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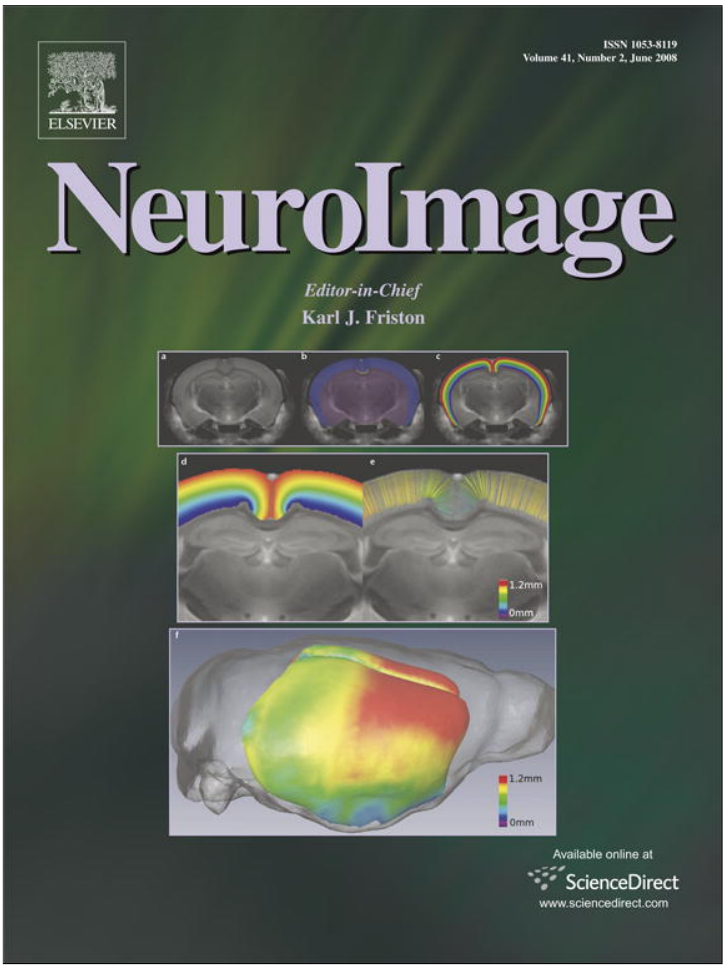

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Oscillatory correlates of intentional updating in episodic memory

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The efficient use of our memory does not only require remembering encoded information, it also requires forgetting old out-of-date information. That such memory updating is part of our memory system is suggested by numerous behavioral studies. The physiological correlates of this process, however, still remain elusive. In this study we explore oscillatory correlates of memory updating as they occur in list-method directed forgetting. In this task, subjects are cued to forget a previously learned word list and to learn a new list of words instead. Such cuing typically leads to forgetting of the first list (List 1) and to memory enhancement of the second (List 2). Measuring EEGs during List-2 encoding, we identified two effects of the forget cue on oscillatory function: an increase in upper alpha power and a reduction in upper alpha phase coupling (11 to 13 Hz). Median-split analyses revealed that the two oscillatory effects were selectively related to the two behavioral effects. Whereas the increase in power was related to List-2 enhancement, the reduced phase coupling was related to List-1 forgetting. Our results point to separate neural origins of forgetting and enhancement and show that alpha oscillations play a critical role in intentional updating of episodic memory.
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Introduction

The efficient use of our memory requires effective updating of the system. Updating reduces the accessibility of irrelevant out-of-date information, like a friend's old home address, and selectively enhances the accessibility of more relevant, newer information, i.e., the friend's current home address. In episodic memory, updating processes can be studied using the directed-forgetting paradigm (Bjork et al., 1968; for reviews, see MacLeod, 1998, or Bäuml, in press). In the list method of this paradigm, subjects 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 (Fig. 1A). After study of List 2, a recall test is conducted in which subjects are asked to recall all of the previously presented items, including those the subjects were originally cued to forget. Compared with remember-cued subjects, who serve as baseline for both List-1 and List-2 recall, forget-cued subjects typically show impaired recall of List-1 items and improved recall of List-2 items. These two effects of the forget cue are referred to as List-1 forgetting and List-2 enhancement. The forgetting reflects the reduced accessibility of the old, out-of-date information, the enhancement reflects the improved access to the more relevant, newer information.

Updating, as it is observed in the directed-forgetting paradigm, is mediated by an intentionally driven process and thus is in stark contrast to updating processes examined in working memory, which occur almost automatically (e.g., Polich, 2007). Updating in directed forgetting has mostly been attributed to a single mechanism, regarded as responsible for both effects of the forget cue, i.e., List-2 enhancement and List-1 forgetting. The selective rehearsal account, for instance, assumes that during List-2 encoding subjects in the remember condition rehearse both the List-2 and the to-be-remembered List-1 items, whereas in the forget condition the forget cue leads to selective rehearsal activities on the List-2 items, thus improving later recall of List 2 at the expense of List 1 (Bjork, 1970). The retrieval inhibition account assumes that, by inhibiting List-1 items, the forget cue reduces accessibility of the List-1 items and, due to the resulting decrease in the items' interference potential, simultaneously improves access to the List-2 items (Geiselman et al., 1983). Finally, the context-change account claims that the forget cue induces a change in subjects' internal context; such context change should impair List-1 recall due to the mismatch between the context at encoding and the context at retrieval and improve List-2 recall due to a reduction in interference (Sahakyan and Kelley, 2002). Selective rehearsal, retrieval inhibition, and the context-change hypothesis reflect one-mechanism accounts of memory updating. List-1 forgetting and List-2 enhancement thus should be the two sides of the same coin and should always occur together.

Indeed, most of the time List-1 forgetting and List-2 enhancement have been found to go together. Very recently, however, some

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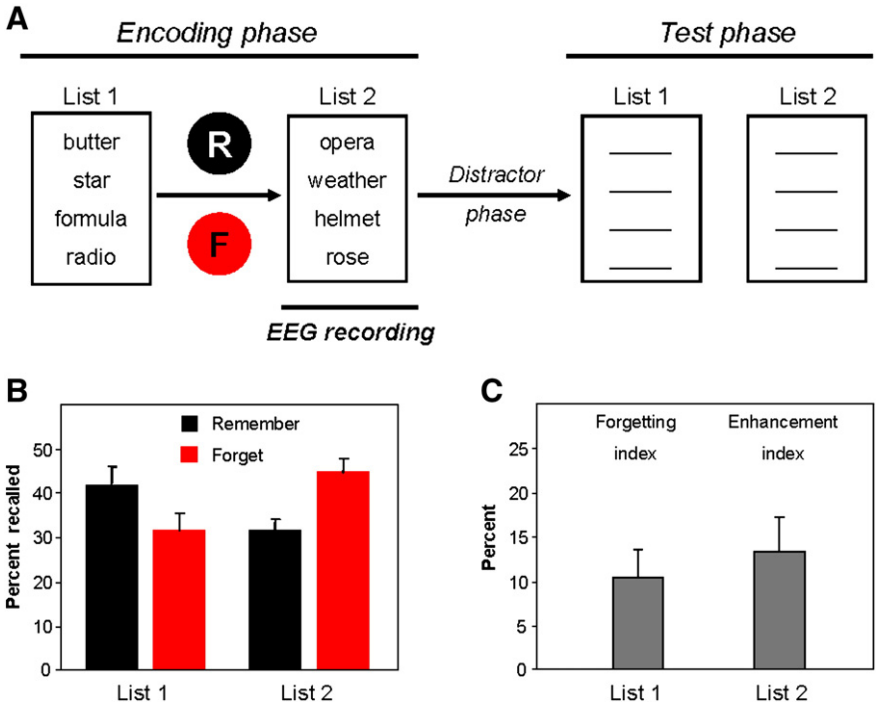

Fig. 1. (A) Depiction of the directed-forgetting procedure. F = presentation of a cue to forget List 1; R = presentation of a cue to remember List 1. (B) Recall data in the present experiment: Regarding List 1, recall was lower in the forget than in the remember condition ($p < .005$); regarding List 2, recall was higher in the forget than in the remember condition ($p < .005$); analysis of variance (ANOVA); error bars: standard errors. (C) Forgetting and enhancement indices: Within-participant forgetting as calculated on the basis of List-1 recall ("Remember" – "Forget"); within-participant enhancement as calculated on the basis of List-2 recall ("Forget" – "Remember"); error bars: standard errors. Forgetting and enhancement are not correlated ($p = .87$).

exceptions to this "rule" have been observed and forgetting has been found to occur without enhancement (Conway et al., 2000; Sahakyan and Delaney, 2003; Zellner and Bäuml, 2006) and enhancement to occur without forgetting (Macrae et al., 1997; Sahakyan and Goodmon, 2007). In particular, whereas List-1 forgetting has been reported to be present in recall but to be absent in recognition, List-2 enhancement has been observed in both recall and recognition (Benjamin, 2006; Sahakyan and Delaney, 2005). These dissociations suggest the action of two separate mechanisms, one mediating List-1 forgetting and the other mediating List-2 enhancement. Consistently, a two-factor account was suggested, according to which List-1 forgetting is caused by retrieval inhibition or, alternatively, a change in subjects' internal context, whereas List-2 enhancement is due to a change in people's List-2 encoding with more elaborate encoding in the forget than in the remember condition (Sahakyan and Delaney, 2003).

While there has been much progress on the cognitive side of list-method directed forgetting in the past 40 years (Bäuml, in press; MacLeod, 1998), to date little effort has been made to understand the physiological mechanisms mediating this intentional forgetting. In this study, we make a first step and explore the electrophysiological correlates of listwise directed forgetting by investigating the effects of the forget cue on oscillatory brain activity. While traditional measures of brain activity have focused on event-related potentials (ERPs), researchers have recently begun to explore the role of oscillations in brain function. Brain oscillations can be measured with the EEG. They are typically divided into different frequency bands, ranging from low frequency bands (delta: 2–4 Hz, theta: 4–7 Hz, alpha: 7–13 Hz) to higher frequency bands (beta: 13–30 Hz, gamma > 30 Hz), and are described by two parameters, power and phase. Whereas power at electrode sites is regarded a measure of local synchrony, phase coupling between electrode sites is regarded a measure of the synchrony between distant neural assemblies (Lachaux et al., 1999).

Brain oscillations have repeatedly been associated with memory processes (for reviews, see Axmacher et al., 2006, or Klimesch, 1999). In episodic memory, mainly gamma oscillations, theta oscillations, and alpha oscillations seem to play a role. Using the subsequent memory paradigm, for instance, several studies have shown that both theta and gamma power during encoding are stronger for items which are recalled on a later memory test (Klimesch et al., 1996; Osipova et al., 2006; Sederberg et al., 2003; Summerfield and Mangels, 2005; see also Sederberg et al., 2006), whereas alpha power during encoding has been found to be weaker for recalled items (Klimesch, 1999; Sederberg et al., 2006). In addition, theta power has been reported to decrease when the lag between encoding and recall of an episode increases (Klimesch et al., 2006b), suggesting that theta power may be sensitive to the overlap between encoding and testing context. Accordingly, theta phase coupling between frontal and parietal electrode sites has been found to distinguish successful from unsuccessful encoding of combined item and context information (Summerfield and Mangels, 2005). Thus, if contextual changes mediate (parts of) the directed forgetting effects, as suggested by the context-change hypothesis (Sahakyan and Kelley, 2002; Sahakyan and Delaney, 2003), theta oscillations might play a crucial role in directed forgetting.

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Oscillations in the alpha frequency range might also play a role in directed forgetting. Whereas former theories suggested that alpha oscillations indicate a passive idling state of the brain (Pfurtscheller et al., 1996), newer theories state that alpha oscillations are critically related to active inhibitory function (for a review, see Klimesch et al., 2007). Consistently, findings in the field of visual perception have shown that alpha amplitudes increase if a visual stimulus has to be ignored (Kelly et al., 2006) and that perception performance is negatively correlated with prestimulus alpha activity (Hanslmayr et al., 2007; Thut et al., 2006). Alpha amplitudes have also been found to increase when subjects inhibit motor responses (Hummel et al., 2002). If inhibition underlies (parts of) the directed forgetting effects, as suggested by the retrieval inhibition hypothesis (Bjork, 1989; Geiselman et al., 1983), alpha oscillations thus might be crucially involved in directed forgetting.

Using the think/no-think paradigm (Anderson and Green, 2001) – a memory variant of the go/no-go paradigm –, a recent fMRI study found intentional forgetting to be correlated with increased BOLD signal in the prefrontal cortex (Anderson et al., 2004), suggesting that intentional forgetting needs top–down control. Electrophysiological studies have repeatedly demonstrated that alpha oscillations are critically related to top–down processes. For instance, alpha power has been found to increase when subjects shift their attention inwards to stored representations and to decrease if attention is shifted outwards (Ray and Cole, 1985). Similarly, alpha phase coupling between anterior and posterior electrode sites has been reported to increase when attention is shifted to a specific stimulus dimension (von Stein et al., 2000). Because directed forgetting reflects intentional forgetting, internally guided top–down processes should be involved, again suggesting that alpha oscillations play a role in this type of forgetting.

In this study, we employed oscillatory measurements of brain activity to examine electrophysiological correlates of directed forgetting. Subjects studied two item lists which they had to recall on a later memory test. Between the study of the two lists, subjects received either a remember cue asking them to remember the first list, or a forget cue asking them to forget the list. Because (part of) the processes mediating directed forgetting seem to operate during List-2 encoding (Pastötter and Bäuml, 2007), we recorded EEGs during study of List-2 items. Doing so, we employed measures of both power and phase coupling. Our goals were to characterize the role of oscillations in directed forgetting and to determine whether enhancement and forgetting in this intentional forgetting are mediated by the same or by different physiological processes.

Materials and methods

Subjects

Twenty-four healthy subjects took part in the experiment on a voluntary basis. The sample consisted of nine males and fifteen females, all of them speaking German as native language. Their mean age was 24.8 years with a range of 19 to 36 years.

Experimental design and procedure

We used a 2×2-design with the within-participants factors of CONDITION (remember/forget) and LIST (List 1/List 2). Conditions differed only in the inter-list cue which stated in the remember condition that List 1 should be remembered and in the forget condition that List 1 should be forgotten. Order of conditions was counterbalanced across participants. 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 later be tested. They were also told that it could happen that, just after presentation, the experimenter declared an item list as no longer relevant and that, in this case, they should try to forget the irrelevant list. A short practice trial with a forget cue followed (for similar design and procedure, see Zellner and Bäuml, 2006).

Both the remember and the forget condition consisted of an encoding phase, a distractor phase, and a test phase. In the encoding phase, two lists were presented to each subject in each of the two conditions. Each list contained 20 semantically unrelated medium-frequency German nouns drawn from the CELEX database. Across lists, the words were matched on frequency and word length. The words were exposed individually for 2 s in the centre of a computer screen. Before presentation of a word, a blank interval was shown for 1450–1550 ms and a fixation cross for 500 ms. Throughout the whole encoding phase no motor responses were required from the subjects.

Remember condition and forget condition differed in the cue provided between List 1 and List 2. In the remember condition, participants were cued to continue to remember the so far seen items (List 1) and to additionally learn another list (List 2). In the forget condition, participants were told that the so far seen items (List 1) will not be tested later and that they therefore should try to forget these items and instead learn another list (List 2). Then, the second list was presented in the same way as the first list. List 2 was always followed by a remember cue. After the encoding phase, the subjects had to count backward for 30 s from a three-digit number as a recency control. Following this distractor phase, a written recall test of both lists was carried out. Subjects were asked to recall the List-1 items first and the List-2 items second (e.g., Sahakyan and Delaney, 2003; Zellner and Bäuml, 2006).

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 surprisingly told to remember 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 she would not deceive the participant again (see also Zellner and Bäuml, 2006). The results from recent work indicate that list-method directed forgetting experiments lead 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 (Barnier et al., 2007; Conway and Fthenaki, 2003; Zellner and Bäuml, 2006). We chose the within-subjects design because it permits a detailled analysis on whether a putative neural correlate of memory updating shows sensitivity to individual differences in the amount of forgetting and enhancement.

Recordings and analysis of EEG data

During the encoding of List 2, EEG data were recorded from 50 Ag/AgCl electrodes arranged according to the extended 10–20 system and mounted in an elastic cap. Additionally, two EOG-channels were recorded. Electrode Cz served as reference electrode. Impedance was kept below 5 kΩ. Bioelectrical signals were digitalized with a sampling rate of 500 Hz. Frequencies between 0.3 and 70 Hz were recorded. EEG recordings were offline re-referenced against average reference, EOG-corrected,

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and visually inspected for remaining artefacts. Thereupon, the recording of the list was separated into 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. After artifact rejection, at least 18 single trials remained for each condition and participant for analysis.

To calculate power, EEG data was transformed using Hanning windowed fast Fourier transformations (FFT, Brain Vision Analyzer Software Brain Products GmBH) with a frequency resolution of 1 Hz. In the first instance, pre-stimulus power (1750 to 750 ms before word onset) and post-stimulus power (250 to 1250 ms after word onset) were calculated separately. After this, because effects of experimental conditions in power did not differ between the pre-stimulus and post-stimulus interval, we included the total length of 4000 ms of single trials in the FFT analysis. Power was calculated and averaged within four frequency bands (theta: 4 to 7 Hz, lower alpha: 8 to 10 Hz, upper alpha: 11 to 13 Hz, lower beta: 14 to 18 Hz), separately for experimental conditions and subjects. Power values of frequency bands entered into repeated measures analyses of variance (ANOVA) with the within-subjects factors CONDITION (remember, forget) and SITE (50 electrodes). Greenhouse–Geisser correction was applied when appropriate.

The phase locking values (PLV) were calculated for each condition and electrode pair from 4 to 18 Hz with a frequency resolution of 1 Hz using the software BESA v5.1.8 (Brain Electrical Source Analysis MEGIS Software). PLV is a measure of frequency-specific phase variability between two signals (Lachaux et al., 1999). Unlike spectral coherence, it is a measure that is independent of amplitude. Electrical activity is taken to be synchronous if the phase lag between two electrodes remains constant throughout the trials. The PLV ranges from 0 meaning maximal phase variability to 1 meaning perfect phase coupling. A common problem with calculating connectivity measures on a scalp electrode level is that volume conduction gives rise to spurious phase coupling. For example, oscillatory activity in one focal brain region is recorded from several electrodes. If this brain region is more active in one condition and less active in the other condition, differences in phase coupling are obtained. In order to diminish the contribution of such an underlying common source, we followed recent work (Sauseng et al., 2008; Summerfield and Mangels, 2005) and calculated phase coupling on the current source density (CSD) profiles. The CSD represents the second spatial derivative of the voltage distribution in the brain tissue and is implicitly reference free. The CSD transformation acts as a spatial filter which removes the influence of very low spatial frequencies, thus largely diminishing the influence of common sources (Lachaux et al., 1999; Nunez et al., 1997). Notice that this method is conservative, because it cannot distinguish between meaningful coupling of nearby sources and volume conduction.

Again, because effects of experimental conditions in phase coupling did not differ between the pre-stimulus (1750–750 ms) and post-stimulus interval (250–1250 ms), we included the total length of 4000 ms of single trials in the PLV analysis. Prior to statistical analysis, PLVs were Fisher-*z*-transformed. For statistical analysis of the PLV, a two-stage procedure was carried out. At first, *t*-tests were calculated for each electrode pair to investigate which electrode pairs show a significant difference between the two conditions. Second, randomization tests (Blair and Karniski, 1993; Hanslmayr et al., 2007), based on 20,000 permutation runs, were 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 the two conditions (remember vs. forget), 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.

Results

Behavioral results

The behavioral results showed the standard pattern of directed forgetting: List-1 forgetting and List-2 enhancement. Regarding List 1, subjects recalled 41.7% of the items in the remember condition and 31.5% in the forget condition. Regarding List 2, subjects recalled 31.5% of the items in the remember condition and 44.6% in the forget condition (Fig. 1B). 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 (Fig. 1C). 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.

Based on a balanced median split on the forgetting index (List 1: remember minus forget) a high-forgetting and a low-forgetting group were formed with counterbalanced order of experimental conditions. Forgetting was significantly induced in the high-forgetting group (20.9%; $t_{11}=5.6$; $p<.001$) but was not induced in the low-forgetting group (−0.4%; $t_{11}<1.0$). Based on a balanced median split on the enhancement index (List 2: forget minus remember), a high-enhancement and a low-enhancement group were formed with counterbalanced order of experimental conditions, respectively. Enhancement was significantly induced in the high-enhancement group (23.0%; $t_{11}=3.6$; $p<.005$) but did not reach significance in the low-enhancement group (3.3%; $t_{11}=1.0$). Split groups based on enhancement and forgetting indices consisted of different subject samples ($\phi=.17$, $p=.41$).

Physiological results: power at electrode sites

Three two-way ANOVAs calculated with theta power (4 to 7 Hz), lower alpha power (8 to 10 Hz), and lower beta power (14 to 18 Hz) as dependent measures revealed neither main effects of CONDITION (all Fs<1) nor CONDITION × SITE interactions (all Fs<1.6). Significant main effects of SITE indicated that theta power and lower alpha power were mainly observed at occipital and central electrode sites (theta: $F(4.7,108.2)=24.6$, $p<.001$; lower alpha: $F(2.7,61.1)=12.2$, $p<.001$), whereas lower beta power was mainly observed at occipital and temporal electrode sites ($F(6.0,138.2)=12.2$, $p<.001$).

A two-way ANOVA calculated with upper alpha power (11 to 13 Hz) as dependent measure revealed a significant main effect of SITE ($F(3.4,77.9)=20.0$, $p<.001$), indicating that upper alpha power was mainly observed at occipital and parietal electrode sites. More important, both a main effect of CONDITION ($F(1,23)=4.3$, $p=.05$) and a CONDITION × SITE interaction ($F(5.9,135.1)=2.2$, $p<.05$) were found, indicating an increase of upper alpha power in the forget condition compared to the remember condition (Fig. 2A). This effect was mostly pronounced at left temporal electrode sites (FC3, FC5, FT7, C3, C5, T7, CP3, CP5, TP7; $t_{23}=2.9$; $p<.01$) and was specific to the upper alpha band. A two-way ANOVA with factors

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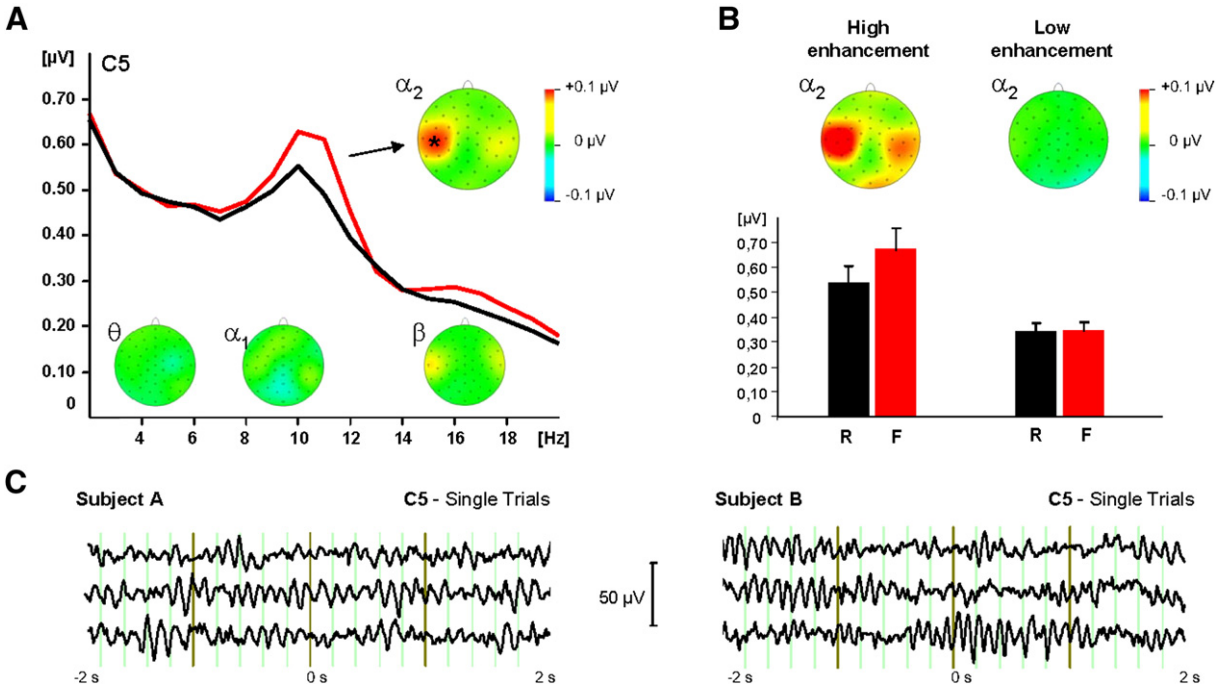

Fig. 2. Electrophysiological data on List-2 encoding: analysis of power. (A) Average scalp distributions of differences in power between the forget and the remember condition for four frequency bands (theta: 4 to 7 Hz, lower alpha: 8 to 10 Hz, upper alpha: 11 to 13 Hz, lower beta: 14 to 18 Hz). Color coding indicates differences in power over an electrode during List-2 encoding. Red means more power in the forget than in the remember condition. Significant differences in power between conditions were only found in the upper alpha frequency band (11 to 13 Hz) over left temporal electrodes (e.g., C5) with larger power in the forget condition (red line) than in the remember condition (black line, $p<.01$). (B) Average scalp distributions of differences in upper alpha power between conditions as a function of the magnitude of List-2 enhancement (high and low enhancement, balanced median split based on behavioral enhancement index). High enhancement is accompanied by a larger difference in upper alpha power over left temporal electrodes between the remember (R) and forget (F) condition ($p<.01$); error bars: standard errors. (C) Three representative single trials of each of two subjects are shown for electrode C5.

CONDITION (remember, forget) and FREQUENCY (lower alpha, upper alpha) revealed a main effect of CONDITION ($F(1,23)=6.0$, $p<.05$) and a CONDITION × FREQUENCY interaction ($F(1,23)=4.3$, $p<.05$). Left temporal electrodes did not show any difference in lower alpha power between conditions ($t_{23}<1$).[1]

Physiological results: phase coupling between electrode sites

Comparing phase coupling across the remember and forget condition, PLV analysis revealed significant differences in the alpha frequency band, mostly pronounced in the upper alpha range (Fig. 3A). No significant effects were found for the other frequency bands. In the upper alpha frequency range, we found 28 electrode pairs with less coupling in the forget condition ($p<.005$; one-tailed) and one electrode pair with less coupling in the remember condition ($p<.005$; one-tailed). The randomization test showed that the upper alpha decoupling in the forget condition was significant ($p<.005$), indicating that in less than 0.5% of the permutation runs 28 or more electrode pairs showed significantly less upper alpha phase coupling in the forget compared to the remember condition. In the lower alpha frequency range, we found 19 electrode pairs with less coupling in the forget condition ($p<.005$; one-tailed) and two electrode pairs with less coupling in the remember condition ($p<.005$; one-tailed). The randomization test showed that the lower alpha decoupling in the forget condition was significant ($p<0.05$).

Relationship between behavioral and physiological effects

To examine the relationship between upper alpha power and List-2 enhancement, left temporal alpha power in the forget and remember conditions were contrasted with the between-subjects factor of enhancement group (high-enhancement vs. low-enhancement group, Fig. 2B). A two-way ANOVA revealed a main effect of CONDITION ($F(1,22)=10.7$, $p<.005$), a main effect of GROUP ($F(1,22)=8.6$, $p<.01$), and a CONDITION × GROUP interaction ($F(1,22)=8.9$, $p<.01$). Power was significantly different between experimental conditions in the high-enhancement group ($t_{11}=3.2$; $p<.01$), with more power in the forget than in the remember condition. In contrast, in the low-enhancement group, no difference in upper alpha power between conditions was found ($t_{11}<1.0$). Contrasting upper alpha power with the factor of forgetting group did not reveal significant differences between subject groups. A two-way ANOVA with factors CONDITION (remember, forget) and GROUP (high-forgetting group, low-forgetting group) revealed a main effect of CONDITION ($F(1,22)=7.6$,

[1] We examined the effects of CONDITION and SITE also in other frequency bands. Two-way ANOVAs calculated with delta power (2 to 4 Hz), upper beta power (20 to 30 Hz), and lower gamma power (30 to 45 Hz) as dependent measures revealed neither main effects of CONDITION nor CONDITION × SITE interactions (all p's >.10).

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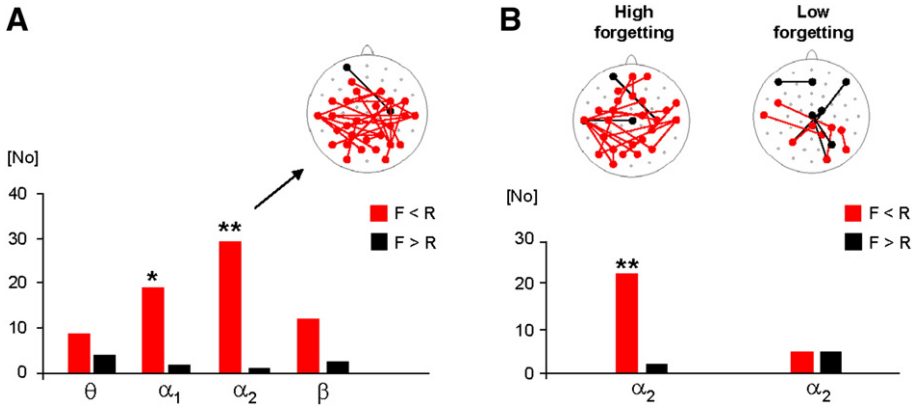

Fig. 3. Electrophysiological data on List-2 encoding: analysis of phase coupling (PLV). (A) A significant difference in phase coupling between the forget (F) and remember (R) condition was found in the alpha frequency band with 28 electrode pairs showing less upper alpha coupling ($p<.005$, based on a randomization test) and 19 electrode pairs showing less lower alpha coupling in the forget than in the remember condition ($p<.05$, based on a randomization test). Red coding corresponds to less phase coupling and black coding to more phase coupling in the forget than in the remember condition ($p<.005$, one-tailed). (B) Differences in upper alpha phase coupling between conditions as a function of the magnitude of List-1 forgetting (high and low forgetting, balanced median split based on behavioral forgetting index). Only high forgetting is accompanied by a significant difference in phase coupling, with 23 electrode pairs showing less phase coupling in the forget than in the remember condition ($p<.005$, based on a randomization test). Red coding corresponds to less phase coupling and black coding to more phase coupling in the forget than in the remember condition ($p<.005$, one-tailed).

$p<.05$), but neither a main effect of GROUP ($F(1,22)<1$), nor a CONDITION × GROUP interaction ($F(1,22)<1$).

To examine the functional relationship between alpha phase coupling and List-1 forgetting, upper and lower alpha phase coupling in the forget and remember condition were contrasted with the between-subjects factor of forgetting group (high-forgetting vs. low-forgetting group, Fig. 3B). In the high-forgetting group, we found 23 electrode pairs with less upper alpha phase coupling in the forget condition ($p<.005$; one-tailed) and two electrode pairs with less coupling in the remember condition ($p<.005$; one-tailed). The randomization test showed that the upper alpha decoupling in the forget condition was significant ($p<.005$) in this group. In contrast, in the low-forgetting group, only five electrode pairs were found with less upper alpha phase coupling in the forget condition ($p<.005$; one-tailed), and also five electrode pairs were found with less coupling in the remember condition ($p<.005$; one-tailed). As indicated by the randomization test, both effects on phase coupling in the low-forgetting group were nonsignificant. Cochran's Q-tests revealed that the number of significant electrode pairs was larger in the high-forgetting group compared to the low-forgetting group with respect to upper alpha decoupling ($\chi^2(1)=11.5$, $p<.001$). Contrasting lower alpha decoupling, no significant difference between forgetting groups was found ($\chi^2(1)=2.6$, $p>.10$). Contrasts of upper alpha phase decoupling with the factor of enhancement group did not reveal any significant differences between subject groups. Both the high- and the low-enhancement group showed 10 electrode pairs with less upper alpha phase coupling in the forget condition than in the remember condition ($p<.005$; one-tailed).

Analysis of possible order effects

In the present experiment, we chose the within-subjects design of directed forgetting, with each subject participating in both the remember and the forget condition. We did this to permit a detailed analysis on whether a putative neural correlate of directed forgetting shows sensitivity to individual differences in amount of List-1 forgetting and amount of List-2 enhancement. Prior behavioral work reported no effect of order of remember and forget condition on subjects' List-1 forgetting and List-2 enhancement (Barnier et al., 2007; Conway and Fthenaki, 2003; Zellner and Bäuml, 2006), thus providing an empirical rationale for our choice of design.

The behavioral results of the present experiment replicate the prior results by indicating that order of remember and forget condition did not influence List-1 forgetting and List-2 enhancement. The same amount of forgetting and enhancement were found regardless of whether the subjects started with the remember condition or the forget condition (t_{22}s<1.60, ps$>.10$). The same result arose for the two identified physiological effects. Order of experimental conditions did not influence the effect in upper alpha power at left temporal electrodes. A three-way ANOVA with factors CONDITION (remember, forget), ORDER (remember first, forget first), and GROUP (high enhancement, low enhancement) replicated the main effect of CONDITION and the reliable CONDITION × GROUP interaction; all other main effects and interactions, however, were nonsignificant (all Fs<1.6).

Order of experimental conditions did also not influence the effect in upper alpha phase coupling. Less phase coupling in the forget than in the remember condition was found both when subjects started with the remember condition (13 pairs, $p<.005$; one-tailed) and when they started with the forget condition (14 pairs, $p<.005$; one-tailed); following Cochran's Q-test, the difference in number of electrode pairs between groups was not significant ($\chi^2(1)<1$). Similarly, following Cochran's Q-test, order of remember and forget conditions did not influence upper alpha phase coupling for the high- and the low-forgetting groups (both $\chi^2(1)$s<1). Thus, order of remember and forget condition had no reliable influence on the above described findings.[2]

[2] In this study, EEG data were recorded during List-2 encoding but not during List-1 encoding. While we found no order effects on the two identified physiological effects during List-2 encoding, given the present within-subjects design, it is in principle possible that order of conditions affected electrophysiological activities during List-1 encoding. A future study is needed to examine how List-1 activity might interact with the present findings.

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Discussion

This is the first study relating memory updating as it is studied in list-method directed forgetting to electrophysiological measurements of brain activity. Prior behavioral work demonstrated that the forget cue per se is not sufficient to create successful directed forgetting but rather that additional List-2 encoding is necessary to induce the effect (Pastötter and Bäuml, 2007). We therefore measured subjects' electrophysiological activity during List-2 encoding. We identified two effects of the forget cue on oscillatory function: an increase in upper alpha power and a reduction in upper alpha phase coupling. Median-split analyses revealed that the two oscillatory effects were selectively related to the two behavioral effects. Whereas the increase in power was related to List-2 enhancement, the reduced phase coupling was related to List-1 forgetting. These findings, together with the observed nonrelationship between forgetting and enhancement, indicate that memory updating in this paradigm is mediated by two separate mechanisms.

Alpha phase coupling and List-1 forgetting

Theories of directed forgetting often assume that, during List-2 encoding, subjects in the remember condition engage in relational encoding of the two lists, whereas in the forget condition they focus on list-specific processing of the List-2 items (see MacLeod, 1998). The observed reduced phase coupling in the forget condition is in line with such a view, indicating that the forget cue led to less coherent activities in the relevant brain structures. Coherent firing between distant neuronal populations has been regarded a mechanism which subserves binding in conscious perception (Gross et al., 2004; Rodriguez et al., 1999) and associative learning (Miltner et al., 1999). The list-specific processing of List-2 items in the presence of the forget cue thus may be expected to lead to less coherent activities in the relevant neural networks and less phase coupling than does the relational processing of the two lists, which is exactly what the present results reveal. Employing quite different paradigms, previous studies reported evidence for an increase in memory performance when certain brain structures are oscillating in synchrony (Fell et al., 2001; Tallon-Baudry et al., 2004; Weiss and Rappelsberger, 2000). The present results extend these findings by demonstrating that the opposite behavior, i.e., forgetting, can occur when the synchrony in oscillations is reduced.

The difference in phase coupling was observed between local and distant electrode sites. Because we carried out CSD transformation (see Materials and methods section), this result points to the action of a cortical network involving multiple superficial sources that reduced their coupling in response to the forget cue presentation. The reduced phase coupling was observed in the alpha frequency range. Following recent results in the field of visual perception which suggest that alpha oscillations serve as an active inhibitory filter for the brain (Hanslmayr et al., 2007; Kelly et al., 2006; Thut et al., 2006; see also Klimesch et al., 2007), the present results suggest that List-1 forgetting reflects retrieval inhibition (Geiselman et al., 1983). Such inhibition may have led to the "unbinding" of List-1 items, leading to less phase coupling in the forget than in the remember condition and a change from relational to list-specific processing of List-2 items. Although, in principle, list-specific processing of List-2 items might also arise as a result of selective rehearsal of List-2 items or the creation of a second, list-specific context cue (see MacLeod, 1998, or Bäuml, in press), the localisation of the present effect in the alpha frequency range favors the inhibition view over noninhibitory accounts of directed forgetting.

Alpha power and List-2 enhancement

The two oscillatory effects that we observed in the present study were both localized in the alpha frequency range. Partly, this may be due to the inhibitory character of the task, partly it may reflect the involvement of top–down processes. Because directed forgetting reflects intentional forgetting, internally guided top–down processes should be involved (Anderson et al., 2004), suggesting a prominent role of alpha frequencies in this type of task (Ray and Cole, 1985; von Stein et al., 2000). Top–down processing may play a particular role for the encoding of List-2 items. It has recently been argued that List-2 enhancement is due to a change in people's encoding with more elaborate List-2 encoding in the forget than in the remember condition (Sahakyan and Delaney, 2003). This change in strategy has been suggested to be mediated by self-induced evaluation of the current study strategy and adjustment of the strategy on the next to-be-encoded list (Sahakyan et al., 2004). Such adjustment should trigger top–down processes, which is likely to induce activities in the alpha frequency range.

Using the subsequent memory paradigm, previous studies on the role of alpha power in episodic encoding reported that decreases in alpha power predict successful encoding of list items (Klimesch, 1999; Sederberg et al., 2006). Because items' alpha power has been found to be higher in middle than in early serial list positions (Sederberg et al., 2006), it was argued that high alpha power reflects divided attention between multiple items during encoding; in contrast, low alpha power was argued to reflect more focused processing of single items, leading to better recall performance. The present results show a different pattern. In the forget condition, subjects showed higher recall *and* higher levels in alpha power than in the remember condition. Moreover, on a median-split basis, increases in subjects' alpha power were related to subjects' List-2 enhancement.

The difference in pattern across these studies may be due to differences in task and data analysis. First, Sederberg et al. (2006) analyzed power changes within word lists, event-related to the presentation of each single item. In our study, we analyzed global power changes between two word lists that followed experimental manipulation. Second, alpha power is usually highest in the prestimulus interval, and high prestimulus alpha power has been found to be positively related to cognitive performance (for a review, see Klimesch et al., 2006a). Prestimulus power is therefore suggested to reflect brain state activity and differences in prestimulus power may reflect the activity of different global mechanisms during information processing. Prestimulus and poststimulus power did not differ in the present experiment. The observed effect of the forget cue on alpha power thus is consistent with the view that the effect reflects general brain state activity and the two cues (remember vs. forget) triggered different types of processes.

Oscillatory correlates and a 2-factor view of memory updating

List-method directed forgetting is generally regarded a case of updating in episodic memory mediated by an intentionally driven process that diminishes accessibility of old, out-of-date information and enhances accessibility of new, more relevant information (e.g., Bjork, 1989). The results of the present study suggest that increased

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alpha power and reduced alpha phase coupling underlie this form of memory updating. In contrast, a number of previous EEG studies have related memory updating processses to the P300 component of the ERP (e.g., Polich, 2007). However, these studies typically addressed updating processes in working memory, which occurs almost automatically and thus differs from memory updating as it is observed in the directed-forgetting paradigm. The present pattern of increased power but reduced phase coupling also suggests that alpha phase coupling was not confounded by increased precision in phase estimation due to stronger signal power. Indeed, increased power might result in increased precision in phase estimation, thus making it more likely to find an increase in phase coupling, which is exactly the opposite to what the present results show.

The present result of two distinct physiological mechanisms mediating the two behavioral effects of directed forgetting can serve as a post-hoc explanation of the previous finding that occasionally forgetting occurs without enhancement (Conway et al., 2000; Sahakyan and Delaney, 2003; Zellner and Bäuml, 2006) and enhancement occurs without forgetting (Macrae et al., 1997; Sahakyan and Goodmon, 2007). In particular, it can account for the fact that List-1 forgetting and List-2 enhancement can be dissociated experimentally. Whereas List-1 forgetting has recently been shown to be present in recall but not in recognition, List-2 enhancement has been found to be present in both types of memory tasks (Benjamin, 2006; Sahakyan and Delaney, 2005). Obviously, forgetting and enhancement are not just the two sides of the same coin, as proposed by most previous accounts of the phenomenon.

The evidence for two distinct physiological mechanisms is consistent with a two-factor view of memory updating, according to which the directed forgetting phenomenon consists of two separate components having different underlying mechanisms. Sahakyan and Delaney (2003) provided such a view, suggesting that List-1 forgetting is caused by a change in internal context in response to the forget cue – or, alternatively, by retrieval inhibition –, whereas List-2 enhancement is caused by a change in people's encoding strategy. Regarding List-2 enhancement, the present results seem in accord with the view that the forget cue changes subjects' encoding strategy for List-2 items. Regarding List-1 forgetting, the present results fit the retrieval inhibition hypothesis better than the contextual change hypothesis. Whereas the finding of reduced coupling in the alpha frequency range is consistent with an inhibitory view (Klimesch et al., 2007), the present null effects in the theta frequency range do not support the contextual-change account, because contextual changes would be expected to induce activities in the theta frequency range (Klimesch et al., 2006b; Sato and Yamaguchi, 2007; Summerfield and Mangels, 2005). A direct examination of oscillatory correlates of context-dependent forgetting will help clarify the issue.

The identification of two distinct oscillatory correlates helps to indicate the number and nature of mechanisms underlying intentional updating in episodic memory. Besides, the identification of the two components is also of interest for studies on the development and neuropsychology of memory updating. The results from developmental studies indicate that updating in episodic memory is not present before middle childhood (Harnishfeger and Pope, 1996; Wilson and Kipp, 1998) and possibly gets deficient again with increasing age (Zacks et al., 1996; but see Zellner and Bäuml, 2006). Moreover, results from neuropsychological work suggest that certain brain lesions induce impairments in memory updating (Conway and Fthenaki, 2003). Extending previous one-factor accounts, the two-factor account permits a separate analysis of the two mechanisms underlying memory updating and thus may improve our understanding of intentional memory updating in young children, older adults, and patient groups.

In sum, relating memory updating as it is studied in list-method directed forgetting with electrophysiological measurements of brain activity we identified two selective effects of the forget cue on oscillatory function. The one effect, a reduction in upper alpha phase coupling, was related to List-1 forgetting, and the other effect, an increase in upper alpha power, was related to List-2 enhancement. Both effects were measured during List-2 encoding, indicating that directed forgetting is not solely the result of retrieval effects at test. The two physiological effects challenge single-mechanism accounts of directed forgetting according to which List-1 forgetting and List-2 enhancement are mediated by the same mechanism and support a two-mechanism view according to which the one effect (reduced coupling) reflects inhibition of out-of-date information (List 1) and the other effect (increase in power) reflects a change in encoding strategy for new material (List 2). Finding both oscillatory effects in the alpha frequency range strengthens the view suggested in prior work that alpha frequencies are related to top–down processes and active inhibitory function.

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