

Assessing the Neural Correlates of Task-unrelated Thoughts during Episodic Encoding and Their Association with Subsequent Memory in Young and Older Adults

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Abstract

Recent evidence indicates that young adults frequently exhibit task-unrelated thoughts (TUTs) such as mind-wandering during episodic encoding tasks and that TUTs negatively impact subsequent memory. In the current study, we assessed age-related differences in the frequency and neural correlates of TUTs during a source memory encoding task, as well as age-related differences in the relationship between the neural correlates of TUTs and subsequent source forgetting effects (i.e., source misses). We found no age-related differences in frequency of TUTs during fMRI scanning. Moreover, TUT frequency at encoding was positively correlated with source misses at retrieval across age

groups. In both age groups, brain regions including bilateral middle/superior frontal gyri and precuneus were activated to a greater extent during encoding for subsequent source misses versus source hits and during TUTs versus on-task episodes. Overall, our results reveal that, during a source memory encoding task in an fMRI environment, young and older adults exhibit a similar frequency of TUTs and that experiencing TUTs at encoding is associated with decreased retrieval performance. In addition, in both age groups, experiencing TUTs at encoding is associated with increased activation in some of the same regions that exhibit subsequent source forgetting effects. ■

INTRODUCTION

During the performance of cognitive tasks, attention often shifts to thoughts that are not conducive to successive task performance (task-unrelated thoughts [TUTs]; Smallwood & Schooler, 2015). Previous studies suggest that the content of TUTs is varied and includes mind-wandering (e.g., thoughts about daily life, current concerns, worries), distractions (e.g., thinking about scanner noise in an fMRI study), and task-related interferences (thoughts related to the appraisal of the current task; Stawarczyk, Majerus, Maquet, & D'Argembeau, 2011). In addition, previous studies indicate that TUTs are associated with decreased performance in a variety of tasks including episodic memory, sustained attention tasks, and reading comprehension (Randall, Oswald, & Beier, 2014; McVay, Meier, Touron, & Kane, 2013; Stawarczyk, Majerus, Maj, Van der Linden, & D'Argembeau, 2011).

In recent years, studies have started to investigate the neural correlates of TUTs (e.g., Stawarczyk, Majerus, Maquet, et al., 2011; Christoff, Gordon, Smallwood, Smith, & Schooler, 2009). In one study, participants were periodically presented with thought probes asking about their attentional focus (on-task or mind-wandering) while they performed a sustained attention to response task (SART; Christoff et al., 2009). There was greater activation in regions including medial pFC, bilateral middle/superior

frontal gyri (MFG/SFG), posterior cingulate, precuneus, bilateral middle temporal cortex, inferior parietal cortex, and medial-temporal lobes preceding mind-wandering reports versus on-task reports. Notably, similar brain regions were also activated when participants made errors on the SART, consistent with the idea that errors in this task are made while participants are engaging in TUTs.

We recently conducted an fMRI study in young adults in which we measured the neural correlates of TUTs during a source memory encoding task (Maillet & Rajah, 2014b). That study was based in part on a meta-analysis of episodic encoding studies that indicated that a set of brain regions including medial pFC, bilateral MFG/SFG, posterior cingulate, precuneus, and inferior parietal cortex are consistently more activated during encoding items later forgotten versus remembered (Kim, 2011), so-called subsequent forgetting effects. The brain regions exhibiting subsequent forgetting effects in this meta-analysis are strikingly similar to the brain regions involved in TUTs in the study by Christoff et al. (2009). We thus reasoned that subsequent forgetting effects may sometimes arise because forgotten encoding items occur during TUT episodes.

However, it is unlikely that the brain regions identified by Christoff et al. (2009) as being involved in TUTs in the SART are always detrimental to episodic encoding. For instance, one of these brain regions, the medial pFC, is thought to be involved in self-referential processes and/or valuation (D'Argembeau, 2013). Although, these cognitive

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processes are recruited during TUT episodes (TUTs tend to be self-referential/related to current concerns; Klinger, 2013; McVay et al., 2013), it is likely that they can also sometimes contribute to successful episodic encoding of word stimuli. In fact, encoding tasks that encourage participants to engage in self-referential processing/valuation (e.g., pleasantness judgments, judging whether adjectives are self-descriptive) promote superior encoding compared with studies using semantic encoding tasks (e.g., man-made/natural judgment; Maillet & Rajah, 2013; Symons & Johnson, 1997). Furthermore, the few fMRI studies that have used self-referential processing/valuation encoding tasks have reported greater activation in medial pFC for subsequently remembered versus forgotten events (e.g., Leshikar & Duarte, 2012; Macrae, Moran, Heatherton, Banfield, & Kelley, 2004). Thus, in Maillet and Rajah (2014b), we included an encoding task manipulation (pleasantness [PLEAS] vs. man-made/natural [MAN] judgments) to test the hypothesis that medial pFC contributes to memory performance when the encoding task involves self-referential processing/valuation but is detrimental to memory performance when it does not.

Three key results emerged from Maillet and Rajah (2014b). First, encoding words preceding TUT reports were associated with higher RT and were forgotten more often than encoding words preceding on-task reports, suggesting that words may be forgotten when they occur during TUT episodes. Second, across encoding tasks, subsequent source forgetting effects (regions more activated when source information was forgotten vs. remembered) were found in brain regions including posterior cingulate, precuneus, right TPJ, and MFG/SFG. Some of these regions, including posterior cingulate and right MFG/SFG, were also activated to a greater extent during TUT versus on-task episodes, suggesting that subsequent source forgetting effects may occur in part because these brain regions are involved in TUTs. Third, consistent with our predictions, we found that medial pFC exhibited an encoding task by subsequent source memory interaction: This region was activated to a greater extent in unsuccessful versus successful encoding in the MAN task and in successful versus unsuccessful encoding in the PLEAS task.

Age-related Differences in Frequency and Neural Correlates of TUTs

In the current study, we used the same paradigm to assess age-related differences in frequency and neural correlates of TUTs during episodic encoding. Based largely on a prominent theory that proposes that aging is associated with a deficit in inhibitory control (Hasher & Zacks, 1988), it is sometimes assumed that older adults exhibit an increase in TUTs compared with their younger counterparts. Inconsistent with this proposal, several behavioral studies have reported that older adults exhibit an overall reduction in TUTs compared with young adults (Maillet &

Schacter, 2016; Zavagnin, Borella, & De Beni, 2014; Maillet & Rajah, 2013; Jackson & Balota, 2012; Krawietz, Tamplin, & Radvansky, 2012). However, it is unclear whether the finding of an age-related reduction in TUTs in behavioral contexts necessarily applies to fMRI studies. fMRI takes place in a relatively uncomfortable and noisy environment in which older participants may have greater trouble concentrating (Stevens, Hasher, Chiew, & Grady, 2008; Gutchess & Park, 2006). Thus, it is arguable that the occurrence of TUTs may disproportionately increase in older versus young adults in fMRI studies (e.g., older adults may be more distracted by the scanner environment than young adults). This could result in an overall similar amount of TUTs in young and older adults or even an increase in TUTs in older relative to young adults during fMRI scanning, although this has never been tested. In the current study, we assessed these possibilities and also hypothesized that TUTs would be negatively associated with retrieval performance in both groups.

The second goal of this study was to assess age-related differences in the neural correlates of TUTs and their relationship to subsequent forgetting effects. fMRI studies have consistently indicated that there are age-related differences in brain activation in regions that in young adults are involved in subsequent forgetting, including posterior cingulate, precuneus, medial pFC, inferior parietal lobes, and MFG/SFG (for meta-analysis, see Maillet & Rajah, 2014a). Although young adults exhibit subsequent forgetting effects in these regions, older adults often exhibit either a reduced difference in activation between forgotten and remembered events compared with young adults (e.g., de Chastelaine, Mattson, Wang, Donley, & Rugg, 2015) or even a reversal of this effect such that there is more activation in remembered versus forgotten events in older adults (e.g., de Chastelaine, Wang, Minton, Muftuler, & Rugg, 2011). This reduction/reversal in subsequent forgetting effects in older adults has been reported both when the memory task involves encoding of single items (Duverne, Motamedinia, & Rugg, 2009; Morcom, Good, Frackowiak, & Rugg, 2003) and item-item associations (de Chastelaine et al., 2011; Miller et al., 2008). In contrast, two recent studies using source memory paradigms have reported group similarities in subsequent forgetting effects in many of these regions (Cansino et al., 2015; Mattson, Wang, de Chastelaine, & Rugg, 2014).

The significance of reductions/reversal in subsequent forgetting effects with age is unclear (for discussion of these effects, see de Chastelaine et al., 2011, 2015; Maillet & Rajah, 2014a; Mattson et al., 2014). In part, this may reflect a lack of understanding of the cognitive processes involved in subsequent forgetting in both age groups. Given preliminary evidence for an association between subsequent source forgetting effects and TUTs in young adults (Maillet & Rajah, 2014b), a key question is whether this association persists in older adults. Indeed, little is known regarding the cognitive processes engaged when

older adults subsequently forget the source of events. On the basis of previous studies using source memory encoding tasks (Cansino et al., 2015; Mattson et al., 2014), we hypothesized that young and older adults would similarly exhibit subsequent source forgetting effects in regions including bilateral MFG/SFG, posterior cingulate, precuneus, and inferior parietal lobe. Furthermore, we predicted that TUTs would be associated with activation in similar brain regions as those exhibiting subsequent source forgetting effects.

Finally, the third goal of this study was to assess whether older adults would exhibit a similar benefit to young adults in retrieval performance from encoding words while making a pleasantness relative to a man-made/natural judgment and whether this is associated with medial pFC activation. Previous behavioral results indicate that young and older adults exhibit similar retrieval benefits from a self-referential/valuation encoding task (Maillet & Rajah, 2013; Gutchess, Kensinger, Yoon, & Schacter, 2007), and fMRI studies have further indicated that medial pFC may be similarly recruited by young and older adults during such tasks (Leshikar & Duarte, 2014). Thus, we expected that during the PLEAS task, but not the MAN task, medial pFC would show a distinct pattern from other brain regions typically involved in subsequent forgetting in both young and older adults. That is, although we expected regions such as precuneus, inferior parietal lobes, and bilateral MFG/SFG to be involved in subsequent source forgetting across tasks, we expected the medial pFC to be involved in subsequent source forgetting in the MAN task, but in subsequent source memory in the PLEAS task.

METHODS

Participants

Twenty young adults (age range = 18–30 years, mean age = 23.4 years, 12 women) and 16 older adults (age range = 60–74 years, mean age = 67.0 years, 11 women) participated in this study. Data from the young adults were previously presented in Maillet and Rajah (2014b). Data from the older adults have not been presented before. Young adults were recruited through online advertisements on university websites in the Montreal area. Older adults were recruited through advertisements in magazines and newspapers. All participants were healthy at the time of testing and had no history of neurological or psychological illness. All participants were right-handed as determined by the Edinburgh inventory (Oldfield, 1971). There were no between-group difference in education (young mean = 16.35, old mean = 16.38; $t(1, 34) = 0.035$, $p = .973$). One additional young adult and three additional older adults were excluded because of a lack of events ($n < 8$) in one condition. The young adult and two older adults were excluded because of lack of TUT events. The other older adult was excluded because of too few source misses in the PLEAS task.

Participants completed a battery of neuropsychological/personality tests including the Montreal Cognitive Assessment Scale (Nasreddine et al., 2005; cut-off > 25), the Beck Depression Inventory (Beck, 1987; Beck, Ward, Mendelson, Mock, & Erbaugh, 1961; cut off < 10), the verbal fluency portion of the Delis–Kaplan Executive Function System (D-KEFS) test, and a 12-item conscientiousness inventory (Costa & McCrae, 1992). Conscientiousness was assessed because of previous evidence of its relation to age-related differences in frequency of TUTs (Jackson & Balota, 2012). Additionally, older adults completed the Geriatric Depression Scale (Brink et al., 1982). Between-group differences in test scores were assessed using t tests.

Behavioral Procedure

Participants visited the Douglas Mental Health University Institute (Montreal, Canada) on two separate occasions. In the first session, they completed the aforementioned neuropsychological tasks and questionnaires and 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 2). Because participants performed a practice version of both the encoding and retrieval task, encoding during fMRI was intentional.

Participants returned for a second session in which fMRI scanning took place. The MRI session began with a 6-min resting state scan (not part of the current study analysis) and a 5-min anatomical scan. Next, participants completed four fMRI runs during which they performed episodic encoding of word stimuli (10 min 20 sec per run). Across the four runs, participants encoded 276 words, 138 while performing a pleasantness judgment and 138 while performing a man-made/natural judgment. Thus, 69 words were encoded in each of the four runs.

Within each run, words were presented in blocks of 4–7. The same encoding task was performed within a block and was switched in the following block. Variable intertrial intervals were presented between encoding words (range = 2.2–6.7 sec, mean = 4 sec). Two and a half seconds after the end of each block, a thought probe was presented asking participants to report the type of thought that they were experiencing the moment the probe came on screen. Participants chose between (1) being concentrated on the task, (2) mind-wandering, (3) task-related interferences, or (4) thinking about internal distractions or external distractions (Stawarczyk, Majerus, Maquet, et al., 2011).

Approximately 10 min following the end of the encoding task, participants performed a source memory retrieval task outside the scanner. During retrieval, all 276 encoding words (138 from the PLEAS task and 138 from the MAN task) and 138 new words were presented in a randomized order, one at a time. Each word appeared on-screen for 4.5 sec, followed by a fixed 1-sec ITI. Participants performed

a four-alternative choice retrieval task in which they were required to decide if a presented word was either (1) old and studied in the PLEAS task, (2) old and studied in the MAN 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) on 33.3% of trials. At the end of the experiment, participants were asked to rate on a scale of 1–10 how motivated they had been to perform the task well, how interested they thought the task was, and how difficult they thought the task was.

Behavioral Analysis

In all behavioral and fMRI analyses, the words directly preceding the thought probes (54 in total) were analyzed separately from all other encoding words (222 total). The words directly preceding thought probes were separated into on-task/TUTs depending on the response given in the thought probe. All other words were divided according to subsequent source memory.

Subsequent Source Memory Task

Five response types were of interest at retrieval: (1) source hit, (2) item recognition without source, (3) item misses (encoding items that received a “new” response), (4) source misattributions (instances where participants falsely claimed to have encoded a word in one task rather than the other), and (5) false alarm to new words. In memory experiments, retrieval performance is often calculated using a single measure, such as Hits – False alarms. In the current experiment, we opted instead to conduct an Age group (young, old) \times Encoding task (PLEAS, MAN) ANOVA on each of the five response types separately. To foreshadow the Results section, age-related differences were observed only in source misattributions, a result that may have been obscured by using a single measure of retrieval performance. Second, we performed a three-way Age group (young, old) \times Encoding task (PLEAS, MAN) \times Retrieval response type (source hit, item recognition without source, item miss, source misattribution) ANOVA on encoding RT.

Task-unrelated Thoughts

To assess age-related differences in frequency of TUTs during fMRI scanning, we conducted an Age group (young, old) \times TUT type (mind-wandering, task-related interferences, distractions) ANOVA. We were also interested in assessing the impact of self-reports of TUTs during thought probes on the encoding events preceding the thought probes. For these analyses, we collapsed mind-wandering, task-related interferences, and distractions into a TUT category and compared it with on-task responses. Age group (young, old) \times TUT (on-task, TUT) ANOVAs were conducted to assess (1) whether encoding

RT was longer when participants reported a TUT and (2) if retrieval of these events was affected.

To assess the impact of frequency of TUT reports during encoding on subsequent retrieval performance across individuals, we also conducted correlations between frequency of TUTs and retrieval performance. We conducted correlations between TUT frequency and (1) frequency of source misses (average of “item recognition without source” and “item miss” responses) and (2) frequency of source misattributions.

fMRI Methods

fMRI Data Collection

The MRI and fMRI data were collected using a 3-T Siemens Trio scanner (Berlin, Germany) 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 (repetition time = 2300 msec, echo time = 2.98 msec, flip angle = 9, 172 1 mm sagittal slices, field of view = 256 mm, 1 mm \times 1 mm \times 1 mm resolution). Following the structural scan, participants performed the aforementioned episodic memory task during four 10.26-min runs while BOLD images were acquired using a fast EPI pulse sequence (repetition time = 2000 msec, echo time = 30 msec, field of view = 256 mm, in-plane resolution = 4 \times 4 \times 4 mm). Three hundred eight fMRI volumes were acquired in each of the four encoding runs, for a total of 1232 in the experiment.

fMRI Data Preprocessing

Preprocessing and analysis of the fMRI data were conducted in SPM8. Images from the first 10 sec of each run were discarded to control for field inhomogeneities. ArtRepair was used to correct for slice and volume artifacts. Scans were spatially realigned to the first scan, using a six-parameter (rigid body) transformation. Scans were normalized to the Montreal Neurological Institute (MNI) EPI template in SPM8, resampled to 2 mm³ voxels, and smoothed using an 8-mm FWHM kernel.

fMRI Analysis

All participants had a minimum of eight events in each of the conditions examined in this experiment. The average number of events for each condition was adequate: PLEAS source hit (young = 63, old = 52), MAN source hit (young = 41, old = 36), PLEAS source miss (young = 35, old = 39), MAN source miss (young = 58, old = 59), on-task (young = 27, old = 30), TUT (young = 27, old = 24). A voxel significance threshold of $p < .001$ with a minimum cluster threshold of 48 voxels (determined using 1000 Monte Carlo simulations; Slotnick, Moo, Segal, &

Hart, 2003) was used to correct for multiple comparisons at $p < .05$ for all analyses, unless otherwise specified. When brain regions exhibited an interaction (e.g., subsequent source memory by encoding task) we used Marsbar (marsbar.sourceforge.net/) to extract their parameter estimates and clarify the interaction.

General linear model. In our previous analysis of these data in young adults (Maillet & Rajah, 2014b), we collapsed “item recognition without source,” “item miss,” and “source misattributions” responses into an “incorrect source” category and contrasted activation in this category versus source hits. However, the behavioral results in this study indicated that, although older adults exhibited no difference in frequency of “item recognition without source” or “item miss” responses compared with young adults, they did exhibit more “source misattributions” compared with young adults. Thus, collapsing across all response types would have resulted in distinct proportions of events from each category in young versus older adults. Thus, in the current study, “item recognition without source” and “item miss” responses were combined in a “source miss” category, whereas source misattributions were modeled separately.

For each participant, nine 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 regression analysis. Encoding words that did not directly precede the thought probes were assigned to one of six regressors: source hit, source miss (“item recognition without source” and “item miss” responses), and source misattributions in each of the two encoding tasks. “Item recognition without source” and “item miss” responses were modeled together as source misses because of lack of events to model them independently. Source misattributions were modeled, but not analyzed any further, because of lack of events. The encoding events directly preceding the thought probes across both encoding tasks were classified as on-task or TUTs based on the participants’ response to the thought probe and modeled as events ($t = 0$).¹ The thought probes themselves were modeled as a single regressor and were not analyzed further, given that we were not interested in brain activation related to reporting that one is on-task or exhibiting a TUT. 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.

To assess brain activation related to subsequent source memory, in the first level of analysis, four contrasts were performed contrasting the following conditions versus baseline: source hits and source misses in each of the two encoding tasks. The contrast results from the individual participants’ analysis were then entered into a second-level, mixed-effects ANOVA, with factors of Age

group (young, old), Subsequent source memory (source hit, source miss), and Encoding task (PLEAS, MAN) to assess main effects and interactions. In addition, to assess brain activation related to exhibiting TUTs, paired t tests were used to compare brain activation for encoding words preceding TUT versus on-task reports and vice versa.

RESULTS

Behavioral Results

Neuropsychology Tests and Questionnaires

Means with standard deviations for neuropsychological tests and questionnaires are listed in Table 1. We found no significant between-group differences in the MOCA ($t(1, 34) = 0.512, p = .612$), the BDI ($t(1, 34) = 0.511, p = .613$), letter fluency ($t(1, 34) = 1.016, p = .317$), category fluency ($t(1, 34) = 0.459, p = .649$) category switching ($t(1, 34) = 0.062, p = .951$), or NEO conscientiousness ($t(1, 34) = 1.243, p = .222$). Older adults had normal Geriatric Depression Scale scores (Table 1).

Following the memory experiment, on a scale of 1–10, we asked participants to rate how interesting and difficult they thought the memory task had been, as well as how motivated they had been to perform well. We found no between-group difference in ratings of interest ($t(1, 34) = 1.175, p = .248$) or difficulty ($t(1, 34) = 1.099, p = .280$). However, older adults reported being more motivated than young adults to perform the task ($t(1, 34) = 2.28, p = .029, d = 0.765$).

Table 1. Neuropsychological Tests and Questionnaires

	Young	Old
Education	16.35 (1.81)	16.38 (2.53)
MOCA	28.15 (1.14)	28.38 (1.5)
BDI	3.1 (3.09)	3.63 (3.03)
DKEFS-Letters	42.85 (11.32)	46.94 (12.8)
DKEFS-Category	46.4 (9.56)	44.88 (10.31)
DKEFS-Category Switch	15.8 (3.16)	15.88 (4.15)
NEO Conscientiousness	36.55 (5.84)	39.06 (6.24)
GDS	N/A	1.19 (1.17)
Interesting	6.5 (2.01)	7.31 (2.12)
Difficult	5.9 (2.1)	6.63 (1.78)
Motivation	7.75 (1.77)	8.88 (0.96)

This table presents group means and standard deviations for young and older adults for neuropsychological tests and questionnaires. MOCA = Montreal Cognitive Assessment; BDI = Beck Depression Inventory; DKEFS = Delis–Kaplan Executive Function System; GDS = Geriatric Depression Scale.

Table 2. Retrieval Response Type and Encoding RT

Response Type	Young		Old	
	Response proportions	Encoding RT	Response proportions	Encoding RT
<i>Pleasantness Task</i>				
Source hit	0.57 (0.18)	1572 (268)	0.47 (0.19)	1702 (175)
Recognition, no source	0.21 (0.14)	1652 (282)	0.17 (0.15)	1888 (297)
Item miss	0.13 (0.09)	1684 (317)	0.19 (0.11)	1735 (203)
Source misattribution	0.09 (0.07)	1727 (280)	0.17 (0.10)	1877 (198)
False alarm to new word	0.03 (0.04)		0.05 (0.03)	
<i>Man-made/Natural Task</i>				
Source hit	0.38 (0.15)	1673 (313)	0.32 (0.15)	1917 (178)
Recognition, no source	0.23 (0.12)	1624 (327)	0.18 (0.13)	1889 (348)
Item miss	0.30 (0.13)	1589 (297)	0.35 (0.11)	1830 (190)
Source misattribution	0.09 (0.08)	1693 (352)	0.14 (0.06)	1912 (208)
False alarm to new word	0.03 (0.05)		0.04 (0.03)	

This table presents the proportion of each retrieval response type as well as the mean encoding RT for each retrieval response type with standard deviations in parentheses. The proportion of responses does not add to 1 because false alarm to new words is also presented.

Encoding RT

Encoding RT data is listed in Table 2. An Age group (young, old) \times Encoding task (PLEAS, MAN) \times Subsequent source memory (source correct, item recognition without source, new, source misattribution) mixed ANOVA revealed a main effect of subsequent source memory ($F(3, 99) = 5.837, p = .001, \eta^2p = .15$), a main effect of Age group ($F(1, 33) = 6.288, p = .017, \eta^2p = 0.160$), an Encoding task \times Subsequent source memory interaction ($F(3, 99) = 4.237, p = .007, \eta^2p = 0.114$), and an Encoding task \times Age group interaction ($F(1, 33) = 5.420, p = .026, \eta^2p = 0.141$). The Encoding task \times Subsequent source memory interaction was due to RT for source hits being faster than all other response types (source misattributions ($t(1, 35) = 5.869, p < .001, d = 0.98$), item recognition without source ($t(1, 34) = 3.616, p < .001, d = 0.61$), item miss ($t(1, 35) = 2.640, p = .012, d = 0.44$)) during the PLEAS task, but RT during item misses being faster than source hits ($t(1, 35) = 3.340, p = .002, d = 0.56$) and source misattributions ($t(1, 35) = 2.664, p = .012, d = 0.44$) in the MAN task. The Encoding task \times Age group interaction was due to young adults having faster RT than older adults in the MAN task ($t(1, 34) = 3.076, p = .004, d = 1.032$), but not in the PLEAS task ($t(1, 34) = 1.984, p = .055$).

Retrieval Performance

The proportions of source hits, source misattributions, words recognized without the source, item misses, and

false alarms are listed in Table 2. We conducted Age group \times Task mixed ANOVAs on each response type individually. The ANOVA for source hits revealed a main effect of Task ($F(1, 34) = 68.781, p < .001, \eta^2p = 0.669$), indicating that both age groups exhibited more source hits during the PLEAS task versus the MAN task. There was no main effect of Age group or interaction (all $ps > .1$).

The mixed ANOVA for item recognition without source revealed a Task main effect ($F(1, 34) = 4.497, p = .041, \eta^2p = 0.117$) because of both age groups exhibiting more of these responses in the MAN task versus the PLEAS task. There was no main effect of Age group or interaction (all $ps > .3$). The mixed ANOVA for item misses similarly revealed a main effect of Task ($F(1, 34) = 86.869, p < .001, \eta^2p = 0.719$) because of both age groups exhibiting more of them in the MAN task versus the PLEAS task. There was no main effect of Age group or interaction (all $ps > .1$). We also conducted a mixed ANOVA on the sum of item recognition without source and item misses because these response types were combined in the fMRI analyses to form a “source miss” category. Similar to the ANOVAs on each individual response type, there was a main effect of Task ($F(1, 34) = 88.053, p < .001, \eta^2p = 0.721$), but no main effect of Age group or interaction (all $ps > .5$).

The mixed ANOVA for source misattributions revealed a main effect of age group ($F(1, 34) = 8.997, p = .005, \eta^2p = 0.209$) because of older adults exhibiting more source misattributions compared with young adults in both encoding tasks. The main effect of Encoding task

and the Encoding task \times Age group interaction were not significant ($p > .2$). Finally, the mixed ANOVA for false alarms to new words revealed no main effects or interactions.

In summary, two key results emerged from the analysis of retrieval responses. First, source retrieval was better for words encoded in the PLEAS task versus the MAN task: Both age groups exhibit more source hits and less source misses (i.e., “item recognition without source” and “item miss” responses) in the PLEAS task versus the MAN task. Second, the only age-related difference was found for source misattributions: In both the MAN and PLEAS tasks, older adults exhibited more of them compared with young adults.

TUT—Behavioral Results

We examined whether there were any age-related differences in frequency of TUT types during the episodic encoding task. In young adults, the percentage of thought probes for which mind-wandering, task-related interferences, and distractions were reported was 8%, 14%, and 28%, respectively. In older adults, they were 6%, 19%, and 20%, respectively. An Age group (young, old) \times TUT type (mind-wandering, task-related interferences, distractions) mixed ANOVA revealed a main effect of TUT type ($F(2, 68) = 12.46, p < .001, \eta^2p = 0.268$), but no main effect of Age group ($F(1, 34) = 0.741, p = .395$) or interaction ($F(2, 68) = 1.942, p = .151$). Post hoc tests indicated that the main effect of TUT type was due to mind-wandering being less frequent than both distractions ($t(1, 35) = 5.101, p < .001, d = 0.85$) and task-related interferences ($t(1, 35) = 3.096, p = .004, d = 0.52$). Distractions were also more frequent than task-related interferences ($t(1, 35) = 2.205, p = .034, d = 0.37$). To be consistent with the analysis of the fMRI data, in the following section, we collapsed mind-wandering, task-related interferences, and distractions into an off-task (TUT) category.

RT for On-task versus TUT Responses

In young adults, we previously reported that RTs for words preceding TUT reports were higher than those preceding on-task reports (Maillet & Rajah, 2014b). Here, we examined whether this effect would also be present in older adults. Encoding RT for words preceding thought probes is listed in Table 3. A TUT (on-task, TUT) \times Age group (young, old) mixed ANOVA for RT for the first word preceding the thought probe revealed a main effect of TUTs ($F(1, 34) = 13.012, p = .001, \eta^2p = 0.277$), but no main effect of Age group ($F(1, 34) = 0.663, p = .421$) or interaction ($F(1, 34) = 2.266, p = .141$). Across age groups, TUT responses were associated with higher RT versus on-task responses for the encoding word preceding the thought probe.

Retrieval Performance for On-task vs. TUT Responses

We examined whether, in addition to being associated with higher RT, encoding words preceding TUT versus on-task reports would be associated with differential retrieval performance (Table 3). An age group \times TUT mixed ANOVA on source hits revealed a main effect of TUTs ($F(1, 34) = 5.687, p = .023, \eta^2p = 0.143$) due to source hits being more frequent for on-task versus TUT responses. There was no main effect of TUTs on either source misattributions ($F(1, 34) = 3.804, p = .06$) or item recognition without source responses ($F(1, 34) = 1.546, p = .222$). However, there was a main effect of TUTs on item misses ($F(1, 34) = 9.059, p = .005, \eta^2p = 0.210$), because of their being more frequent for TUT versus on-task trials. There was no Age group \times TUT interaction for any retrieval response type (all $ps > .5$), indicating that the impact of TUTs on retrieval performance was similar in young and older adults. Thus, in summary, words directly preceding TUT reports were associated with fewer source hits and more item misses compared

Table 3. Retrieval Response Types and Encoding RT for Words Preceding Thought Probes

Retrieval Response Type	Young		Old	
	On Task	TUT	On Task	TUT
Source hit	0.51 (0.16)	0.43 (0.17)	0.42 (0.18)	0.36 (0.19)
Recognition, no source	0.21 (0.17)	0.25 (0.12)	0.16 (0.14)	0.18 (0.15)
Item miss	0.18 (0.11)	0.26 (0.15)	0.24 (0.15)	0.32 (0.18)
Source misattribution	0.09 (0.09)	0.08 (0.09)	0.17 (0.08)	0.14 (0.08)
Encoding RT	1484 (244)	1676 (453)	1617 (191)	1696 (190)

This table presents the proportion and standard deviation of each retrieval response type and encoding RT for words preceding thought probes. The data are separated according to whether participants reported being on-task or exhibiting a TUT during the thought probe.

Table 4. Main Effect of Subsequent Source Memory and Subsequent Source Memory \times Age Group Interaction

<i>Hemisphere</i>	<i>Brain Region</i>	<i>Brodmann's Area</i>	<i>MNI Coordinates</i>	<i>Cluster Size</i>	<i>Peak t Value</i>
<i>Group Similarities: Source Hits vs. Source Misses</i>					
Left	Inferior frontal gyrus	47/45	-42 30 -12	1193	6.45
			-42 26 -2		5.93
			-54 30 12		5.53
Left	Cerebellum		-24 -32 -26	115	4.99
Left	Superior frontal gyrus	6/8	-10 38 58	241	4.32
			-8 30 64		3.96
			-4 26 48		3.91
<i>Group Similarities: Source Misses vs. Source Hits</i>					
Bilateral	Precuneus	7	6 -78 50	3665	5.62
			-4 -76 52		5.08
			4 -66 60		4.72
Right	Superior frontal gyrus	9	38 52 24	300	5.12
			28 56 30		3.9
			36 40 40		3.86
Right	Middle frontal gyrus	6	28 -2 56	417	4.3
			38 4 54		3.88
			32 -4 48		3.35
Right	Temporoparietal junction	40	48 -48 54	984	4.19
			58 -36 44		4.03
			60 -42 34		4
Left	Middle frontal gyrus	46/9	-36 48 22	49	4
Left	Superior temporal gyrus	22	-60 -38 12	77	3.87
Left	Inferior parietal lobe	40	-32 -30 50	69	3.45
<i>Group by Subsequent Source Memory Interaction</i>					
Right	Caudate		14 12 8	254	4.33
Left	Caudate		-10 10 6	490	4.26
			-22 8 8		3.86
			-24 20 -2		3.66
Left	Inferior frontal gyrus	44/6	-50 8 32	206	4.1
Left	Inferior frontal gyrus	46	-48 34 4	73	3.87
Left	Anterior medial prefrontal	8/9	-10 56 30	132	3.84
			0 50 20		3.43

This table presents the random effects between-group SPM8 results. The t values represent the value for the local maxima which had a $p < .001$ and spatial extent threshold of $k > 48$. The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

with words directly preceding on-task reports in both age groups.

Correlations between TUTs and Retrieval Performance

Results in the previous section indicate that encoding events occurring in the moment directly preceding reports of exhibiting a TUT are more likely to be forgotten. We also assessed whether, across different individuals, frequency of TUT reports correlates with retrieval performance. To be consistent with the fMRI data, we averaged the proportion of “item recognition without source” and “item miss” responses across tasks in each participant across encoding tasks (i.e., source misses) and correlated this with frequency of TUTs. In young adults, there was a trend for TUT frequency to be positively correlated with source misses ($r = .419, p = .066$). In older adults, the correlation between TUTs and source misses was positive, but not significantly so ($r = .301, p = .258$). Across all 36 participants in this study, there was a significant positive correlation between TUT frequency and source misses ($r = .365, p = .029$), even after controlling for age group ($r = .374, p = .027$). In contrast, there was no significant relationship between TUT and source misattributions either in young ($r = -.173, p = .466$) or older adults ($r = -.172, p = .524$). The across-group correlation was not significant ($r = -.218, p = .202$) even after partialling out age group ($r = -.172, p = .323$). Thus, in summary, individuals that exhibited more TUTs exhibited more source misses, but not more source misattributions.

fMRI Results

Age Group by Encoding Task \times Subsequent Source Memory ANOVA

First, we were interested in assessing brain regions exhibiting subsequent source forgetting effects, that is, brain regions more active during source misses versus source hits. We conducted an Age group (young, old) \times Encoding task (PLEAS, MAN) by subsequent source memory (remembered, forgotten) mixed ANOVA. Results for the main effect of Subsequent source memory and the Age \times Subsequent source memory interaction are shown in Table 4 and Figure 1. Source misses were associated with greater activation in precuneus, bilateral MFG/SFG, right TPJ, and left TPJ. The reverse contrast revealed greater activation in left ventrolateral pFC, cerebellum, and superior medial pFC during source hits versus source misses. Five regions in the left posterior inferior frontal gyrus, anterior medial pFC, and bilateral caudate exhibited a subsequent source memory by age group interaction. Beta estimates extracted from all five brain regions indicated that young adults exhibited greater activation for source hits versus source misses (all $ps < .003$) whereas

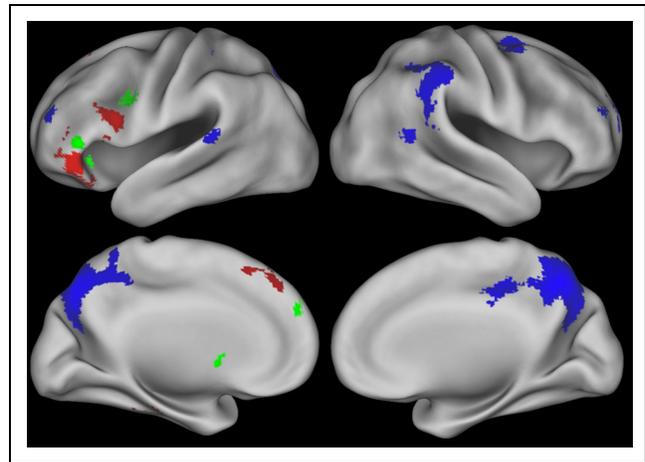


Figure 1. This figure depicts group similarities in regions more activated for source hits versus source misses (red) and source misses versus source hits (blue). The brain regions exhibiting an age group by subsequent source memory interaction are displayed in green. Caret was used to create the figure. Please note that some smaller activations identified in each contrast may not show up with Caret.

older adults did not exhibit any difference in activation between these conditions (all $ps > .05$).

We also examined age-related differences in brain activation as a function of Encoding task (Table 5 and Figure 2). The main effect of encoding task indicated that, independent of subsequent source memory, both age groups activated anterior cingulate/medial pFC, bilateral middle temporal gyri, posterior cingulate, and left inferior frontal gyrus in the PLEAS task versus the MAN task. The reverse contrast revealed greater activation in bilateral superior parietal lobe, right MFG, and left precentral gyrus. Age-related differences in activation in the two encoding tasks were observed in four regions. One region, in anterior medial pFC, was recruited by young to a greater extent in the PLEAS task versus the MAN task ($p < .001$), whereas there was no difference in activation in old ($p > .1$). The other three regions, in left superior pFC and left intraparietal sulcus, were recruited by older adults in the MAN task versus the PLEAS task (all $ps < .006$), with no difference in activation in young (all $ps > .05$).

Lastly, we assessed age-related similarities and differences in brain regions exhibiting an interaction of encoding task and subsequent memory (Table 6). Only group similarities were identified. Both age groups exhibited greater activation for source hits versus source misses in two subregions of left inferior/middle FG in the MAN task, but not in the PLEAS task (Region 1: MNI coordinates: $[-44\ 6\ 30]$, Peak $T = 4.66$, cluster size = 225; Region 2: MNI coordinates: $[-48\ 30\ 18]$, Peak $T = 3.8$, cluster size = 161). Beta estimates from these two regions confirmed that they both exhibited a Subsequent source memory \times Encoding task interaction because of greater activation for source hits versus misses in the MAN task (all $ps < .001$), but no difference in activation between source hits and source misses in the PLEAS task (all $ps > .2$).

Table 5. Main Effect of Encoding Task and Encoding Task by Age Group Interaction

<i>Hemisphere</i>	<i>Brain Region</i>	<i>Brodmann's Area</i>	<i>MNI Coordinates</i>	<i>Cluster Size</i>	<i>Peak t Value</i>
<i>Group Similarities: Pleasantness vs. Man-made/Natural Task</i>					
Left	Medial prefrontal cortex	8/9	-8 54 40	4452	8.25
			-4 54 6		7.77
			-6 52 14		7.51
Left	Inferior temporal gyrus	21	-60 -14 -24	281	5.95
Left	Inferior frontal gyrus	47	-38 20 -20	365	5.09
			-28 14 -20		5.01
			-44 28 -12		4.81
Right	Superior temporal gyrus	38	46 12 -38	60	4.65
Left	Posterior cingulate	23/31	-4 -50 26	94	3.88
Left	Superior temporal gyrus	39	-58 -60 32	48	3.67
			-54 -68 30		3.39
<i>Group Similarities: Man-made/Natural vs. Pleasantness Task</i>					
Bilateral	Superior parietal lobe/precuneus	40/7	-44 -46 60	5404	6.16
			44 -46 46		5.76
			-38 -46 66		5.65
Right	Superior frontal gyrus	6	32 2 66	703	5.06
			32 6 56		4.64
Right	Precentral gyrus	6	42 8 32	353	4.63
Left	Precentral gyrus	6	-26 -6 54	481	4.42
			-28 0 64		4.36
			-24 -6 74		3.47
Right	Anterior middle frontal gyrus	10	36 56 2	192	3.81
Right	Middle/superior frontal gyrus	9	42 38 32	127	3.76
			40 46 26		3.35
<i>Encoding Task by Age Group Interaction</i>					
Left	Precentral gyrus	4/3/6	-36 -14 58	620	4.29
			-36 -28 64		3.54
			-16 -12 58		3.4
Left	Anterior medial prefrontal cortex	9	-4 62 22	54	3.91
Left	Inferior/superior parietal lobe	40/7	-44 -40 60	92	3.58
			-34 -44 60		3.43
Left	Middle frontal gyrus	9	-40 40 30	52	3.58

This table presents the random effects between-group SPM8 results. The *t* values represent the value for the local maxima which had a *p* < .001 and spatial extent threshold of *k* > 48. The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

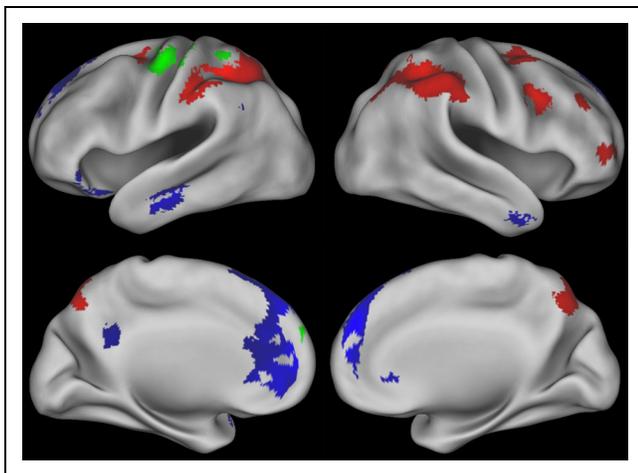


Figure 2. This figure depicts group similarities in regions more activated in the man-made/natural versus the pleasantness task (red) and the pleasantness versus the man-made natural task (blue). The brain regions exhibiting an age group by encoding task interaction are displayed in green. Caret was used to create the figure. Please note that some smaller activations identified in each contrast may not show up with Caret.

No brain region was identified as exhibiting greater activation in source hits versus misses only in the PLEAS task. In our previous analysis of this data set in young adults (Maillet & Rajah, 2014b), we found a cluster in medial pFC that exhibited this effect. We were thus surprised not to find any effect in the between-group analysis in this study. We conducted separate within-group ANOVAs looking for regions exhibiting greater activation in source hits versus misses only in the PLEAS task in each age group. In young adults, a single cluster in ventral medial pFC was found ($p < .001$; MNI coordinates: $[-2\ 42\ 0]$; cluster size = 79). Post hoc tests revealed that activation in this region was greater for source hits versus misses in the PLEAS task ($p = .03$), but greater for source misses versus hits in the MAN task ($p = .01$), similar to our previous report. In contrast, the within-group whole-brain ANOVA in older adults did not reveal any significant activation in medial pFC for this contrast, even at a reduced $p < .005$ threshold.

We next assessed whether the ventral medial pFC effect in young adults was driven by RTs (which also exhibited an Encoding task \times Subsequent source memory interaction). We thus repeated the within-group whole-brain ANOVAs, controlling for RT. In young adults, the ventral medial pFC was observed, but only at a reduced $p < .005$ threshold (MNI coordinates: $[-4\ 44\ -2]$, cluster size = 74). Thus, while controlling for RTs did slightly reduce the significance of this effect, the effect does not appear to reflect an artifact of RTs differences between tasks.

Brain Regions Involved in TUTs

Next, we assessed brain regions that were more active during encoding events directly preceding TUTs relative

to on-task reports. We expected to find similar regions for TUT versus on-task trials as we found for source misses versus source hits. The results from this analysis are presented in Table 6. Encoding words preceding TUT reports versus on-task reports were associated with greater activation in precuneus, bilateral MFG/SFG, right lateral temporal cortex, and right insula. No brain region was significantly more active for on-task versus off-task trials, and no region was differentially activated with age in either contrast.

We examined which brain regions were more active during both TUT versus on-task trials and source misses versus source hits (each contrast individually thresholded at $p < .001$, $k = 48$). We observed a conjunction in right MFG/SFG. When the cluster extent threshold was lowered to $k = 15$, a conjunction was also observed in left MFG/SFG and precuneus (Table 7; Figure 3).

DISCUSSION

In the current study, we measured frequency of TUTs in young and older adults during a source memory encoding task. Compared with young adults, older adults exhibited a similar amount of source misses, which we define as instances where participants either forgot the word entirely or remembered the word but forgot its source. However, older adults exhibited at a greater amount of source misattributions, which we define as instances where participants falsely claim to have studied a word in one task rather than the other. Thus, older adults' reduced behavioral performance on the source memory task was attributable primarily to their tendency to exhibit source misattributions, a result that has been obtained in some prior studies (e.g., Cohen & Faulkner, 1989).

We found no age-related differences in frequency of TUTs. In addition, TUTs at encoding were positively associated with source misses in both age groups. Furthermore, TUTs and source misses were associated with activation in similar brain regions including bilateral middle/superior FG and precuneus. Lastly, in young adults, we observed greater activation for source hits versus source misses in medial pFC in the PLEAS task. In the following sections, we discuss each of these results in greater detail.

Age-related Differences in Frequency of TUTs

Recently, many behavioral studies have found age-related reductions in frequency of TUTs across different cognitive tasks including working memory, reading comprehension, sustained attention tasks, and episodic memory encoding (Zavagnin et al., 2014; Maillet & Rajah, 2013; Jackson & Balota, 2012; Krawietz et al., 2012). Behavioral studies are usually conducted in quiet and comfortable environments. In these settings, age-related reductions

Table 6. Brain Regions Involved in Exhibiting TUTs

<i>Hemisphere</i>	<i>Brain Region</i>	<i>Brodmann's Area</i>	<i>MNI Coordinates</i>	<i>Cluster Size</i>	<i>Peak t Value</i>
<i>Group Similarities: Encoding Trials Preceding TUT vs. On-task</i>					
Right	Middle frontal gyrus	6	28 0 44 42 0 38 36 0 60	751	4.76 4.65 3.68
Right	Clastrum/insula		42 8 -6 34 20 -14 54 4 10	439	4.57 3.86 3.79
Right	Middle/superior frontal gyrus	8/9/10	36 40 40 34 58 8 28 58 22	434	4.51 3.82 3.63
Right	Lateral temporal cortex	21	46 -12 -16 38 -2 -20	157	4.39 3.84
Left	Middle/superior frontal gyrus	9/10	-34 46 32 -30 56 22 -34 50 12	141	4.27 3.86 3.83
Right	Superior medial frontal gyrus	6	12 12 50 16 16 58	286	4.23 3.97
Right	Precuneus	7	14 -76 58 10 -66 66	54	4.08 3.5
Left	Superior medial frontal gyrus	6	-18 -4 50 -14 0 58 -8 6 56	150	4.01 3.88 3.68

This table presents the random effects between-group SPM8 results. The t values represent the value for the local maxima which had a $p < .001$ and spatial extent threshold of $k > 48$. The cluster size refers to the total number of voxels included in the voxel cluster. The stereotaxic coordinates are measured in mm.

in TUTs are primarily attributable to a reduction in mind-wandering, rather than task interferences or distractions (Zavagnin et al., 2014). However, fMRI studies take place in a relatively uncomfortable and noisy environment. It

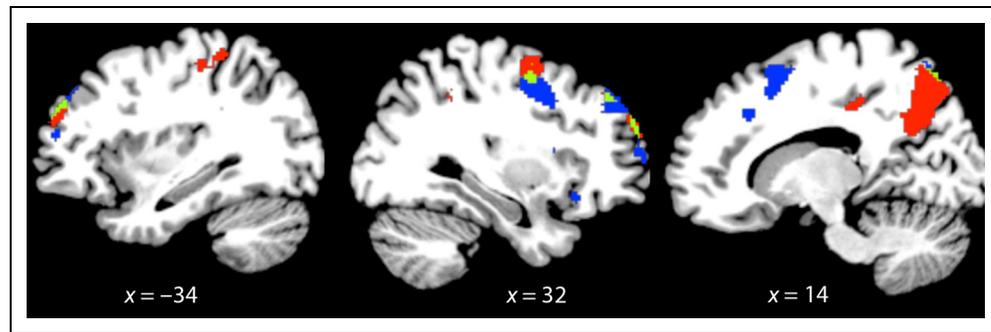
is possible that, under these conditions, older adults may be more distracted by the scanner environment or by feelings of discomfort (Stevens et al., 2008; Gutchess & Park, 2006).

Table 7. Conjunction Analysis

<i>Hemisphere</i>	<i>Brain Region</i>	<i>Brodmann's Area</i>	<i>MNI Coordinates</i>	<i>Cluster Size</i>
Right	Precuneus	7	10 -78 54	22
Right	Middle/superior frontal gyrus	8/9	38 52 24 36 40 40 24 60 22	135
Right	Middle frontal gyrus	6	30 -4 54 38 4 52	106
Left	Middle frontal gyrus	9	-36 48 26	30

This table presents the results from a conjunction analysis between two contrasts: TUT versus on-task, and source miss versus source hit. Each contrast was individually thresholded at $p < .001$, $k > 15$.

Figure 3. This figure depicts groups similarities in regions more activated for source misses versus source hits (red), TUT versus on-task events (blue), and the overlap between these two contrasts (green).



In the current study, we measured frequency of mind-wandering, task-related interferences, and internal/external distractions. In both age groups, distractions were the most commonly reported TUT type, indicating that participants do indeed get distracted by the scanner environment. In contrast, participants exhibited very little mind-wandering. Thus, it appears that compared with behavioral paradigms that tend to promote higher levels of mind-wandering compared with distractions (e.g., Zavagnin et al., 2014), this relationship is flipped in fMRI studies (see also Stawarczyk, Majerus, Maquet, et al., 2011). However, we did not find a disproportionate increase in distractions in older adults. In fact, although older adults exhibited numerically lower amounts of TUTs, we observed no significant age-related differences in frequency of any TUT type. Thus, unlike previous behavioral studies, young and older adults may exhibit a similar frequency of TUTs in fMRI environments. It is at present unclear what led to this null finding. Older adults did exhibit numerically lower amounts of TUTs compared with young; thus, one possibility is that a higher sample size would have yielded different results. Unlike some previous behavioral studies (Maillet & Rajah, 2013; Jackson & Balota, 2012; Krawietz et al., 2012), we found no age-related differences in task interest, task difficulty of conscientiousness scores between young and older adults. Krawietz et al. (2012) reported that, after accounting for age-related differences in task interest, age-related reductions in TUTs were no longer significant. Thus, another possibility is that the age equivalence in task interest may have contributed to the similar TUT rates in the current study. Alternatively, Gutchess and Park (2006) noted that the ongoing task may need to be relatively complex for age-related differences in vulnerability to distraction manifest. Thus, it is possible that a more difficult task would have yielded different results. More generally, because this is the first study to measure age-related differences in TUTs during a cognitive task, future studies are needed to ascertain the precise factors influencing rates of TUTs in an fMRI environment.

The behavioral impact of TUTs on task performance was very similar in young and older adults. Across age groups, words directly preceding thought probes in which participants reported exhibiting TUTs versus being

on-task were associated with increased RT and were more often forgotten at retrieval. Furthermore, across both age groups, there was a positive correlation between TUT frequency and source misses. In contrast, there was no association between TUT and source misattributions, and if anything, this association was negative. Thus, TUTs appear to primarily reduce the quality of ensuing memories (i.e., source misses) rather than promoting false memories (i.e., source misattributions).

Taken together, our results suggest that TUTs are unlikely to contribute to age-related reductions in performance on source memory tasks. This is indicated first by the result that older adults do not exhibit an increase in frequency of TUTs compared with young adults. Second, age-related reductions in performance on the source memory task used in the current study were due to an age-related increase in source misattributions, which were not significantly associated with TUT frequency. Thus, age-related differences in retrieval performance in source memory tasks may be due to mechanisms other than TUTs that contribute to older adults making false attributions of source.

Neural Correlates of Subsequent Source Forgetting Effects and TUTs

Given the behavioral association between TUTs and source misses reported above, one may expect the neural correlates of TUTs and subsequent source forgetting (i.e., source misses) to be similar. We found no age-related differences either in regions associated with source misses versus source hits or in regions activated during TUT versus on-task events. Across age groups, source misses were associated with activation in bilateral middle/superior pFC, bilateral inferior parietal lobe, precuneus, and left superior temporal gyrus. Note that although the contrast used here (source misses vs. source hits) differs from the more commonly used forgotten versus remembered contrast, the regions identified in both contrasts appear to be highly similar (compare with Kim, 2011). In addition, the finding of age-related similarities in subsequent source memory effects in the current study is consistent with two recent studies that also used source memory encoding tasks (Cansino et al., 2015; Mattson et al., 2014) despite

differences in the contrasts used in these studies compared with the present one (in the current study, item misses and words recognized with the source were combined in a “source miss” category and contrasted against source hits, whereas in these two studies, only items recognized without the source [but not item misses] were contrasted against source hits).

Across age groups, TUTs were associated with activation in bilateral MFG/SFG, precuneus, right insula and right lateral temporal cortex. All of these brain regions have previously been identified in previous studies of TUTs (Fox, Spreng, Ellamil, Andrews-Hanna, & Christoff, 2015). The similarity between regions more activated for TUT versus on-task episodes and those exhibiting subsequent source forgetting effects is illustrated in Figure 3. Overlapping activation between subsequent source forgetting effects and TUTs was found in bilateral MFG/SFG and precuneus. The overlap in brain activation between subsequent source forgetting effects and TUTs, as well as the behavioral association between TUTs and source misses provides evidence that subsequent source forgetting effects may in part reflect the occurrence of TUTs in both age groups. The precuneus may be involved in memory retrieval, scene construction, or monitoring on internal and external milieu (Stawarczyk, Majerus, Maquet, et al., 2011; Andrews-Hanna, Reidler, Sepulcre, Poulin, & Buckner, 2010; Hassabis, Kumaran, & Maguire, 2007). The MFG/SFG may be involved in executive control processes recruited during TUT episodes (e.g., for planning future events), in conflict detection aimed at bringing attention back on task, or in meta-awareness (Maillet & Rajah, 2014b; Christoff et al., 2009).

Two unresolved questions in the literature are (1) why older adults exhibit reductions/reversals in subsequent memory effects in studies using item encoding or item–item encoding and (2) why such effects are not observed during source memory encoding, such as in the current study. Although our study was not designed to answer these questions directly, we briefly speculate as to why these effects may occur. First, our result of age similarities in the association between TUTs and source misses, at both a behavioral and neural levels, provides preliminary evidence that the cognitive processes engaged when young and older adults encode events whose source will later be forgotten may be similar, at least within the context of fMRI. More research will be needed to confirm this association. However, these preliminary results suggest that reductions/reversals in subsequent memory effects, when they do occur, occur because of age-related differences in activation during successful rather than unsuccessful encoding.

Why would such effects occur in encoding of single item and item–item associations, but not in source memory encoding? One key difference between source memory and other paradigms is that these tasks restrict the potential types of details that are relevant for successful performance. In contrast, item recognition tasks can be

performed by remembering a variety of features, including perceptual details, thoughts, feelings, and emotions. In these tasks, there exists a possibility that young and older adults may rely on different features: for example, whereas young adults may rely more on perceptual details, older adults may rely more on spontaneously occurring personal thoughts and feelings (Hashtroudi, Johnson, & Chrosniak, 1990) or on prior knowledge (Umanath & Marsh, 2014), both of which are known to recruit regions such as posterior cingulate, precuneus, inferior parietal lobes, and SFG (Fox et al., 2015; Binder & Desai, 2011). In contrast, source memory tasks can only be performed by recollecting the precise feature being measured in a given study (e.g., encoding task, spatial location). Thus, one speculative possibility is that reductions/reversals in subsequent memory effects with age occur only during encoding of single items or item–item associations because of age-related differences in the features of encoding events that ultimately lead to successful retrieval.

Contribution of Medial pFC to Subsequent Source Memory in Young and Older Adults

In both age groups, retrieval was better for words encoded in the PLEAS task versus the MAN task, consistent with prior findings (Maillet & Rajah, 2013). In both age groups, the encoding task main effect indicated that a large region of medial pFC was activated to a greater extent in the PLEAS task versus the MAN task, which may be due to the former task engaging valuation (D’Argembeau, 2013) or self-referential processes (Gusnard, Akbudak, Shulman, & Raichle, 2001) to a greater extent.

In our previous analysis of this data set in young adults, we found that a dorsal portion of the medial pFC was involved in subsequent source memory across encoding tasks (MNI peak coordinates: [−6 54 44], [−6 58 16], [−6 58 30]). In the current analysis, we found that a similar dorsal region of medial pFC [−10 56 30] was involved in subsequent source memory across tasks, but only in young adults. We previously suggested that the task-independent subsequent source memory effect in this region may reflect internally directed attention to task-relevant cognitive operations at encoding which was necessary for successful source recollection. Thus, one possibility is that older adults recruited these processes to a lesser extent than young at encoding. In our previous analysis of this data set in young, we also found a more ventral region of medial pFC that was involved in subsequent source memory in the PLEAS task, but in subsequent source forgetting in the MAN task (MNI peak coordinates: [−2 56 8]). Although the ventral region was not identified in the between-group ANOVA, within-group analyses revealed that a similar region (MNI coordinates: [−2 42 0]) exhibited this effect in young adults, but not in older adults. We previously suggested that this more ventral region may be involved in self-referential evaluation/valuation of verbal stimuli, which would have been led

to subsequent source memory only in the PLEAS task. Our results regarding age-related differences in this effect are inconclusive—it is possible that not enough power was available in the current experiment to detect it in older adults.

Limitations and Future Directions

In the current study, we used a source memory paradigm that allowed us to dissociate source misses from source misattributions. These two types of source errors are usually not distinguishable in fMRI studies that use forced-choice designs (e.g., when participants are forced to choose one source or the other). This paradigm revealed that age-related reductions in source memory performance are due primarily to source misattributions (a finding that we had not predicted). A limitation of the current study is that we were unable to assess the neural correlates of source misattributions because of a lack of events. However, our results do reveal that, unlike source misses, source misattributions are not associated with frequency of TUTs. We are not aware of any studies that have assessed age-related differences in the neural correlates of encoding events later associated with source misattributions. It will be important for future studies to assess this to better understand why their frequency increases with age.

Another limitation of the current study is that, because of small event numbers, we were unable to assess age-related differences in the neural correlates of specific TUT types such as mind-wandering, task-related interferences, and distractions. Although our results reveal that there are age similarities in brain activation that collapsed across these thought types, it is possible that age differences would emerge if these thought types were considered individually.

Acknowledgments

This work was supported by CIHR operating grant #MOP126105 and an FRQ-S, Research Scholar-Junior 2 award to M. N. Rajah, as well as by a Natural Science and Engineering Research Council of Canada PGS D award to D. Maillet.

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Note

1. In the current study, TUTs were modeled as events given that our goal was to assess similarities in neural activation between TUTs and source misses (which are also modeled as events). In contrast, two previous studies (Stawarczyk, Majerus, Maquet, et al., 2011; Christoff et al., 2009) using block designs have modeled TUTs as 10-sec epochs preceding the thought probe. To determine whether these different methods (event vs. epoch) make a big impact on the results, we also tried modeling TUT as an epoch starting at the onset of the second word preceding the thought probe and ending at the onset of the thought probe. These epochs lasted on average approxi-

mately 12 sec. In general, this method yielded similar activation for TUT versus on-task events as the contrast reported in this article in regions including posterior cingulate/precuneus, right MFG/SFG, and right lateral temporal cortex. However, a few differences emerged. Most notably, only the contrast reported in the article yielded activation in left MFG/SFG.

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