great personal significance. Participants were instructed not to listen to their recordings after dictating them.

The median number of recordings made for the Personal Episodic and General Semantic conditions was 71 and 41, respectively (for PE: range 58–500; for GS, range 16–206). Of these, 10 recordings per condition were randomly selected for this study. This oversampling reduced the novelty of the recording activity as well as the predictability of which recordings would be used in the study. As a result of the high degree of effort and commitment to participate in this study, the sample size was small. This was offset by the high potency of the prospective retrieval cues for the production of a vivid recollection during MEG scanning.

Memory retrieval in the MEG

Recordings were edited to 30 s in length and randomized by condition. The experimental run was preceded by four 'practice' memories (two per condition) to allow acclimation to the MEG environment and ensure compliance with instructions. Each recording was preceded by a 30 s fixation (rest, eyes open) condition. At the onset of the recording, participants closed their eyes and heard the title that they had created. While listening to the recording, they were instructed to mentally re-experience the events (Personal Episodic) or to think about the semantic information (General Semantic). After each recording, participants opened their eyes and verbally assigned ratings on four scales: re-experiencing of thoughts, emotions, visual images, and the ease or speed with which the event was reactivated. Participants also rated, from 1 to 10, the 'overall' vividness of recollection, anchored by 'no recollection' and 'vivid recollection' at either end and how easily the episode came to mind, anchored by 'very difficult' and 'very easy'. Thirty seconds were allotted for the ratings. The same ratings were collected in response to the General Semantic recordings in order to assess for the presence of intrusive episodic thoughts and to confirm that the Personal Episodic recordings evoked a higher degree of re-experiencing. Following the 30 s rating period, participants were cued to fixate again for 30 s in advance of the next recording.

MEG data acquisition and preprocessing

MEG recordings were made in a magnetically shielded room by using a 150-channel CTF system with SQUID-based axial gradiometers (VSM MedTech Ltd., Coquitlam, BC, Canada). Neuromagnetic signals were digitized continuously at a sampling rate of 312.5 Hz. Analyses were conducted using SPM8 (http://www.fil.ion.ucl.ac.uk/spm) and with custom-made MATLAB scripts. The MEG data from each block were high-passed filtered at 0.2 Hz using a 5th-order Butterworth filter and epoched from −1000 ms to 30,000 ms relative to the start of the memory retrieval period of each trial.