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Oscillatory correlates of autobiographical memory

Gennady G. Knyazev^{a,*}, Alexander N. Savostyanov^{a,b,c}, Andrey V. Bocharov^{a,b}, Elena A. Dorosheva^{a,b}, Sergej S. Tamozhnikov^a, Alexander E. Saprigyn^a^a Institute of Physiology and Basic Medicine, Siberian Branch of the Russian Academy of Medical Sciences, Novosibirsk, Russia^b Novosibirsk State University, Novosibirsk, Russia^c Tomsk State University, Tomsk, Russia

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ABSTRACT

Recollection of events from one's own life is referred to as autobiographical memory. Autobiographical memory is an important part of our self. Neuroimaging findings link self-referential processes with the default mode network (DMN). Much evidence coming primarily from functional magnetic resonance imaging studies shows that autobiographical memory and DMN have a common neural base. In this study, electroencephalographic data collected in 47 participants during recollection of autobiographical episodes were analyzed using temporal and spatial independent component analyses in combination with source localization. Autobiographical remembering was associated with an increase of spectral power in alpha and beta and a decrease in delta band. The increase of alpha power, as estimated by sLORETA, was most prominent in the posterior DMN, but was also observed in visual and motor cortices, prompting an assumption that it is associated with activation of DMN and inhibition of irrelevant sensory and motor areas. In line with data linking delta oscillations with aversive states, decrease of delta power was more pronounced in episodes associated with positive emotions, whereas episodes associated with negative emotions were accompanied by an increase of delta power. Vividness of recollection correlated positively with theta oscillations. These results highlight the leading role of alpha oscillations and the DMN in the processes accompanying autobiographical remembering.

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1. Introduction

Recollection of events from one's own life is referred to as autobiographical memory. During this recollection, the self is projected back through time and spatially and temporally bounded scene is reconstructed. It may be accompanied by strong emotions (Spreng et al., 2008). Brain activation during resting conditions has been called the default mode of brain function and a set of regions showing a consistent pattern of deactivation during the initiation of task-related activity was called the default mode network (DMN, Raichle et al., 2001). Driven by an internal mode of cognition, the default mode may set the stage for self-projection or scene construction (Gusnard et al., 2001; Raichle and Gusnard, 2005), thus enabling a functional overlap between autobiographical memory

and the default mode of brain function. Indeed, meta-analyses of functional magnetic resonance imaging (fMRI) studies using activation likelihood estimation demonstrate that these two domains have a common neural base (Spreng et al., 2008). However, the earlier vision of the DMN as a functionally homogeneous system that is broadly associated with internally directed cognition is now challenged by recent findings showing the functional heterogeneity of the DMN (Laird et al., 2009; Leech et al., 2011). An fMRI study of the topography and response profile of human parietal regions inside and outside the DMN during episodic memory retrieval showed an activation of posterior nodes of the DMN, but also more anterior and dorsal parietal regions that were anatomically separate from the DMN (Sestieri et al., 2011). The results of this study suggest that DMN parietal regions directly support memory retrieval, whereas non-DMN parietal regions are more involved in post-retrieval processes, such as memory-based decision-making. Robust functional dissociation within the DMN was also noted. Whereas posterior nodes of the DMN were significantly activated during memory retrieval, an anterior DMN node in medial prefrontal cortex was strongly deactivated (Sestieri et al., 2011). This latter finding demonstrates functional heterogeneity rather than homogeneity within the DMN during episodic memory retrieval.

Autobiographical memory, however, entails a complex set of operations, which besides self-reflection include episodic memory, emotion, visual imagery, attention, executive functions, and semantic processes

Abbreviations: ANOVA, analysis of variance; DMN, default mode network; EEG, electroencephalogram; ERSP, event-related spectral perturbations; FDR, False Discovery Rate; fMRI, functional magnetic resonance imaging; GLM, general linear model; ICA, independent component analysis; LORETA, low-resolution brain electromagnetic tomography; MEG, magnetoencephalogram; PFC, prefrontal cortex; SICA, spatial independent component analysis; sLORETA, standardized low-resolution brain electromagnetic tomography; TICA, temporal independent component analysis

* Corresponding author at: Institute of Physiology and Basic Medicine, SB RAMS, Timakova str., 4, Novosibirsk 630117, Russia. Tel.: +7 383 334 81 94; fax: +7 383 332 42 54.

E-mail address: knyazev@physiol.ru (G.G. Knyazev).

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(Svoboda et al., 2006). Correspondingly, in fMRI studies of autobiographical retrieval, activation of many cortical areas beyond the DMN has been documented. Particularly the medial temporal-lobe, and the hippocampal complex more specifically, is often referred to as the 'hub' of the autobiographical memory system (Moscovitch et al., 2005). Furthermore, the link between controlled retrieval processes in autobiographical memory and activations in lateral prefrontal cortex (PFC), i.e., the classical working memory (WM) areas, was detected by an early positron emission tomography study (Conway et al., 1999) and was supported by subsequent meta-analyses (Svoboda et al., 2006).

The overwhelming majority of this evidence is based on fMRI findings. Understanding brain function however is not possible without a comparison of the evidence coming from different methodological domains. Particularly, electro/magneto-encephalographic (EEG/MEG) data are very important because these methods have excellent temporal resolution and provide evidence for oscillatory processes in the brain at time scales relevant for the dynamics of cognitive operations. EEG studies have revealed robust EEG correlates of memory processes. Most studies emphasize a critical role of hippocampal theta in memory encoding and retrieval (e.g., Buzsaki, 2005; Düzel et al., 2010; Foster et al., 2013; Jensen and Lisman, 2005; Kahana et al., 2001; Nyhus and Curran, 2010; Stella and Treves, 2011; Vertes, 2005), although involvement of other rhythms is also acknowledged. It has been suggested that theta and alpha oscillations reflect control processes in two memory systems, a working memory and a complex knowledge system that comprises semantic long-term memory, respectively (Klimesch, 1999; Klimesch et al., 2010). In a series of studies, Conway and coauthors have shown changes in slow cortical potentials while participants retrieved autobiographical memories and then held them in mind. In these studies, 14 electrodes located at the 10–20 system coordinates and referred to the linked mastoids were used. Both frontal and posterior effects were found and the results suggest that the left frontal negativity primarily reflects cortical activation associated with the operation of a complex retrieval process, whereas the later temporal and occipital negativity reflects activation corresponding to the formation and maintenance of a detailed memory (Conway et al., 2001, 2003).

Most of these studies were performed in the 'pre-DMN' era and, apart from the Conway et al.'s work, they did not specifically address autobiographical memory. In recent years, a number of studies have found robust EEG correlates of DMN activity. These studies used either simultaneous EEG and fMRI registration or functional correlates of DMN activity that are known from fMRI studies (see Knyazev, 2013b for a review). However, an EEG confirmation (or refutation) of the link between autobiographical memory and DMN is still lacking in the literature, as well as the evidence on the involvement in these processes the traditional EEG frequency bands. With regard to the latter, it is important to take into account the existing evidence on EEG correlates of DMN activity and self-referential processes in general.

Simultaneous EEG-fMRI studies have mostly shown a positive association of DMN activity with alpha and beta (Brookes et al., 2011; Hlinka et al., 2010; Jann et al., 2009, 2010; Mantini et al., 2007; Mo et al., 2013; Ros et al., 2013; Sadaghiani et al., 2010, 2012; Wu et al., 2010) and a negative association with theta (Meltzer et al., 2007; Mizuhara et al., 2004; Scheeringa et al., 2008; White et al., 2012) and delta (Hlinka et al., 2010) oscillations. Gamma power shows positive correlations with DMN BOLD signal at rest (Mantini et al., 2007), but it has been shown that low frequency oscillations (<20 Hz), and not gamma activity, predominantly contribute to inter-areal BOLD correlations and influence local processing by modulating gamma activity within individual areas (Wang et al., 2012). EEG correlates of self-referential processes are most frequently found in brain regions overlapping with the DMN; spontaneous self-referential mentation is mostly associated with the alpha frequency band (Cannon and Baldwin, 2012; Knyazev, 2013a, 2013b; Knyazev et al., 2011, 2012, 2013). Summing up, existing evidence appears to converge in showing that in resting conditions, self-related thoughts are accompanied by an increase of spectral power in cortical regions

overlapping with the DMN and these changes are most consistently found in the alpha frequency band. The association between alpha oscillations and the default mode of brain function is in line with longstanding observations of enhanced alpha activity during mental imagery and internally oriented attention (e.g. Cooper et al., 2003, 2006; Klinger et al., 1973; Ray and Cole, 1985a, 1985b). It is also in line with the proposed role of alpha oscillations in top-down processes and inhibition of sensory perception (Klimesch et al., 2007).

In this study, we aimed to investigate EEG spectral power changes in participants who retrieved autobiographical memories and then held them in mind. We expected that this process would be accompanied by an increase of spectral power in the alpha frequency band and this increase would be most prominent in cortical regions overlapping with the DMN. Because we were explicitly interested in the comparison of our results with the existing fMRI framework, the study design and methods of EEG data analysis were chosen so that they would maximally match the relevant fMRI studies.

2. Material and methods

2.1. Participants

The data were collected in a sample of 47 participants (20 men; age range of 18 to 48 years, mean = 24.2, SD = 7.5). The sample consisted of healthy volunteers who received a sum equivalent to about 5% of the monthly living wage for participation. All subjects were consistently right-handed. Handedness was confirmed using the Annett handedness questionnaire and the criterion for consistent right-handedness as proposed by Annett (1970). All applicable subject protection guidelines and regulations were followed in the conduct of the research in accordance with the Declaration of Helsinki. All participants gave informed consent to the study. The study has been approved by the Institute of Physiology and Fundamental Medicine ethical committee.

2.2. Procedures

Participants sat in a soundproof and dimly illuminated room. First, the spontaneous EEG was registered during about 12 min including alternating 2 min intervals with eyes open and eyes closed. All following instructions were auditory and were given via loudspeaker. The participant was asked to close his/her eyes and after few seconds, the following instruction was given: "Please try to remember as vivid as possible an episode from your past. Please press the button when you have chosen the appropriate episode and started to recall it. Please press the button again when the remembrance is vivid." To press the button, all participants used the index finger of his/her dominant hand. After 60 s. following the second button-press, the participant was asked to evaluate the strength of positive and negative emotion and vividness of the recollection using the five-point Likert scale. After that, the participant performed 60 trials of a simple attention task (a GO-NO-GO task, where he/she had to press a button upon presentation of high-pitched tone (20% of trials) and refrain from doing so upon presentation of low-pitched tone) and after a short break proceeded to the next trial of autobiographical remembering. The insertion of intermittent GO-NO-GO task between episodes of autobiographical remembering was made in order to switch over participants' attention from internal to external processing, thus allowing starting the next episode afresh. In addition, in fMRI research, the switching from external to internal processing is the usual way to study DMN-related processes (e.g., Harrison et al., 2008). The participant was asked to keep his/her eyes closed both during the memory and during the attention tasks. Each participant completed ten paired memory-attention blocks. Between each attention and memory task episodes, there was a 20 s. break, which was followed by the instruction to start the next memory trial. For the analysis, the last but 1 s before the instruction was chosen

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