

## Dissociable roles of default-mode regions during episodic encoding

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### ABSTRACT

We investigated the role of distinct regions of the default-mode network (DMN) during memory encoding with fMRI. Subjects encoded words using either a strategy that emphasized self-referential (pleasantness) processing, or one that emphasized semantic (man-made/natural) processing. During encoding subjects were intermittently presented with thought probes to evaluate if they were concentrated and on-task or exhibiting task-unrelated thoughts (TUT). After the scanning session subjects performed a source retrieval task to determine which of two judgments they performed for each word at encoding. Source retrieval accuracy was higher for words encoded with the pleasantness vs. the man-made/natural task and there was a trend for higher performance for words preceding on-task vs. TUT reports. fMRI results show that left anterior medial PFC and left angular gyrus activity was greater during successful vs. unsuccessful encoding during both encoding tasks. Greater activity in left anterior cingulate and bilateral lateral temporal cortex was related successful vs. unsuccessful encoding only in the pleasantness task. In contrast, posterior cingulate, right anterior cingulate and right temporoparietal junction were activated to a greater extent in unsuccessful vs. successful encoding across tasks. Finally, activation in posterior cingulate and bilateral dorsolateral prefrontal cortex was related to TUT across tasks; moreover, we observed a conjunction in posterior cingulate between encoding failure and TUT. We conclude that DMN regions play dissociable roles during memory formation, and that their association with subsequent memory may depend on the manner in which information is encoded and retrieved.

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### Introduction

The default-mode network (DMN) refers to a set of regions including medial prefrontal cortex (mPFC), posterior cingulate cortex (PCC), inferior parietal lobes (IPL), and lateral temporal cortex (LTC) (Buckner et al., 2008). A formal characterization of this network came from task-based meta-analyses which found that these regions were activated to a greater extent during passive resting-state conditions compared to a variety of externally-driven and cognitively demanding tasks, such as visual search and episodic memory retrieval (Nyberg et al., 1996; Shulman et al., 1997). More recently, similar task-related reductions in activity in DMN regions has been reported during episodic encoding studies (e.g., Daselaar et al., 2004). Furthermore, a recent meta-analysis indicated that increased activation in all major DMN regions during episodic encoding, including ventral medial PFC, PCC, bilateral IPL and LTC is predictive of retrieval failure (Kim, 2010). It has been suggested that since successful encoding requires externally-directed attention, activation in DMN regions should be suppressed, reflecting down-regulation of task-unrelated thoughts (TUT) (Daselaar et al., 2009; Shrager et al., 2008), defined here as thoughts that are not relevant to encoding items. This

suggestion is consistent with behavioral evidence indicating that the frequency of TUT at encoding is negatively correlated with retrieval performance in young adults (Maillet and Rajah, 2013; Seibert and Ellis, 1991); and is also compatible with evidence that DMN regions are involved in TUT at rest and during some cognitive tasks such as the sustained attention to response task (Andrews-Hanna et al., 2010a; Christoff et al., 2009; Stawarczyk et al., 2011). However, to our knowledge, the hypothesis that activation in DMN regions during episodic encoding reflects TUT has never been directly tested.

Furthermore, although the majority of the literature indicates that activation in DMN regions is suppressed during successful episodic encoding, these studies have mostly used semantic encoding tasks, such as judging whether words are man-made/natural (Kim, 2010). Such tasks are known to deactivate DMN regions (e.g., Lustig et al., 2003). In contrast, increased activation in some DMN regions has been observed during successful encoding when the encoding task emphasized subjective evaluation of stimuli in relation to oneself. For example, successful encoding using both pleasantness judgments, or judging whether adjectives are descriptive of oneself have both been associated with activation in mPFC (e.g., Leshikar and Duarte, 2012; Macrae et al., 2004; Maillet and Rajah, 2011; Shrager et al., 2008; Zierhut et al., 2010) and at least one study using pleasantness judgments has also reported correct subsequent memory effects in IPL (Schott et al., 2011). Moreover, encoding using such self-referential strategies results in better memory compared to semantic and perceptual

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encoding tasks (e.g., Leshikar and Duarte, 2012; Mailliet and Rajah, 2013). It has been suggested that this increase in memory is due to the superior organizational and elaborative processes associated with encoding information in relation to the self (Rogers et al., 1977; Symons and Johnson, 1997). In contrast, in another fMRI study where subjects encoded words using a pleasantness judgment, it was found that activation in left mPFC predicted retrieval success; but, activation in right mPFC, PCC/precuneus, and bilateral temporoparietal junction predicted retrieval failure (Shrager et al., 2008). Taken together, these studies suggest that when self-referential encoding strategies are used, a subset of DMN regions may be involved in encoding success, while a distinct set of regions may be involved in encoding failure, perhaps due to TUT.

These results are consistent with evidence that the DMN can be fractionated into distinct subsystems, only some of which are preferentially recruited during self-referential processing. For example, Andrews-Hanna et al. (2010b) reported that a dorsal medial PFC subsystem, which included regions such as dorsal medial PFC, LTC, temporal pole and temporoparietal junction was preferentially activated when people made self-relevant decisions. In addition, Andrews-Hanna et al. (2010b) identified a distinct subsystem, which included retrosplenial cortex and IPL, that was preferentially engaged when individuals constructed mental scenes based on memory. More recently, Qin and Northoff (2011) performed a quantitative meta-analysis indicating that in contrast to other DMN regions, only the ventral anterior cingulate (ACC) was preferentially recruited during self-referential decisions. In another meta-analysis, Kim (2012) reported evidence that a subsystem including anterior medial PFC and posterior cingulate mainly supports self-referential processes, while regions including IPL and LTC were involved in memory retrieval. Thus, although there is some inconsistency, these results converge to suggest a particularly important role of mPFC in self-referential processes, which is in agreement with studies indicating that this region is involved in encoding success when items are encoded in relation to the self.

These prior studies also suggest that other DMN regions, including PCC, IPL and LTC, are involved in encoding failure regardless of whether the encoding task is self-referential or semantic because the cognitive processes subserved by these regions are recruited to a greater extent during TUT relative to encoding items using these strategies. Previous studies suggest that the content of TUT during the performance of a cognitive task in an fMRI scanner is varied and may include: mind-wandering (e.g. thoughts about the past or the future), distractions involving monitoring of the internal or external environment (e.g. thinking about how hungry one is, thinking about scanner noise etc.), and task-related interferences (e.g. thoughts related to the appraisal of the current task) (Stawarczyk et al., 2011). These thoughts may recruit cognitive processes that have been associated with PCC, LTC and IPL such as, scene construction (Hassabis et al., 2007), memory retrieval (Kim, 2012; Wagner et al., 2005), internally focused attention (Buckner et al., 2008), prospection (Addis et al., 2007), and monitoring of internal/external milieu (Raichle et al., 2001).

The current study was designed to investigate the role of distinct DMN regions during encoding of word stimuli. We used fMRI to examine regional activity while subjects performed self-referential (pleasantness) and semantic (man-made/natural judgment) encoding of verbal stimuli. We pseudo-randomly inserted thought probes throughout the encoding task that asked subjects to provide self-reports of their current mental state (Christoff et al., 2009; Stawarczyk et al., 2011). During thought probes, subjects reported whether they were focused on task, or whether they were exhibiting TUT (i.e. mind-wandering, task-related interferences or distractions) (Stawarczyk et al., 2011). Ten minutes after fMRI scanning, subjects performed a source memory retrieval task for encoded stimuli.

The first goal of this study was to directly test the hypothesis that due to its involvement in self-referential processes, mPFC would be activated to a greater extent in successful vs. unsuccessful encoding of

verbal items when a pleasantness but not when a man-made/natural encoding strategy is used. Also, based on findings that retrosplenial cortex/PCC, IPL and LTC may be recruited during in processes such as construction of mental scenes (Andrews-Hanna et al., 2010b; Hassabis et al., 2007) and/or memory retrieval (Kim, 2012; Wagner et al., 2005), and that these regions have been involved in encoding failure even when a self-referential task is used (Shrager et al., 2008), we predicted that these regions would be activated to a greater extent in unsuccessful vs. successful encoding of word stimuli independently of the task. In addition, we tested the hypothesis that the DMN regions activated in unsuccessful vs. successful encoding would also be activated to a greater extent when subjects were off-task (exhibiting TUT) vs. on-task. To identify the neural correlates of TUT during episodic memory encoding, we contrasted the activation in encoding trials preceding TUT (off-task) reports with the activation in encoding trials preceding on-task reports. Reaction times for the events preceding thought probes were used as an objective measure for whether the TUT episode, whose occurrence was measured during the thought probe, extended to the preceding encoding event. Specifically, we predicted that if this was the case, encoding trials in which TUT occurred would be associated with longer reaction times vs. those where no TUT occurred.

## Methods

### Subjects

Twenty-one, right-handed, healthy adults (age range 18–30, mean age = 23.33, 12 women) participated in the study. Participants reported no history of psychiatric illness, neurological disorders, or substance abuse and were healthy at time of testing. Participants had a minimum of high school education (mean education = 16.35 year). Volunteers were recruited with advertisements on university websites in the city of Montreal. All participants signed a consent form approved by the ethics boards of the Douglas Mental Health University Institute.

### Behavioral methods

Participants visited the Douglas Mental Health University Institute on two separate occasions. In the first session, they completed a series of neuropsychological tasks including the Montreal Cognitive Assessment Scale (Nasreddine et al., 2005) (cut-off > 25) and the Beck Depression Inventory (Beck, 1987; Beck et al., 1961) (cut off < 10). They also completed the Edinburgh inventory (Oldfield, 1971), and were all right-handed according to this test. Finally, participants performed a practice version of the fMRI task in a mock MRI scanner, which familiarized them with the memory task and thought classification prior to the fMRI session (session two).

Participants returned for a second session to perform an episodic memory task for words, while undergoing fMRI scanning. The MRI session consisted of an anatomical scan (5 min) and 4 fMRI encoding runs (each 10 min 20 s). Thus, in total, the encoding portion of the experiment lasted approximately 41 min. The stimuli used in the memory task were 414 French nouns of 3–11 letters, taken from Desrochers and Thompson (2009) and the OMNILEX database (<http://www.omnilex.uottawa.ca/scrServices.asp>). The experiment was carried out in French, given that Montreal is a primarily French-speaking city. In total, 414 nouns were used: 276 served as encoding words, while the other 138 were used as distractors at retrieval. Half of the words were used in the pleasantness task, while the other half was used in the man-made/natural task. The words were not switched across the pleasantness and man-made/natural task for different subjects. However, T-tests indicated that words used in pleasantness encoding, man-made/natural encoding and words used as distractors in the retrieval task were matched for number of letters (mean with standard deviation: 6.46 (1.82), 6.68 (1.67) and 6.60 (1.74) respectively), number of syllables (mean with standard deviation: 2.05 (0.68), 2.02 (0.72)

and 2.00 (0.71) respectively), frequency ratings (mean with standard deviation: 3.49 (1.15), 3.30 (1.11) and 3.47 (1.08) respectively) and imageability ratings (mean with standard deviation: 4.48 (1.5), 4.43 (1.62) and 4.62 (1.56) respectively). Half of the words in all tasks represented man-made objects (e.g., pencil, computer, car), and the other half were natural (e.g., cat, apple, rose).

During each encoding run, subjects were presented with words, one at a time, in the center of the screen for 2.5 s/word. They were asked to answer one of two questions for each word during encoding: 1) determine whether it was man-made (semantic encoding task) or 2) judge if they think the word was pleasant (self-referential encoding task). The question to be answered on any given trial was indicated by an appropriate cue, presented below each word (“Pleasant?” or “Man-made?”). For both encoding tasks, participants answered “yes” with button 1 and “no” with button 2. Encoding trials were separated by a variable inter-trial interval (ITI) of either 2.2, 4.0, or 6.7 s (mean = 4.3 s) which served to add jitter to the fMRI acquisition sequence, allowing dissociation of event-related changes in BOLD activity (Dale, 1999). Participants were informed that a retrieval task would follow; thus encoding was intentional.

Participants performed the same encoding task for 4, 5, 6 or 7 consecutive words. After 4–7 words, there was a 2.5 sec ITI, followed by a thought probe was presented on screen for 7 s. Following the thought probe, the encoding task was switched for the next 4–7 words.

During the thought probe subjects were asked to report the type of thought that they were experiencing the moment the probe came on screen (Christoff et al., 2009; Stawarczyk et al., 2011). In accordance with the methods used by Stawarczyk et al. (2011), subjects chose between 1) being concentrated on the task, 2) mind-wandering (e.g. I thought about my personal worries, I thought about something that happened in the past or future, etc.), 3) task-related interferences (e.g. I thought about how long, boring, easy or hard the task was, etc.), or 4) thinking about internal distractions (e.g. feeling uncomfortable, thinking about back pain, etc.) or external distractions (e.g. thinking about scanner noise). Note that we use the term “task-unrelated thought (TUT)” to refer to mind-wandering, task-related interferences and distractions. Although it may appear contradictory that we included task-related interferences as a component of task-unrelated thought, our use of the term TUT is meant to refer to a collection of thoughts that are not relevant to encoding words, rather than thoughts unrelated to the task itself. Participants were familiarized with the thought classification, and given examples of each category during the practice session. In total, there were 54 thought probes across the four encoding runs (13 or 14 per run).

Approximately 10 min following the end of the encoding task, subjects performed a source memory retrieval task outside of the scanner. During retrieval, all 276 encoding words (138 in the pleasantness task, and 138 in the man-made/natural task), mixed with 138 new words, were presented one at a time. Each word appeared on-screen for 4.5 s, followed by a fixed 1 s ITI. Subjects were asked to choose whether each word was 1) old and studied in the pleasantness task, 2) old and studied in the man-made task, 3) old (but no recall of the encoding task) or 4) new. The correct response was 1) on 33.3% of trials, 2) on 33.3% of trials and 4) and 33.3% of trials.

#### *fMRI data acquisition*

The MRI and fMRI data were collected using a 3 T Siemens Trio scanner at the Douglas Mental Health University Institute Brain Imaging Centre. A standard whole-head coil was used, and cushions were inserted to stabilize head motion. A high-resolution structural scan was acquired using a 5.03 min gradient-echo (GRE) sequence (TR = 2300 ms, TE = 2.98 ms, flip angle = 9, 172 1 mm sagittal slices, field of view = 256 mm, 1mm × 1mm × 1mm resolution). Following the structural scan, subjects performed the aforementioned episodic memory task during four 10.26 min runs while blood-oxygen-level-

dependent (BOLD) images were acquired using a fast echo-planar imaging (EPI) pulse sequence (TR = 2000 ms, TE = 30 ms, field of view = 256 mm, in-plane resolution = 4 × 4 × 4mm). 308 fMRI volumes were acquired in each of the four encoding runs, for a total of 1232 in the experiment.

#### *Behavioral data analysis*

##### *Event trial classification*

We analyzed the behavioral data in a way that matched the fMRI data analysis (see later section). Specifically, the 276 encoding events were divided into those directly preceding the thought probes (n = 54), and those that did not (n = 222). Words directly preceding thought probes were classified as either “on-task” or “off-task”, depending on the answer provided during the thought probe. Off-task trials were those in which subjects responded that they were exhibiting any type of TUT (mind-wandering, task-related interferences or distractions), while on-task trials were those in which they responded that they were concentrated on the task, irrespective of subsequent memory. The encoding trials that did not directly precede thought probes were divided into “correct pleasantness encoding” (PleasCor), “incorrect pleasantness encoding” (PleasIncor), “correct man-made/natural encoding” (ManCor) and “incorrect man-made/natural encoding” (ManIncor). Correct events were those words that were subsequently remembered and attributed to the correct encoding task (correct source). Incorrect events were all other events types, in which the source was forgotten (source misattribution, item recognition with no recollection of source, and missed words). We chose to combine these events types due to the small number of “misses” in the pleasantness task (mean = 14). As noted in a previous study using this methodology, this means that our behavioral and fMRI results distinguish encoding events for which the source was later remembered vs. forgotten, but do not speak to the question of events later attracting a correct recognition judgment without source vs. misses (Gottlieb et al., 2010). However, we did conduct exploratory analyses using only misses, reported in section 3.2.3.

##### *Reaction time*

We analyzed encoding reaction time data primarily to test the hypothesis that encoding trials directly preceding on-task reports would be associated with faster reaction times compared with encoding trials preceding off-task reports. A two-tailed paired samples *t*-test was used to assess this hypothesis. A separate two-way encoding task (man-made/natural vs. pleasantness) by subsequent memory (correct vs. incorrect) ANOVA was used to analyze RT on the remaining encoding trials which did not directly precede the thought probes.

We also examined whether retrieval RT differed as a function of encoding task or subsequent memory. A two-way encoding task (man-made/natural vs. pleasantness) by subsequent memory (correct vs. incorrect) ANOVA was used to analyze the retrieval RT.

##### *Retrieval performance*

We analyzed the retrieval performance data in order to answer two questions: 1) is source memory better for words encoded in the pleasantness vs. man-made/natural task and 2) is source memory better for words directly preceding on-task vs. off task reports. We analyzed retrieval performance using an index which assessed the probability of correctly remembering the source, while correcting for response bias. Specifically, for each task, retrieval performance was computed as (% Source Hit – (% source misattribution + % false alarm)/2). A two-tailed paired *t*-test was used to compare retrieval performance in the two tasks, for words which did not directly precede the thought probes.

The (% Source Hit – (% source misattribution + % false alarm)/2) measure could not be used to compare performance on encoding trials preceding on-task vs. off-task reports; this is because “false alarms”

cannot be attributed to on-task or off-task trials (they can only be attributed to the pleasantness or the man-made/natural task). Thus, to compare performance on on-task vs. off-task trials, we compared (% of source hits – % source misattribution) using a paired *t*-test.

### fMRI data analysis

#### fMRI data preprocessing

Pre-processing and analysis of the fMRI data was conducted in SPM8 (<http://www.fil.ion.ucl.ac.uk/spm/>). Images from the first 10 s of each run were discarded to control for field inhomogeneities. All scans were then spatially realigned to the first scan, using a 6 parameter (rigid body) transformation. Next, the scans were normalized to the MNI EPI template in SPM8, resampled to 2 mm cubic voxels and smoothed using an 8 mm full-width at half maximum (FWHM) kernel.

#### fMRI general linear model

For each subject, seven regressors were modeled in an event-related manner ( $t = 0$ ), convolved with the SPM canonical hemodynamic response function and its temporal derivative, and entered into a general linear model (GLM) regression analysis. Encoding events directly preceding the thought probes ( $n = 54$ ) were analyzed separately from other encoding events ( $n = 222$ ), and classified as either “on-task” or “off-task”, depending on the answer provided during the thought probe. Because of the small amount of trials available, we did not examine on-task and off-task events separately for each encoding task. The thought probes themselves were also modeled as a regressor, but were not analyzed further (Christoff et al., 2009). The encoding trials that did not directly precede thought probes were divided into “correct pleasantness encoding” (PleasCor), “incorrect pleasantness encoding” (PleasIncor), “correct man-made/natural encoding” (ManCor) and “incorrect man-made/natural encoding” (ManIncor). Correct events were those words that were subsequently remembered and attributed to the correct encoding task (correct source). Incorrect events were all other events types, in which the source was forgotten (source misattribution, old with no recollection of source, and forgotten words). Serial correlations were accounted for using an autoregressive AR(1) model. A high-pass filter cut-off of 128 was used, and no global normalization was performed. Finally, movement parameters were included as regressors of no interest.

Two separate second level random effect fMRI analyses were conducted. The first analysis was conducted on the encoding trials which did not directly precede thought probes (classified as PleasCor, PleasIncor, ManCor and ManIncor), while the second was conducted on encoding trials directly preceding the probes (classified as on-task or off-task). Results were considered significant if they exhibited  $p < .001$  with a cluster size greater than 10 voxels (Forman et al., 1995).

#### fMRI analysis of regions involved in the main effect of subsequent memory, encoding task, and subsequent memory by encoding task interaction

The first fMRI analysis used data from all 21 subjects included in this study. We performed the following 4 *t*-contrasts for each subject: PleasCor vs. baseline, PleasIncor vs. baseline, ManCor vs. baseline and ManIncor vs. baseline. These contrasts were entered in a two-way subsequent source memory-by-encoding task repeated measures ANOVA. We assessed brain regions involved in the main effect of encoding

task, the main effect of subsequent source memory and the encoding task-by-subsequent source memory interaction. Main effects were exclusively masked with the subsequent memory-by-encoding task *F* interaction at a very liberal threshold ( $p < 0.05$ ) to ensure that they were not driven by it (e.g., Prince et al., 2009).

#### fMRI analysis of regions involved in TUT

For the second fMRI analysis, we used a sub-sample of 14 subjects (out of 21) that had at least 14 on-task and 14 off-task events to examine the brain regions involved in exhibiting TUT (mean of 26 on-task and 27 off-task events across the 14 subjects). First, 2 *t* contrasts were performed for each subject (off-task vs. on-task and on-task vs. off-task). Next, two one-sample group level *t*-tests were performed on these *t*-contrasts to test the null hypothesis that there were no differences in activation between these conditions. Although we acknowledge that this is a relatively small sample size, a similar sample size ( $n = 15$ ) was used in a previous study of mind-wandering (Christoff et al., 2009). In addition, the regions identified in our TUT contrast were largely overlapping with those found in previous studies (Christoff et al., 2009; Stawarczyk et al., 2011).

Finally, to assess the regions involved both in encoding failure and in exhibiting TUT, we performed a conjunction in SPM8 between the off-task vs. on-task and the main effect of encoding failure (both contrasts individually thresholded at  $p < 0.001$ ). The conjoint probability for the conjunction is very conservative ( $p < 0.00001$ ) (Fisher, 1950; Lazar et al., 2002).

We used Mango (<http://ric.uthscsa.edu/mango/download.html>) and Caret ([http://brainvis.wustl.edu/wiki/index.php/Main\\_Page](http://brainvis.wustl.edu/wiki/index.php/Main_Page)) to display the fMRI results for the Figures. Marsbar (<http://marsbar.sourceforge.net/>) was used to extract parameter estimates of the ROIs plotted in Fig. 2.

## Results

### Behavioral results

#### Encoding reaction time

Encoding reaction times are listed in Table 1. We analyzed the impact of encoding task-type (man-made/natural vs. pleasantness) and subsequent memory (correct vs. incorrect) on encoding RT using a two-way task repeated measures ANOVA. There was a significant task-by-subsequent source memory interaction ( $F(1,20) = 24.202$ ,  $p < 0.001$ ,  $\eta^2p = 0.548$ ), and a significant main effect of subsequent source memory on encoding RT ( $F(1,20) = 4.707$ ,  $p = 0.042$ ,  $\eta^2p = 0.191$ ). There was no main effect of task-type on encoding RT ( $p = 0.97$ ). The significant interaction was due to subjects responding faster during correct vs. incorrect events in the pleasantness task ( $F(1,20) = 31.827$ ,  $p < 0.001$ ,  $\eta^2p = 0.614$ ), with no such effect in the man-made/natural task ( $F(1,20) = 1.294$ ,  $p = 0.269$ ).

We also compared encoding RT for words preceding on-task reports vs. off-task reports. Subjects responded that they were on-task on 51% of probes, and off-task on 48% of probes. This proportion was similar when thought probes followed the man-made/natural encoding task (49% on-task, 51% off-task) and the pleasantness encoding task (52% on-task, 47% off-task). Across encoding tasks, TUT were composed of 18% mind-wandering, 31% task-related interferences and 50% internal/external distractions. To be consistent with the fMRI data, we examined

**Table 1**  
Reaction time with standard error.

	Subjective Correct	Subjective Incorrect	Objective Correct	Objective Incorrect	On-Task	Off-Task
Encoding Reaction Time (ms)	1586 (58)	1731 (56)	1679 (66)	1639 (62)	1487 (52)	1710 (101)
Retrieval Reaction Time (ms)	2076 (85)	2242 (89)	2246 (82)	2153 (87)	2114 (69)	2079 (82)

Note: This table presents the mean encoding reaction times in for each condition, with standard error in parentheses. “On-Task” refers to encoding events preceding thought probes in which subjects reported being concentrated on the task. “Off-task” refers to encoding events preceding thought probes in which subjects reported exhibiting task-unrelated thoughts.

RT in the encoding trials preceding on-task vs. off-task trials, collapsed across encoding task type and TUT type. A repeated measures ANOVA revealed that subjects responded significantly faster in the encoding trials preceding on-task vs. off task reports ( $F(1,20) = 12.071, p = 0.002, \eta^2p = 0.376$ ). This result supports our interpretation that the TUT episode encompassed the encoding trial preceding the thought probe.

#### Retrieval accuracy and reaction time

The proportion of correct source, source misattribution, words recognized without the source, misses and false alarms is listed in Table 2. A paired *t*-test on the (% Source Hit – (% source misattribution + % false alarm)/2) measure indicated that source memory performance was better for words encoded in the pleasantness vs. man-made/natural task ( $F(1,20) = 59.462, p < 0.001, \eta^2p = 0.748$ ). As can be seen in Table 2, the reduced source memory performance in the man-made/natural task is attributable to a greater amount of misses in this task ( $T(1,20) = 57.699, p < 0.001, \eta^2p = 0.743$ ); there were no differences in either source misattributions ( $T(1,20) = 0.71, p = 0.944$ ) or words recognized without the source ( $T(1,20) = 1.66, p = 0.112$ ).

A two-way repeated measures ANOVA on retrieval RT with factors of task (man-made/natural vs. pleasantness) and subsequent memory (correct vs. incorrect) revealed a significant interaction ( $F(1,20) = 24.927, p < 0.001, \eta^2p = 0.555$ ), but not main effect of task ( $F(1,20) = 2.184, p = 0.155$ ) or subsequent memory ( $F(1,20) = 0.155, p = 0.698$ ). The interaction was due to significantly faster RT in correct retrieval events studied in the pleasantness vs. man-made task ( $F(1,20) = 13.21, p = 0.002, \eta^2p = 0.398$ ), but faster RT for incorrect events in the man-made vs. the pleasantness task ( $F(1,20) = 11.865, p = 0.003, \eta^2p = 0.372$ ).

We also examined retrieval performance for words preceding on-task vs. off-task reports. As explained in the methods section, we compared the % of source hits – % source misattribution for each condition. A repeated measures ANOVA indicated that there was a trend for subjects to exhibit higher retrieval performance for words preceding on- vs. off-task reports ( $F(1,20) = 2.866, p = 0.1, \eta^2p = 0.125$ ). To further understand this trend, we computed exploratory *t*-tests on the different retrieval response types. Subjects exhibited more source hits for on-task vs. off task trials ( $F(1,20) = 5.837, p = 0.025, \eta^2p = 0.226$ ). Although subjects exhibited numerically higher source misattributions in on-task vs. off-task trials, this difference was not significant ( $F(1,20) = 0.763, p = 0.393$ ). Subjects exhibited significantly more misses for off-task vs. on task trials ( $F(1,20) = 5.447, p = 0.03, \eta^2p = 0.214$ ). Finally, we also examined whether retrieval RT differed according to on-task vs. off-task reports at encoding. We found no significant difference in retrieval RT between words preceding on-task vs. off-task reports at encoding ( $F(1,20) = 0.555, p = 0.465$ ). Thus in summary, in addition to being associated with higher encoding reaction

times (previous section), encoding trials preceding off-task reports were also associated with subtle changes in subsequent memory compared to on-task trials (more misses and less source hits).

#### fMRI results

##### Main effect of encoding task

The main effect of encoding task identified regions which were activated to a greater extent when making a pleasantness vs. man-made/natural judgment or vice-versa, independent of whether subjects correctly remembered the source of encoding events or not. A group of regions including anterior mPFC, anterior cingulate cortex (ACC), bilateral inferior/middle temporal gyri, bilateral angular gyri, PCC and bilateral cerebellum was identified in the pleasantness vs. the man-made/natural task. In contrast, greater activation in the man-made/natural vs. the pleasantness task was identified in bilateral ventrolateral/dorsolateral PFC and bilateral intraparietal sulcus extending into superior parietal lobe. A complete list of regions identified by the main effect of task can be found in Table 3.

##### Main effect of subsequent source memory

Regions including medial anterior PFC, left angular gyrus and left lateral PFC were activated to a greater extent in correct vs. incorrect source memory encoding, independently of encoding task. In contrast, the right precuneus/PCC, right ACC, right temporoparietal junction and right anterior superior frontal gyrus were activated to a greater extent during incorrect vs. correct source encoding events. A complete list of regions identified by the main effect of subsequent source memory can be found in Table 4.

One hypothesis regarding encoding failure effects is that they represent attention to *personal* thoughts and feelings irrelevant to the encoding task. To the extent that regions involved in encoding failure are involved in processing personal/subjective information, they may also be involved in making personal self-referential (pleasantness) judgments. To examine whether any of the regions involved in incorrect source memory encoding were also involved in making personal judgments, we masked the incorrect vs. correct main effect contrast by the pleasantness vs. man-made/natural main effect contrast (both contrasts thresholded at  $p < 0.001$ ). A single region, the right ACC (MNI coordinates: [6 42 -6]; cluster size = 17; *T* value = 3.55), was identified by this analysis. For completeness, we also examined whether any regions were involved in both the incorrect vs. correct main effect and the man-made/natural vs. pleasantness main effect contrast (both contrasts thresholded at  $p < 0.001$ ). One region in right parietal lobe (MNI coordinates: 52 -42 42, cluster size = 20) showed this effect.

##### Task by subsequent source memory interaction

The task by subsequent source memory interaction identified regions that were related to correct vs. incorrect source encoding in the pleasantness, but not the man-made/natural task (no regions were found for the opposite effect at  $p < 0.001$  (uncorrected,  $k > 10$ )). These regions included: left ACC/anterior mPFC, bilateral middle/superior temporal gyrus, bilateral anterior parahippocampal gyrus and left hippocampus. A complete list of regions identified by the interaction can be found in Table 5.

Incorrect encoding in the current study included source misattributions, events recognized without the source and forgotten events (misses). As previously mentioned in section 3.1.2, although the proportion of source misattributions and events recognized without the source did not differ in the man-made/natural vs. the pleasantness tasks, there was a significantly higher number of forgotten trials in the man-made/natural vs. the pleasantness task. Thus, it is possible that areas identified by the Task by Subsequent source memory interaction were biased by the greater amount of misses in the man-made/natural task relative to other trial types (rather than actual differences in successful vs. unsuccessful pleasantness, compared to man-made/

**Table 2**  
Retrieval accuracy performance with standard error.

Response type	Pleasantness task	Man-made task	On-task	Off-task
% Source Hit	0.57 (0.04)	0.38 (0.03)	0.51 (0.03)	0.44 (0.04)
% Recognition, no source	0.21 (0.03)	0.23 (0.03)	0.21 (0.04)	0.24 (0.03)
% Misses	0.13 (0.02)	0.30 (0.03)	0.19 (0.02)	0.25 (0.03)
% Source misattribution	0.09 (0.02)	0.09 (0.02)	0.09 (0.02)	0.07 (0.02)
% False alarms	0.03 (0.01)	0.03 (0.01)		
% Source Hit – ((% false alarm + % source misattribution)/2)	0.51 (0.04)	0.31 (0.03)		

Note: This table presents the retrieval performance data for each condition. "Recognition, no source" refers to words when subjects correctly responded that they had seen a word before, but did not remember its source. "Source misattribution" refers to responding that a word studied in the pleasantness task was studied in the man-made/natural task and vice-versa. "On-Task" refers to retrieval performance for encoding words preceding thought probes in which subjects reported being concentrated on the task. "Off-task" refers to retrieval performance for encoding words preceding thought probes in which subjects reported exhibiting task-unrelated thoughts.

**Table 3**  
ANOVA encoding task main effect.

Hemisphere	Brain region	Brodman area	MNI coordinates	Cluster size	Peak T value
<i>Pleasantness vs. man-made/natural encoding task</i>					
Bilateral	Anterior medial PFC	10/9	−2 62 20	2673	7.83
Left	Cerebellum		26 −86 −36	338	6.26
Right	Temporal pole	21/38	48 12 −36	99	5.65
Left	Middle/inferior temporal gyrus	20/21/38	−56 −8 −26	452	5.32
	Parahippocampal gyrus		−46 14 −32		5.17
Left	Anterior cingulate	32/10	−12 36 −10	27	5.1
Left	Angular gyrus/supramarginal gyrus	39/40	−54 −68 28	415	4.7
Bilateral	Posterior cingulate	31/23	−4 −54 22	247	4.55
Left	Anterior medial PFC	10	−12 −52 32	13	3.99
Left	Cerebellum		−24 −86 −38	32	3.85
Right	Angular gyrus	39	60 −58 20	30	3.57
Right	Middle temporal gyrus	21	50 −42 0	34	3.44
<i>Man-made/natural vs. pleasantness encoding task</i>					
Left	Precentral gyrus/middle/inferior frontal gyrus	6/9/44	−44 2 32	926	6.05
Left	Intraparietal sulcus	7/40	−34 −44 42	1921	5.96
Right	Intraparietal sulcus	7/40	44 −44 48	1318	5.3
Right	Insula/inferior frontal gyrus	47	32 24 −4	518	5.22
	Insula/frontal operculum		−32 18 6	175	4.68
Right	Precentral gyrus/middle/inferior frontal gyrus	6/44/9	32 10 54	341	4.68
Right	Precentral gyrus/middle/inferior frontal gyrus	6/44/9	46 10 30	865	4.58
Right	Middle/inferior frontal gyrus	46/44	44 20 28		4.26
Left	Frontal pole	10	36 54 6	208	4.33
Left	Middle/superior frontal gyrus	6	−28 0 58	178	4.27
Left	Lateral globus pallidus		−16 0 10	92	3.95
Right	Caudate		12 6 4	112	3.92
Right	Thalamus		10 −10 8		3.47
Left	Inferior temporal/fusiform gyrus	37	−50 −56 −16	37	3.82
Right	Paracingulate/superior frontal gyrus	32/6	6 16 50	48	3.69
Right	Inferior frontal gyrus	13	42 8 16	17	3.38

Note: This table presents the random effects within-group SPM8 results. The t-values represent the value for the local maxima which had a  $p < .001$  and spatial extent threshold of  $k > 10$ . The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

natural encoding). To address this issue, we re-calculated the interaction contrast after excluding all encoding events subsequently judged as recognized without the source, or in which the source was misattributed (leaving only “misses” as incorrect events, as is often done in the subsequent memory literature). This ensured that incorrect encoding was made up of the same trial types in both tasks. This analysis revealed activation in many of the same regions, including in left ([−

20 2 −14],  $p < 0.0001$ , cluster size = 117) and right ([22 6 −16]  $p = 0.002$ , cluster size = 24) anterior parahippocampal gyrus, left ACC/anterior mPFC ([−14 40 18],  $p = 0.001$ , cluster size = 46) and right middle/superior temporal gyrus ([58 10 −6],  $p = 0.001$ , cluster size = 18), although at a reduced,  $p < 0.005$  threshold. The reduced p values are likely attributable to the fact that there were few misses, particularly in the pleasantness task. However, this analysis reveals that it

**Table 4**  
ANOVA main effect of subsequent source memory.

Hemisphere	Brain region	Brodman area	MNI Coordinates	Cluster size	Peak T value
<i>Correct vs. incorrect source encoding</i>					
Left	Inferior/Middle frontal gyrus	46/45/47	−46 26 18	11,029	9.18
Right	Cerebellum/Inferior temporal gyrus		34 −76 −40	3351	5.55
Left	Angular gyrus	39	−44 −66 28	439	5.39
Right	Inferior frontal gyrus	47	36 34 −14	297	5.18
Left	Medial anterior PFC	10	−14 58 18	77	4.75
Right	Cingulate gyrus	33/24/32	10 8 28	138	4.15
Left	Amygdala/hippocampus		−24 −8 −18	25	4.12
Left	Brain stem		−12 −20 −18	116	3.75
Left	Cingulate gyrus	24	−6 2 30	20	3.72
Right	Cerebellum		26 −38 −30	54	3.7
Left	Lateral occipital cortex	18	−34 −88 −8	51	3.65
Left	Lateral occipital cortex/superior parietal lobule	7/19	−28 −64 40	47	3.58
Left	Lingual gyrus	19/30	−16 −48 −2	26	3.58
Right	Occipital pole	18	24 −102 6	102	3.54
Left	Middle temporal gyrus	22/21	−54 −44 2	16	3.45
Left	Occipital pole	18	36 −92 −6	35	3.34
<i>Incorrect vs. correct source encoding</i>					
Bilateral	Precuneus posterior cingulate	7/31	8 −78 50	2165	5.01
Right	Temporoparietal junction middle temporal gyrus	40/22/39	58 −44 38	581	4.79
Right	Cingulate gyrus	24/31/7	6 −22 40	67	4.09
Right	Lateral frontal pole	10	24 62 12	26	3.62
Right	Anterior cingulate	32/24	6 42 −2	24	3.55

Note: This table presents the random effects within-group SPM8 results. The t-values represent the value for the local maxima which had a  $p < .001$  and spatial extent threshold of  $k > 10$ . The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

**Table 5**  
ANOVA interaction: Regions involved in correct source encoding only in the pleasantness task.

Hemisphere	Brain region	Brodmann area	MNI coordinates	Cluster size	Peak T value
<i>Interaction: Correct vs. incorrect source only in the pleasantness task</i>					
Left	Medial temporal lobe/amygdala/putamen	34/28/38	−20 4 −14	396	5.93
Left	Precentral gyrus	6	−34 −12 64	366	4.57
Bilateral	Cingulate gyrus/supplementary motor cortex	24/32/6	−8 −2 50	562	4.34
Right	Medial temporal lobe/amygdala/putamen	34/28/38	20 6 −14	142	4.06
Left	Medial temporal lobe	36	−44 −34 −10	43	4.05
Left	Anterior cingulate	32/9	−14 40 18	111	3.91
Left	Postcentral gyrus/supramarginal gyrus/superior parietal lobule	3/40	−50 −24 54	167	3.86
Right	Caudate		18 10 18	33	3.78
Left	Anterior medial PFC/anterior cingulate	10/32	−4 54 6	166	3.73
			−8 42 0		3.71
Left	Inferior/middle/superior temporal gyrus	21/20/22	−62 −16 −18	12	3.7
Right	Superior temporal gyrus	38	56 12 −8	25	3.62
Left	Hippocampus		−32 −18 −14	26	3.56
Right	Precentral gyrus/middle frontal gyrus	6	38 −8 62	29	3.54

Note: This table presents the random effects within-group SPM8 results. The t-values represent the value for the local maxima which had a  $p < .001$  and spatial extent threshold of  $k > 10$ . The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

is unlikely that activation in these regions was driven by a different distribution of events in the two tasks.

We note an interesting hemispheric effect in ACC: both left and right ACC exhibited a pleasantness vs. man-made/natural main effect, indicating that these regions may be involved in processing subjective/personal information. However, left ACC exhibited a subsequent source memory by task interaction, while right ACC exhibited an encoding failure main effect. A summary of the effects found in ACC and the rest of mPFC is illustrated in Fig. 1.

#### Regions involved in exhibiting TUT during episodic encoding

We examined the brain regions related to exhibiting TUT by contrasting activation in encoding trials preceding off-task vs. on task reports (Table 6). Increased activity in PCC/retrosplenial cortex, lingual gyrus and bilateral DLPFC was observed during encoding events preceding off- vs on-task events. We observed no significant increases in brain activity during encoding events preceding on-task vs. off-task reports at  $p < 0.001$ .

We conducted a conjunction analysis to determine whether the regions activated in encoding events preceding off-task vs. on-task reports overlapped with regions involved in incorrect vs. correct encoding (both individual contrasts thresholded at  $p < 0.001$ ). Thus, the conjoint probability of finding an effect was  $0.001 * 0.001 = 0.00001$ . A single region in PCC ([−14 66 22], cluster size = 48) was identified in the conjunction (Fig. 2).

#### Correlations between brain activation and behavioral measures

In the previous sections we presented results of contrasts that compared brain activation during correct vs. incorrect encoding and on-task vs. off-task events. Here, we further investigated whether individual differences in activation during successful encoding relates to behavioral measures of interest. We selected four regions of interest from the aforementioned contrasts: 1) the ventrolateral PFC region (identified in the correct vs. incorrect main effect; peak: [−46 26 18]), 2) the precuneus/PCC (identified in the incorrect vs. correct main effect; peak: [8 −78 50]) and 3) the left ACC (showing a correct vs. incorrect effect only in the pleasantness task; [peak = −14 40 18]) and 4) the left anterior medial PFC (showing a correct vs. incorrect main effect [−14 58 18]). Left VLPFC was selected because it is one of the regions that has most commonly been associated with successful verbal encoding (Blumenfeld and Ranganath, 2007; Kim, 2010; Wagner et al., 1998). Left ACC was included because it was activated to a greater extent in correct vs. incorrect events only in the pleasantness task, which was one of our key predictions. PCC was included because we predicted that this region would be involved in encoding failure and TUT. Left anterior medial PFC was selected because of our a-priori interest in this region, and the interesting effect (correct vs. incorrect main effect)

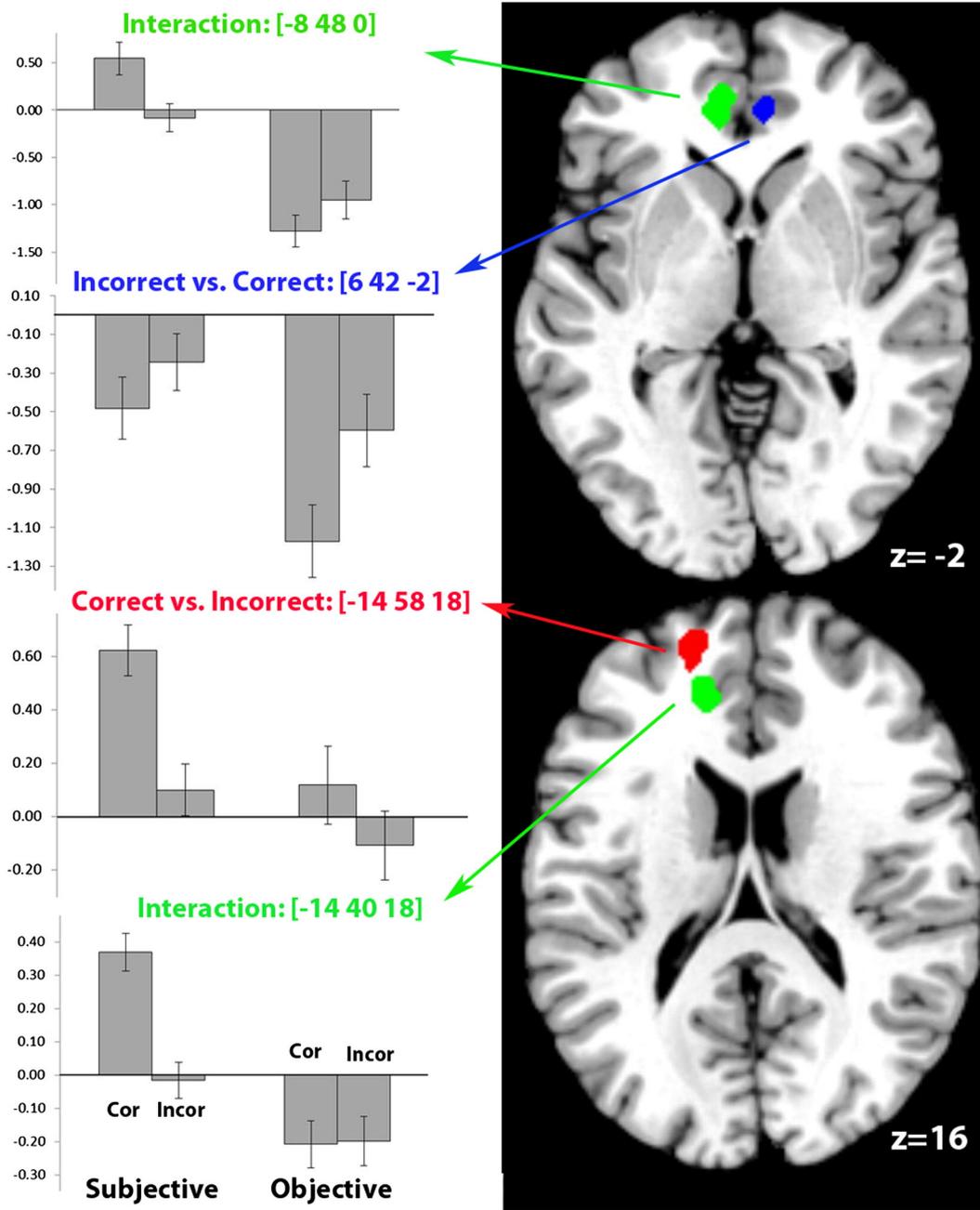
observed in this region. We related activation in these four regions during successful encoding to retrieval performance, encoding RT and frequency of off-task thought reports. The results are presented in Table 7. We present an overview of these correlations here, by mentioning those that reached trend level for significance ( $r > 0.37$ ,  $p < 0.1$ , 2-tailed). Activation in left VLPFC during successful encoding was positively related to retrieval performance in the pleasantness task ( $r = 0.47$ ,  $p = 0.03$ ). Activation in precuneus/PCC during successful encoding was negatively related to retrieval performance in the man-made/natural task ( $r = -0.37$ ,  $p = 0.098$ ). Activation in left ACC during successful encoding was positively related to retrieval performance in the pleasantness task ( $r = 0.38$ ,  $p = 0.089$ ). We also performed stepwise multiple regressions using activation in these four regions during successful encoding as independent variables, and retrieval performance, encoding RT and frequency of off-task thought in each task separately. A model with only activation in left VLPFC was the best predictor of retrieval performance in the pleasantness task ( $F(1,20) = 5.281$ ,  $p < 0.33$ , adjusted R squared = 0.176). No other model reached significance.

## Discussion

The goal of this study was to investigate the role of distinct DMN regions in episodic memory encoding. Subjects encoded word stimuli using a self-referential (pleasantness) and a semantic (man-made/natural) task. During encoding subjects were intermittently presented with thought probes to evaluate if they were concentrated and on-task or exhibiting task-unrelated thoughts (TUT). In the next sections we first discuss the behavioral results, and then discuss the fMRI results in relation to our specific hypotheses.

#### Behavioral results

Behavioral results indicated that retrieval performance was better for words encoded self-referentially vs. semantically, consistent with previous research (e.g., Leshikar and Duarte, 2012; Maillat and Rajah, 2013). Encoding RT was significantly faster for successfully vs. unsuccessfully encoded words in the self-referential, but not the semantic task. It is possible that words for which subjects can more easily judge as pleasant or not, because they are more salient/meaningful for a given participant, are easier to remember than words for that are harder for subjects to classify as pleasant/unpleasant. On the other hand, the easiness with which a word can be classified as man-made or natural may not have an influence of whether this word will be remembered or not. In addition, retrieval RT was significantly faster for source hits in the pleasantness vs. the semantic task, but faster for incorrect events in the man-made vs. pleasantness task. These results may indicate that

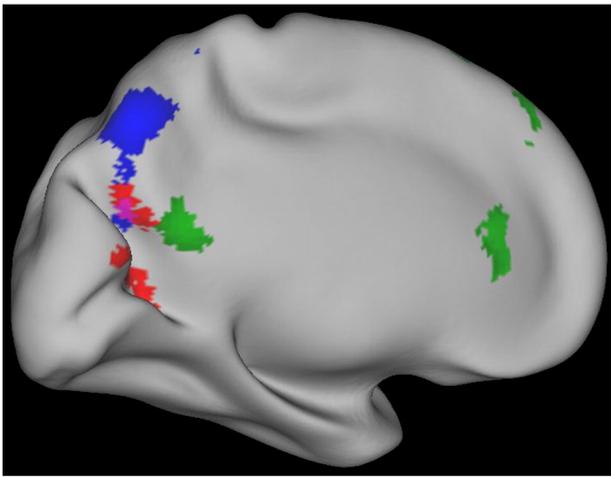


**Fig. 1.** Summary of fMRI results in the medial prefrontal cortex. One region exhibited a correct vs. incorrect source memory effect, one exhibited an incorrect vs. correct source memory main effect, and two exhibited a subsequent memory-by-encoding task interaction. A bar graph of the mean parameter estimates, with standard error, for each of these four areas is presented.

**Table 6**  
Brain regions involved in task-unrelated thoughts.

Hemisphere	Brain region	Brodmann area	MNI coordinates	Cluster size	Peak T value
Left	Posterior cingulate/retrosplenial cortex	31/18/30	-10 -68 22	239	5.07
			-22 -58 0		4.88
			-14 -62 12		4.48
Left	Left dorsolateral PFC	9	-34 38 38	36	4.95
Bilateral	Lingual gyrus	18	0 -72 14	66	4.55
Right	Thalamus		20 -28 0	11	4.53
Right	Right dorsolateral PFC	9	32 46 34	56	4.32
Right	Lingual gyrus	18	6 -68 -2	11	4.1

Note: This table presents the random effects within-group SPMS results. The t-values represent the value for the local maxima which had a  $p < .001$  and spatial extent threshold of  $k > 10$ . The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.



**Fig. 2.** Summary of fMRI results in the left posterior cingulate/precuneus region. Regions depicted in blue exhibited an incorrect vs. correct source memory main effect. Regions depicted in red were identified in the off-task > on-task t-contrast. The region depicted in purple represents the overlap between these two effects. Finally, regions depicted in green exhibited pleasantness vs. man-made/natural encoding task main effect.

for words that were correctly retrieved, retrieval judgments were easier to make in the pleasantness vs. the man-made task, perhaps because these memories were stronger. On the other hand, if memories were indeed stronger for words encoded in the pleasantness task vs. man-made task, this may have resulted in subjects hesitating more in the pleasantness vs. the man-made retrieval task for incorrect events (considering that they may have in fact have judged this word as pleasant/unpleasant) before ultimately making a mistake.

Our behavioral results indicate that TUT is frequent during episodic memory encoding. Indeed, subjects reported exhibiting a TUT on 48% of thought probes. In comparison, another study reported that subjects experienced TUTs on approximately 68% of thought probes during a sustained attention to response task (SART) (Stawarczyk et al., 2011). This reduction in TUT during episodic memory encoding may be due to this task being more demanding than the SART, which is quite repetitive and monotonous (Smallwood and Schooler, 2006). Moreover, 50% of TUTs in our study were internal/extraction distractions. This indicates that the majority of TUTs during episodic encoding in an fMRI scanner in young adults may be related to monitoring of internal and external milieus, rather than mind-wandering or thoughts related to the appraisal of the task. Finally, we found an association between TUT and performance on the memory task. First as we had predicted, RT for words preceding on-task reports were significantly faster than those preceding TUT reports. Second, we found that subjects exhibited more source hits and fewer misses for encoding trials preceding on-task vs. off-task

**Table 7**  
Correlations between activation in regions of interest and behavioral measures.

	Retrieval performance		Reaction time		Off-task thought	
	Pleas	Man	Subj	Man	Subj	Man
Left VLPFC	0.47**	0.30	−0.04	−0.05	−0.34	0.00
Left ACC	0.38*	0.11	−0.30	0.19	−0.16	−0.01
Precuneus/PCC	−0.05	−0.37*	0.26	0.01	−0.15	0.12
Anterior medial PFC	0.17	0.10	−0.26	0.24	−0.27	0.19

Note: This table presents correlations between activation in left ventrolateral prefrontal cortex (VLPFC), left anterior cingulate cortex (ACC), precuneus/posterior cingulate (PCC) and anterior medial PFC during successful encoding and three behavioral measures: retrieval performance, reaction time and frequency of off-task thoughts. Pleas = pleasantness task. Man = man-made/natural task. \*\*: significant at  $p < 0.05$ . \* Trend for significance ( $p < 0.1$ ).

reports, consistent with prior evidence of a negative relationship between TUT and memory performance (Mailet and Rajah, 2013; Seibert and Ellis, 1991; Smallwood et al., 2003).

*Left anterior medial PFC and angular gyrus are activated to a greater extent in correct vs. incorrect encoding across tasks*

We had not predicted that any DMN region would be activated to a greater extent in correct vs. correct encoding across tasks. Based on previous findings, one would instead expect a particularly important role for the left inferior frontal gyrus in successful encoding of verbal material (Kim, 2010; Wagner et al., 1998). In agreement with these findings, the most prominent region involved in encoding success across tasks was a large region spanning the left inferior and middle frontal gyri. This may reflect the role of this region in controlled semantic elaboration, which promotes successful verbal encoding (Wagner et al., 1998).

Interestingly however, we also found encoding success effects across encoding tasks in DMN regions including left anterior medial PFC (MNI coordinates:  $[-14\ 58\ 18]$ ), left angular gyrus ( $[-44\ -66\ 28]$ ). This result was unexpected, given that neither of these regions is usually involved in encoding success when semantic encoding strategies are used. One possibility is that these regions were involved in encoding success because of the specific requirements of the source retrieval task. In the current study, the source retrieval task required subjects to identify which of two encoding judgments had been performed on a given word. In other words, the retrieval task required subjects to distinguish which of two cognitive operations (i.e. task-relevant thoughts) they had performed on a given word at encoding (Johnson et al., 1993). This is different from retrieval tasks traditionally used in the literature that only require subjects to recall whether or not a stimulus was seen or not – in these cases, retrieval of the cognitive operation performed at encoding is not required. Similarly, retrieval of the cognitive operations is not required in other source retrieval tasks that emphasize memory for perceptual aspects of the stimuli (e.g. determining if a word presented in red or green/on the left or right). Thus one possibility is that task-independent encoding success effects in anterior medial PFC and angular gyrus reflects internally directed attention to task-relevant cognitive operations at encoding which was necessary for successful source recollection. This suggestion is compatible with proposals that the angular gyrus is involved in internally focused attention (but note that this role is typically emphasized at retrieval, e.g. Daseelaar et al., 2009; Wagner et al., 2005).

Another study that assessed subsequent memory for encoding task (distinguishing between words and pictures judged as living/non-living vs. smaller/bigger than a shoebox) also identified a very similar region of left medial anterior PFC to the one observed in the current study (MNI:  $[-10\ 66\ 16]$ ) (Dulas and Duarte, 2011). In addition, we note that previous studies have also implicated this region specifically in retrieval of which of two encoding tasks was performed (Dobbins and Wagner, 2005; Simons et al., 2005). For example, in Simons et al. (2005), at encoding, subjects either judged whether stimuli were pleasant/unpleasant or related more to entertainment or politics. Two source retrieval tasks were administered: in one, subjects had to remember which of the two encoding tasks they had performed on the stimulus, while in the other, they had to remember whether the stimulus had been presented on the left or right of the screen (spatial source). Compared to the spatial source task, recollection of encoding task recruited left anterior medial PFC (MNI:  $[-9\ 63\ 21]$ ). The authors suggested that this region may be involved in the coordinated control of internally generated information. Thus, when considered along with findings from other studies, our results suggest that the anterior medial PFC may be important both in encoding and retrieving the cognitive operation performed on encoding stimuli. Furthermore, our results emphasize that the association between encoding activation in regions of DMN, such as left anterior medial PFC and angular gyrus, and retrieval performance

may critically depend on the nature of the retrieval task (Morris et al., 1977; Rugg et al., 2008; Tulving and Thompson, 1973).

*Left ACC and bilateral LTC are activated to a greater extent in correct vs. incorrect encoding using a pleasantness task*

The main effect of encoding task indicated that the medial PFC (including ACC), PCC, bilateral angular gyrus, bilateral LTC and cerebellum were activated to a greater extent when making a pleasantness vs. man-made/natural judgment during verbal encoding, independent of whether subjects correctly remembered the source of encoding events or not. However, it is unlikely that all these regions are involved specifically in self-referential processes. Indeed, prior experimental studies (Grady et al., 2012; Grigg and Grady, 2010) in addition to recent meta-analysis (Qin and Northoff, 2011) have indicated that most of these DMN regions are recruited not only when making self-referential judgments, but also when making judgements about personally known people, and about widely-known but not personally known figures. Thus in the current study, it is possible that some of these DMN regions may have been recruited in during pleasantness vs. man-made/natural encoding due to their more general involvement in internally directed attention and/or subjective evaluation processes (Buckner et al., 2008; Legrand and Ruby, 2009; Spreng, 2012).

Furthermore, although many DMN regions were recruited to a greater extent in a pleasantness vs. man-made/natural encoding, only a subset of them were involved in correct vs. incorrect encoding in the pleasantness task. Consistent with our hypothesis, left ACC, spreading into anterior medial PFC was one of these regions. Bilateral LTC were also involved in correct vs. incorrect encoding in the pleasantness task only. On the other hand, there was a trend in all three regions in the opposite direction (i.e. incorrect vs. correct) in the man-made/natural task (illustrated for left ACC in Fig. 1). Thus one possibility is that these regions were involved in successful encoding only in the pleasantness task due to their involvement in self-referential evaluation of verbal encoding stimuli (e.g., Andrews-Hanna et al., 2010b). In contrast, self-referential evaluation of verbal material in the man-made/natural task may have been detrimental to source memory retrieval, since it could have led to a source misattribution (judging that one had encoded a word in the pleasantness task instead of the man-made/natural task).

*PCC is involved both in encoding failure and exhibiting TUT*

A major goal of this study was to test that hypothesis that the DMN regions activated to a greater extent in incorrect vs. correct encoding would be activated to a greater extent in encoding trials preceding off-task vs. on-task reports. In the current study, encoding failure was associated with increased activity in precuneus, PCC, right temporoparietal junction, right ACC and right anterior lateral PFC. All of these regions are commonly associated with encoding failure (Kim, 2010). Furthermore, exhibiting TUT was associated with increased activation in lingual gyrus, bilateral dorsolateral PFC and a region of PCC which overlapped with the one involved in incorrect source encoding. Thus, the same region of PCC was involved in encoding failure and exhibiting TUT during episodic encoding.

The exact cognitive mechanism subserved by this region of PCC during episodic encoding is unclear. The area encompassed by this regional activation did not overlap with a more anterior and ventral region of PCC that was involved in the pleasantness vs. man-made/natural encoding task main effect (see Fig. 2), making it unlikely that it subserves self-referential processes (see Huijbers et al., 2012 for a related discussion). Instead, one possibility is that PCC is involved in “scene construction” processes, or memory retrieval, necessary when an individual imagines an alternate scenario from the one currently being experienced (Andrews-Hanna et al., 2010b; Buckner and Carroll, 2007; Hassabis and Maguire, 2009; Hassabis

et al., 2007; Wagner et al., 2005). Alternatively, given that the majority of TUT in the current experiment were related to thinking about internal/external distractions (e.g. thinking about MRI scanner noise, or how uncomfortable one is in the scanner), PCC may also be involved in monitoring of the internal and external milieu (Raichle et al., 2001; Stawarczyk et al., 2011).

Apart from PCC, we observed a mismatch between regions involved in exhibiting TUT and in encoding failure. Specifically, exhibiting TUT was related to bilateral DLPFC activation, while encoding failure was related to activation in right ACC and right temporoparietal junction. Although not the focus of our study, DLPFC regions similar to the ones we observed in the current study during TUT (MNI: [−34 38 38] and [32 46 34]) were identified in a meta-analysis of encoding failure (TAL: [−36 30 38] and [34 32 42]) (Kim, 2010). Furthermore, when both contrasts were individually thresholded at  $p < 0.005$ , we observed a conjunction between the encoding failure contrast and the off-task vs. on-task contrast in right DLPFC (MNI: [34 40 40]; cluster size = 27). Christoff et al. (2009) observed DLPFC and dorsal ACC involvement in mind-wandering episodes during a sustained attention to response task, and proposed that activation in these regions may reflect either 1) multitasking (coordination of TUT and task performance), 2) conflict detection aimed at bringing attention back to the task or 3) detecting conflict with the TUT episode itself. Alternatively, this region may be involved in monitoring of internal and external milieu.

In contrast to DLPFC, right ventral ACC was associated with encoding failure, but not in exhibiting TUT. However, two previous experiments have found that ventral ACC is involved in TUT during the sustained attention to response task (Christoff et al., 2009; Stawarczyk et al., 2011). In addition, Stawarczyk et al. (2011) contrasted activation during different types of TUT, and found that some DMN regions including ventral mPFC were particularly involved in mind-wandering, compared to task-interferences and internal/external distractions. The authors suggested that this region may be involved in monitoring the self-relevance of the ongoing contents of consciousness. In the present experiment, we had too few TUT events to examine different thought types individually and mind-wandering represented only 18% of TUT events. Thus, if right ventral ACC is particularly involved in mind-wandering, it is possible that averaging across other TUT types prevented this region from reaching significance in the current experiment. However, consistent with a particularly important role for this region in self-referential processes (Qin and Northoff, 2011; Qin et al., 2010), we found that right ACC exhibited not only an incorrect vs. correct main effect, but also a pleasantness vs. man-made/natural encoding task main effect. It will be important for future studies to further examine the mismatch between TUT and incorrect encoding observed here to test this hypothesis. Finally, right temporoparietal junction was also involved in encoding failure. However, this region was not involved in TUT or in the pleasantness vs. man-made/natural encoding task main effect in our study; thus our experiment does not offer any explanation for the involvement of this region in encoding failure.

No regions were identified in the on-task vs. off-task contrast in our study. One may have expected regions activated in correct vs. incorrect events to also be activated in encoding events preceding on-task vs. off-task reports. We have noted that differences in retrieval performance for encoding events preceding on-task vs. off-task events were very subtle; in other words, successful encoding sometimes occurred even when subjects reported being off-task (and vice-versa), possibly diluting the effect. Another possibility, although speculative, is that subjects are also encoding the contents of their off-task thoughts, thus recruiting regions part of traditional encoding networks. Both of these factors could have contributed to the null results in this study.

In closing, we would like to re-emphasize some of the main limitations of the current study. First we used a small sample of subjects ( $n = 14$ ) to examine activation during off-task vs. on-task events. Second, for all fMRI contrasts in the current study, we used

an uncorrected threshold of  $p < 0.001$ . Using this threshold, it is possible that some of the results reported in this paper are false positives; however we believe that the use of this threshold in the current study represented a good compromise between type 1 and type 2 errors. Further studies are required to replicate these findings and to see whether they generalize to other types of encoding tasks. Third, in the current study, we collapsed across different TUT types; it would be interesting to examine activation during different types of TUT to determine the relative involvement of distinct brain regions in specific thought types during episodic encoding. Finally, in the current fMRI study there was a fixed ITI of 2.5 sec between the on- and/or off-task encoding events and the subsequent thought probe. In rapid event-related fMRI studies variable ITIs between events are recommended for optimally discriminate activity associated with neighbouring event-types. Thus, due to the fixed ITI between on- and/or off-task events and the thought probe, it may be that there was residual activity related to the thought probe which was associated with on- and/or off-task events. However, we do not think this was the case since: i) residual activity associated with the thought probe would have to be correlated with either the on- and/or off-task events, for this to occur, and ii) off- and on-task events were both followed by identical thought probes, so activity associated with the probe would likely be controlled for in a contrast of these event-types. Moreover, previous studies, employing similar designs, have reported activity in similar brain regions during mind-wandering (Christoff et al., 2009; Stawarczyk et al., 2011).

## Conclusions

In summary, our experiment presents evidence that DMN play dissociable roles during episodic encoding of verbal material. In contrast to the general finding that all major DMN regions are involved in encoding failure (Kim, 2010), our experiment demonstrates that many of these regions, including left ACC, left anterior medial PFC, left angular gyrus and bilateral LTC can be involved in encoding success in some memory paradigms. We propose that the encoding strategy used, as well as the specific requirements of the retrieval task may be critical in determining the nature of the association between activation in specific DMN regions and retrieval success. For example, in the current study, left ACC and bilateral LTC were involved in encoding success only in the pleasantness task, suggesting that these regions were modulated primarily the nature of the *encoding* task. Left anterior medial PFC and left angular gyrus were involved in encoding success across tasks. As previously discussed, this may reflect the role of these regions in internally-directed attention to cognitive operations (i.e. task-relevant thoughts), which was a specific requirement of the subsequent source *retrieval* task. Finally, our experiment also demonstrates for the first time an overlap between encoding failure and exhibiting TUT in the PCC.

## Disclosure statement

There are no conflicts of interest for any of the authors regarding the study presented in this article. All authors have reviewed the contents of the manuscript being submitted and approve of its contents and validate the accuracy of the data. The data contained in the manuscript being submitted has not been previously published nor has it been submitted elsewhere, and will not be submitted elsewhere, while under consideration in *NeuroImage*.

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