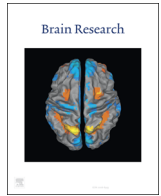




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Research Report

Electrophysiological evidence during episodic prospection implicates medial prefrontal and bilateral middle temporal gyrus

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ABSTRACT

fMRI studies have implicated the medial prefrontal cortex and medial temporal lobe, components of the default mode network (DMN), in episodic prospection. This study compared quantitative EEG localized to these DMN regions during prospection and during resting and while waiting for rewards. EEG was recorded in twenty-two adults while they were asked to (i) envision future monetary episodes; (ii) wait for rewards and (iii) rest. Activation sources were localized to core DMN regions. EEG power and phase coherence were compared across conditions. Prospection, compared to resting and waiting, was associated with reduced power in the medial prefrontal gyrus and increased power in the bilateral medial temporal gyrus across frequency bands as well as greater phase synchrony between these regions in the delta band. The current quantitative EEG analysis confirms prior fMRI research suggesting that medial prefrontal and medial temporal gyrus interactions are central to the capacity for episodic prospection.

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1. Introduction

The default mode network (DMN) is a set of widely distributed, but functionally connected brain regions including the medial prefrontal cortex (MPFC), posterior cingulate cortex/precuneus (pC) and bilateral middle temporal gyrus (MTG; Laird et al., 2009; Raichle et al., 2001). The DMN is active during wakeful rest. It is also associated with a range of introspective self-referential cognitive states such as episodic prospection (Spreng and Grady, 2010), autobiographical memory (Addis et al., 2007; Spreng et al., 2009), mind wandering (Christoff et al., 2009) and moral decision making (Reniers et al., 2012). Although differing in terms of their specific content these mental processes share common features, i.e. they all involve shifting individual's perspective from the present context to an alternative temporal (past or future) or locational (here or there) or social (me or other) context. The DMN plays an important role in the integration of autobiographical information driving decisions relating to desired future states (Sonuga-Barke and Fairchild, 2012). Central to this is episodic prospection – the ability to mentally 'imagine' or 'preview' possible future events and states (Boyer, 2008; Lin and Epstein, 2014). Functional magnetic resonance imaging (fMRI) studies have

implicated the medial prefrontal cortex and medial temporal lobe as a putative neural network underpinning episodic prospection (Buckner et al., 2008) working with MPFC and MTG to facilitate processes of self-projection into the future (Bar, 2009; Buckner and Carroll, 2007). This is consistent with the research showing that MTG provides the foundation for internal mentation during autobiographical memory retrieval (Fox et al., 2015; Li et al., 2014; Tulving, 2002), while MPFC is implicated in self-related simulations (Kim, 2012; Szpunar et al., 2007) and complex perspective-taking processes (Van Hoek et al., 2013).

The neural correlates of introspective, self-referential cognition and the resting brain have been investigated previously using a range of different methods such as fMRI and electroencephalography (EEG) recordings (Christoff, 2012; Helps et al., 2010; Helps et al., 2009; Helps et al., 2008; Knyazev, 2013; Knyazev et al., 2012; Smallwood et al., 2012; Spreng et al., 2009). Nevertheless, studies of the association between episodic prospection and the DMN have been limited solely to fMRI. Although a considerable amount is known about activations of the DMN regions during episodic prospection, the connective pattern between core DMN hubs and the roles of different DMN regions in introspective processes remain a matter of debate. Compared to fMRI, EEG provides a direct measure of neural activity with excellent temporal resolution to the millisecond range, and so EEG is well placed to assess the functional coupling of brain oscillations. Previous research has demonstrated a direct connection in resting state functional connectivity between the DMN as identified by

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fMRI blood-oxygen-level dependent (BOLD) signals and EEG oscillations in very low frequency (Hiltunen et al., 2014), and higher frequency domains (Laufs et al., 2003; Mantini et al., 2007). Strong association between fMRI BOLD signals and EEG oscillations have been observed in anterior MPFC, one of the DMN hubs, during cognitive task performance in both healthy volunteers (Meltzer et al., 2007; Scheeringa et al., 2009), and a clinical sample with attention-deficit/hyperactivity disorder (ADHD; Cannon et al., 2011; 2012). Taken together, EEG offers an ideal platform to investigate brain oscillations during episodic prospection.

In the current research, we extend previous literature to present the first study of episodic prospection using EEG signals localized to the DMN regions. To study prospection we asked participants to consider the use of money in future scenarios. Participants were instructed to imagine themselves actually experiencing and spending money in the scenario compared with a condition when they were asked to estimate the values of items that could be purchased in the scenario (Benoit et al., 2011). The imagine condition is designed to involve the recollection of autobiographical or contextual memory, whereas the estimate condition aims to elicit semantic or declarative memory processes. Previous EEG-based studies have demonstrated that EEG correlates can effectively differentiate episodic and semantic memory processes (See Klimesch (1999) for a detailed review). For example, Klimesch and colleagues measured patterns of event-related desynchronization or synchronization (i.e. the percentage of band power decrease or increase in a test interval as compared to a reference interval), during semantic and episodic memory tasks. In the semantic memory task, participants were asked to judge whether the concept-feature pairs were semantically congruent. In the episodic memory task, which followed the semantic task without warning, participants were asked to report whether specific concept words were actually presented with feature words. Despite the two tasks sharing the same feature words, the extent of alpha power suppression, particularly in the upper alpha band, was related to semantic memory performance, whereas the theta power increase was correlated with encoding new information into episodic memory (Klimesch et al., 1997; Klimesch et al., 1994). Therefore, we anticipated there might be differences in EEG activity between the imagine and estimate conditions.

There were two more control conditions of interest: resting and waiting. These allowed the differentiation of specific EEG correlates relating to prospection from those activated during similar brain states. Although both episodic prospection and resting states activate some common neuroanatomical regions within the DMN they are not identical states. For instance, spontaneous thoughts generated during rest are unconstrained and lack a specific objective, whereas prospective thoughts involve definite scenarios and often have a clear temporal focus. In this sense prospection has a more goal-directed and effortful nature than resting. It also involves systematic accessing and integrating memories about prior experiences with thoughts about future possibilities. Given this we expected to see a degree of suppression of core DMN hubs such as the MPFC (seen in goal-directed tasks) and increased activation of MTG (seen in autobiographical memory tasks) during episodic prospection relative to that seen in the pure resting state.

The brain states occurring when individuals are actually waiting for future events also provides an interesting contrast with the process of prospection about those events. Recent EEG studies observed the attenuation of EEG power within the frontal regions when individuals were 'waiting' for rewards compared to when they were resting (Hsu et al., 2013). The waiting-induced attenuation of neural oscillations was localized to midline brain structures overlapping with the DMN regions, suggesting the suppression may be caused by the goal-directed nature of waiting (Hsu et al., 2015). However, there was no evidence of increased

MTG activation during waiting, suggesting that once the decision to wait had been taken there was limited prospective thinking. Moreover, previous research has demonstrated that episodic prospection reduces the discounting of future rewards in healthy volunteers (Benoit et al., 2011; Peters and Büchel, 2010), but see negative findings in patients with amnesia (Kwan et al., 2012; Kwan et al., 2015). It is not clear how episodic prospection contributes to the tolerance of delay during waiting. A direct comparison of neural oscillations between prospection and waiting state would provide evidence of the impact of prospective thinking on impulsive decision making.

To increase the power and sensitivity of the study we employed a hypothesis driven, region of interests (ROI) strategy and focused on the signals sourced to the core DMN regions including the bilateral MTGs, MPFC and pC regions. We predicted that: (i) compared to resting, prospection would be associated with lower activity within the MPFC given its more goal-directed nature; (ii) compared to both resting and waiting conditions prospection would be associated with higher activity in the MTG and higher coherence between MTG and MPFC given its likely use of autobiographical and self-referential elements. (iii) These effects would be most pronounced in the condition where individuals were asked to imagine spending money rather than just estimating the cost of things.

2. Results

2.1. The comparison between the imagine and estimate conditions

Participants reported a significantly higher emotion intensity and vividness of experience in the imagine condition compared to estimate condition (emotion intensity: $t(21)=3.69$, $p=.001$; vividness of experience: $t(21)=3.83$, $p=.001$). The mean and SD of scores on Consideration of Future Consequences questionnaire (CFC, mean \pm SD=42.41 \pm 4.90) in this study were similar to those reported in the initial paper of CFC by Strathman et al. (1994), showing that our participants' ability to consider their future fell in the normal range. The differences in EEG power and phase coherence between the imagine and estimate conditions were tested using two-way repeated measure ANOVAs for each frequency band respectively. There was no significant difference in EEG power between the two conditions (delta: $F(1, 57)=1.72$, $p=.21$; theta: $F(1, 57)=0.35$, $p=.85$; alpha: $F(1, 57)=3.48$, $p=.08$; beta: $F(1, 57)=.14$, $p=.71$). The imagine condition induced a significantly higher level of coherence across the DMN region pairs in the alpha band ($F(1, 95)=4.28$, $p=.05$) compared to the estimate condition. The differences of phase coherence in the delta, theta or beta bands failed to achieve statistical significance (delta: $F(1, 95)=1.72$, $p=.21$; theta: $F(1, 95)=0.09$, $p=.77$; beta: $F(1, 95)=2.76$, $p=.11$).

2.2. The comparisons of EEG correlates among the imagine, resting and waiting conditions

The 3 (Condition: imagine, resting and waiting) \times 4 (Region: LMTG, MPFC, pC, RMTG) repeated measures ANOVA with power as the dependent variable showed significant main effects of condition and region, as well as a significant condition by region interaction across all frequency bands (delta: condition: $F(2, 38)=31.07$, region: $F(3, 57)=30.15$, interaction: $F(6, 114)=31.07$; theta: condition: $F(2, 38)=20.41$, region: $F(3, 57)=15.14$, interaction: $F(6, 114)=23.66$; alpha: condition: $F(2, 38)=20.08$, region: $F(3, 57)=17.34$, interaction: $F(6, 114)=25.44$; beta: condition: $F(2, 38)=53.15$, region: $F(3, 57)=18.11$, interaction: $F(6, 114)=19.55$, all $p < .001$). Table 1 provides the statistical information of follow-

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