Brain Oscillations Mediate Successful Suppression of Unwanted Memories

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To avoid thinking of unwanted memories can be a successful strategy to forget. Studying brain oscillations as measures of local and inter-regional processing, we shed light on the neural dynamics underlying memory suppression. Employing the think/no-think paradigm, 24 healthy human subjects repeatedly retrieved (think condition) or avoided thinking of (no-think condition) a previously learned target memory upon being presented with a reminder stimulus. Think and no-think instructions were delivered by means of a precue that preceded the reminder by 1 s. This allowed us to segregate neural control mechanisms that were triggered by the precue from the effect of suppression on target memory networks after presentation of the reminder. Control effects were reflected in increased power in the theta (5–9 Hz) frequency band in the medial and dorsolateral prefrontal cortex and higher long-range alpha (10–14 Hz) phase synchronization. Successful suppression of target memories was reflected in a decrease of theta oscillatory power in the medial temporal lobes and reduced long-range theta phase synchronization emerged after presentation of the reminder. Our results suggest that intentional memory suppression correlates with increased neural communication in cognitive control networks that act in down-regulating local and inter-regional processing related to memory retrieval.

Keywords: brain oscillations, forgetting, inhibitory control, memory suppression, think/no-think

Introduction

To intentionally avoid and suppress particular mental representations is a powerful capability of the human mind. There is accumulating evidence that this ability extends to the episodic memory domain (Anderson and Huddleston 2012). The intentional suppression of unwanted memories may be a successful strategy to forget what we prefer not to think about (Anderson and Green 2001; but see, e.g., Bulevich et al. 2006).

In the laboratory, the neurocognitive processes mediating forgetting by voluntary suppression can be investigated by means of the so-called think/no-think (T/NT) paradigm (Anderson and Green 2001). In the T/NT paradigm, participants are repeatedly cued to either suppress (NT condition) or retrieve (T condition) memories when being presented with a reminder stimulus. On a behavioral level, such memory suppression leads to forgetting of NT items when compared with never-cued baseline items (Anderson and Green 2001; Hanslmayr, Leipold, et al. 2010; Waldhauser, Lindgren, et al. 2012). fMRI studies suggest that voluntary memory suppression is the result of a dynamic interaction between two systems: (1) A prefrontal control system that down-regulates (2) a distributed hippocampal/posterior cortical system, which presumably stores memory traces and their sensory representations (Anderson and Hanslmayr 2014; Anderson et al. 2004;

Depue et al. 2007; Benoit and Anderson 2012). Owing to their crucial role in orchestrating neural activity in distributed cell assemblies (Fries 2005), brain oscillations are strongly implicated during this interaction. To date, however, little is known about how brain oscillations mediate voluntary memory suppression.

In the present study, we re-analyzed EEG data from a previously published event-related potential study (Hanslmayr et al. 2009), where we utilized a modified T/NT paradigm. Therein, participants first studied face–word pairs until a high learning criterion. In a subsequent T/NT Phase, participants received an anticipatory T/NT Cue, which preceded the reminder (face) stimulus by 1 s (Fig. 1*A*). This spaced delivery of the T/NT Cue and the Reminder allowed us to separate the 2 aspects of memory suppression: The initiation of executive control in response to the T/NT Cue and the actual down-regulation of storage-related brain systems in response to the reminder. Employing time–frequency analysis in terms of oscillatory power and phase synchronization as measured by EEG, we shed light on the dynamic oscillatory interaction of brain networks underlying voluntary memory suppression.

Like other forms of inhibitory control, memory suppression presupposes the recruitment of control mechanisms that act in the suppression of target networks (e.g., Aron 2007; Mecklinger et al. 2009). In the EEG, these control mechanisms are evident in increased frontal theta oscillatory activity, which has been localized to medial and lateral prefrontal cortex regions during response conflict (Hanslmayr et al. 2008), memory interference (Staudigl et al. 2010), and memory suppression (Depue et al. 2013). Crucially, top-down cognitive control in general and memory suppression in particular also rely on enhanced fronto-parietal communication (Corbetta and Shulman 2002; Paz-Alonso et al. 2013) that is reflected in increased phase synchronization in the alpha frequency band (Sauseng et al. 2005; Sadaghiani et al. 2012). Taken together, these findings suggest that memory suppression should in part be mediated by increased prefrontal theta (5–9 Hz) oscillatory power and higher phase coupling in the alpha (10–14 Hz) band.

Successful memory retrieval is usually reflected in increased oscillatory power in the theta band (Düzel et al. 2003; Osipova et al. 2006; Nyhus and Curran 2010). Previous studies demonstrated that memory-related theta power effects in the medial temporal lobe are volume conducted to the scalp and can be picked up by surface sensors, particularly at posterior sites (Guderian et al. 2009; Staudigl and Hanslmayr 2013). Retrieval and memory maintenance is also characterized by increased phase synchronization in the theta band, which appears to be generated by hippocampo-cortical feedback loops (Guderian and Düzel 2005; Osipova et al. 2006; Cashdollar et al. 2009). Based on data showing that memory suppression decreases retrieval-related hippocampal activity (e.g., Anderson et al.
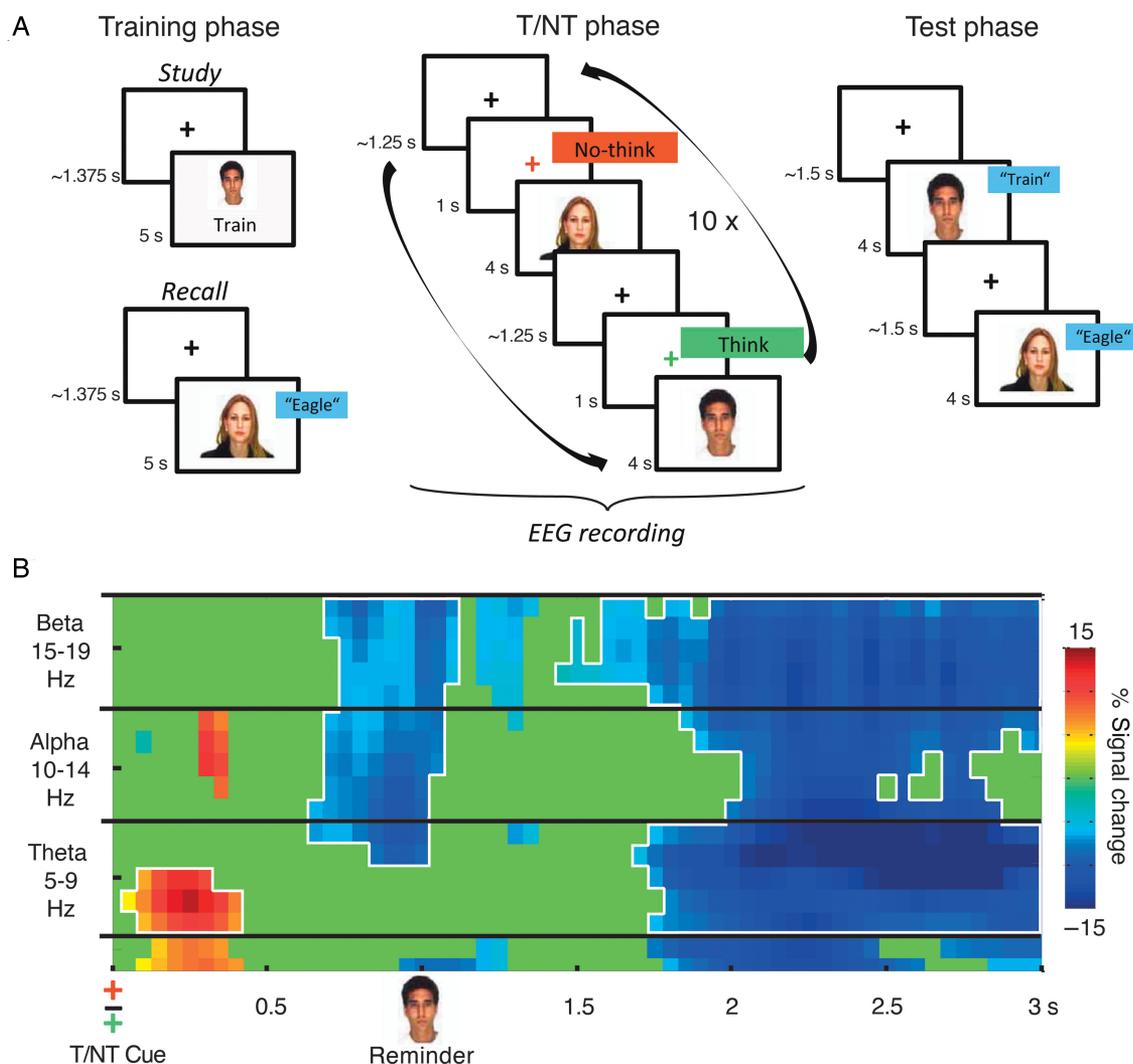
Figure 1. (*A*) Experimental procedure, trial sequence, and stimulus timing for T and NT items, baseline items not shown. (*B*) Power difference between NT and T conditions (NT–T), averaged across all electrode sites. Power values are masked with the results of a continuous Wilcoxon signed-rank test over 10 ms and 1 Hz time–frequency bins. Only differences with $P < 0.05$ (one-tailed) are shown. Significant clusters surviving permutation-based correction are framed in white. Black lines indicate upper and lower borders of the frequency bands of interest.

2004), we expected the NT condition to be characterized by reduced theta power in posterior and medio-temporal lobe regions and attenuated theta long-range phase synchronization. However, in addition to the expected decrease of theta oscillatory activity, memory suppression might also reflect decreased phase synchronization in the alpha frequency band. This would correspond to findings from encoding tasks, showing that decreased alpha phase synchronization correlates with lower memory performance (Bäuml et al. 2008; Hansl-mayr et al. 2012). Thus, we expected an additional decrease of alpha synchronization as a marker of reduced retrieval, which is to be separated from increased synchronization in the same frequency range reflecting fronto-parietal inhibitory control.

Two recent studies explored brain oscillatory correlates of voluntary memory suppression in the T/NT paradigm (Depue et al. 2013; Ketz et al. 2014). The study by Depue et al. (2013) reports an increase of theta and alpha oscillatory power in the NT condition when compared with the T condition. In contrast, Ketz et al. (2014) attributed that theta power increases solely to the T condition, whereas memory suppression in the NT condition was characterized by a power increase in the

alpha frequency range. These partly contradictory results could be due to the fact that both studies were unable to clearly separate the oscillatory correlates of increased prefrontal cognitive control from those related to the down-regulation of the hippocampo-cortical memory storage system. Also, phase synchronization was not explored in both studies. Our modified T/NT procedure allowed us to close these gaps by temporally segregating cognitive control from memory suppression effects.

Materials and Methods

Participants

Twenty-four volunteers (mean age: 21.5, range: 19–25 years; 14 females) participated in the experiment. All participants were right-handed, native German speakers, and had normal or corrected-to-normal vision. No participant reported any history of neurological disease. All subjects gave written informed consent and received course credits or monetary reward for participation.

Materials

Fifty-four faces with a neutral expression were used as reminder stimuli, and 54 semantically unrelated words served as targets.

The faces were drawn from the AR Face Database by Martinez and Benavente (1998). The word material was chosen such that each of the 54 words belonged to a different semantic category (Battig and Montague 1969; Mannhaupt 1983).

Procedure

The experimental session consisted of 2 blocks, each including a complete T/NT procedure (training phase, T/NT phase, and testing phase; Depue et al. 2006; Hanslmayr et al. 2009). Accuracy was recorded by key press of the experimenter in all phases of the experiment.

Training Phase

In each of the 2 blocks, participants first went through 2 study–test cycles (Fig. 1A, left). In each of the 2 cycles, participants studied 27 face–word pairs including 3 filler items. This was followed by a cued recall test during which the face of a face–word pair was presented as a reminder stimulus for the target word. Each study trial started with a fixation cross with variable duration (1.25–1.5 s), followed by a face–word pair; participants were instructed to memorize the face–word pairs. Each test trial consisted of a fixation cross with variable duration (1.25–1.5 ms), followed by a face; participants were instructed to overtly recall the associated target word when being presented with the face. Mean recall performance at the end of the second study–test cycle was 80.75% (SD = 11.25) averaged across blocks; no participant recalled <50% of the target items.

Think/No-Think Phase

In each block, 8 faces of the 27 face–word pairs were repeated 10 times during the T/NT phase and served as NT items, and another 8 face–word pairs were repeated 10 times and served as T items. Eight face–word pairs did not occur during the T/NT phase and served as a behavioral baseline. The material was counterbalanced across the 3 item types and the 2 blocks. To familiarize participants with the NT instruction before the T/NT phase, participants performed 15 NT practice trials during which each of the 3 filler items was repeated 5 times. For the NT trials, participants received a direct suppression instruction, to avoid thinking about the previously learned item by pushing the target item out of consciousness. The subjects were told to keep fixation on the reminder stimulus, and they were discouraged from generating other associations to the reminder. Each trial in the T/NT phase started with a fixation cross, which turned either red or green after a variable delay (1–1.5 s) to precue participants on whether to prepare for thinking of a previously studied item (T: green) or prepare for not letting a previously studied item enter consciousness (NT: red; Fig. 1A, middle). The T/NT cue was followed by a face, which served as the reminder stimulus. The sequence of items was pseudorandomized, with the restriction that the same condition (T vs. NT) did not occur >3 times in a row.

Test Phase

During the test phase, all previously studied targets from the T, NT, and baseline conditions were tested by means of a cued recall task (Fig. 1A, right). A trial in the testing phase consisted of a fixation cross with variable duration (1.25–1.750 s), followed by the face of a previously studied cue–target pair presented as a memory cue. Participants were instructed to recall and verbally report the word that was initially associated with the face during presentation of the memory cue.

EEG Recording

The EEG was recorded with a Brainamp MR+ amplifier (Megis, BrainVision) from 63 Ag–AgCl electrodes positioned according to the extended 10–10 system. EEG was referenced to FCz during recording and digitally re-referenced against the average of all electrodes. Vertical and horizontal eye movements were recorded by 2 additional channels to control for eye movements and blinks. Impedances were kept <10 kΩ, and the sampling rate was set to 500 Hz. Signals between 0.1 and 250 Hz were recorded, and a notch filter was set at 50 Hz. Before analysis, the EEG data were corrected for electro-oculogram (EOG) artifacts using calibration data to generate individual artifact coefficients and the principal component analysis (PCA) method (for details,

see Ille et al. 2002). All epochs containing remaining artifacts as identified by careful visual inspection were excluded from further analyses.

EEG Analysis

In contrast to our previous study, that is ERP study, on the same data set (Hanslmayr et al. 2009), we focused our analysis entirely on the contrast between T and NT conditions and high versus low forgetters collapsed across both halves of the TNT phase. This was done to be able to directly link our analyses to fMRI studies that typically employ a similar approach (e.g., Anderson et al. 2004). However, we cross-checked our analyses with our previous approach (Hanslmayr et al. 2009) that focused on the second half of the TNT phase as the part of the experiment that most strongly results in successful memory suppression. Second-half data (not reported) yielded largely similar results as the present analysis using data collapsed across both halves.

Continuous EEG was epoched from −0.5 to 3 s around onset of the precue. EEG analysis was carried out in MATLAB (version R2010a; The MathWorks, Inc., Natick, MA, USA) using the FieldTrip toolbox (Oostenveld et al. 2011) and self-written codes. We applied 21 Morlet wavelets, each with a width of 5 cycles of its center frequency period to derive a time–frequency representation from the EEG signal from 1 to 20 Hz. To avoid filter artifacts at the edges of the epochs, the data were filtered in a larger time interval, but analyses were restricted to the 3.5-s epochs. The resulting time–frequency data were down-sampled to 10 ms time-bins to facilitate data handling.

Sensor-Level Analysis

To quantify event-related power modulations, poststimulus power change was calculated in relation to a baseline period (−0.5 to 0 s precue; Pfurtscheller and Aranibar 1977). Phase synchrony between electrode sites was quantified as phase-locking values (PLVs; Lachaux et al. 1999), using the phase estimates from the wavelet transformation. In order to minimize effects of volume conduction, current source density transformation was applied to the EEG data before PLV calculation using the CSD toolbox (http://psychophysiology.cpmc.columbia.edu/Software/CSDtoolbox/index.html; Kayser and Tenke 2006). PLVs were calculated for all possible pairs of electrodes in a frequency range from 1 to 20 Hz. PLVs range from 0 to 1, indicating maximal phase variability and maximal phase synchrony, respectively. The measure is independent of amplitude. The same amount of trials as for the condition containing the lower number of trials was randomly selected for the condition containing the higher number of trials, and phase estimates were averaged across 50 randomizations. This was done before calculating PLVs since trial numbers can bias phase synchronization measures.

Source Localization

We identified source activity for the obtained EEG power effects in the theta frequency band in order to gain a deeper understanding of their functional significance. We compared source activity between think and no-think conditions (NT–T) after correcting for baseline source activity for each condition. In order to warrant stable estimation of sources and still allow for baseline correction with time–frequency data uncontaminated by filter artifacts, time windows of 1 s length were chosen. Thus, power at the center frequency of 7 Hz was localized in time intervals of 0–1 and 1.5–2.5 s. The 2 time windows were chosen so that they should capture neural activity related to the differences of theta power between conditions in the interval following the TNT cue and the reminder. We expected generators of the early theta power increase in the NT condition to be localized in the medial and dorsolateral prefrontal cortex (PFC), corresponding to activity identified in fMRI studies on memory suppression (Anderson et al. 2004; Benoit and Anderson 2012). For the decreases of theta power, we expected generators in the medial temporal lobe (MTL) (Anderson et al. 2004; Benoit and Anderson 2012). It should be noted, however, that source localization of deep-brain generators such as the hippocampus or MTL can be problematic (Quraan et al. 2011). Thus, we were prepared to rather find reductions in cortical areas involved in memory retrieval and sensory processing such as the inferior parietal and visual cortices, potentially communicating with the hippocampal formation (Depue et al. 2007; Cabeza 2008). In addition, we also explored

cortical sources of power differences between NT and T conditions in the alpha and beta frequency band. Our hypotheses concerning these frequency bands were less clear-cut than for the theta band. As indicated by studies on motor inhibition (e.g., Swann et al. 2009), we expected an interplay of alpha/beta power decreases in frontal areas as a marker of higher prefrontal cortical activity (Hanslmayr et al. 2011; Scheeringa et al. 2011) and increases in downstream areas such as the MTL reflecting inhibition of retrieval-related processing areas (Waldhauser, Johansson, et al. 2012).

We employed the Dynamic Imaging of Coherent Sources (DICS) beamforming approach to identify sources of oscillatory activity after calculating the cross-spectral density matrix (Gross et al. 2001). Because trial numbers can bias source localization, values of the condition containing the higher number of trials were averaged across 50 randomizations, selecting the same amount of trials as for the condition containing the lower number of trials. DICS constructs adaptive spatial filters to localize power for each grid point in the entire brain (Gross et al. 2001). For each individual and each time period of interest, filters were calculated using the baseline periods (−1 to 0 s) and activity of 1 s length following the precue or the reminder, including the trials from both conditions. The resulting average source estimate for each condition in the time intervals of interest was corrected for source activity in the baseline interval and subsequently statistically compared with the other condition. Statistical results of the comparison between conditions were interpolated to the standard Montreal Neurological Institute (MNI) brain.

Statistical Methods

The analysis of the behavioral and EEG data was based only on those face–word pairs for which participants could recall the target item correctly in the second study–test cycle of the training phase (Anderson et al. 2004; Waldhauser, Lindgren, et al. 2012). For statistical comparisons of all behavioral data, one-tailed t-tests with the α-level set to 0.05 were used.

Our EEG analysis focused on 3 frequency bands spanning a range of 5 Hz around a center frequency: theta (5–9 Hz) centered around 7 Hz, alpha (10–14 Hz) with a center of 12 Hz, and lower beta (15–19 Hz) around 17 Hz. This selection was based on statistically guided inspection of EEG power. This initial screening was done to identify potential time windows of interest. In order to prevent that selection of time windows is biased by false-positive results, we conducted a cluster-based permutation test. In a first step, we identified clusters of adjacent time–frequency bins with a significant ($P < 0.05$) difference between T and NT conditions by means of running Wilcoxon signed-rank tests, averaged across all electrode sites (Fig. 1B). Secondly, we randomly swapped the values for T and NT conditions across subjects in 1000 randomizations. In analogy to the original data, clusters of adjacent significant time–frequency bins were identified. Thirdly, the cluster sizes (i.e., number of adjacent significant time–frequency bins) of the original data were tested against the cluster-size distribution from the 1000 randomizations, such that only clusters bigger than random clusters at a predefined alpha-level were considered significant (see Maris and Oostenveld 2007, for a similar approach). Alpha levels were adapted with a step-wise Bonferroni correction, dividing an alpha level of 0.05 by the number of comparisons. Thus, the first cluster of the real data was considered significant when it was bigger than 95% (uncorrected) of the randomized clusters, the second cluster was considered significant when it was bigger than 97.5% of the second largest clusters ($P < 0.05/2$), given that a first cluster was identified in the randomization procedure, and so forth. Based on these results, both power and PLV were analyzed in 3 time windows with a minimum length of 0.5 s (0–0.5, 0.5–1, and 1.5–3 s after onset of the T/NT-precue). This allowed us to identify the topographical distribution of the significant differences between conditions in the time windows defined on the basis of the cluster-based running Wilcoxon test. The topographical EEG power differences between conditions in each time window and frequency band were analyzed by means of nonparametrical Wilcoxon signed-rank tests (one-sided) using all 63 electrode sites. For PLVs, Wilcoxon signed-rank tests (one-sided) were calculated for each electrode pair. PLVs between 2 electrode sites were considered significant when PLVs differed with $P < 0.005$ between conditions. A randomization approach was used to correct for multiple comparisons across electrode sites (Blair and Karniski 1993; Hanslmayr et al. 2009). Here, it is tested how often the result of the first step can be obtained when randomly shuffling values between conditions in 1000 iterations. The resulting probability is denoted as P_{corr}.

Source statistics of power were calculated using dependent t-tests for the comparison between conditions ($P < 0.05$, one-tailed) in time windows of 1 s (0–1, 1.5–2.5 s; see above). Analyses were corrected for multiple comparisons using a cluster-based permutation approach (Maris and Oostenveld 2007).

In order to reveal a possible relationship between brain activity and subsequent forgetting, we divided our participants into high and low forgetters by a median split based on NT–baseline forgetting scores within the 6 counterbalancing groups. We employed independent t-tests for comparing NT–T differences in EEG power between high and low forgetters at the source level ($P < 0.05$, one-tailed). Analyses were corrected for multiple comparisons using a cluster-based permutation approach (Maris and Oostenveld 2007). We also contrasted PLV at the selected center frequencies between the 2 subgroups. Differences between subgroups at the scalp level were always tested by means of nonparametric Mann–Whitney U-tests that were controlled for multiple comparisons through randomization (Blair and Karniski 1993; Hanslmayr et al. 2009). Between group analyses were restricted to time windows and frequency bands that yielded significant effects in the overall analysis. Following the same approach, based on the overall results, we also investigated the relationship between phase synchronization and power. Median splits on power and PLV values were performed on the mean difference values between T and NT conditions for each subject, taking into account only those electrodes/electrode pairs that were significant in the overall analysis comparing T and NT conditions in the whole sample.

Results

Behavioral Results

As reported in our previous study (Hanslmayr et al. 2009), recall in the NT condition (84.4%, SD = 19.4) was significantly reduced when compared with baseline (93.4%, SD = 14.4; $t_{(23)} = 3.08$; $P < 0.005$). Recall in the T condition (93.8%, SD = 9.5) did not differ significantly from baseline ($t_{(23)} = 0.10$; $P > 0.5$).

EEG Oscillations

In order to identify time windows and frequency bands of interest, we inspected EEG power differences between NT and T conditions by means of continuous Wilcoxon signed-rank tests, averaged across all electrode sites (Fig. 1B). Seven clusters emerged in the time–frequency space of which 3 survived the permutation statistic. The biggest cluster started at 1.45 s and lasted until the end of the epoch, comprising significant effects in all frequency bands from 5 to 19 Hz ($P < 0.05$). The second cluster ranged from 0.7 to 1.15 s and 8 to 19 Hz ($P < 0.025$). The third cluster ranged from 0.05 to 0.45 s and from 5 to 8 Hz ($P < 0.017$). Based on these findings, 3 time windows of interest were selected to further investigate the topographical distribution of effects, 0–0.5, 0.5–1.0, and 1.5–3.0 s after the T/NT Cue. We focused on the same frequency bands and time windows as in the EEG power analyses to reveal patterns of inter-regional communication by comparing indices of electrode phase coupling (PLV) between T and NT conditions.

T/NT Cue-Related Effects

Power

With onset of the T/NT Cue, we observed an early (0–0.5 s) increase in theta (5–9 Hz) power for the NT condition. This early

increase in theta power was evident over frontal and parietal electrode sites, and was driven by a significant increase of theta power in the NT condition when compared with the T condition as revealed in a nonparametric Wilcoxon test ($P_{corr} <$ 0.05; Fig. 2A, left). No significant effects in alpha and beta power were observed in this time window ($P_{corr} > 0.10$). In the subsequent time window (0.5–1.0 s), the theta power effect was reversed, with the NT condition now showing decreased power relative to the T condition ($P_{corr} < 0.05$; Fig. 2A, right). Baseline-corrected source activity at 7 Hz was contrasted between T and NT conditions for the whole time interval following the T/NT Cue (0–1.0 s). This analysis revealed that the theta power increase in the NT condition was driven by sources in the left dorsolateral prefrontal cortex, corresponding to BA 9/46 (Fig. 2B), and also comprising portions of the anterior cingulate cortex (BA 32).

Central to our hypothesis, we explored whether the reported theta power effects on the source level were functionally relevant for forgetting. To this end, we tested whether EEG power differences between conditions (NT–T) differed between high and low forgetters. A stronger prefrontal theta power increase (NT > T) was expected for high forgetters compared with low forgetters in the T/NT Cue interval, indicating efficient cognitive control. High forgetters showed a stronger theta power increase (NT > T) compared with low forgetters in the PFC, comprising the left and right middle frontal gyrus (~BA 8/9/46, Fig. 2C). In the same time window, high forgetters also showed theta power

decreases in the left inferior temporal gyrus (~BA 20/37), left fusiform gyrus (~BA 37), left parahippocampal gyrus (~BA 36), the left inferior parietal lobe (BA 40), and the primary visual cortex (~BA 17/18, Fig. 2C).

Significant power effects during the T/NT Cue interval also emerged in the other 2 frequency bands. In the alpha and beta band, significantly less power in the NT compared with the T condition was observed in the time window of 0.5–1.0 s after the T/NT Cue (both $P_{corr} < 0.05$). The alpha effect had a largely left hemispheric distribution, whereas the beta difference displayed a more parietal effect on the scalp (Fig. 2D,E).

Source localization of these effects most prominently revealed large decreases of alpha and beta oscillatory power in the prefrontal cortex and additional foci in the MTL (alpha) and the visual cortex (beta; Supplementary Fig. 1A and Supplementary Material, Results). Comparing high and low forgetters revealed differences in power in the dorsal parietal cortex, anterior cingulate cortex, and left MTL (Supplementary Fig. 1B and Supplementary Material, Results).

Phase Synchronization
With onset of the T/NT Cue, a significant increase in phase synchronization emerged in the alpha frequency band for the NT condition compared with the T condition ($P_{corr} < 0.01$, Fig. 3A, middle). Increased phase synchronization was observed between frontal and parietal/occipital electrodes, and also at parietal and occipital electrode pairs. Such an increase in
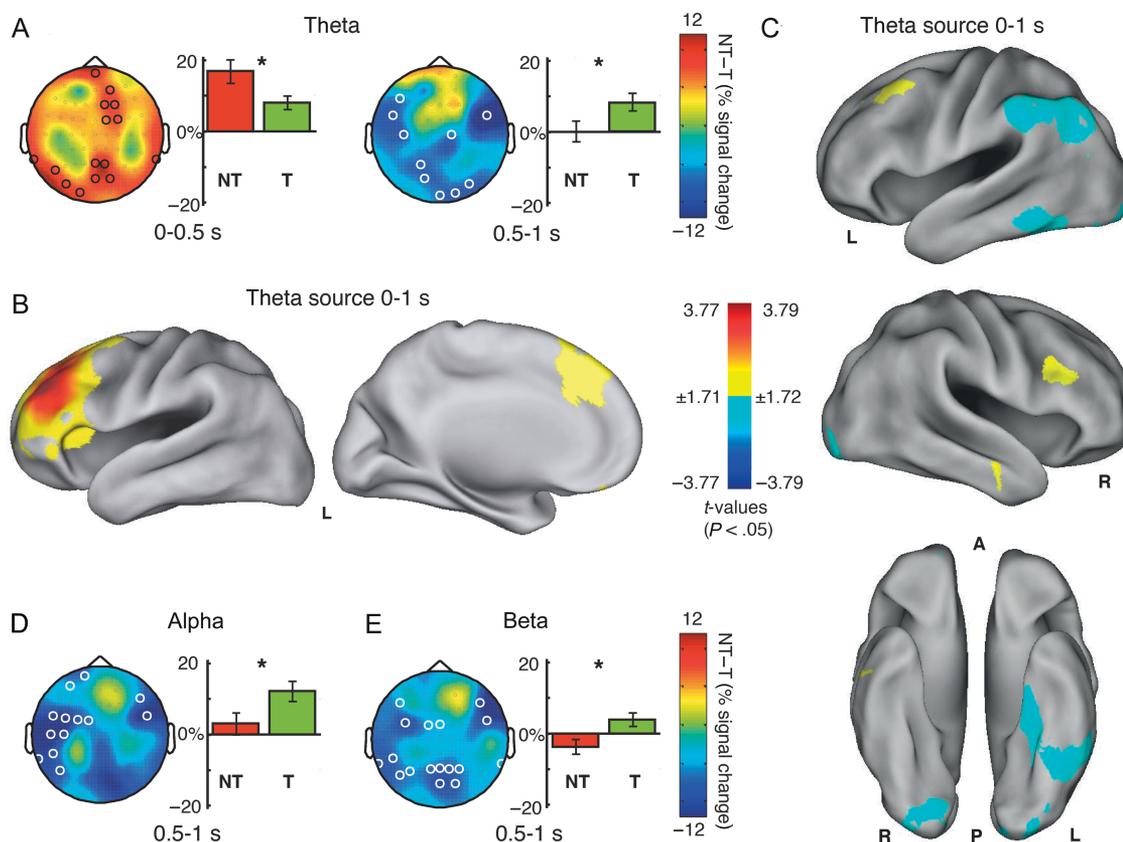
Figure 2. Significant ($P_{corr} < 0.05$) EEG power differences between NT and T conditions in the theta (A), alpha (D), and beta (E) frequency bands for the 0–0.5 and 0.5–1 s time windows following the T/NT-Cue. Headplots depict topographical distribution of NT–T power differences, and bar graphs depict power values within conditions at the significant electrode sites. Black (white) circles indicate electrodes for which NT > T (NT < T) power in the respective time–frequency windows. Significant overall effects are marked by asterisks. Significant ($P < 0.5$) NT–T theta (7 Hz) power differences at the source level (B) between conditions (NT–T) and (C) high and low forgetters (NT–T) for the 0–1 s time window.
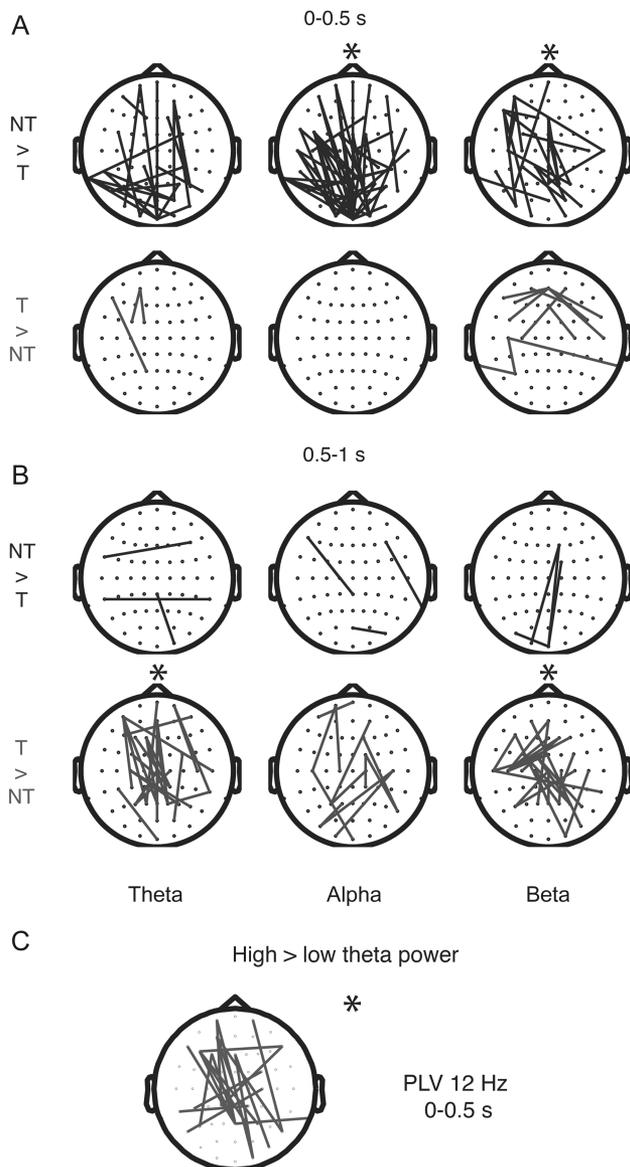
Figure 3. PLV differences between NT and T conditions in the 0–0.5 s (*A*) and 0.5–1 s (*B*) time windows. Lines display electrode pairs for which significant (*P* < 0.005) differences in PLVs were obtained between conditions (NT > T = upper rows, T > NT = lower rows). (*C*) T/NT-Cue-related (0–0.5 s) alpha (12 Hz) PLV difference (NT–T) between subjects showing high and low theta power differences in the same time window. Significant overall effects (P_{corr} < 0.05) are marked by asterisks.

phase synchronization for NT trials was also observable in the beta frequency band (P_{corr} < 0.05, Fig. 3*A*, right), but did not reach significance in the theta frequency band (P_{corr} > 0.05, Fig. 3*A*, left). In the following time window, from 0.5 to 1.0 s, the difference between T and NT conditions reversed (Fig. 3*B*, lower row). Here, we observed a decrease in phase synchronization for the NT condition in the theta frequency band (P_{corr} < 0.05), mostly between frontal and parietal electrodes, and in the beta frequency band (P_{corr} < 0.05), between frontal and central and between central and parietal electrodes.

High and low forgetters were also contrasted based on their NT–T differences in phase synchronization. In the T/NT Cue interval (0–0.5 s), no significant differences in phase synchronization in any of the 3 frequencies were observed. In addition, we tested whether alpha phase coupling and theta power increases in the T/NT Cue interval were also related. This was

done by splitting the sample based on median theta power difference (NT–T, 0–0.5 s) and contrasting alpha PLV differences (NT–T, 0–0.5 s) between the 2 groups. The results show that subjects with high theta power differences also showed higher differences in the alpha PLV compared with those with low theta power differences (P_{corr} < 0.05; Fig. 3*C*), mostly between frontal and parietal electrodes.

Reminder-Related Effects

Power

A pronounced decrease in theta power (no-think < think) was evident, starting around 0.5 s after presentation of the reminder (1.5–3.0 s following the T/NT Cue; Fig. 1*B*). This theta power difference was widespread, affecting almost all electrodes (P_{corr} < 0.001, Fig. 4*A*). Source localization of this theta power decrease for the NT condition (1.5–2.5 s) revealed a distributed network of neural generators (Fig. 4*B*). In the left hemisphere, decreased theta power was evident in the fusiform gyrus, the superior temporal gyrus, and the postcentral gyrus (~BA 37/22/40/42/43). Reduced theta power in the right hemisphere was localized to the superior temporal gyrus close to the temporal pole (~BA 22/38) and to superior temporal and inferior parietal regions (~BA 40). In addition, we identified decreased theta power in the precentral gyrus (BA 4) and the right lateral PFC.

A stronger decrease in theta power (NT < T) for high forgetters in MTL and posterior sensory processing regions was expected, as this should indicate successful suppression of retrieval-related activity. Pronounced decreases in theta power (NT < T) in the left hemisphere were observed for high compared with low forgetters (Fig. 4*C*). These effects were evident in the inferior and medial temporal cortex, being most pronounced in the parahippocampal cortex (~BA 35) and the fusiform gyrus (~BA 20, Fig. 4*C*).

Power decreases were not restricted to the theta frequency range. Power in the alpha (P_{corr} = 0.009) and beta (P_{corr} > 0.001) bands displayed a similar pattern, exhibiting less power in the no-think compared with the think condition (Fig. 4*D,E*). Source localization of these effects revealed a decrease of alpha and beta oscillatory power in the prefrontal cortex and in the visual cortex for the beta frequency band (Supplementary Fig. 2*A* and Supplementary Material, Results). The comparison between high and low forgetters showed alpha and beta power increases in the dorsal parietal, prefrontal, and anterior cingulate cortices (Supplementary Fig. 2*B* and Supplementary Material, Results). In addition, we observed increased alpha and beta oscillatory power in retrieval processing regions for high forgetters such as the inferior parietal cortex, occipital cortex, and the MTL.

Phase Synchronization

In the reminder-related time window, a 2-fold phase synchronization pattern emerged. A pronounced PLV decrease for the NT condition arose in all 3 frequency bands (all P_{corr} < 0.001, Fig. 5*A*, lower row). Decreased phase synchronization was widespread, comprising reduced interhemispheric and frontoparietal long-range coupling and also reduced short-distance coupling between electrodes. At the same time, we also observed an increase in phase synchronization for the no-think condition in the alpha and beta frequency band (both P_{corr} < 0.05, Fig. 5*A*, upper row) that was most pronounced between
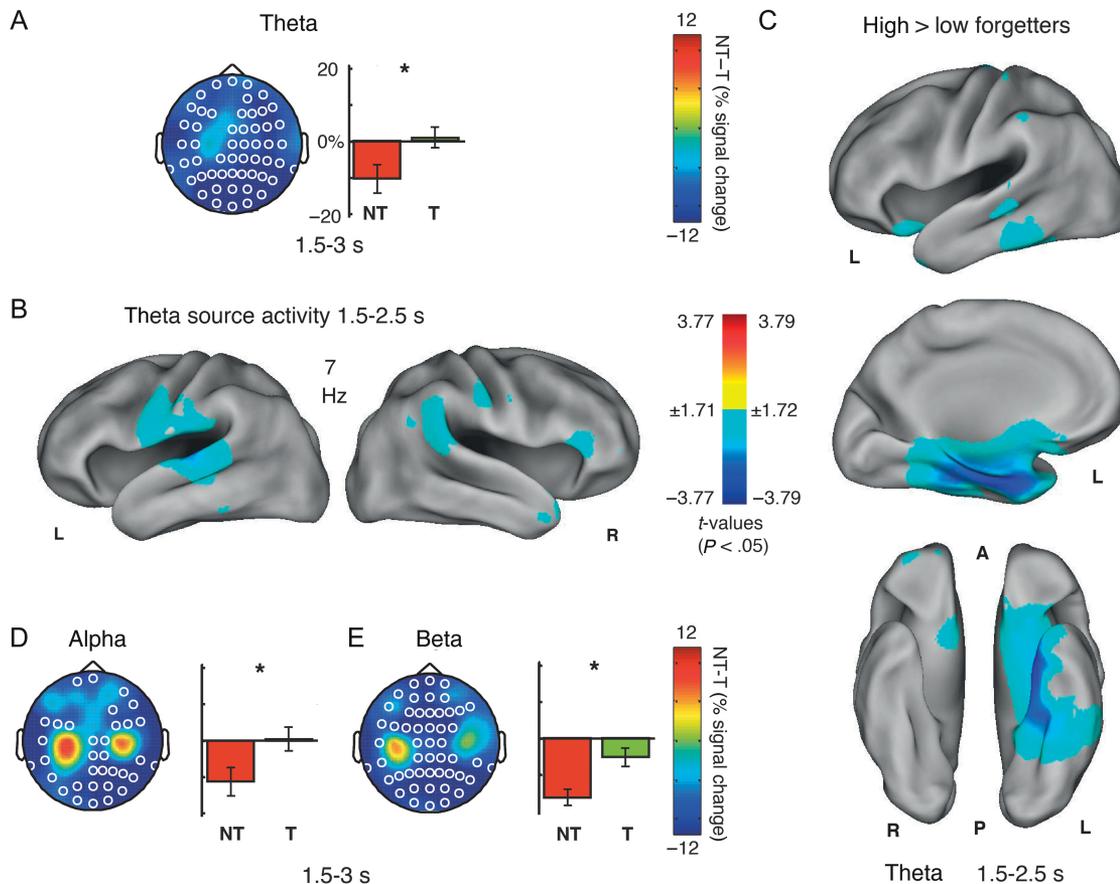
Figure 4. Significant ($P_{corr} < 0.05$) EEG power differences between NT and T conditions in the theta (*A*), alpha (*D*), and beta (*E*) frequency bands following the reminder stimulus from 1.5 to 3 s. Headplots depict topographical distribution of NT–T power differences and bar graphs depict power values within conditions at the significant electrode sites. White circles indicate electrodes for which power in the NT condition is lower than for the T condition. Significant overall effects are marked by asterisks. Significant ($P < 0.5$) NT–T theta (7 Hz) power differences at the source level (*B*) between conditions (NT–T) and (*C*) high and low forgetters (NT–T) for the 1.5–2.5 s time window.

frontal/frontocentral and centroparietal electrodes. No NT-related phase synchronization increase was observed in the theta band ($P_{corr} > 0.5$).

During the reminder interval (1.5–3 s), phase synchronization at 7 Hz was lower in the NT compared with the T condition for high forgetters relative to low forgetters ($P_{corr} < 0.01$; Fig. 5*B*). No differences at the alpha and beta center frequencies emerged in this comparison.

Due to the presumed role of alpha phase synchronization in top-down inhibitory control (Klimesch 2012), we expected alpha phase synchronization to be involved in the down-regulation of memory-related activity. Therefore, we tested whether higher alpha PLVs predict lower theta power in the reminder-related interval as a marker of reduced retrieval processing. We performed a median split based on mean alpha PLV differences (NT–T) and compared subjects with high PLV with those exhibiting low PLV differences. Confirming our hypothesis, subjects with high NT–T alpha phase coupling showed stronger theta power differences (NT–T) at 7 Hz in the same time window ($P_{corr} < 0.001$; Fig. 5*C*). This suggests that alpha phase coupling is related to a decrease of reminder-related theta power.

Discussion

The current study sheds light on the brain oscillatory dynamics underlying voluntary memory suppression in the T/NT task (Anderson and Green 2001). Using a modified version of the T/NT paradigm (Hanslmayr et al. 2009; Hanslmayr, Leipold, et al. 2010), we were able to temporally segregate the oscillatory correlates of the initiation of cognitive control processes as triggered by the T/NT cue, from the actual effects of the suppression of specific target memories. Consistent with our hypothesis, 2 main findings emerged: first, upon presentation of the T/NT cue, higher prefrontal theta power was triggered by the NT compared with the T condition. This pattern was paralleled in fronto-parietal alpha phase synchronization. Secondly, upon presentation of the reminder stimulus, a sustained and widespread decrease in theta power and phase synchronization was evident, localized to posterior sensory regions and the MTL when comparing high with low forgetting subjects. These results confirm and extend previous EEG (Depue et al. 2013; Ketz et al. 2014) and fMRI studies (Anderson et al. 2004; Depue et al. 2007; Benoit and Anderson 2012) in suggesting a dynamic interaction between a prefrontal cognitive control network and a hippocampo-cortical memory storage network (Anderson and Hanslmayr 2014). In the following, we will discuss how activity in each of these networks and in their interaction is reflected in the reported results. We will also discuss the effects in the other frequency bands that were not expected (e.g., the beta frequency band).

Control Network

We observed a pronounced increase in theta power over frontal and parietal electrode sites immediately after delivery
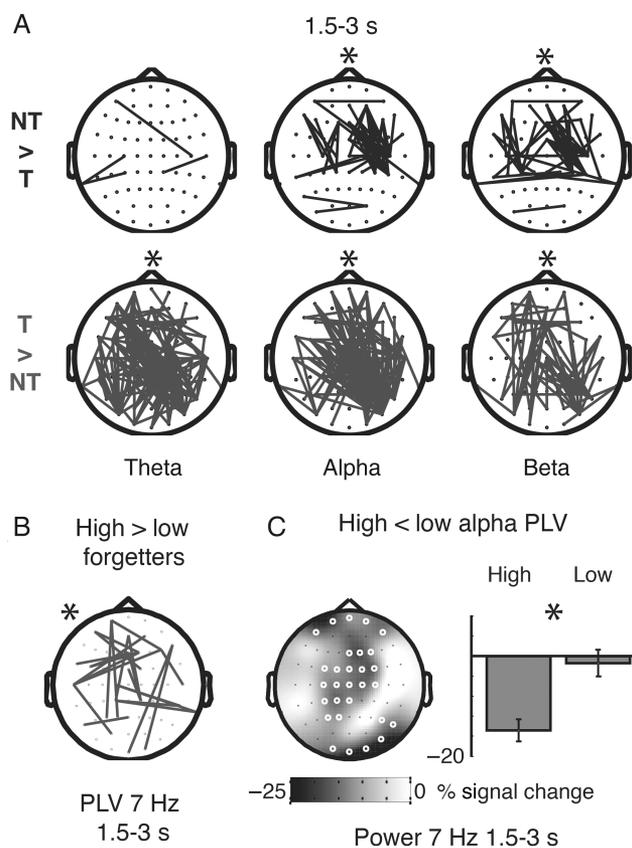
Figure 5. (*A*) PLV differences between NT and T conditions in the 1.5–3 s time window. Lines display electrode pairs for which significant (*P* < 0.005) differences in PLVs were obtained between conditions (NT > T = upper row, T > NT = lower row). (*B*) Reminder-related (1.5–3 s) theta (7 Hz) PLV differences between high and low forgetters. Significant overall effects (P_{corr} < 0.05) are marked by asterisks. (*C*) Reminder-related (1.5–3 s) theta (7 Hz) power differences between subjects showing high and low alpha PLV differences in the same time window.

of the NT cue. Increases in theta power with a similar frontal and parietal distribution on the scalp have previously been reported in T/NT studies (Depue et al. 2013; Ketz et al. 2014) and other forgetting paradigms (Hanslmayr, Staudigl, et al. 2010; Staudigl et al. 2010; Waldhauser, Johansson, et al. 2012). More generally, similar prefrontal theta power effects were observed in cognitive control tasks that require interference processing and conflict adaptation (Hanslmayr et al. 2008; Pastötter et al. 2013). In line with these studies, the reported theta power increases in response to the NT cue were localized to the medial and lateral prefrontal cortex. fMRI studies employing the T/NT paradigm report activity in similar brain regions, although these studies highlight the role of the right lateral PFC in contrast to our finding of mostly left lateralized and medial sources (Anderson et al. 2004; Depue et al. 2007; Benoit and Anderson 2012). It is possible that EEG beamforming, in contrast to fMRI, failed to identify right PFC sources in the overall analysis, since it can have problems to detect bilaterally correlated sources (Dalal et al. 2006). However, contrasting high versus low forgetters in our study revealed a clear activation in the right lateral PFC. This suggests that the left PFC, together with structures such as the anterior cingulate cortex, serves to generally initiate executive control, whereas the right PFC is the decisive brain region in the successful direct suppression of unwanted memories (Benoit and

Anderson 2012). Strikingly, the theta effect occurred before presentation of the actual reminder stimulus. Thus, theta effects appear to be independent of the reactivation of the to-be-suppressed memory representation (cf. Anderson et al. 2004; Hanslmayr, Staudigl, et al. 2010; Staudigl et al. 2010; Waldhauser, Johansson, et al. 2012). In line with our previous ERP study, our data suggest that the observed cognitive control mechanisms can be triggered voluntarily (Hanslmayr et al. 2009). This active control process appears to reflect a preparation for upcoming episodic inhibition, leading to later forgetting of the target items. Such a result is in line with studies on task-switching, showing that the execution of an upcoming task can be initiated by the presentation of a preceding indicative cue (e.g., Nicholson et al. 2005).

Increases in prefrontal theta power were paralleled by increases in long-range phase synchronization in the alpha and beta frequency band. Intriguingly, subjects who exhibited high theta power in response to the T/NT cue also showed high alpha phase synchronization in the same time window. The two effects therefore appear to be linked, and both likely reflect the action of a top-down control network, which prepares the brain to suppress the memory associated with an upcoming reminder. Enhanced alpha phase synchronization was not restricted to the T/NT cue interval, however. Alpha phase synchronization remained at a high level also during the presentation of the reminder, correlating on a between-subject level with decreased theta power in the same time window. This latter result is suggestive of a sustained top-down fronto-parietal control network (Sadaghiani et al. 2012; Paz-Alonso et al. 2013; Sauseng et al. 2013) in the service of suppressing theta synchrony in memory-related networks, which would otherwise readily reinstate the unwanted memory trace (Fuentemilla et al. 2014). Importantly, the timing of the late effect roughly coincides with ERP effects related to cognitive control that were reported in previous studies to immediately precede and sustain a reduction of recollection (Bergström et al. 2009; Mecklinger et al. 2009; Waldhauser, Lindgren, et al. 2012).

Memory Network

Suppression of specific memories was associated with a pronounced decrease in theta power, starting ∼0.5 s after presentation of the reminder. Importantly, successful memory retrieval is typically associated with increased oscillatory power in the theta frequency band (Nyhus and Curran 2010). Enhanced theta power during memory tasks was source-localized to the MTL in various MEG studies (Guderian et al. 2009; Staudigl and Hanslmayr 2013). Comparing high and low forgetters on the source level showed that high forgetting subjects were indeed characterized by a pronounced decrease of theta power in MTL regions (Fig. 4*C*). Although source localization results, especially from EEG data, should always be interpreted with caution, these results converge with previous fMRI studies (Anderson et al. 2004; Depue et al. 2007; Benoit and Anderson 2012). Voluntary suppression of memories therefore seems to induce a decrease of theta power in retrieval-related brain networks, which correlates with later forgetting. Although the contrast between NT and T conditions across all subjects did not reveal reduced theta power in the MTL, the regions observed in the overall contrast overlap with areas revealed in previous fMRI studies which also report decreased BOLD in the superior and medial temporal gyri, the parietal cortex, and

the fusiform gyrus (Anderson et al. 2004; Depue et al. 2007; Benoit and Anderson 2012).

Pronounced reductions were also evident in theta phase synchronization, suggesting that memory suppression affects a larger network of brain areas involved in the retrieval and post-retrieval processing of the target memory. This finding suggests that not only local synchronization (power) is reduced, but also communication between brain areas involved in memory processing. In line with the reduced power in the MTL, this result could reflect a reduction of synchrony within hippocampo-cortical feedback loops (Guderian and Düzel 2005; Cashdollar et al. 2009).

In addition to the suppression effects in the reminder interval, we observed a decrease in theta power and phase synchronization already preceding the onset of the reminder in the NT condition when compared with the T condition. This is in line with our previous study (Hanslmayr et al. 2009), suggesting a preparatory effect triggered by the T/NT cue. The difference between T and NT conditions appears to be driven by a relative increase in theta power for the T condition, as opposed to below-baseline power for the NT condition. Increased theta power before the onset of a reminder stimulus has been shown to reflect enhanced memory-related processing (Addante et al. 2011). Our data suggest that subjects prepare for retrieval following a think cue, while they successfully avoid retrieval preparation in the no-think condition (Hanslmayr et al. 2009). Although such an interpretation seemingly speaks against active inhibitory effects, the anticipatory avoidance of retrieval processing was related to later forgetting. High forgetters displayed reduced theta power in inferior temporal, ventral parietal, and occipital areas before onset of the face stimulus, suggesting that the early decrease in theta power is a correlate of reduced visual and bottom-up attentional processing of the reminder stimulus in the NT condition relative to the T condition for high forgetters when compared with low forgetters (Depue et al. 2007; Cabeza 2008). Such a mechanism could be the reason for why memory suppression can be boosted by giving an anticipatory cue, before the reminder appears (Hanslmayr, Leipold, et al. 2010).

Effects in Other Frequency Bands

Apart from the reported results confirming our hypotheses, additional time–frequency patterns arose. The power decrease during and before the reminder interval was not restricted to the theta frequency band, but was also observed in the alpha and beta frequency range. As evident from the source localization results, the power decrease in the alpha and beta frequency band was generated by cortical sources quite different from the theta effects. Alpha and beta power decreased in frontal, temporal, and occipital regions in the NT task when compared with the T condition. Recent studies point to an inverse relationship between alpha/beta power and BOLD response (Hanslmayr et al. 2011; Scheeringa et al. 2011). In this line, the occipital decrease in beta power could reflect the higher visual processing of the NT cue and the reminder stimulus, as a response to the instruction in the experiment to focus on the cue and stimulus instead of retrieving the target memory. The prefrontal decrease of alpha and beta power could be a correlate of higher activation in top-down control areas, including the inferior frontal gyrus, a region that is involved in inhibitory control (Aron et al. 2004; Swann et al.

2009). The anticipatory power decrease in the left temporal lobe during the T/NT cue interval could reflect preparation of MTL regions for the upcoming suppression task, or retrieval of instructions associated with the cue, or even the retrieval of substitutional memories, but this effect is difficult to be interpreted at present.

The comparison between high and low forgetters revealed increased alpha and beta power in the anterior cingulate cortex and the dorsal parietal cortex, regions involved in error monitoring and top-down control of memory retrieval (Menon et al. 2001; Cabeza et al. 2008), with the latter region known to operate in the alpha frequency band (Capotosto et al. 2009). These sources converge with fMRI studies investigating the control of memory intrusions in the T/NT paradigm (Levy and Anderson 2012). Remarkably, we also observed an increase in alpha and beta power in MTL and inferior parietal areas for high forgetters during both T/NT cue and reminder intervals. Taken together with the findings on phase synchronization, these effects suggest the active inhibition of retrieval-related brain areas via modulations of the alpha and beta frequency bands (Waldhauser, Johansson, et al. 2012).

Taken together, the findings on alpha and beta power differences between conditions and high and low forgetters point to additional processes that might mediate intentional memory suppression. This being said, it has to be noted that the observed effects were less clear and more scattered than the theta power effects. The interplay of increased and decreased alpha and beta power in the various regions and its role for suppression-induced forgetting deserves further investigation in future studies.

A similar ambiguous pattern was observed in phase synchronization measures. PLVs were not only decreased in the theta frequency range, but were also decreased in the alpha and beta range. Phase synchronization in the alpha frequency band is assumed to reflect neural timing that can enhance memory-related processing and facilitate communication between brain areas (Klimesch et al. 2008). Interestingly, alpha and beta phase de-synchronization has recently been found during intentional forgetting paradigms (Bäuml et al. 2008; Hanslmayr et al. 2012; Sauseng et al. 2013), which has been interpreted as an effective mechanism to decrease synaptic plasticity in the service of suppressing irrelevant memories (Anderson and Hanslmayr 2014). In line with theoretical notions suggesting that alpha oscillations play a complex role in gating neural timing that can have both detrimental as well as enhancing effects on communication between cell assemblies (Klimesch et al. 2007), our data suggest a two-fold role of alpha phase synchronization in orchestrating memory suppression. Future studies will have to clarify how increases of alpha/beta synchronization as correlates of enhanced top-down control can be separated from decreased synchronization in the same frequency band as a marker of reduced memory processing.

Conclusions

Replicating and extending previous EEG studies and converging with fMRI research, our study shows that voluntary memory suppression is the result of the dynamic interaction between a cognitive control network and a hippocampo-cortical memory storage network. The suppression of unwanted memories is achieved by the rapid recruitment of cognitive

control, reflected in high prefrontal theta power. Sustained cognitive control is mediated by a network operating in the alpha/beta frequency range, arguably involved in monitoring and coordinating the avoidance of memory retrieval during the presentation of the reminder. The effect of this suppression of specific memories is evident in decreased local and wide spread theta synchrony, likely reflecting the active down-regulation of a hippocampo-cortical memory storage network.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/.

Notes

Conflict of Interest: None declared.

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