B R A I N R E S E A R C H 1 1 7 2 (2007) 1 1 0 - 1 2 3

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Research Report

Source-retrieval requirements influence late ERP and EEG memory effects

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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.

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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

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^{0006-8993/\$ –} see front matter \circledast 2007 Elsevier B.V. All rights reserved. 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 sensoryspecific 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 intertrial coherence measure applied to single-trial data, Makeig

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Table 1 – Performance measures for old/new discrimination and for source memory (probability of correct and incorrect source judgments for old items, probabilities of correct rejection of new items, the corresponding reaction times, and source

accuracy							
Retrieval condition	Hits	False alarms	Pr	Br			
Task Location	.85 (.02) .87 (.02)	.06 (.02) .06 (.02)	.79 (.04) .81 (.04)	.21 (.03) .29 (.03)			
	Source correct		Source incorrect		New		Source accuracy
	р	RT	р	RT	р	RT	
Task Location	.61 (.03) .52 (.02)	1367 (56) 1197 (56)	.24 (.02) .35 (.02)	1465 (81) 1235 (63)	.94 (.02) .93 (.02)	858 (38) 847 (36)	.72 (.02) .60 (.02)
Standard errors of	of the means (SEM	I) are given in paren	theses. Reactions	times (RTs) are disp	layed in ms. Pr: dis	scrimination index	; Br: Bias index.

et al. (2002) demonstrated stimulus-induced phase resetting of frequencies below 12 Hz and suggested this was the main generation mechanism for the averaged N1 component in a spatial visual selective attention task. Conversely, examining amplitude variance in single-trial auditory MEG data, Mäkinen et al. (2005) found that a phase reorganization of ongoing EEG activity induced by auditory stimuli was not responsible for the generation of the event-related response. However, Klimesch et al. (2006b) have shown that amplitude variance does not index phase resetting.

Using intracranial recordings in epilepsy patients, Fell et al. (2004) was able to show that the hippocampal P300 response to target stimuli in a visual oddball paradigm is produced by both stimulus-related phase locking and power changes in the delta and theta range, whereas the AMTL-N400, a negativity generated in the rhinal cortex, is associated with phase locking and a later additional power increase. In a study on the influence of the hippocampus on language processing, Meyer et al. (2005) obtained phase synchronization within the gamma band between the rhinal cortex and the hippocampus that preceded the respective ERP components in both regions.

Few studies so far have examined the spectral characteristics of recognition memory ERPs. Klimesch et al. (2000) obtained an oscillatory old/new effect – an increase of induced spectral power in the delta and theta frequency range for studied (old) words relative to new words – with the same temporal and topographic characteristics as the ERP old/new effect. Using MEG recordings, Düzel et al. (2005) found differences in spectral power between hits and correct rejections in the theta range; that is, for frequencies higher than the dominant frequency of the event-related field old/new effect. In contrast, phase locking differences between old and new items were most pronounced in the delta band, the dominant frequency range of the field differences.

This brief overview suggests that late ERP components most likely reflect modulations in the delta and theta frequency range. It is an open issue, however, whether late ERP effects can be accounted for by inter-trial phase locking as suggested by oscillatory models or by an additional stimulus-evoked increase in spectral power in the respective frequency ranges as suggested by evoked models. Here we examined whether LPN amplitude modulations reflect enhanced phase locking precision of ongoing EEG activity across single trials as revealed by enhanced intertrial phase locking, or enhanced EEG power that would reflect the activation of a larger number of neural assemblies. If the LPN reflects phase locking of ongoing EEG activity, we would expect these two variables to be affected similarly by the same experimental manipulation. Conversely, if the LPN is caused by enhancement in EEG power, LPN amplitude and EEG power measures should show similar functional sensitivity. Subjects performed four study-test blocks with two alternating study tasks. Pictures were used as stimuli. Test phases included two retrieval conditions: subjects either had to discriminate between pictures studied in the lower or upper part of the screen and new pictures (Location condition), or between the two tasks performed in the study phase and new pictures (Task condition).

2. Results

2.1. Behavioral data

An overview of the behavioral data is given in Table 1. Old/new discrimination was similar in the Location (Pr=.81) and the Task condition (Pr=.79) [F(1,15)=1.2, ns]. However, a comparison of source memory accuracies revealed superior performance in the Task (.72) as compared to the Location condition (.60) [F(1,15)=19.05, p<.001]. Response bias tended to be higher (more liberal) in the Location (.29) than the Task condition (.21) [F(1,15)=3.61, p=.073].

A two-way ANOVA on reaction–time measures (Type and Retrieval Condition as factors) showed two significant main effects and a reliable interaction [F(2,30) = 24.24, p < .001]. Follow-up analyses revealed the following pattern: source incorrect>source correct>new. While the two retrieval conditions did not differ in the time needed for correct rejections, both types of 'old' responses were slower in the Task as compared to the Location condition, and incorrect source judgments in the Task condition were slower than all other responses.

2.2. ERP data

Grand averages for correct and incorrect source judgments for old pictures and correct rejections of new pictures at three anterior frontal and parieto-occipital electrodes are depicted in Figs. 1A and B, separately for the two retrieval conditions.



Fig. 1 – Grand average ERPs for correct and incorrect source judgments and correct rejections depicted separately for the two retrieval conditions at anterior frontal and parieto-occipital electrode sites (A and B). Topographical maps show the scalp distribution of the late negative going old/new effect associated with accurate source memory as a function of retrieval condition (C and D).

Both retrieval conditions were associated with an early parietal old/new difference that was largest between 300 and 700 ms. The ensuing prefrontal old/new effect and the parieto-occipitally focused negative-going old/new effect (i.e. the late posterior negativity) were modulated by the specific source-retrieval requirements.

A large number of ERP studies have reported two separable ERP correlates of recognition memory in the 300 to 700 ms time range, namely a 300 to 500 ms old/new effect at frontal sites – the putative ERP correlate of familiarity – and a 400 to 800 ms effect at parietal sites – the putative ERP correlate of recollection (Mecklinger, 2006; Rugg and Curran, 2007). Yet, the main focus of the present study is on the functional significance of the LPN and its reflection in ongoing EEG activity; it does not address the familiarity/recollection issue and therefore we refrained from further subdividing this early time interval. Rather, we opted to examine the ERP effects in longer time intervals, allowing for a better comparison with the wavelet-based measures of EEG activity that lack the high temporal resolution of ERP measures (Sinkkonen et al., 1995).

In the early time window (300-700 ms), there was a main effect of Type [F(2,30)=15.67, p<.001] and an interaction between Retrieval Condition and Anterior/Posterior [F(1,15)= 9.69, *p*<.01]. The main effect was because recognized pictures elicited more positive-going ERPs than correct rejections, irrespective of source-memory accuracy. The interaction indicated that the Task condition in general evoked more positive ERPs than the Location condition at anterior frontal sites [F(1,15)=19.77, p<.001] but not at parieto-occipital sites [F(1,15)<1, ns]. The ANOVA in the middle time window (700-1200 ms) revealed a three-way interaction between Retrieval Condition, Anterior/Posterior, and Type [F(2,30)=5.34, p<.05]. Subsidiary analyses showed that the only reliable old/new effects associated with recognized pictures were evident over anterior frontal regions in the Task condition [cf. Fig. 1; F(2,30)= 7.42, p<.01].

In addition to lower-order interactions, a Retrieval Condition × Type × Anterior/Posterior interaction was observed in the final time window [1200–1800 ms; F(2,30) = 3.55, p < .05]. Follow-up analyses showed that the prefrontal old/new effect observed in the middle time window remained reliable only for incorrect source judgments in the Task condition [main effect of Type: F(2,30) = 3.78, p < .05]. Furthermore, both retrieval conditions were associated with reliable negative-going old-new differences at parieto-occipital sites for correct and incorrect source attributions [Task: F(2,30)=15.65, p<.001; Location: F(2,30)=8.73, p<.01], confirming the presence of an LPN in both retrieval conditions. An ANOVA performed on difference measures (source correct-new and source incorrect-new) revealed that the LPN was greater in magnitude in the Task as compared to the Location retrieval condition, irrespective of source accuracy [F(1,15)=5.08, p<.05]. The ANOVA conducted on the rescaled difference measures revealed a Condition × Anterior/Posterior × Laterality interaction [F(14,210) = 2.97, p < .05], suggesting that the scalp distribution of the LPN differed as a function of Retrieval Condition (see Figs. 1C and D). Post-hoc tests showed that while the Location condition was associated with an effect centered at parieto-occipital sites, the Task condition was characterized by a more broadly distributed effect along the midline channels.

2.3. EEG data

The time-frequency plots in Fig. 2 show the time courses of the phase locking index (PLI) and whole power for all frequencies at a posterior parietal electrode (POZ) in color coded form (A and B for phase locking and C and D for whole power). As apparent from Fig. 2, effects of Task and Type on PLI and whole power are most pronounced in the delta (1–4 Hz) and theta (4–8 Hz) frequency ranges. Figs. 3 and 4 illustrate the mean values of PLI and whole power in the delta and theta frequency ranges for the 300 to 700 ms and the 1200 to 1800 ms time windows, for both tasks and all three response types, respectively. For reasons of clarity, the analyses of PLI and whole power will be restricted to the early and late time window, in which old/new effects and



Fig. 2 – Time-frequency plots for correct and incorrect source judgments and correct rejections are depicted separately for the two retrieval conditions at the POZ electrode for phase locking index (A and B) and EEG power (C and D). Scalp topography of delta phase locking (1–4 Hz) associated with accurate source memory as a function of retrieval condition (E and F).



Fig. 3 – Mean values (±1 SE) of the phase locking index (PLI) measures at the POZ electrode (site) for the delta (upper part) and theta (lower part) frequency range. PLI is shown for the early and late time interval for both retrieval conditions and the three response types.



Fig. 4 – Mean values (±1 SE) for whole power measures at the POZ electrode (site) for the delta (upper part) and theta (lower part) frequency range. Power is shown for the early and late time interval for both retrieval conditions and the three response types.

Table 2 – Results of the Retrieval Condition, Type, Anterior/Posterior, and Laterality ANOVAs performed for the phase locking index and EEG power in the delta and theta frequency ranges

Frequency band	df	F-value		
and effect		300–700	1200–1800	
		ms	ms	
Delta (1–4 Hz)				
Phase locking index:				
TYPE	2,28	11.91***	21.22***	
Source inc>New	1,14	25.45***	26.10***	
Source cor>New	1,14	5.78*	21.17***	
Source inc>Source cor	1,14	5.79*	5.39*	
COND	1,14	-	4.23 ^a	
TYPE×AP	2,28	-	3.36 ^a	
Anterior: Task>Location	1,14	-	3.89 ^a	
EEG power:				
TYPE	2,28	4.76*	-	
Source inc>New	1,14	6.77*	-	
Source cor>New	1,14	3.93 ^a	-	
COND×TYPE	2,28	4.43*	-	
Task: Source inc>New	1,14	6.57*	-	
Task: Source cor>New	1,14	5.02*	-	
Theta (4–8 Hz)				
Phase locking index:				
TYPE	2,28	31.12***	86.22***	
Source inc>New	1,14	45.89***	182.97***	
Source cor>New	1,14	7.11*	41.68***	
Source inc>Source cor	1,14	37.75***	-	
COND	1,14	6.39*	8.74**	
COND×TYPE	2,28	9.58**	4.35*	
Source inc: Task>Location	1,14	18.06***	7.54**	
Task: Source inc>Source cor	1,14	31.28***		
Task: Source inc>New	1,14	49.24***	-	
EEG power:				
TYPE	2,28	5.42*	5.11*	
Source inc>New	1,14	6.14*	-	
Source cor>New	1,14	4.88*	-	
New>Source inc	1,14	-	6.34*	
New>Source cor	1,14	-	6.04*	
COND×TYPE	2,28	3.36 ^a	0.40	
Source cor: Task>Location	1,14	5.54*	-	
New: Task>Location	1,14	4.70*	-	

Note. TYPE (source correct vs. source incorrect vs. new); COND (Retrieval Condition: Task vs. Location); AP (Anterior vs. Posterior); LAT (left vs. midline vs. right). ***p < .001, *p < .01, *p = .05, $^{a}p = .10$.

LPN effects were most pronounced. Table 2 shows the results of the overall ANOVAs.

The early parietal ERP old/new effect (300–700 ms) was reflected in enhanced PLI and whole power for old vs. new responses (as compared to new responses) in the delta and theta frequency ranges, with these old/new differences being more pronounced in the Task than in the Location condition. In the late LPN time interval (1200–1800 ms), in the delta and theta ranges, the PLI was larger for both old vs. new responses (relative to new responses) and also larger in the Task than in the Location condition; a pattern of results that is highly similar to the one obtained for LPN amplitude. No modulations were found for whole power in the delta range, whereas theta power was enhanced for old relative to new responses. An additional effect that was present in both time intervals is the enhancement of theta phase locking for incorrect responses in the Task condition (cf. Fig. 3). These observations could be confirmed by a series of statistical analyses.

2.3.1. 300 to 700 ms

In the early time window, PLI values in the *delta range* were higher for old responses than for new responses, irrespective of source accuracy [source incorrect vs. new:, p<.001; source correct vs. new: p<.05]. PLI values were also larger for incorrect than for correct source judgments [p<.05]. Parallel to the enhanced delta PLI values, delta power was also larger for old than for new responses. This main effect of Type was embedded in a Retrieval Condition × Type interaction. Subsidiary analyses showed that this interaction reflects the fact that there was a power increase for old responses relative to new responses in the Task condition [source incorrect: p<.05; source correct: p<.05], but not in the Location condition.

As for the delta frequency range, in the *theta band*, phase locking was higher for old responses than for new responses irrespective of source accuracy [source incorrect vs. new: p<.001; source correct vs. new: p<.05]. The PLI values were also larger for incorrect than for correct source judgments [p<.001]. Theta phase locking was more pronounced in the Task than in the Location condition. In addition, a Retrieval Condition×Type interaction was obtained. It shows that PLI values for incorrect source judgments (but not the other two responses) were larger in the Task than in the Location condition [p<.001]. Also, within the Task condition, theta phase locking was larger for incorrect old responses than for the other two response types [source incorrect vs. source correct: p<.001; source incorrect vs. new: p<.001].

EEG power in the theta band (as in the delta band) was enhanced for old responses, irrespective of source accuracy [source incorrect vs. new p < .05; source correct vs. new: p < .05]. In addition, the interaction between Retrieval Condition and Type was marginally significant, reflecting that correct source judgments tended to evoke more theta power in the Task condition than in the Location condition [p < .05]. For new responses, theta power over parieto-occipital sites was higher in the Task condition than in the Location condition [p < 0.05]. For phase locking in both the delta and theta frequency range, no effects of retrieval condition at either electrode region were obtained.

To summarize, in the early (300 to 700 ms) time interval, EEG power and phase locking in the delta and theta band were enhanced for old responses relative to new responses, irrespective of source accuracy. In contrast to the ERP old/ new effects, no interactions between the Anterior/Posterior factor and the Type or Retrieval Condition factors were obtained, suggesting that power and phase locking modulations were more widespread across the scalp than the corresponding ERP measures. As old/new effects were found for both power and phase locking in the low-frequency range, it is reasonable to assume that both enhanced inter-trial timing and power contribute to ERP old/new effects. In addition to the old/new effects, there was a selective enhancement in theta phase locking for incorrect responses in the Task condition, for which longest response times were obtained.

2.3.2. 1200-1800 ms

In the 1200–1800 ms time window, *delta* phase locking was more pronounced for both types of old responses than for new responses [source incorrect vs. new: p<.001; source correct vs. new: p<.001], and also larger for incorrect than for correct source judgments [p<.05]. In addition, a marginally significant effect of Retrieval Condition suggested that delta phase locking tended to be larger in the Task condition than in the Location condition. Furthermore, a Type by Anterior/Posterior interaction suggests that at anterior recordings, delta phase locking tended to be larger in the Task condition than in the Location condition, whereas no such Retrieval Condition effects were obtained at posterior recordings. In contrast to the analyses in the 300 to 700 ms time interval, for the delta EEG power, no significant effects of Type or Retrieval Condition were obtained.

Phase locking in the *theta* frequency range was more pronounced in the Task than in the Location condition and also more pronounced for old than for new responses, irrespective of source accuracy [source incorrect vs. new: p<.001; source correct vs. new: p<.001]. Moreover, a Retrieval Condition × Type interaction was obtained, indicating that theta PLI values were larger in the Task than in the Location condition for incorrect source judgments. Theta power was larger for new responses than for both types of old responses [new vs. source incorrect, p<.05; new vs. source correct p<.05].

To summarize, the analyses of the late time interval revealed enhanced PLI in the delta and theta ranges both for old responses relative to new responses irrespective of source accuracy, and for the Task as compared to the Location condition. This speaks for a close functional relationship between LPN amplitude and phase locking in the lowfrequency range. No such modulations were obtained for delta and theta power; however, theta power was enhanced for new as compared to old responses in this late time interval. In addition, as in the early interval, there was a selective enhancement of theta phase locking for incorrect responses in the Task condition.

There could be an objection to the aforementioned results: phase locking effects were located at the lower end of the frequency range, where transient effects of Gabor filtering may have affected the calculation of power and phase values. We therefore recalculated both measures using the upper portion of the delta frequency range (3.15–4.05 Hz) only. As in the initial analysis of the whole delta frequency range, there again was a significant effect of Type for PLI [F(2,28)=34.99, p<.001] and a marginally significant main effect of Retrieval Condition [F(1,14)=3.94, p=.06]. Again, no significant effects were observed for delta EEG power.

Given the high functional similarity between phase locking and the LPN, in a final analysis, we examined topographical aspects of both measures. The scalp topography analysis of the LPN revealed a significant Retrieval Condition × Anterior/Posterior × Laterality interaction, reflecting the more centro-parietal topography of the LPN in the Task condition. However, neither for delta phase locking nor for theta phase locking were any interactions involving the Anterior/Posterior and/or the Laterality factor obtained, suggesting that the topographic distribution of the EEG measures were highly similar across tasks and response types.

3. Discussion

The present study investigated whether specific sourceretrieval requirements affect late ERP memory effects and how these ERP amplitude modulations are reflected in EEG power and EEG phase locking. In particular, we were interested in whether LPN amplitude is enhanced in a source retrieval situation in which multiple source specifying attributes (representing the task performed at study) can be retrieved and integrated with recognized items as compared to a situation in which only one feature (i.e. study location) is diagnostic for the source judgments. A second issue addressed was concerned with the mechanisms contributing to the generation of ERP old/new and LPN effects. Do ERP amplitude differences result from a more precise timing of ongoing EEG activity across single trials as measured by the phase locking index (PLI), or from a larger amount of neural assemblies being activated as revealed by changes in whole power, or do they result from a combination of both?

The longer response times and superior source accuracy in the Task condition support the view that more source specifying attributes were retrieved and evaluated in the Task condition than in the Location condition. The similar levels of old/new discrimination in both tasks further suggest that the source manipulation did not affect accuracy of item recognition memory.

3.1. ERP and oscillatory old/new effects

As expected, reliable old/new effects in the 300 to 700 ms range were obtained in both tasks. The ERP old/new effects were paralleled by EEG power enhancements and increases in phase locking for old relative to new responses in the delta and theta frequency range, irrespective of task. This high functional resemblance of the ERP old/new effect and EEG power and phase locking modulations in the delta/theta frequency range supports the view that the ERP old/new effects are produced by both power changes *and* phase locking. Consistent with prior studies, these oscillatory old/new effects were restricted to the delta and theta frequency range (Düzel et al., 2005; Jacobs et al., 2006; Klimesch et al., 2000).

Enhanced phase locking and EEG power for correctly retrieved items relative to new items may reflect better synchronization and enhanced activation in widespread neural networks – including the medial temporal lobes – in support of successful memory performance. Consistent with the present results, increases in theta power in the first several hundred milliseconds after the (re)presentation of retrieval cues have been related to the selective activation of (memory) stored information relevant for search and retrieval processes (Klimesch et al., 2000, 2006a).

Another effect was obtained for theta phase locking: in both the early and late time interval, phase locking of theta activity was enhanced for incorrect source judgments in the Task condition, for which longest response times were obtained.



Fig. 5 – Mean values (±1 SE) of the phase locking index (PLI) measures at the FPZ electrode (site) for the theta frequency range. PLI is shown for the middle time interval for the Task condition and the three response types.

Additional analysis of the middle (700 to 1200 ms) time window¹ (Fig. 5) revealed that this effect was present throughout the whole trial, though more accentuated over frontal recording sites in the middle time period. An objection against this result could be that trial numbers were lower in the two conditions with incorrect source judgments as compared to correct and new judgments. As PLI measures tend to be larger with smaller sample size, the enhanced theta phase locking during incorrect source judgments in the Task condition could result from differences in sample size. However, a closer look at the results shows that in both the early and late time windows, the Retrieval Condition × Type interaction reflects the fact that theta phase locking was larger for incorrect judgments in the Task condition relative to the Location condition, for which PLI estimates were derived from comparable trial numbers. Thus, we feel safe to conclude that it is rather unlikely that the latter effect arose from between-condition differences in sample size. Increases in theta power at fronto-midline recording sites have been reported to emerge in demanding task situations characterized by high working memory load, response conflict, and a high likelihood of erroneous responses (Jacobs et al., 2006; Luu et al., 2004; Mecklinger et al., 1992). A large variety of studies have also found enhanced negativities in response-locked ERPs following errors or correct responses given in situations of high response conflict (i.e. the error-related negativity, ERN). Dipole analyses suggest that the ACC contributes to the generation of the ERN and the mid-frontal theta rhythm (Dehaene et al., 1994; Luu et al., 2004). On the basis of these findings, it has recently

been proposed that the ERN may reflect a phase reset of ongoing theta activity (Tucker and Luu, 2006; but see Yeung et al., 2007). This phase reset may be initiated by decrements of dopaminergic input to the ACC and may contribute to the coordination of activation of multiple cortical assemblies in highly demanding and conflicting task situations (Tucker and Luu, 2006). The selective increase in theta phase locking preceding and following erroneous source memory responses in the Task condition, which also yielded the longest response times, is consistent with the aforementioned view.

3.2. The retrieval of source specifying information

In the late time interval, positive slow wave activity was most pronounced for incorrect source judgments in the Task condition at anterior recordings. This effect was paralleled by a selective enhancement of anterior delta phase locking in the same experimental condition. Given that response times were slower in the Task than in the Location condition, and additionally prolonged for incorrect source judgments in the former condition, the ERP slow wave and PLI results presumably reflect enhanced PFC involvement in situations of high response uncertainty.

In contrast to the early old/new effect, the LPN at posterior recordings was enhanced when study task rather than study location was the relevant source-memory demand. This result is consistent with the view that the LPN is sensitive to the amount of source specifying information available during source judgments. The more information can be retrieved and evaluated from the study episode, the larger the LPN. The observation that the LPN was not affected by the correctness of source judgments is consistent with prior studies (Senkfor and Van Petten, 1998; Wilding and Rugg, 1996; Friedman et al., 2005) and suggests that the information searched for and retrieved does not have to be accurate. Rather, any contextual attribute relevant for the task at hand may be activated and integrated with the recognized picture. For example, remembering a picture from the study episode may lead to the reexperience of the operations performed (or potentially performed) at study in the Task condition, or to a visualization of the location at which it was (or potentially was) presented. In both cases, an integrated representation of the item-context conjunction is generated and continuously evaluated (Johansson and Mecklinger, 2003).

The topographical analysis showed that the LPN in both tasks was generated by at least partly non-overlapping neural generators (Rugg and Coles, 1995). Retrieving the study location elicited a parieto-occipitally focused effect, whereas retrieving the study task gave rise to a more widespread effect with a less posterior maximum. As both effects overlap at parietal sites, the present results are consistent with the view that the LPN reflects processes tied to both sensory-specific search and the binding of contextual information to a recognized item. The larger amplitude and broader distribution observed when study task was the relevant source feature is in agreement with the idea that a wider range of contextual attributes or more general source-specifying information are available for reconstructing the previous interaction with an item as compared to its location (see Friedman et al., 2005, for similar arguments).

¹ For theta phase locking in the middle (700 to 1200 ms) time window, in addition to lower-order effects, there were interactions between Retrieval Condition and Type [F(2,28)=4.63, p<.05], and between Retrieval Condition, Type, and Anterior/Posterior [F(2,28)= 3.45, p=.058]. The two-way interaction indicated that incorrect source judgments in the Task condition yielded higher PLI values than in the Location condition [F(1,14)=5.33, p<.05]. The three-way interaction indicates that at anterior frontal regions phase locking for incorrect source judgments was higher in the Task than in the Location condition [F(1,14)=9.73, p<.01], whereas for correct source judgments a Location>Task pattern was obtained [F(1,14)=11.51, p<.01]. Reliable effects of Type were obtained at anterior sites for both source conditions [Task F(2,28)=31.67, p<.001; Location F(2,28)=14.20, p<.001].

The analysis of EEG data reveals important additional insights into the functional characteristics and the neurophysiological mechanisms of the LPN. The LPN was associated with enhanced phase locking in the delta and theta range, while no elevations of delta and theta EEG power were obtained in the LPN time window. The parallel effects of Response Type and Retrieval Condition for LPN amplitude and phase locking of theta and delta frequencies strongly suggest that the LPN is generated by more precise timing of slow frequencies across single trials. EEG power seems to be of minor relevance for the generation of the LPN. In other words, the enhancement of LPN amplitude does not necessarily reflect activation in a larger amount of neural assemblies, but rather a stimulus-evoked enhancement in precision of timing of ongoing theta and delta frequencies.

The following objection could be raised against the view that LPN reflects enhanced phase locking of delta and theta oscillations in the absence of power changes: task specific topographies were obtained for the LPN but not for the phase locking measures. It is important to note, however, that the topographic variability of the phase locking measures was much higher than for the LPN amplitude measures. In fact, adjusting standard deviations at the mean values across the 24 electrodes entering topographic analyses the variability scores were .55 for LPN amplitude and .81 for delta PLI (collapsed across task). This suggests that, due to their large topographic variability, PLI measures may have lacked the sensitivity to detect task-specific topographical differences. Conversely, the finding that the LPN and PLI, though functionally similar show different scalp topographies, could also mean that they are reflections of different neurophysiological events that occur in parallel and share the same functional sensitivity. Further studies will be required to obtain a more detailed picture of the neurophysiological mechanisms underlying LPN generation.

Neuropsychological and neuroimaging evidence suggests that posterior parietal brain regions play an important role in relating objects to one another (Humphreys and Riddoch, 1992) and in allocating attention to feature conjunctions (e.g. Corbetta et al., 1995; Corbetta and Shulman, 2002) or internal mnemonic representations (Wagner et al., 2005). On the basis of these observations and the present findings, it is conceivable that posterior parietal regions mediate the binding of a recognized item with contextual attributes during memory retrieval. They may support the allocation of attention to these retrieved memories and keep them accessible for other processes. The phase locking analysis further suggests that enhanced phase precision of ongoing delta and theta activity in these regions is the most likely mechanism underlying this binding/integration function.

Another result in the late time interval merits some further elaboration: while theta power was larger for old than for new responses in the early time interval, a reversed pattern (new>old) for theta power emerged in the late time interval. Consistent with prior studies that have shown theta power to be related to the encoding of new information and also positively correlated with subsequent memory performance (Klimesch, 1999), the present theta power enhancement may reflect the encoding of new information into episodic memory. In the aforementioned studies, encoding related increases of theta power were found in the first 500 ms after stimulus presentation. Given the delayed character of theta power enhancements in the present study, it is reasonable to assume that when participants are engaged in the retrieval of itemcontext conjunctions and the initiation and execution of motor responses, the encoding of new information is postponed to a post-response time period.

3.3. The functional significance of inter-trial timing

A final issue concerns the functional role of stimulus-induced phase reset. The observation that theta phase locking in the presented study was observed in multiple conditions and time windows suggest that it supports more general processing functions that can be activated under various task demands (Klimesch et al., 2006a). From an ERP perspective, enhanced phase locking of low-frequency oscillations across single trials decreases inter-trial variability and by this directly reduces latency variability of averaged ERP components. On the level of single trials, phase reset may be related to the control of cortical activation (Hanslmayr et al., 2007; Klimesch et al., 2006b). In fact, bipolar signals with alternating polarities reflect the alternation between phases of low and high excitability of the underlying neural assemblies. Consistent with this view, late ERP components, such as the P300 or other late slow waves, have been taken to reflect thresholds for the excitability of underlying cortical networks (Birbaumer et al., 1990; Elbert and Rockstroh, 1987). Phase synchronization of ongoing EEG rhythms by external events may secure brain regions to be set in an excitatory or inhibitory state when a stimulus is processed (Klimesch et al., 2006b). Delta and in particular theta frequencies are fast enough to show several oscillations, i.e. phases of excitation and inhibition, per trial. Phase locking of delta and theta frequencies in the LPN interval may thus reflect the coordination of excitability of cortical brain regions supporting search and retrieval of item-attribute conjunctions in the response and post-response period. Phase locking and power enhancement in the delta and theta range in the time interval of the old/new effect allows the integration of information in distributed networks by the medial-temporal lobes (Lisman, 2005). Phase reset of ongoing oscillatory theta activity may thus reflect the coordination of activity in brain networks in response to relevant events. An important issue for further research is how the large scale coordination of excitability as reflected in low-frequency timing processes across trials is functionally related to phase alignments across cortical regions (cf. Von Stein et al., 1999) and how these interactions are related to memory processes.

In conclusion, the present results provide further support for the view that the search for and the retrieval of attribute conjunctions from a prior study episode is reflected in the LPN. The LPN was not affected by source memory accuracy and was larger in a situation in which multiple source-specifying features were available for the source decision. This is consistent with the view that any contextual attributes available for a source decision may be activated and integrated with other mnemonic information to form a bound representation of a study episode. Posterior parietal regions presumably play an important role in the allocation of attention to these bound representations and in keeping them accessible for continuous evaluation or other post-response processes.

4. Experimental procedures

4.1. Participants

Sixteen healthy undergraduate students (8 females) at Saarland University were paid 5.5€ per hour for their participation. The participants had normal or corrected-to-normal vision, were right handed as determined by self report, and their mean age was 23 years (range: 19–26).

4.2. Stimuli, design, and procedure

Four hundred and eighty pictures from the International Affective Pictures System (IAPS; Lang et al., 1993) served as stimulus material. The pictures were divided into 16 sets to allow for counterbalancing as described below and were matched with respect to valence and arousal. The experiment consisted of four study-test blocks and four picture sets were assigned to each of these blocks. Study lists were formed by combining two sets (i.e. 60 pictures) and test lists by combining all four sets (i.e. 60 old and 60 new pictures). Pictures were $\sim 12 \times 10 \text{ cm}^2$ and were displayed on a black background. Pictures were presented alternately at an upper and lower screen position during study phases, and centrally during test phases.

Participants alternated between two tasks during the study phases, in which they were to: (a) decide whether the presented picture was taken indoor or outdoor or (b) judge whether they (while imagining being the photographer) would approach or withdraw from the depicted object or scene. The encoding task was manipulated on a trial-by-trial basis and each study trial began with a 1-s cue to inform participants of their upcoming task ('Indoor/outdoor?' or 'Approach/withdraw?'). This cue was followed by a centered 2-s fixation cross that after 1 s moved to the upper or lower part of the screen to approximately align with the center of the subsequently presented picture. Study pictures were presented for 2 s and the trial ended with a 2-s response window (blank screen). Following a short break, participants were informed about the retrieval condition relevant for the ensuing memory test. In the Task condition, participants had to discriminate between pictures that had required an indoor/ outdoor or an approach/withdraw decision, and new pictures. For the Location condition, participants were told to discriminate between pictures studied at the upper or lower part of the screen, and new pictures. Retrieval condition was kept constant within each test phase and was manipulated across study-test blocks, with order counterbalanced across subjects. Test trials began with a 1-s display of a row of fixation crosses followed by a single 1-s fixation cross and a 500-ms empty screen. Test pictures were presented for 300 ms and were followed by a 2200ms response window. Participants were instructed to use the index and middle finger of one hand for the two source judgments and the index finger of the other hand to reject new pictures (hand/finger-to-response mapping was counterbalanced across participants). For counterbalancing, the 16 picture sets were rotated through the levels of study location, study task, old/new status, and retrieval condition across participants. Presentation order of both study and test items was pseudorandom (not more than 3 consecutive items of the same type).

4.3. Electrophysiological methods

Electroencephalograms were recorded using 61 Ag/AgCl scalp electrodes referenced to the left mastoid and later re-referenced off-line to the average of the left and right mastoids. Additional electrodes placed above and below the right eye and outside the outer canthi of both eyes recorded vertical and horizontal electrooculograms. All channels were amplified with a bandpass from DC to 100 Hz (16-bit resolution; 500 Hz sampling rate; $<5 \text{ k}\Omega$ inter-electrode impedance). Epoch duration was 2200 ms including a 200-ms pre-stimulus period used for baseline correction. ERP averages were formed for correct and incorrect source judgments and correct responses to new items in the two retrieval conditions.

4.4. Data analyses

Data were analyzed with repeated-measures analyses of variance (ANOVA). The Greenhouse–Geisser adjustment for non-sphericity was used where appropriate and the corrected *p*-values are reported together with the uncorrected degrees of freedom. Bonferroni correction was used for multiple comparisons.

4.4.1. Behavioral data

Hit responses were calculated as the sum of correct and incorrect source judgments, separately for both tasks. Old-new discrimination was calculated as $\Pr[p(hit)-p(false alarm)]$ and source-memory accuracy by dividing the probability of a correct source judgment by the probability of a correct 'old' response [p(correct source)/p(correct source+incorrect source)]. Response bias (Br) was defined as FA/[1-(hit-false alarm)] (cf. Snodgrass and Corwin, 1988).

4.4.2. ERP and EEG data

ERP waveforms were quantified as the mean amplitudes in three consecutive time windows (300–700 ms, 700–1200 ms, and 1200–1800 ms) that correspond well with those used in previous research, encompassing the parietal, the prefrontal, and the late posterior ERP memory effects. For the sake of simplicity and comparability with the EEG measures, we report the results of a hypothesis-driven approach focusing on the anterior frontal (FP1, FPZ, FP2) and parieto-occipital (PO3, POZ, PO4) sites, at which the late ERP modulations were maximal.

The spectral information of the EEG data was determined on the basis of high time–frequency resolution Gabor wavelet analyses, which were calculated in small frequency bins of 0.5 Hz and then averaged in frequency bands with a width of 2 Hz (for details see Schack et al., 2001). The time–frequency resolution of the Gabor filter was controlled by the gamma parameter (in our case γ =1). Frequencies between 1 and 20 Hz were used. Whole power was determined on a single trial basis and than averaged across trials. *Phase synchronization* across single trials was measured using the phase locking index (PLI). The PLI is a measure of phase variability at a certain time point and ranges from 0, which is maximal phase variability, to 1, which reflects perfect phase locking (Schack and Klimesch, 2002). The phases were calculated for each single trial.

The ERP mean amplitude measures, the PLI, and whole power were analyzed in the three consecutive time windows mentioned above. The ANOVAs included the factors Retrieval Condition (Task vs. Location), Type (source correct, source incorrect and new), Anterior/Posterior, and Laterality. Followup analyses were performed to elucidate effects involving the factors of Type and Retrieval Condition. For reasons of simplicity, only effects involving the factors Retrieval Condition and Type in the overall analyses will be reported. The scalp topographies of selected effects were also examined after being normalized by the vector scaling procedure to remove between-condition differences using data from 24 channels (McCarthy and Wood, 1985).

Acknowledgments

This research was supported by the German Research Society (grant FOR448). The authors are grateful to Anne-Cécile Treese, Andrea Gäbel, and Christoph Schwanck for help with data collection.

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