

The Neural Correlates of Cognitive Control: Successful Remembering and Intentional Forgetting

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Abstract

■ The ability to control how we process information by remembering that which is important and forgetting that which is irrelevant is essential to maintain accurate, up-to-date memories. As such, memory success is predicated on both successful intentional encoding and successful intentional forgetting. The current study used an item-method directed forgetting paradigm to elucidate the cognitive and neural processes that underlie both processes while also examining the relationship between them to understand how the two may work together. Results indicated that encoding-related processes in the left inferior PFC and medial-temporal lobe (MTL) contribute to subsequent memory success, whereas inhibitory processes in the right superior frontal gyrus and right inferior parietal lobe contribute to subsequent

forgetting success. Furthermore, connectivity analyses found a negative correlation between activity in the right superior frontal cortex and activity in the left MTL during successful intentional forgetting but not during successful encoding, incidental forgetting, or incidental encoding. Results support the theory that intentional forgetting is mediated by inhibition-related activity in the right frontal cortex and the interaction of this activity with that of encoding-related activity in the MTL. Further support for this inhibitory-related account was found through a clear dissociation between intentional and incidental forgetting, such that intentional forgetting was associated with regions shown to support inhibition, whereas incidental forgetting was associated with regions supporting encoding. ■

INTRODUCTION

In a world in which information is constantly changing, the ability to update our memory store is critical. Accordingly, the cognitive control of memory is predicated on recognizing the differences between two types of information, relevant and irrelevant, and acting accordingly. With regard to memory encoding, whereas relevant information must be successfully incorporated into long-term memory so that it can be retrieved at a later time, irrelevant information must be forgotten so that it is not stored in long-term memory and cannot interfere with the retrieval of other memories. To date, the majority of research related to the cognitive control of memory has focused on processes supporting successful encoding and retrieval (for meta-analysis, see Spaniol et al., 2009) as well as processes supporting the suppression and forgetting of information already stored in long-term memory (for a review, see Anderson & Huddleston, 2012). Far less research has focused on the method(s) by which intentional forgetting, occurring at the time of encoding, can successfully prevent irrelevant information from being encoded into long-term memory. The current study aims to investigate the cognitive control of memory during encoding by elucidating the cognitive and neural processes underlying both successful encoding, as well as the means by which intentional forgetting disrupts encoding.

One experimental paradigm utilized for investigating control processes that mediate memory success is the directed forgetting (DF) paradigm. In item-method DF, participants are presented with a series of items (e.g., words), each followed by an instruction to either remember or forget the item. It is theorized that the item is held in working memory until the memory instruction is given; at which point, participants engage in cognitive processes aimed at carrying out the specific memory instruction (Paz-Caballero, Menor, & Jimenez, 2004; Basden & Basden, 1996). Traditionally, research has posited that, when given an instruction to remember, individuals engage in deep encoding aimed at supporting later memory for the to-be-remembered (TBR) item (Basden & Basden, 1996). When given an instruction to forget, individuals forgo this deep processing, resulting in decay of the memory trace, causing forgetting. However, recently, it has been suggested that an instruction to forget is accompanied by active, inhibition-related processing that is aimed at halting further processing of the item and blocking the encoding of the item into long-term memory (Fawcett & Taylor, 2008; Zacks, Radvansky, & Hasher, 1996). Thus, these two separable mechanisms, differential encoding and goal-directed inhibition, are posited to work together to exert control over memory encoding. Considering this, the DF paradigm not only allows for the study of both encoding and inhibition, but because only a subset of items are subsequently successfully remembered or forgotten, this paradigm presents the additional opportunity to study

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both attempt and success, as it pertains to remembering and forgetting.

With regard to the cognitive mechanisms underlying each process, it is theorized that successful encoding of the TBR items occurs because they undergo enhanced, intentional encoding as compared with the to-be-forgotten (TBF) items (Basden & Basden, 1996). As such, this differential encoding results in a higher rate of retrieval for TBR than TBF items. Previous research using general encoding paradigms suggests that the encoding attempt is associated with increased activity in the left PFC (Wagner et al., 1998; Kapur et al., 1996; Demb et al., 1995), whereas encoding success is also mediated by increased activity in the medial-temporal lobe (MTL) as well as increased activity in the early visual cortex (Kim & Cabeza, 2007; Gutchess et al., 2005; Schacter et al., 1999; Fernandez et al., 1998; Kelley et al., 1998; Kapur et al., 1996). Although support for differential encoding has been shown in numerous behavioral studies using the DF paradigm (Lee & Lee, 2011; Quinlan, Taylor, & Fawcett, 2010; Hourihan & Taylor, 2006; MacLeod, 1999; Wetzel & Hunt, 1977; Woodward, Bjork, & Jongewar, 1973), little imaging data has been collected to support this theory. In the first study to use fMRI to investigate DF, Reber et al. (2002) focused entirely on encoding processes. In accord with the previous literature, researchers found that increased activity in the left inferior PFC supported the encoding attempt, whereas greater activation in the MTL was found for subsequently remembered items, as opposed to subsequently forgotten items, regardless of whether they had been marked as TBR or TBF (Reber et al., 2002). However, a second study (Wylie, Foxe, & Taylor, 2008) did not find MTL activity associated with successful remembering but rather found increased MTL activity for intentional forgetting. This discrepancy calls into question the role of the MTL in intentional remembering and intentional forgetting. One contributing factor to this inconsistency may be the use of a yes/no recognition task in the foregoing DF studies. The use of such a recognition test not only collapses across qualitative differences in memory (i.e., recollection and familiarity), which are known to be mediated by distinct subsystems of the MTL (e.g., Diana, Yonelinas, & Ranganath, 2007; Yonelinas, Otten, Shaw, & Rugg, 2005), but also includes guessing within each response. As such, this study was not able to isolate the neural processes associated with pure recollection and forgetting. The current study aims to isolate intentional encoding processes that lead to recollection and examine the role of the MTL in recollection-based encoding as well as successful forgetting.

Although differential encoding enhances MTL activity and successful memory, it is posited that inhibition promotes successful forgetting by suppressing the processes that are necessary for encoding, including that of the MTL. With regard to the DF paradigm, it is theorized that the presentation of a cue to forget initiates an inhibitory process that prevents further encoding of TBF items, thus facilitating the forgetting of irrelevant information. It is, of course, possible that forgetting occurs not because the encoding of TBF

items is actively prevented but more simply because attention is diverted away from these items, leading to the passive decay of the memory trace. Examining intentional forgetting within the domain of neuroimaging research would greatly enhance our ability to distinguish between these two possible mechanisms. If, as the recent neuroimaging literature suggests, forgetting occurs as the result of an active inhibitory mechanism, one would expect that regions involved in top-down inhibition and intentional forgetting would suppress encoding-related activity within the MTL during trials in which a participant is instructed to forget and in which the item is successfully forgotten. On the other hand, if the TBF instruction merely operates to divert attention away from the item, one would not expect to see this direct interaction between attention-related activity and encoding-related activity within the MTL.

With regard to top-down inhibition processes, inhibition has primarily been studied with respect to the inhibition of a motor response or action. Successful inhibition of overt motor responses has been associated with increased neural activity in the right inferior frontal gyrus, right middle frontal gyrus, right medial frontal gyrus, and the basal ganglia (Levy & Wagner, 2011; Boehler, Appelbaum, Krebs, Hopf, & Woldorff, 2010; Chevrier, Noseworthy, & Schachar, 2007; Aron & Poldrack, 2006; Garavan, Ross, & Stein, 1999; Konishi et al., 1999). Moreover, research has demonstrated that, compared with other executive processes such as response shifting, response inhibition preferentially activates the right inferior PFC and bilateral temporal-parietal junction (Hedden & Gabrieli, 2010). The few studies that have examined non-motor-related inhibition (such as those of retrieval suppression) have also reported similar patterns of activation in frontal and parietal regions. For example, the use of a think/no-think (TNT) paradigm has shown increased activity in both superior/middle and inferior PFC associated with memory suppression trials (i.e., no-think trials; Depue, Curran, & Banich, 2007; Anderson et al., 2004). Furthermore, both Anderson and Depue (Depue et al., 2007; Anderson et al., 2004) found a relationship between increased activity in the right PFC and reduced activity in the hippocampus. Specifically, Anderson et al. (2004) showed that, across participants, greater memory inhibition was associated with a greater hippocampal decrease for suppressed memories, and Depue et al. (2007) found that, over repeated retrieval suppression attempts, right PFC activity exhibited increases in activity, whereas hippocampal activity exhibited decreases. Both researchers theorized this to be evidence for a top-down, inhibitory relationship between the right PFC and the MTL during retrieval suppression. Although this hippocampal deactivation was not directly linked to inhibition-related activity in the right PFC and parietal cortex, these studies provide preliminary evidence for an account of inhibition that is based on one region (e.g., right PFC) increasing in activation to suppress the activation of another region (e.g., MTL). More direct evidence for the role of inhibition supporting successful forgetting at the time of

encoding theory can be obtained by examining the connectivity between regions presumed to support inhibition (i.e., right PFC and parietal lobes) and encoding (i.e., MTL), particularly when information is being forgotten. Thus, we attempt to extend the theories articulated both by Anderson and Depue (Depue et al., 2007; Anderson et al., 2004) by using a within-subject connectivity method that will directly examine interactions between inhibitory and encoding-related regions on a trial-by-trial basis.

To our knowledge, only one study has attempted to examine the link between intentional forgetting and encoding-related processes. In analyzing the fluctuations of the MTL during a DF task using intracranial ERPs, Ludwig et al. (2010) reported decreased negativity in the hippocampus during intentionally forget trials. Although the authors used this finding to conclude that a cue to forgotten items causes suppression of encoding-related activity, two significant limitations lead to difficulty in the interpretability of these results. First, the authors did not find evidence of differential encoding, as a cue to remember did not lead to increased encoding-related activity. Second, because the intracranial ERPs were only implanted in one specific region (only in the hippocampus), the observed decrease in hippocampal activity could not be directly related to suppression from another region. As noted, current theory suggests that this inhibition arises from processing within the right PFC and/or parietal cortex. But again, the exact locale of this encoding-related inhibition has yet to be determined. The spatial resolution of fMRI allows for us to determine, with increased precision, the location of inhibitory-related intentional forgetting.

Whereas a vast number of neuroimaging studies have investigated retrieval suppression in the TNT paradigm (Anderson & Huddleston, 2012), only a few neuroimaging studies have investigated the neural processes involved in intentional forgetting within the DF paradigm. Whereas ERP studies have generally converged on the finding that TBF items promote a right-lateralized, frontal pattern of activity that may represent inhibitory activity (Paz-Caballero et al., 2004; Ullsperger, Mecklinger, & Muller, 2000), an fMRI study conducted by Wylie and colleagues (2008) found intentional forgetting to be associated with activity in the right superior frontal gyrus and right inferior parietal lobe. Although generally consistent with the aforementioned motor-related inhibition studies, the locale of the frontal activation identified in the fMRI study differs from the locale of the inhibition-related activity found in most motor-inhibition tasks (i.e., inferior right PFC; Aron & Poldrack, 2006; Aron, Fletcher, Bullmore, Sahakian, & Robbins, 2003; Rubia, Smith, Brammer, & Taylor, 2003; Garavan et al., 1999; Jonides, Smith, Marshuetz, Koeppe, & Reuter-Lorenz, 1998). Thus, results call into question whether this activity observed in DF studies truly reflects inhibition or is associated with diverting attention, or reflexive reorienting, from the presented item (e.g., Levy & Wagner, 2011). Alternatively, the discrepancy between motor inhibition studies and the DF study by Wylie et al.

(2008) may reflect functional organization within the right PFC where motor inhibition is mediated by right inferior PFC and inhibition of a cognitive task (such as memory encoding) is mediated by right middle and superior PFC. Support for this theory comes from neuroimaging studies examining the TNT paradigm, which find increased activity for no-think trials (retrieval suppression) in the right dorso-lateral PFC (Depue et al., 2007; Anderson et al., 2004) and has been suggested by Anderson and colleagues (Anderson & Huddleston, 2012; Anderson & Weaver, 2009).

Regardless of the mechanism, these data suggest that both right PFC and parietal regions are part of a network that supports intentional forgetting in a way that is different from incidental forgetting. However, the Wylie et al. (2008) study did not fully dissociate processes involved in intentional and incidental forgetting. Thus, it is unclear if incidental forgetting represents a weaker form of intentional forgetting or if it is mediated by distinct neural processes. If the two are truly separate cognitive operations, they should be mediated by separable neural processes, with incidental forgetting mediated by regions involved in encoding attempt and intentional forgetting mediated by regions involved in cognitive control and inhibition.

Finally, the parietal lobe, as it pertains to inhibition, has largely been ignored with respect to studies of motor inhibition and retrieval suppression. Although activity in the right inferior parietal lobe is often observed during inhibition-related tasks, its contribution to task success is seldom discussed from a theoretical standpoint (Kramer, Knight, & Munte, 2011; Hedden & Gabrieli, 2010; Aron & Poldrack, 2006; Rubia et al., 2001; Garavan et al., 1999). It has been theorized that the parietal lobe may facilitate the withdrawal of a motor response (Garavan et al., 1999) or provide increased attentional resources for the viewing of infrequent stimuli (Boehler et al., 2010). As such, it is unclear whether the parietal lobe directly contributes to inhibition or whether it supports a secondary function that is a by-product of many inhibitory-related tasks. Even more ambiguity is introduced when considering the presence of parietal lobe activity during DF studies. Wylie et al. (2008) reported increased activity in the right inferior parietal lobe for successful forgetting, but ERP-related DF literature cites the opposite, with similar parietal lobe activity for TBR but not TBF items (Paz-Caballero et al., 2004). Thus, continued research regarding intentional forgetting is needed to move toward a better understanding of the role of the parietal lobe in successful forgetting.

The current experiment aims to clarify the aforementioned issues regarding the cognitive and neural basis of intentional remembering and forgetting. First, we aim to investigate the neural correlates underlying both attempted and successful encoding of relevant information. We predict that encoding attempt of semantic information will be accompanied by neural activity in the left inferior PFC and early visual regions. Encoding success, on the other hand, will recruit not only the left PFC and visual cortex but also the left MTL. Second, we aim

to investigate the neural correlates underlying both attempted and successful forgetting of irrelevant information. As noted above, intentional forgetting is posited to be mediated by inhibition. Considering this, we predict that both forgetting attempt and success will be accompanied by activity in the right PFC and inferior parietal cortex. Within the PFC, we further predict inhibition-related activity to be localized to the middle and/or superior PFC, as opposed to the inferior right PFC, given that forgetting-related inhibition is related to inhibition of cognitive, not motor-related, processes. This is based on evidence showing that retrieval inhibition recruits the middle frontal gyrus and dorsolateral PFC, whereas motor inhibition has been localized to the inferior frontal cortex. Third, to directly investigate the relationship between inhibition-related activity and encoding-related processing, we aimed to investigate the interaction between regions associated with intentional forgetting and those associated with successful encoding. If, as theorized, intentional forgetting is associated with inhibition of encoding, there should exist a negative relationship between activation associated with intentional forgetting and encoding-related regions. That is, if inhibitory processes are responsible for preventing items from being encoded into long-term memory, then it should do so by interrupting or suppressing encoding-related activity. Specifically, we predict that inhibition-related activity in the right superior PFC will exhibit negative connectivity with the MTL, a region shown to be at the core of successful memory processes. We will investigate whether the same relationship exists for the parietal lobe to determine whether these regions play similar or different roles in supporting inhibition. Although the existence of such a negative correlation could not be used to infer that the PFC suppresses encoding-related MTL activity, such a finding would contribute to the development of a theory based on an interaction between these areas. Finally, we aim to investigate neural differences that distinguish between intentional and incidental forgetting. Doing so would provide firm evidence that these are indeed two separate forms of forgetting and, as such, are mediated by dissociable cognitive processes. Specifically, we predict that incidental forgetting stems from encoding failure and would be associated with activity similar to that seen for encoding attempt, whereas intentional encoding is driven by inhibition-related processing.

METHODS

Participants

Twenty-seven adults between the ages of 18–26 years ($M = 21.11$ years, $SD = 1.79$ years) participated for monetary compensation. The data of two participants were lost due to scanner malfunction, and another was excluded due to the participant's failure to follow instructions. Thus, 24 participants were included in the final analysis. All were right-handed, healthy, English speakers who had passed a cognitive assessment composed of the Mini-Mental State

Examination and sections of the Wechsler Adult Intelligence Scale (version III). All participants provided written informed consent, and the Pennsylvania State University Institutional Review Board approved all procedures.

Materials

Three hundred sixty nouns were chosen from the Medical Research Council Psycholinguistic Database (http://websites.psychology.uwa.edu.au/school/MRCDatabase/uwa_mrc.htm). Words had an average Kucera–Francis written frequency of 110 (range = 50–275) and an average concreteness of 433 (range = 254–600). One hundred of the words were randomly selected to be marked as to-be-remembered (TBR) during encoding, another 100 were marked as to-be-forgotten (TBF) during encoding, and the remaining 160 were used as “new” items during the recognition test at retrieval.

Procedure

The experiment employed a traditional item-method DF paradigm. During the encoding phase, each of the 200 words appeared individually on the screen for 1000 msec and was followed by the presentation of a fixation cross that remained for 2000 msec. After this period, a group of five colored pound signs were presented for 3000 msec (see Figure 1). Participants were instructed that words followed by green pound signs should be remembered (TBR items), as they would appear on an upcoming memory test. Words followed by red pound signs should be forgotten (TBF items), as they would not be on the memory test (see Figure 1). The encoding trials were broken into five blocks of 40 words, with TBR and TBF items appearing in a pseudo-random order, such that no more than three of the same trial type appeared sequentially. Each trial lasted for 8000 msec, which included a jittered fixation cross that lasted between 1500 and 3000 msec (average = 2000 msec).

Following encoding, participants completed a 10-min matrix-reasoning task as interference. The task was taken

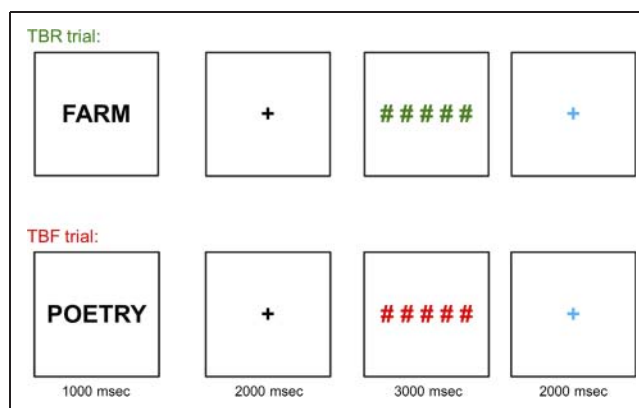


Figure 1. Schema of encoding trials, in which participants are instructed to remember words associated with green pound signs and forget those associated with red pound signs.

from the Wechsler Adult Intelligence Scale III and required participants to select one of four options to complete a given pattern. The interference task was followed by a retrieval task that included 360 words: the 100 TBR items and 100 TBF items from encoding and 160 new words. Each word appeared individually on the screen for 2500 msec, and participants made a remember/know/new memory decision during that time (see Yonelinas & Jacoby, 1995, for a review). A jittered fixation cross, identical to that in encoding, followed the presentation of the word. It was stressed to the participants that their memory response should not depend on whether the word had been marked as TBR or TBF during the study phase but should instead depend only on whether the word was old or new. The retrieval task was divided into five blocks of 52 words each.

Image Acquisition

Imaging data of both encoding and retrieval were acquired in a 3-T Siemens Magnetom Trio MRI scanner (Siemens, Erlangen, Germany). Functional encoding data were obtained in five 5.60-min runs, each consisting of 165 volumes. Functional retrieval data were collected and will be reported in a subsequent article. Encoding images were collected using an EPI sequence with a 2-sec repetition time (TR), 30-msec echo time, 240-mm field of view, and a 70° flip angle. Thirty-four slices were acquired per TR, with a slice thickness of 3.8 mm, resulting in 3.8 mm³ isotropic voxels. Structural images were acquired during the interference task, using a T1-weighted magnetization prepared rapid gradient echo (MP RAGE), with a TR of 2300 msec, an echo time of 3.41 msec, a 230-mm field of view, and a voxel size of 0.9 mm³.

Image Processing

Preprocessing and statistical analyses were performed using SPM software in MATLAB (SPM 8; Wellcome Department of Cognitive Neurology, London, United Kingdom). First, time-series data were corrected for differences in slice acquisition time. Images were then spatially realigned to the first functional run of encoding and were subsequently checked for movement artifacts using a time-series diagnostic function TSDiffAna (Freiburg Brain Imaging, Freiburg, Germany) in MATLAB (MathWorks). No individual moved more than 3 mm in any direction, in any run. Thus, no data were removed because of motion artifacts. The functional images were then normalized using the Montreal Neurological Institute template and converted to Talairach space (Talairach & Tournoux, 1988). Finally, images were smoothed using an 8-mm Gaussian smoothing kernel.

Data Analysis

For each participant, trial-related activity was modeled with a stick function corresponding to stimulus onsets, convolved with a canonical hemodynamic response func-

tion within the context of the general linear model, as implemented in SPM8. Confounding factors (head motion, magnetic field drift) were also included in the model. Statistical parametric maps were identified for each participant by applying linear contrasts with the parameter estimates (beta weights) for the events of interest, resulting in a *t* statistic for every voxel.

Given that our study goal was to examine cognitive and neural activity associated with the cognitive control of memory, we focused our analysis on neural activity associated with the onset of memory cues (TBR/TBF cues). In accord with previous DF analyses (Wylie et al., 2008), word-related activity was also modeled yet treated as a regressor of no interest. Encoding trials were coded using a subsequent memory design. Given memory instructions (TBR/TBF) and the subsequent memory scoring (recollection/familiarity/forget), the model included six trial types of interest: (1) TBR-recollection: intentional remembering, (2) TBR-forget: incidental forgetting, (3) TBF-recollection: incidental remembering, and (4) TBF-forget: intentional forgetting. Subsequent familiarity [(5) TBR-familiarity and (6) TBF-familiarity] was also modeled and included in analyses examining encoding and forgetting attempt.

Encoding attempt activity was defined as activity associated with all TBR trials compared with TBF trials. Encoding success was defined by comparing activity associated with TBR-recollection with TBF-forget. Likewise, forgetting attempt was defined as activity associated with all TBF trials compared with TBR trials, and forgetting success was defined by comparing activity associated with TBF-forget trials with TBR-recollection trials. Activity related to successful remembering and forgetting was modeled with these particular contrasts because we specifically wanted to investigate neural differences between two types of successful cognitive control processes (successful encoding and successful forgetting). Lastly, the dissociation between intentional forgetting and incidental forgetting was examined by comparing activity associated with the two conditions, TBF-forget and TBR-forget.

To obtain results that were corrected for multiple comparisons, we used Monte Carlo simulations (www2.bc.edu/slotnick/scripts.htm) to define individual voxel and cluster extent thresholds (e.g., Garoff-Eaton, Kensinger, & Schacter, 2007; Slotnick & Schacter, 2004, 2006; Slotnick, Moo, Segal, & Hart, 2003; Forman et al., 1995). In this study, an individual voxel threshold of $p < .005$ was used in combination with a cluster extent threshold of 13 resampled voxels (823 mm³), which yielded results corrected for multiple comparisons at $p < .05$.

Connectivity Analysis

To investigate whether activity associated with intentional forgetting reflects inhibition of encoding processes, we conducted a psychophysiological interaction (PPI) analysis. Seed voxels for the PPI analysis were chosen from the

subset of regions found to be significantly active for successful intentional forgetting. Specifically, we used the peak voxel from activated clusters in the right medial frontal gyrus (BA 8), right superior frontal gyrus (BA 10), and right inferior parietal lobe (BA 40; see Table 3 for seed peaks). Choice of these seeds was based on both previous evidence implicating the right PFC and parietal lobe in inhibitory processing and the identification of these regions as the location of task-specific forgetting success in the current study. A 4-mm sphere of voxels was drawn around each peak, and the time course of TBF-forget trials was extracted for each seed region. The time courses were then compared with the time courses of voxels within the MTL. We focused our PPI analysis within the MTL because both previous evidence and our current study have implicated the MTL in mediating encoding success. The same time course extraction procedure was also conducted for TBR-recollection, TBF-recollection, and TBR-forget trials.

RESULTS

Behavioral Results

Whereas the traditional DF paradigm (with the use of a yes/no recognition test) allows for only one measure of memory control the current DF paradigm (with recognition responses separating recollection, familiarity, and forgetting) allows for the calculation of both a directed remembering and a directed forgetting effect. With regard to recollection, participants exhibited a significant remembering effect, $t(23) = 5.57, p < .0001$, such that they had a greater rate of intentional remembering (TBR-recollection: $M = 0.43, SD = 0.19$) than incidental remembering (TBF-recollection: $M = 0.26, SD = 0.14$). Conversely, participants had a higher rate of familiarity for TBF items ($M = 0.35, SE = 0.02$) compared with TBR items ($M = 0.30, SE = 0.02$), $t(23) = 2.17, p < .05$. Lastly, participants exhibited significant directed forgetting, $t(23) = 5.85, p < .0001$, such that they had a greater rate of intentional forgetting (TBF-forget: $M = 0.39, SD = 0.14$) than incidental forgetting (TBR-forget: $M = 0.27, SD = 0.12$; see Table 1).

Neuroimaging Results

Encoding Attempt and Encoding Success

Encoding attempt was associated with significant clusters of neural activity in the left inferior (BA 45) and left

middle (BA 6) frontal gyrus, left cuneus (BA 18), middle cingulate gyrus (BA 32), and right medial occipital gyrus (BAs 19 and 18). Encoding success was associated with neural activity in the left middle frontal gyrus (BA 11), left hippocampus and parahippocampal gyrus (PHG; BAs 28 and 35), right cuneus (BAs 17 and 18), left inferior temporal gyrus (BA 37), left superior parietal lobe (BA 7), middle and right superior frontal gyrus (BA 6), and right medial frontal gyrus (BA 32; Table 2, Figure 2).

Forgetting Attempt and Forgetting Success

Forgetting attempt was associated with significant clusters of activity in the right superior frontal gyrus (BA 8), right inferior parietal lobe (BA 40), left cingulate gyrus (BA 24), left postcentral gyrus (BAs 1–3), left superior occipital gyrus (BA 19), and right/middle precuneus (BAs 5 and 7). Forgetting success was associated with significant clusters of activity in the right superior frontal gyrus (BAs 8 and 10), right inferior parietal lobe (BA 40), middle superior frontal gyrus (BA 9), right medial frontal gyrus (BA 8), left postcentral gyrus (BA 3), left cingulate gyrus (BA 23), and middle precuneus (BA 7; see Table 3, Figure 2).

Connectivity Analysis

When the time courses of seed regions in the right superior and medial frontal gyrus (BAs 10 and 8, respectively) were analyzed during TBF-forget trials, they were each found to negatively interact with a cluster in the left MTL. Specifically, activity in BA 10 was negatively correlated with a cluster of voxels in the left hippocampus (peak: $-34, -18, -16$; $k = 1207 \text{ mm}^3$), and activity in BA 8 was negatively correlated with a cluster of voxels in the left PHG (BA 28; peak: $19, -14, -19$; $k = 549 \text{ mm}^3$). No significant interaction was found between the time course of voxels in the right inferior parietal lobe or PFC and any MTL region during TBR-forget, TBR-recollection, TBF-recollection, or TBR-forget trials. Thus, although activity in the right PFC predicted a decrease in MTL activity during successful forgetting trials, it did not predict a similar decrease in activity for incidental forgetting, successful recollection, or incidental recollection.

Intentional and Incidental Forgetting

Contrasts between intentional and incidental forgetting revealed large neural differences between these two different behavioral outcomes. Compared with incidental forgetting, intentional forgetting was associated with greater activity in the right superior parietal lobe (BA 7), left inferior parietal lobe (BA 40), left superior parietal lobe (BAs 5 and 7), right postcentral gyrus (BAs 1 and 2), and right precuneus (BA 7). Incidental forgetting, on the other hand, was associated with greater activity in the left inferior frontal gyrus (BA 47), left superior frontal gyrus (BA 6), middle cingulate gyrus (BA 32), left superior

Table 1. Rate of Response as a Function of Trial Type

Word Type	Recollection Mean (SE)	Familiarity Mean (SE)	New/Forget Mean (SE)
TBR	0.43 (0.04)	0.30 (0.02)	0.26 (0.02)
TBF	0.26 (0.03)	0.35 (0.02)	0.39 (0.03)
Foil	0.11 (0.03)	0.34 (0.03)	0.66 (0.05)

TBR = to be remembered; TBF = to be forgotten; SE = standard error.

Table 2. Intentional Encoding

	BA	H	Coordinates (T&T)			t	mm ³
			x	y	z		
Encoding Attempt							
Superior frontal gyrus	6	M	−7	12	68	4.22	933
Inferior frontal gyrus	45	L	−48	24	22	3.16	713
Cingulate gyrus	32	M	−4	29	36	3.65	2030
Medial occipital gyrus	19, 18	R	26	−100	15	4.79	5103
Early visual cortex	18	L	−11	−104	−2	3.86	823
Lenticular nucleus	−	L	−15	9	−4	3.18	768
Successful Encoding							
Middle and inferior frontal gyrus	11	L	−52	28	22	5.07	28588
Middle frontal gyrus	11	L	−19	37	−18	3.56	878
Medial frontal gyrus	32	R	11	29	36	3.58	878
Superior frontal gyrus	6	R	41	−6	62	4.03	823
	6	M	−4	12	61	5.43	16187
Subcallosal gyrus	25	L	−15	8	−14	5.09	5981
Striatum		R	11	9	2	3.59	2030
		L	−19	9	−4	5.02	8341
Hippocampus/PHG	28, 35	L	−26	−17	−12	3.94	3676
Fornix	−	L	−30	−31	1	3.83	988
Superior temporal gyrus	38	L	−52	19	−11	4.47	1591
Inferior temporal gyrus	37	L	−59	−50	−14	4.16	878
Superior parietal lobe	7	L	−30	−65	51	3.31	878
Fusiform gyrus	37	L	−59	−50	−14	4.16	878
Early visual cortex	17, 18	R	19	−100	1	8.30	22662

BA = Broadmann's area; H = hemisphere; *t* = statistical *t* value; T&T = Talairach and Tournoux coordinates; R = right; L = left; M = midline.

parietal lobe (BA 7), and bilateral cuneus (BAs 17 and 18; see Table 4, Figure 3).

DISCUSSION

The current study had four main findings. With regard to intentional encoding, results showed that encoding attempt was mediated by the left inferior frontal gyrus and early visual cortex, whereas encoding success was additionally mediated by the left hippocampus and PHG. With regard to intentional forgetting, forgetting attempt was mediated by the right superior frontal gyrus and right inferior parietal cortex, whereas forgetting success was additionally mediated by the right medial frontal gyrus. A PPI analysis found that the right superior and medial frontal gyrus exhibited negative connectivity with two separate

clusters in the left MTL (left hippocampus and PHG) during successful forgetting, suggesting that the right superior PFC plays a role in inhibition-based suppression of encoding-related processing. No such relationship was seen between these regions during successful encoding, incidental encoding, or incidental forgetting. Finally, results showed that intentional and incidental forgetting are dissociable on the neural level. Whereas intentional forgetting was associated with neural activity in the right parietal cortex, incidental forgetting was associated with neural activity in the left inferior frontal gyrus. Each finding is discussed individually in more detail below.

Intentional Encoding

Regarding the neural correlates mediating intentional encoding, our results converge on both the existing behavioral

and neuroimaging literature and lend support to the current theoretical framework that has been provided regarding differential encoding. Specifically, encoding attempt was associated with increased activity in the left inferior frontal gyrus, regardless of a memory outcome. These results suggest that viewing a cue to remember promotes encoding-related processes in a way that viewing a cue to forget does not, even if the item is later forget. Similar patterns of activity have been reported in other studies when focusing on encoding-related activity without separating trials by one's subsequent memory response (Wagner et al., 1998; Kapur et al., 1996; Domb et al., 1995). Specifically, the left inferior frontal gyrus has been linked to retrieval of semantic knowledge (Domb et al., 1995; for a review, see Gabrieli, Brewer, & Poldrack, 1998; Gabrieli et al., 1996). For example, Gabrieli and colleagues (1996) reported increased activity in the left inferior PFC when participants were required to make a semantic decision regarding a word as opposed to making a perceptual-based decision about the word. Although our study involved no such explicit encoding task, participants were aware that they would eventually be asked to retrieve TBR items and may have engaged in deep semantic processing to try to remember the TBR items. Such a strategy supports the theory

of differential encoding believed to underscore the memory difference between TBR and TBF items. Although the left inferior frontal gyrus was also shown to be more active for intentional remembering compared with intentional forgetting, the pattern of parameter estimates observed in this region suggests that, in general, this region is upregulated during the presentation of TBR items, as compared with TBF items, with a graded pattern of responding across TBR trial types (see Figure 2A). Accordingly, results suggest that, although this region is modulated by encoding success, it primarily engaged during encoding attempt and intent.

In addition to increased activity in the left PFC, a cue to remember also elicited increased activity in early visual cortex (BA 18). Although activity in this region has previously been associated with successful encoding of pictures (Gutches et al., 2005), it is interesting to note that, in the current study, this activity is associated with the memory cue that followed the item presentation and was not associated with the presentation of the item itself. We propose that this activity may be indicative of the recapitulation of item-specific sensory details (Slotnick & Schacter, 2004, 2006; Okado & Stark, 2003) that support encoding of item details. That is, we suggest that, when

Table 3. Intentional Forgetting

	BA	H	Coordinates (T&T)			t	mm ³
			X	Y	Z		
<i>Forgetting Attempt</i>							
Superior frontal gyrus	8	R	22	40	39	4.47	2085
Cingulate gyrus	24	L	−15	0	41	4.26	768
Postcentral gyrus	3, 1, 2	R	59	−26	42	4.63	22717
Postcentral gyrus	1, 2	L	−67	−22	32	3.62	1207
Precuneus	5, 7	L	−11	−36	53	4.24	9438
Inferior parietal lobe	40	R	52	−44	43	4.27	4993
Superior occipital gyrus	19	L	−30	−74	20	3.34	1975
<i>Successful Forgetting</i>							
Superior frontal gyrus ^a	10	R	26	57	14	3.87	1646
	9	M	7	61	27	3.43	1152
	8	R	19	22	53	3.92	878
Medial frontal gyrus ^a	8	R	26	36	39	5.16	5542
Cingulate gyrus	23	L	−19	−56	16	3.61	713
Postcentral gyrus	3	L	−63	−18	42	3.83	1043
Precuneus	7	M	4	−47	50	6.12	14431
Inferior parietal lobe ^a	40	R	48	−44	43	4.03	1646

BA = Broadmann's area; H = hemisphere; *t* = statistical *t* value; T&T = Talairach and Tournoux coordinates; R = right; L = left; M = midline.

^aThe peak voxel of each of these regions was used as a seed region for the PPI analyses.

Table 4. Intentional and Incidental Forgetting

	BA	H	Coordinates (T&T)			t	mm ³
			x	y	z		
Intentional Forgetting							
Postcentral gyrus	1, 2	R	63.11	−25.4	45.49	4.91	3841
Superior parietal lobe	7	R	18.56	−46.34	63.81	3.66	1701
	5, 7	L	−25.99	−42.53	67.07	3.47	1866
Precuneus	7	R	22.27	−32.67	45.85	4.68	3018
Inferior parietal lobe	40	L	−66.83	−22.46	31.52	4.89	1482
Incidental Forgetting							
Inferior frontal gyrus	47	L	−44.55	40.75	−15.29	4.17	2524
Inferior frontal gyrus	47	L	−51.98	26.7	−5.12	3.98	6420
Superior/medial frontal gyrus	6	L	−25.99	22.52	56.91	5.72	14267
Cingulate gyrus	32	M	0	28.92	39.32	4.43	4061
Superior frontal gyrus	6	M	0	12.13	67.79	3.92	878
Superior parietal lobe	7	L	−29.7	−61.56	50.75	4.42	1536
Early visual cortex	18	R	18.56	−104.09	1.43	3.97	1646
	17	L	−11.14	−104.25	−1.72	3.42	823

BA = Broadmann's area; H = hemisphere; *t* = statistical *t* value; T&T = Talairach and Tournoux coordinates; R = right; L = left; M = midline.

presented with a cue to remember, participants engage in the retrieval of sensory-related details of the item presentation in a manner similar to the recapitulation of sensory details that is experienced during successful retrieval. The retrieved details are then integrated into the encoding episode and support later memory for the TBR items. Alternatively, a cue to remember could lead participants to engage in imagery-related processing associated with the TBR items, with greater imagery leading to successful encoding. Additional research is needed to distinguish between these theoretical accounts.

Interestingly, a recent study by Sergent, Ruff, Barbot, Driver, and Rees (2011) found that auditory cues presented after the offset of visual cues (targets) increased activity in the early visual cortex and were associated with increased ability to accurately report the location of the (visual) targets. As this memory facilitation only occurred when the auditory cue was presented 200 msec after the target but not when it was presented 1000 msec after the target, the authors suggest the presence of a critical window in which recapitulation of visual information in visual cortex can benefit behavioral performance. The current results expand on this finding by suggesting that activity in early visual cortex can be recruited up to 2000 msec after stimulus offset, while still aiding behavioral performance. Additionally, our results illustrate that this activity can be successfully recruited differentially, based on the type of postcue stimulus that is provided. That is, although Sergent

et al. (2011) reported differential early visual activity when comparing cued trials to uncued trials, our study suggests that this region may also respond to different types of cues, as evidenced by increased activity for TBR as compared with TBF cues.

Taken together, the foregoing activation patterns support the theory that TBR items undergo differential processing as compared with TBF items. Specifically, a cue to remember promotes intentional encoding processes that serve to enhance the representation of the word through semantic elaboration and recapitulation of sensory details associated with the item. However, encoding attempt alone does not beget successful subsequent memory. Along with the left inferior frontal gyrus and early visual cortex, successful encoding was also mediated by activity in the left superior parietal cortex (BA 7), left inferior temporal gyrus (BA 37), and left hippocampus/ PHG (BAs 28 and 35). The superior parietal cortex has been shown to mediate increased attentional control (Corbetta & Shulman, 2002) and has been implicated in successful encoding (for a review see Uncapher & Wagner, 2009). Specifically, this region is most often associated with successful retrieval (Donaldson, Petersen, & Buckner, 2001; Konishi, Wheeler, Donaldson, & Buckner, 2000; for a review, see Wagner, Shannon, Kahn, & Buckner, 2005) and retrieval of item-specific details (i.e., recollection; Wheeler & Buckner, 2004; Dobbins, Rice, Wagner, & Schacter, 2003; Henson, Rugg, Shallice, Josephs, & Dolan, 1999). For example, Henson

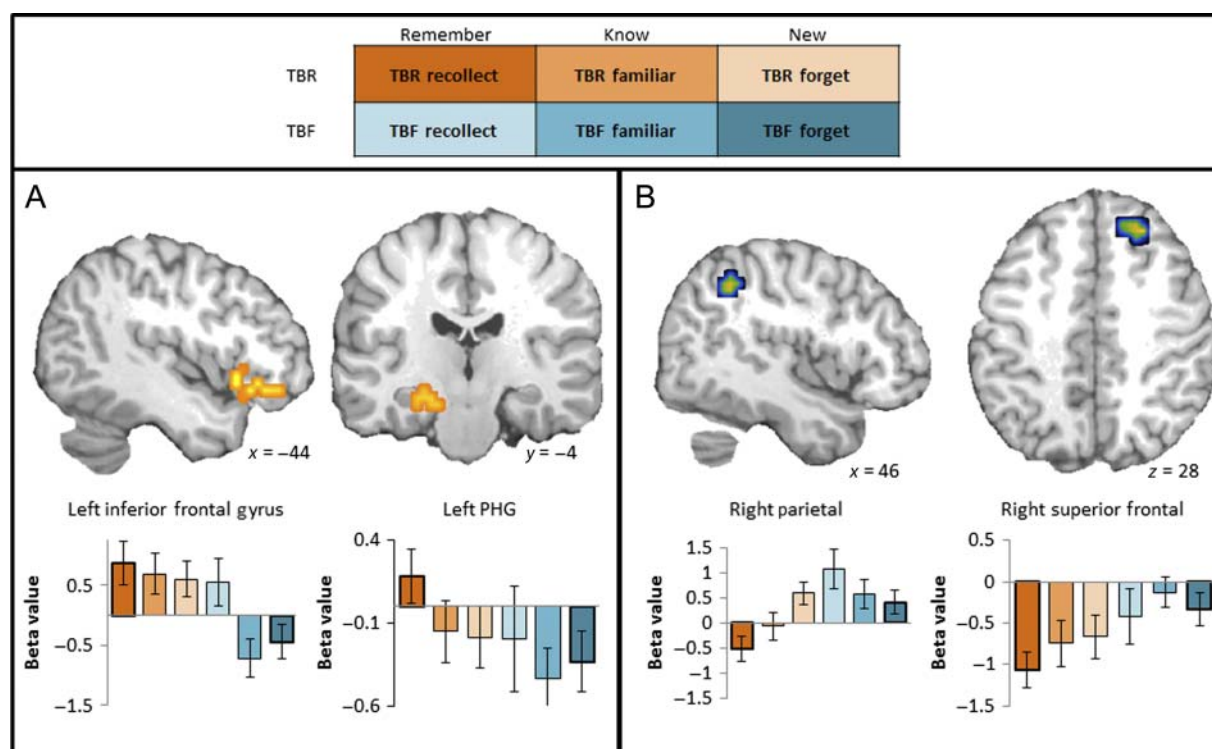
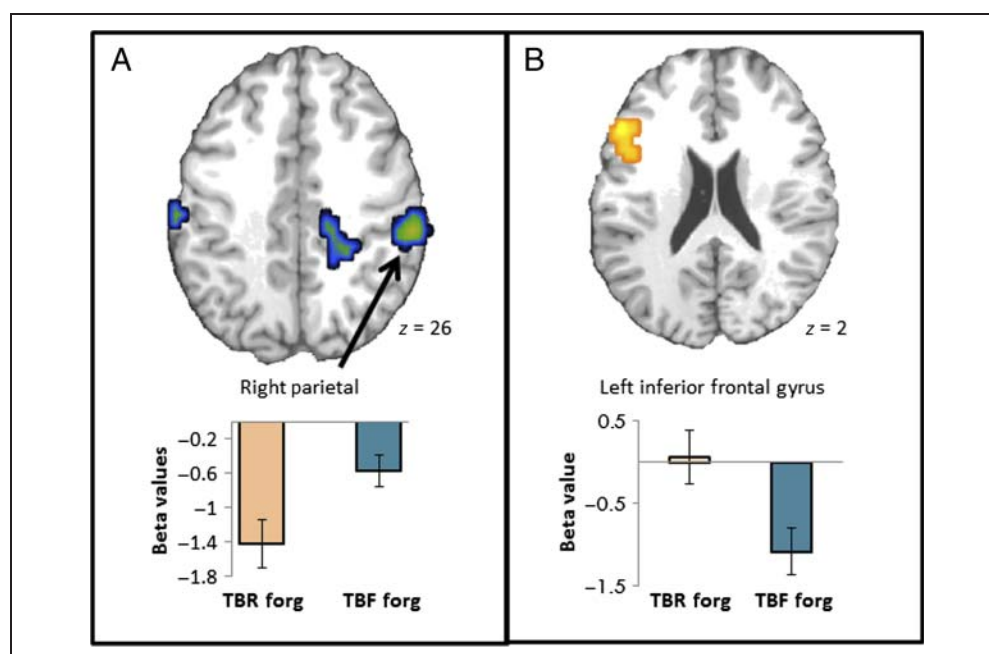


Figure 2. (A) Areas significantly more active for successful intentional remembering than successful intentional forgetting, including the left inferior frontal gyrus and left PHG. (B) Areas significantly more active for successful intentional forgetting than successful intentional remembering, including the right parietal lobe and right superior frontal gyrus. See Tables 2 and 3 for coordinates of peak activation.

et al. (1999) reported increased activity in the left superior parietal lobe during a recognition test for correct recollection responses as opposed to correct familiar responses and concluded that this activity was related to a reinstatement of words from the encoding period. The current results

afford a similar conclusion, particularly given that this activity was associated not only with a presentation of a cue to remember but also with subsequent successful recollection of the item. Thus, in accord with the recapitulation theory described above, we propose that increased activity in the

Figure 3. (A) The right parietal cortex was significantly more active for intentional forgetting than incidental forgetting, whereas (B) the left inferior frontal gyrus was more active for incidental forgetting than intentional forgetting. See Table 4 for coordinates of peak activation.



left superior parietal lobe, in conjunction with activity in early visual cortex, supports the recapitulation of the stimuli leading to subsequent recollection.

Finally, results also show that the hippocampus/PHG supports successful intentional remembering. The role of the MTL in supporting encoding success has been well documented (e.g., Kim & Cabeza, 2007; Schacter et al., 1999; Fernandez et al., 1998; Kelley et al., 1998; Kapur et al., 1996). The current study expanded this previous research in observing MTL activity associated not with the TBR item *per se* but with the TBR instruction cue associated with subsequently recollected items. Moreover, although the MTL was associated with successful intentional encoding, it was not found to be differentially active during either encoding attempt or intentional forgetting. In fact, neural activity within this MTL cluster suggests that this activity is driven primarily by an increased hippocampal gyrus and PHG activity during TBR-recollection trials, compared with all other trial types. Thus, unlike previous DF results, which have observed MTL activity for both successful encoding and intentional forgetting (Wylie et al., 2008) and encoding success without examining activity associated with intentional forgetting (Reber et al., 2002), the current study supports a role of the MTL solely for encoding success. Unfortunately, we cannot offer a satisfying explanation as to why Wylie and colleagues (2008) observed MTL activity associated with intentional, as opposed to incidental, forgetting. Although Wylie and colleagues did find MTL activity associated with encoding success, it is unclear whether (1) the two clusters of activity overlapped and (2) how MTL activity in forgetting contrasts related to encoding success activity in the same region. Considering the fact that MTL activity was not expected for forgetting, future research is necessary to reconcile this finding with the current literature. Taken together, the current results provide support for the presence of differential encoding within the DF paradigm and are the first to identify MTL activity only for items that are both instructed to be remembered and subsequently recollected. Overall, results suggest that individuals are able to discriminate between which should be remembered and which should be forget and recruit the neural networks required to successfully execute successful encoding processes.

Intentional Forgetting

Regarding the neural correlates of intentional forgetting, our results suggest that both forgetting attempt and forgetting success are mediated by activity in the right PFC and right parietal lobe. Specifically, the right superior frontal gyrus and inferior parietal lobe were active for both forgetting attempt and successful intentional forgetting. With regard to the right superior PFC, the pattern of neural activity shows the opposite pattern of that observed in the left PFC. That is, activity in the right superior PFC is upregulated in response to a cue to forget, as compared with a cue to remember, with a graded

pattern of responding across all trial types (see Figure 2B). Behavioral theory posits that intentional forgetting and forgetting success in the DF paradigm is mediated by one's ability to inhibit the encoding of the presented item. As such, increased activation in both the right PFC and parietal lobe have been interpreted as reflecting inhibitory processing [with much of this evidence supported by cognitive tasks requiring inhibition of a motor response (Kramer et al., 2011; Levy & Wagner, 2011; Hedden & Gabrieli, 2010; Aron & Poldrack, 2006; Aron et al., 2003; Rubia et al., 2001; Garavan et al., 1999)].

Although the right PFC has generally been shown to play a reliable role in tasks that involve inhibitory responses (Wylie et al., 2008; Aron & Poldrack, 2006; Anderson et al., 2004; Aron et al., 2003; Rubia et al., 2003; Garavan et al., 1999; Jonides et al., 1998), our current findings contribute to a slowly emerging pattern of results regarding a more specific inhibitory-related dissociation within this region. Specifically, it has been shown that tasks requiring the inhibition of a motor response (e.g., go/no-go and stop-signal tasks) rely on activation of the right inferior PFC (Aron & Poldrack, 2006; Aron et al., 2003; Rubia et al., 2003; Garavan et al., 1999; Jonides et al., 1998). However, the few studies that have employed tasks that are clearly inhibitory-related and yet do not involve a motor response (e.g., think-no-think; DF) report increased activation in the right PFC, superior to that observed in motor inhibition (i.e., middle frontal gyrus and superior frontal gyrus; Wylie et al., 2008; Depue et al., 2007; Anderson et al., 2004). For example, when participants are instructed to make a keypress any time the letter "X" appears on the screen, except if an "X" had also been presented on the previous trial, the inferior frontal gyrus is active during trials in which the keypress to a second "X" must be inhibited (Garavan et al., 1999). However, when a participant must inhibit a cognitive process such as suppressing the retrieval of a learned association (e.g., Anderson et al., 2004), similarly right lateralized but middle frontal gyrus activity is observed. This dissociation may reflect a functional dissociation within the right PFC with regard to different aspects of stimuli processes (e.g., Anderson & Huddleston, 2012; Anderson & Weaver, 2009). That is, although the right inferior PFC may inhibit activation in regions responsible for executing a motor task, more superior regions in the right PFC appear to inhibit activation in regions associated with more cognitive-based tasks (e.g., encoding and retrieval in memory).

With regard to the parietal lobe, research in the area of cognitive control denotes an important role of this region in supporting both motor inhibition (for a review, see Simmonds, Pekar, & Mostofsky, 2008) and retrieval suppression (for a review, see Anderson & Huddleston, 2012). For example, with regard to motor inhibition, Boehler and colleagues (2010) found the right inferior parietal cortex to be active for successful stop-signal trials as compared with successful go trials (in a go/no-go task) as well as for trials in

which participants received a stop signal and were required to inhibit a motor response (stop-relevant), as compared with trials when participants received a stop signal but were required to provide the motor response anyway (stop-irrelevant). As such, the authors concluded that the right inferior parietal lobe supports the successful withholding of a motor response. In addition, extensive research in the TNT paradigm finds the parietal episodic memory effect to be reduced as a result of retrieval suppression, such that activity in this region is an indicator of the degree to which a stimulus has been suppressed (Anderson & Huddleston, 2012; Bergstrom, Velmans, & Richardson-Klavehn, 2007). Our data regarding parietal lobe activation both compliment and extend this research, supporting the notion of its importance in successful inhibitory processes but also demonstrating that its function may be quite different from that of the PFC and may be more strongly related to a diversion of attention.

As noted above, we found the right inferior parietal lobe to be active in response to both a cue to forget compared with a cue to remember and in our measure of forgetting success. Examining the parameter estimates across all trial types in this cluster showed that, unlike the linear trend observed in the frontal regions, activity in the parietal lobe appears to be upregulated for TBF items as well as for items that were incidentally forget, thus suggesting that this region may support attentional processes that are diverted both when an item is attempted to be forget and when it is successfully forget (regardless of attempt). In an attempt to further clarify the role of the parietal cortex with regard to cognitive control processes associated with intentional forgetting, we looked for evidence of inhibition using functional connectivity analyses (see below). Although the parietal lobe did appear to support intentional forgetting, our results showed no evidence for a role of this region in the inhibition of encoding-related regions (i.e., MTL). Thus, we propose that the inferior parietal lobe may be associated with the withdrawal of attentional processes that support successful forgetting by withdrawing from encoding-related activities (see also Levy & Wagner, 2011).

Finally, the reported results regarding intentional forgetting illustrate an overall pattern with regard to the lateralization of successful encoding and successful forgetting. Whereas encoding attempt and success were shown to be strongly left lateralized, intentional forgetting was strongly right lateralized. Thus, with respect to the localization of inhibitory processes, our results contribute to the growing body of literature that has demonstrated the hemispheric lateralization of many cognitive processes (Aron & Poldrack, 2006; Vigneau et al., 2006; Garavan et al., 1999; Kelley et al., 1998; Zatorre, Evans, Meyer, & Gjedde, 1992). In summary, our results support the theory that the inhibition required to prevent encoding may be part of a larger and more general right-lateralized inhibitory network (Kramer et al., 2011; Hedden & Gabrieli, 2010; Wylie et al., 2008; Aron & Poldrack, 2006; Anderson et al., 2004; Garavan et al., 1999).

Although reporting right-lateralized activity for tasks that require inhibition is not a particularly new finding, our interpretation of the types of processes for which this activity is required is new. Garavan et al. (1999) suggested two possible explanations for the right parietal lobe activity that they isolated in their study of response inhibition. They proposed that this activity was due either to the retraction of the motor response necessary to not respond during no-go trial or that it was part of an increased attention-related network that was recruited as a result of the presentation of these less-frequent trials. Our results, however, suggest that the right parietal and PFC regions are responsible for more than these two roles. The use of a DF paradigm elicited robust right-lateralized activity in response to TBF trials, despite the fact that these trials did not require the inhibition of a motor response and were presented with equal frequency as compared with TBR trials.

Connectivity Analysis

Whereas inhibition is defined as a mental process imposing restraint on behavior or another mental process, the inhibition theory of DF posits that intentional forgetting is a cognitive process that actively inhibits the encoding of unneeded information (rather than forgetting as the passive decay of the memory trace). As noted, a direct link between inhibition-related processing in the right superior PFC and inferior parietal cortex and encoding-related processing in the MTL is necessary to confirm this behavioral theory. Considering this, we examined the relationship between both the right superior PFC and inferior parietal cortex with that of the MTL during both intentional remembering and intentional forgetting. Specifically, we investigated the presence of potential correlations (or the lack thereof) between the time course of voxels active in inhibitory and encoding processes. As such, inhibition would be supported by a negative relationship between activation in regions associated with intentional forgetting (i.e., right PFC) and those associated with intentional remembering (i.e., MTL). Moreover, it was hypothesized that this relationship would be present during successful intentional forgetting but not during remembering.

Results showed a significant negative correlation between the time courses of the right superior frontal gyrus and the left hippocampus as well as between the right middle frontal gyrus and the left PHG. Although these negative correlations were observed during trials in which the stimuli were intentionally forget, they were absent during trials in which the stimuli were intentionally remembered, incidentally remembered, or incidentally forget, suggesting a specific inhibitory role of this region in successful intentional forgetting. As noted, the right middle and superior frontal gyri have been associated with inhibitory processes across several previous studies examining nonmotor inhibition (Wylie et al., 2008; Depue et al.,

2007; Anderson et al., 2004), and these studies have theorized that activity in this region may mediate activity within MTL during memory control processes. However, to our knowledge, this is the first study to directly link increased activation in the right PFC to reduced activity in the MTL within participants. Although the MTL, including the PHG, is critical to successful encoding, our results provide novel evidence supporting a theory of intentional forgetting that is based on the active inhibition of encoding processes in this region. Furthermore, the lack of any correlation (neither positive nor negative) between these regions during encoding attempt and success indicates that this negative coupling between the right PFC and MTL is not an invariable state but one that is specifically engaged following explicit instructions to forget information. Although we acknowledge that causality cannot be inferred from the negative relationship observed in the PPI analyses, these results, in combination with other neuroimaging data supporting the role of PFC as the locus of inhibitory processing, strongly support the behavioral theory regarding successful forgetting in DF as one mediated by active inhibition of encoding. A lack of significant correlations between the right inferior parietal cortex and any MTL region suggests that, unlike the right PFC, the parietal cortex does not engage in active inhibition but perhaps supports intentional forgetting by a diversion of attention away from irrelevant stimuli.

To our knowledge, ours is the first study that has used functional connectivity analyses to support the theory of active inhibition in cognitive control of memory encoding (see a recent study by Benoit & Anderson, *in press*, for similar work in the area of retrieval inhibition). The analysis overcomes limitations in previous studies that only theorized such a relationship and provides a clearer and more complete view of the cognitive mechanism underlying intentional forgetting in the DF paradigm. Moreover, our results contribute to the existing literature related to the cognitive control of memory in that they emphasize the separate contributions of PFC and the parietal lobe to intentional and successful forgetting. Despite these advances, the current analysis cannot distinguish between two possible inhibitory processes, encoding preemption and memory disruption. That is, it remains unclear whether the right PFC inhibits subsequent memories by preventing sensory information from reaching the hippocampus for processing or whether PFC inhibits an already-formed (or partially formed) memory within the hippocampus (similar to the mechanism proposed in retrieval inhibition). Future research is needed to distinguish between these possible mechanisms and determine the directionality and potential causality of the negative coupling observed between the right PFC and MTL.

Intentional and Incidental Forgetting

The final goal of this study was to investigate the dissociation between intentional and incidental forgetting.

Behaviorally, many studies have posited that, whereas incidental forgetting arises from a failure of encoding, intentional forgetting is driven by a separable and active inhibitory process. This theory is supported by the vast amount of behavioral literature that shows increased forgetting of TBF items compared with forgetting associated with TBR items (for a review, see Basden, Basden, & Gargano, 1993). Despite these behavioral results, no study has shown a true dissociation in the neural correlates underlying each type of forgetting. The current results show that, when directly compared, intentional forgetting was associated with increased activity in the right superior parietal lobe, whereas incidental forgetting was associated with activity in the left inferior frontal gyrus, left superior frontal gyrus, early visual cortex, and left superior parietal lobe.

Our results not only exhibit a clear dissociation between the neural correlates mediating each type of forgetting but also support the behaviorally based theory that forgetting of TBF items is an active goal-driven process and is not simply mediated by the absence of encoding-related activity. If forgetting of TBF items was simply because of the passive decay of information, one would expect to see a pattern of activity similar to that of TBR items, with simply less encoding-related activity. This, however, is not the case. Unlike the left-lateralized incidental forgetting, intentional forgetting was driven by right-lateralized parietal activity, which has already been theorized to strongly contribute to cognitive control processes and intentional redirection of attentional resources (Boehler et al., 2010; Wylie et al., 2008; Garavan et al., 1999).

Incidental forgetting, on the other hand, does appear to be mediated by regions associated with encoding attempt (Slotnick & Schacter, 2004, 2006; Okado & Stark, 2003; Corbetta & Shulman, 2002; Gabrieli et al., 1996; Demb et al., 1995). As such, results suggest that, during the presentation of a cue to remember, participants engage in encoding-related activity, but despite this attempt, the amount of encoding may not be sufficient to preserve successful encoding of the item. Other regions found to be significantly more active for incidental than intentional forgetting (specifically, BAs 7 and 32) were recently reported as part of a meta-analysis examining the neural correlates of subsequent forgetting (Kim, 2011). These regions have been posited to be involved in the default-mode network, thus suggesting that this activity may be indicative of decreased attention or mind wandering (Kim, 2011). The lack of significantly greater PFC activity for intentional as compared with incidental forgetting suggests that this region is recruited, to some extent, during a failed encoding attempt. As noted previously, however, this region was not found to be directly inhibiting the MTL during incidental forgetting, as it did during intentional forgetting. Considering this, we posit that the below-threshold right PFC activity that appears during incidental forgetting is the result of an encoding attempt that utilizes regions more widespread than the typical encoding network and, as a result, is unsuccessful. As such, results suggest that

incidental forgetting is the result of an encoding attempt but ultimate failure. Although Wylie et al. (2008) also found evidence for intentional forgetting, they did not examine the neural correlates associated with incidental forgetting and thus were unable to conclude that these separate forms of forgetting are truly mediated by separable neural correlates. This is the first study to directly compare differences in the neural correlates that are associated with intentional and incidental forgetting and thus the first to conclude that incidental and intentional forgetting are driven by two separable cognitive processes.

Conclusion

The current study investigated the cognitive control processes that mediate successful memory—including both intentional remembering and intentional forgetting. Whereas intentional remembering was found to be mediated by a left-lateralized network of PFC and MTL regions, intentional forgetting was mediated by a right-lateralized network that included the superior frontal gyrus and inferior parietal cortex. Although previous studies have suggested that intentional forgetting is driven by inhibitory processes that emanate from the right PFC, ours is the first study to directly link increased activity in the right superior PFC to suppression of activity in encoding-related regions (e.g., MTL). Finally, our results demonstrate a clear dissociation between incidental and intentional forgetting, indicating that, whereas the former is mediated by encoding attempt, the latter is driven by a combination of active inhibition and diversion of attention. In conclusion, these findings provide both strong and novel support for the identification of the right superior PFC as a critical region for the active inhibition of encoding. Furthermore, we have provided evidence for the neural basis in support of the two-theory account of intentional forgetting, such that differential encoding and attentional inhibition both contribute to the cognitive control of memory.

Acknowledgments

Awarded to N. A. D.: Grant sponsor: NSF; Grant number: 1025709. Portions of this research were conducted while N.A.D. was an AFAR Research Grant recipient from the American Federation for Aging Research.

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