available at www.sciencedirect.com
ScienceDirect
www.elsevier.com/locate/brainres
ELSEVIER
BRAIN RESEARCH

Research Report

Source-retrieval requirements influence late ERP and EEG memory effects

Axel Mecklinger[a,*], *Mikael Johansson*[b], *Mauricio Parra*[a], *Simon Hanslmayr*[c]

[a]*Experimental Neuropsychology Unit, Department of Psychology, Saarland University, 66123 Saarbrücken, Germany*
[b]*Neuropsychology Unit, Department of Psychology, Lund University, Sweden*
[c]*Department of Experimental Psychology, Institute of Psychology, Regensburg University, Germany*

ARTICLE INFO

Article history:
Accepted 24 July 2007
Available online 14 August 2007

Keywords:
Episodic memory
Source memory
Event-related potential
ERP old/new effect
Late posterior negativity
Phase locking
Oscillation

ABSTRACT

The present study examined whether event-related potential (ERP) memory effects and measures of ongoing EEG activity (power and phase locking) are sensitive to varying source retrieval requirements in recognition memory. ERP old/new effects were obtained in two distinct source-memory tasks. Functionally related EEG power and phase locking effects were found in the delta and theta frequency range. A late posterior negativity (LPN) was larger for old than new responses irrespective of source accuracy. It was also larger when participants were required to judge how they had previously interacted with a recognized picture as compared to judging its study location. This result is consistent with the view that the LPN reflects processes in the service of reconstructing previous episodes by integrating recognized items with task-relevant contextual attributes, and that LPN amplitude is related to the amount of contextual features available for forming such an integrated representation. Phase locking of ongoing delta and theta activity (but not EEG power) was functionally equivalent to LPN amplitude modulations, suggesting that stimulus-induced concentration of delta and theta phases without stimulus-induced power changes may be the neural mechanism of LPN generation. In addition, sustained enhancements of phase-locking precision in the theta range were observed for erroneous and delayed source judgments, suggesting that theta-phase locking is related to the coordination of multiple cortical assemblies in highly demanding task situations.

1. Introduction

The ability to mentally travel backward in time and reexperience a previous event tied to its spatiotemporal context is considered the hallmark of episodic memory, separating it from other forms of memory. In order to remember a past experience, external and/or internal cues interact with stored memory traces to reconstruct the previous episode and give rise to a recollective experience (cf. Tulving, 1983). It is generally assumed that the retrieval of contextual information is mediated by a consciously controlled search process relying on the integrity of the medial temporal lobe and the prefrontal cortices (Yonelinas, 2002). The present study focuses on one important aspect of episodic memory, namely, our ability to recover specific contextual information that allows us to infer the sources of our memories.

Event-related potentials (ERPs) have proven sensitive to mnemonic processing engaged at the time of retrieval (see Friedman and Johnson, 2000, for a review). A robust finding is

---

[*] *Corresponding author.* Fax: +49 681 3026516.
E-mail address: mecklinger@mx.uni-saarland.de (A. Mecklinger).

doi:10.1016/j.brainres.2007.07.070

that correctly recognized old items elicit more positive-going ERPs as compared to correctly rejected new items from approximately 300 ms post-stimulus onset. This old–new difference has been fractionated into several old/new effects. A phasic, parietally distributed effect is considered to index recollection, as it is sensitive to the amount of accurately retrieved information. A more sustained right frontal effect is generally attributed to various control processes associated with memory retrieval. In addition to these positive-going old/new effects, a number of recent ERP studies of episodic memory have revealed a late, posteriorly distributed negative-going slow wave (LPN) onsetting at around the time of the response, which is also sensitive to the old/new status of the test probes (for a review, see Johansson and Mecklinger, 2003). The LPN is observed under two classes of experimental conditions: one class comprises item recognition tasks with high demands on action monitoring arising from response conflict (Herron, 2007). The other class of studies typically employs source-memory tasks in which participants either have to discriminate between new and old items from different sources (e.g. Johansson et al., 2002) or in which they are given test probes from different sources and have to single out items from a particular target source (e.g. Cycowicz et al., 2001; Friedman et al., 2005) .

Participants in the study of Cycowicz et al. (2001) encoded line-drawings of common objects outlined in either red or green. In the subsequent test phase, they were presented with old and new stimuli (outlined in black) and instructed to either (a) respond 'old' to items previously presented in only one of the two study colors and 'new' to all other test items or (b) give mere old–new judgments. Interestingly, while both types of memory tasks elicited early parietal old/new effects, only the former task was associated with a prominent LPN old/new difference. Based on its parieto-occipital topography, Cycowicz et al. (2001) proposed that the effect reflects the activation of sensory-specific areas supporting the reinstatement of the drawing in its previous study color.

Friedman et al. (2005) found LPNs of similar magnitude in two conditions in which the color of items was or was not changed from study to test. As in the former condition study and test features varied, they took their results as evidence against the view that the LPN mainly reflects reactivation of representations in visual areas stemming from the study phase and rather suggested that the LPN is related to the reactivation of more general source-specifying information.

On the basis of their review, Johansson and Mecklinger (2003) suggested that the LPN reflects processes that attempt to reconstruct the study episode by retrieving and evaluating attribute conjunctions (item + contextual information) and that take place while or even after memory judgments are made. According to this view, the LPN reflects processes that form and retain an integrated representation of a recognized item bound to task-relevant contextual attributes when such information is not readily recovered by the test probe or needs continued evaluation. Inherent in the account is the idea that prefrontal cortices exert a top–down influence on posterior cortical regions in that they select appropriate attributes to search and bind to the recognized item in order to allow the reconstruction of a previous episode. The LPN would thus not be tied solely to the activation of sensory-specific areas, but also to the engagement of posterior brain areas subserving the binding of a recognized item to any contextual attributes not necessarily visuo-perceptual, but defined by task requirements. It follows that the LPN should be larger in a task situation in which multiple source-specifying attributes can be retrieved and evaluated.

In the present study, we address this issue by directly examining the LPN in a within-subject design, manipulating source-retrieval requirements under otherwise identical test conditions. Participants encoded pictures presented in one of two locations on the screen (top vs. bottom), performing one of two study tasks ('indoor/outdoor?' vs. 'approach/withdraw?'). Location and study task were manipulated in an orthogonal fashion during study. At test, this made possible a comparison of source memory relying on study location on the one hand (Location condition) and source memory based on operations performed at encoding (Task condition) on the other hand. Even though the two source tasks may have also differed on other dimensions, like the presence or absence of sensory information, it should be noted that only one feature (study location) is available for the source decision in the Location condition, whereas multiple contextual attributes (related to the decision made in the study task) are available for the source decision in the Task condition. Thus, if the LPN is related to the retrieval and evaluation of attribute conjunctions, one would expect larger LPN amplitudes for source memory judgments in the Task condition, where more contextual details are available for reconstructing the previous study episode.

In addition to the standard ERP averaging approach, we also applied EEG power and phase locking analyses. By the combined examination of experimental effects on LPN amplitude, EEG power, and EEG phase locking, we will be able to examine whether LPN amplitude increases result from a higher precision in inter-trial timing, from a larger amount of neural assemblies being activated, or from a combination of both (see below). To obtain a more coherent picture of the relationship between memory-related ERP effects and ongoing EEG activity, combined ERP / EEG analyses were also conducted for ERP old/new effects.

1.1. *EEG power and phase locking*

A recent debate deals with the EEG mechanisms contributing to averaged event-related potentials (ERPs). In more detail, it is at issue whether averaged ERP components result from an increase in stimulus-evoked EEG power or from a reorganization of ongoing neural EEG activity in the sense of a more precise timing (phase locking) of oscillations in some frequency ranges, or from a combination of both (see e.g., Fell et al., 2004; Makeig et al., 2002; for a discussion see Hanslmayr et al., 2007). Two types of models can be distinguished: evoked models emphasize the evoked nature of neural responses and assume that a stimulus evokes an additive neural population response in every single trial. Conversely, oscillatory models focus on the oscillatory nature of neural responses and assume that a stimulus induces phase locking of ongoing oscillatory EEG rhythms in each trial (see e.g. Fell et al., 2004).

The empirical evidence with respect to these two models is mixed (e.g. Hanslmayr et al., 2007; Makeig et al., 2002; Shah et al., 2004; Yeung et al., 2004). Using an event-related inter-trial coherence measure applied to single-trial data, Makeig