Updating Processes in Episodic Memory

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Abstract

The efficient use of episodic memory does not only require to remember new information, it also requires to forget old information. That such memory updating is part of our memory system is suggested by behavioral studies examining both contextual and intentional memory updating. The electrophysiological correlates of episodic memory updating, however, still remain elusive. To investigate episodic memory updating, the context-change paradigm and the directed-forgetting paradigm can be used. In the directed-forgetting paradigm, subjects are cued to intentionally forget a previously learned item list and to learn a new list of items instead. In the context-change paradigm, subjects are cued to change their internal context between the learning of two lists. Both forms of cuing typically lead to forgetting of the first list and to memory enhancement of the second. The standard explanation of these effects is that forgetting and enhancement are mediated by a single mechanism: context differentiation in contextual memory updating and retrieval inhibition in intentional memory updating. In four experiments the necessity of new learning after cue presentation and the electrophysiological (EEG) correlates of forgetting and enhancement as they occur in these paradigms were explored. In both paradigms, forgetting of the first list was only observed when a second list was learned after cuing. Analysis of oscillatory EEG activity revealed that the forgetting in contextual memory updating was accompanied by an increase of theta phase coupling between scalp electrodes which is suggested to reflect the establishment of a new mental List-2 context. On the other hand, the forgetting in intentional memory updating was accompanied by a decrease of upper alpha phase coupling which is suggested to reflect an inhibitory disintegration of the to-be-forgotten information. Thus, phase coupling mediated the forgetting both in contextual and intentional memory updating, but in different frequency bands. In both paradigms, memory enhancement was accompanied by an increase in upper alpha band power which is suggested to reflect a change of encoding strategy after cuing. In sum, the present experiments revealed separate neural origins of forgetting and memory enhancement and thus point to a two-mechanism view of episodic memory updating.

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Chapter 1

Introduction

The company ”Lacuna Inc.” is the brainchild of Dr. Howard Mierzwiak who, after years of dedicated research, has developed a cutting-edge, non-surgical procedure for the focused erasure of troubling memories. ”Lacuna Inc.” was founded to provide a state of the art research facility for the development of this procedure. Over the years as the project has progressed from a mere idea into a full-blown medical service, ”Lacuna Inc.” has grown right along with it. Now a full service clinic with a highly trained staff, ”Lacuna Inc.” is just starting to tap into its potential. With hundreds of satisfied customers already, ”Lacuna Inc.” is developing a strong reputation in the medical community. The procedure is offered to men and women of all ages, and it is perfectly safe. So how does the procedure work?

Step One: The initial meeting. The first meeting with Dr. Mierzwiak serves primarily as an introductory meeting where the patient will be given a tour of the facility and a chance to meet the staff. After that, the patient will sit down for a consultation with Dr. Mierzwiak. While the possibilities for this procedure are endless, it is important that the patient and the doctor have a full understanding of each other’s expectations for the patient’s personal case. This helps the Lacuna team tailor the procedure to best serve the patient.

Step Two: Preparing for the procedure. After a patient decides of the specifics of what memory he/she is going to have erased, there is some initial preparation that goes into a successful procedure. The patient is instructed to collect any items or mementos that have any ties to the memory that is being targeted. These items will be used by the Lacuna team during and disposed of following the procedure. This is to ensure that the patient won't have any unexplainable items after the memory erasure.

Step Three: Mapping the memory. The team of Lacuna technicians will use the information they have received and the items brought in by the patient to create a map of the memory. They will then use this map to extract the memory from the patients mind.

Step Four: The procedure. Following the map created specifically for every patient, Dr. Mierzwiak and his team will begin to erase the target memory. The procedure works on a reverse timeline, which means it begins with the most recent memories and goes backwards in time. This approach is designed to target the emotional core that every memory builds on. By eradicating the core, Dr. Mierzwiak is able to make the entire memory dissolve. When the patient wakes up from the surgery, they remember nothing of the targeted memory and the brain is up to store new memories.

Of course, "Lacuna Inc." is a fictional company in the 2004 romance film "Eternal Sunshine of the Spotless Mind" by Charlie Kaufman and Michel Gondry. The characters of Joel and Clementine used this procedure to erase their memories of their love affair. As part of the screenwriting and promotion for the film, a back-story for the technology was made, including a spoof website for "Lacuna Inc." which is the source for the presented four-step procedure. Today, such targeted memory erasure of episodes is a fictional procedure.

1.1 Retrieval competition and memory updating

Quite contrary to the idea of memory erasure, experimental research has shown that, in large part, episodic forgetting does not occur because stored information is destroyed or erased, but because, although available, information becomes less accessible in large and growing networks in the brain (Melton, 1963; Tulving, 1983). The amount of information stored in our memory exceeds by far the amount of information that we can actually retrieve from it and, thus, episodic forgetting often occurs because retrieval of specific memories fails (for a review, see Roediger & Guynn, 1996). Indeed, in a series of experiments, Tulving and colleagues showed that retrieval failure represents a major source of forgetting (for a review, see Tulving, 1983). More precisely, they demonstrated that the accessibility of memories strongly depends on appropriate retrieval cues that can be used to evoke previously encoded information (e.g. Tulving & Pearlstone, 1966; Tulving & Psotka, 1971). For example, participants performed much better in a recognition task than in an uncued free recall test, suggesting that they know more than a free recall indicates (Tulving & Pearlstone, 1966). In addition, Tulving argued that successful retrieval depends on the similarity of encoding and retrieval operations. Retrieval cues have been shown to be most effective if the information in the cue resembles the information of the original encoding (e.g. Tulving & Osler, 1968; Tulving & Thomson, 1973). This interaction between encoding and retrieval processes becomes most apparent in studies that have shown that recall can be impaired by simply changing physical context between encoding and retrieval (e.g. Godden & Baddeley, 1975; Smith, Glenberg, & Bjork, 1978).

Various experimental work has shown that context can affect memory performance. Context at the time of encoding has been manipulated through various means to change external and subjects' internal contexts. Researchers have manipulated moods, arousal level, alcohol and marijuana intoxication, and so forth. Many of these experiments have simultaneously manipulated the context at encoding and retrieval in order to evaluate the context dependency of memory. Perhaps the most exotic manipulation is that of Godden and Baddeley (1975), who had divers learn and retrieve material either while underwater or while sitting on land. Cue-dependent forgetting theorists maintain that "memory for an event is always a product of information from two sources," the memory trace and the retrieval cue, the latter being "the information present in the individual's cognitive environment when retrieval occurs" (Tulving, 1974, p.74). Thus, retrieval processes are always bound to those of encoding and storage. How an episode is encoded and stored determines how well it can be retrieved later and what cues will affect its retrieval. As Tulving put it, "recollection of an event, or a certain aspect of it, occurs if and only if properties of the trace of the event are sufficiently similar to the retrieval information" provided in the retrieval cues. Maximizing the (contextual) similarity between study and test benefits retention and the greater the overlap between encoding and retrieval conditions, the greater positive transfer will be.

However, even if the appropriate cue for specific information is provided, retrieval can still fail because of retrieval competition of similar memories that are related to a cue. Retrieval competition means that specific information sharing a common retrieval cue competes for recall once the cue is provided. The more interfering information competes under a specific retrieval cue, the poorer the recall for any one piece of this information will be (Roediger, 1973; Tulving & Pearlstone, 1966). For example, imagine a scene in an American court room: a judge, two lawyers, the accused, a jury, and so on. Each of these persons experiences all about the same event, listens to the same testimonies, is introduced to the same witnesses. Nevertheless, when asking these persons about specific facts of the scene several years later, recall success will significantly differ between them. While the accused, the jury and the witnesses will remember many specific and facts of a unique court scene, the judge and the lawyers will do poorly because they experienced too many similar events prior and subsequent to this specific event. In fact, corresponding evidence comes from studies in single-list and multiple-list paradigms. In single-list paradigms, recall performance is reduced and slowed down when the number of competing list items increases (Watkins, 1975). As too many information is related to a specific cue, the cue is said to be overloaded (Earhard, 1967; Watkins & Watkins, 1975). In multiple-list paradigms, both the prior and the subsequent encoding of information can impair later memory for the targeted list, which is known as proactive and retroactive interference (Müller & Pilzecker, 1900; Underwood, 1957; for a review, see Crowder, 1976). Thus, retrieval competition constrains goal-directed retrieval of relevant memories.

The critical question in research of episodic memory updating is how to reduce competition from irrelevant information in order to facilitate retrieval of specific target memories. With reference to the court room scene, lawyers and witnesses deliberately or inadvertently communicate both admissible and inadmissible information to the jury. Thus, the question is whether the members of the jury are able to disregard inadmissible and irrelevant information and base their decision on admissible information only. Episodic memory updating might help to ignore false information like inadmissible information in the court room (for a review, see Kassin & Studebaker, 1998). Another relevant form of memory updating may concern the application to clinical contexts, like the forgetting of traumatic memories. From a historical standpoint, the notion that motivated forgetting should play a major role in repression mechanisms, as hypothesized by Freud and others, traces back more than a century. A third and common form of memory updating concerns the facility to replace old out-of-date information with new up-to-date information, like a new computer password in the office or a new phone number after removal. Thereby, the action of different mechanisms that serve episodic memory updating has been suggested. Each of these mechanisms operates to overcome retrieval competition of irrelevant information and to enhance processing of relevant information. At least three mechanisms have been suggested: blocking, retrieval inhibition and context differentiation.

Blocking refers to the inaccessibility of irrelevant information as a by-product of strengthening relevant information. Because retrieval competition is strength dependent, strengthening the representation of the relevant information (e.g. by means of additional encoding) blocks access to related but irrelevant information on a later recall test (McGeoch, 1942; Raaijmakers & Shiffrin, 1981; Rundus, 1973). More precisely, it is assumed that if the relevant information is represented in memory more strongly than the irrelevant information, the sampling of the relevant information will be favored at test. This sampling blocks the recall of the irrelevant information and makes it less accessible. Thereby, blocking does not affect the irrelevant information itself or the retrieval routes between the irrelevant information and its cue. Thinking of the court-room scene, a lawyer can strengthen his arguments by repeating them in the final speech to the jury. As a consequence, the jury's memory of repeated arguments will be enhanced but sampling of not repeated information will be blocked.

Retrieval inhibition can lead to the updating of irrelevant information through deactivation of some of its retrieval routes (for a review of inhibitory processes in episodic memory, see Bäuml, in press). More precisely, route deactivation refers to the weakening of the retrieval route between the irrelevant information and its cue, making the irrelevant information less accessible (Melton & Irwin, 1940; Geiselman, Bjork, & Fisher, 1983) without affecting the representation or availability of the irrelevant information itself. Route deactivation is suggested to mediate some form of intentional memory updating (Bäuml, in press). Intentional memory updating occurs in response to explicit or implicit cues to forget, initiated either by ourselves or others, in both real-world and laboratory situations (for a review, see Johnson, 1994, or MacLeod, 1998). With reference to the court-room scene, this form of updating may be initiated by the judge's demand to disregard nonevidentiary sources of information. Thus, if a lawyer or a witness communicates inadmissible information, and if the opposing lawyer objects, the judge will strike the evidence from the record and admonish the jury to disregard it. In other words, the judge wants the jury to forget the inadmissible information and remember relevant information only.

Context differentiation can lead to a reduction in the accessibility of encoded information by reducing the similarity between encoding and retrieval context. This might be achieved by changing physical or mental context after encoding of previous information. As a consequence, retrieval competition of previously encoded material should be reduced as different context information is connected to the items' representations encoded before and after the context change. Indeed, such contextual memory updating has guided much research in memory and is captured in the notions of encoding specificity (Tulving & Osler, 1968; Tulving & Thomson, 1973) and transfer-appropriate processing (Morris, Bransford, & Franks, 1977). With reference to the courtroom scene, lawyers can induce context changes to reduce recall performance of previously listened to information, e.g. the brought forward arguments of the opposing lawyer. This might be achieved by inducing emotions or arousal to change the jury members' mental contexts.

The principles of retrieval competition, retrieval inhibition and context differentiation are essential for current accounts of episodic memory updating. In this dissertation, two forms of episodic memory updating were investigated: contextual memory updating and intentional memory updating. The former is meant to be mediated by context differentiation, the latter by route deactivation. These mechanisms reduce accessibility of irrelevant information without necessarily strengthening the relevant information (unlike blocking). An empirical and theoretical review of contextual and intentional memory updating is given in the following sections of Chapter 1. As demonstrated in Chapter 2, electrophysiological measurements can be used to investigate the underlying mechanism(s) of contextual and intentional memory updating. In particular, the potential of analyses of oscillatory brain activity to study memory processes is highlighted. In Chapter 3, the experiments of the dissertation are presented. Both behavioral and electrophysiological experiments were run to investigate episodic memory updating. In Chapter 4, the results of the experiments are discussed and theoretical implications are given that may be examined in further experiments.

1.2 Contextual memory updating

In context-dependent-memory research, first-order and second-order paradigms can be contrasted (Bjork & Richardson-Klavehn, 1988). First-order paradigms are those in which a single context at encoding is either matched or mismatched to the context at retrieval. Second-order paradigms are those which use multiple contexts at encoding. Various studies using first-order paradigms showed that changes of both physical environment (e.g., Godden & Baddeley, 1975; Smith et al., 1978; for a review, see Smith & Vela, 2001) and internal state or mood between study and test (e.g., Eich, 1980; Macht, Spear, & Levis, 1977; for a review, see Eich, 1989) can reduce recall of previously learned material as they enhance the contextual mismatch between study and test. Retrieval is context dependent and memory is best when testing occurs in the same context in which learning took place. What subjects learned when drunk they remember better when drunk than when sober, and vice versa (Goodwin et al., 1969). Thus, the major determinant of context-dependent memory effects in first-order paradigms is the encoding-retrieval similarity of context as the degree of overlap between encoding and retrieval features determines retrieval success (Tulving, 1979, 1983).

The overlap principle of contextual features is consistent with the notion of encoding specificity (Tulving & Thomson, 1973) and basic to many current computational models of memory, such as the search of associative memory (SAM) model (Raaijmakers & Shiffrin, 1981). SAM and most other current models use mechanisms that incorporate contextual associations and the principle of cue-dependent memory. It is postulated that contextual cues fluctuate over time, leading to mismatches between encoding contexts and the retrieval context that can account for a variety of memory effects (Mensink & Raaijmakers, 1988). The more the contextual cues fluctuate over time, the less likely it is that the information can be retrieved at test if the appropriate contextual cues are missing. Thereby, the effects of context fluctuation or experimental manipulations of context diminish as the use of noncontextual cues, at learning or test, is supported. In addition, the effects of a context change from study to test can be diminished or even eliminated if the encoding context can be reinstated physically or mentally at test (Godden & Baddeley, 1980; Smith, 1979).

The notion of encoding-retrieval similarity plays an important role for the retrieval success in episodic memory which refers to memory for personally experienced past events (Tulving, 1983) and contextual memory updating in particular. But it is important to regard that episodic memory does not work in isolation. Episodic memory interacts very closely with semantic memory which refers to general knowledge of the world (Tulving, 2002). In particular, the storage of new information into episodic memory is directly associated with semantic memory processes (Baddley, 1984; Cabeza & Nyberg, 2000; Roediger, 1984). Therefore, in some cases a cue that differs from the original encoded episode can provoke its recall better than a literal copy of the episode itself (Tulving & Thomson, 1973).

In first-order paradigms, context-dependent memory effects are typically found in free recall but not in recognition (Godden & Baddeley, 1980; Jacoby, 1983; Smith et al., 1978). This dissociation can be best explained by the outshining hypothesis (Smith, 1988, 1994; Smith & Vela, 2001) which is based on the idea that when noncontextual cues are used, the effects of contextual cues are diminished or even eliminated. Recognition tests provide more noncontextual cues than free recall tests and therefore show less context dependence. In addition, there are generally no context-dependent memory effects on priming in implicit tasks (Parker, Gellatly, & Waterman, 1999; Parker, Waterman, & Gellatly, 2000). On the basis of the recollection/familiarity distinction, these findings suggest that effects in contextual memory updating reflect primarily a deficit in recollection and not in familiarity.

In second-order paradigms, the number of physical or internal contexts at encoding is manipulated. A commonly found context-dependent memory effect is the reduction of interference which occurs when different lists of items are learned in different contexts. The results of such studies are quite consistent, showing reduced proactive interference (Dallet & Wilcox, 1968) and retroactive interference (Eckert, Kanak, & Stevens, 1984; Greenspoon & Ranyard, 1957). Thus, these studies indicate that context information can decrease interference among sets of learned items with different contextual referents provided that appropriate cuing at test allows for reaccessing the different referents. Otherwise, the accessibility for the different contextual episodes would be reduced leading to context-dependent forgetting like in the context-change paradigm.

In the context-change paradigm both sides of contextual memory updating - forgetting and enhancement - can be examined. Participants typically study two lists of items and, after the presentation of List 1, either receive or not receive a cue to change their internal context before studying List 2 (Delaney & Sahakyan, in press; Sahakyan & Delaney, 2003, 2005; Sahakyan, & Kelley, 2002). After study of List 2, a recall test is conducted in which participants are asked to recall all of the previously presented items. Compared to uncued participants, cued participants show impaired recall of List-1 items and improved recall of List-2 items, referred to as the forgetting and enhancement. The List-1 forgetting is meant to be caused by the contextual mismatch between encoding of List-1 items and test induced by the context change (first-order effect). The List-2 enhancement is meant to arise from reduced proactive List-1 interference caused by the introduction of the new context previous to List-2 encoding (second-order effect).

The context-change paradigm provides good evidence for contextual updating in episodic memory. As a one-mechanism account context differentiation invokes the same mechanism to explain the forgetting and the enhancement of contextual memory updating. However, contrary to a one-mechanism account, it has recently been shown that forgetting may occur without enhancement in the context-change paradigm (Aslan & Bäuml, 2007; Sahakyan & Delaney, 2003). Instead, the enhancement was suggested to depend on additional factors like the adoption of more effective encoding strategies in response to the context change (Sahakyan & Delaney, 2003, 2005; Sahakyan, Kelley, & Delaney, 2004). It was argued that a strategy-based explanation provided a better account of the enhancement in memory updating than did the previous mechanism of context differentiation. Indeed, Sahakyan and Delaney's (2003) findings showed that efficient encoding strategies on List-2 learning can explain the enhancement without the need for a forgetting-related mechanism that produces an escape from proactive interference. Thus, Sahakyan and colleagues suggested that forgetting and enhancement may have different underlying mechanisms in contextual memory updating.

1.3 Intentional memory updating

Various work showed that an intention to forget typically leads to episodic memory updating. In the laboratory, intentional memory updating can be investigated with the list-method directed-forgetting paradigm (Bjork, LaBerge, & LeGrand, 1968). In this paradigm it was demonstrated that previously encoded material can be intentionally forgotten, making it less accessible on later recall attempts. In the list-method directed-forgetting paradigm, participants study two lists of items and, after the presentation of List 1, receive a cue to either forget or continue remembering this list before studying list 2 (Bjork, LaBerge, & LeGrand, 1968; for a review, see Johnson, 1994, or MacLeod, 1998). After study of List 2, a recall test is conducted in which participants are asked to recall all of the previously presented items, including both to-be-forgotten and to-be-remembered items. Compared with remember-cued participants, forget-cued participants typically show impaired recall of List-1 items, referred to as forgetting, and improved recall of List-2 items, referred to as enhancement. Thus, directed-forgetting effects provide evidence for intentional memory updating which is reflected by reduced accessibility for the old information and enhanced accessibility for the new information. Directed forgetting does not disappear if money is offered for recalled List-1 items, indicating that the effect is not due to demand characteristics (MacLeod, 1999).[1]

There is relatively broad agreement in the literature that directed forgetting on the list-method task manifests itself at the retrieval stage and is caused by retrieval inhibition. More specifically, when subjects are told to forget preceding information and are then presented with new information to learn, a process is initiated that inhibits the subsequent retrieval of the to-be-forgotten information. By inhibiting the List-1 items, the forget cue reduces proactive interference from List 1 and thus facilitates retrieval of List-2 items (Bjork, 1989). Primary evidence for this comes from studies comparing performance in the forget condition with performance in a condition with only a single list to learn. Because the level of performance in the forget condition and such a no-proactive-interference condition did not statistically differ, participants in the forget condition were said to escape from proactive interference (Bjork & Bjork, 1996; Bjork & Woodward, 1973). Furthermore, whereas this updating process inhibits the retrieval of the to-be-forgotten material, it leaves its strength in memory unaffected. By

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[1] In the literature, two different directed forgetting tasks have actually been used: the list-method and the item-method task. In contrast to the list-method task, in the item-method task, participants study a list of items and the exposure of each item is followed closely by the cue either to remember it or to forget it. On a later memory task, to-be-remembered items are typically better recalled than to-be-forgotten items (for a review, see MacLeod, 1998).

this view, List-1 items are less accessible, but remain available in memory. As a one-mechanism account retrieval inhibition invokes the same mechanism to explain the forgetting and the enhancement of intentional memory updating.

Retrieval inhibition of the to-be-forgotten material may arise from some form of deactivation of the retrieval route between the irrelevant information and its cue (Geiselman, Bjork, & Fisher, 1983; Melton & Irwin, 1940; for a review, see Bäuml, in press). Such an inhibitory mechanism weakens the associations between a cue and the to-be-forgotten material without affecting the representations of the to-be-forgotten items itself. As a consequence, route deactivation results in a loss of retrieval access to List-1 items rather than in a loss of the items' availability (Tulving, 1974; Tulving & Pearlstone, 1966). Support for the inhibitory route-deactivation account comes from a number of findings. First, the forgetting occurs in free recall but not in recognition or implicit memory tests (e.g. Basden, Basden, & Gargano, 1993; Block, 1971; MacLeod, 1999). Impairments on List-1 recognition, however, were found when participants were required to make source memory judgments (Geiselman et al., 1983). On the basis of the recollection/familiarity distinction, these findings suggest that the forgetting in intentional memory updating reflects primarily a deficit in recollection and not in familiarity. Second, in a relearning paradigm, to-be-forgotten items are relearned as readily as to-be-remembered items (Geiselman & Bagheri, 1985; Reed, 1970). Third, the forgetting extends to incidentally learned items (e.g. Geiselman et al., 1983). Being part of the same episode as intentionally learned words, incidentally learned words were also rendered inaccessible by the forget cue. Forth, inhibition can be released and its potential proactive interference reinstated by the reexposure of to-be-forgotten items (Basden et al., 1993; Bjork & Bjork, 1996; Goernert & Larson, 1994).

However, noninhibitory one-mechanism accounts of list-method directed forgetting have been suggested as well (see MacLeod, 1998). A prominent noninhibitory account of directed forgetting is the selective-rehearsal explanation which assumes that differential rehearsal of List-1 items after forget cue presentation accounts for the directed-forgetting effect. The proposal is that a forget cue between lists stops rehearsal of List-1 items and causes selective rehearsal of List-2 items, whereas a remember cue between lists causes nonselective rehearsal of both List-1 and List-2 items (Bjork, 1970; for a review, see Sheard & MacLeod, 2005). Because the selective-rehearsal explanation attributes directed forgetting to differences in encoding, effects both on recall and recognition of intentionally learned items should be observed. However, the failures to find directed forgetting on recognition and the finding that directed forgetting extends to incidentally learned items are inconsistent with the selective-rehearsal explanation.

A more recent noninhibitory account of list-method directed forgetting is the context-change explanation (Sahakyan & Kelley, 2002). Here, the proposal is that directed forgetting is a variant of context-dependent forgetting. It was argued that one strategy that would allow participants to intentionally forget List 1 in directed forgetting would be to deliberately attempt to alter their internal context cues, creating a larger than normal change of context between lists. Accordingly, the forget cue should create a second context cue and, regarding List 1, should lead to a mismatch between the context at encoding and the context at retrieval. In this way, the effect of the forget cue should mimic a change in internal context similar to the one created by imagination tasks. Consistent with this hypothesis, Sahakyan and colleagues found that a change in internal context can simulate typical directed forgetting data, and that not only context-dependent forgetting but also directed forgetting can be reduced if at test the original List-1 encoding context is reinstated (Sahakyan & Delaney, 2003; Sahakyan & Kelley, 2002).

Contrary to one-mechanism accounts, however, it has recently been shown that forgetting may occur without enhancement (Conway et al., 2000; Sahakyan & Delaney, 2003; Zellner & Bäuml, 2006) and enhancement may occur without forgetting (Bäuml, Aslan, & Kuhbandner, 2007; Benjamin, 2006; Macrae, Bodenhausen, Milne, & Ford, 1997). Therefore, two-mechanism accounts have emerged that attribute the forgetting and the enhancement of directed forgetting to different mechanisms (Sahakyan & Delaney, 2005). The forgetting is explained by invoking retrieval inhibition or context differentiation, whereas the enhancement is explained by invoking an encoding-strategy-change explanation (Sahakyan & Delaney, 2003, 2005). It was proposed that the enhancement of directed forgetting is attributed to better encoding of the second list because forget group participants often adopt better encoding strategies on the second list. Indeed, Sahakyan and Delaney (2003) showed that the enhancement was abolished when subjects' encoding strategy at List-2 learning was induced to be the same in both the remember and forget condition. Thus, it was argued that a strategy-based explanation provided a better account of the enhancement in memory updating than did the previous mechanisms of retrieval inhibition or context differentiation. Consequently, one-mechanism accounts would have to be modified to assume that retrieval inhibition or contextual shifts somehow result in more efficient List-2 encoding for some participants in order to fully explain the enhancement of memory updating.

In sum, both contextual and intentional memory updating are reflected by reduced accessibility for the still available old information and enhanced accessibility for the new information. Contextual memory updating, as investigated in the context-change paradigm, has originally been explained with a one-mechanism account. The proposal is that context differentiation between lists leads to forgetting which is meant to be caused by the contextual mismatch at retrieval and enhancement which is meant to arise from reduced proactive interference. Intentional memory updating, as investigated in the directed forgetting paradigm, has also been explained with a one-mechanism account. The proposal is that retrieval inhibition leads to forgetting of List-1 items and enhancement of List-2 items which is meant to arise from reduced proactive interference. Recently, two-mechanism accounts that attribute the forgetting to retrieval inhibition or context differentiation and the enhancement to a change to a superior encoding strategy have been suggested. In this dissertation, behavioral experiments together with electrophysiological experiments were run to help discovering exactly which and how many mechanisms mediate contextual and intentional memory updating, to what extent they are functionally or neurally equivalent, and whether they are inhibitory or noninhibitory in nature.

Chapter 2

Electrophysiology of memory processes

For over a century, scientists have used measures of brain activity to gain insights into perceptual, cognitive, and motor functions and have developed a variety of methods to measure brain activity. On the one hand, hemodynamic methods have been developed to indirectly measure brain activity by recording changes in vascular variables that are linked to changes in neural activity. On the other hand, electromagnetic methods have been developed to directly measure brain activity by recording the electromagnetic fields generated by certain neuronal populations. These approaches provide complementary views on neural activity and differ in their relative strengths in determining when versus where neural activity takes place.

Electrical activity changes rapidly over time but has a spatially extended field. There is an increasing number of researchers analyzing the electroencephalogram (EEG) to investigate cortical functioning, mostly by applying event-related brain potential (ERP) measures (for a review, see Handy, 2005, or Rugg, 1995). ERPs are changes in the brain's electrical activity time-locked to some experimental condition or event such as the presentation of a stimulus. The magnitude of these changes is small in comparison to the amplitude of the background EEG which constitutes the noise from which the ERP signal has to be extracted. ERP waveforms with satisfactory signal-to-noise ratios are obtained by averaging the EEG samples from a number of trials belonging to the same experimental condition. The averaged waveforms represent estimates of time-locked neural activity elicited by the presentation of stimuli belonging to different experimental conditions. By recording EEGs from multiple scalp electrode sites, ERPs can be analyzed in their temporal and spatial characteristics. There is a relatively long history of studies that employed ERPs to investigate the electrophysiological correlates of human memory and the ERP has been shown to be useful for studying cognitive function and memory (for a review, see Rugg & Allan, 2000). But there are important limitations of the use of ERPs in memory research because ERP waveforms can only be used to study processes that are time-locked to an event or stimulus.

On the other hand, EEG data can also be investigated in the frequency domain and it has been convincingly demonstrated that assessing oscillatory activity within specific frequency bands can yield insights into the functional correlations of these signal (for an overview, see Buzsáki, 2006, or Herrmann, Grigutsch, & Busch, 2005). The question is, whether different oscillations in different frequency bands reflect different cognitive processes. In contrast to ERP measures, analyses of oscillatory activity can be used to study processes that are not time-locked to a detectable event. This dissertation focuses exclusively on measures of oscillatory brain activity deduced from the EEG.

2.1 Oscillatory brain activity

Selective information processing requires exact timing and coherent neuronal activation of numerous and widely distributed functional areas of the brain, which are believed to be established by oscillations (Fries, 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001). It is assumed that synchronization of neuronal discharges subserves the integration of many dimensions of a cognitive act, including perceptual binding, memory, and motor planning. As functionally specialized cortical areas are distributed and spread over the cortex, they have to cooperate in a dynamic organization of information processing within local and global cortical networks which passively store information via their synaptic weights (Hebb, 1949) and become active when a particular information has to be accessed (Fuster, 1997). For example, central to the classical binding problem, at the level of visual feature binding, there is evidence that the firing of neurons signaling different features of the same object is synchronized, whereas the firing of the same neurons is uncorrelated if they discharge in response to separate perceptual objects (e.g. Singer, 1999; Varela et al., 2001).

Analysis of EEG oscillations traces back to the beginning of EEG-based research. Berger (1929) was the first to describe oscillations in different frequency bands which are present in the human brain and showed that the dominant rhythm in the human scalp EEG ranges from about 8 to 13 Hz. This frequency band was designated alpha as it was the first to be observed. Occipito-parietal alpha oscillations are most dominant when subjects have their eyes closed and are suppressed and substituted by the faster beta oscillations ranging from about 15 to 30 Hz when subjects open their eyes. Following this consecutive ordering, Adrian (1942) referred to oscillations from about 30 to 80 Hz as gamma waves. Unlike alpha in the human EEG, theta is the dominant rhythm of lower mammals and shows a much wider frequency range than in humans, namely from about 3 to 12 Hz. Theta is most easily recorded from the hippocampus but occurs in other cortical and subcortical structures as well. In humans the theta frequency ranges from about 4 to 8 Hz. In addition to these frequency bands, there are various others, ranging from very slow oscillations (<1 Hz) (Leopold, Murayama, & Logothetis, 2003) to high-frequency (100-200 Hz) (Ylinen et al., 1995) and ultra-fast oscillations (600 Hz) (Curio, 1999). However, no sharp boundaries between the relevant frequency bands should be drawn as there are interindividual differences between subjects and intraindividual differences during a cognitive task. For example, alpha frequency varies as a function of age, neurological diseases, brain volume and task demands (for a review, see Klimesch, 1999). Regarding the factor age, older people may show an alpha peak frequency of 7 Hz or lower (Brenner et al., 1986). As for the alpha band, there are no clear criteria for other frequency bands and broad-band analyses must be interpreted with caution. By analyzing narrow frequency bands instead, the danger that frequency specific effects are undetected or cancel each other out can be reduced.

Oscillations are characterized by their phase and amplitude. The phase of an EEG oscillation ranges between 0 and 2π. The amplitude (square root of power) is typically between 0 and 10 μV. At every point in time one can determine the phase and amplitude of an oscillation. According to a classification by Galambos (1992), there are spontaneous, evoked and induced oscillations, all of which are differentiated by their degree of phase locking to an experimental condition or stimulus. Spontaneous activity is completely uncorrelated with the occurrence of an experimental condition. Evoked oscillations are strictly phase-locked to the onset of an experimental condition across trials. They usually result from any kind of sensory event, such as visual stimulation, and are visible in the averaged event-related potential (ERP). Induced activity is correlated with an experimental condition but is not strictly phase-locked to its onset and, thus, not visible in the averaged ERP.

Two scales of neuronal synchrony can be distinguished - local synchrony and global synchrony (Varela et al., 2001). Local synchrony concerns neural assemblies which are distributed over a local area. When recording EEG from surface electrodes, local synchrony can be operationalized by measuring the oscillatory power over an electrode reflecting the spatial summation of the underlying neuronal activity. Analyzing oscillatory power in a given frequency band, tonic and event-related power changes can be distinguished. Tonic power refers to the induced activity that is not event-related on a trial per trial basis. It can be measured in some type of baseline condition, e.g. eyes closed or a pre-stimulus reference interval. Tonic changes in power occur over the life cycle and in response to circadian rhythms (for a review, see Klimesch, 1999). Event-related changes in power can be measured in different ways, but the basic idea is that some type of baseline condition which reflects the tonic aspect (e.g. a pre-stimulus interval) is compared with some type of task condition (e.g. a post-stimulus interval). Event-related changes in ongoing EEG activity can consist of either decreases or increases in power compared to the reference interval. These changes are considered to be due to a decrease or an increase in synchronous firing of the underlying neuronal populations. The former case is called event-related desynchronization (ERD) (Pfurtscheller & Aranibar, 1977) and the latter event-related synchronization (ERS) (Pfurtscheller, 1992). Both tonic power and event-related power changes have been shown to be related to cognitive processing and memory performance in particular (Klimesch, 1999). Thereby, investigating the functional relationship between tonic power and event-related changes, researchers showed that event-related changes are strongly influenced by tonic power in the pre-stimulus interval (Doppelmayr, Klimesch, Pachinger, & Ripper, 1998; Fingelkurts, Fingelkurts, Krause, & Sams, 2002; Lehman, Michel, Pal, & Pascual-Marqui, 1994).

Global synchrony concerns assemblies which are farther apart in the brain such as, for example, assemblies between occipital and frontal lobes or across hemispheres. But of course, there is no simple continuum from strictly local to global networks. Global synchrony can be operationalized by measuring oscillatory phase coupling between electrodes reflecting the dynamic phase relationship between two neural assemblies independently of their amplitude. In contrast to local power changes, phase coupling enables to monitor increasing and decreasing synchronization between different brain regions more or less engaged in a cognitive task. The phase locking value (PLV) is such a measure of frequency-specific phase coupling between two signals that is independent of amplitude (Lachaux et al., 1999). Thereby, oscillatory activity is taken to be synchronous if the phase lag between two electrodes remains constant throughout the trials. The PLV ranges from 0.0 meaning maximal phase variability to 1.0 meaning perfect phase coupling. Frequency coherence is another measure that has been extensively used to investigate global synchrony. It is estimated by calculating the correlation coefficient of two signals and, thus, mixes the effects of amplitude and phase in the interrelations between the signals. However, to narrow the analysis down to global synchrony, methods that focus exclusively on phase information - like PLV - should be favored (Friston, 1997; Varela et al., 2001). Both phase coupling and coherence have been shown to be related to cognitive processing and memory performance in particular. It has been argued that coherent firing between distant neuronal populations is a mechanism which subserves binding in conscious perception (Gross et al., 2004; Rodriguez et al., 1999) and associative learning (Miltner et al., 1999). In addition, employing quite different paradigms, previous studies reported evidence for an increase in memory performance when certain brain structures are oscillating in synchrony (e.g. Fell et al., 2001; Tallon-Baudry, Mandon, Freiwald, & Kreiter, 2004; Weiss & Rappelsberger, 2000).

Both oscillatory power of local signals and phase synchronization across recording sites can be chosen as indicators of local and global processing. It may be hypothesized that the selective information processing, which underlies episodic memory updating, is accompanied by changes in power or phase of oscillations in different frequency bands. As suggested by Klimesch (1999), in particular, two frequency bands are related to memory performance: theta (4 to 8 Hz) and upper alpha (10 to 13 Hz).[1] It is assumed that episodic memory processes are reflected by theta oscillations in a cortico-hippocampal network, whereas semantic memory processes are reflected by upper alpha oscillations in a thalamo-cortical network. Thus, in the following two sections, findings that theta and upper alpha oscillations reflect cognitive performance and memory performance in particular are reviewed.

2.2 Theta oscillations and episodic memory

Theta oscillations recorded from the hippocampus of lower mammals (e.g. rodents) are one of the best documented biological rhythms (for a review, see Kahana, Seelig, & Madsen, 2001). Animal research revealed that in response to increasing demands, hippocampal theta synchronizes. This synchronization can be explained in terms of an increase in duration and rhythmicity of hippocampal burst firing with the same frequency as theta. Although most studies of rodent theta have focused on hippocampal theta, prominent theta activity has also been recorded from many extrahippocampal regions,

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[1] Other frequency bands have also been shown to be related to cognitive performance and memory processes. For example, gamma oscillations (30 to 80 Hz) have been shown to be involved in both perceptual and memory processes (e.g. Fell et al., 2001; Sederberg et al., 2003, 2007; for a review, see Jensen, Kaiser, & Lachaux, in press). In this dissertation, analyses of oscillatory brain activity will focus on the theta and alpha frequency bands.

including cingulate cortex and neocortex. In accordance, human theta does not appear to be restricted to hippocampal sites, but rather appears over widespread regions of the neocortex. It was hypothesized that hippocampal theta may be induced into the cortex via cortico-hippocampal feedback loops and, thus, can even be detected by scalp-recorded EEG signals (Klimesch, 1999). In addition, theta oscillations recorded from the cortex might be, in part, generated distinctly from theta oscillations found in the hippocampus (Kahana et al., 2001). Thus, theta oscillations in the range of about 4 to 8 Hz are most likely generated in cortico-hippocampal as well as in cortico-cortical feedback loops.

Animal studies focusing on the hippocampal theta have provided good evidence that theta synchronization is related to the encoding of new information (Buzsáki et al., 1994; O'Keefe & Burgess, 1999). First, long-term potentiation in rats is highly sensitive to the phase of the hippocampal theta rhythm, with potentiation favored at the peak of the theta cycle and depotentiation favored at its trough (Hölscher, Anwyl, & Rowan, 1997; Huerta & Lisman, 1993). Second, in map-based navigation, the coding of spatiotemporal context and place information in the rat hippocampus is mediated by the phase of hippocampal theta (Skaggs, McNaughton, Wilson, & Barnes, 1996) and it is assumed that episodic memory representations may have evolved from mechanisms serving navigation (Buzsáki, 2005). Third, blocking theta oscillations by lesioning hippocampal structures produces severe impairments in memory function (Mizumori & Leutgeb, 1999). Thus, there has been much progress in understanding the crucial role played by the theta rhythm in the organization and timing of neuronal activity in the hippocampus of lower mammals. Human EEG recordings at the scalp provide a means of investigating theta oscillations in the human brain. Although these recordings have a lower signal-to-noise ratio compared to local field potentials of individual pyramidal cells in rodents, theta oscillations can nonetheless be detected at the human scalp provided they are synchronous over large regions of cortex and high in amplitude.

Human scalp, depth, and subdural recording studies have shown that theta power responds selectively to the encoding of new information in episodic memory. Klimesch et al. (1996, 1997b) calculated theta band power changes during encoding and compared words which could be remembered later with those which could not be remembered. Klimesch and colleagues found significant increases in cortical theta power (ERS) during the encoding of words that were subsequently recalled or correctly recognized. By controlling for unspecific factors, such as attentional demands, task difficulty and cognitive load, it was assumed that the only difference between the later remembered and not remembered words referred to the actual establishment of an episodic memory trace. Similarly, intracranial EEG recordings have confirmed that temporo-frontal neocortical sites exhibit local increases in power during successful encoding (Sederberg et al., 2003). Whereas Sederberg et al. (2003) reported increases in cortical theta power, Fell et al. (2003) found no changes in hippocampal theta power during encoding of subsequently recalled words. These different findings are in line with the assumption that cortical theta oscillations are, in part, generated distinctly from theta oscillations found in the hippocampus (Kahana et al., 2001).

Doppelmayr et al. (1998) showed that the reactivity in theta band power (ERS) which reflects task performance can be predicted from the amount of tonic theta power as measured during a reference interval (e.g. a pre-stimulus interval). Small reference power is related to large theta ERS or increase in power. Accordingly, one could expect that good as compared to bad memory performers show less tonic power in the theta band. This hypothesis was clearly supported by two studies of the Klimesch group (Klimesch, Vogt, & Doppelmayr, 2000; Vogt, Klimesch, & Doppelmayr, 1998).

With respect to global synchrony, long-range coherent activity was shown to be increased during the encoding of words that were later successfully recalled. Weiss and Rappelsberger (2000) reported that subsequently recalled words elicited higher long-range synchrony than not recalled words within different frequency bands, including the theta band. Especially, theta coherence between left frontal and parieto-occipital electrodes increased which might reflect an enhanced cooperation between these regions during the encoding of subsequently recalled words (Sarnthein et al., 1998; Sauseng et al., 2004; Weiss, Müller, & Rappelsberger, 2000). Similarly, Fell et al. (2003)

found enhanced theta coherence between intracranially recorded electrodes during the encoding of subsequently recalled words. Thus, increased global synchrony the theta band is suggested to be related to successful encoding of episodic information.

As it is assumed that theta oscillations primarily reflect episodic memory processes, theta should be sensitive to manipulations of the encoding context. Therefore, Summerfield and Mangels (2005) investigated local and global synchrony of theta oscillations during item-context encoding. EEGs were recorded while subjects encoded words presented in one of four different colors representing a type of intrinsic context. Consistent with previous studies (Klimesch et al., 1996; Sederberg et al., 2003), increases in theta ERS over frontal areas were observed during the encoding of words that were later correctly recognized. Coherence analysis revealed that the item-context binding of words and colors was associated with global synchrony in the theta band between frontal and posterior electrode sites bilaterally. Whereas local synchrony in the theta band was predictive of subsequent item memory, global synchrony predicted the retrieval success of context. Thus, authors confirmed the importance of fronto-posterior coherence in the encoding phase and presented evidence that it is the degree to which this coherence is sustained that predicts associative item-context encoding.

In rodents, in the frame of spatial navigation, hippocampal theta activity is well elucidated. Recently, theta phase coding has been suggested to be a neural mechanism for both cognitive map memory in rodents and episodic memory in humans (Buzsáki, 2005). However, the importance of theta synchrony for episodic memory in humans has only been shown with verbal item material (Klimesch et al., 1996; Summerfield & Mangels, 2005; Weiss & Rappelsberger, 2000). Therefore, Sato and Yamaguchi (2007) investigated scalp EEG activity during performance of a object-place memory task to include the spatial dimension that is essential for both episodic memory and cognitive map memory. Comparable to Summerfield and Mangels's (2005) study, global theta coherence was found to increase in relation to subsequently successful recall of objects' place. Thus, this finding suggests the human theta dynamics in common with rodents in episodic memory formation.

2.3 Upper alpha oscillations and semantic memory

Past animal work implicates the thalamus as an important neuronal oscillator of alpha rhythms because substantial relations between rhythmic activity of the thalamus and the neocortex in animals were found (Andersen & Andersson, 1968; Lopes da Silva, van Lierop, Schrijer, & Storm van Leeuwen, 1973). It is a well-established finding that the reticular nucleus of the thalamus plays a key role in the control of rhythmic EEG activity in the mammalian brain, particularly during sleep (for a review, see Steriade, 2001). In addition, cortical alpha oscillations might be, in part, generated distinctly from a thalamic pacemaker in cortico-cortical feedback loops (Klimesch, 1999). Thus, alpha oscillations in the range of about 8 to 13 Hz are most likely generated in thalamo-cortical as well as in cortico-cortical feedback loops (Steriade, Jones, & Llinas, 1990).

Both upper alpha power and upper alpha phase coupling (10 to 13 Hz) have been shown to be related to cognitive performance and memory performance in particular.[2] Whereas theta oscillations may primarily reflect processes of episodic memory, upper alpha oscillations can be considered as a functional correlate of semantic long-term-memory processes (for a review, see Klimesch, Doppelmayr, & Hanslmayr, 2006). Klimesch, Schimke and Schwaiger (1994) were the first to show a specific relationship between upper alpha ERD and semantic memory processes. Their results demonstrated that upper alpha shows a larger ERD in a more semantic as compared to a more episodic encoding task. Indeed, upper alpha ERD responds primarily to semantic processing and neither to episodic or working memory processes nor to more general task demands such as task difficulty or attention (Klimesch et al., 1997a).

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[2] There is strong evidence for the view that there is no single alpha rhythm but instead a population of different alpha rhythms (for a review, see Basar & Bullock, 1992). Lower alpha (8 to 10 Hz) is topographically widespread over the entire scalp and probably reflects general attentional demands. Upper alpha (10 to 13 Hz) is topographically restricted to occipito-parietal electrode sites and appears functionally related to semantic processes (for a review, see Klimesch, 1999).

This does not mean that upper alpha is completely irrelevant for episodic memory or working memory, as there are good reasons to assume that at least part of episodic and working memory can be understood in terms of transiently activated (semantic) long-term memories (Fuster, 1997). Thus upper alpha ERD should play an important role in most memory tasks but will be most sensitive to semantic processing demands. The interplay of episodic memory and semantic memory may be reflected by co-activation of upper alpha with other frequencies, e.g. theta, that are related to central executive functions. Interestingly, Neubauer, Freudenthaler, and Pfurtscheller (1995) found smaller upper alpha ERD or even ERS for good performers in a non-semantic working memory task. Thus, pronounced upper alpha ERD can be observed in a semantic long-term memory task but less ERD or even ERS can be observed in a working memory task in which knowledge from semantic long-term memory is irrelevant. Doppelmayr et al. (2005) suggested that the finding of ERS in these working memory tasks may indicate the ability to avoid activation of a system that is not directly task relevant. Accordingly, upper alpha ERD would reflect focused activation and ERS inhibition of task-irrelevant processes (Klimesch et al., 2006).

In semantic long-term memory tasks, good performers show larger magnitude of upper alpha ERD as compared to bad performers. But upper alpha ERD does not depend only on task type or stimulation but also on tonic power as measured during a reference interval (e.g. a pre-stimulus interval) in a sense that large reference power is associated with large ERD and good performance (for a review, see Klimesch, 1999). Indeed, several studies imply that good memory performance is related to large alpha power in the reference interval but to small power during task performance (Doppelmayr et al., 2002; Klimesch et al., 2000; Vogt et al., 1998). This is in accordance with findings that tonic upper alpha power is related to cognitive processing capacity which depends on factors like age or neurological diseases (for a review, see Klimesch, 1999). Accordingly, tonic upper alpha power and ERD are positively correlated to (crystallized) intelligence as semantic long-term memory performance represents an essential aspect of intelligence (Doppelmayr et al., 2002).

But is the relationship between the dynamics of alpha oscillations and cognitive performance just correlative or causal in nature? Applying repetitive transcranial magnetic stimulation in the upper alpha frequency range in the pre-stimulus reference interval, Klimesch, Sauseng, and Gerloff (2003) enhanced tonic power in the upper alpha band. As a result, both upper alpha ERD and task performance were enhanced. This finding provides good evidence for the functional relevance of local synchrony in the upper alpha band for the implementation of memory performance. On the basis of this finding, Hanslmayr et al. (2005) tested whether neurofeedback training can enhance cognitive performance similarly. Authors showed that success in neurofeedback training led to a significant increase in reference upper alpha power and was positively correlated with the improvement in cognitive performance.

Early findings that alpha amplitude was attenuated by eyes opening or visual stimulation inspired the idea that alpha oscillations function as an idling rhythm (Adrian & Matthews, 1934). Today, the idling hypothesis has been largely overtaken by a framework where alpha oscillations reflect a level of cortical inhibition (Klimesch, 1996; Klimesch, Sauseng, & Hanslmayr, 2007). Klimesch (1996) proposed that small alpha amplitudes are a signature of regions of active neuronal processing, whereas large alpha amplitudes reflect the inhibition of task-irrelevant cortical areas. Regarding memory processes, Klimesch et al. (2007) suggested that large alpha-amplitude oscillations during memory retention inhibit the retrieval of memorized items. Thus, according to the inhibition hypothesis, large alpha oscillations reflect the suppression of unattended or ignored stimuli. Although a number of findings support the inhibition hypothesis, it was recently questioned. Palva and Palva (2007) argued that it may be unfeasible to deduce that large alpha amplitudes correspond to inhibited cortical states. These authors suggest that alpha oscillations may reflect active processing in task-relevant networks or active inhibition of task-irrelevant regions, or both. Moreover, they link alpha band oscillations to the mechanisms of short-term memory and attention. Thus, the functional significance of alpha-amplitude dynamics remains a central objective in future research. Furthermore, Klimesch et al. (2006) suggested the use of other measures - particularly phase sensitive measures - to study memory processes and to evaluate an oscillation's functional significance in general.

With respect to global synchrony, coherent upper alpha activity has been shown to be increased during the encoding of words that were later successfully recalled (Weiss & Rappelsberger, 2000). Authors suggested that coherence in the upper alpha band might be correlated with the semantic part of the task. As mentioned earlier, in this study, recalled nouns were correlated with higher coherence in various frequency bands. It is assumed that coherence in the different frequency bands yield different functional contributions to the mnemonic information processing. Obviously, later recalled words were embedded within more complicated networks of interactions in different frequency bands between various brain regions than not recalled words. A higher degree of semantic associations during the encoding phase of later recalled items is reflected by enhanced upper alpha coherence, respectively.

To summarize, memory processes are accompanied by changes in power and phase of oscillations in the theta and upper alpha frequency band. It is assumed that episodic memory processes are reflected by theta oscillations, whereas semantic memory processes are reflected by upper alpha oscillations. Episodic and semantic memory networks cooperate in a dynamic organization within both local and global cortical networks. It may be hypothesized that similar processes are involved in episodic memory updating and, thus, measurement of oscillatory brain activity might be used to examine forgetting and enhancement both in contextual and intentional memory updating.

Chapter 3

The present experiments

Both behavioral and electrophysiological experiments were run to investigate which processes mediate contextual and intentional memory updating, to what extent they are functionally or neurally equivalent, and whether they are inhibitory or noninhibitory in nature. The goal of the behavioral *Experiment 1a* was to replicate the detrimental and beneficial effects of episodic memory updating: contextual memory updating in the context-change paradigm and intentional memory updating in the directed-forgetting paradigm.

In intentional memory updating, research has shown that recall of List-1 items is not impaired if participants are instructed to forget List 1 after encoding of List 2 (Roediger & Tulving, 1979; Woodward, Park, & Seebohm, 1974). Furthermore, the forget cue per se does not appear to be sufficient to induce List-1 forgetting and subsequent List-2 encoding seems necessary to create the effect (Gelfand & Bjork, 1985, described in Bjork, 1989). Thus, for successful intentional memory updating, the intention to forget out-of-date information should arise directly after List-1 learning but before the encoding of the subsequent up-to-date information (List 2). But to date, the latter finding has only been reported as part of a conference paper. Therefore, the first goal of *Experiment 1b* was to reexamine the crucial role of List-2 encoding for successful intentional forgetting. In contextual memory updating, the question is whether changes in internal context are sufficient to induce context-dependent forgetting or if subsequent learning is necessary. Although classical studies using first-order paradigms showed context-dependent forgetting without subsequent learning, with weaker environmental manipulations or manipulations of internal states, like mood induction, context changes sometimes failed to generate a context-dependent forgetting (Eich, 1985; Fernandez & Glenberg, 1985).

Experiment 2 was conducted to correlate contextual memory updating as it is studied in the context-change paradigm with electrophysiological measurements of oscillatory brain activity. It is assumed that both theta and upper alpha oscillations reflect memory processes (Klimesch, 1999). Particularly the theta band was suggested to play an important role in episodic memory and global synchrony of theta oscillations was shown to be related to retrieval success of contextual information (Summerfield & Mangels, 2005). As it has recently been shown that forgetting may occur without enhancement in the context-change paradigm (Aslan & Bäuml, 2007; Sahakyan & Delaney, 2003), a one-mechanism account, like context differentiation, may not be sufficient to explain both enhancement and forgetting. Therefore, analyses of local and global synchrony in the upper alpha and theta band might reveal the number of mechanisms that mediate the pattern of forgetting and enhancement in contextual memory updating.

Experiment 3 was conducted to correlate intentional memory updating as it is studied in the directed-forgetting paradigm with oscillatory brain activity. An interesting question in intentional memory updating is whether the underlying processes are inhibitory or noninhibitory in nature. According to the inhibition hypothesis, upper alpha oscillations reflect some form of cortical inhibition (Klimesch, 1996; Klimesch et al., 2007). Therefore, measurements of synchrony in the upper alpha band should be sensitive to intentional memory updating. Otherwise, if intentional memory updating is based on context differentiation as suggested by Sahakyan and Kelley (2002), synchrony in the theta band should mediate the pattern of forgetting and enhancement. But again, as previous studies have shown that forgetting can occur without enhancement (Conway et al., 2000; Sahakyan & Delaney, 2003; Zellner & Bäuml, 2006) and enhancement without forgetting (Bäuml et al., 2007; Benjamin, 2006; Macrae et al., 1997), analyses of local and global synchrony in the upper alpha and theta band might help to reveal the number of mechanisms underlying intentional memory updating.

Memory updating and the role of post-cue encoding

3.1 Experiment 1a

The goal of *Experiment 1a*[1] was to replicate the detrimental and beneficial effects of intentional memory updating in the directed-forgetting paradigm (Bjork, 1989) and unintentional memory updating in the context-change paradigm (Sahakyan & Kelley, 2002). Because it has recently been shown that forgetting may occur without enhancement, *Experiment 1a* was run to check for possible effects of procedure and/or material which could mask memory updating effects in the later experiments. Only if both forgetting and enhancement of memory updating can be observed in *Experiment 1a*, then the following behavioral and electrophysiological experiments will be conclusive. In addition, data of *Experiment 1a* can serve as baseline for comparison with data of *Experiment 1b* investigating the crucial role of post-cue encoding.

3.1.1 Methods

Participants

One hundred sixty-two healthy students of the University of Regensburg took part in the experiment on a voluntary basis. The sample consisted of

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[1] Parts of the experiment were accepted for publication in Pastötter, B., & Bäuml, K.-H. (in press). The crucial role of post-cue encoding in directed forgetting and context-dependent forgetting. *Journal of Experimental Psychology: Learning, Memory, and Cognition.*

62 males and 100 females. Their mean age was 23.5 years with a range of 18 to 49 years. All participants spoke German as native language. They were tested individually with 54 participants in each of the three experimental conditions.

Material

Forty-five unrelated German nouns of medium frequency were drawn from the CELEX database using the Wordgen v1.0 software toolbox (Duyck, Desmet, Verbeke, & Brysbaert, 2004). Three lists of 15 words each were prepared. Across lists, words were matched on frequency and word length. The assignment of items to lists was constant for all participants. Item order within lists was random for each participant. Each list was equally often used in the remember condition, the context-change condition and the forget condition and served equally often as the first and the second presented list.

Experimental Design

A 3 × 2 mixed design with the between-participants factor CUE (remember, context change, forget) and the within-participants factor LIST (List 1, List 2) was used. Two lists of words were learned. Conditions differed in which cue was provided after List-1 encoding. In the remember condition, List 1 was followed by a cue to remember the items; in the forget condition, List 1 was followed by a cue to forget the items; in the context-change condition, List 1 should be remembered and was followed by a mental context change. Mean recall frequency was used as dependent variable. Items were counted as correctly recalled if they were recalled with the correct list.

Procedure

Participants were informed about the general nature of the experiment. They were told that they had to learn some items and that their memory for these items would be tested later on. They were also told that it could happen that, just after presentation, the experimenter would declare an item list as no longer relevant and that, in this case, they should try to forget the related list.

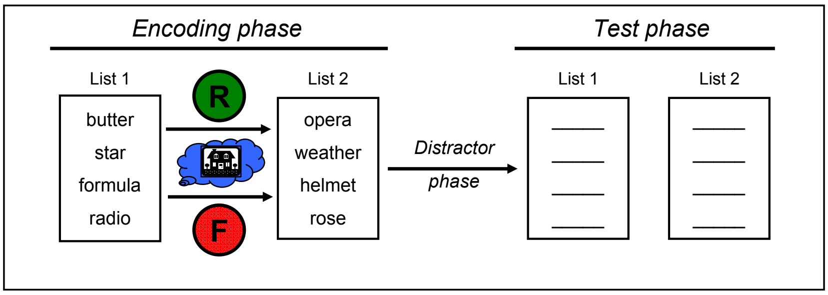

Figure 3.1: Depiction of the procedure in *Experiment 1a.* R = presentation of a cue to remember List 1; thought bubble = imagination of parents' house; F = presentation of a cue to forget List 1. List-1 items were tested first and List-2 items second.

Each participant took part in one experimental condition, the remember condition, the context-change condition or the forget condition. Each experimental condition consisted of an encoding phase, a distractor phase, and a test phase (Fig. 3.1). In the encoding phase, two lists were presented to each participant in each of the three conditions. The words were read out individually by the experimenter at a rate of about 2 s per word. Conditions differed in the instruction given after List-1 learning. In the remember condition, participants were instructed to remember List 1. In the forget condition, List 1 was followed by a cue to forget the list. In the context-change condition, participants were instructed to remember List 1, and, additionally, were asked to imagine their parents' house, to mentally walk through it for 30 s and to tell the things they imagine. In both the remember condition and the forget condition, the cue was followed by backward counting from a three-digit number for an equivalent time to bar participants from rehearsal of List-1 items. Thereupon, in all conditions, participants learned a second list of items which was followed by a remember cue and a 30-s backward counting task as distractor phase and recency control. Following this distractor phase, a written free recall test of both lists was carried out. Participants were asked to recall List-1 items first and List-2 items second. Recall time for each list was 60 s.

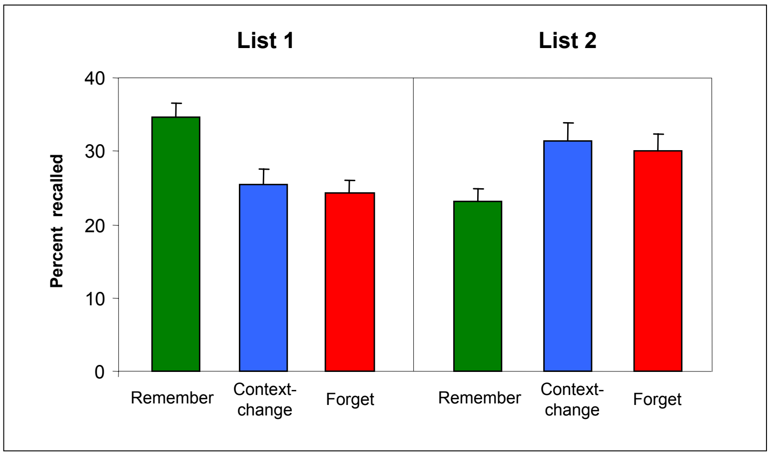

Figure 3.2: Recall data: Regarding List 1, forgetting was observed both in contextual memory updating ($p < .005$) and intentional memory updating ($p < .001$). Regarding List 2, enhancement was observed both in contextual memory updating ($p < .01$) and intentional memory updating ($p < .025$). Analyses of variance (ANOVA); error bars: standard errors.

3.1.2 Results

Regarding List 1, participants recalled 34.6% of the items in the remember condition, 25.6% in the context-change condition and 24.3% in the forget condition. Regarding List 2, participants recalled 23.1% of the items in the remember condition, 31.4% in the context-change condition and 30.0% in the forget condition (Fig. 3.2).

The forgetting indices in contextual memory updating (9.0%) and intentional memory updating (10.2%) were calculated as the difference in List-1 recall between the remember and the context-change condition and the remember and the forget condition, respectively. The enhancement indices in contextual memory updating (8.3%) and intentional memory updating (6.9%) were calculated as the differences in List-2 recall between the context-change and the remember condition or the forget condition and the remember condition, respectively.

Regarding List-1 forgetting, a one-way analysis of variance revealed a significant effect of CUE ($F(2, 159) = 8.6, p < .001$). Post-hoc analysis revealed that the effect arose from forgetting in both in contextual memory updating ($t_{106} = 3.2$; $p < .005$) and intentional forgetting ($t_{106} = 3.9$; $p < .001$).

Regarding List-2 enhancement, a one-way analysis of variance revealed a significant effect of CUE ($F(2, 159) = 4.0, p < .025$). Post-hoc analysis revealed that the effect arose from enhancement both in contextual memory updating ($t_{106} = 2.7$; $p < .01$) and intentional memory updating ($t_{106} = 2.3$; $p < .025$).

In addition, intrusion errors were analyzed. The mean proportion of List-2 intrusions during List-1 recall was 2.6% in the remember condition, 3.7% in the forget condition, and 2.6% in the context-change condition. One-way analysis of variance on proportion of intrusions of List-2 items during List-1 recall showed no effect of the between-participants factor of CUE ($F(2, 159) < 1$). The mean proportion of List-1 intrusions during List-2 recall was 2.0% in the remember condition, 2.8% in the forget condition, and 2.7% in the context-change condition. One-way analysis of variance on proportion of intrusions of List-1 items during List-2 recall showed no effect of the between-participants factor of CUE ($F(2, 159) < 1$).

3.1.3 Discussion

Experiment 1a replicates Sahakyan and Kelley's (2002) observation that comparable forgetting and enhancement effects in memory updating can be found in the directed-forgetting and the context-change paradigm. Compared with remember-cued participants, both forget-cued participants and participants who's internal context was changed showed impaired recall of List-1 items and improved recall of List-2 items.

Participants were asked to recall List-1 items before List-2 items, thus following prior work in which contextual and intentional memory updating were compared (Sahakyan & Delaney, 2003; Sahakyan & Kelley, 2002). Three previous studies addressed the issue of whether recall order affects directed forgetting, thus examining a possible role of retrieval strategies or output interference in this type of forgetting. In each of these studies, experiments were conducted in which half of the participants recalled List 1 before List 2 and the other half recalled List 2 before List 1. Consistent across the single studies, recall order did not affect the results, neither List-1 forgetting nor List-2 enhancement (Barnier et al., in press; Geiselman et al., 1983; Zellner & Bäuml, 2006), which suggests that retrieval strategies and output interference are not a major factor in this type of forgetting (but see Golding & Gottlob, 2005, for an output order effect when using a within-subjects directed forgetting design, in which there is only a forget but not a remember condition). It therefore appears likely that the present pattern of results would not have changed if recall order of the two lists (in the List-2-encoding condition) had been reversed.

These results provide evidence for both contextual and intentional memory updating in the present experimental design and, therefore, masking effects of either material or procedure can be excluded for the following behavioral and electrophysiological experiments.

3.2 Experiment 1b

In intentional memory updating, the forget cue per se does not appear to be sufficient to induce List-1 forgetting. Rather, subsequent List-2 encoding seems necessary to create the effect. Corresponding evidence comes from an experiment by Gelfand and Bjork (1985; described in Bjork, 1989), in which participants learned a list of ten nouns (List 1) and then received a cue to either forget or continue remembering this list. Immediately after cuing, one group of participants learned a second list of ten nouns (List 2), another group rated a list of ten adjectives, and a third group of participants did nothing while "the experimenter fumbled around killing time" (p. 320). After this interpolated activity, a recall test was conducted in which participants were asked to recall the List-1 items, regardless of initial cuing. Forgetting of List 1 was observed only when the learning of List-2 was interpolated. Following Bjork (1989), this result indicates that successful directed forgetting depends on resetting the learning process, as initiated by the study of List-2 items.

The first goal of *Experiment 1b*[2] was to examine whether mental context changes also need subsequent learning of new material to induce forgetting of List-1 items. In first-order paradigms, when using weaker environmental manipulations, like simple room changes, or manipulations of internal states, like mood induction, context changes sometimes failed to generate a context effect, which led to concerns about its reliability (e.g., Eich, 1985; Fernandez & Glenberg, 1985). These findings provided some demonstration that changes in internal context may not be sufficient to induce contextual memory updating. Indeed, by running experiments with second-order paradigms, researchers showed that mood induction differentiates context only when participants learn two or more word lists in different moods (Bower, Monteiro, & Gilligan, 1978; Schare, Lisman, & Spear, 1984). A second goal of *Experiment 1b* was to reexamine the previously reported crucial role of List-2 encoding for successful intentional forgetting. To date, this finding has only been reported as part of a conference paper. A reexamination of the finding appears timely.

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[2] Parts of the experiment were accepted for publication in Pastötter, B., & Bäuml, K.-H. (in press). The crucial role of post-cue encoding in directed forgetting and context-dependent forgetting. *Journal of Experimental Psychology: Learning, Memory, and Cognition.*

3.2.1 Methods

Participants

One hundred sixty-two healthy students of the University of Regensburg took part in the experiment on a voluntary basis. The sample consisted of 71 males and 91 females. Their mean age was 23.5 years with a range of 18 to 43 years. All participants spoke German as native language. They were tested individually with 54 participants in each of the three experimental conditions.

Material

The same material as in *Experiment 1a* was used. Each list was equally often used in the remember condition, the context-change condition and the forget condition.

Experimental Design

A one-factor design with three levels of the between-participants factor CUE (remember, context change, forget) was used. In contrast to *Experiment 1a* no second list was learned. Conditions differed in the encoding phase. In the remember condition list learning was followed by a cue to remember these items. In the context-change condition the list should be remembered and participants were instructed to change their internal cognitive context. In the forget condition the learned list should be forgotten. Mean recall frequency was used as dependent variable. For power analysis, the G*Power v2.0i software was used (Erdfelder, Faul, & Buchner, 1996).

Procedure

The procedure was identical to the procedure of *Experiment 1a*, with the exceptions that participants counted backward for another 30 s instead of

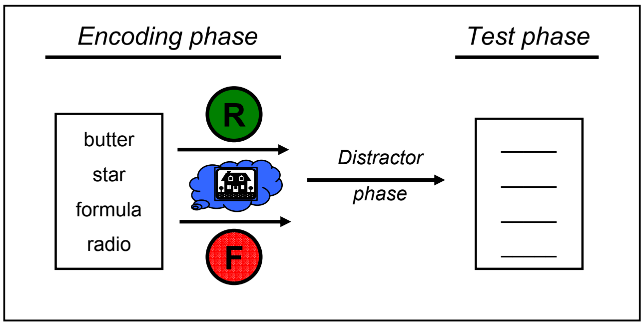

Figure 3.3: Depiction of the procedure in *Experiment 1b.* R = presentation of a cue to remember the list; thought bubble = imagination of parents' house; F = presentation of a cue to forget the list.

List-2 learning and a written recall test of only one list (Fig. 3.3).

3.2.2 Results

The results showed that new learning is necessary to induce both context-dependent forgetting and intentional forgetting. Participants recalled 42.5% of the items in the remember condition, 40.6% in the context-change condition and 40.6% in the forget condition (Fig. 3.4). A one-way analysis of variance revealed no significant effect of CUE ($F(2, 159) < 1$).

A power analysis was conducted to determine the probability with which an effect of a given size could be detected in the present data set. A review of the literature suggests that the typical detrimental effects found in most studies on context-dependent forgetting and intentional forgetting are of a large size according to Cohen's (1988) effect size conventions. Given a total sample size of $N = 162$ and an α-level of .05, a large effect of size $f = .40$ could be detected with a probability of .996.

A comparison of results between *Experiment 1a* and *Experiment 1b* suggests that the effect of CUE on List-1 recall depended on whether List-2 items were to be encoded or not. Consistently, a 3 × 2 analysis of variance on pro-

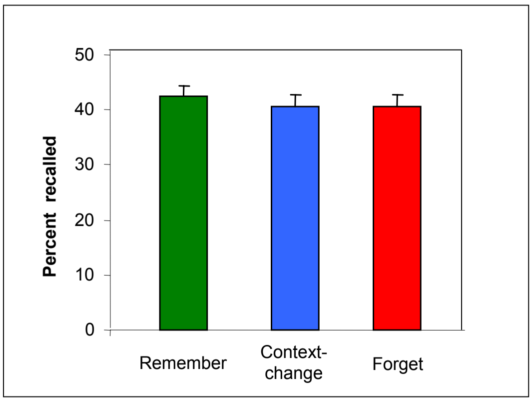

Figure 3.4: Recall data: Recall did not change across conditions: neither context-dependent forgetting nor intentional forgetting was found; analysis of variance (ANOVA); error bars: standard errors.

portion of List-1 recall with the factors of CUE (remember, forget, context change) and ENCODING (List-2 encoding, no List-2 encoding) showed a main effect of CUE ($F(2, 318) = 4.8$, $p < .01$), a main effect of ENCODING ($F(1, 318) = 67.2$, $p < .001$), and an interaction between the two factors ($F(2, 318) = 3.1$, $p < .05$).

3.2.3 Discussion

In *Experiment 1b*, Gelfand and Bjork's (1985) observation that the presence of the forget cue in intentional memory updating is not sufficient to induce List-1 forgetting was replicated. The subsequent learning of further items is necessary to induce the effect, indicating that some resetting of the learning process is a pre-condition for successful forgetting (Bjork, 1989). Going beyond this prior work, the present results suggest that a change in internal context, as realized through an imagination task, is also not sufficient to induce List-1 forgetting. Rather, the context change induces forgetting only when there is subsequent learning of new material in the new internal context. As holds for intentional memory updating, some resetting of the learning process seems to be necessary for successful contextual memory updating.

The result of *Experiment 1b* that context-dependent forgetting needs learning of new material after the context change seems to disagree with other results in the literature, in which context-dependent forgetting was found without resetting the learning process. In their classical study, Godden and Baddeley (1975), for instance, found reliable context-dependent forgetting when letting divers learn and recall word lists on land or underwater. However, when using weaker environmental manipulations context changes sometimes failed to generate a context effect (e.g., Eich, 1985; Fernandez & Glenberg, 1985). The present results provide another demonstration that changes in internal context may not be sufficient to induce context-dependent forgetting. In addition, however, the results suggest that changes in internal context can become effective when followed by subsequent learning of further material. This suggestion is in line with research showing that mood induction differentiates context only when participants learn two or more word lists in different moods (Bower, Monteiro, & Gilligan, 1978; Schare, Lisman, & Spear, 1984). It indicates that also weak context changes can induce forgetting, though apparently only when encoding of further material follows the context change.

From a theoretical point of view, one could argue that context changes should lead to forgetting of List-1 items regardless of whether List-2 learning is present or absent. Indeed, if the nonoverlap between the retrieval context and the encoding context is what underlies the decrease in recall of List-1 items (e.g., Mensink & Raaijmakers, 1988), then forgetting of List 1 should arise irrespective of whether List-2 items were encoded or not. However, there are at least two possible reasons why a context change in the absence of List-2 encoding may not produce forgetting of List-1 items. The first reason is that in the presence of List-2 learning the retrieval cues at test have to differentiate between pre-cue and post-cue information. In the absence of List-2 learning, no such differentiation is needed, which may lead to better List-1 recall in the absence than in the presence of List-2 learning. The second reason is that the encoding of List-2 items may have provided an opportunity to strengthen the representation of the new context, which may have made it hard for the participants to mentally reinstate the List-1 context at test. In contrast, in the absence of List-2 learning, no such strengthening of the context representation may have taken place and the List-1 context may have been fairly easy to reinstate at test. Indeed, context effects have generally been found to be rather small in first-order paradigms, in which context differentiation appears needless and reinstatement of the original context may be easy (e.g., Eich, 1985; Fernandez & Glenberg, 1985).

The present results reveal a parallel between directed forgetting and context-dependent forgetting by identifying a common necessary condition for successful forgetting. Previous studies identified further parallels. One such parallel is the demonstration that both directed forgetting and context-dependent forgetting are present in recall but not in recognition (Basden, et al., 1993; Godden & Baddeley, 1980; MacLeod, 1999; for exceptions, see Benjamin, 2006, or Sahakyan & Delaney, 2005, who show List-2 improvement in recognition). A second parallel is that both forms of forgetting are present in explicit but not in implicit memory tests (Basden et al., 1993; Parker, Gellatly, & Waterman, 1999). A third parallel is that both directed forgetting and context-dependent forgetting can be reduced if the original List-1 context is reinstated at test (Godden & Baddeley, 1980; Sahakyan & Kelley, 2002).

The present results thus are consistent with the hypothesis that context-dependent forgetting and directed forgetting are mediated by the same mechanisms (Sahakyan & Kelley, 2002). On the other hand, the results do not reject the claim that different mechanisms mediate the two forms of forgetting. For instance, while context-dependent forgetting may reflect an encoding/retrieval mismatch, directed forgetting may well be mediated by retrieval inhibition. In fact, it has repeatedly been argued that inhibition should be initiated only if there is post-cue encoding of competing material, triggering inhibitory processes on the to-be-forgotten List-1 items (Barnier et al., in press; Conway et al., 2000). By varying the potential of lists to interfere, Conway et al. (2000) found that directed forgetting was reduced when list-2 learning was disrupted by a secondary task which was meant to dampen list-2 interference. In addition, the forget cue does not create forgetting if it is presented after the encoding of List-2 encoding but only if it is presented before List-2 encoding (Bjork, 1970). The present results are also consistent with the view that context-dependent forgetting reflects an encoding/retrieval mismatch, whereas directed forgetting is mediated by selective rehearsal (Sheard & MacLeod, 2005). This holds although in the present experiment rehearsal of List-1 items in the remember condition may be expected to take place not only in the presence of List-2 learning but during the interpolated distractor task as well.

Although the present results do not answer the question of whether context-dependent forgetting and directed forgetting are mediated by the same mechanism(s) or by different mechanisms, they suggest an important parallel between the two forms of forgetting. This parallel may be of some use for work that investigates the neural correlates of context-dependent forgetting and directed forgetting. Although the exact nature of the underlying mechanism(s) of episodic memory updating is not yet fully known, the parallels identified between directed forgetting and context-dependent forgetting provide important insights into the relation between the two forms of memory updating. The present observation that directed forgetting and context-dependent forgetting depend on subsequent learning of interfering material, may help clarify whether the two forms of memory updating are equivalent on a neural basis. Because the mechanism(s) underlying the two forms of updating should be active during List-2 encoding, they should be observable in imaging or electrophysiological data when comparing neural activities during List-2 encoding after a forget cue and after a context change. Therefore, *Experiment 2* and *Experiment 3* were conducted to correlate contextual and intentional memory updating with electrophysiological measurements of oscillatory brain activity during List-2 encoding.

Electrophysiology of contextual memory updating

3.3 Experiment 2

Memory enhancement and forgetting in contextual memory updating are assumed to be mediated by context differentiation between lists which is caused by the mental context change previous to List-2 encoding. List-1 forgetting is meant to be caused by the contextual mismatch and the List-2 enhancement is meant to arise from the reduced List-1 interference. Electrophysiological measurements of oscillatory brain activity can be employed to examine if such a one-mechanism account can explain both enhancement and forgetting in contextual memory updating.

Contrary to a one-mechanism account, it has recently been shown that forgetting may occur without enhancement in the context-change paradigm (Aslan & Bäuml, 2007; Sahakyan & Delaney, 2003). A possible reason that may have contributed to the failure to find List-2 enhancement in these studies is that List-1 items were tested first and List-2 items second. The prior recall of List-1 items may have reinstated the original learning context of this list and, in this way, may have attenuated the effects of the context-change manipulation on List-2 recall. Thus, in the present *Experiment 2*, testing order of List-1 and List-2 items was manipulated to control for a possible output order effect.

Based on the results of *Experiment 1b* it can be assumed that the mechanism(s) underlying contextual memory updating in the context-change paradigm operate(s) at the time of List-2 encoding following the change of mental context. Thus, EEGs were recorded during the encoding of List-2 items. It is hypothesized that especially the theta frequency band (4 to 8 Hz) plays an important role in contextual memory updating because previous research has shown its relation to episodic memory (Klimesch, 1999) and context processing (Summerfield & Mangels, 2005). Moreover, it is hypothesized that the upper alpha frequency band (10 to 13 Hz) is related to the enhancement in contextual memory updating. Because upper alpha is meant to reflect semantic (deep) memory processing, changes in this frequency band might support Sahakyan and Delaney's (2003) encoding-strategy explanation of enhancement in memory updating.

3.3.1 Methods

Participants

Forty-eight healthy students of the University of Regensburg took part in the experiment on a voluntary basis. The sample consisted of 25 males and 23 females. Their mean age was 23.6 years with a range of 19 to 38 years. All participants were right-handed, had normal or corrected-to-normal vision, and spoke German as native language.

Material

One hundred twenty unrelated German nouns of medium frequency were drawn from the CELEX database using the Wordgen v1.0 software toolbox (Duyck et al., 2004). Six lists of 20 words each were prepared. Across lists, the words were matched on frequency and word length. The assignment of items to lists was constant for all participants. Item order within lists was random for each participant. Each list was equally often used in the remember condition and in the context-change condition and served equally often as the first and the second presented list.

Experimental Design

A 2 × 2 × 2 design with the within-participants factors CUE (remember, context-change) and LIST (List 1, List 2), and the between-participants factor TEST (List 1 tested first, List 2 tested first) was used. In the context-change condition participants were instructed to change their internal cognitive context after List-1 learning. In the remember condition participants simply waited for an equivalent time for the experimenter to present List 2. Order of conditions was counterbalanced. In the test phase either List-1 items or List-2 items were tested first. Mean recall frequency was used as behavioral dependent variable. Mean power at electrode sites and phase locking values (PLV) between electrodes were used as physiological dependent variables.

Procedure

Participants were informed about the general nature of the experiment. They were told that they had to learn some items and that their memory for these items would be tested later on.

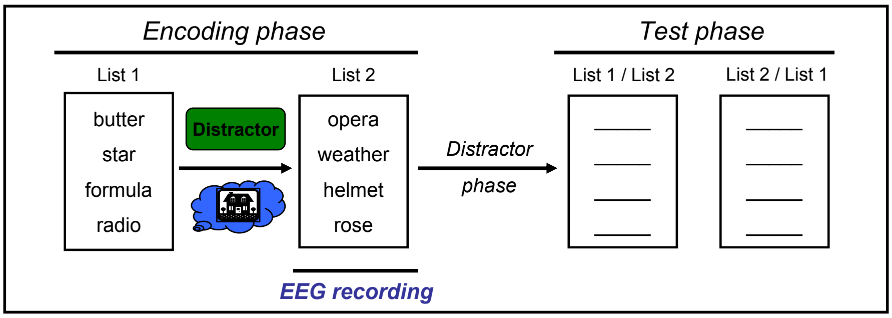

Figure 3.5: Depiction of the procedure in *Experiment 2*. Distractor in the remember condition; imagination of parents' house in the context-change condition. Either List-1 items or List-2 items were tested first.

Each participant took part in both experimental conditions, the remember condition and the context-change condition. Both conditions consisted of an encoding phase, a distractor phase, and a test phase (Fig. 3.5). In the encoding phase, two lists were presented to each participant in each of the two conditions. The words were exposed individually for 2000 ms in the centre of a computer screen. Before presentation of a word, a blank interval and a fixation cross were presented, the first for 1450-1550 ms and the second for 500 ms (see below). Throughout the whole encoding phase no motor responses were required from the participants. In both conditions, List 1 was followed by the instruction to remember the list. The two experimental conditions differed in the interlist phase after the cue to remember List 1. In the context-change condition, participants were asked to imagine their parents' house, to mentally walk through it for 45 s and to tell the things they imagine. In the remember condition participants simply waited for an equivalent time for the experimenter to present List 2. To bar participants from rehearsal of List-1 items in the waiting period, the experimenter did some smalltalk and pretended to check the instruments. List 2 was again followed by a remember cue. After the encoding phase, participants had to count backward for 30 sec from a three-digit number as a recency control. Following this distractor phase, a written recall test of both lists was carried out. Participants were asked to recall either List-1 items or List-2 items first. Recall time for each list was 90s.

Recordings of EEG data

During the encoding of List 2, EEG data were recorded from 62 Ag/AgCl electrodes arranged according to the extended 10-20 system and mounted in an elastic cap. Additionally, two EOG-channels were recorded. Electrode FCz served as common reference. Impedance was kept below 5 kΩ. Bioelectrical signals were digitalized with a sampling rate of 500 Hz. Frequencies between 0.1 and 70 Hz were recorded. EEG recordings were offline re-referenced against average reference, EOG-corrected, and visually inspected for remaining artifacts. Thereupon, the recording of the list was separated in 20 single trials having a length of 4000 ms (+/− 50 ms) and consisting of the following sequence: a blank interval of variable duration between 1450 ms and 1550 ms, the presentation of a fixation cross for 500 ms, and the presentation of a word for 2000 ms (Fig. 3.6). A part of the blank interval was used as pre-stimulus interval with a length of 1000 ms: 1750 ms to 750 ms before stimulus onset. Relating differences in oscillatory activity between conditions both to the forgetting of List-1 items and the enhancement of List-2 items, the pre-stimulus interval was chosen for analysis as it minimizes the superposition of List-2 encoding. After artifact correction, at least 17 single trials remained for each condition and participant for analysis.

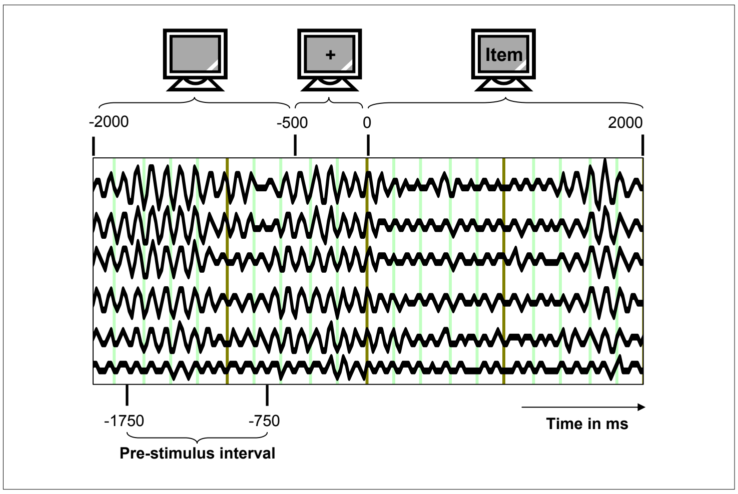

Figure 3.6: Typical example of an EEG epoch in the encoding phase. A single trial consisted of the following sequence: a blank interval of variable duration between 1450 ms and 1550 ms, the presentation of a fixation cross for 500 ms, and the presentation of an item for 2000 ms. A fixed part of the blank interval was used as pre-stimulus interval with a length of 1000 ms.

Analyses of EEG data

Tonic power in the pre-stimulus interval is highly predictive of post-stimulus power and event-related changes (Doppelmayr et al., 1998; Fingelkurts et al., 2002; Lehman et al., 1994). Therefore, power analysis was restricted to tonic power in the pre-stimulus interval of List-2 item presentation in the remember and context-change condition. Tonic power was calculated for each electrode and frequency from 4 to 20 Hz on the basis of a Hanning windowed fast Fourier transformation with a resolution of 1 Hz (Brain Vision Analyzer Software ©BrainProducts GmBH). Power was collapsed over the pre-stimulus interval of 1 s (1750 to 750 ms before stimulus onset) during the presentation of List-2 items. T-tests were calculated for each electrode to investigate which electrodes showed a significant difference between conditions ($p < .05$; two-tailed). Only results for electrodes and frequency bands which show a p-level of smaller than .05 will be reported.

The phase locking value (PLV) was calculated for each electrode pair and frequency from 4 to 20 Hz with a frequency resolution of 2 Hz. PLV was calculated using the software BESA (Brain Electrical Source Analysis ©MEGIS Software). Like power, PLV was collapsed over the pre-stimulus interval of 1 s (1750 to 750 ms before stimulus onset) during the presentation of List-2 items. Prior to statistical analysis PLV was Fisher-z-transformed. For statistical analysis of PLV a two-stage procedure was carried out. At first, t-tests were calculated for each electrode pair to investigate which electrode pairs showed a significant difference between conditions ($p < .005$; one-tailed). Second, a randomization test (Blair & Karniski, 1993), based on 20.000 permutation runs, was carried out to control for type I errors due to multiple testing. This procedure evaluates whether a given number of electrode pairs, exhibiting a significant difference between conditions is expected by chance. If the p-value of this randomization test is below .05, less than 5% of the permutation runs exhibited equal or more electrode pairs with a significant difference between the two conditions. Only results for frequency bands which show a p-level of smaller than .05 (two-tailed) in the randomization test will be reported.

3.3.2 Results

Behavioral results

The behavioral results showed both sides of contextual memory updating in the context-change paradigm. The forgetting was calculated as the difference in List-1 recall between the remember and the context-change condition. Participants recalled 40.8% of List-1 items in the remember condition and 31.3% in the context-change condition when List 1 was tested first, compared to 40.2% in the remember condition and 34.0% in the context-change condition when List 1 was tested second (Fig. 3.7A). Analysis of variance with the factors CUE (remember, context-change) and TEST (List 1 tested first, List 2 tested first) revealed a main effect of CUE ($F(1,46) = 7.9$, $p < .01$), but neither a main effect of TEST ($F(1,46) < 1$) nor a CUE × TEST interaction ($F(1,46) < 1$). Thus, the forgetting (7.9%) was observed independent of testing order.

The enhancement was calculated as the difference in List-2 recall between the context-change and the remember condition. Participants recalled 43.7% of List-2 items in the remember condition and 51.5% in the context-change condition when List 2 was tested first, compared to 33.5% in the remember condition and 40.8% in the context-change condition when List 2 was tested second (Fig. 3.7A). Analysis of variance with the factors CUE (remember, context-change) and TEST (List 1 tested first, List 2 tested first) revealed a main effect of CUE ($F(1,46) = 11.5$, $p < .005$) and a main effect of TEST ($F(1,46) = 4.2$, $p < .05$). Analysis did not show a CUE × TEST interaction ($F(1,46) < 1$). Thus, the enhancement (7.5%) was observed independent of testing order with larger recall quotes when List 2 was tested first. Across individuals, the forgetting and the enhancement did not correlate ($r = -.09, p = .56$; Fig. 3.7B).

Physiological results

Two separate electrophysiological mechanisms underlying contextual memory updating in the context-change paradigm were identified: an increase of pre-stimulus upper alpha power - selectively associated with enhancement - and an increase in pre-stimulus theta phase coupling - selectively associated with forgetting.

Significant differences in pre-stimulus power between conditions were only found in the upper alpha band (11 to 13 Hz). Figure 3.8A shows the results from the upper alpha power analysis. Left temporal electrodes (T7, TP7, P7, PO7, CP5, P5) showed significant differences in upper alpha power between the remember and the context-change condition with larger upper alpha power in the context-change than in the remember condition ($t_{47} = 3.2$;

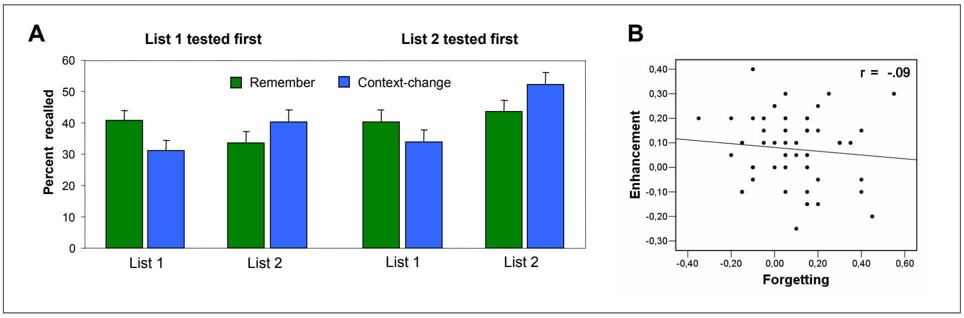

Figure 3.7: (A) Recall data separated for testing order of lists: Regarding List 1, recall was lower in the context-change than in the remember condition ($p < .01$); regarding List 2, recall was higher in the context-change than in the remember condition ($p < .005$); analysis of variance (ANOVA); error bars: standard errors. (B) Spearman rank correlation: Forgetting and enhancement are not correlated ($p = .56$). Forgetting was calculated on the basis of List-1 recall ('Remember' - 'Context-change'); enhancement was calculated on the basis of List-2 recall ('Context-change' - 'Remember').

$p < .005$). No significant effect was found for other frequency bands (Fig. 3.9A).

To examine the functional relationship between the neural effect in upper alpha power and the behavioral effects of contextual memory updating, differences in upper alpha power between the context-change and remember condition were analyzed whether they were predictive of individual differences in the amount of forgetting and enhancement. Although differences in upper alpha power between conditions were neither correlated with enhancement ($r = -.18, p = .23$) nor with forgetting ($r = .16, p = .28$), overall alpha power over left temporal electrodes was found to be predictive of enhancement ($r = .32, p < .05$; Fig. 3.10A). No correlation between overall alpha power and the amount of forgetting was found ($r = -.04, p = .80$).

A significant difference in pre-stimulus phase coupling between conditions was only found in theta band (4 to 8 Hz). Comparing theta phase cou-

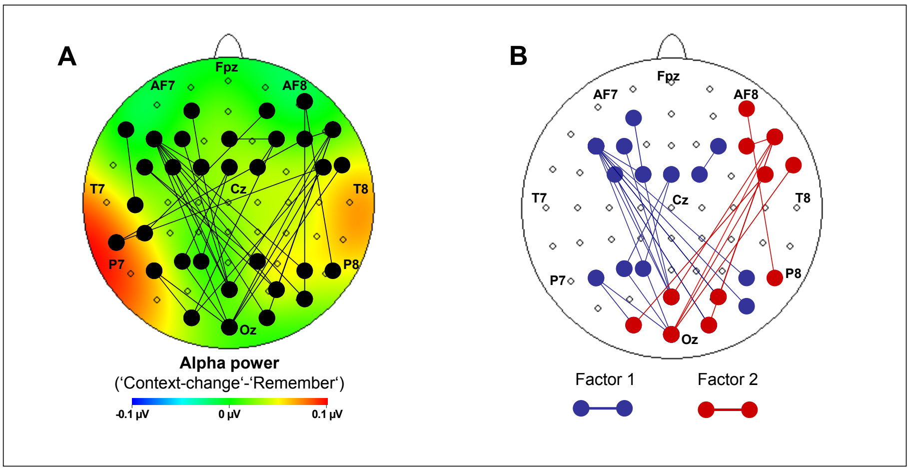

Figure 3.8: Electrophysiological correlatives of contextual memory updating. (A) Average scalp distribution of differences in upper alpha power and theta phase coupling between the context-change and the remember condition. Color coding indicates the difference in upper alpha power over an electrode during the pre-stimulus interval. Red means more alpha power in the context-change than in the remember condition ($p < .025$). Black lines correspond to more theta phase coupling ($p < .005$) in the context-change than in the remember condition. (B) Results of the factor analysis: Blue lines correspond to the electrode pairs loading on factor 1, red lines to the electrode pairs loading on factor 2.

pling across the remember and context-change condition, 35 electrode pairs showed more coupling in the context-change condition ($p < .005$; one-tailed) and seven electrode pair showed more coupling in the remember condition ($p < .005$; one-tailed). Figure 3.8A shows the difference in pre-stimulus theta phase coupling of electrode pairs with more coupling in the context-change condition. The randomization test showed that this difference between conditions was not expected by chance ($p < 0.025$), indicating that in less than 2.5% of the permutation runs 35 or more electrode pairs showed significantly more phase coupling in the context-change condition compared to the remember condition. No significant effect was found for other frequency bands (Fig. 3.9B).

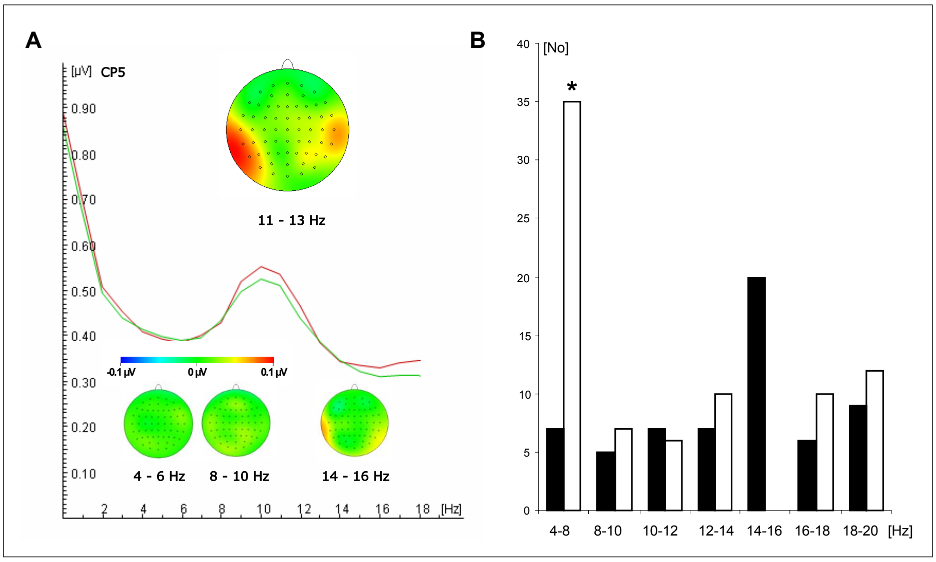

Figure 3.9: Electrophysiological data of different frequency bands. (A) Significant differences in pre-stimulus power between conditions were only found in the upper alpha band (11 to 13 Hz) over left temporal electrodes (e.g. CP5) with larger upper alpha power ($p < .005$) in the context-change (red line) than in the remember condition (green line). (B) A significant difference in pre-stimulus phase coupling (PLV) between conditions was only found in theta band (4 to 8 Hz) with 35 electrode pairs showing more coupling in the context-change than in the remember condition ($p < .025$).

The differences in theta phase coupling of the 35 electrode pairs were put to factor analysis. Two factors emerged accounting for 35% of total variance. Factor 1 consisted of 18 left fronto-parietal, factor 2 of nine right fronto-parietal electrode pairs (Fig. 3.8B), which suggests the action of two separate networks. Examining the functional relationship between this neural effect in phase coupling and the behavioral effects, a significant correlation between increased right fronto-parietal phase coupling (factor 2) and the amount of forgetting was found. More phase coupling in the context-change than in the remember condition was accompanied by poorer List-1 recall in the context-change condition compared to the remember condition ($r =$

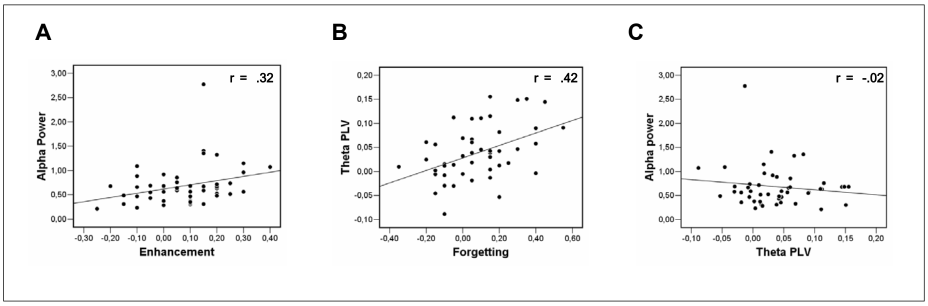

Figure 3.10: Spearman rank correlations. (A) Temporal pre-stimulus alpha power and the enhancement are positively correlated ($p < .05$). (B) The difference in pre-stimulus theta phase coupling (Factor 2) and the forgetting are positively correlated ($p < .005$). (C) Overall alpha power and the differences in phase coupling are not correlated ($p = .81$).

$.42, p < .005$; Fig. 3.10B). No correlation between increased phase coupling and the amount of enhancement was found ($r = -.08, p = .61$). Additionally, no correlation between overall alpha power and theta phase coupling was found ($r = -.02, p = .88$; Fig. 3.10C; see Table 3.1 for a summary of all the relevant Spearman rank correlations).

3.3.3 Discussion

Experiment 2 was conducted to correlate contextual memory updating as it is studied in the context-change paradigm with electrophysiological measurements of oscillatory brain activity. Regarding the forgetting in contextual memory updating, the findings suggest that the effect is due to an increase in theta phase coupling which might reflect the establishment of a new List-2 context leading to context differentiation between lists. This is suggested because the behavioral effect is accompanied by a selective increase in theta phase coupling, which points to more coherent activities in the relevant brain structures. The finding that context-dependent forgetting induces coupling in the theta frequency range is in agreement with recent work showing the im-

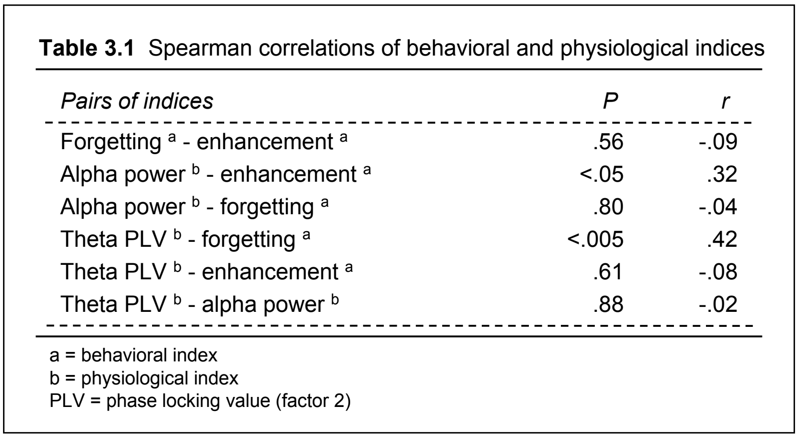

Table 3.1 Spearman correlations of behavioral and physiological indices

Pairs of indices	*P*	*r*
Forgetting ^{a} - enhancement ^{a}	.56	-.09
Alpha power ^{b} - enhancement ^{a}	<.05	.32
Alpha power ^{b} - forgetting ^{a}	.80	-.04
Theta PLV ^{b} - forgetting ^{a}	<.005	.42
Theta PLV ^{b} - enhancement ^{a}	.61	-.08
Theta PLV ^{b} - alpha power ^{b}	.88	-.02

a = behavioral index
b = physiological index
PLV = phase locking value (factor 2)

Table 3.1: Spearman rank correlations of behavioral and electrophysiological data. Theta phase coupling (PLV) in the right fronto-parietal network (red lines in Fig. 3.8B) and forgetting: more theta phase coupling in the context-change than in the remember condition involves more forgetting of List-1 items ($p < .005$). Alpha power (temporal) and enhancement: more overall alpha power involves more enhancement of List-2 items ($p < .05$). Just like the behavioral data, the electrophysiological correlatives of forgetting and enhancement do not cohere.

portance of global theta synchrony during successful memory encoding (Weiss & Rappelsberger, 2000) and in context processing in particular (Summerfield & Mangels, 2005).

The second behavioral effect of contextual memory updating, the enhancement, is not related to phase coupling but is due to pre-stimulus upper alpha power over left temporal electrodes. Using other paradigms, previous work already found evidence that pre-stimulus alpha power is related to semantic memory performance (Doppelmayr et al., 2002; Klimesch et al., 2000, 2003; Vogt et al., 1998) indicating that similar processes may be involved in the enhancement effect of contextual memory updating and more standard memory enhancement effects. Thus, the increase of upper alpha power might reflect a change to a deeper encoding strategy that enhances memory performance (Sahakyan & Delaney, 2003, 2005). Finding the two underlying physiological mechanisms to operate during the encoding of the new information fits with the picture suggested from *Experiment 1b* which showed that the context change alone is not sufficient to induce contextual memory updating and that the additional encoding of new information, e.g., List-2 items, is necessary to create the effect.

The correlational data of *Experiment 2* suggest that two mechanisms mediate the pattern of forgetting and enhancement in contextual memory updating. This conclusion arises partly on the basis of the noncorrelation between behavioral enhancement and forgetting. More crucially, however, it arises because two separate physiological mechanisms were identified, which supposedly mediate the two behavioral effects. These results can serve as a post-hoc explanation of the previous finding that occasionally forgetting occurs without enhancement (Aslan & Bäuml, 2007; Sahakyan & Delaney, 2003). In particular, the findings reject one-mechanism accounts of contextual memory updating, according to which forgetting and enhancement are just the two sides of the same coin, at least in the context-change paradigm.

Electrophysiology of intentional memory updating

3.4 Experiment 3

In intentional memory updating, memory enhancement and forgetting occur typically together, which is consistent with the view that the two components are mediated by the same mechanism (Bjork, 1989; Geiselman et al., 1983; MacLeod, 1998). Contrary to this standard theory, however, it has recently been shown that forgetting may occur without enhancement (Conway et al., 2000; Sahakyan & Delaney, 2003; Zellner & Bäuml, 2006) and enhancement may occur without forgetting (Bäuml et al., 2007; Macrae et al., 1997). These dissociations suggest a two-mechanism theory of intentional memory updating according to which updating consists of two separate components (Sahakyan & Delaney, 2003, 2005). Therefore, as in *Experiment 2*, electrophysiological measurements of oscillatory brain activity were employed to examine whether enhancement and forgetting in intentional memory updating are regulated by the same or by different physiological mechanisms.

Based on the results of *Experiment 1b* it can be assumed that the mechanism(s) underlying intentional memory updating in the directed-forgetting paradigm operate(s) at the time of List-2 encoding following the forget cue. Thus, EEGs were recorded during the encoding of List-2 items. It is hypothesized that the upper alpha frequency band (10 to 13 Hz) plays an important role in intentional memory updating because previous research suggested its inhibitory function (Klimesch et al., 2007). On the other hand, if context-dependent forgetting and directed forgetting were mediated by the same mechanism, the neural activities during List-2 encoding after the forget cue should resemble the neural activities after the cue to change context. In this case, directed forgetting should be accompanied by an increase in theta phase coupling. In addition, because upper alpha is also meant to reflect semantic memory processing, changes in this frequency band might support Sahakyan and Delaney's (2003) encoding-strategy explanation of enhancement in episodic memory updating.

In contrast to *Experiment 2*, all participants were asked to recall List-1 items before List-2 items. Three previous studies addressed the issue of whether recall order affects directed forgetting, thus examining a possible role of retrieval strategies or output interference in this type of forgetting. In each of these studies, experiments were conducted in which half of the participants recalled List 1 before List 2 and the other half recalled List 2 before List 1. Consistent across the single studies, recall order did not affect the results, neither List-1 forgetting nor List-2 enhancement (Barnier et al., in press; Geiselman et al., 1983; Zellner & Bäuml, 2006).

3.4.1 Methods

Participants

Twenty-four healthy students of the University of Regensburg took part in the experiment on a voluntary basis. The sample consisted of nine males and fifteen females. Their mean age was 24.8 years with a range of 19 to 36 years. All participants were right-handed, had normal or corrected-to-normal vision, and spoke German as native language. None of them experienced a directed-forgetting experiment before.

Material

The same material as in *Experiment 2* was used. Each list was equally often used in the remember condition and in the forget condition and served equally often as the first and the second presented list.

Experimental Design

A 2 × 2 design with the within-participants factors CUE (remember, forget) and LIST (List 1, List 2) was used. Conditions differed in the encoding phase. In the remember condition List 1 was followed by a cue to remember these items. In the forget condition List 1 should be forgotten. Order of conditions was counterbalanced. Mean recall frequency was used as behavioral dependent variable. Mean power over electrodes and PLV between electrodes were used as physiological dependent variables.

Procedure

Participants were informed about the general nature of the experiment. They were told that they had to learn some items and that their memory for these items would be tested later on. They were also told that it could happen that, just after presentation, the experimenter would declare an item list as no longer relevant and that, in this case, they should try to forget the related list and instead learn another list.

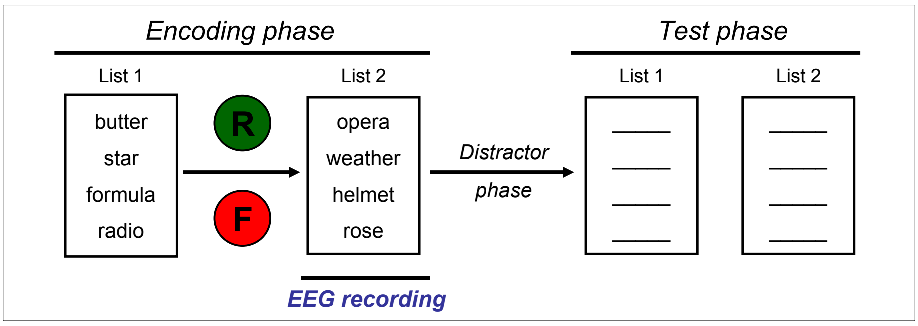

Figure 3.11: Depiction of the directed-forgetting procedure in *Experiment 3a.* F = presentation of a cue to forget List 1; R = presentation of a cue to remember List 1.

Each participant took part in both experimental conditions, the remember condition and the forget condition. Both conditions consisted of an encoding phase, a distractor phase, and a test phase (Fig. 3.11). In the encoding phase, two lists were presented to each participant in each of the two conditions. The words were exposed individually for 2000 ms in the centre of a computer screen. Before presentation of a word, a blank interval and a fixation cross were presented, the first for 1450-1550 ms and the second for 500 ms (see below). Throughout the whole encoding phase no motor responses were required from the participants. The two experimental conditions differed only in the instruction given between List 1 and List 2. In the remember condition, List 1 was followed by the instruction to remember the list, whereas in the forget condition, List 1 was followed by a cue to forget the list. List 2 was always followed by a remember cue. After the encoding phase, the participants had to count backward for 30 sec from a three-digit number as a recency control. Following this distractor phase, a written recall test of both lists was carried out. Participants were asked to recall List-1 items first and List-2 items second. The recall time for each list was 90s.

Participants who completed the remember condition first and the forget condition second experienced no unexpected events until the test phase of the forget condition when they were, to their surprise, told to recall the forget items. Participants who completed the forget condition first and the remember condition second were confronted with the surprise test after their first trial. In this case, the experimenter assured firmly that the participant would not be deceived again.

Many previous directed forgetting studies employed a between-participants design, in which each single participant accomplished either the forget condition or the remember condition. Recent experiments in our laboratory (Zellner & Bäuml, 2004, 2006) and other laboratories (Conway & Fthenaki, 2003), however, indicate that the experiment leads essentially to the same results irrespective of whether each participant accomplishes both the remember and the forget condition, or accomplishes just one of the two conditions. Here, the within-participants design was chosen because it permits a detailed analysis on whether a putative neural correlate of memory updating shows sensitivity to individual differences in the amount of updating-induced forgetting and enhancement.

Recordings of EEG data

The recording of EEG data was identical to the recording of *Experiment 2*. Accordingly, the recording of List 2 was separated in 20 single trials having a length of 4000 ms (+/− 50 ms) and consisting of the following sequence: a blank interval of variable duration between 1450 ms and 1550 ms, the presentation of a fixation cross for 500 ms, and the presentation of a word for 2000 ms. As in *Experiment 2*, a part of the blank interval was used as pre-stimulus interval with a length of 1000 ms: it started 1750 ms and ended 750 ms before the onset of the word. In order to minimize noise in the signal, peripheral electrodes were excluded and 50 electrodes were kept for further analysis. After artifact correction, at least 18 single trials remained for each condition and participant for analysis.

Analyses of EEG data

The analyses of EEG data were identical to the analyses of *Experiment 2*.

3.4.2 Results

Behavioral results

The behavioral results showed both sides of intentional memory updating in the directed-forgetting paradigm. Regarding List 1, participants recalled 41.7% of the items in the remember condition and 31.5% in the forget condition. Regarding List 2, participants recalled 31.5% of the items in the remember condition and 44.6% in the forget condition (Fig. 3.12A). The forgetting (10.2%) was calculated as the difference in List-1 recall between the remember and the forget condition, the enhancement (13.1%) as the difference in List-2 recall between the forget and the remember condition. Using pairwise t-test analysis (two-tailed), a separate analysis of the two behavioral effects showed that both the forgetting ($t_{23} = 3.13, p < .005$) and the enhancement ($t_{23} = 3.27, p < .005$) were significant. Across individuals, the forgetting and the enhancement did not correlate ($r = .16, p = .46$; Fig. 3.12B).

Physiological results

Two separate and unrelated electrophysiological mechanisms underlying intentional memory updating in the directed forgetting paradigm were identified: an increase of pre-stimulus alpha power - selectively associated with enhancement - and a decline of pre-stimulus alpha phase coupling - selectively associated with forgetting.

Significant differences in pre-stimulus power between conditions were only found in the upper alpha band (11 to 13 Hz). Figure 3.13A shows the results from the alpha power analysis. Left temporal electrodes (T7, TP7, FC5, C5, CP5, C3, CP3) showed significant differences in upper alpha power between

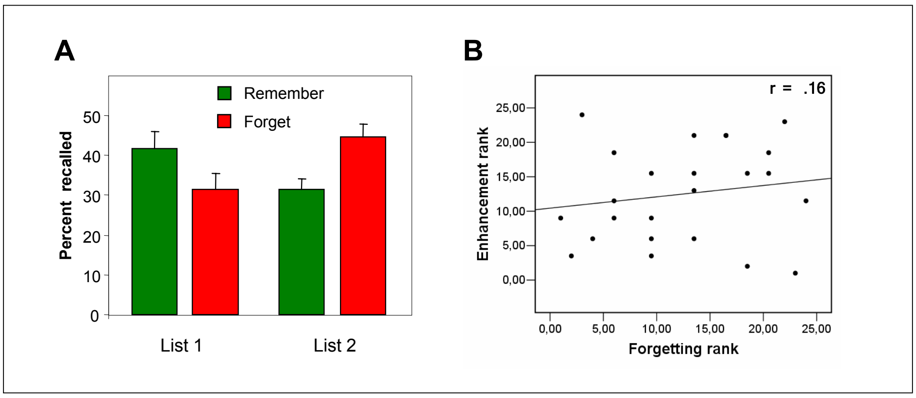

Figure 3.12: (A) Recall data: Regarding List 1, recall was lower in the forget than in the remember condition ($p < .005$); regarding List 2, recall was higher in the forget than in the remember condition ($p < .005$); analysis of variance (ANOVA); error bars: standard errors. (B) Spearman rank correlation: Forgetting and enhancement are not correlated ($p = .46$). Forgetting was calculated on the basis of List-1 recall ('Remember' - 'Forget'); enhancement was calculated on the basis of List-2 recall ('Forget' - 'Remember').

the remember and the forget condition with larger upper alpha power in the forget than in the remember condition ($t_{23} = 2.86$; $p < .01$). No significant effect was found for other frequency bands (Fig. 3.14A).

To examine the functional relationship between the neural effect in upper alpha power and the behavioral effects, individual differences in alpha power were analyzed whether they were predictive of individual differences in the amount of forgetting and enhancement. A significant nonparametric Spearman rank correlation between the increased temporal alpha power and the amount of enhancement was found. More upper alpha power in the forget than in the remember condition was accompanied by better List-2 recall in the forget condition compared to the remember condition ($r = .57$, $p < .005$; Fig. 3.15A). Contrariwise no significant correlation between upper alpha power and the amount of forgetting was found ($r = .11, p = .60$).

Significant difference in pre-stimulus phase coupling between conditions

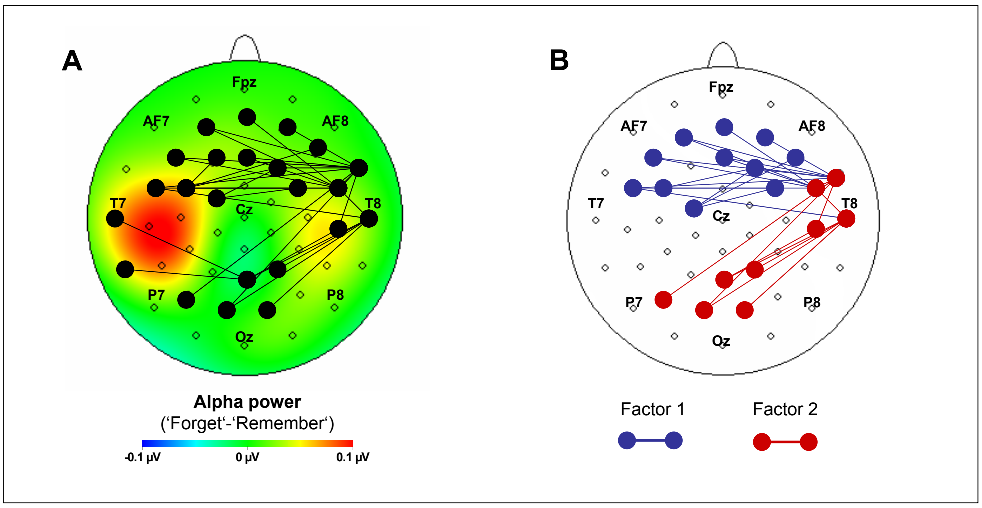

Figure 3.13: Electrophysiological correlatives of intentional memory updating. (A) Average scalp distribution of differences in upper alpha power and upper alpha phase coupling between the forget and the remember condition. Color coding indicates the difference in upper alpha power over an electrode during the pre-stimulus interval. Red means more upper alpha power in the forget than in the remember condition ($p < .01$). Black lines correspond to less upper alpha phase coupling ($p < .005$) in the forget than in the remember condition. (B) Results of the factor analysis: Blue lines correspond to the electrode pairs loading on factor 1, red lines to the electrode pairs loading on factor 2.

were found in a frequency range from 10 to 16 Hz, mostly pronounced in the upper alpha band (10 to 12 Hz). Comparing phase coupling across the remember and forget condition, 31 electrode pairs showed less upper alpha phase coupling in the forget condition ($p < .005$; one-tailed) and three electrode pairs showed less upper alpha phase coupling in the remember condition ($p < .005$; one-tailed). Figure 3.13A shows the difference in pre-stimulus alpha phase coupling of electrode pairs with less coupling in the forget condition. The randomization test showed that the decoupling in the forget condition was significant ($p < 0.01$), indicating that in less than 1% of the

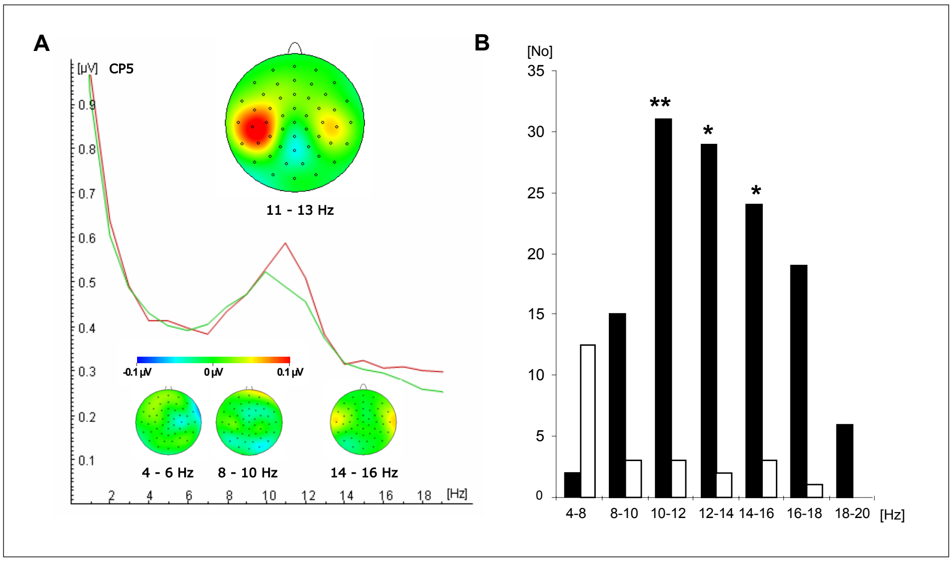

Figure 3.14: Electrophysiological data of different frequency bands. (A) Significant differences in pre-stimulus power between conditions ($p < .05$; two-tailed) were only found in the upper alpha band (11 to 13 Hz) over left temporal electrodes (e.g. CP5) with larger upper alpha power in the forget (red line) than in the remember condition (green line). (B) Significant differences ($p < .005$) in pre-stimulus phase coupling (PLV) between conditions ($p < .05$; two-tailed, based on 20.000 randomizations) were found in a frequency range from 10 to 16 Hz, mostly pronounced upper alpha band (10 to 12 Hz) with 31 electrode pairs showing less coupling in the forget than in the remember condition ($p < .01$).

permutation runs 31 or more electrode pairs showed significantly less upper alpha phase coupling in the forget compared to the remember condition. Significant effects of decoupling in the forget condition were also found for frequencies ranging from 12 to 16 Hz (Fig 3.14B) and these were highly comparable to the effect in the upper alpha band. Indeed, by collapsing PLV over a frequency range from 10 to 18 Hz, 28 electrode pairs showed less phase coupling in the forget condition ($p < .005$; one-tailed) and not one showed less phase coupling in the remember condition ($p < .005$; one-tailed). Figure 3.16 shows the topography of differences in phase coupling of electrode

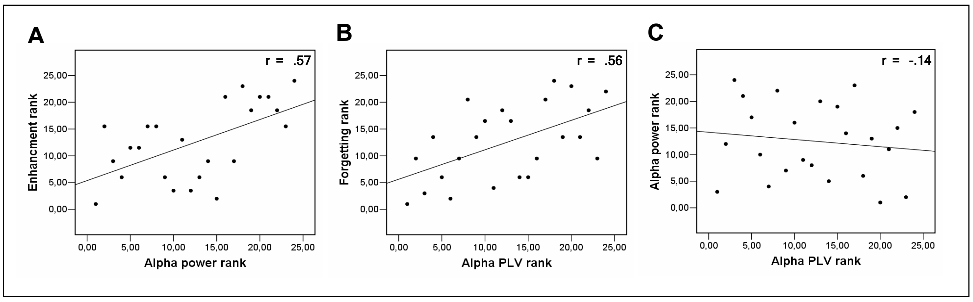

Figure 3.15: Spearman rank correlations. (A) The difference in pre-stimulus upper alpha power ('Forget' - 'Remember') and the enhancement are positively correlated ($p < .005$). (B) The difference in pre-stimulus upper alpha phase coupling ('Remember' - 'Forget') and the forgetting are positively correlated ($p < .005$). (C) The differences in upper alpha power and phase coupling are not correlated ($p = .50$).

pairs from 10 to 18 Hz with less coupling in the forget than in the remember condition. The randomization test showed that the decoupling in this broad band analysis was significant ($p < 0.025$).

The differences in phase coupling of the 31 electrode pairs in the upper alpha band were put to factor analysis. Two factors emerged accounting for 47% of total variance. Factor 1 consisted of 18 fronto-temporal, factor 2 of nine tempo-parietal electrode pairs (Fig. 3.13B), which suggests the action of two separate networks. Examining the functional relationship between this neural effect in phase coupling and the behavioral effects, a significant correlation between decreased tempo-parietal phase coupling (factor 2) and the amount of forgetting was found. Less upper alpha phase coupling in the forget than in the remember condition was accompanied by poorer List-1 recall in the forget condition compared to the remember condition ($r = .56, p < .005$; Fig. 3.15B). No correlation between decreased phase coupling and the amount of enhancement was found ($r = -.01, p = .96$). Additionally, no correlation between alpha power and phase coupling was found ($r = -.14, p = .50$; Fig. 3.15C; see Table 3.2 for a summary of all the relevant

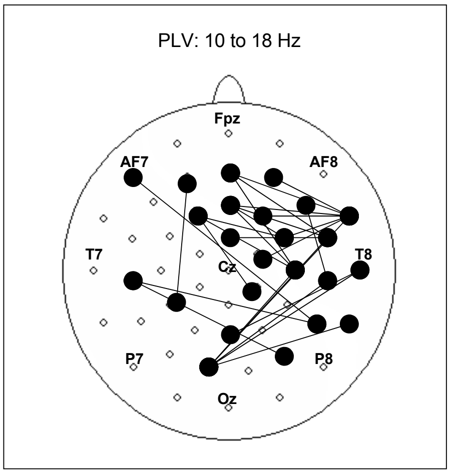

Figure 3.16: Broad band analysis from 10 to 18 Hz of PLV revealed a significant difference in phase coupling between the forget and the remember condition ($p <$ .025) with less phase coupling in the forget than in the remember condition. 28 electrode pairs (black lines) showed less phase coupling in the forget than in the remember condition ($p <$ .005). No electrode pair showed less phase coupling in the remember than in the forget condition ($p <$ .005).

Spearman rank correlations).

3.4.3 Discussion

Experiment 3 was conducted to correlate intentional memory updating as it is studied in the directed forgetting paradigm with electrophysiological measurements of oscillatory brain activity. Regarding the one behavioral effect of intentional memory updating, the reduced accessibility of the out-of-date List-1 information, the findings suggests that the effect is due to the disintegration of memory networks involved in the representation of this information. Such a disintegration is suggested because the forgetting is accompanied by a selective decrease in upper alpha phase coupling, which points to less coherent activity in the relevant brain structures. The results of *Experiment 3* demonstrate that intentional forgetting occurs when the

Table 3.2 Spearman correlations of behavioral and physiological indices

Pairs of indices	*P*	*r*
Forgetting [a] - enhancement [a]	.46	.16
Alpha power [b] - enhancement [a]	<.005	.57
Alpha power [b] - forgetting [a]	.60	.11
Alpha PLV [b] - forgetting [a]	<.005	.56
Alpha PLV [b] - enhancement [a]	.96	-.01
Alpha PLV [b] - alpha power [b]	.50	-.14

a = behavioral index
b = physiological index
PLV = phase locking value (factor 2)

Table 3.2: Spearman rank correlations of behavioral and electrophysiological data. Upper alpha phase coupling (PLV) in the tempo-parietal network (red lines in Fig. 3.13B) and forgetting: less upper alpha phase coupling in the forget than in the remember condition involves more forgetting of List-1 items ($p < .005$). Upper alpha power (temporal) and enhancement: more alpha power in the forget than in the remember condition involves better recall of List-2 items ($p < .005$). Just like the behavioral data, the electrophysiological correlatives of forgetting and enhancement do not cohere.

synchrony of upper alpha oscillations is reduced after the forget cue.

The present finding of a phase decoupling in the upper alpha frequency range thus may reflect the partial loss of access to List-1 items or route deactivation of List-1 items in response to the forget cue. Such an interpretation is consistent with behavioral results showing directed forgetting in recall but not in recognition (Geiselman et al., 1983; MacLeod, 1998). The interpretation that intentional forgetting induces route deactivation or "unbinding" in the alpha frequency range also agrees with other recent work showing the importance of alpha oscillations in top-down processing (Klimesch et al., 2007; Sauseng et al., 2005; von Stein, Chiang, & Knig, 2000; Thut, Nietzel, Brandt, & Pascual-Leone, 2006).

Consistent with the inhibition account of directed forgetting, the correlation of forgetting and phase decoupling suggests that the forget cue leads to a disintegration of networks representing List 1, thus pointing to the action of an inhibitory mechanism. Alternatively, the differences in upper alpha phase coupling might also be attributed to selective rehearsal of List-2 items. According to this view, nonselective rehearsal of List-2 items in the remember condition would be reflected by an increase in upper alpha phase coupling. Thus, the positive correlation of forgetting and upper alpha phase coupling might also be explained by selective rehearsal. In contrast, because phase coupling differences between conditions in *Experiment 2* and *Experiment 3* were found in different frequency bands, directed forgetting does not seem to be a variant of context-dependent forgetting as suggested by Sahakyan and colleagues (Sahakyan & Delaney, 2003; Sahakyan & Kelley, 2002).

The second behavioral effect of intentional memory updating, the memory enhancement for the more relevant, newer information, is not related to phase coupling but is due to an increase in pre-stimulus upper alpha power. On the basis of previous EEG studies (Hanslmayr et al., 2005; Klimesch et al., 1997, 2003), the correlation of enhancement and pre-stimulus upper alpha power suggests that the forget cue improves encoding of List-2 items. The finding is comparable with the differences in upper alpha power between experimental conditions in contextual memory updating (*Experiment 2*). Thus, the increase of upper alpha power might reflect a change to a deeper encoding strategy that enhances memory performance (Sahakyan & Delaney, 2003, 2005) in both contextual and intentional memory updating. Again, finding the two underlying physiological mechanisms to operate during the encoding of the new information fits with the picture suggested from *Experiment 1b* which showed that the presence of the forget cue alone is not sufficient to induce intentional memory updating.

The findings of *Experiment 3* suggest that two mechanisms mediate the pattern of forgetting and enhancement in intentional memory updating. First, behavioral enhancement and forgetting did not correlate. Second, two separate physiological mechanisms were identified, which supposedly mediate the two behavioral effects. These results can serve as a post-hoc explanation of the previous finding that occasionally forgetting occurs without enhancement (Conway et al., 2000; Sahakyan & Delaney, 2003; Zellner & Bäuml, 2006) and enhancement occurs without forgetting (Macrae et al., 1997).

This two-mechanism explanation of intentional memory updating is similar in character to two-mechanism accounts suggested on the basis of behavioral data (Sahakyan and Delaney, 2003, 2005). However, in contrast to the context-change hypothesis of directed forgetting (Sahakyan & Kelley, 2002) the present results suggest that this form of episodic forgetting is not caused by context differentiation which should be accompanied by an increase of theta coupling (*Experiment 3*). Instead, the finding that directed forgetting induces "unbinding" in the upper alpha frequency band best fits with some form of retrieval inhibition in top-down processing (Klimesch et al., 2007).

Chapter 4

General discussion

The present experiments revealed both behavioral and electrophysiological findings in the study of episodic memory updating. *Experiment 1a* was run to replicate the previous observations of both detrimental and beneficial effects of memory updating. Contextual memory updating as studied in the context-change paradigm arose from cuing participants to change their mental context between the learning of two lists. Intentional memory updating as studied in the directed-forgetting paradigm arose from cuing participants to forget a first list and to remember a second list of items. Both forms of updating were characterized by the forgetting of pre-cue items and memory enhancement of post-cue items in a final free recall test. The results of *Experiment 1b* showed that cues to forget or to change context are not sufficient to induce forgetting. Rather, the subsequent learning of post-cue items, that is to say memory updating, is necessary to induce the forgetting.

The results of *Experiment 1* suggest that the mechanisms underlying memory updating are active during the encoding of post-cue items and, thus, they could be observable in electrophysiological brain activity during List-2 encoding. Indeed, analyses of oscillatory brain activity in *Experiment 2* and *Experiment 3* revealed the electrophysiological mechanisms of episodic memory updating during the encoding of post-cue items. However, contrary to one-mechanism accounts of episodic memory updating, both contextual and intentional memory updating are best explained with two underlying electrophysiological mechanisms.

Forgetting in contextual memory updating was accompanied by an increase of theta phase coupling between scalp electrodes which is suggested to reflect the integration of contextual information that differentiates between List-1 and List-2 contexts. Accordingly, Summerfield and Mangels (2005) argued that global synchrony of theta oscillations plays an important role in episodic memory and context-dependent memory in particular. More precisely, they showed that, whereas theta power was predictive of subsequent item memory, global synchrony predicted the retrieval success of context. In addition, Sato and Yamaguchi (2007) found an increase of theta coherence for subsequently successful recall of objects' place. Therefore, in *Experiment 2*, the increase of theta phase coupling is suggested to reflect the establishment of a new List-2 context leading to context differentiation between lists. As a consequence, at test forgetting can be observed because of the contextual encoding-retrieval mismatch.

Forgetting in intentional memory updating was accompanied by a reduction of upper alpha phase coupling between scalp electrodes. Klimesch et al. (2007) suggested that upper alpha power may be a marker of inhibitory processes. In particular, large alpha-amplitude oscillations are meant to reflect active retrieval inhibition of memorized items during memory retention. According to Bäuml (in press) this form of inhibition is best described as item suppression that implies a loss in availability of the memory representation itself (Anderson & Spellman, 1995; Postman, Stark, & Fraser, 1968). However, forgetting in intentional memory updating may be best explained by some form of route deactivation between the memory representation and its cue which does not affect the representation of the to-be-forgotten information itself. Therefore, the reduction in upper alpha phase coupling between scalp electrodes in intentional memory updating is suggested to reflect route deactivation of to-be-forgotten material which reduces accessibility but leaves the availability of representations unaffected.

As noninhibitory accounts of intentional memory updating, the selective-rehearsal and context-change explanation have been suggested. However, the latter is not supported by the present data. In *Experiment 3*, no increase of theta phase coupling was observed which is suggested to be a correlate of contextual memory updating in *Experiment 2.* Thus, the forgetting in intentional memory updating does not seem to be a variant of context-dependent forgetting. On the other hand, the selective-rehearsal explanation can't be ruled out by the present electrophysiological results. The positive correlation of forgetting and upper alpha phase coupling might also be explained by more nonselective rehearsal with more upper alpha phase coupling in the remember condition compared to the forget condition during List-2 encoding. Nevertheless, on the basis of previous behavioral findings, the selective-rehearsal explanation of intentional memory updating remains questionable as the failures to find directed forgetting on recognition and implicit memory tasks (Basden et al., 1993; Block, 1971; MacLeod, 1999) and the findings that directed forgetting extends to incidentally learned items (Geiselman et al., 1983) are inconsistent with an explanation that is solely based on differences in encoding processes.

As one-mechanism accounts, context differentiation in contextual memory updating and retrieval inhibition or selective rehearsal in intentional memory updating invoke the same mechanism to explain the forgetting and the enhancement. Each account attributes the enhancement to a single mechanism that produces an escape from proactive interference. However, Sahakyan and Delaney (2003) showed that only those participants that switched from a shallow to a deep encoding strategy escaped from proactive interference. Their data suggests that efficient encoding strategies on List-2 learning can explain the enhancement without the need for a forgetting-related mechanism that produces an escape from proactive interference.

In accordance with this suggestion, Sahakyan and Delaney (2003) analyzed retrospective reports of study strategies from participants in the Sahakyan and Kelley (2002) study. Participants in the forget and context-change condition reported switching to a superior encoding strategy on List 2 more often than did participants in the remember condition. Further evidence for the encoding-strategy explanation comes from studies using recognition at test. Investigating intentional memory updating with recognition, no forgetting was found, but enhancement emerged (Benjamin, 2006; Sahakyan & Delaney, 2005). The absence of forgetting in recognition is consistent with previous research reporting similar findings (Basden et al., 1993). More interesting is the finding of significant enhancement which would be expected in recognition if enhancement arose from shifting to a better encoding strategy. Thus, there are a number of findings providing evidence that forgetting and enhancement do not occur simultaneously suggesting that they may have different underlying mechanisms.

In addition, Sahakyan and Delaney (2003) examined the role of encoding strategies in both contextual and intentional memory updating. By manipulating levels of processing during List-2 encoding they showed that enhancement was abolished when List-2 encoding strategy was induced to be the same both in the remember and forget condition. The forgetting was observed regardless of encoding strategy. Therefore, a two-mechanism account was suggested on the basis of these behavioral data (Sahakyan & Delaney, 2003, 2005). The encoding strategy explanation of enhancement in memory updating is based on the idea that segmentation of lists in the context-change and forget condition might lead to a performance evaluation (Sahakyan, Delaney, & Kelley, 2004). Segmentation might lead participants to engage in an assessment of their own performance after List 1, leading some participants to recognize that their encoding strategy was not going to lead to good recall performance. In the remember condition participants may be more likely to treat the two lists as parts of the same episode and, therefore, may less likely assess their List-1 performance between lists and fail to recognize an inefficient strategy.

Accordingly, the electrophysiological results of *Experiment 2* and *Experiment 3* reject one-mechanism accounts and suggest that at least two mechanisms mediate the pattern of forgetting and enhancement in episodic memory updating. Both in contextual and intentional memory updating the enhancement was not related to phase coupling but was due to an increase in pre-stimulus upper alpha power over temporal electrodes. This increase in power is suggested to reflect a change of encoding strategy to a deeper (more semantic) level of processing (Sahakyan & Delaney, 2003, 2005).

Upper alpha oscillations respond primarily to semantic processing and several studies imply that good memory performance is related to large alpha power in the pre-stimulus interval (Doppelmayr et al., 2002; Klimesch et al., 2000; Vogt et al., 1998). By applying repetitive transcranial magnetic stimulation in the upper alpha frequency range in the pre-stimulus reference interval, Klimesch et al. (2003) enhanced both tonic power and performance. Therefore, the present finding of enhanced upper alpha power in the pre-stimulus interval of the forget and context-change condition might reflect the shift to a deeper, more semantic encoding strategy as suggested by Sahakyan and Delaney (2003, 2005). Indeed, a magnetoencephalographic study (Walla et al., 2001) showed that left temporal brain activity depends on depth of word encoding. Deep semantic encoding elicited higher brain activity in left temporal brain areas than shallow perceptual encoding. In general, depth of encoding-related increases in activity are more commonly seen on the left ventral stream, because deep encoding is nearly always synonymous with encoding for meaning, and, therefore, depends on left-lateralized language mechanisms (for a review, see Martin, 1999). Thus, the present finding of increased upper alpha power at left temporal electrode sites fits with the hypothesis of an encoding-strategy change that underlies the enhancement in both intentional and contextual memory updating. Concerning the correlational data of the present experiments, although individual differences in upper alpha power were not predictive of enhancement in contextual memory updating, it might be argued that these differences strongly rely on individual overall power as interindividual differences in overall alpha power are striking and participants with pronounced overall power tend to show more variance over trials and experimental conditions.

The present electrophysiological results point to separate mechanisms underlying forgetting and enhancement in episodic memory updating. However, real evidence for a dissociation of the underlying mechanisms might be found only by demonstrating that the mechanisms are acting independently. Recent behavioral findings might be helpful to show such dissociations of mechanisms. Sahakyan and Delaney (2003) manipulated encoding strategy both in contextual and intentional memory updating. Instructing participants to encode lists by using the same strategy led to significant forgetting but abolished the enhancement. Therefore, such a manipulation might lead to differences in theta or upper alpha phase coupling but not to differences in upper alpha power between experimental conditions. Indeed, the preliminary results of a current EEG experiment investigating intentional memory updating are consistent with this assumption (unpublished data). By presenting List-2 items together with meaningful environmental sounds, we tried to equilibrate participants' level of List-2 processing between the remember and forget condition. Although significant List-1 forgetting and upper alpha decoupling were observed, neither List-2 enhancement nor differences in upper alpha power between conditions emerged.

On the other hand, investigating intentional memory updating, Bäuml et al. (2007) induced different moods in participants immediately after they received the forget cue. Positive mood is meant to impair executive functioning (for a review, see Mitchell & Phillips, 2007) and thus should reduce the forgetting of the out-of-date information. In accordance, the forget cue induced forgetting of to-be-forgotten information only in neutral mood but not when the subjects were in positive mood. Inducing participants to encode lists with positive mood led to significant enhancement but abolished the forgetting. Thus, induction of positive mood might lead to differences in upper alpha power but not to differences in phase coupling between conditions. Such experimental demonstrations would nicely show that the mechanisms of episodic memory updating are independent indeed.

Sophisticated memory updating does not erase the old information in order to facilitate retrieval of new information. The present experiments showed that forgetting in memory updating is related to changes in phase coupling in the theta or upper alpha frequency band. Previous behavioral studies showed that both forms of forgetting can be reduced or even eliminated and, thus, forgotten information can be reaccessed, either by context reinstatement or release of inhibition. In this regard, it might be hypothesized that phase coupling in the theta and upper alpha frequency range is sensitive to context reinstatement and release of inhibition.

Context reinstatement has been shown to reduce context-dependent forgetting (e.g. Godden & Baddeley, 1980; Smith, 1979). Investigating contextual memory updating, Sahakyan and Kelley (2002) instructed participants to mentally reinstate List-1 context prior to the recall test. Participants who experienced a context change between lists benefited from context reinstatement in their List-1 recall performance more than did those in the standard remember group and the forgetting was almost eliminated. *Experiment 2* showed that forgetting in contextual memory updating is related to an increase of theta phase coupling. Therefore, context reinstatement should be accompanied by changes in theta phase coupling. It might be hypothesized that context reinstatement prior to the recall test reduces or even eliminates the differences both in List-1 recall and theta phase coupling between experimental conditions.

In intentional memory updating, it was shown that inhibition can be released and the forgetting can be reduced or even eliminated (Basden et al., 1993; Bjork & Bjork, 1996; Goernert & Larson, 1994). Authors showed that part-list reexposure of to-be-forgotten items prior to the recall test can reinstate their potential interference and reduce the forgetting. Thus, it might be hypothesized that part-list reexposure of to-be-forgotten material prior to the final recall test reduces or even eliminates the difference both in List-1 recall and upper alpha phase coupling between experimental conditions. Thus, there is at least behavioral evidence that episodic memory updating does not result in a "spotless" mind and does not work like a memory-deletion devise as suggested in the 2004 romance film "Eternal Sunshine of the Spotless Mind". Future electrophysiological experiments will have to show the role of phase coupling in context reinstatement and release of inhibition.

Physiological studies of both contextual and intentional memory updating across the life span might help to understand developmental changes of episodic memory processes in young children and older adults. Indeed, processing of context information (Craik, 1986; Craik & McDowd, 1987; Smith, 1977) and inhibitory processes (Hasher & Zacks, 1988) have been suggested to depend on development and represent the most prominent accounts of age-related changes in memory performance (for a review of memory in early childhood, see Rovee-Collier & Hayne, 2000; for a review of memory in older adults, see Balota, Dolan, & Duchek, 2000). Therefore, it would be interesting to contrast previous findings and theoretical accounts of age-related differences in memory performance and memory updating with the evolvement of oscillatory brain activity in the human brain.

Alpha peak frequency changes across the lifespan with an increase in childhood (Hughes, 1987; Somsen et al., 1997) and a decrease in the elderly (Köpruner, Pfurtscheller, & Auer, 1984). As alpha peak frequency is supposed to reflect speed of information processing (Klimesch, 1999), it might lead to age-related cognitive changes in multiple task domains. According to the speed-of-processing account, age differences in memory do not reflect changes in memory processing per se, but instead merely reflect age differences in the speed of processing (Salthouse, 1988).

Concerning global synchrony, alpha and theta coherence increases in childhood (Barry et al., 2004; Marosi et al., 1992; Thatcher, 1992) and decreases in the elderly (Duffy, Mcanulty & Albert, 1996; Kikuchi et al., 2000). Context differentiation obviously develops very early in life (Hayne, Rovee-Collier, & Borza, 1991; Rovee-Collier, 1997) but retrieval of context declines with age, a finding that has been associated with declining frontal lobe efficiency (Craik, Morris, Morris, & Loewen, 1990; Trott et al., 1999). Thus, it might be assumed that differences in theta phase coupling between experimental conditions and the forgetting in contextual memory updating might be observed in early childhood but are less pronounced in late development. Regarding intentional memory updating, previous behavioral studies challenged the hypothesis of a general inhibitory deficit by showing that both age groups do show intact inhibition in some episodic memory tasks (e.g. Aslan, Bäuml, & Pastötter, 2007; Zellner & Bäuml, 2005, 2006). Indeed, intentional memory updating is present from middle childhood (Harnishfeger & Pope, 1996; Wilson & Kipp, 1998) and remains stable in older subjects (Zellner & Bäuml, 2006, but see Zacks, Radvansky, & Hasher, 1996). Therefore, it might be argued that upper alpha decoupling in children can be observed as soon as alpha peak frequency shifts have progressed and different frequency bands have become functionally differentiated. As the shift in alpha peak frequency in older people is less pronounced than in children, the inhibitory function of upper alpha decoupling should largely remain.

Concerning local synchrony, tonic upper alpha and theta power change with age. From early childhood to adulthood there is a strong increase in upper alpha power but a decrease in theta power (Somsen et al., 1997). In contrast, older people show a decrease in upper alpha power and an increase in theta power (Christian, 1997; Obrist, 1954). Regarding event-related power changes in memory tasks, both children and older adults show greater alpha ERS and smaller theta ERS during encoding and smaller alpha ERD and theta ERS during retrieval compared to young adult (Krause, Salminen, Sillanmäki, & Holopainen, 2001). In this dissertation, I argue that enhancement in contextual and intentional memory updating may be due to changes of encoding strategy which are related to tonic upper alpha power. As encoding strategies gradually develop in early childhood (Gathercole, 1998) and are less spontaneously initiated by older people (Hultsch, 1969), differences in pre-stimulus upper alpha power between experimental conditions and the enhancement in memory updating should not be observed in early and late development. Eventually, the suggested two-mechanism account of episodic memory updating permits separate analyses of mechanisms and thus may improve the understanding of episodic memory updating in young children and older adults.

In this dissertation, four experiments were reported that addressed the role of updating processes in episodic memory. The behavioral experiments revealed the crucial role of post-cue encoding both in context-dependent forgetting and directed forgetting. To return to the introductive courtroom scene, both a change of jury members' mental contexts and the judge's demand to disregard irrelevant information should be followed by the presentation of new information. The present electrophysiological experiments revealed that episodic memory updating is best explained with a two-mechanism account. Forgetting in contextual memory updating was accompanied by an increase of theta phase coupling between scalp electrodes which is suggested to reflect the establishment of a new List-2 context leading to context differentiation between lists. Forgetting in intentional memory updating was accompanied by a reduction of upper alpha phase coupling between scalp electrodes which is suggested to reflect the inhibitory disintegration of to-be-forgotten material. Enhancement in both contextual and intentional memory updating was accompanied by an increase of tonic upper alpha power at left temporal electrode sites which is assumed to reflect a change of participants' encoding strategy. With reference to the court room scene, these findings suggest that the forgetting of inadmissible information can be induced separable of the subsequent memory enhancement that follows either demands to disregard irrelevant information or mental changes of context. In sum, combining behavioral and electrophysiological data with current theoretical accounts of episodic memory updating, the present experiments suggest that while context differentiation in contextual memory updating and retrieval inhibition in intentional memory updating provide the best explanations for the forgetting, the enhancement appears to be due to encoding-strategy changes in both forms of episodic memory updating.

Chapter 5

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