



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 (Craig 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 (Craig 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 adaption 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 (Bäuml 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

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