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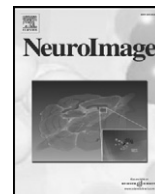
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Oscillatory brain activity before and after an internal context change – Evidence for a reset of encoding processes

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ABSTRACT

Prior behavioral work has shown that changing context during encoding can influence long-term memory performance. The present study examined the neural correlates of such context effects by analyzing oscillatory brain activity during the encoding of words, both before and after a context change. Participants studied two lists of items and, after the presentation of List 1, were either cued to change their internal context through a simple imagination task, or not. Replicating the behavioral work, the change in context led to forgetting of the first list (List 1) and to memory enhancement of the second (List 2). Measuring EEGs during encoding of the two lists, the context change was found to affect oscillatory brain activity. Whereas an increase of theta and alpha power from List-1 to List-2 encoding was found when the context was left unchanged, a slight theta and alpha power decrease was found when the context was changed. In addition, median split analysis revealed that alpha power during List-2 encoding was related to the enhancement effect of the context change. The results suggest that a change in internal context can lead to a reset of encoding processes, thus pointing to a crucial role of encoding processes in context-dependent memory.

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Introduction

Changes in context can affect memory performance on a later recall test. For instance, when subjects study a set of material in one spatial context (e.g., on land) and are later tested on the studied material in a different spatial context (e.g., under water), then recall performance is typically lower than in a condition in which the spatial context was not changed between study and test (e.g., tested on land; Godden and Baddeley, 1975). Context changes, however, can also be beneficial for memory performance. For instance, when several lists of items are studied in different physical contexts (e.g., different rooms), then recall of the single lists is typically better compared to a condition in which the single lists are studied in the same physical context (e.g., the same room; Smith, 1982). Such beneficial and detrimental effects of context changes are not restricted to physical (external) context changes but do also arise for internal context changes, like changes in subjects' mood or subjects' physiological states (for reviews, see Eich, 1989, or Smith and Vela, 2001).

Beneficial and detrimental effects of a context change

Using an internal context-change manipulation, Sahakyan and Kelley (2002) recently introduced a paradigm in which beneficial and detrimental effects of a context change can be examined simultaneously. Participants study two lists of items and, after the presenta-

tion of List 1, are either cued to change their internal context through a simple imagination task (context-change condition) or do not receive such a cue (no-change condition). After study of List 2, a recall test is conducted in which participants are asked to recall all previously presented items. The typical finding in this paradigm is that the imagination task enhances recall of List 2 and impairs recall of List 1, reflecting the beneficial and the detrimental memorial effect of a context change (Aslan and Bäuml, 2008; Pastötter and Bäuml, 2007; Sahakyan and Delaney, 2003; Sahakyan and Kelley, 2002).

The two, opposing effects of a context change are consistent with standard views on context-dependent memory, including computational models, like the comprehensive search of associative memory model (SAM, Mensink and Raaijmakers, 1988) or the temporal context model (TCM, Howard and Kahana, 2002). In these models, the beneficial effect of a context change on List-2 performance is explained by an improved interference situation at test. Initially, at encoding, our memory system binds each item to the current representation of the mental context. A change of context between study of the two lists then alters the mental context for List-2 encoding, leading to specific context cues for the two lists. Because the specific List-2-context cue reduces interference from List 1 at test, recall performance on List 2 should be enhanced compared to the same-context condition. In contrast, because the new mental context is still active at test, a mismatch between study and testing context for List-1 items should arise, lowering recall of List-1 items compared to the same-context condition (encoding-specificity principle; see Tulving and Thomson, 1973).

While standard views on context-dependent memory emphasize the important role of retrieval processes at test to explain the

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memorial effects of a context change, they largely ignore the possible role of encoding for these modulations in memory performance. Such a position is justified with regard to List 1, because List-1 encoding precedes the context manipulation and thus should not differ between experimental conditions. Regarding List-2 encoding, however, this theoretical position might be premature. Indeed, results from recent studies examining oscillatory brain activity during encoding of single lists suggest that context changes may not only affect retrieval processes at test but may already influence the encoding of material studied subsequently to the context change. These studies are described next.

Oscillatory brain activity and encoding

When investigating encoding processes, physiological studies often use the subsequent-memory paradigm showing that brain activity during encoding can predict which items will subsequently be remembered or forgotten (for a review, see Paller and Wagner, 2002). Besides using traditional measures of hemodynamic brain activity and brain potentials, researchers have recently begun to examine the role of oscillatory brain activity for memory performance (for reviews, see Axmacher et al., 2006; Klimesch, 1999; or Jensen et al., 2007). Generally, oscillations across different frequency bands have been shown to be predictive of subsequent-memory performance. Whereas stimulus-induced theta (4 to 8 Hz) and gamma power (>30 Hz) have been found to be positively related to subsequent-memory performance, alpha (10 to 14 Hz) and beta power (15 to 25 Hz) have been reported to be negatively related to retrieval success (Caplan and Glaholt, 2007; Klimesch et al., 1996a,b; Osipova et al., 2006; Sederberg et al., 2003, 2007).

More specifically, Sederberg et al. (2006) recently examined the change of stimulus-induced power as a function of items' serial position in a list. They found that theta and alpha power increased from early to middle serial positions at widespread electrodes over the scalp. The authors argued that, with cumulative list length, increases of theta and alpha power might reflect a shift from focused to more divided encoding; due to memory load, inattention might increase and lead to unsuccessful encoding of middle-list items. In fact, increases of theta and alpha power with memory load have been reported in both episodic and working memory tasks (Jensen et al., 2002; Jensen and Tesche, 2002; Klimesch et al., 1999; Onton et al., 2005). In contrast to theta and alpha power, Sederberg et al. (2006) showed that high-frequency beta and gamma power can account for subsequent-memory effects for early-list items only, thus predicting the primacy effect in single-list learning.

If theta and alpha power increase with the encoding of multiple items, such increases should not only be found within lists. Rather, if two lists were to-be-encoded successively, similar increases in theta and alpha power should arise from the first to the second to-be-encoded list, thus generalizing the single-list finding to two-list paradigms. In particular, such putative increases in theta and alpha power across two lists might be expected to be disrupted if the context is changed between List-1 and List-2 encoding. After a change in context, List-2 items are bound to a new context cue, thus possibly reducing memory load for List-2 items and increasing attention for item encoding. If so, less theta power and less alpha power should be observed during List-2 encoding when the context was changed between study of the two lists than when the context was not changed, reflecting a (partial) reset of encoding processes. The question of whether context changes can induce such a reset of encoding processes has not been addressed to date.

The present experiment

An experiment is reported which addresses the issue. Participants studied two item lists which they had to recall on a later memory test. Between the study of the two lists, participants were either cued to

change their internal context through a simple imagination task, or they did not receive such a cue (e.g., Pastötter and Bäuml, 2007; Sahakyan and Kelley, 2002). We recorded electroencephalograms (EEGs) during the study of the two lists and focused on stimulus-induced power changes during the encoding of items. Extending the findings from Sederberg et al. (2006) from the single-list paradigm to the present two-list paradigm, we expected an increase in both theta and alpha power from List-1 to List-2 encoding when the context was unchanged between study of the two lists. When the context was changed, we expected lower theta and alpha power during List-2 encoding than without such a context change. By comparing List-2 encoding activity across context conditions, the results will indicate whether memorial consequences of a context change are already reflected in differences in List-2 encoding. Such a result would point to a particular role of encoding processes in context-dependent memory.

Methods

Participants

Forty-eight healthy students (25 males and 23 females) at Regensburg University, Germany, participated in the experiment. Their mean age was 23.6 years ($SD=3.2$). All participants were right-handed, had normal or corrected-to-normal vision, and spoke German as native language. Participants were paid 15 Euros or received course credit for participation.

Material

Eighty unrelated German nouns of medium frequency were drawn from the CELEX database using the Wordgen v1.0 software toolbox (Duyck et al., 2004). Four 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 no-change condition and the context-change condition, and served equally often as the first and second presented list.

Behavioral design

The experiment had a 2×2 behavioral design with the within-participants factor of *context* (no change, context change) and the between-participants factor of *output order* (List 1 tested first, List 2 tested first). First, conditions differed in whether, after List 1 encoding, participants' internal context was changed or not. In the context-change condition, List 1 was followed by a mental context change; in the no-change condition, participants' internal context was not changed. Second, conditions also differed in whether List-1 items or List-2 items were to be recalled first at test. Mean recall frequency was used as dependent variable. List-1 recall was analyzed separately from List-2 recall (e.g., Pastötter and Bäuml, 2007; Sahakyan and Kelley, 2002). Items were counted as correctly recalled if they were recalled with the correct list.

Procedure

Both the no-change condition and the context-change condition consisted of an encoding phase, a distractor phase, and a test phase (Fig. 1A). Prior to the encoding phase, participants were informed about the general nature of the experiment. They were told that they had to learn some words and that their memory for these words would be tested later on. In the encoding phase, two lists of words were presented. 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

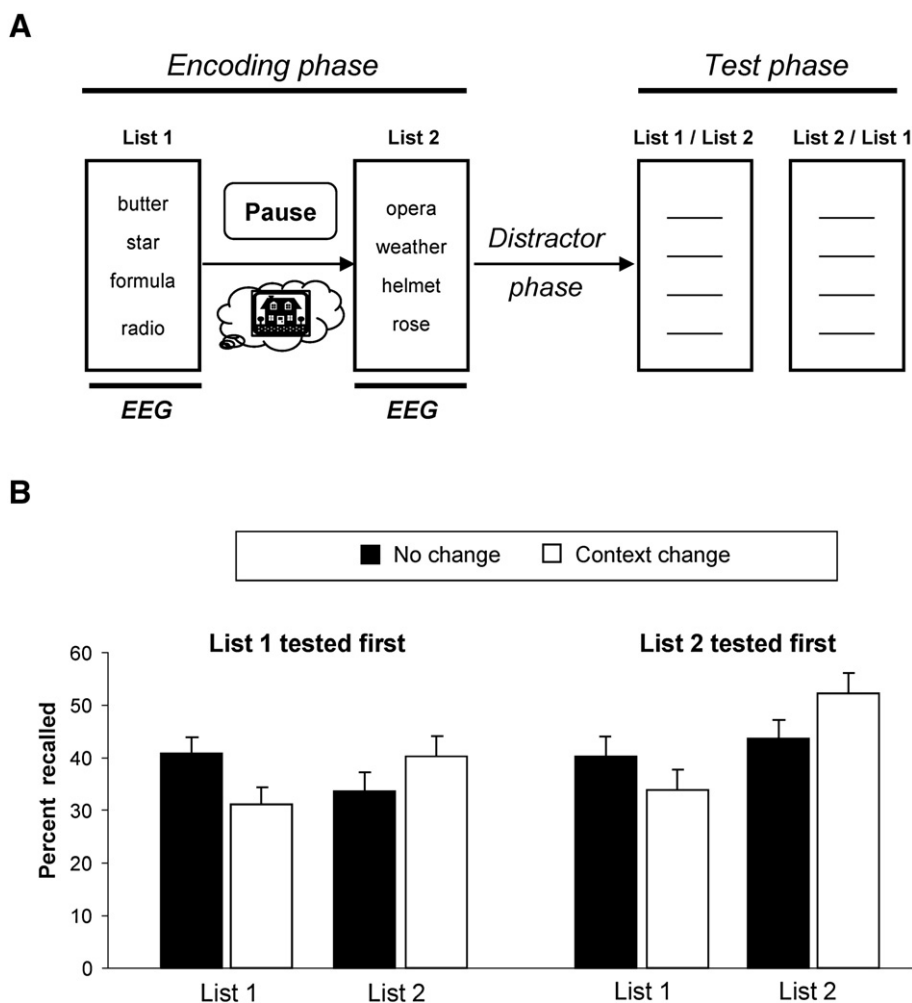


Fig. 1. Depiction of the procedure and behavioral results. (A) Experimental manipulation of context conditions (no change, context change) during encoding: pause in the no-change condition; imagination of parents' house in the context-change condition. At test, either List-1 items or List-2 items were tested first. (B) Mean recall frequency as a function of list (List 1, List 2), context (no change, context change), and test (List 1 tested first, List 2 tested first). Error bars: standard errors.

and the second for 500ms. Conditions differed in the procedure after List-1 encoding. In the context-change condition, participants were subject to an internal context change. They were asked to imagine their parents' house, to mentally walk through it, and to tell their imaginations to the experimenter. They were told to use the next 45s for this task. The purpose of the task was to shift the participants' mental context from studying words in an experiment to something quite different (e.g., Pastötter and Bäuml, 2007; Sahakyan and Kelley, 2002). In the no-change condition, participants waited for an equivalent amount of 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. In the distractor phase, participants had to count backward from a random three-digit number for 30s as a recency control. In the test phase, a recall test was carried out. The participants were asked to write down as many List-1 or List-2 items they could remember. Recall of the two lists was done on separate sheets of papers. Output order of lists was manipulated between subjects. Recall time for each single list was 90s.

Recordings of EEG data

During the encoding phase of lists, EEGs were recorded from 63 Ag/AgCl electrodes arranged according to the extended 10–20 system and mounted in an elastic cap (BrainCap64, EasyCap). Vertical and horizontal eye movements were recorded from two additional

channels. Electrode FCz served as common reference. Signals were digitalized with a sampling rate of 500Hz and amplified between 0.3 and 70Hz with a notch filter at 50Hz to remove line noise (BrainAmpMR plus, Brain Products). Impedance was kept below 5kΩ. EEG recordings were offline re-referenced against average reference and EOG-corrected using calibration data to generate individual artifact coefficients (Ille et al., 2002).

Analyses of EEG data

EOG-corrected recordings of each list were segmented into 4000ms epochs ranging from 2000ms preceding stimulus onset to 2000ms after stimulus onset. After rejection of artifact contaminated epochs, at least 17 single trials remained for each list, condition, and participant for further analyses. In the no-change condition, 19.0 List-1 trials (SD=0.4) and 18.8 List-2 trials (SD=0.6) were accepted for analyses; in the context-change condition, 19.0 List-1 trials (SD=0.4) and 18.9 List-2 trials (SD=0.5) were accepted, respectively.

Using the short-time-Fourier-transformation algorithm implemented in BESA (Brain Electrical Source Analysis© MEGIS Software v5.1.8) oscillatory power data was filtered in a frequency range from 2 to 45Hz. Analogous to a Morlet wavelet, time–frequency resolution was set to 50ms and 1Hz for the theta (4 to 8Hz) and alpha band (10 to 14Hz), 25ms and 2Hz for the beta band (16 to 26Hz), and 10ms and 5Hz for the gamma band (30 to 45Hz). Because we were interested in induced power changes, not phase-locked to stimulus onset, the

averaged evoked signal was subtracted from all single trials prior to Fourier transformation. To examine differences in event-related power between conditions, the ERD/ERS method was used (Pfurtscheller and Aranibar, 1977). This method examines stimulus-induced power changes by calculating the percentage of power decrease (event-related desynchronization, ERD) or power increase (event-related synchronization, ERS) in relation to a pre-stimulus interval which was set to 1500ms to 1000ms prior to stimulus onset.

For statistical analysis, ERD/ERS values were collapsed in order to obtain four frequency bands – theta (4 to 8Hz), alpha (10 to 14Hz), beta (16 to 26Hz), and gamma (30 to 45Hz) – and four time windows – T1 (0 to 500ms), T2 (500 to 1000ms), T3 (1000 to 1500ms), and T4 (1500 to 2000ms). To examine differences in stimulus-induced power changes between conditions, pair-wise contrasts were calculated for each frequency band and time window. To account for multiple testing, a two-stage randomization procedure was carried out. At first, Wilcoxon tests were calculated for each electrode in order to investigate which electrodes differ between conditions ($p < 0.05$; two-tailed). Thereafter, a randomization test using 2000 permutations was run (Blair and Karniski, 1993; Hanslmayr et al., 2007). This procedure evaluates whether a given number of electrodes, exhibiting a significant difference between two conditions, is expected by chance. If the p -value (p_{corr}) of this randomization test is below 0.05, less than 5% of the permutation runs exhibited equal or more electrode sites with a significant difference between conditions. Only if the randomization test exhibited a significant difference between conditions, power data was averaged across all significant electrodes for the specific frequency band and time window and entered into repeated measures analyses of variance (ANOVA) with the within-subjects factors of list (List 1, List 2) and context (context change, no [context] change).

We also examined differences in phase coupling between experimental conditions during List-2 encoding. By calculating phase locking values on current source density (CSD) profiles for each condition and electrode pair across frequency bands and time windows, we were able to measure synchrony between distant neural assemblies (Lachaux et al., 1999; Nunez et al., 1997). As indicated by randomization tests (Blair and Karniski, 1993), no differences between experimental conditions were found. We also extended analysis to pre-stimulus and post-stimulus intervals separately, and again did not find any effect on phase coupling. Therefore, in the Results section, we do not report on the detailed statistical findings from these analyses.

Results

Behavioral results

List-1 recall

When List 1 was tested first, participants recalled 40.8% of the List-1 items in the no-change condition and 31.3% of the items in the context-change condition; when List 2 was tested first, 40.2% of the List-1 items were recalled in the no-change condition and 34.0% in the context-change condition (Fig. 1B). Analysis of variance with the factors of *context* and *output order* revealed a main effect of *context* ($F(1, 46) = 7.9, p < .01$), with higher recall in the no-change condition than the context-change condition. However, neither a main effect of *output order* ($F(1, 46) < 1$) nor a *context* × *output order* interaction was found ($F(1, 46) < 1$). Thus, significant List-1 forgetting was present independent of output order.

List-2 recall

When List 1 was tested first, participants recalled 33.5% of the List-2 items in the no-change condition and 40.8% of the items in the context-change condition; when List 2 was tested first, 43.7% of the List-2 items were recalled in the no-change condition and 51.5% in the context-change condition (Fig. 1B). Analysis of variance with the

factors of *context* and *output order* revealed a main effect of *context* ($F(1, 46) = 11.5, p < .005$), with higher recall in the context-change condition than the no-change condition, and a main effect of *output order* ($F(1, 46) = 4.2, p < .05$), with higher recall when the list was tested first than when it was tested second. However, no *context* × *output order* interaction emerged ($F(1, 46) < 1$). Thus, significant List-2 enhancement was present independent of output order.

Median split data

Based on a balanced median split on the enhancement index as calculated on the basis of List-2 recall (context change minus no change), a high-enhancement and a low-enhancement group were formed with counterbalanced order of experimental conditions. Enhancement was significantly induced in the high-enhancement group (50.0% vs. 34.6%; $t_{23} = 7.1; p < .001$) but was not induced in the low-enhancement group (42.3% vs. 42.7%; $t_{23} < 1$). Based on a balanced median split on the forgetting index as calculated on the basis of List-1 recall (no change minus context change), a high-forgetting and a low-forgetting group were formed, respectively. Forgetting was significantly induced in the high-forgetting group (48.5% vs. 25.2%; $t_{23} = 8.7; p < .001$) but was not induced in the low-forgetting group, which even showed better List-1 recall in the context-change condition (32.5% vs. 40.0%; $t_{23} = 3.7; p < .05$). Split groups based on the enhancement and forgetting index consisted of different subject samples ($\phi = -.17, p = .25$). Consistently, a correlation of forgetting and enhancement index across individuals showed that these behavioral effects were not mutually dependent ($r = -.10, p = .48$).

Physiological results

No-change condition

Our first goal was to examine whether the single-list findings from Sederberg et al. (2006) extend to the present two-list paradigm. We thus determined which frequency bands and time windows exhibited significant differences in oscillatory activity between List-1 and List-2 encoding in the no-change condition. Randomization tests revealed a significant increase in theta power from 500 to 1000ms ($p_{\text{corr}} < .01$) and a significant increase in alpha power from 500 to 1500ms across lists ($p_{\text{corr}} < .01$, Fig. 2A). In contrast, beta and gamma power did not differ between lists in any time window. To assess the timing of significant differences in theta and alpha power, we calculated time-frequency spectrograms of power averaged across those electrodes exhibiting significant differences for the two frequency bands. Fig. 2A shows that differences between lists began approximately 500ms following the onset of each item presentation with more theta and alpha power during List-2 encoding than during List-1 encoding. For both frequency bands, not a single bin was found showing less theta or alpha power during List-2 than during List-1 encoding.

Context-change condition

In the next step we analyzed oscillatory activity when the context was changed between study of the two lists. Comparison of activity during item encoding before and after the context change revealed a slight decrease in power from List-1 to List-2 encoding in both the theta ($p_{\text{corr}} = .07$) and the alpha frequency range ($p_{\text{corr}} = .06$) in the time window from 500 to 1000ms (Fig. 2B). Again, beta and gamma power did not differ between lists. Time-frequency analysis of power averaged across those electrodes exhibiting significant differences for the two frequency bands showed that differences between lists were mostly pronounced from 500 to 1000ms following the onset of each item.

Comparison of experimental conditions

Having observed the topography and timing of effects between the encoding of lists for the no-change and context-change condition separately, we directly compared oscillatory List-2 activity between

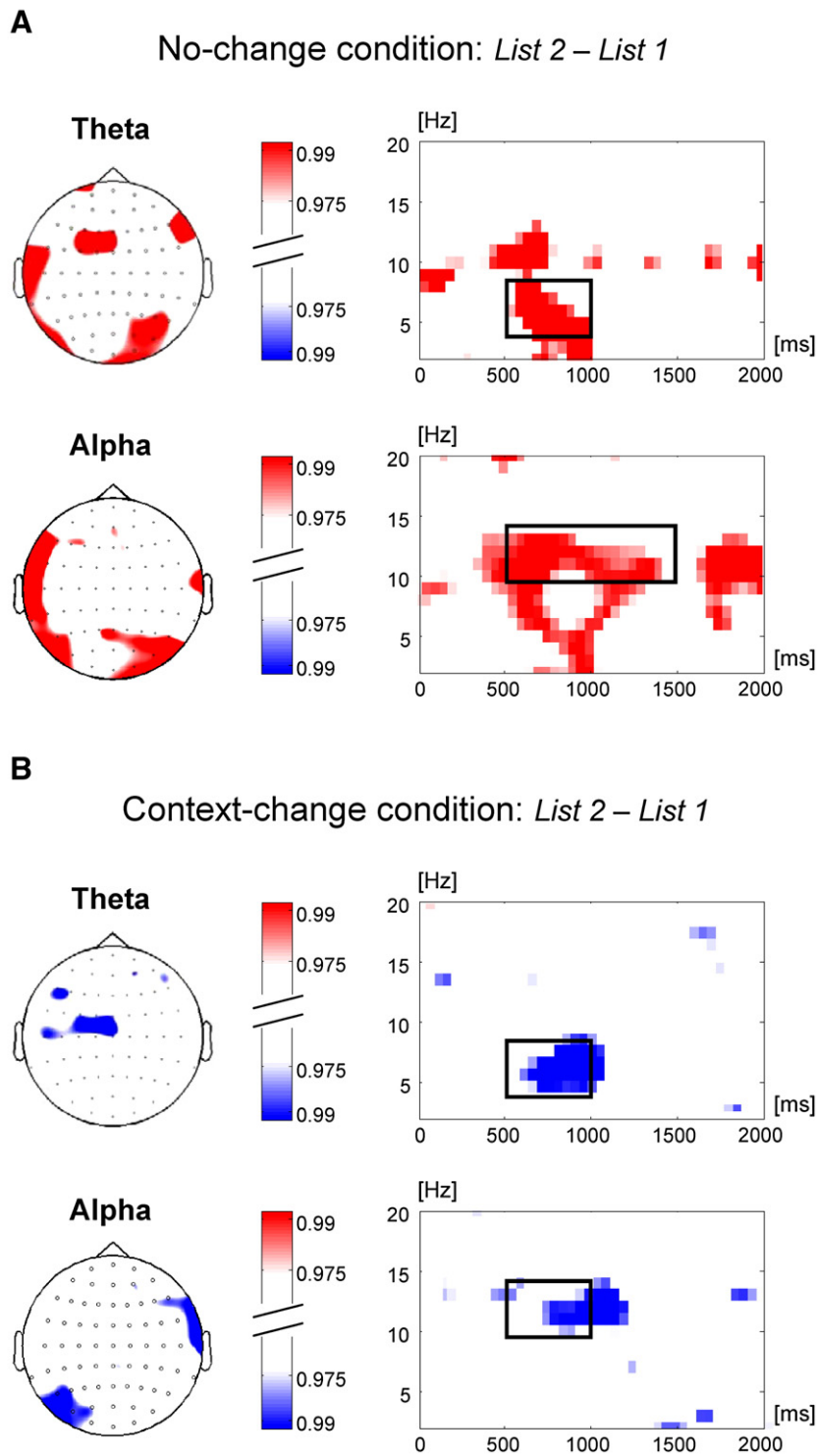


Fig. 2. Comparison of oscillatory activity between List-1 and List-2 encoding. (A) Power data in the no-change condition. Scalp topographies depict the electrodes that exhibited significant differences in theta (4 to 8 Hz, 500 to 1000 ms) and alpha power (10 to 14 Hz, 500 to 1500 ms) between List-1 and List-2 encoding (scaling is based on Wilcoxon tests, $p < 0.05$, two-tailed; randomization testing, see Methods). Red areas denote an increase in theta and alpha power from List-1 to List-2 encoding (p_{corr} 's $< .01$). No electrode showed a decrease in theta or alpha power across lists (blue areas). Time–frequency spectrograms show the timing of significant differences in power between lists averaged across corresponding electrodes. (B) Power data in the context-change condition. Scalp topographies depict the electrodes that exhibited significant differences in theta (500 to 1000 ms) and alpha power (500 to 1000 ms) between List-1 and List-2 encoding. Blue areas denote a decrease in theta ($p_{\text{corr}} = .07$) and alpha power ($p_{\text{corr}} = .06$) from List-1 to List-2 encoding. No electrode showed an increase in theta or alpha power across lists. Time–frequency spectrograms show the timing of significant differences in power between lists averaged across corresponding electrodes.

experimental conditions. Randomization tests revealed significant differences between conditions in the theta ($p_{\text{corr}} < .01$) and alpha frequency range ($p_{\text{corr}} < .001$) from 500 to 1000ms following stimulus onset. Beta and gamma power did not differ between conditions in

any time window of List-2 encoding. Fig. 3A shows scalp topographies of electrodes that exhibited significant differences in theta and alpha power from 500 to 1000ms. Time–frequency analysis revealed that differences between conditions began approximately 500ms

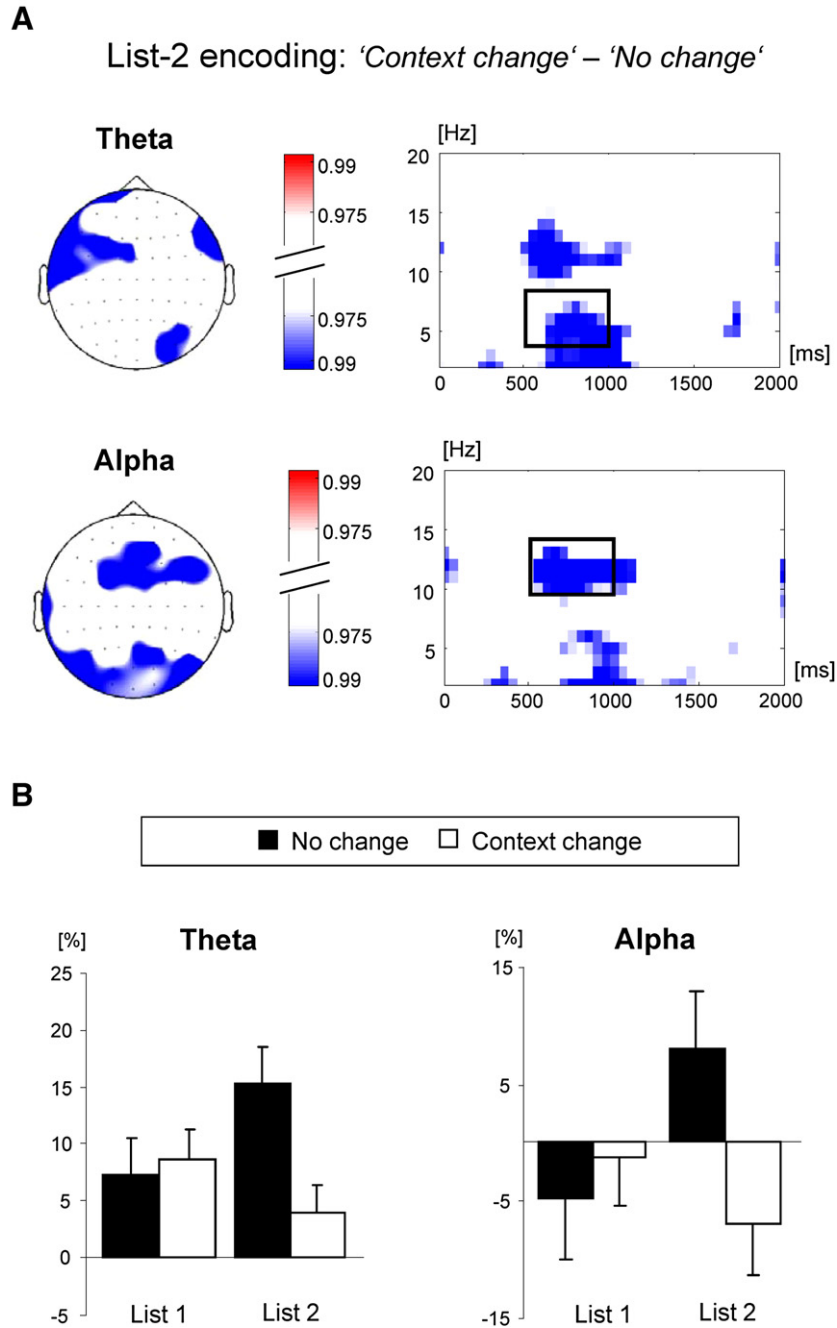


Fig. 3. Comparison of oscillatory activity between the no-change and context-change conditions. (A) Power data during List-2 encoding. Scalp topographies depict the electrodes that exhibited significant differences in theta (500 to 1000 ms) and alpha power (500 to 1000 ms) between the no-change and context-change conditions (scaling is based on Wilcoxon tests, $p < 0.05$, two-tailed; randomization testing, see Methods). Blue areas denote less theta ($p_{\text{corr}} < .01$) and alpha power ($p_{\text{corr}} < .001$) in the context-change condition compared to the no-change condition. No electrode showed more power in the context-change condition. Time–frequency spectrograms show the timing of significant differences in power between conditions averaged across corresponding electrodes. (B) Theta and alpha power averaged across those electrodes showing significant differences between experimental conditions during List-2 encoding for each frequency band (500 to 1000 ms) as a function of list (List 1, List 2) and context (no change, context change). Error bars: standard errors.

following the onset of each item presentation, with less theta and alpha power in the context-change than the no-change condition, and diminished 500ms later.

The differences in theta and alpha power between conditions interacted with List-1 and List-2 encoding. Theta power averaged across electrodes showing significant differences between experimental conditions during List-2 encoding from 500 to 1000ms entered into a two-way ANOVA with the within-subjects factors of list (List 1, List 2) and context (no change, context change). Analysis revealed a *list* × *context* interaction ($F(1, 47) = 10.5, p < .005$), which was due to an increase of theta power from List-1 to List-2 encoding in the

no-change condition ($t_{47} = 2.4; p < .05$) and a marginal decrease from List-1 to List-2 encoding in the context-change condition ($t_{47} = 1.8; p = .07$, Fig. 3B). Similarly, alpha power averaged across electrodes showing significant differences during List-2 encoding from 500 to 1000ms entered into a two-way ANOVA with the within-subjects factors of list (List 1, List 2), and context (no change, context change). Analysis revealed a *list* × *context* interaction ($F(1, 47) = 18.9, p < .001$), which was due to an increase of alpha power from List-1 to List-2 encoding in the no-change condition ($t_{47} = 2.8; p < .01$) and a marginal decrease from List-1 to List-2 encoding in the context-change condition ($t_{47} = 1.7; p = .09$, Fig. 3B).

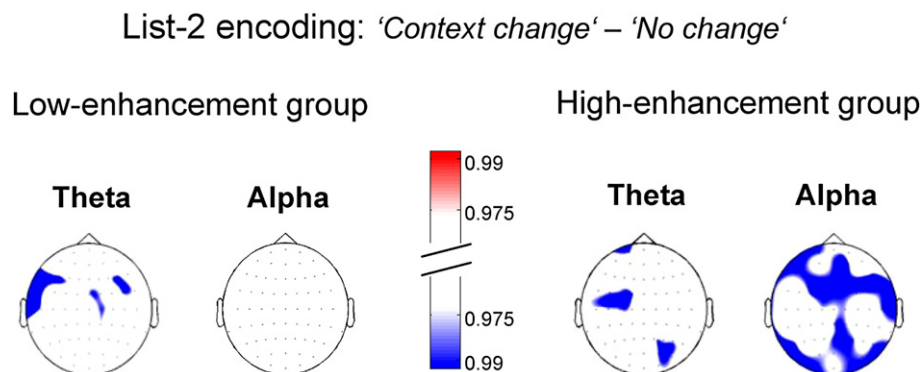


Fig. 4. Relationship between behavioral and oscillatory effects. Power data during List-2 encoding differentiated by enhancement groups. Scalp topographies depict the electrodes that exhibited significant differences in theta (500 to 1000 ms) and alpha power (500 to 1000 ms) between the no-change and context-change condition (scaling is based on Wilcoxon tests, $p < 0.05$, two-tailed; randomization testing, see Methods). Both enhancement groups showed less theta power in the context-change condition compared to the no-change condition (blue areas, $p_{\text{corr}} < .05$). The high-enhancement also showed less alpha power in the context-change condition compared to the no-change condition (blue areas, $p_{\text{corr}} < .001$).

Relationship between behavioral and physiological effects

In order to relate behavioral and physiological data, theta and alpha power averaged across those electrodes exhibiting significant differences between conditions during List-2 encoding were contrasted with the between-subjects factors of forgetting and enhancement group. Concerning alpha power as dependent measure, a four-way ANOVA with the between-subjects factors of enhancement (high, low) and forgetting (high, low), and the within-subject factors of list (List 1, List 2) and context (no change, context change) revealed a $list \times context$ ($F(1, 44) = 16.5$, $p < .001$) and a $list \times context \times enhancement$ interaction ($F(1, 44) = 4.3$, $p < .05$). Both interactions were due to a $list \times context$ interaction in the high-enhancement group ($F(1, 23) = 18.6$, $p < .001$) but not the low-enhancement group ($F(1, 23) < 1$). In the high-enhancement group, alpha power slightly increased from List-1 to List-2 encoding in the no-change condition (10.6%), but decreased in the context-change condition (–15.1%). Analysis of theta power as dependent measure revealed neither main effects nor interactions of between-subjects factors *enhancement* (high, low) and *forgetting* (high, low).

So far statistical analyses were based on the average power of preassigned electrodes showing significant differences between conditions during List-2 encoding across all subjects. We finally determined scalp topographies depicting significant differences between conditions separately for the low- and high-enhancement group (Fig. 4). Randomization tests revealed that both groups showed less theta power in the context-change condition compared to the no-change condition ($p_{\text{corr}} < .05$). In contrast, only the high-enhancement group showed a difference in alpha power between experimental conditions, with less alpha power during List-2 encoding when the context was changed between lists than when it was left unchanged ($p_{\text{corr}} < .001$).

Discussion

We replicated prior behavioral work on context-dependent memory (e.g., Pastötter and Bäuml, 2007; Sahakyan and Kelley, 2002) by showing that a change in internal context between the study of two lists can improve later recall of the subsequently encoded material (List-2 enhancement) and impair recall of the previously encoded items (List-1 forgetting). We extended the prior work by exploring oscillatory brain activities during encoding of the two lists, both when participants' internal context was changed between study of the two lists and when it was left unchanged. When the context was left unchanged, both theta and alpha power increased from List-1 to List-2 encoding. In contrast, when the context was changed, no such increase in power was observed and even a slight decrease in theta

and alpha power emerged. Moreover, median split analysis revealed that the decrease in alpha power from List-1 to List-2 encoding was related to List-2 enhancement. The results point to a particular role of encoding processes in context-dependent memory.

Effects of context changes on encoding processes

The results in the no-context-change condition extend recent findings from the single-list paradigm to the present two-list paradigm. In the single-list paradigm, Sederberg et al. (2006) demonstrated that theta and alpha oscillations increase in amplitude with increasing number of to-be-encoded items in a list. They argued that, with increasing number of to-be-encoded items, a shift from focused to more divided encoding takes place and encoding gets impaired, be it through an increase in memory load due to there being more items to encode (Jensen et al., 2002; Klimesch et al., 1999) and/or decreased attention. Consistent with this view, recent work suggests a strong link between alpha oscillations and attention on the one hand (for a review, see Palva and Palva, 2007) and theta oscillations and memory load on the other (for a review, see Jensen, 2006). Generalizing the results from the single-list paradigm, in the present two-list paradigm we found a similar increase in theta and alpha power from List-1 to List-2 encoding when the context was left unchanged between study of the two lists. Following Sederberg et al. (2006), this result suggests that, when holding study context constant, the study of a second list is accompanied by a shift to more divided encoding, with increased memory load and/or inattention compared to study of the first list. An increase in amount of the to-be-encoded material thus seems to impair the encoding of items regardless of whether the increase occurs within or across lists.

In contrast to the no-context-change condition, we did not find any increase in theta and alpha power from List-1 to List-2 encoding when the context was changed between study of the two lists. Together with the findings from the no-context-change condition, this result suggests that changing context between lists can abolish the memory load and inattention effects that supposedly build up when the study context is left unchanged, suggesting that some reset of encoding processes takes place when the context is changed. Remarkably, even a slight decrease in theta and alpha power was observed from List-1 to List-2 encoding when the context was changed between the two lists. In fact, participants with a high amount of List-2 enhancement showed a reliable decrease in alpha power from List 1 to List 2 at widespread electrodes over the scalp. It thus seems that changing context between lists can even enhance attentional resources, boosting encoding processes for the subsequently studied material. This interpretation is in line with research on human and animal

learning, indicating that, when subjects learn a set of material, they also learn how to learn the same or similar material more effectively in the future (e.g., Postman, 1971).

The question may arise of whether there is a simple relationship between the present effects in theta and alpha activity and the subsequent-memory effect, i.e., the often observed differences in encoding activity between later remembered and later forgotten items (Paller and Wagner, 2002). Because there were not enough trials for such analysis in the present study, we did not calculate oscillatory activity for remembered and forgotten items separately. From the literature, evidence for a possible relation between the present results and subsequent-memory effects is provided by the fact that the present finding of a reduction in alpha power after a context change is in line with the typical finding of reduced alpha power for remembered compared to forgotten items (e.g., Klimesch et al., 1996b). However, no such link is provided between the present finding of a reduction in theta power and subsequent-memory effects; theta power for subsequently remembered items is typically higher than theta power for forgotten items (e.g., Caplan and Glaholt, 2007; Klimesch et al., 1996a). Thus, there may be no simple relation between the present results on the effects of context changes and subsequent-memory effects.

Implications for theoretical accounts of context-dependent memory

The standard view on context-dependent memory emphasizes the role of retrieval processes to account for both the beneficial and detrimental effects of context changes (Howard and Kahana, 2002; Mensink and Raaijmakers, 1988; Sahakyan and Kelley, 2002; Tulving and Thomson, 1973). Accordingly, the beneficial effect of a context change between the study of two lists is often explained through reduction of proactive interference from List-1 items, supposedly caused by the specificity of the List-2-context cue at test. However, in contrast to this pure retrieval-based view, in the present experiment a context change was found to affect the subsequent encoding of List-2 items and to induce a reset of encoding processes, making encoding of the List-2 items comparable to encoding of the List-1 items. In particular, the encoding processes after the context change were predictive for List-2 enhancement. These results challenge a purely retrieval-based view on context-dependent memory and point to an additional role of encoding processes in context-dependent memory.

While the present results identify an oscillatory correlate of the beneficial effect of a context change (List-2 enhancement), no such correlate arose for the detrimental effect of the context change (List-1 forgetting). In the present study, we measured EEGs during List-2 encoding. Finding no oscillatory correlate for List-1 forgetting thus may indicate that context-dependent forgetting is not caused during List-2 encoding. Indeed, as incorporated in many computational models (e.g., Mensink and Raaijmakers, 1988), the new context cue may be established in direct response to the context-change task, so that the new context cue is already built up before List-2 encoding starts. Then, at test, List-1 forgetting is caused by the mismatch between study and testing context for List-1 items, reflecting a pure retrieval explanation of List-1 forgetting. Following this view, encoding mechanisms would contribute to List-2 enhancement but not to List-1 forgetting.

The suggested view that List-2 encoding plays no role for List-1 forgetting in context-dependent memory appears inconsistent with a recent behavioral study from our lab (Pastötter and Bäuml, 2007). In this study, evidence was provided that, after an internal context change, List-2 encoding is necessary to cause List-1 forgetting. As one explanation of this finding, we suggested that the encoding of List-2 items may provide an opportunity to strengthen the representation of the new context, which may increase the contextual encoding/retrieval mismatch for List-1 items at test and thus increase List-1 forgetting. We did not identify an oscillatory correlate for such a

strengthening of context representation in the present study, nor did we find any other correlate of List-1 forgetting. Further work appears necessary to clarify the exact relation between the behavioral and the physiological results.

Context-dependent forgetting vs. directed forgetting

Using a related two-list paradigm, called list-method directed forgetting, Bäuml et al. (2008) recently reported an experiment in which subjects were provided a forget cue between the study of two lists, asking them to intentionally forget the previously presented list (List 1) and focus on the encoding of a new list (List 2). Replicating prior behavioral work, the forget cue led to forgetting of the first list and to memory enhancement for the second list, relative to a control condition in which no such cue was provided (for reviews on directed forgetting, see MacLeod, 1998, or Bäuml, 2008). More important, analysis of oscillatory activity during List-2 encoding revealed that whereas alpha phase coupling between electrode sites was reduced in response to the forget cue and was related to List-1 forgetting, alpha power increased and was related to List-2 enhancement.

Phase coupling between electrode sites is regarded a measure of the synchrony between distant neural assemblies (Lachaux et al., 1999). Following the view that alpha oscillations can serve as an active inhibitory filter for the brain (Hanslmayr et al., 2007; Klimesch et al., 2007; Thut et al., 2006), the phase coupling finding thus was interpreted as evidence that, in the presence of the forget cue, subjects actively inhibit retrieval routes to List-1 items, inducing less coherent activities in the relevant brain structures. Finding no such inhibitory signature in the present context paradigm supports the suggested view that context-dependent forgetting reflects a contextual encoding/retrieval mismatch and is noninhibitory in nature (e.g., Mensink and Raaijmakers, 1988). At the same time, the finding challenges the view that directed forgetting is mediated by internal context changes (Sahakyan and Kelley, 2002).

A comparison of power results of the present context-change experiment and the directed-forgetting study shows a more complex picture. In the present context-change experiment, analysis of tonic alpha power (not locked to stimulus presentation) during List-2 encoding, including the total length of 4000ms of single trials, revealed an increase of alpha power in the context-change condition compared to the no-change condition ($p_{\text{corr}} < .01$), thus mimicking the power results in the directed-forgetting study (Bäuml et al., 2008). In contrast to the present experiment, reexamination of the power data from the directed-forgetting study, however, revealed no stimulus-induced power changes during List-2 encoding after the forget cue was provided, in neither the theta nor the alpha frequency band. This difference in results may be due to a real functional difference in List-2 enhancement between the context-change paradigm and the directed-forgetting paradigm, but it may also be due to the smaller statistical power that was present in the directed-forgetting study. Further research is needed to examine the similarities and dissimilarities of List-2 encoding processes between the two experimental paradigms in more detail.

Conclusions

Using a two-list paradigm, the present results extend evidence from single-list paradigms by demonstrating that, with an increase in amount of to-be-encoded material, increases in theta and alpha power arise, likely to reflect a shift from a more focused to a more divided encoding of material. More important, the present results indicate that a change in context between the study of two lists can undo this increase in low-frequency power and may even lead to a slight power decrease. The results are consistent with the view that context changes induce a reset of encoding processes, holding memory load

and attention at high levels. The findings thus point to a crucial role of encoding processes in context-dependent memory.

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