

ERPs and Neural Oscillations during Volitional Suppression of Memory Retrieval

Brendan Eliot Depue¹, Nick Ketz^{1*}, Matthew V. Mollison^{1*},
Erika Nyhus², Marie T. Banich^{1,3}, and Tim Curran¹

Abstract

■ Although investigations of memory and the dynamics of ERP components and neural oscillations as assessed through EEG have been well utilized, little research into the volitional nature of suppression over memory retrieval have used these methods. Oscillation analyses conducted on the Think/No-Think (TNT) task and volitional suppression of retrieval are of interest to broaden our knowledge of neural oscillations associated not only during successful memory retrieval but also when retrieval is unwanted or suppressed. In the current study, we measured EEG during a TNT task and performed ERP and EEG spectral power band analyses. ERP results replicated other researchers' observations of increases in 500–800 msec parietal effects for items where retrieval was instructed to be elaborated compared with being sup-

pressed. Furthermore, EEG analyses indicated increased alpha (8–12 Hz) and theta (3–8 Hz) oscillations across parietal electrodes for items that were instructed to be suppressed versus those to be elaborated. Additionally, during the second half of the experiment (after repeated attempts at control), increases in theta oscillations were found across both frontal and parietal electrodes for items that were instructed to be suppressed and that were ultimately forgotten versus those ultimately remembered. Increased alpha power for items that were instructed to be suppressed versus elaborated may indicate reductions of retrieval attempts or lack of retrieval success. Increased theta power for items that were instructed to be suppressed versus elaborated may indicate increased or prolonged cognitive control to monitor retrieval events. ■

INTRODUCTION

Memory for episodic events influences our thinking when approaching and planning new goal-related behavior. Attention to relevant memories can be seen as beneficial, whereas continued attention to irrelevant memories can be unwanted during the planning and execution of such behavior. Flexibly modulating memory retrieval can thus be seen as an important function that subserves the maintenance of relevant versus irrelevant memory. Indeed, this process becomes highly apparent when past events include painful reminders of trauma or unwanted memory episodes.

Recent research has suggested that attempts to suppress or modulate the retrieval of such memory events is under our volitional control, indicating that cognitive control can influence long-term memory retrieval (Depue, Banich, & Curran, 2006; Anderson & Green, 2001; Bjork, Bjork, & Anderson, 1998; Bjork, 1989; Geiselman, Bjork, & Fishman, 1983). Some studies have used the Think/No-Think (TNT) task, to illustrate such volitional control over memory episodes. During the TNT paradigm, individuals learn cue–target pairings (words or pictures) to a high degree

of accuracy. Subsequently, they are shown only the cues repeatedly. For some cues, they are instructed to suppress retrieval of the related target, whereas for other cues, they are instructed to elaborate retrieval of the related target. Individuals then perform a cued recall test that compares performance on suppressed and elaborated trials as well as items that were initially learned but were never elaborated or suppressed (baseline trials). In many of these studies, items that are instructed to be suppressed (No-Think [NT] trials) are recalled at a significantly lower rate than items instructed to be elaborated (Think [T] trials). Crucially, items that are instructed to be suppressed also are recalled less than baseline items that reflect normal memory function (Lambert, Good, & Kirk, 2010; Nørby, Lange, & Larsen, 2010; Paz-Alonso, Ghetti, Matlen, Anderson, & Bunge, 2010; Salame & Danion, 2007; Depue et al., 2006; Wessel, Wetzels, Jelicic, & Merckelbach, 2005; Levy & Anderson, 2002; Anderson & Green, 2001).

Several fMRI studies indicate that volitional control over memory retrieval may be mediated by lateral prefrontal cortical (LPFC) regions exerting influence over the medial-temporal lobe (MTL) declarative memory system (Butler & James, 2010; Depue, Banich, & Curran, 2007; Anderson, Ochsner, & Kuhl, 2004). Representative of this finding, increases in LPFC activity are consistently found during the suppression of NT items, as compared with the elaboration of T items. Additionally, decreases in

¹University of Colorado-Boulder, ²Brown University, ³University of Colorado-Denver

*These authors contributed equally to this work.

hippocampal or MTL activity are also found during the suppression of NT items, as compared with T items (Butler & James, 2010; Depue et al., 2007; Anderson et al., 2004). Increased LPFC activity correlates with decreased hippocampal/MTL activity both within participants (over the time course of NT trials) and across participants, as well as correlating with increases in the ability to behaviorally suppress retrieval, suggesting the possibility that LPFC–hippocampal/MTL interactions leads to successful suppression (Depue & Banich, 2012; Depue, Burgess, Willcutt, Ruzic, & Banich, 2010; Depue et al., 2007). Furthermore, the strength of correlations between activity in the LPFC and hippocampal/MTL increase as repetition increases, suggesting that as cognitive control is repetitively invoked, suppression over memory retrieval becomes more likely (Depue & Banich, 2012; Depue et al., 2007, 2010). This learning of control is also reflected in behavioral findings that show increases in suppression at 10, but not 5, repetitions during the TNT task (Hanslmayr, Leipold, Pastötter, & Bäuml, 2009; Depue et al., 2006). Recently, a study by Benoit and Anderson (2012) also indicated that different neural circuitries are involved in memory suppression dependent on whether individuals were instructed to think of something else versus instructed to not think of a substitution (direct suppression) while they engaged in suppression. The differences in these two strategies provided an interesting dissociation within left (substitution) versus right (direct suppression) LPFC and further reinforce that memory suppression involves top-down cognitive/inhibitory control that putatively interacts with the hippocampal/MTL memory system.

Similarly, ERPs measured during the TNT task have consistently indicated reductions of the parietal old/new effect for NT trials, as compared with T trials (Bergstrom, de Fockert, & Richardson-Klavehn, 2009; Mecklinger, Parra, & Waldhauser, 2009; Bergstrom, Velmans, de Fockert, & Richardson-Klavehn, 2007). The parietal old/new effect is thought to index the recollection of event details (reviewed by Rugg & Curran, 2007), which may depend on the hippocampus because amnesic patients with hippocampal damage show markedly reduced parietal ERP old/new effects (Addante, Ranganath, Olichney, & Yonelinas, 2012; Düzel, Vargha-Khadem, Heinze, & Mishkin, 2001). Therefore, these results possibly indicate a modulation of hippocampal/MTL retrieval during volitional suppression of memory. Another study (Hanslmayr et al., 2009) indicated early and late slow wave components during NT trials that were found across frontal (early) and parietal (late) electrodes. These components were highly correlated, suggesting a possible role of top-down frontal control over parietal regions during the TNT task. Similarly, Chen et al. (2012) show increases in both early P1 and N2 components for NT as compared with T trials across frontal and parietal electrodes, reflecting increases in attention/cognitive control.

Research investigating the role of neural oscillations underlying episodic memory function has indicated that

oscillations within different power bands (e.g., theta, alpha, beta, gamma) may reflect different characteristics of memory processes (Fell & Axmacher, 2011; Freunberger, Werkle-Bergner, Griesmayr, Lindenberger, & Klimesch, 2011; Klimesch, Sauseng, & Hanslmayr, 2007; Palva & Palva, 2007; Jacobs, Hwang, Curran, & Kahana, 2006; Sauseng, Klimesch, Schabus, & Doppelmayr, 2005; von Stein & Sarnthein, 2000; Klimesch, 1999). For instance, increased oscillations in the alpha spectrum are thought to underlie task disengagement, when irrelevant stimuli are to be ignored or filtered, selective attention and cortical inhibition (Freunberger et al., 2011; Klimesch et al., 2007). Increased oscillations in the theta spectrum have been found in various studies for correct recognition memory of a wide variety of stimuli (for a review, see Nyhus & Curran, 2010; Sauseng et al., 2005; von Stein & Sarnthein, 2000). Increased theta in hippocampal regions during retrieval has been suggested to modulate the amount of neural firing to amplify relevant and simultaneously suppress irrelevant information (Klimesch et al., 2007). Phase synchronization or coherence (i.e., the timing of neural oscillations between discrete brain regions) of theta oscillations has been considered an important indicator of top-down control and communication between PFC and hippocampus/MTL, perhaps guiding episodic memory retrieval (Kahana, Seelig, & Madsen, 2001; Klimesch, 1999; Klimesch et al., 1996).

Given the power of electrophysiological methods to provide insights into memory processes, we sought to examine both the ERP waveform and EEG oscillatory power band dynamics of the TNT task. Because previous studies conducting ERPs on the TNT task have shown that the parietal old/new effect is reduced for NT, as compared with T trials, but no ERP baseline was incorporated, we wished to compare baseline trials against T and NT trials. This is of interest to determine how possible reductions in parietal effects specifically for NT trials compare to a perceptual stimulus baseline (pB). The pB condition was included to hold recollection effects for the cue constant, although, because the pB condition was unpaired with any target, comparison of the recollection/retrieval of the target could be assessed across conditions.

Because of the prominent role oscillations are hypothesized to play in memory, we further wished to assess alpha and theta band oscillations occurring in the TNT task. Alpha oscillations are thought to index task disengagement, filtering out irrelevant information or cortical inhibition. Thus, we hypothesized that increased alpha oscillations would be associated with NT as compared with T trials. Theta oscillations have been found across frontal electrodes and are thought to reflect increases in cognitive control (Klimesch, 1999). Moreover, increases in theta oscillations across frontal and parietal electrodes have also been implicated in increased communication important for memory processes (Kahana et al., 2001; Klimesch, 1999; Klimesch et al., 1996). Thus, we hypothesized greater increases in theta oscillations for NT than T trials. This assumption is based on previous findings indicating that NT as compared

with T trials, consistently engage PFC more, indicated by increased BOLD response in fMRI studies, as well as showing correlations of BOLD response between PFC and hippocampus/MTL (Depue et al., 2007, 2010; Anderson et al., 2004).

METHODS

Participants

Fifty-one undergraduates from the University of Colorado at Boulder participated in the experiment for credit, as part of the requirement for undergraduate psychology courses. Fifteen individuals were eliminated for bad EEG data resulting from having fewer than 20 artifact-free trials per condition ($n = 10$; before splitting conditions by first vs. second half of TNT phase), excessively noisy EEG ($n = 4$), and excessive blinking ($n = 1$). Another seven individuals eliminated for ceiling effects or insufficient baseline performance ($\leq 25\%$) in the behavioral task, resulting in 29 individuals on which final analyses were conducted (mean age = 19.64, range = 18–24; 15 women).

Behavioral Paradigm

The TNT paradigm was utilized using face–picture pairs. Forty-four faces (female) previously normed as having a neutral expression were used. Forty images were selected from the International Affective Picture Series (IAPS), negative in emotional content (Lang, Bradley, & Cuthbert, 1995). We chose to use negative valenced images as they have been shown to elicit greater cognitive control than neutral stimuli in our past research (Depue et al., 2006). An fMRI study further supports this idea and indicates that negative, as compared with neutral, material recruits control mechanisms to a greater degree (Butler & James, 2010). Furthermore, our use of negative-valenced images has provided a neural framework for investigating memory suppression in several studies and highlights the ecological validity of using negative valenced material, as it may relate to clinical disorders of recurrent traumatic memories (Depue et al., 2007, 2010). Pictures were selected at a median level of negative affect on a scale of 1–9 (mean = 4.1, $SD = .55$). Because the IAPS has no relatedness scores, two independent raters selected pictures to have as minimal relatedness in content as possible to eliminate possible grouping effects. All stimuli were pseudorandomly assigned to condition, such that the faces equally appeared in each condition by counterbalancing. The 44 faces were assigned to either: (1) T, (2) NT, (3) recall baseline (rB), and (4) perceptual baseline (pB). The first three conditions (T/NT/rB) were pseudorandomly paired with IAPS pictures ($n = 40$), whereas the remaining four faces (pB) were presented with no IAPS pictures and served as a pure perceptual baseline. The experiment was designed with E-Prime software (Psychology Tools, Inc., Pittsburgh, PA), which was used to

display the stimuli and record performance on a Dell computer.

The experimental procedure was divided into three phases: training, experimental, and testing. During the training phase, participants learned 40 face–picture pairs. Participants first viewed each pair (4 sec) and, after 20 pairs, were shown a face (4 sec) and asked to select which of two pictures was originally paired with the face. Both of the two pictures came from the training phase so that novelty of one choice could not be used as a potential alternative cue for recognition. The four unpaired perceptual baseline faces (pB) were also randomly intermixed in the training (2 per set) to control for repetition effects, participants were instructed to simply view these faces. This procedure continued in sets of 20 until the participant could recognize the correct picture previously paired with a face with 97.5% accuracy (39 items) over all 40 pairs (average training sets = 2 ± 1).

In the experimental phase, participants saw the face for only 32 of the 40 pairs, half of these being relegated to the T condition and half to the NT condition. The eight remaining pairs served as the rB and thus were not shown again until testing. The four unpaired pB faces were also presented during the experimental phase. In all conditions, a trial consisted of presentation of a face for 3.5 sec, followed by a 500-msec intertrial interval. The color of a border around the faces indicated the condition: green for the T condition, red for NT condition, and yellow for pB condition. Identical to our recent work with the TNT (Depue et al., 2006, 2007, 2010), in the T condition participants were told “Think of the picture previously associated with the face,” whereas in the NT condition, they were told “Do not let the previously associated picture come into consciousness.” During the pB condition, participants were instructed to “Passively view the face.” Within each condition (T/NT/pB), participants viewed faces 12 times. Because we were interested in general suppression effects and the efficacy of such, we did not provide any strategy to participants other than those above.

During the test phase, participants were shown each of the 40 faces (4 sec) from the training phase (16 T, 16 NT, 8 rB) and were told to write down a brief description of the picture originally associated with it. These data provided the accuracy measures. The eight faces not shown in the experimental phase served as the rB condition, used to assess an individual’s baseline memory ability for face–picture pairs when no cognitive control over retrieval is required, and with which the T and NT conditions could be compared.

Electrophysiological Recording

A 128-channel HydroCel Geodesic Sensor Net (Tucker, 1993) was used to measure the EEG at the scalp using a central vertex reference (Cz) with a sampling rate of 250 Hz and a bandpass hardware filter from 0.1 to 100 Hz. The net was connected to an AC-coupled, high-input

impedance amplifier (200 M Ω , Net Amps, Electrical Geodesics, Inc., Eugene, OR). The electrodes were adjusted until impedance measurements were less than 50 k Ω .

Electrophysiological Data Processing

A 60-Hz digital notch filter was applied to the continuous EEG recordings to remove electrical line noise before epoching the EEG from 1000 msec before to 1700 msec after each stimulus of the TNT phase. Trials were discarded from analysis if more than 20% of the channels were bad (average amplitude over 100 μ V or voltage fluctuations of greater than 50 μ V between adjacent samples). Individual bad channels were replaced on a trial-by-trial basis with a spherical spline algorithm (Srinivasan, Nunez, Tucker, Silberstein, & Cadusch, 1996). Eye blinks were corrected using an ICA-based approach implemented in the ERP PCA Toolkit (Dien, 2010). EEG was baseline-corrected with respect to the 1 sec prestimulus interval of each trial average referenced (Dien, 1998), corrected for the polar average reference effect (Junghöfer, Elbert, Tucker, & Braun, 1999). ERP and EEG analyses were done in MATLAB (version R2011a; The MathWorks, Inc., Natick, MA) using the FieldTrip toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011) and in-house scripts.

RESULTS

Behavioral

Behavioral results from the testing phase of the TNT task for 29 participants (Figure 1) showed that, after the 12 repetitions of cues, recall significantly differed for T and NT items ($t(28) = -4.66, p < .00001$). Furthermore, there was a significant increase in recall for T items compared with rB ($t(28) = 1.91, p = .028$). Conversely, there was a

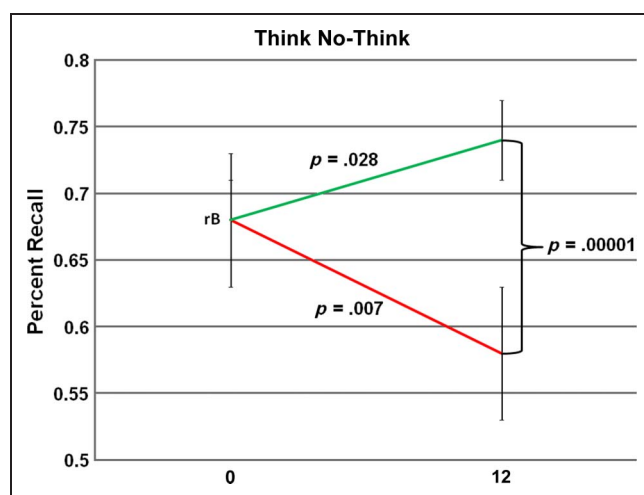


Figure 1. Behavioral data from the TNT. Green represents T trials, and red represents NT trials. 0, 12 refer to the number of repetitions. rB = recall baseline trials. Error bars represent SEM.

significant decrease in recall for NT items relative to rB ($t(28) = -2.54, p = .007$). Thus, the behavioral results replicate patterns typically found with this paradigm. Because we excluded a significant portion of participants due to EEG artifact, we also include the overall behavioral results for 45 of the 51 participants (six removed for not achieving initial learning, <25% accuracy) to establish the behavioral effect was robust in the larger sample. Recall significantly differed for T and NT items ($t(44) = -4.51, p < .00001$). Furthermore, there was a significant increase in recall for T items compared with rB ($t(44) = 1.71, p = .028$). Conversely, there was a significant decrease in recall for NT items relative to rB ($t(44) = -2.44, p = .016$).

ERP

The parietal old/new effect was analyzed over two posterior-superior regions near the standard P3 and P4 sites from 500–800 msec after test stimulus onset. We grouped the electrodes into two a priori ROIs based on those used in other studies and baseline corrected across the 200 msec before stimulus onset (e.g., Curran & Hancock, 2007; Curran, DeBuse, & Leynes, 2007; Curran, DeBuse, Woroch, & Hirshman, 2006; Curran & Friedman, 2004). The shaded regions in Figure 2 illustrate these ROIs, and only data from electrodes that fell into these ROIs were analyzed. Grand-averaged ERP waveforms were created by averaging ERPs from the channels within each region and across participants. Because our paradigm did not require participants to make standard old/new judgments, we simply refer to these ERP effects as parietal effects for the remainder of the results.

A two-way ANOVA conducted on the mean amplitude for Condition (T/NT) and Subsequent Memory (R/F) examining the parietal effect (500–800 msec) centered on right and left posterior superior (RPS, LPS) ROIs. Results indicated a significant main effect for Condition ($F(1, 27) = 19.56, MSE = 1.35, p = .0001$; Figure 2), but no main effect of Subsequent Memory or an interaction. Because our previous fMRI research has indicated a difference in engagement of cognitive control regions across the time course of repetitions (Depue et al., 2007), we examined patterns for the first versus second half of the experimental phase. A two-way ANOVA conducted on mean amplitude for Condition (T/NT/pB) and Experimental Half examining the parietal effect (500–800 msec) centered on RPS and LPS ROIs indicated a significant main effect for Condition ($F(2, 26) = 17.76, MSE = 1.90, p = .00001$; Figure 2), but no main effect of Experimental Half nor an interaction between these two factors.

To further investigate the differences between conditions and assess the increase/decrease of the mean of the parietal effect, we conducted several pairwise t tests, collapsed over subsequent memory and experimental half. Parietal amplitudes were more positive for T versus NT (T: $M = 1.71, SEM = 0.25$; NT: $M = 0.72, SEM = 0.14$; $t(27) = 4.41, p = .0002$) and T versus pB (T: $M = 1.71,$

corrected $p = .05$, 200–600 msec, 3–8 Hz; Figure 4A–C). An analogous interaction between the NTR and pB trials, similarly indicated a reduction of theta power across frontal electrodes between the first and second half of the subsequently remembered trials (NTR2–NTR1) that was larger than the first versus second half difference for perceptual baseline trials (pB2–pB1; cluster corrected $p = .04$, 200–600 msec, 3–8 Hz; Figure 4C). Taken together, these interactions suggest that increased theta power for NT forgotten and pB, as compared with NT remembered trials, was dependent on the difference between experimental half. During the second half alone, there was a significant increase in theta across frontal and parietal electrodes between forgotten and remembered (NTF2 vs. NTR2; cluster corrected $p < .01$, 280–680 msec, 3–8 Hz; Figure 4D–F), neither condition was significantly different than pB2. Therefore, during the second experimental half, NT trials that were subsequently forgotten yielded greater theta power than trials that were ultimately remembered.

In summary, centro-parietal alpha was increased for NT over T trials, and neither of these conditions significantly differed from pB trials that were numerically intermediate. Centro-parietal theta showed a NT = pB > T pattern. More constrained analyses examining subsequent memory and experimental half resulted in a significant interaction across halves, which suggests that NT trials that were forgotten and pB trials yield increased theta as experimental repetitions increased, as compared with NT trials that were remembered. Within the second experimental half, significant increases in theta across frontal and parietal electrodes were found for NT trials that were forgotten, as compared with remembered.

DISCUSSION

In the current study, we sought to examine the parietal ERP effects and EEG oscillations during volitional memory suppression. Indicating that participants were able to

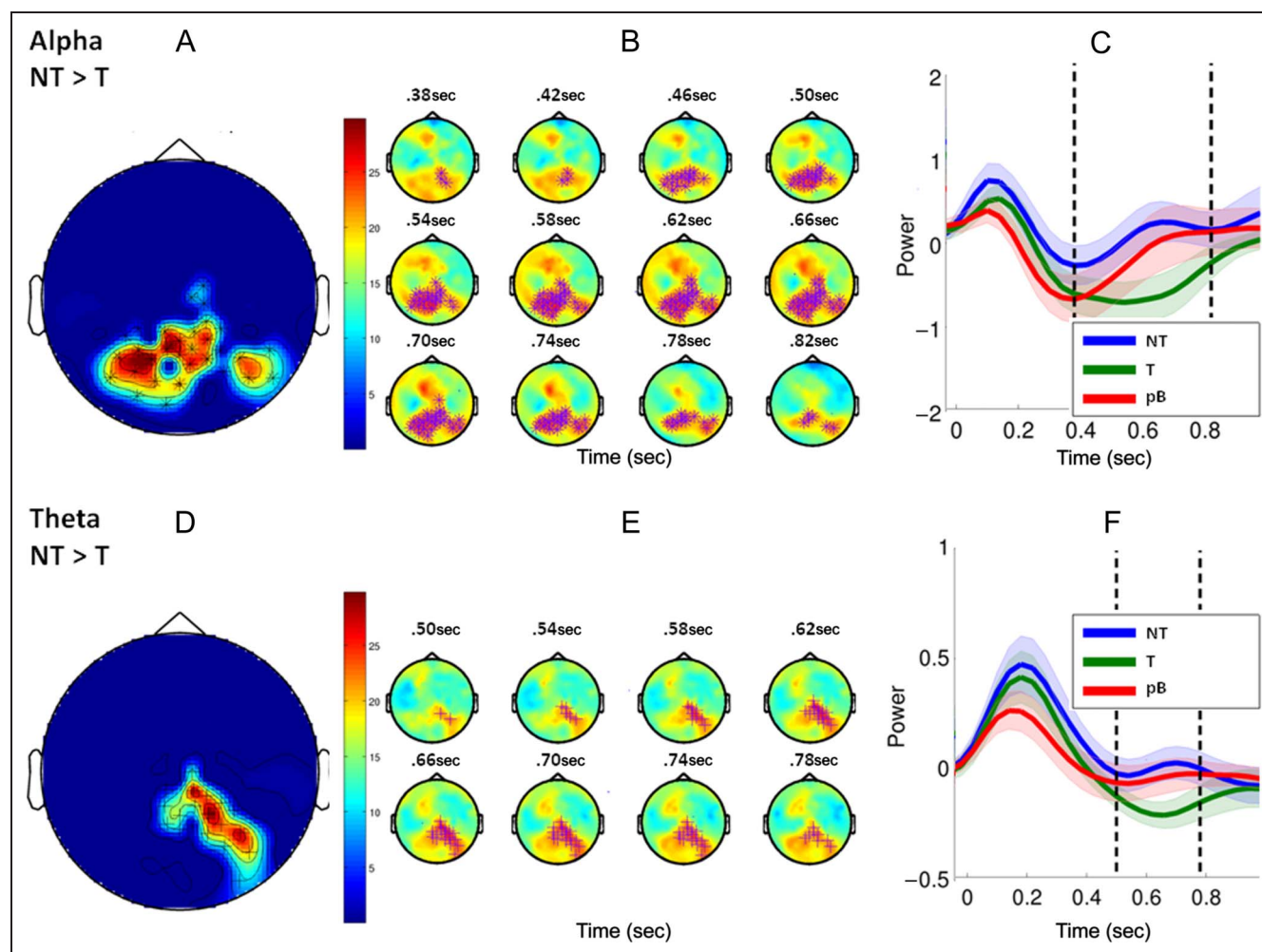


Figure 3. Alpha and theta power over scalp distribution (NT = No-Think, T = Think, pB = Baseline), $^+p < .05$, $^*p < .01$. (A) Increased alpha collapsed across the significant time window for No-Think versus Think trials (color scale represents level of t statistic). (B) The timing of the effects. (C) Average trial power across the epoch for each condition and SEM around the amplitude. (D) Increased theta collapsed across the significant time window for No-Think versus Think trials (color scale represents level of t statistic). (E) The timing of the effects. (F) Average trial power across the epoch for each condition and SEM around the amplitude.

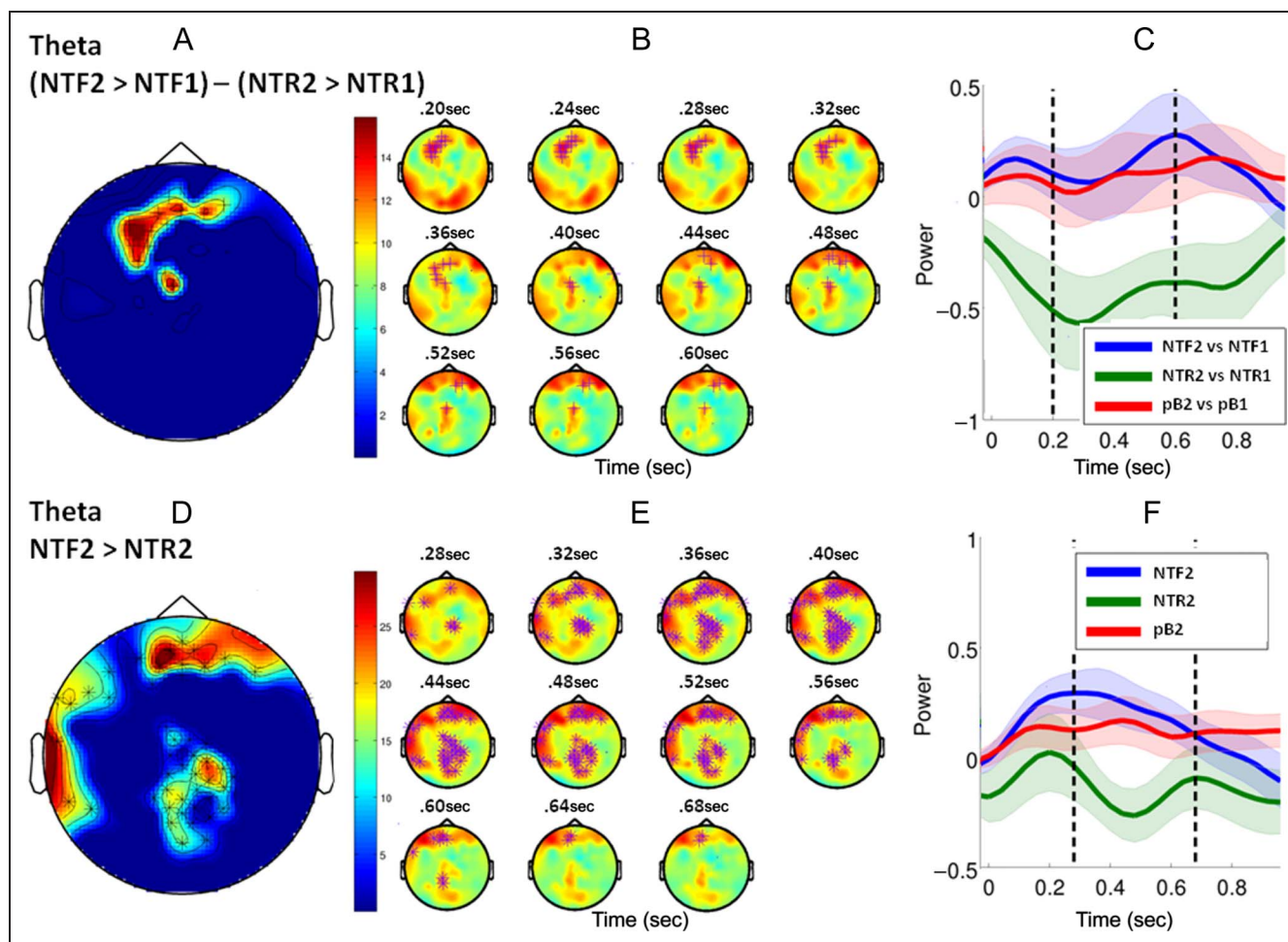


Figure 4. Theta power over scalp distribution (NT = No-Think, T = Think, pB = Baseline), ⁺ $p < .05$, ^{*} $p < .01$. (A) Increased theta collapsed across the significant time window for the interaction of No-Think forgotten versus No-Think remembered trials by experimental half [(NTF2-NTF1)–(NTR2-NTR1)] (color scale represents level of *t* statistic). (B) The timing of the effects. (C) Average trial power across the epoch for each condition and SEM around the amplitude. (D) Increased theta collapsed across the significant time window for No-Think forgotten versus No-Think remembered trials during the second experimental half (NT2F, NT2R; color scale represents level of *t* statistic). (E) The timing of the effects. (F) Average trial power across the epoch for each condition and SEM around the amplitude.

volitionally suppress memory retrieval, behavioral results revealed suppression of NT items below T and baseline items. ERP results indicated increased parietal effects for T, as compared with NT and pB trials consistent with the waveform and temporal window (500–800 msec) of the parietal old/new effect commonly observed in memory paradigms. Investigating EEG oscillatory analyses revealed increases in both alpha and theta power for NT as compared with T trials across parietal electrodes. Increases in theta power were observed in NT trials that were forgotten, as compared with remembered dependent on experimental half, suggesting greater theta power for NT forgotten trials as repetition increased across frontal electrodes. Increased theta power was also seen within the second experimental half for NT trials that were forgotten versus remembered across both frontal and parietal electrodes.

Our finding of increases in the ERP parietal effect for T trials, as compared with NT trials, is consistent with other researchers' results in the TNT paradigm (Bergstrom

et al., 2007, 2009; Hanslmayr et al., 2009). Furthermore, we present a novel finding in that NT trials did not differ in parietal effects from the pB condition, which were not paired with any target stimuli. Interestingly, comparing NT and pB trials represents a contrast that assesses the amount of recollection when stimuli were not paired with a target (pB) to a condition in which individuals attempt to suppress a paired target. Although there likely is some recollection of the face that occurs during these trials when presented with the cue, this processing should be similar across the two conditions. Therefore, examining the parietal effects between the paired (either T and/or NT) and unpaired (pB) conditions putatively measures recollection processes of the paired associate/target, as well as being sensitive to retrieval attempts that theoretically are decreased for NT and pB conditions. Equivalency in the parietal effects for NT and pB trials suggests that attempting to avoid or suppress recollection lessens the retrieval or attempts at retrieval of the associated memory.

One possible alternative explanation for the equivalency of NT and pB trials is that the relative frequency of pB trials is less than NT trials, and therefore, pB trials may elicit a heightened parietal positivity due to their relative novelty. However, other research has suggested that such probability effects are spatio-temporally dissociable from parietal old/new effects (Herron, Henson, & Rugg, 2004). The parietal effects found in the current study may well be associated or consistent with the standard parietal old/new effect that has been illustrated in recognition memory paradigms (as reviewed by Rugg & Curran, 2007). Therefore, the ERP results may indicate a decrease in recollection processes during NT trials. Because parietal old/new effects are reduced by hippocampal/MTL damage (Addante et al., 2012; Düzel et al., 2001) and recollection processes have been linked to the hippocampal complex/MTL region (as review by Eichenbaum, Yonelinas, & Ranganath, 2007), it is possible these regions have been modulated to reduce the recollection/retrieval process during NT trials, as would be expected due to fMRI studies showing reduced hippocampal activity during NT trials (Butler & James, 2010; Depue et al., 2007, 2010; Anderson et al., 2004).

In support of the modulation of recollection/retrieval processes as illustrated by the parietal effects, increases in alpha and theta power, which have been consistently linked to memory processes, were apparent for NT, as compared with T trials. Previous research examining alpha oscillations has indicated their involvement in numerous, albeit converging processes applicable to behavior that may be invoked during volitional memory suppression. Increases in alpha oscillations have been described to be present in brain regions that are thought to be task deactivated or when irrelevant stimuli need be ignored (Freunberger et al., 2011; Klimesch et al., 2007). Conversely, when these neural regions become engaged alpha oscillations decrease, generally known as “alpha suppression” (Klimesch, 1999). More recently researchers have argued that increases in alpha may also indicate brain regions that are under the influence of top-down cognitive (Palva & Palva, 2007) or inhibitory control (Klimesch et al., 2007). Increases in alpha across parietal electrodes found in the current study are concordant with any or all of these observations. As such, decreases in alpha in T, as compared with NT and pB trials, could indicate a sensitivity to increases in retrieval processes (e.g., attempts or success) and therefore an engagement of the brain regions underlying these results, which have been linked to decreases in alpha power (Klimesch et al., 2007). Therefore, the results indicate increases of retrieval attempts or success in T conditions and decreases in NT and pB conditions, which is concordant with elaborated versus suppressed retrieval, respectively.

Consistent with the results from alpha oscillation, theta oscillations were also increased for NT as compared with T trials. As previously mentioned, increases in theta have been demonstrated in memory paradigms and are thought to be a possible indicator of PFC-hippocampal/MTL com-

munication (Klimesch et al., 2007; Sauseng et al., 2005; von Stein & Sarnthein, 2000). Our current findings may also mirror these results, as we observed increased theta across parietal electrodes for NT, as compared with T trials, in general. On inspection of Figures 3 and 4, this result appears to be driven by decreases in theta power for T (see Figure 3) and NTR trials (see Figure 4) than pB and NTF trials. Therefore, to reconcile these findings, we suggest that the decrease in theta for T and NTR versus both pB and NTF trials could be associated with cognitive control processes monitoring the outcome of a retrieval attempt, which would determine the success of such an event. In the case of T and NTR trials, decreased theta may reflect successful retrieval, even when retrieval is unwanted (i.e., NTR trials). Therefore, monitoring of retrieval attempts is likely faster and less resource dependant for T and NTR than NTF trials, in which an individual may continue to monitor retrieval, to establish they are successfully suppressing. Although speculative, this view also is parsimonious with increased theta during pB trials. In the current experimental setting, the majority of trials require either elaborating or suppressing retrieval, and therefore, during pB trials, individuals may continue to monitor retrieval as a de facto state of any given trial. In summary, decreases in theta may reflect when something is retrieved versus unretrieved and monitoring the outcome of retrieval attempts, which is likely dependent on PFC-hippocampal interaction.

The timing (~200–800 msec) of the major differences between conditions in both alpha and theta power increases suggest that both oscillations may be in response to the stimulus cue, as opposed to being invoked in a more tonic fashion across trials. Therefore, the increase in both power bands for NT compared with T trials appears to be transient. Speculatively, these findings suggest that attempts at volitionally reducing retrieval involve heightened communication between PFC and hippocampus/MTL, as indicated by increased theta across parietal and frontal electrodes. Moreover, the possible consequence of increased cognitive/inhibitory control over the hippocampus/MTL is reflected in increased alpha across parietal electrodes. Both findings can be viewed as being phasic in nature, as compared with proactive task sets or tasks goals that might invoke cognitive/inhibitory control in a more tonic or sustained nature. The precise interaction between power bands and their timing and contributions to proactive control provides an interesting question for future study.

Thus, whereas most current research focuses on increased theta oscillatory dynamics during successful retrieval or WM operations, the findings are likely reflective of communication between different neural regions (i.e., PFC-hippocampal/MTL; Klimesch et al., 2007; Sauseng et al., 2005). Conversely, the current study examines when retrieval is unwanted and thus volitional suppression is engaged. That being said, communication between PFC-hippocampus/MTL should also be evoked to modulate or lessen the amount of retrieval. One alternative interpretation that has been suggested to explain memory

suppression as assessed by the TNT paradigm (Depue, 2012; Tomlinson, Huber, Rieth, & Davelaar, 2009; Hertel & Calcaterra, 2005) may also be associated with increased theta during NT trials (as our results indicate). This interpretation suggests that individuals are simply learning/focusing on alternative memory representations to distract themselves from the original memory target/pairing. Although this interpretation is consistent with increased theta, it is less consistent with the current ERP findings that indicate reductions in parietal effects for NT trials. It is likely these parietal effects are associated with recollection/retrieval processes; thus, NT trials reflect less recollection/retrieval, as well as increased theta, perhaps indicating PFC–hippocampal/MTL communication during suppression.

In summary, the current study has indicated that, when elaboration and suppression were compared with a perceptual baseline condition, the suppression condition showed no differences in parietal ERP effects, perhaps indicating reduced or down-modulated recollection processes during these trials. The ERP results, therefore, have extended and replicated previous findings of increased parietal ERP effects for elaboration of memory, as compared with volitional memory suppression. Furthermore, increases in both alpha and theta oscillations were associated with memory suppression across parietal electrodes, as well as increases in theta across frontal and parietal electrodes both when suppression is successful and after increased attempts at suppression. These latter findings are novel, in that they extend current theories of neural oscillations suggesting that theta oscillations increase not only when memory retrieval occurs but also when retrieval is unwanted and may be reduced. Speculatively, they provide insight into the dynamics of PFC–hippocampal/MTL communication that undoubtedly underlies what information is ultimately retrieved, thus dictating the constant ebb and flow of relevant versus irrelevant memories that are used to guide human behavior.

Acknowledgments

This research was funded by NIH grant MH64812 and NSF grant SBE-0542013 to the Temporal Dynamics of Learning Center (an NSF Science of Learning Center). We thank Chris Bird for research assistance.

Reprint requests should be sent to Brendan Eliot Depue, Department of Psychology and Neuroscience, University of Colorado at Boulder, 345 USCB, Boulder, CO 80309, or via e-mail: depue@colorado.edu.

REFERENCES

- Addante, R. J., Ranganath, C., Olichney, J., & Yonelinas, A. P. (2012). Neurophysiological evidence for a recollection impairment in amnesia patients that leaves familiarity intact. *Neuropsychologia*, *50*, 3004–3014.
- Anderson, M. C., & Green, C. (2001). Suppressing unwanted memories by executive control. *Nature*, *410*, 366–369.
- Anderson, M. C., Ochsner, K. N., & Kuhl, B. (2004). Neural systems underlying the suppression of unwanted memories. *Science*, *303*, 232–235.
- Benoit, R. G., & Anderson, M. C. (2012). Opposing mechanisms support the voluntary forgetting of unwanted memories. *Neuron*, *76*, 450–460.
- Bergstrom, Z., de Fockert, J., & Richardson-Klavehn, A. (2009). ERP and behavioral evidence for direct suppression of unwanted memories. *Neuroimage*, *48*, 726–737.
- Bergstrom, Z., Velmans, M., de Fockert, J., & Richardson-Klavehn, A. (2007). ERP evidence for successful voluntary avoidance of conscious recollection. *Brain Research*, *1151*, 119–133.
- Bjork, E. L., Bjork, R. A., & Anderson, M. C. (1998). Varieties of goal-directed forgetting. In J. M. Golding & C. M. MacLeod (Eds.), *Intentional forgetting: Interdisciplinary approaches* (pp. 103–137). Mahwah, NJ: Erlbaum.
- Bjork, R. A. (1989). Retrieval inhibition as an adaptive mechanism in human memory. In H. L. Roediger, III & F. I. M. Craik (Eds.), *Varieties of memory and consciousness: Essays in honour of Endel Tulving* (pp. 309–330). Hillsdale, NJ: Erlbaum.
- Butler, A. J., & James, K. H. (2010). The neural correlates of attempting to suppress negative versus neutral memories. *Cognitive, Affective, & Behavioral Neuroscience*, *10*, 182–194.
- Chen, C., Liu, C., Huang, R., Cheng, D., Wu, H., Xu, P., et al. (2012). Suppression of aversive memories associates with changes in early and late stages of neurocognitive processing. *Neuropsychologia*, *50*, 2839–2848.
- Curran, T., DeBuse, C., & Leynes, P. A. (2007). Conflict and criterion setting in recognition memory. *Journal of Experimental Psychology: Learning, Memory, & Cognition*, *33*, 2–17.
- Curran, T., DeBuse, C., Woroch, B., & Hirshman, E. (2006). Combined pharmacological and electrophysiological dissociation of familiarity and recollection. *Journal of Neuroscience*, *26*, 1979–1985.
- Curran, T., & Friedman, W. J. (2004). ERP old/new effects at different retention intervals in recency discrimination tasks. *Cognitive Brain Research*, *18*, 107–120.
- Curran, T., & Hancock, J. (2007). The FN400 indexes familiarity-based recognition of faces. *Neuroimage*, *36*, 464–471.
- Depue, B. E. (2012). A neuroanatomical model of prefrontal inhibitory modulation of memory retrieval. *Neuroscience and Biobehavioral Reviews*, *36*, 1382–1399.
- Depue, B. E., & Banich, M. T. (2012). Increased inhibition and enhancement of memory retrieval are associated with decreased hippocampal volume. *Hippocampus*, *22*, 651–655.
- Depue, B. E., Banich, M. T., & Curran, T. (2006). Suppression of emotional and non-emotional content in memory: Effects of repetition on cognitive control. *Psychological Science*, *17*, 441–447.
- Depue, B. E., Banich, M. T., & Curran, T. (2007). Prefrontal regions orchestrates the suppression of memory via a two phase process. *Science*, *317*, 215–219.
- Depue, B. E., Burgess, G. C., Willcutt, E. G., Ruzic, L., & Banich, M. T. (2010). Inhibitory control of memory retrieval and motor processing associated with the right lateral prefrontal cortex: Evidence from deficits in individuals with ADHD. *Neuropsychologia*, *48*, 3909–3917.
- Dien, J. (1998). Issues in the application of the average reference: Review, critiques, and recommendations. *Behavior Research Methods, Instruments and Computers*, *30*, 34–43.
- Dien, J. (2010). The ERP PCA Toolkit: An open source program for advanced statistical analysis of event-related potential data. *Journal of Neuroscience Methods*, *187*, 138–145.

- Düzel, E., Vargha-Khadem, F., Heinze, H.-J., & Mishkin, M. (2001). Brain activity evidence for recognition without recollection after early hippocampal damage. *Proceedings of the National Academy of Sciences*, *98*, 8101–8106.
- Eichenbaum, H., Yonelinas, A. P., & Ranganath, C. (2007). The medial temporal lobe and recognition memory. *Annual Review of Neuroscience*, *30*, 123–152.
- Fell, J., & Axmacher, N. (2011). The role of phase synchronization in memory processes. *Nature*, *12*, 105–118.
- Freunberger, R., Werkle-Bergner, M., Griesmayr, B., Lindenberger, U., & Klimesch, W. (2011). Brain oscillatory correlates of working memory constraints. *Brain Research*, *1375*, 93–102.
- Geiselman, R. E., Bjork, R. A., & Fishman, D. L. (1983). Disrupted retrieval in directed forgetting: A link with posthypnotic amnesia. *Journal of Experimental Psychology: General*, *112*, 58–72.
- Hanslmayr, S., Leopold, P., Pastötter, B., & Bäuml, K.-H. (2009). Anticipatory signatures of voluntary memory suppression. *The Journal of Neuroscience*, *29*, 2742–2747.
- Herron, J. E., Henson, R. N., & Rugg, M. D. (2004). Probability effects on the neural correlates of retrieval success: An fMRI study. *Neuroimage*, *21*, 302–310.
- Hertel, P. T., & Calcaterra, G. (2005). Intentional forgetting benefits from thought substitution. *Psychonomic Bulletin & Review*, *12*, 484–489.
- Jacobs, J., Hwang, G., Curran, T., & Kahana, M. J. (2006). EEG oscillations and recognition memory: Theta correlates of memory retrieval and decision making. *Neuroimage*, *32*, 978–987.
- Junghöfer, M., Elbert, T., Tucker, D. M., & Braun, C. (1999). The polar average reference effect: A bias in estimating the head surface integral in EEG recording. *Clinical Neurophysiology*, *110*, 1149–1155.
- Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current Opinion in Neurobiology*, *11*, 739–744.
- Klimesch, W. (1999). EEG alpha and theta oscillations reflect cognitive and memory performance: A review and analysis. *Brain Research Reviews*, *29*, 169–195.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: The inhibition-timing hypothesis. *Brain Research Reviews*, *53*, 63–88.
- Klimesch, W., Schimke, H., Doppelmayr, M., Ripper, B., Schwaiger, J., & Pfurtscheller, G. (1996). Event-related desynchronization (ERD) and the Dm effect: Does alpha desynchronization during encoding predict later recall performance? *International Journal of Psychophysiology*, *24*, 47–60.
- Lambert, A. J., Good, K. S., & Kirk, I. J. (2010). Testing the repression hypothesis: Effects of emotional valence on memory suppression in the think–no think task. *Consciousness and Cognition*, *19*, 281–293.
- Lang, P. J., Bradley, M. M., & Cuthbert, B. N. (1995). *The International Affective Picture System (IAPS)*. Gainesville, FL: University of Florida, Center for Research in Psychophysiology.
- Levy, B. J., & Anderson, M. C. (2002). Inhibitory processes and the control of memory retrieval. *Trends in Cognitive Neuroscience*, *6*, 299–305.
- Maris, E., & Oostenveld, R. (2005). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190.
- Mecklinger, A., Parra, M., & Waldhauser, G. T. (2009). ERP correlates of intentional forgetting. *Brain Research*, *1255*, 132–147.
- Nørby, S., Lange, M., & Larsen, A. (2010). Forgetting to forget: On the duration of voluntary suppression of neutral and emotional memories. *Acta Psychologica*, *133*, 73–80.
- Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews*, *34*, 1023–1035.
- Oostenveld, R., Fries, P., Maris, E., & Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *156869*, 1–9.
- Palva, S., & Palva, M. (2007). New vistas for α frequency band oscillations. *Trends in Neurosciences*, *30*, 150–158.
- Paz-Alonso, P. M., Ghetti, S., Matlen, B. J., Anderson, M. C., & Bunge, S. A. (2010). Memory suppression is an active process that improves over childhood. *Frontiers in Human Neuroscience*, *3*, 24.
- Rugg, M. D., & Curran, T. (2007). Event-related potentials and recognition memory. *Trends in Cognitive Science*, *6*, 251–257.
- Salame, P., & Danion, J. M. (2007). Inhibition of inappropriate responses is preserved in the think–no-think and impaired in the random number generation tasks in schizophrenia. *Journal of the International Neuropsychological Society*, *13*, 277–287.
- Sauseng, P., Klimesch, W., Schabus, M., & Doppelmayr, M. (2005). Fronto-parietal EEG coherence in theta and upper alpha reflect central executive functions of working memory. *International Journal of Psychophysiology*, *57*, 97–103.
- Srinivasan, R., Nunez, P. L., Tucker, D. M., Silberstein, R. B., & Cadusch, P. J. (1996). Spatial sampling and filtering of EEG with splinelaplacians to estimate cortical potentials. *Brain Topography*, *8*, 355–366.
- Tomlinson, T. D., Huber, D. E., Rieth, C. A., & Davelaar, E. J. (2009). An interference account of cue-independent forgetting in the no-think paradigm. *Proceedings of the National Academy of Sciences*, *106*, 15588–15593.
- Tucker, D. M. (1993). Spatial sampling of head electrical fields: The geodesic sensor net. *Neurophysiology*, *87*, 145–163.
- von Stein, A., & Sarnthein, J. (2000). Different frequencies for different scales of cortical integration: From local gamma to long range alpha/theta synchronization. *International Journal of Psychophysiology*, *38*, 301–313.
- Wessel, I., Wetzels, S., Jellicic, M., & Merckelbach, H. (2005). Dissociation and memory suppression: A comparison of high and low dissociative individuals performance on the think–no think task. *Personality and Individual Differences*, *39*, 1461–1470.