



## Brain oscillatory subsequent memory effects differ in power and long-range synchronization between semantic and survival processing



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### ABSTRACT

Memory crucially depends on the way information is processed during encoding. Differences in processes during encoding not only lead to differences in memory performance but also rely on different brain networks. Although these assumptions are corroborated by several previous fMRI and ERP studies, little is known about how brain oscillations dissociate between different memory encoding tasks. The present study therefore compared encoding related brain oscillatory activity elicited by two very efficient encoding tasks: a typical deep semantic item feature judgment task and a more elaborative survival encoding task. Subjects were asked to judge words either for survival relevance or for animacy, as indicated by a cue presented prior to the item. This allowed dissociating pre-item activity from item-related activity for both tasks. Replicating prior studies, survival processing led to higher recognition performance than semantic processing. Successful encoding in the semantic condition was reflected by a strong decrease in alpha and beta power, whereas successful encoding in the survival condition was related to increased alpha and beta long-range phase synchrony. Moreover, a pre-item subsequent memory effect in theta power was found which did not vary with encoding condition. These results show that measures of local synchrony (power) and global long range-synchrony (phase synchronization) dissociate between memory encoding processes. Whereas semantic encoding was reflected in decreases in local synchrony, increases in global long range synchrony were related to elaborative survival encoding, presumably reflecting the involvement of a more widespread cortical network in this task.

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### Introduction

Memory is crucially shaped by the way information is processed during encoding (Craik and Lockhart, 1972). This impact of varying encoding tasks on later memory performance has been known for decades and is a defining part of several theoretical and functional frameworks of memory (Craik and Lockhart, 1972; Fuster, 1997; Morris et al., 1977; Tulving and Thomson, 1973). However, little is known about the underlying neural mechanisms of successful memory formation in different encoding tasks. The neural correlates of successful memory formation can be investigated with the so-called Subsequent Memory Paradigm. In this paradigm, neural activity during encoding is contrasted between items that are later remembered and items that are later not remembered. Subsequent Memory Effects (SMEs) have been investigated by numerous fMRI, ERP, and brain oscillation studies (Hanslmayr et al., 2012a Paller and Wagner, 2002), but only few have investigated the impact of different encoding

tasks on SMEs. In line with the process view of memory encoding, several neuro-cognitive studies found dissociable SMEs in different encoding tasks (e.g. Hanslmayr et al., 2009; Otten and Rugg, 2001a, b; Schott et al., 2011).

However, the interpretation of the results is to some degree limited as these studies typically contrast a shallow encoding task, usually focused on some alphabetical or phonological feature, with a deep, semantic encoding task, that requires the processing of an item in regard to a single semantic feature (e.g. animacy). These tasks do not only differ in their amount of phonological or semantic processing, but also in other respects, for example in encoding efficiency. As semantic encoding leads to higher subsequent memory than shallow encoding, the reported effects may not specifically reflect semantic feature processing, but also efficient memory processing. To clarify this issue, SMEs elicited by semantic feature processing have to be contrasted with SMEs elicited by other equally efficient, or even more efficient encoding tasks. Encoding strategies that promote higher memory performance than semantic feature judgment are usually intentional tasks, that involve usage of more complex strategies like organizing material, mental imagery or mnemonic systems (for review of effective encoding strategies Worthen and Hunt, 2008).

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An incidental encoding task (i.e. the subjects do not know of a later memory test) that promotes very high memory performance and involves a similar judgment procedure as typical semantic encoding tasks, is the survival processing task (Nairne et al., 2007). During survival encoding, subjects are asked to imagine being stranded in a foreign land without basic supplies and their task is to rate presented items for relevance in such a scenario. Judging items for their survival value results in superior memory compared to several other efficient encoding tasks, including semantic processing (Nairne and Pandeirada, 2008). Survival processing was first introduced as an effective encoding strategy based on special adaptation of memory to survival related information (Nairne et al., 2007). Following research suggested that the effectiveness of survival processing can be explained by the utilization of several proximate encoding mechanisms (Howe and Otgaar, 2013). Survival processing is regarded to rely less on semantic item-specific processing, but more on relational processing of the items (Burns et al., 2011). Further, it has been shown that survival processing also relies on the richness and distinctiveness of the encoding context (Kroneisen and Erdfelder, 2011). On a neural level this elaborative encoding process might be reflected in increased engagement of widespread cortical networks.

A measure of cortical communication in cortical networks is brain oscillatory activity (Fries, 2005). Brain oscillations are assumed to be involved in memory formation as they enable communication within local and distant cortical cell assemblies and thereby shape synaptic plasticity (Buzsaki and Draguhn, 2004; Fell and Axmacher, 2011). Oscillatory activity recorded by scalp electrodes is a tool to measure memory related changes in local and global communication. Thereby, phase synchrony between electrodes indicates synchrony between distant cell assemblies enabling more global communication, whereas oscillatory power presumably reflects the amount of local synchrony in a cell assembly measured by an electrode (Lachaux et al., 1999; Varela et al., 2001).

Several studies investigated changes in oscillatory power related to successful memory formation (Axmacher et al., 2006; Düzel et al., 2010; Hanslmayr et al., 2012a Klimesch et al., 2008). The typical findings in these studies are positive theta (4–8 Hz) and gamma (>40 Hz) power SMEs, i.e., increases in power for subsequently remembered compared to subsequently forgotten items during item processing (Klimesch et al., 1997; Osipova et al., 2006; Summerfield and Mangels, 2005). A different picture arises in the alpha (8–12 Hz) and beta (12–30 Hz) frequency range in which negative SMEs are usually observed, i.e., decreases in alpha and beta power for remembered vs. forgotten items (see Hanslmayr et al., 2012a; for a review). Recently, successful memory encoding has not only been related to effects during item presentation, but also to oscillatory activity preceding item presentation. For instance, positive pre-stimulus theta SMEs have been reported before the successful encoding of an item (Fell et al., 2011; Gruber et al., 2013; Guderian et al., 2009). In addition to these memory related changes in power, several studies found a positive relationship between long range phase synchronization in different frequency bands and memory encoding (Bäumel et al., 2008; Fell et al., 2001; Hanslmayr et al., 2012b; Summerfield and Mangels, 2005; Weiss and Rappelsberger, 2000).

Whether and how these brain oscillatory SMEs vary with encoding tasks is still unknown. To the best of our knowledge, only one prior study compared brain oscillatory SMEs in a shallow, alphabetical task and a deep, semantic feature judgment task (Hanslmayr et al., 2009). The results showed that the negative SMEs in alpha and beta power were specifically obtained in the semantic feature condition, but not in the shallow encoding condition (Hanslmayr et al., 2009). In contrast, positive SMEs in theta power were specifically obtained in the shallow, but not in the semantic encoding condition, suggesting that alpha/beta power decreases specifically reflect semantic feature memory encoding. However, as explained above, semantic and non-semantic encoding tasks differ not only in the level of semantic processing, but also in

encoding efficiency. Therefore these results could also reflect efficient encoding instead of semantic encoding.

To investigate the question of whether two efficient encoding tasks lead to dissociable brain oscillatory SMEs and to further elucidate the role of global and local synchrony in memory formation, the present study compares brain oscillatory SMEs elicited by a classical semantic encoding task with the more elaborative survival processing task. Subjects judged words during encoding either for survival relevance (survival task) or for animacy (semantic task). A colored fixation cross was presented 1000 ms before item presentation as encoding task cue (Fig. 1A) to dissociate item-related encoding processes from pre-item encoding processes. If alpha/beta power decreases specifically reflect semantic feature processing, and not efficient encoding in general, similar results as reported by Hanslmayr et al. (2009) should arise when comparing semantic feature processing with the more efficient survival encoding. The putative more complex processing during the survival judgment might engage a more widespread cortical network which should be reflected by increases in long range phase synchrony between distant electrodes (PLV). In addition, we aimed to replicate the positive SME in theta power preceding item presentation, and to clarify whether this pre-item effect dissociates between the two encoding tasks (Gruber and Otten, 2010; Otten et al., 2006).

## Material and methods

### Subjects

18 healthy volunteers participated in the experiment. Data from two subjects were excluded because total trial number was less than 14 trials in one of the conditions. All of the 16 participants included in data analysis were students aged between 20 and 28 years ( $M = 23.75$ ,  $SD = 2.24$ ). Five of them were male and one of them was left-handed. They reported no history of neurological or psychiatric diseases, had normal or corrected to normal vision and were native German speakers. All subjects received 20 € compensation or course credit for participation. Participants signed informed consent at the beginning of the experiment.

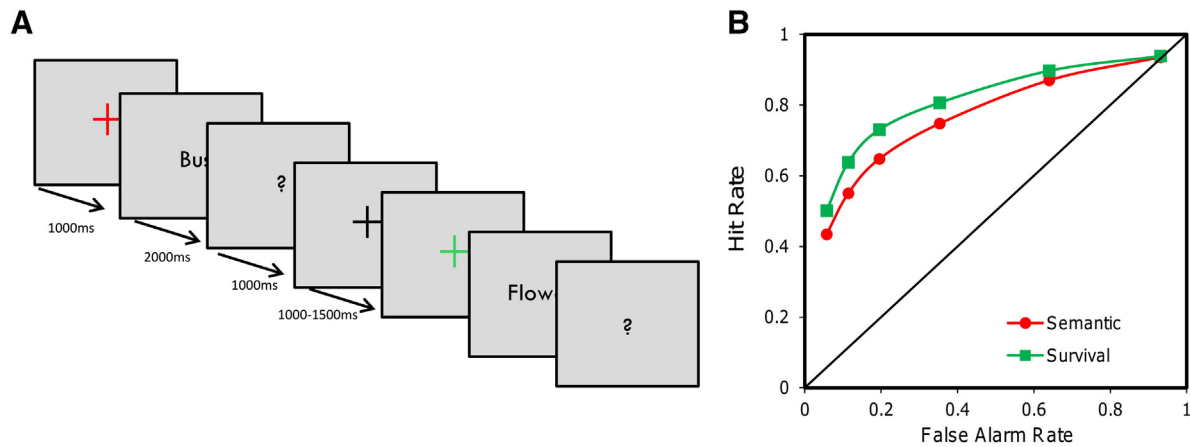
### Material

All items were randomly chosen from CELEX Database (Baayen et al., 1995). Words were neither specifically related to animacy nor survival. Three word lists containing 150 words each were constructed. Across lists the words were matched according to word frequency, word length and for survival and animacy relatedness. Across subjects word material was counterbalanced, as each list was used equally often in the semantic encoding condition, survival encoding condition and as new words during recognition. Sequence of words and conditions was randomized for each subject. Additionally, twenty randomly chosen words were used during the practice phase.

### Procedure

Each subject was tested individually in a quiet surrounding seated in front of a PC screen. The experiment consisted of an encoding phase, a distractor phase and a recognition phase.

At the beginning of the encoding phase participants received a printed instruction containing the semantic and survival task instructions. In the semantic task condition they were instructed to judge words if they are animated or are related to something animated. Subjects were instructed to give subjective ratings on a six point scale. This graded response was applicable as some words were not specifically animated or unanimated (e.g. harmony). The survival task instruction was a German translation of the survival processing strategy proposed by Nairne et al. (2007): “In this task we would



**Fig. 1.** (A) Experimental procedure: Subjects performed an incidental encoding task judging words randomly intermixed for survival relevance and animacy on a scale from 1 to 6. Which encoding task should be performed, was indicated by a colored fixation cross preceding the item, allowing dissociating pre-item task related activity from item-related activity. (B) Memory performance for both conditions is shown by means of item recognition ROCs. Hit (y-axis) and false alarm rates (x-axis) are depicted for the semantic and survival condition. Hit and false alarm rates were obtained by cumulating responses over confidence ratings, starting with the sure old confidence rating. Recognition performance was significantly higher for words encoded in the survival condition than in the semantic condition.

like you to imagine that you are stranded in the grasslands of a foreign land, without any basic survival materials. Over the next few months, you'll need to find steady supplies of food and water and protect yourself from predators. We are going to show you a list of words, and we would like you to rate how relevant each of these words would be for you in this survival situation. Some of the words may be relevant and others may not – it's up to you to decide."

They received no information about the following memory test and they received no instruction to memorize the words. Participants were especially reminded to switch between encoding conditions and to give a response on each trial. The experiment started with a practice phase consisting of twenty items to familiarize the participants with the judgment and response process and to check if the subjects had understood the instructions. During encoding participants judged 150 items for survival value and 150 items for animacy. The sequence of semantic and survival trials was randomized. Each trial started with a fixation cross presented for a variable time (1000–1500 ms) followed by a colored fixation cross, the encoding task cue, presented for 1000 ms, indicating whether the following item should be judged for animacy or survival. The color of the encoding task cue was counterbalanced across subjects. After the cue, the to-be-judged word was presented for 2000 ms. Subjects were instructed not to respond until a question mark appeared after 2000 ms to avoid contamination of movement related activity. Subjects then indicated their survival or animacy judgment using a one to six scale on a computer keyboard in front of them. The assignment of the keys was counterbalanced across subjects. The whole encoding phase lasted for ca. 25 min with a variable pause after half of the trials.

The encoding phase was followed by a distractor task in which subjects discriminated high and low tones for ten minutes. Afterwards participants received the instructions for the surprise recognition test. During the recognition phase 300 words which were shown in the encoding phase were presented again, randomly mixed with 150 new words. Subjects gave recognition confidence judgments using the same response buttons from 1 to 6 as during the encoding task. Subjects were instructed to use the extreme points of the scale for very sure old and very sure new judgments and the intermediate points as varying levels of uncertainty. Subjects were especially reminded to use the whole scale according to their subjective recognition and to answer on each trial. A trial during recognition consisted of a fixation cross presented for variable duration (1000–1500 ms) and the word presented for 2000 ms, followed by a question mark requesting a response. The recognition phase lasted for about 35 min.

### Electrophysiological recording

During encoding, distractor and recognition phase, the EEG was recorded from 61 equidistant active electrodes (ActiCAP, Montage 10, Brain Products, Gilching, Germany). Impedances were kept below 20 k $\Omega$ . Signals were recorded with a sampling rate of 500 Hz and amplified between 0.15 and 100 Hz with a notch filter at 50 Hz to remove line noise (BrainAmpMR plus, BrainVision Recorder, Brain Products, Gilching, Germany). The EEG was initially recorded against a reference electrode placed at FCz and was later rereferenced against average reference.

### Behavioral data

Behavioral data was analyzed utilizing a modeling approach to obtain bias free measures of memory strength. A single process unequal variance model was used, as it provided a good fit to recognition data in other studies (Dunn, 2004; Spitzer and Bäuml, 2007; Wixted, 2007).

This model assumes that recognition is based on a single process which represents memory strength. Memory strength can be modeled using signal detection theory (for details, see Macmillan and Creelman, 2005). It is assumed that the probabilities of old and new words eliciting a certain memory strength can be modeled using normal distributions, with the distribution of new words set to  $N(0,1)$  and the mean  $d'$  and standard deviation  $\sigma$  of the distribution of the old items varying freely according to the data.  $d'$  in this model can be interpreted a measure of memory performance. The model assumes that subjects respond with a certain confidence rating  $i$ , whenever their subjective memory strength exceeds a certain criterion  $c_i$  (see supplemental figure 1) The parameters ( $d'$ ,  $c_1$ – $c_5$ ,  $\sigma$ ) were estimated from the data utilizing a maximum likelihood procedure. This procedure also yields a  $\chi^2$ -distributed  $G^2$  statistic to test the goodness of fit of the assumed model (for more details and specific equations see Spitzer and Bäuml, 2007). For each condition and each subject parameters were estimated separately. In order to compare recognition performance, nonparametric Wilcoxon signed-rank tests were used to compare  $d'$  in the semantic and survival condition.

### EEG

Data was analyzed using MATLAB (The Mathworks, Inc., Munich, Germany), in-house MATLAB scripts, and FieldTrip (<http://www.ru>).

nl/neuroimaging/fieldtrip), an open-source Matlab toolbox developed at the Donders Institute for Brain, Cognition, and Behaviour (Nijmegen, The Netherlands) (Oostenveld et al., 2011).

Hits and misses were classified using the recognition confidence ratings. In contrast to binary yes/no ratings, confidence ratings provide a more fine grained scale of memory performance that allow classifying hits and misses independent of individual response bias. To enhance signal to noise ratio for analyzing SMEs only words receiving the highest confidence rating were classified as hits (see Otten and Rugg, 2001a,b; Otten et al., 2006 for a similar trial definition).

To classify misses, the same signal detection theory approach was used as for analyzing behavioral memory performance. For each subject single process unequal variance models were fitted irrespective of encoding condition to obtain individual criterion measures  $c_i$  for each confidence rating  $i$ . The location of these criteria  $c_i$  relative to the neutral criterion represents the response bias of a certain rating  $i$ . The neutral response criterion represents the criterion with zero bias. A criterion  $c_i$  that is lower than the neutral criterion, indicates that a rather low memory strength is necessary for a subject to use this rating  $i$ . The assumed underlying memory strength of such a rating  $i$  is more likely elicited by a new word than old word. Consequently an old word receiving such a rating  $i$  elicits a feeling of remembering similar to a completely new word and thus it can be assumed that most words receiving this rating  $i$  were not successfully encoded (the underlying model is illustrated in supplemental figure 1). Accordingly, misses were classified by the relative position of the estimated criterion  $c_i$  of the given confidence rating  $i$  to the neutral response criterion.

The location of this neutral criterion was calculated for each subject. A rating  $i$  was classified as miss if the corresponding estimated criterion  $c_i$  was less than the criterion nearest to the neutral criterion (the same approach was used by Hanslmayr et al., 2009). This approach is further illustrated in the supplementary material (see supplemental figure 1). For seven subjects the ratings from 3 to 6 were classified as misses, for another seven subjects ratings from 4 to 6 and for two subjects ratings from 2 to 6. This procedure was utilized to enhance signal to noise ratio, as misclassification of misses is minimized. We showed this by calculating SMEs using a fixed criterion for the classification of misses instead of individual one. Using a fixed criterion effectively reduced the number of miss trials for 9 subjects. This led to a decrease from on average 41 miss trials to 35 trials per condition. All effects and topographies remained qualitatively similar (see supplemental figure 2). However, the effects were slightly decreased showing that a fixed criterion decreased the signal-to-noise ratio of the oscillatory memory effects.

Before analysis the EEG was segmented in epochs from 2500 ms preceding word onset to 2500 ms after word onset. The EEGs were corrected for blinks and eye movements, using Independent Component Analysis. Remaining artifacts, due to muscle activity or poor EOG correction, were excluded by careful visual inspection. Mean trial number for semantic hits was 61 (ranging from 25 to 117), for semantic misses 48 (ranging from 26 to 83), for survival hits 70 (ranging from 23 to 129), and for survival misses 36 (ranging from 14 to 73).

For time–frequency power analysis the EEG epochs were subjected to a Gabor transformation, which transforms a signal into a complex time–frequency signal, from which the power information can be extracted. The data were filtered in a frequency range of 1–30 Hz and for 30–100 Hz. The filter parameter for time–frequency resolution ( $\gamma$ ) was set to 1 for the lower frequencies and to  $2\pi$  for the higher frequencies, to accommodate for the different time frequency characteristics in the lower and higher frequency bands. Power values were calculated for each single trial, and averaged across trials within the four conditions (later remembered, later forgotten for semantic and survival processed items). These power values were then baseline corrected using a 500 ms baseline interval preceding task cue onset.

The resulting power values represent percentage signal change with respect to that baseline (Pfurtscheller and Aranibar, 1977).

For long range phase synchrony analysis the EEG epochs were first current source density transformed and then phase locking values (PLV; see Lachaux et al., 1999 for details) were calculated for each possible electrode pair, but excluding neighboring pairs, in time–frequency bins of 50 ms and 1 Hz using FieldTrip. Current source density transformation was carried out to diminish the effect of volume conduction on phase synchrony (Nunez et al., 1997). High PLVs indicate a high consistency in phase differences between an electrode pair across trials. Hence PLV is a measure of global synchronization and global communication. As unequal trial numbers influence phase measures, PLVs were calculated on a subsample of trials containing as many trials as the condition with the least trials. E.g., if one subject had only 20 semantic misses, then PLVs for all other conditions for this subject were calculated only for a randomly selected subsample of 20 trials. In order to not produce a bias because of the random selection of such a subsample of trials, PLVs for each condition were calculated for 100 randomly selected sets of trials (e.g. 100 times 20 trials were randomly selected) for each condition and then averaged.

For statistical analysis of time–frequency data and PLVs a nonparametric two stage randomization process was used to minimize influences from outliers and to account for multiple testing (see Blair and Karniski, 1993). At a first level, Wilcoxon signed rank tests were used to assess, which and how many electrodes/electrode pairs exhibit a significant difference between conditions for a time–frequency window of interest. The threshold for significance was set to 0.05 for power values and to 0.005 for PLVs. A higher threshold was used for PLVs because of the high number of statistical comparisons. Then, to correct this result for multiple comparisons a permutation test was used. The test used 1000 permutation runs shuffling the assignment of the conditions randomly for each subject. After each run a Wilcoxon signed rank test was calculated returning the number of electrodes/electrode pairs showing a significant difference between the randomly assigned conditions. After 1000 permutation runs this procedure yields a distribution of the number of significant electrodes in a sample with randomly assigned conditions. This distribution then constitutes an approximation of the probability distribution under the null hypothesis. A significant difference between conditions is indicated, if the number of electrodes/electrode pairs showing a significant difference between the two conditions is less likely than  $p_{\text{corr}} = 0.05$  according to the generated distribution. This procedure therefore effectively controls for type-I errors due to multiple testing and was applied in several previous studies from our lab, investigating power (Hanslmayr et al., 2009) and phase synchrony (Hanslmayr et al., 2007, 2012b).

To assess if subsequent memory effects (hit–miss) differed significantly between semantic and survival encoding, differences of hits and misses for power values and PLVs were calculated in both conditions. These differences were then compared using the same nonparametric randomization procedure for the time–frequency windows in which SMEs were found in one of both conditions. This comparison is equivalent to a two-way ANOVA interaction analysis.

## Results

### Behavioral results

For the ROC analysis the hit and false alarm rates were cumulated over the five criterion points, starting with the highest confidence rating. By plotting cumulated false alarm rates against cumulated hit rates ROC curves are obtained, which illustrate recognition performance. The closer the ROC curve is to the left upper corner of the graph, the higher is the recognition performance. ROCs for both encoding conditions are presented in Fig. 1B. Single process unequal-variance signal detection models were fitted to the data for every subject and every condition to obtain individual memory

performance parameters. In order to evaluate the goodness of fit to our data  $\chi^2$ -tests were carried out. The signal detection model fit the data of all subjects adequately as indicated by non significant maximum likelihood tests (all  $p$ s > 0.28). Recognition performance  $d'$  in both conditions was very high. However, in the survival condition  $d'$  was significantly higher than in the semantic condition ( $d'$ : 2.03 vs. 1.57;  $Z = -3.15$ ;  $p < 0.005$ ).

To control for rating during encoding as potential confounding factor, the mean ratings for hits and misses for each condition were calculated. A two-way ANOVA was carried out on the mean ratings with the factors encoding condition (semantic vs. survival) and subsequent memory (hit vs. miss). A significant main effect for subsequent memory ( $F(1,15) = 6.36$ ,  $p < 0.05$ ) was obtained, which was due to subsequent hits receiving higher ratings during encoding than misses. However, and most importantly, no main effect of encoding condition ( $F(1,15) = 0.01$ ,  $p > 0.9$ ) and no significant interaction effect between encoding conditions and subsequent memory emerged ( $F(1,15) = 1.07$ ,  $p > 0.3$ ). This shows that differences found in SMEs between conditions are not confounded by differences in ratings during encoding.

Additionally, reaction time data during encoding was analyzed. Subjects were not allowed to respond until 2 s after word presentation onset (see Fig. 1A). Thus, to analyze reaction time the median reaction time between rating button press and question mark presentation was calculated for each subject and condition. A two-way ANOVA was carried out on the mean RTs with the factors encoding condition (semantic vs. survival) and subsequent memory (hit vs. miss). A significant interaction effect was found ( $F(1,15) = 4.99$ ,  $p < 0.05$ ). This interaction effect was due to a significant difference between hits and misses in the semantic condition (482 ms vs. 538 ms,  $T = -2.35$ ;  $p < 0.05$ ), that was not evident in the survival condition (493 ms vs. 487 ms,  $T = 0.56$ ). There was no significant main effect of encoding condition ( $F(1,15) = 1.52$ ,  $p > 0.2$ ).

### Oscillatory power

Following previous work (Hanslmayr et al., 2009), time frequency data was analyzed in the theta (5–8 Hz), alpha (8–12 Hz), beta1 (15–19 Hz) and beta2 (23–28 Hz) frequency range. In a first step, significant differences between hits and misses (SMEs) were identified for each condition separately. Then, differences between these SMEs were contrasted for time frequency windows, in which SMEs were found. The time–frequency diagrams of SMEs averaged over all electrodes are depicted in Fig. 2, separately for the two encoding conditions, showing clusters of significant time–frequency bins in the theta, alpha, and beta frequency range. SMEs were also analyzed in the gamma frequency range (30–100 Hz). However, no significant effects were found in this frequency band.

In the semantic encoding condition, SMEs were found after item presentation in the alpha, beta1, and beta2 frequency range (see Fig. 2A). Semantic hits were related to a more pronounced alpha power decrease than semantic misses (800–2000 ms, 8–12 Hz,  $p_{\text{corr}} < 0.001$ , see Fig. 3A). This effect showed a widespread topography involving frontal, parietal, and occipital electrodes. Successful later remembering was also related to a beta1 power decrease (300–2000 ms, 15–19 Hz,  $p_{\text{corr}} < 0.05$ , see Fig. 3B) at central and posterior electrodes, and a decrease in beta2 power (0–1500 ms, 23–28 Hz,  $p_{\text{corr}} < 0.001$ , see Fig. 3C) at posterior electrodes.

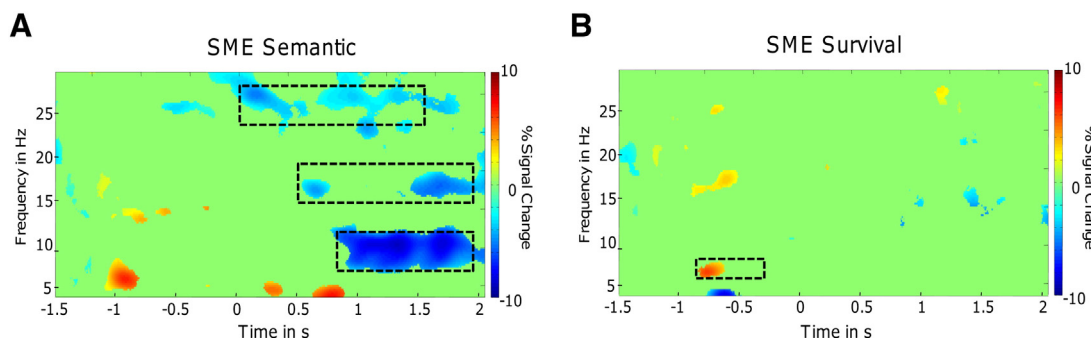
In the survival encoding condition, a significant difference between hits and misses was only found related to the task cue in the theta frequency range –900 to –300 ms before item presentation (5–8 Hz,  $p_{\text{corr}} < 0.05$ , see Figs. 2B and 3D) at central and left parietal electrodes. Later remembered survival processed words elicited a stronger theta power increase than later forgotten words in this pre-item interval. Significant SMEs after item presentation were not evident in any frequency band.

To investigate differences in SMEs between semantic and survival processing, differences between hits and misses for the two conditions were compared. This was done for time–frequency windows in which significant SMEs were found in one of the two conditions. SMEs for survival and semantic processing did not differ for the pre-item theta SME (–900 to –300 ms before item presentation, 5–8 Hz). This was confirmed by an additional analysis, which revealed a significant main effect of subsequent memory for pre-item theta power comparing hits and misses irrespective of encoding condition (Fig. 4). This can also be seen in Fig. 5D, showing a comparable positive theta SME in both conditions. Concerning alpha power, the SMEs differed significantly between the two encoding conditions (800–2000 ms, 8–12 Hz,  $p_{\text{corr}} < 0.05$ , Fig. 5A), demonstrating a significantly stronger SME at fronto-central electrodes in the semantic than in the survival condition. The beta2 SME (0–1500 ms, 23–28 Hz,  $p_{\text{corr}} < 0.05$ , Fig. 5C) was also significantly stronger for the semantic condition than the survival condition at posterior electrodes. A similar tendency, yet not quite significant, was found for beta1 power (300–2000 ms, 15–19 Hz,  $p_{\text{corr}} < 0.1$ , Fig. 5B) at left posterior electrodes. This picture is also evident for the mean over all electrodes (Fig. 5D).

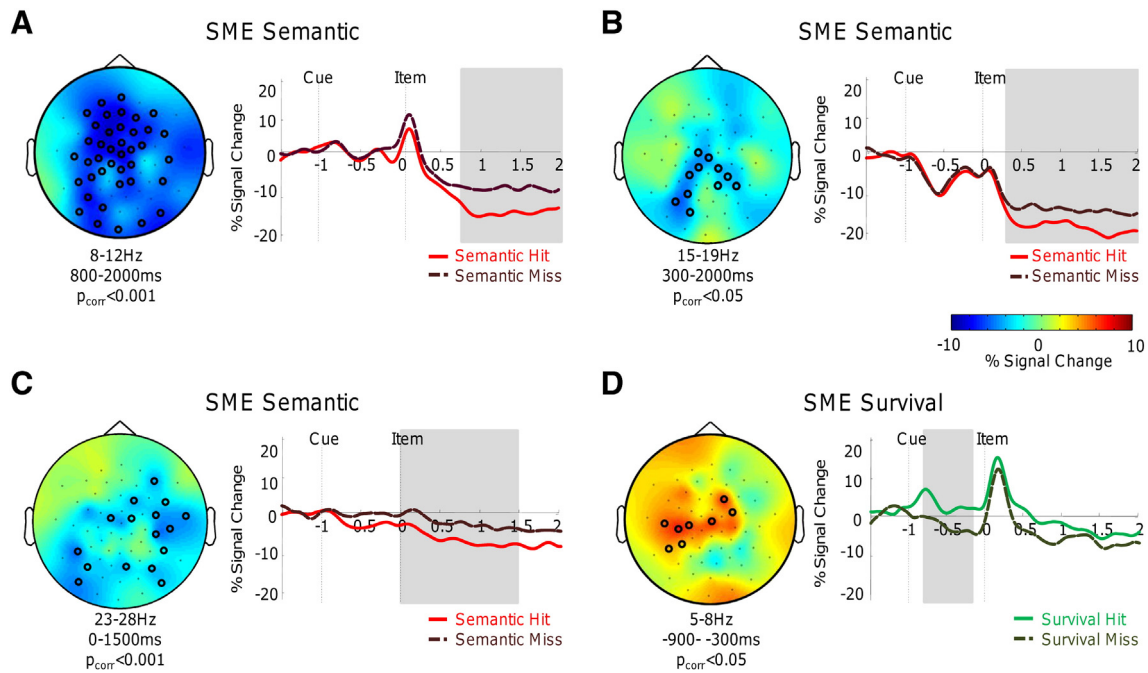
To investigate whether differences of SMEs arose because of generally higher or lower power levels in one of the encoding tasks, hits for both conditions were compared with each other for the time frequency windows in which SMEs were found. No differences were found in power between semantic hits and survival hits in those time–frequency ranges (all  $p_{\text{corr}} > 0.3$ ).

### Phase synchrony

Phase synchrony SMEs were analyzed for the frequency bands in which oscillatory power SMEs were found, albeit in differing time

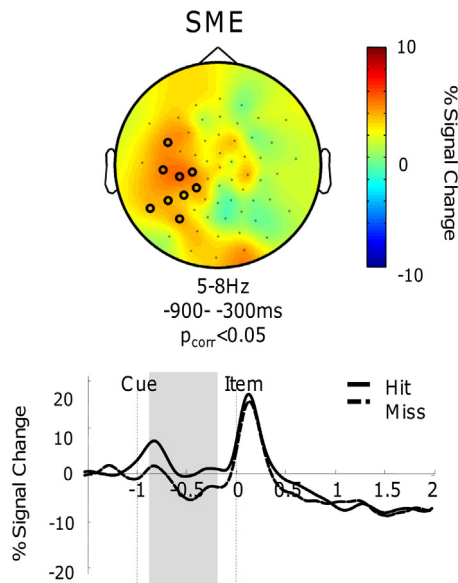


**Fig. 2.** Time–frequency plots of oscillatory SMEs averaged across all electrodes for (A) semantic encoding and (B) survival encoding. Time–frequency bins showing no significant differences as obtained by non-parametric Wilcoxon tests comparing hits and misses for each time–frequency bin are masked in green. Red/blue indicates more/less power for hits than misses, respectively. Time–frequency windows, in which significant SMEs were found, are highlighted in dashed boxes.



**Fig. 3.** Oscillatory power subsequent memory effects (SMEs) are shown for both conditions separately. (A) In the semantic processing condition a negative SME was found in alpha power (8–12 Hz) from 800–2000 ms post item presentation; (B) in beta1 power (15–20 Hz) 300–2000 ms post item presentation, and (C) in beta2 power (23–29 Hz) 0–1500 ms post item presentation. (D) In the survival encoding condition subsequently remembered words were associated with a theta power (5–8 Hz) increase in the pre-item interval (–900 to –300 ms). Circles in the topography plots highlight significant electrodes. Red/blue indicates more/less power for hits than misses, respectively. Time courses of power increases/decreases for hits and misses collapsed across all electrodes that showed significant SMEs are depicted on the right for the respective time–frequency window. Time windows of significant SMEs are highlighted by gray boxes.

windows. As a measure of phase synchrony, the phase locking value (PLV) was calculated for each electrode pair excluding neighboring pairs. PLVs between hits and misses in each condition were contrasted in time bins of 500 ms in the same frequency bands in which power SMEs emerged. The identical frequency bands were analyzed, because



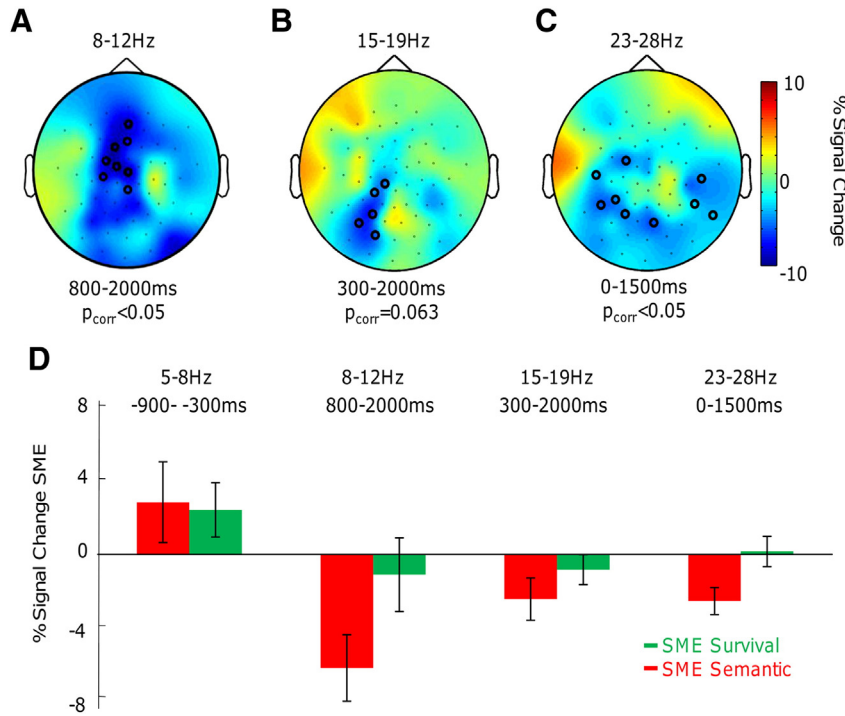
**Fig. 4.** Pre-item theta SME (5–8 Hz, 900–300 ms before item presentation) irrespective of encoding condition. The pre-item theta effect showed no interaction of subsequent memory and encoding condition. However, pooled for hits and misses of both conditions a significant main effect of subsequent memory was obtained. Circles highlight significant electrodes in the topography plots and red indicates more power for hits than misses. Time courses of power depict average power collapsed across all electrodes that showed a significant SME in the respective time–frequency window.

both encoding conditions are hypothesized to differ in the amount of local and global synchrony, but not in the involvement of differing frequency bands. Effects were analyzed in consecutive, non-overlapping bins of 500 ms, as the time course of local and global effects might differ. Additionally, comparing PLVs in 500 ms time windows allows obtaining stable effects lasting several cycles of an oscillation and reduces the total number of tests. If a significant effect was found in two consecutive 500 ms time bins, the time windows were merged.

In the survival condition, significant phase synchrony SMEs were found in the alpha frequency range (500–1000 ms, 8–12 Hz, 21 significant pairs,  $p_{\text{corr}} < 0.05$ , Fig. 6A) and in the beta1 frequency range (0–1000 ms, 15–19 Hz, 28 significant pairs,  $p_{\text{corr}} < 0.01$ , Fig. 6A). Survival hits showed an increase in alpha and beta1 PLV compared to survival misses. No significant SMEs were evident in the theta frequency band and in the semantic condition. In the same time window in which the positive survival alpha phase synchrony SME was observed, a marginally significant negative SME (a decrease in PLV for hits compared to misses) was obtained in the semantic condition (500–1000 ms, 8–12 Hz, 18 significant pairs,  $p_{\text{corr}} < 0.1$ , Fig. 6B). Comparing the phase synchrony SMEs in the time–frequency windows of the alpha and beta1 survival SMEs with semantic SMEs revealed significant differences between phase synchrony SMEs. The encoding related increase in alpha and beta1 phase synchrony SMEs was significantly larger in the survival condition than in the semantic condition (500–1000 ms, 8–12 Hz, 23 significant pairs,  $p_{\text{corr}} < 0.05$ , 0–1000 ms, 15–19 Hz, 28 significant pairs,  $p_{\text{corr}} < 0.01$ , Fig. 6C). This pattern of results is also evident in the mean PLVs averaged over all electrode pairs showing a significant difference in SMEs between conditions (Fig. 6D).

## Discussion

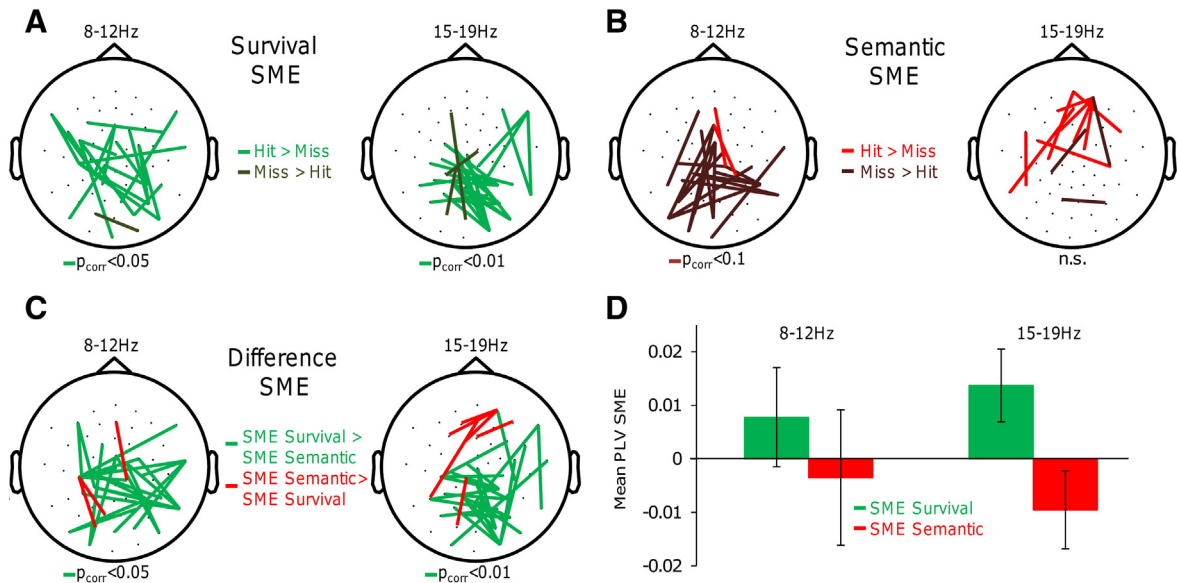
In the present study, we investigated whether brain oscillatory activity related to successful memory encoding differs between two



**Fig. 5.** Differences between power SMEs are shown for both conditions. (A) SMEs for survival and semantic processing differed significantly in alpha power (8–12 Hz, 800–2000 ms), with the semantic condition eliciting a stronger negative SME than the survival condition. (B) SMEs in beta1 power (15–19 Hz, 300–2000 ms) showed a marginally significant difference between the two encoding conditions. (C) SMEs in beta2 power (23–28 Hz, 0–1500 ms) also differed significantly between both encoding conditions. Blue indicates stronger negative SMEs for the semantic encoding conditions, circles in the topography plots highlight significant electrodes. (D) Mean power of hits–misses collapsed across all electrodes for the respective time windows and frequency bands. Error bars indicated standard errors.

highly efficient encoding tasks, a semantic feature processing and a survival judgment task. Indeed, SMEs in both encoding tasks were dissociable. Successful encoding in the semantic processing condition was characterized by a decrease in alpha and beta power, whereas

successful encoding in the survival processing condition was related to an increase in long range phase synchrony in the alpha and beta1 frequency bands and to a higher recognition performance. These results replicate prior findings (Hanslmayr et al., 2009). Going beyond



**Fig. 6.** Results of the phase synchronization analysis. SMEs in phase synchrony were compared for frequency bands in which significant power SMEs were obtained. (A) Long range synchrony in the alpha band (8–12 Hz, 500–1000 ms) and beta1 band (15–19 Hz, 0–1000 ms) increased significantly for subsequently remembered words compared to forgotten words in the survival condition. (B) In the semantic condition this effect was not evident. In the alpha band there was even a non-significant tendency (8–12 Hz, 500–1000 ms) of a negative semantic phase synchrony SME. (C) The alpha and beta1 phase synchrony SMEs differed significantly between survival and semantic encoding. (D) Mean phase locking values for the respective time windows and frequency bands are shown for hits and misses of both conditions, collapsed across all electrodes showing a significant interaction. Error bars indicated standard errors.

prior work this study shows that two highly efficient encoding tasks differing in processing complexity lead to dissociable SMEs in local and global synchrony measures.

This specific relationship of alpha/beta power decreases to successful encoding in a semantic task across two studies further corroborates the close relationship between semantic encoding and alpha/beta power decreases. These specific beta power decreases in the semantic condition are also consistent with findings linking negative beta power SMEs to BOLD signal increases in the left inferior prefrontal gyrus (Hanslmayr et al., 2011), a brain region that is reliably activated during encoding (Kim, 2011) and semantic processes (Binder et al., 2009) and has been shown to support semantic memory encoding (Otten and Rugg, 2001b).

Encoding in the survival processing condition was associated with increases in alpha and beta long range phase synchronization. Phase synchronization has been generally proposed as a mechanism facilitating communication between distant cortical areas (Fries, 2005; Varela et al., 2001) and especially alpha and beta phase synchrony has been related to cortico-cortical communication (Buffalo et al., 2011; Donner and Siegel, 2011; von Stein et al., 2000). The phase synchrony SMEs found specifically in the elaborative survival condition might therefore indicate communication in large cortical networks involved in the different processes underlying the survival task. Increases in phase synchronization related to memory formation have been reported by several other studies in various frequency bands. Weiss and Rappelsberger (2000) reported increases in global synchronization related to encoding success in several frequency bands. Other studies specifically related increases in theta synchronization to item context binding (Summerfield and Mangels, 2005) and alpha phase synchrony to binding mechanisms in episodic memory (Bäuml et al., 2008). In intracranial recordings phase synchronization in the gamma and theta frequency was found to support episodic memory encoding (Burke et al., 2013; Fell et al., 2001). The results of local synchrony SMEs in the item feature based semantic task, and global synchrony SMEs in the more elaborative survival task, suggests that encoding in the survival task relied on a more widespread cortical network. Potentially, this increase in cortical communication indexes the concurrent processing of the items in regard to several dimensions (e.g. Is the item eatable/drinkable/useful as a tool/weapon?, images of using the item in different survival situations) that lead to the encoding of a contextual rich episodic memory and consequently to a higher chance of successful later retrieval ( Craik and Tulving, 1975; Klein and Saltz, 1976).

As survival processing also requires semantic processing of the items, it was surprising that no SMEs in alpha or beta power were found. To investigate if alpha/beta power generally differed between tasks or only between SMEs, power for semantic hits and survival hits was contrasted in the time–frequency windows of the SMEs. No differences in alpha/beta power were evident between hits of both encoding conditions. Alpha and beta power therefore do not generally differ between semantic and survival judgments, but differ in whether they predict later remembrance of the item in that condition. Assuming that decreases in local alpha/beta synchronization indexes information processing (Hanslmayr et al., 2012a) this indicates that in both tasks a similar amount of semantic processing is employed. However, only in the animacy condition does this semantic processing shape later memory, whereas in the survival condition these item feature related processes did not influence subsequent memory to the same extent.

In contrast to the alpha power decrease and phase synchronization SMEs, the pre-item theta SME for survival processed words did not differ between conditions. As can be seen in Fig. 5D, the increase in theta power for hits compared to misses was very similar for both conditions, and pooling both conditions yielded a significant SME (Fig. 4). These results replicate previous findings, demonstrating that pre-item theta power does not differ between deep and shallow

encoding tasks (Guderian et al., 2009). Therefore, the prestimulus theta SME seems not connected to task specific processing, but may rather reflect motivational preparatory processes as reported by Gruber et al. (2013). This unspecificity for content also resembles results during retrieval showing that theta power does not vary during retrieval of different kinds of materials, whereas alpha and beta power varies material specific (Khader and Rösler, 2011).

Importantly, the reported dissociable SMEs are not confounded by task related differences in reactions times or ratings during encoding. To check for possible differences, reaction times and ratings were contrasted for hits and misses in both conditions. There was an effect of ratings being higher for later remembered words, but this effect did not vary with encoding condition. Reaction times of the survival condition and semantic condition did not differ. However, reaction times for semantic hits were slightly faster than for semantic misses (~50 ms). No such difference was evident in the survival condition. Since this difference was evident approximately 2500 ms after word presentation and therefore at least 500 ms after the reported SMEs, it presumably did not influence the reported memory effects.

The present results show that two tasks, which are classically labeled as “deep encoding tasks” elicit dissociable SMEs. Interestingly, both encoding tasks elicited SMEs in the alpha/beta and theta frequency range. Whereas theta power effects have been reported in several memory studies and are generally thought to be related to contextual episodic memory encoding (Axmacher et al., 2006; Nyhus and Curran, 2010), beta effects have only been reported in some studies (Hanslmayr et al., 2009, 2012a,b). However, beta oscillations have been connected to semantic and language processes (for a review see Weiss and Mueller, 2012), which are processes presumably underlying both encoding tasks. The differences in local/global beta synchrony between both tasks presumably indexes the size of networks involved in the task reflecting the task complexity. This parallels findings that increasing long-range phase synchrony is related to more demanding working memory tasks (Cashdollar et al., 2009; Sauseng et al., 2005). The present findings in the alpha/beta band also fit the theory that alpha and lower beta oscillations reflect operations in a very broadly defined knowledge system (Klimesch, 2012; Klimesch et al., 2010). Semantic and survival processing lead to information processing indexed by alpha/beta power decreases (Hanslmayr et al., 2012a), but survival processing might involve a stronger interaction between different cortical areas.

The present results also have implications for the ongoing debate concerning the nature of the survival processing advantage. Nairne and Pandereida (2008) claimed that this encoding advantage arises from the fact that our brains have been shaped by evolution and that this particular encoding scenario makes use of these old, evolutionary modules that are tuned to process survival related information (see also e.g. Aslan and Bäuml, 2012). The need for this evolutionary explanation is much debated (Howe and Otgaar, 2013). Several studies show that the survival advantage is based on more proximate mechanisms such as novelty, contextual, relational or schematic processes (e.g. Butler et al., 2009; Kroneisen and Erdfelder, 2011; Kroneisen et al., 2012; Soderstrom and McCabe, 2011). These processes might best be subsumed as elaborative encoding processing. As the semantic feature judgment task and the survival task differ not only in the alleged evolutionary importance of the task but also in processing complexity and many other respects, the present study is clearly not designed to reveal a potential evolutionary survival module underlying the survival processing task. However, increases in phase synchrony related to successful encoding have also been found in studies that did use mere intentional encoding strategies (Weiss and Rappelsberger, 2000). Therefore increases in alpha/beta phase synchrony do not seem to reflect activation of a special survival module.



## Conclusion

The present study compared a semantic encoding task with a survival processing task. Both tasks are classically considered as “deep” encoding tasks. However, the present study shows that encoding related activity is significantly different in both tasks. This pattern of results supports the process view of memory illustrated by several cognitive theories of memory. The dissociation of global and local synchrony SMEs related to a semantic feature and an elaborative encoding task indicate the potential dissociable role of local and global synchrony measures in memory formation. Additionally, these results emphasize the important role of encoding strategies usage on SMEs. Consequently, task instructions in memory encoding studies have to be considered as important contributing factors.

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## Conflict of interest

The authors declare no competing financial or other interests.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.neuroimage.2013.04.121>.

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