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Age-related differences in agenda-driven monitoring of format and task information

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ABSTRACT

Age-related source memory deficits may arise, in part, from changes in the agenda-driven processes that control what features of events are relevant during remembering. Using fMRI, we compared young and older adults on tests assessing source memory for format (picture, word) or encoding task (self-, other-referential), as well as on old–new recognition. Behaviorally, relative to old–new recognition, older adults showed disproportionate and equivalent deficits on both source tests compared to young adults. At encoding, both age groups showed expected activation associated with format in posterior visual processing areas, and with task in medial prefrontal cortex. At test, the groups showed similar selective, agenda-related activity in these representational areas. There were, however, marked age differences in the activity of control regions in lateral and medial prefrontal cortex and lateral parietal cortex. Results of correlation analyses were consistent with the idea that young adults had greater trial-by-trial agenda-driven modulation of activity (i.e., greater selectivity) than did older adults in representational regions. Thus, under selective remembering conditions where older adults showed clear *differential* regional activity in representational areas depending on type of test, they also showed evidence of disrupted frontal and parietal function and reduced item-by-item modulation of test-appropriate features. This pattern of results is consistent with an age-related deficit in the engagement of selective reflective attention.

1. Introduction

Normal aging is associated with a disproportionate decrement in the ability to correctly recollect specific features of events (source memory), relative to less specific forms of memory such as old–new recognition (see Cansino (2009), Craik and Rose (2012), Daselaar and Cabeza (2008), Grady (2008), Henkel, Johnson, and De Leonardis (1998), Naveh-Benjamin and Ohta (2012), Park and McDonough (2013), Park and Reuter-Lorenz (2009), for reviews). The use of neuroimaging in source memory studies with healthy older adults is beginning to yield important information about the relative impact of aging on the various, intertwined factors involved in source memory (e.g., encoding features and binding them together, controlled reflective attention to particular features during remembering), but there is still much to be learned. In particular, little is known about age-related changes in the neural correlates of selective, agenda-driven processes engaged during remembering—that is, those processes involved in determining which features are sought, revived, and used in making a specific memory attribution (see Johnson, Hashtroudi, and Lindsay (1993), Mitchell and Johnson (2009), for further discussion and reviews). This is the focus of the current study.

Source memory is related to encoding activity in representational regions associated with the processing of specific features, such as perceptual processing of color or location (Uncapher, Otten, & Rugg, 2006; Uncapher & Rugg, 2009), and auditory or visual information (Gottlieb, Uncapher, & Rugg, 2010). In addition, consistent with the context reinstatement hypothesis (Tulving and Thomson, 1973), the extent to which this activity (or pattern of activity) is recapitulated at test is related to episodic memory accuracy (see Rissman and Wagner (2012) for a review). But there also is behavioral (Lindsay & Johnson, 1989; Marsh & Hicks, 1998) and neuroimaging (Johnson, Kounios, & Nolde, 1997; Nolde, Johnson, & D'Esposito, 1998; see also, McDuff, Frankel, & Norman, 2009) evidence that remembering does not depend only on what is "there," but also on what the rememberer "looks for" and how they use or evaluate (e.g., weight) what they find (Johnson et al., 1993). That is, the same encoded information can give rise to different memory outcomes and/or brain activity depending on participants' agendas during remembering, which affect not only what they "look for," but also what they "look at" among activated information. Similar concepts include, for example, "retrieval orientation" (e.g., Rugg and Wilding (2000)),

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"domain-sensitive biasing" (e.g., Dobbins and Wagner (2005)), and "cue-based planning" (e.g., Dobbins and Han (2006)), except that these other concepts focus more on the "looking for" than the "looking at" aspect of remembering.

There are several reasons to expect that older adults may be less able to adopt and/or carry out agendas to look for and/or evaluate specific information during remembering. Older adults are less able to, or slower to, constrain retrieval to task relevant information (Dew, Buchler, Dobbins, & Cabeza, 2011; Duverne, Motamedinia, & Rugg, 2009; Jacoby, Bishara, Hessels, & Toth, 2005). Hasher and Zacks and colleagues have reported considerable evidence that older adults are more distracted by task irrelevant information in many contexts (e.g., Campbell, Grady, Ng, & Hasher, 2012; Hasher & Zacks, 1988). Evaluating based on an agenda presumably involves not only looking for the appropriate information, but also selectively attending to (i.e., "looking at") a subset of activated information; older adults have deficits in selective reflective attention (Higgins & Johnson, 2009; Mitchell, Johnson, Higgins, & Johnson, 2010; Oberauer, 2001; Raye, Mitchell, Reeder, Greene, & Johnson, 2008). Consistent with evidence that areas of lateral frontal and parietal cortex are involved in reflective monitoring of information (Cabeza, Ciaramelli, & Moscovitch, 2012; Chun & Johnson, 2011; Ciaramelli, Grady, & Moscovitch, 2008; Nelson et al., 2010), there is evidence of age-related differences in activity in both lateral prefrontal cortex (PFC) and lateral parietal regions associated with memory monitoring (e.g., Daselaar, Fleck, Dobbins, Madden, and Cabeza (2006), McDonough, Wong, and Gallo (2012), Mitchell, Raye, Johnson, and Greene (2006), Morcom, Li, and Rugg (2007)).

To investigate agenda-dependent source memory, studies often contrast a single source identification test with old–new recognition (ON) (see Mitchell and Johnson (2009) for a review). Of course, old–new recognition may be agenda-driven, but it is less selective in the features that are relevant and can be based on a general feeling of familiarity (Jacoby, 1991; Mandler, 1980). Nevertheless, although ON and source identification tests typically differ in the specificity of the information *required*, the same information that is relevant for a source judgment is also relevant for an ON judgment (though typically not vice versa). In other words, although specific features are not *necessary* to make an old–new discrimination, they may be used under some circumstances, especially when the old–new test occurs in the context of a source identification task. Hence, for investigating agenda-driven source monitoring, there should be an advantage to contrasting two source identification tests that direct participants to different classes of features (e.g., format, task).

Some aging studies have included two types of source test (e.g., spatial and temporal), but collapsed across them in analyses in order to, for example, compare accurate source decisions on old items with correct rejections (e.g., Duarte, Henson, and Graham (2008)). We are aware of only two fMRI studies that assessed age-related differences comparing two different source identification tests, and both focused primarily on changes in PFC. In a short-term source memory task designed to minimize retrieval demands and highlight activity associated with selective evaluation of format or location information relative to item recognition, older adults showed source test deficits in left lateral PFC (Mitchell et al., 2006). A study reported by Rajah, Languay, and Valiquette (2010) used a mini-blocked test design, and showed age-related deficits in memory for spatial and temporal information associated with age differences in activity in right dorsolateral and left anterior prefrontal cortex, respectively. The current design is an advance in that it assesses trial-by-trial selectivity of source monitoring in distinct representational areas, as well as frontal and parietal areas involved in source monitoring. Similarities and differences in young and older adults' brain activity under these circumstances should help clarify the nature of age-related changes in the processes involved in selective targeting of specific features according to an agenda.

We combined fMRI with a procedure that used short study-test cycles to assess young and older adults' source memory for item format and encoding task information. In each cycle, participants saw eight labels of concrete objects presented sequentially; for half there was a corresponding picture above the label. For half of each format condition (word only, word+picture), participants were asked to indicate whether they liked the object, and for the other half whether Sarah Palin would like the object (me–Sarah encoding task). (Given that Sarah Palin was the 2008 Republican candidate for vice president, and that she continued to be in the news, we expected our participants would have a sense of her as a person on which to base their "like" judgment.) Next, participants were shown six labels successively; two trials tested whether the item was shown at encoding with a picture or only as a word (format: PW), two whether participants did the "like" task for me or Sarah (task: MS), and two whether the item was old or new (ON).

We chose these two features (format and encoding task) because processing of these two types of information should generate activity in distinct brain regions. There is considerable evidence that (in young adults) both encoding and remembering visual information are associated with activity in posterior sensory regions, including parahippocampal gyrus, fusiform gyrus, and middle occipital cortex (Kensinger & Schacter, 2006; Slotnick, Thompson, & Kosslyn, 2012; Takahashi, Ohki, & Miyashita, 2002; Wheeler, Petersen, & Buckner, 2000), and that greater activity is associated with better memory for specific detail (Garoff, Slotnick, & Schacter, 2005; Kensinger & Schacter, 2007). There is evidence of age-related changes in the processing of visual information by posterior brain areas during both passive viewing and memory tasks (Carp, Park, Polk, & Park, 2011; Chee et al., 2006; Park et al., 2004; Payer et al., 2006), though the extent to which, and circumstances under which, these age differences reflect differences in perceptual vs. reflective processing remains to be clarified (Mitchell et al., 2010; see also, Chee et al., 2006).

On the other hand, previous findings across a range of tasks suggest that anterior and posterior midline regions (medial prefrontal cortex [mPFC] and posterior cingulate/precuneus) play a role in processing and/or representing person information (see Denny, Kober, Wager, and Ochsner (2012), Murray, Schaer, and Debbané (2012), Northoff et al. (2006), for reviews and meta-analyses). An additional reason to expect activity in mPFC to be associated with our encoding task is that, in source memory tasks, activity in medial and lateral anterior PFC is associated with records of reflective cognitive operations, such as those engaged by evaluative judgment tasks, even when they do not explicitly reference the self (e.g., Dobbins and Wagner (2005), Kensinger and Schacter (2006), Mitchell et al. (2008), Simons, Henson, Gilbert, and Fletcher (2008), Turner, Simons, Gilbert, Frith, and Burgess (2008), Vinogradov et al. (2006)). Several studies show that older adults' memory, including memory for details, can benefit from self-referential processing as much as young adults', though this does not completely ameliorate age-related deficits (Dulas, Newsome, and Duarte (2011), Gutchess, Kensinger, Yoon, and Schacter (2007), Hamami, Serbun, and Gutchess (2011)). Also, evidence suggests that there may be age-related changes in medial frontal activity during encoding or remembering person or task information (Feyers, Collette, D'Argembeau, Majerus, and Salmon (2010), Gutchess, Kensinger, and Schacter (2010), Mitchell et al. (2009)). Other data suggest young and older adults' brain activity often looks fairly similar under these circumstances (Dulas et al. (2011), Gutchess, Kensinger, and Schacter (2007), but see Li, Morcom, and Rugg (2004)).

Thus, there was reason to believe that our format manipulation should engage posterior visual cortex and our me–Sarah encoding task should engage mPFC. We also expected at least a subset of these areas to be active again during remembering of this information (Wheeler et al., 2000). We should emphasize that our major interest was not in directly comparing memory for format and task information, per se. Rather, we used two classes of information with clear neural markers to investigate potential age-related changes in selective processing of different classes of features in the service of agenda-driven source memory. Assuming prefrontal and parietal regions are flexibly engaged in reviving and monitoring information in response to current agendas, we also should expect to see differences in activity in prefrontal and/or parietal regions depending on type of test. Aside from differences in regional activity, under at least some circumstances, young and older adults can show different patterns of correlations between areas even when regional differences are negligible (e.g., Davis, Dennis, Daselaar, Fleck, and Cabeza (2008), Feyers et al. (2010), Grady et al. (1994); see Grady (2012), Park and McDonough (2013), for recent reviews). Hence, we also conducted targeted correlations using representational regions and parietal regions as seeds. Of interest were differences in young and older adults' patterns of regional activity and correlations between regions across source tests.

In sum, to further understanding of older adults' source memory deficits, we used a source feature identification procedure that included two different types of features to assess age-related changes in the neural correlates of agenda-driven source monitoring. Our primary analyses focused on three specific questions about activity during test trials: (a) Did regional activity in format- and task-sensitive regions show differential activity during test, depending on the type of source test (Picture–Word vs. Me–Sarah), and, assuming so, did selectivity in activity differ for young and older adults? (b) Were PFC and/or parietal regions differentially engaged in the two age groups during the two source tests? (c) Were there age-related differences in the trial-by-trial correlation of activity in these regions of interest (i.e., functional connectivity)? Together, the pattern of results should clarify age-related changes in agenda-driven modulatory processes underlying selective monitoring (access and evaluation) of source information.

2. Methods

2.1. Participants

Young participants ($n=21$ [17 females], M *age*$=21.3$ yr [$SD=2.0$ yr; range=18–27 yr]) were college students; older participants ($n=18$ [11 females], M *age*$=71.2$ yr [$SD=5.4$ yr; range=64–82 yr]) were healthy, independently living adults from surrounding communities. All participants self-reported being in good health, with no history of stroke, serious heart disease, or primary degenerative neurological disorder. On a scale from 1 to 5, where 1=*excellent*, older adults ($M=1.4$) reported feeling better physically the day of the scan than did young adults ($M=2.0$) ($t[37]=2.57$, $p<.05$), but young and older participants rated their physical health over the past year similarly ($M_s=1.7$ for both groups). Ratings of mood (also a 5-point scale) showed no differences between the groups for mood the day of the scan ($M_s=2.0$, 1.6 for young and older adults, respectively; $p>.10$), but older adults' ratings of their mood over the past year ($M=1.7$) were higher than those of young adults ($M=2.2$) ($t[37]=2.72$, $p=.01$). All participants had normal, or corrected to normal, vision and none were taking psychotropic medications. Older adults scored high on the Folstein Mini Mental State Examination (MMSE; M ($n=17$)$=29.2$ [$SD=1.1$]; max possible=30; the MMSE was not administered to one participant due to time constraints). There were no age-group differences on an abbreviated version of the verbal subscale of the WAIS ($M_{young}=22.3$ [$SD=4.5$], $M_{older}=19.6$ [$SD=5.5$], $p>.05$; max possible=30) or education level (reported in years, 12=high school diploma; $M_{young}=14.9$ [$SD=1.5$], $M_{older}=15.4$ [$SD=2.5$], $p>.05$). All participants were paid. The Human Investigation Committee of Yale University approved the protocol; informed consent was obtained from all participants.

2.2. Design

The 2 (Age: young, older) × 2 (Encoding Format: picture+word [*picture*], word only [*word*]) × 2 (Encoding Task: me, Sarah) × 3 (Test Condition: me/Sarah [*MS*], picture/word [*PW*], old/new [*ON*]) mixed design included Age as a between-subjects factor and Encoding Format (hereafter referred to as *Format*), Encoding Task (hereafter referred to as *Task*), and Test Condition (hereafter referred to as *Test*) as within-subjects factors.

2.3. Stimuli

Stimuli were drawn from several sources, mostly the Internet. They were full-color photographs of natural and man-made objects on light yellow backgrounds (300 × 300 pixels). Each object was sized to take up as much of the 300 × 300 square as possible. Corresponding labels were single words that, as agreed upon by two of the authors, clearly described the object at the basic or subordinate level. No objects had the same label.

2.4. Procedure

Participants were verbally instructed on the tasks outside the scanner and practiced using stimuli not included in other phases. Instructions were clarified as necessary, and participants were permitted to practice until they were comfortable with the tasks.

Each of the six runs had three study/test cycles composed of eight study items and six test items. As shown in Fig. 1, each study cycle began with a 4 s cue period during which participants saw the word *LIKE* (2 s, with 1 s blank before and after) to remind them of the task. This was followed by eight items (4 s each) with format (word, picture) and encoding task (me, Sarah) orthogonally crossed: There were four word only and four word plus picture items, and for half of each

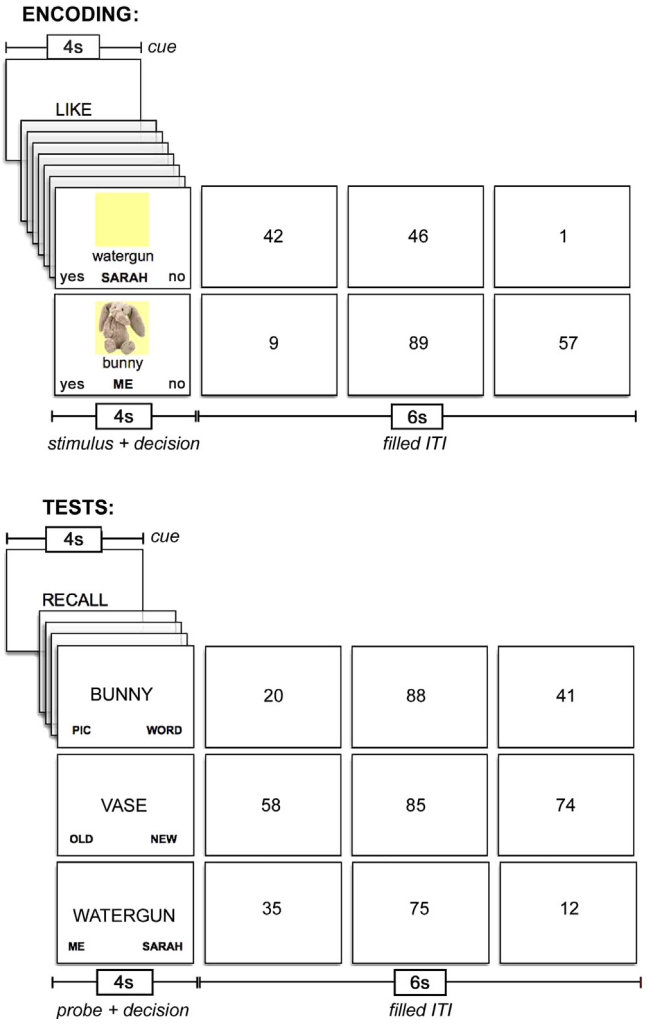

Fig. 1. Procedure and event timeline.

participants decided if they liked the item (*me*) and for the other half they decided if Sarah Palin would like the item (*Sarah*). Word labels appeared in lower case, cues in upper case. The four possible feature pairings (word–Sarah, word–me, picture–Sarah, picture–me) were pseudorandomly presented such that each feature and feature pairing appeared nearly equally often in each ordinal position across the session and across participants. Responses were collected via fiber optic response pads held in each hand; participants pressed a button with their left index finger for *yes* and a button with their right index finger for *no*.

After all eight study items were presented, participants saw the cue *RECALL* (2 s, with 1 s blank before and after) followed by the labels of five of the encoded items (i.e., old) and one new item (not seen elsewhere in the study), presented in all capital letters (4 s each). For two of the old items participants were cued via the words *PIC* and *WORD* on the screen below the test probe (see Fig. 1) to decide if it had been presented at encoding with a picture (left index finger) or as just a word (right index finger)(*picture–word test*, *PW*), for two of the old items participants were cued via the words *ME* and *SARAH* to decide if they had done the "like" judgment for themselves (left index finger) or Sarah Palin (right index finger) (*me–Sarah test*, *MS*), and for one of the old items and the one new item they were cued with the words *OLD* and *NEW* to make an old (left index finger)–new (right index finger) discrimination (*old–new test*, *ON*).[1] The tests were pseudorandomly presented such that across the session, each test type tested each encoding item type (e.g., word–Sarah) equally often. Across 12 different combinations of encoding and test lists, each test type appeared equally often in each ordinal position and tested nearly equal numbers of encoding items from every possible lag. Some of the 12 different combinations of encoding and test lists were repeated across participants; young and older adults received parallel orders.

Each stimulus in both the encoding and test phases was followed by a 6 s inter-trial interval (ITI) during which three random numbers (one or two digits each) were shown for 750 ms each and participants were instructed to think "odd" or "even," depending on the number. This was a relatively easy filler task used to discourage participants from thinking of the stimuli between trials.

There were 36 encoding trials per person for each of the four item types (word–me, word–Sarah, picture–me, picture–Sarah), resulting in 180 brain images per item type per person. Likewise, there were 36 test trials per person for each of the three test types (PW, MS, ON), again resulting in 180 brain images per person per test type.

2.5. Imaging details

After anatomical localizer scans, functional images were acquired on a 3.0 T Siemens Trio scanner with a single-shot echoplanar gradient-echo pulse sequence (TR=2000 ms, TE=25 ms, flip angle=80°, FOV=240). The 36 oblique axial slices were 3.5 mm thick (0 mm skip) with an in-plane resolution of 3.75×3.75 mm; they were aligned with the AC–PC line. Each run began with 12 s of blank screen to allow tissue to reach steady state magnetization and was followed by a 1 min rest interval.

2.6. fMRI analyses

2.6.1. Preprocessing

Data were motion-corrected using a six parameter automated algorithm (AIR; Woods, Cherry, & Mazziotta, 1992). A 12 parameter AIR algorithm was used to co-register participants' images to a common (young) reference brain. Data were mean-normalized across time and participant and spatially smoothed (3D, 8 mm FWHM Gaussian kernel).

2.6.2. ANOVA

The data were analyzed with a voxel-based Analysis of Variance (ANOVA) with participant as a random factor and all other factors fixed, using NeuroImaging Software (Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, and the Neuroscience of Cognitive Control Laboratory, Princeton University). This approach does not require predefining the shape of the hemodynamic response; the hemodynamic response was derived empirically and conditions of interest were directly compared. We were interested in identifying areas showing event-related changes in activity in response to the stimulus on each trial (i.e., transient responses), rather than more sustained "set effects," and hence included Time Within Trial (i.e., image, times 1–5) as a factor. For encoding activity, the ANOVA used a 2 (Age: young, older) × 2 (Format: picture, word) × 2 (Task: me, Sarah) × 5 (Time: 1–5) design, and we examined the following *F*-maps to identify regions sensitive to Format, Task, and their interaction with Age: Format × Time Within Trial (time 1–5) $p < 10^{-14}$; Age × Format × Time $p < .000001$; Task × Time $p < .000001$; Age × Task × Time $p < .001$. For test activity, the ANOVA used a 2 (Age: young, older) × 3 (Test: MS, PW, ON) × 5 (Time: 1–5) design and included correct trials only. We examined the following *F*-maps: Test X Time interaction $p < .000001$, Age × Test × Time interaction $p < .001$. For both the encoding and the test phase analyses, we used a 10 contiguous voxel constraint (Forman et al., 1995). The more liberal of these thresholds ($p < .001$, 10 contiguous voxels) provides an adequate balance between Type I and Type II errors (Lieberman & Cunningham, 2009) in identifying age-related differences; more stringent thresholds were applied in cases where it was necessary in order to better isolate reasonably distinct regions of activity.

In both encoding and test phases, for each region of activity identified in the ANOVA, planned comparisons (e.g., young vs. older within each test type) were conducted on mean percent signal change from time 1 at times 3–5, averaged across trials (because of the lag in the hemodynamic response, this range included the peak activation). That is, planned subsequent comparisons were conducted using mean percent signal change for the time period of interest only on clusters identified in an initial ANOVA.

2.6.3. Between-region correlations using seed regions from the ANOVA

We also conducted a set of targeted correlations using representational regions (medial PFC and parahippocampal gyrus) and lateral parietal regions identified during the test phase as seeds in whole brain correlational analyses. These correlations assessing relations among regions involved correct trials only. For each correct trial in the experiment, for each voxel, we calculated the peak in percent change in activity from time 1 across times 3, 4, and 5 (i.e., the point among times 3–5 where the activity's difference from t1 had the largest absolute value, which could be negative if a voxel showed deactivation). The between-region correlations are between the resulting series of trial-by-trial peak percent changes (one series per participant, per voxel, per condition).[2] The local maxima of key regions identified in the ANOVA described above were used as "seeds" and correlated with every other voxel in the brain, producing a correlation map for each participant, in each condition, for each seed region. These correlations were then normalized via the Fisher *r*-to-*z* transformation and used to create several group-level statistical maps: *t*-maps contrasting age groups within each test condition (resulting from independent-samples *t*-tests), *t*-maps contrasting test conditions within each age group (resulting from repeated-measures *t*-tests), and *t*-maps of the interaction contrasts between age group and test condition (resulting from independent-samples *t*-tests on between-condition differences in z-transformed correlations), all within seed regions. These statistical maps were

[1] Some investigators advocate including a "don't know" response option on source tests to minimize the impact of "guessing" on accuracy and neural activity measures (see Rugg and Morcom (2005) for a discussion). From the source monitoring perspective (Johnson et al., 1993), all source decisions are attributions (i.e., "best guesses") based on available information and influenced by many factors such as metacognitive abilities, current agendas and criteria, and so on. Including a "don't know" response is likely to increase the proportion of correct responses that are high confidence responses (and conversely to reduce the number of low confidence, but potentially correct, responses), and perhaps differentially so for different age groups. Asking for a source judgment for each item, on the other hand, assesses neural activity associated with making source attributions across the range of subjective experiences participants might have. For our current question regarding the neural activity associated with selective focus on different classes of source information (format vs. task), maximizing the number of source attributions made seemed more appropriate. In any event, analyses of test fMRI data were confined to correct trials.

[2] The rationale behind correlating peaks in the raw data rather than using beta-series correlation (e.g., Rissman, Gazzaley, and D'Esposito (2004)) or psychophysical interaction methods (PPI; e.g., Friston et al. (1997)) is two-fold: First, as with our ANOVA approach and unlike beta-series correlation or PPI, our correlation method does not require assuming a specific HRF. This means the analyses are sensitive to correlations between areas (and involving different participant groups) with HRFs of somewhat different shapes or that peak at different delays. Second, compared to PPI (though in common with beta-series correlation), this method allows specific statements about the nature of the relationship between areas in each condition. As noted by Friston et al., "psychophysiological interaction means that the contribution of one area to another changes significantly with the experimental or psychological context" (p. 218). Hence, a PPI result indicates that activity in a seed correlates with the difference in activity between conditions at some other location, implying that the correlations between seed and target activity differ by condition but giving no indication of the strengths or (crucially) signs of those correlations. A PPI result of A > B (which is really A–B > 0) could indicate any of the following: a positive relationship in both conditions, with the correlation in condition A larger in magnitude (e.g., .4 > .2); a negative relationship in both conditions, with the correlation in condition B larger in magnitude (e.g., −.2 > −.4); a relationship only in condition A, where the correlation is positive (e.g.,.2 > 0); a relationship only in condition B, where the correlation is negative (e.g., 0 > −.2); or a positive relationship in condition A and a negative relationship in condition B, regardless of the magnitude of the correlation in either condition (e.g.,.4 > −.2,.3 > −.3, and .2 > −.4). Each of these cases could lead to a different interpretation but, to our understanding, PPI offers no way to distinguish them. The approach we used provides specific information about the nature of the relationship in each condition (rather than only information about the relationship between the relationships).

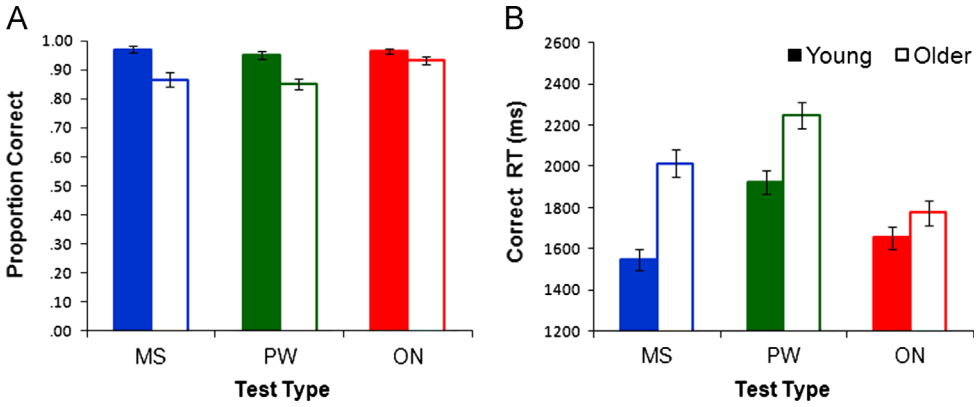

Fig. 2. Behavioral data. (A) Accuracy expressed as proportion correct for each age group for each test. (B) Mean response latencies for each age group for each test. Errors bars are the standard error of that mean.

thresholded to create ROIs in a manner similar to that used with the *F*-maps from the original ANOVA described above. Because these planned comparisons involved a limited number of pre-identified ROIs as seeds, we used a threshold of a minimum of six contiguous voxels, each significant at $p < .01$ to find regions of correlated activity. Given we used single voxels as seeds, the statistics reported in the Results section are for correlations between the local maximum (i.e., peak voxel) in the seed and in the resulting region; the actual *p*-values for each of these comparisons are reported in text.

All statistical maps, for both the ANOVAs and correlations, were transformed to Talairach and Tournoux space using AFNI (Cox, 1996), and areas of activation were localized using AFNI and Talairach Daemon software (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997) as well as manually checked with the Talairach and Tournoux atlas (1988). All coordinates are reported in Talairach and Tournoux space (1988).

3. Results

3.1. Behavioral data

3.1.1. Encoding task performance

Participants' proportions of yes/no responses on the encoding task (i.e., me-Sarah "like task") were submitted to a 2 (Age: young, older) × 2 (Format: picture, word) × 2 (Task: me, Sarah) × 2 (Response: yes, no) ANOVA. There was no main effect of age, nor did age interact with any of the factors (all $ps > .10$); thus young (overall *M* yes = .70) and older adults' (overall *M* yes = .72) pattern of responding at encoding did not significantly differ. A parallel analysis using participants' mean response times to make their yes/no responses on the encoding task showed that older adults ($M = 2067$ ms) were slower overall than young adults ($M = 1848$ ms; $F[1,37] = 4.07$, $p = .05$), and there was an Age × Format × Task interaction ($F[1,37] = 5.44$, $p < .05$). Whereas young adults did not show a Format × Task interaction ($p > .50$), older adults did ($F[1,17] = 9.96$, $p < .01$): For older adults, responses to picture–me items ($M = 1865$ ms) were faster than word–me items ($M = 1930$; $t[17] = 2.13$, $p < .05$), but word–Sarah items ($M = 2060$ ms) were faster than picture–Sarah items ($M = 2100$ ms; $t[17] = 2.35$, $p < .05$). However, when participants' median RTs were used in the analysis, age did not interact with any of the factors (all $ps > .10$). Hence, overall, young and older adults' overt attention to the manipulated features at encoding appeared to be relatively similar.

3.1.2. Memory performance

Fig. 2A shows accuracy scores for young and older adults for each test type (mean proportion correct computed across both decisions within a test, i.e., number of correct picture [me, old] decisions + correct word [Sarah, new] decisions/ number of PW [MS, ON] trials with a response). A 2 (Age: young, older) × 3 (Test: MS, PW, ON) ANOVA showed that the main effect of Age ($F[1,37] = 22.43$, $p < .0001$), and the main effect of Test ($F[2,74] = 8.88$, $p < .0001$), were superceded by an Age × Test interaction ($F[2,74] = 5.94$, $p < .01$). Although young adults performed better than older adults in all conditions (all $ts > 2$, $ps < .05$), the difference between young and older adults was greater for the MS and PW tests (both *M differences* = .10) than the ON test (*M difference* = .03). In addition, whereas older adults demonstrated significantly poorer performance on the source memory tests than the old–new test ($F[2,34] = 8.30$, $p = .001$; MS = PW < ON), young adults' performance did not differ among the tests ($F[2,40] = 1.68$, $p > .10$).

Fig. 2B shows young and older adults' mean response times (RTs) on correct trials for each test. A 2 (Age: young, older) × 3 (Test: MS, PW, ON) ANOVA showed that the main effect of Age ($F[1,37] = 16.45$, $p < .0001$), and the main effect of Test ($F[2,74] = 78.22$, $p < .0001$), were superceded by an Age × Test interaction ($F[2,74] = 15.13$, $p < .0001$). Older adults were significantly slower than young adults on both the MS (*M difference* = 466; $t[37] = 5.54$, $p < .0001$) and the PW (*M difference* = 322; $t[37] = 3.82$, $p < .0001$) tests, but not the ON test (*M difference* = 120; $t[37] = 1.49$, $p > .10$). In addition, whereas young adults were fastest on MS trials followed by ON and then PW, older adults were fastest on ON trials followed by MS and then PW. Hence, young adults were especially fast to access information about the encoding judgment they made; in fact, they were faster even than to make an old/new response.

Overall test performance was high, but we replicated the common finding of disproportionate source relative to old–new deficits in older compared to young adults (see Cansino (2009), Johnson et al. (1993), Mitchell and Johnson (2009), for reviews). In addition, although based on RTs the PW task was more difficult than the MS task, accuracy for the two tests was equal in each age group. Thus, fMRI analyses of the test-phase data for the two source tests were based on a comparable number of observations within each age group.

3.2. fMRI data

3.2.1. Encoding

Consistent with the expectation that medial PFC would be recruited in a task requiring judgments about the self and another person, both young and older adults showed greater activity (i.e., less deactivation) for me than Sarah trials in an area of ventral medial PFC (anterior cingulate cortex that extends into medial frontal gyrus and caudate, BA 24,10,32; Fig. 3A; $F[1,37] = 28.89$, $p < .0001$) and greater activity for Sarah than me trials in an area of more dorsal medial PFC (superior, medial frontal gyri,

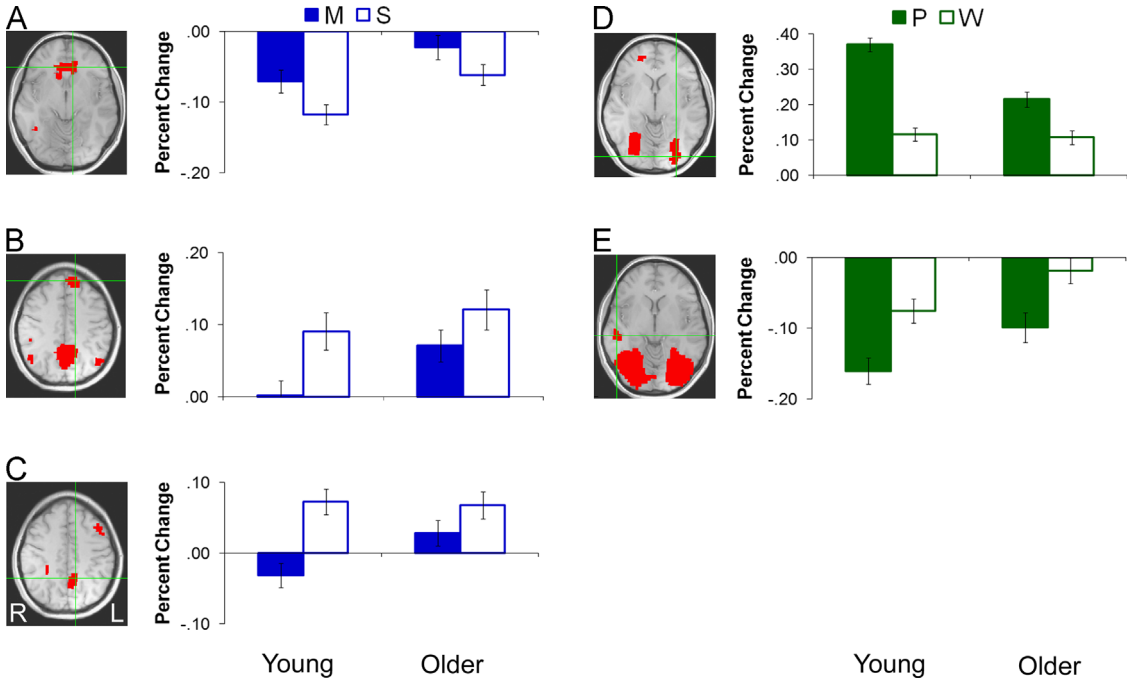

Fig. 3. Regions showing differential activity at encoding related to task (left) and format (right). (A) An area of anterior cingulate cortex, extending into medial frontal gyrus and caudate (BA 24,10,32; $x=-9$, $y=32$, $z=-1$) that shows less deactivation for me than Sarah trials that does not interact with age. (B) Area of left superior, medial frontal gyri (BA 9,8,6; $x=-14$, $y=44$, $z=36$) that shows greater activity for Sarah than me trials that does not interact with age. (C) Area of medial precuneus, posterior cingulate (BA 31,7; $x=-11$, $y=-47$, $z=37$) that shows Sarah > me, more so for young than older adults. (D) Bilateral regions of middle occipital, lingual, and parahippocampal gyri (extending into cuneus on the right; BA 19,18,37; $x=-28$, $y=-83$, $z=0$), showing picture > word and attenuated differences in older adults (bar graph is for left region, right looks nearly identical). (E) Area of right superior, middle temporal gyri (BA 22,21,41; $x=49$, $y=-27$, $z=1$) where word > picture and no age difference. Crosshairs indicate the local maximum for the region. Bar graphs are the mean percent change from time 1 averaged across times 3–5; error bars are the standard error of that mean. Coordinates are Talairach & Tournoux.

BA 9,8,6; Fig. 3B; $F[1,37]=40.64$, $p<.0001$). This is consistent with previous findings of greater ventral medial PFC activity for self-related processing and greater dorsal medial PFC activity for other-related processing (e.g., Mitchell, Macrae, and Banaji (2006), see Amodio and Frith (2006), Denny et al. (2012), Murray et al. (2012), for reviews). There was also an area of medial posterior cortex (precuneus, posterior cingulate cortex; BA 31,7; Fig. 3C) where Sarah > me for both young ($p<.0001$) and older ($p<.05$) adults, but more so for young adults ($F[1,37]$ for the interaction = 10.47, $p<.01$).

Also as expected, both young and older participants showed greater activity for pictures than words (both $ps<.0001$) in bilateral visual cortex (middle occipital, lingual, and parahippocampal gyri; BA 19,18,37; Fig. 3D). This difference was greater for young than older adults ($F[1,37]$ for the interaction = 56.72, $p<.0001$), consistent with evidence that older adults show less category specificity during both passive viewing and memory tasks (Carp et al., 2011; Chee et al., 2006; Park et al., 2004; Payer et al., 2006). Indeed, there were no P > W areas at our threshold that did not show age effects (see Supplementary Table 1). Fig. 3E shows an area where both young and older adults showed greater activity (i.e., less deactivation) for words than pictures: right superior, middle temporal gyri (BA 22,21,41) ($F[1,37]=68.13$, $p<.0001$).

Supplementary Table 1 shows all feature-sensitive areas at encoding.

3.2.2. Test

3.2.2.1. Representational areas. Fig. 4A shows an area of medial frontal gyrus extending slightly into anterior cingulate cortex and superior frontal gyrus (BA 10,32,9) that demonstrated the pattern MS ($M=-.05$) = ON ($M=-.07$) > PW ($M=-.15$) ($F[2,74]=24.78$, $p<.0001$), with $O>Y$ for all tests. The local maximum of this region is 6.03 voxels from the area that showed $M>S$ at encoding. Similar mPFC activity has been associated with source memory for encoding task in other studies (Simons et al., 2008). In addition, this region is similar to those found to be more active when people accurately recognize information that had been encoded in a self-referential manner (Benoit, Gilbert, Volle, & Burgess, 2010). Most notable, similar mPFC regions have been found to be active when people accurately remember the source of an object for which they made self- vs. external judgments (*do you find it pleasant [self]* vs. *what is the dominant color [external]*; Leshikar & Duarte, 2012).

Fig. 4B shows an area of precuneus, extending into cingulate gyrus and superior parietal lobule (BA 7,31) that demonstrated the pattern MS ($M=.13$) > PW ($M=.09$) = ON ($M=.08$) ($F[2,74]=13.37$, $p<.0001$), and activity did not differ significantly between young and older adults for any of the tests. The local maximum of this area is 2.19 voxels from the area in Fig. 3C that showed Sarah > me at encoding.

Fig. 4C shows an area of left parahippocampal gyrus (extending into the hippocampus and fusiform gyrus; BA 35,36,37) with the pattern PW ($M=.08$) > MS ($M=.05$) > ON ($M=.03$) ($F[2,74]=18.07$, $p<.0001$). In this region, the level of activity did not differ significantly between young and older adults on any test.

Fig. 4D shows an area that included left middle and inferior temporal gyri and, to a lesser extent, middle occipital gyrus (BA 37,19) that demonstrated PW ($M=.09$) > MS ($M=.03$) = ON ($M=.04$) ($F[2,74]=18.21$, $p<.0001$); activity did not differ between young and older adults in MS or ON, but $Y>O$ in PW.

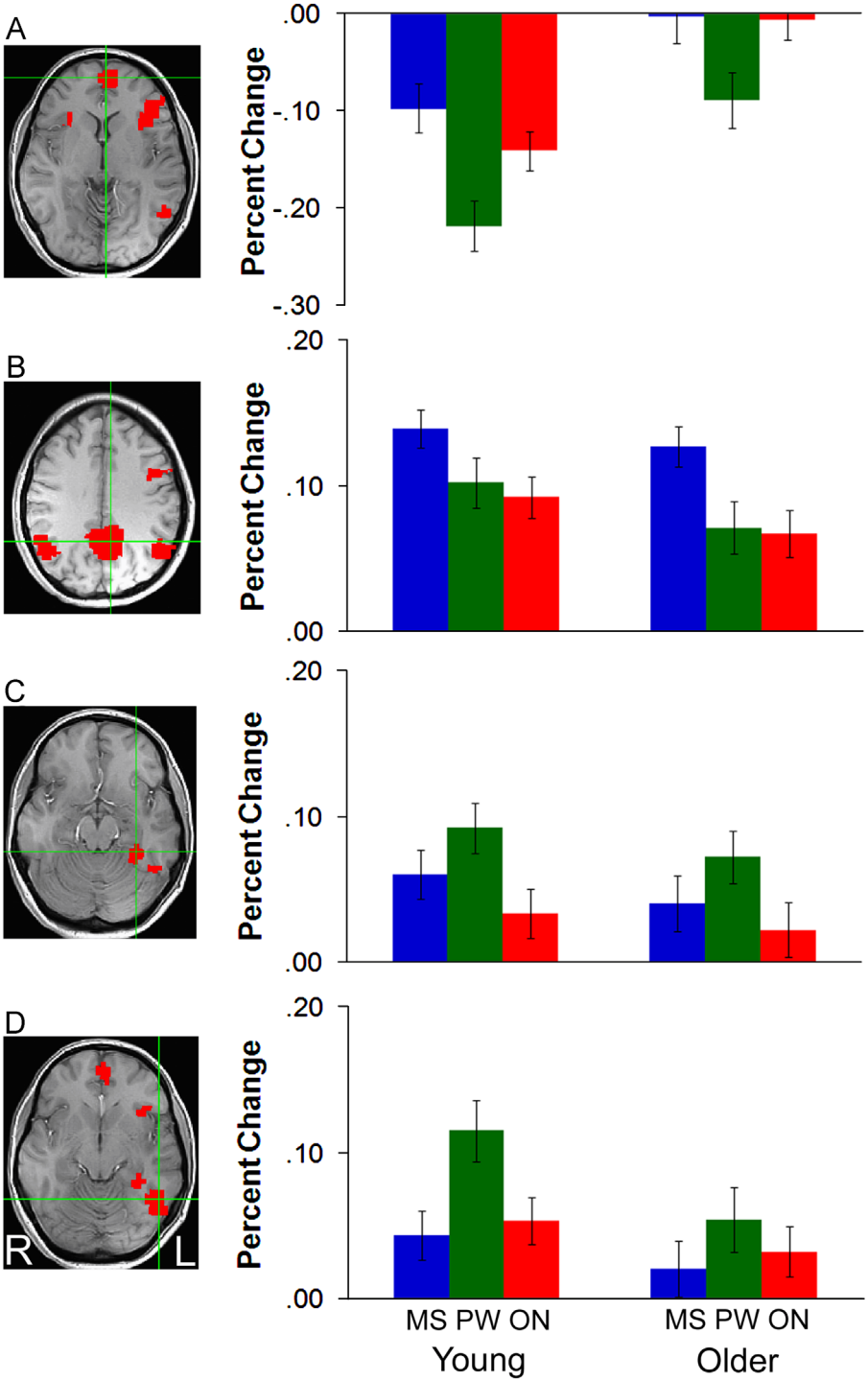

Fig. 4. Representational areas showing differential activity as a function of source test, and no interaction with age. (A) Area of medial prefrontal cortex (medial frontal gyrus, anterior cingulate cortex, superior frontal gyrus; BA 10,32,9; $x=-3$, $y=55$, $z=3$) (B) Area of precuneus, cingulate gyrus, superior parietal lobule (BA 7,31; $x=-7$, $y=-52$, $z=31$). (C) Area of left parahippocampal gyrus (into hippocampus, fusiform gyrus; BA 35,36,37; $x=-31$, $y=-39$, $z=-9$). (D) Area of left middle and inferior temporal gyri (includes a bit of middle occipital gyrus; BA 37,19; $x=-47$, $y=-52$, $z=-4$). Crosshairs indicate the local maximum for the region. Bar graphs are the mean percent change from time 1 averaged across times 3–5; error bars are the standard error of that mean. Coordinates are Talairach & Tournoux.

Overall, the pattern of findings is consistent with the expectation that visual perceptual information would be more important for discriminating format than for discriminating encoding task features and anterior and posterior medial areas would be more important for discriminating task features. Moreover, for the most part, older adults looked similar to young adults with respect to *differential* regional activity at test for correct trials in medial PFC and posterior representational areas. Although we cannot know from these data whether young and older adults activated the same information within a class (i.e., same amount, exact type [picture, word], equally differentiated, and so on), the pattern of activity does suggest they were remarkably similar in the selectivity with which brain areas associated with an appropriate *class* of information for a given test were activated.

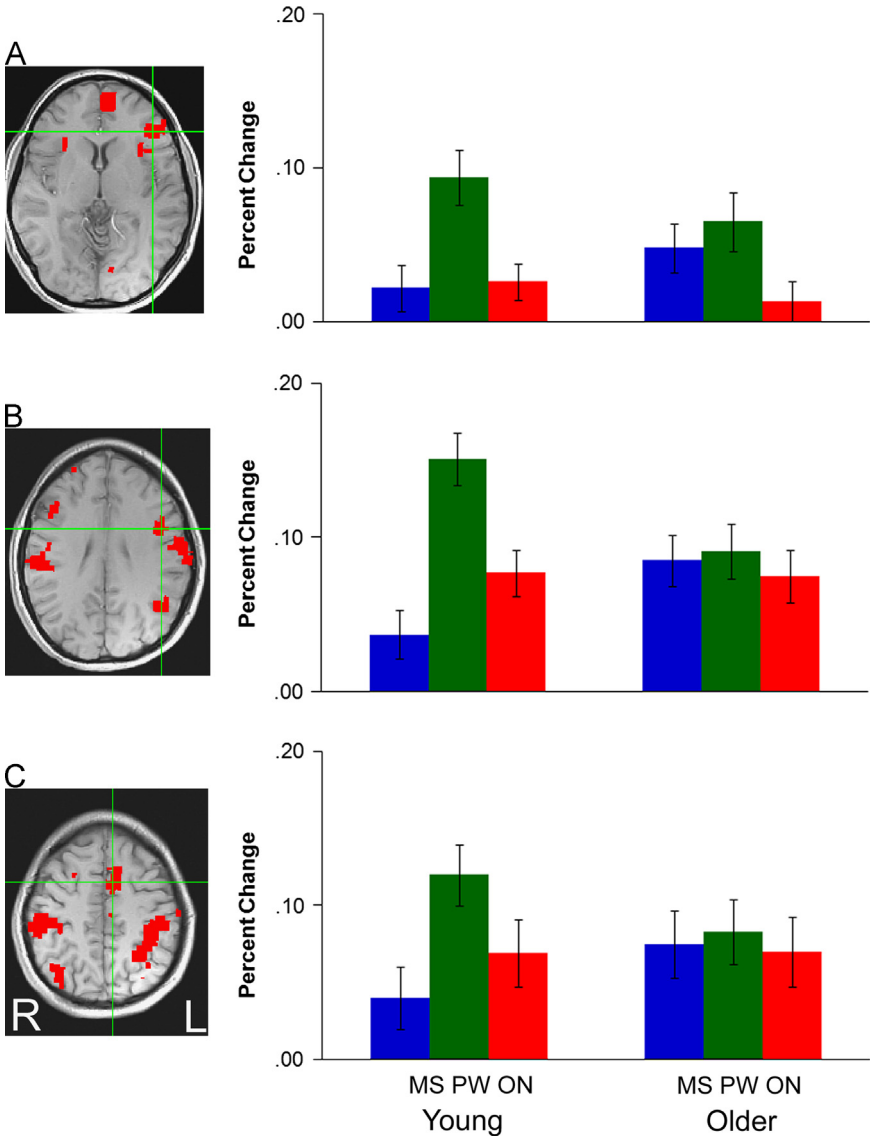

Fig. 5. Prefrontal control and monitoring areas where young adults showed significant differences in activity between PW and MS, but older adults did not. (A) Area of left lateral inferior frontal gyrus, extending slightly into insula and middle frontal gyrus (BA 47,46,45; $x=-41$, $y=30$, $z=6$). (B) Area of left inferior frontal gyrus, extending into middle frontal gyrus and precentral gyrus (BA 44,9,6; $x=-43$, $y=3$, $z=27$). (C) Area of anterior cingulate cortex extending into medial frontal gyrus (BA 32,6; $x=-7$, $y=8$, $z=44$). Crosshairs indicate the local maximum for the region. Bar graphs are the mean percent change from time 1 averaged across times 3–5; error bars are the standard error of that mean. Coordinates are Talairach & Tournoux.

3.2.2.2. Prefrontal control and monitoring areas. Fig. 5A shows a region of left lateral inferior frontal gyrus, extending slightly into insula and middle frontal gyrus (BA 47,46,45) where PW ($M=.08$) > MS ($M=.04$) = ON ($M=.02$) ($F[2,74]=16.89$, $p<.0001$). Although this area did not show an interaction with age when all conditions were included, a subsequent ANOVA including only PW and MS trials showed an Age × Test interaction ($F[1,37]=8.50$, $p<.0001$) because PW > MS for young ($p<.001$) but not older ($p>.10$) adults. We should note that, as in many other source memory studies (see Mitchell & Johnson, 2009, for a review and discussion), there was also a much smaller (12 voxels) area of right inferior frontal cortex. It was slightly less lateral and anterior ($x=27$, $y=19$, $z=2$; Insula, IFG; BA 47), and although it showed a similar pattern of activity, the Age × Test interaction using only PW and MS trials failed to reach significance ($p=.27$; see Supplementary Table 2).

Fig. 5B shows another region of left inferior frontal gyrus, extending into middle frontal gyrus and precentral gyrus (BA 44,9,6) that is posterior and superior to the area in Fig. 5A. This region interacted with age ($F[2,74]=8.02$, $p=.001$), showing no age differences for ON, but opposite age effects in the two source tests: O > Y in MS and Y > O in PW (both $p<.05$). Young adults showed PW > ON > MS ($F[2,40]=15.13$, $p<.0001$) but older adults' activity did not differ between the conditions. Young adults' activity showed modulation relative to ON such that the more difficult test (PW), as indicated by RTs, produced more activity than the easier test (MS). Older adults, on the other hand, showed both more activity on MS than young adults and less activity on PW. This pattern suggests that young adults were recruiting this control area appropriately, perhaps to foreground relevant information in the face of interference (e.g., Jonides, Smith, Marshuetz, Koeppe, and Reuter-Lorenz (1998)), but older adults did (or could) not.

Fig. 5C shows a region of anterior cingulate cortex, medial frontal gyrus (BA 32,6) where PW ($M=.13$) > MS ($M=.06$) = ON ($M=.08$) ($F[2,74]=8.86$, $p<.0001$), and $Y=O$ in all conditions. Nevertheless,

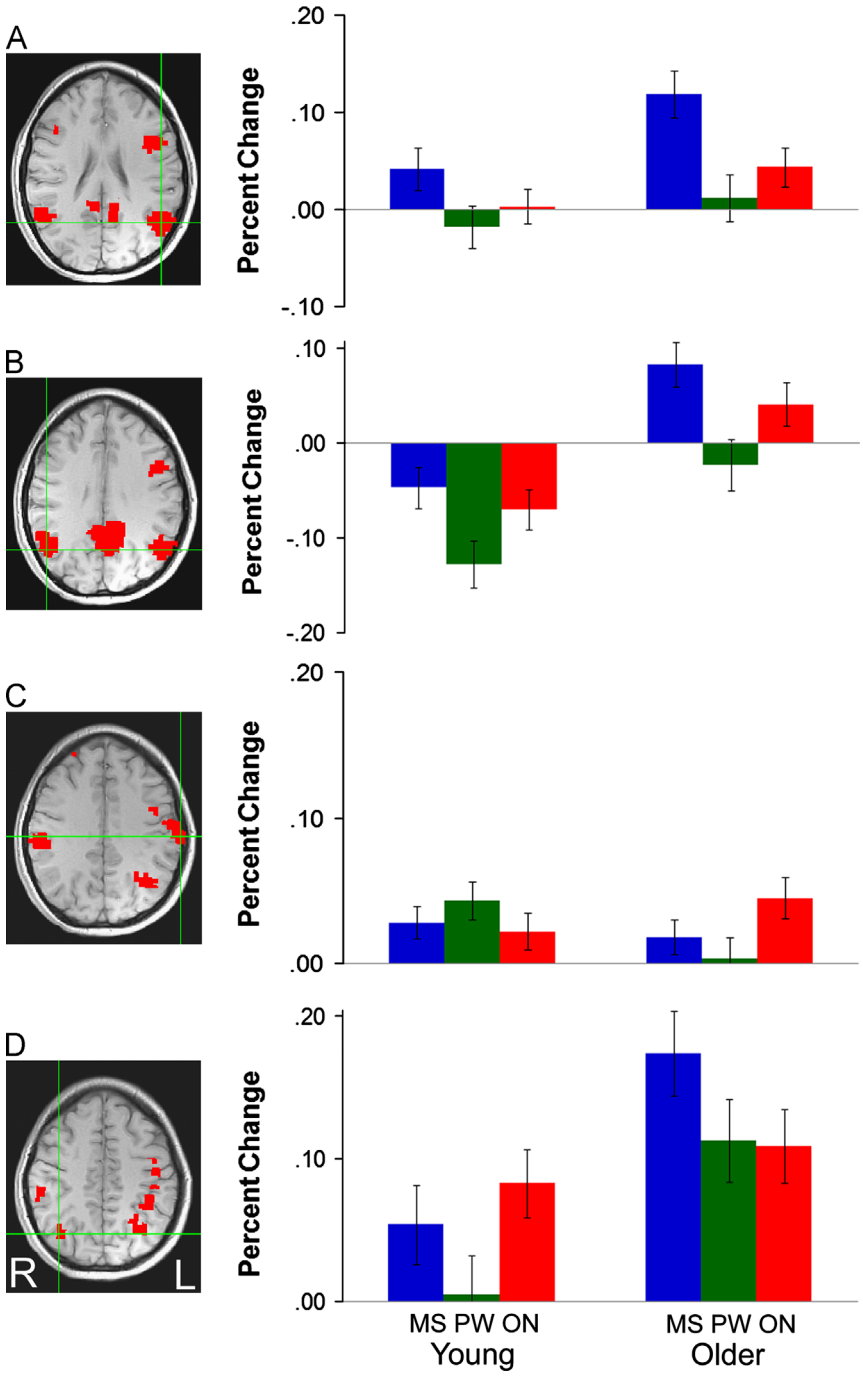

Fig. 6. (A, B) Bilateral parietotemporal regions (A: $x=-46$, $y=-60$, $z=24$; B: $x=47$, $y=-61$, $z=29$) that demonstrated greater activity in MS than PW that did not interact with age. (C) Area of left post- and pre-central gyri, inferior parietal lobule (BA2,4,40) where $Y>O$ for PW only. (D) Area of right inferior parietal lobule, angular gyrus (BA39,40,7; $x=36$, $y=-60$, $z=39$) where $O>Y$ for MS and PW tests. Crosshairs indicate the local maximum for the region. Bar graphs are the mean percent change from time 1 averaged across times 3–5; error bars are the standard error of that mean. Coordinates are Talairach & Tournoux.

an ANOVA including only PW and MS trials showed an Age × Test interaction ($F[1,37]=5.59$, $p=.02$) because PW > MS for young ($p=.001$) but not older adults ($p>.10$). Again, the lack of differentiation among the source tests in older adults implies that they did not recruit this control region differentially depending on test type.

Overall, the fact that older adults showed less selectivity in prefrontal control regions, but similar selectivity to young adults in representational areas, suggests that older adults' difficulty in source monitoring was not that they did not know where to look for the relevant category of information, but rather, they were less selective in what else they looked at.

3.2.2.3. Temporal and parietal areas. Fig. 6A and B shows bilateral regions with their local maxima in middle temporal gyrus, and including a bit of superior temporal gyrus, as well as inferior parietal lobule extending into angular and supramarginal gyri (BA 39,40,[19] on the left and BA 39,40 on the right). In both areas, there was greater activity in MS than PW and no significant interaction with age. The left region showed MS ($M=.08$) > ON ($M=.02$) = PW ($M=-.003$) ($F[2,74]=15.49$, $p<.0001$); O > Y for MS trials ($p<.05$), but O = Y for PW and ON. The right region showed MS (.02) ≥ ON (−.01) > PW (−.08) ($F[2,74]=21.49$, $p<.0001$); O > Y in all conditions ($ps<.01$).

Fig. 6C and D show additional inferior parietal regions that demonstrated Age × Test interactions, and an age effect for at least one of the source tests. The area in Fig. 6C included left post- and pre-central gyri, extending into inferior parietal lobule (BA2,4,40). This area demonstrated an age effect in PW only: Y > O (p=.05). Fig. 6D shows a small region of right inferior parietal lobule, angular gyrus (BA 39, 40,7) where older adults showed greater activity than young adults for both of the source tests (p's < .01), but not ON.

Supplementary Tables 2 and 3 show all regions that were differentially active between tests.

3.3. Targeted correlational analyses

3.3.1. Compared to older adults, young adults showed greater reciprocal activity between representational areas at test

We also conducted planned correlation analyses using seeds from Fig. 4A and C to identify areas whose correlation with these representational seeds showed an Age × Test interaction (see *Methods*). These analyses identified areas where young and older adults showed different relationships between the seed and another area for the two source tests. For simplicity, we report in text the findings for the test type that showed a significant age effect as this drove the Age × Test interaction in each case. Overall, the pattern is consistent with the hypothesis of greater agenda-driven selectivity at test among young than older adults'.

Using the medial frontal gyrus, anterior cingulate region shown in Fig. 4A as a seed identified a region of right parahippocampal gyrus, slightly extending into hippocampus (x=24, y=−45, z=3). For PW trials, young (z=−.172, p < .01), but not older (z=.086, p > .05), adults showed a significant negative correlation in activity between the regions (t[37] for the age effect=3.57, p=.001; t[37] for the interaction=4.33, p < .0001). Using the parahippocampal, fusiform area shown in Fig. 4C as a seed identified for MS trials a region of anterior cingulate cortex, medial frontal gyrus (−14,47,4) where young (z=−.087, p < .05), but not older (z=.079, p > .05), adults had a significant negative correlation in activity between the regions (t[37] for the age effect=2.43, p < .05; t[37] for the interaction =3.95, p < .0001). The local maximum of this resulting area was similar to the mPFC area shown in Fig. 4A. In short, even though older adults looked similar to young adults at test with respect to the selectivity of regional activity of task and format representational areas (Fig. 4A and C), the pattern of correlations was different for young and older adults. The greater reciprocal activity between PFC and posterior representational areas for young than older adults on PW and MS trials, for task and format information, respectively, is consistent with the idea that young adults were more likely than older adults to selectively attend to the features most relevant to the target source discrimination. That is, young adults showed greater agenda-driven modulation of activity on an item-by-item basis.

3.3.1.1. Young adults showed evidence of greater connectivity between parietal and frontal areas. Current theoretical characterizations of reflective attentional processes emphasize interactions between frontal and parietal areas (Chun & Johnson, 2011; Ciaramelli et al., 2008; Nelson et al., 2010), and hence we conducted additional correlational analyses using the parietal regions in Fig. 6 as seeds.

Using the area in Fig. 6A as a seed, we identified three frontal areas. For an area of right medial frontal, superior, middle frontal gyri (23,18,50), on PW trials, young (z=.106, p < .05) but not older (z=−.051, p > .05) adults showed a positive correlation (t[37] for the age effect =2.08, p < .05; t[37] for the interaction =3.85, p < .0001). Both the seed area and the resulting mPFC area are similar to regions included in Nelson et al.'s (2010) angular gyrus-medial PFC module that purportedly is involved in reinstating context-specific (perhaps especially perceptual) information. For an area of right middle, superior frontal gyrus (25, −13, 64), on MS trials, young adults (z=.179, p < .01) showed a positive correlation whereas older adults (z=−.071, p < .05) showed a small, but significant, negative correlation (t[37] for the age effect =4.43, p < .0001; t[37] for the interaction=3.14, p < .01). This frontal area is similar to an area that was included in Nelson et al.'s (2010) posterior inferior parietal–superior frontal gyrus module that they argue is involved in post-retrieval/response monitoring. Finally, for a more ventral (and anterior) area of right superior, middle frontal gyri (21,43,−15), on MS trials, young (z=−.185, p < .01) but not older (z=−.006, p > .05) adults showed a negative correlation (t[37] for the age effect=3.97, p=.001; t[37] for the interaction=3.52, p < .01).

Using the area in Fig. 6B as a seed identified two frontal regions: there was an area of left inferior frontal gyrus (−19,11,12) where, on PW trials, young adults (z=.168, p < .01) showed a positive correlation but older adults (z=−.010, p > .05) did not (t[37] for the age effect=2.91, p < .01; t[37] for the interaction=3.90, p < .0001). There was also an area of medial frontal gyrus (−10,39,29) where, on MS trials, older (z=.256, p < .01) but not young (z=.083, p > .05) adults showed a positive correlation (t[37] for the age effect=2.30, p < .05; t[37] for the interaction= 4.04, p < .0001).

Using the area in Fig. 6C as a seed identified two areas: For an area of medial frontal gyrus/anterior cingulate cortex (6,43,−9), young (z=−.096, p < .05), but not older (z=.032, p > .05), adults showed a significant negative correlation in PW (t[37] for the age effect=2.53, p < .05). Also, in MS, older (z=−.096, p < .01), but not young (z=.050, p > .05), adults showed a significant negative correlation (t[37] for the age effect =2.09, p < .05; t[37] for the interaction=3.67, p=.001). For an area of right middle frontal gyrus, precentral gyrus (36, −1,39), in PW, young (z=.175, p < .01), but not older (z=.017, p > .05), adults showed a positive correlation (t[37] for the age effect=2.78, p < .01; t[37] for the interaction=3.23, p < .01).

When the area in Fig. 6D was used as a seed, we did not find any frontal regions that were differentially correlated between young and older adults.

In sum, there were fewer significant *differential* correlations in older than young adults with frontal areas when parietal areas were used as seeds. From the view of models associating inferior parietal cortex with bottom-up attention to salient information (e.g., active representations in a memory task; Cabeza et al., 2012; Ciaramelli et al., 2008), this pattern is consistent with other behavioral and neuroimaging studies in the literature (see Healey, Campbell, and Hasher (2008), for a review) showing that young adults are better than are older adults at modulating attention to ignore non-target information.

4. Discussion

Behaviorally, we saw the usual pattern of accuracy and response latency in that older adults showed a source memory deficit compared to young adults that was disproportionate to their deficit in old–new recognition (see Cansino (2009), Johnson et al. (1993), Mitchell and Johnson (2009), for reviews).

With respect to brain activity, at encoding young and older adults both showed differential activity in expected representational regions: anterior and posterior medial cortex associated with task (Fig. 3, left) and areas including middle occipital and parahippocampal gyri associated with format (Fig. 3, right). Consistent with evidence of age-related deficits in posterior visual

cortex (Carp et al., 2011; Park et al., 2004; Payer et al., 2006), the greater activity associated with pictures than words in young adults was attenuated in older adults in parahippocampal gyrus (Fig. 3D). Whether this attenuation reflects actual decrements in the efficacy of this area (e.g., less distinct neural processing in perception, Carp et al., 2011), or group differences in perceptual and/or reflective attention during encoding (Gazzaley, Cooney, Rissman, and D'Esposito, 2005), is not entirely clear from these findings. But other evidence suggests young and older adults may look more similar during perception in posterior representational regions under conditions of more tightly constrained attention (e.g., Chee et al. (2006), Mitchell et al. (2010)).

Our primary questions concerned age differences in brain activity at test. Both young and older adults showed selective, agenda-driven activity at test in representational regions that were similar to those seen at encoding. That is, both groups showed greater activity in anterior and posterior medial areas in making judgments about task (Fig. 4A and B), and greater activity in posterior areas (including parahippocampus, hippocampus, fusiform gyrus and middle and inferior temporal gyri) in making judgments about format (Fig. 4C and D). Thus, although older adults may have shown somewhat less activity overall than young adults in some representational areas, their pattern of activity among source test conditions (PW and MS) looked agenda-driven and remarkably like young adults'.

At the same time, correlational analyses using representational areas as seeds revealed that, for both PW and MS tasks, young adults showed evidence of a reciprocal relation between medial prefrontal cortex and posterior (e.g., middle occipital, middle temporal, and parahippocampal gyri) activity consistent with the idea that, on an item-by-item basis, young adults were selectively focusing on the most relevant source features for the respective task and format tests. Older adults did not show similar evidence of this item-by-item reciprocal selective focus.

During selective reflection (refreshing one of two active representations), older adults show intact enhancement of target information but disrupted suppression of non-target information (Mitchell et al., 2010; see also Gazzaley et al., 2005). This invites the speculation that in the current study the relatively intact differential regional activation in target areas for older adults may represent an overall intact activation of a class or category of information across trials in target regions (i.e., average enhancement), but the lack of a reciprocal trial-by-trial relation between target and non-target representational areas reflects a disruption in corresponding item-by-item suppression of less diagnostic information. Evidently, older adults appropriately initiated processes to access the correct type of features in representational areas—that is, to "look for" the most relevant category of information. Hence, the selectivity of regional representation-related activity was similar for the two groups. Nevertheless, because memory representations are multi-faceted, more than the most-relevant feature may be revived during remembering. For example, activating the visual characteristics of the picture might incidentally revive information about the encoding task (e.g., "That's the blue hydrangea that I said I liked"), or other normatively non-diagnostic information (e.g., "That picture reminded me of the hydrangeas I used to grow in the yard"). Consistent with a deficit in inhibitory processes (Hasher & Zacks, 1988), older adults may pay more attention to active non-target features (have less control in what they "look at"), which may or may not be helpful for the current source judgment.

Although speculative, the specific areas that were found as correlates when representational areas were used as seeds may offer clues about potential age differences in the extent to which young and older adults selectively ignored the arguably salient but non-target manipulated features within a class for each test (i.e., "visual/pictorial" information for MS, "me" information for PW). When the left parahippocampal/fusiform area shown in Fig. 4C was used as a seed, on MS trials, for young but not older adults, activity was negatively correlated with activity in a region of mPFC that was very similar to that shown in Fig. 4A. This negative correlation for MS trials suggests that greater trial-by-trial focus on information diagnostic of "self" as the target of the encoding task (see e.g., Denny et al. (2012), Murray et al. (2012), for reviews) was associated with less focus on non-diagnostic (format) information. When the mPFC region shown in Fig. 4A was used as a seed, on PW trials, for young but not older adults, activity was negatively correlated in a region of *right* parahippocampal gyrus/hippocampus (opposite the *left* region in Fig. 4C). Right posterior visual areas (e.g., fusiform gyrus), compared to left, tend to be involved in processing more specific visual features, as opposed to semantic information (Simons, Koutstaal, Prince, Wagner, & Schacter, 2003; see also, Garoff et al., 2005). Hence, this negative correlation for PW trials suggests that, for young adults only, greater focus on the most diagnostic (specific visual/pictorial) information was associated with less focus on non-diagnostic (self or person task) information. Together, the pattern of regional activity and correlations between representational areas suggests a difference in the extent to which young and older adults modulate, on an item-by-item basis, which of the various activated specific features they attend to ("look at"), rather than a difference in what class of information they "look for."

If a disruption in reflective attention contributes to the lack of trial-by-trial reciprocity in older adults' activity in representational areas, there should be some evidence of this in brain areas involved in monitoring at test—that is, areas involved in selecting information and evaluating the amount/qualities of mental content with respect to task agendas. Indeed, there were marked differences in the extent to which the two groups differentially engaged areas of prefrontal and parietal cortex during the source tests.

Regions of left lateral PFC and ACC (Fig. 5) showed evidence of decreased age-related modulation of control as a function of monitoring demands (also McDonough et al. (2012)). A region of left inferior frontal gyrus (Fig. 5A) showed greater activity in PW (the more difficult task as demonstrated by RTs) than MS for young but not older adults. Similar regions of left inferior frontal gyrus are active across a wide range of source memory tests (see Badre and Wagner (2007), Mitchell and Johnson (2009) for reviews). Whether activity in this region is related to pre-probe monitoring (e.g., agenda setting such as planning what to focus on, Dobbins and Han (2006), Han, O'Connor, Eslick, and Dobbins (2012)) or post-probe retrieval and/or evaluation (Dobbins and Han (2006), Mitchell, Johnson, Raye, and Greene (2004)) cannot be ascertained from these data alone. We do note, however, that this region is closer to areas shown to be active (in young adults) in response to a source memory probe than to areas active in response to a cue about the type of upcoming source task (Dobbins and Han (2006)): Our area is 3.55 voxels from one of Dobbins and Han's probe sensitive regions (−40,44,2), and 2.67 voxels from another (−48,33,−2), but our area is further from their cue sensitive areas (8.03 voxels from −54,3,17; 8.17 voxels from −37,2,23) (MNI (SPM) to Talairach conversion instantiated in *GingerALE* v2.1; 〈http://www.brainmap.org〉). This suggests the current region is more likely involved in source monitoring provoked by specific test probes rather than specific task sets (Mitchell et al., 2004). This would be expected given that the cue for each test came up with the probe. The finding of an age-related deficit in this area is consistent with our previous findings from a short-term source monitoring study (Mitchell, Raye, et al., 2006). Together with the lack of age differences in the selectivity of activity in representational areas, these findings suggest that, at

least under these circumstances (limited set of to-be-remembered items, delays of no more than 2.5 min), aging is associated with a deficit in item-by-item evaluation of revived information during specific source remembering (as opposed to, for example, difficulty with directed retrieval, per se).

A slightly more posterior and superior area of left inferior frontal gyrus (Fig. 5B) also showed the pattern PW > MS for young but not older adults. This area is near an area where older adults showed a deficit, relative to young adults, in a study in which participants had to refresh (i.e., foreground) one of three active words ($x=-36$, $y=3$, $z=26$; Raye et al., 2008; also Jonides, Marshuetz, Smith, Reuter-Lorenz, & Koeppe, 2000). Older adults' pattern of activity in the current study suggests that they either cannot engage this area for resolving interference or do not engage this area *selectively* to foreground the most relevant information depending on the interference present at test.

At the same time, older adults showed greater activity overall than young adults in regions of lateral parietal cortex (Fig. 6). Lateral posterior parietal cortex is active when people make various kinds of source judgments (e.g., Dobbins and Wagner (2005), Leshikar and Duarte (2012), Simons et al. (2008), Simons, Owen, Fletcher, and Burgess (2005), Simons, Davis, Gilbert, Frith, and Burgess (2006)), and is more active for correct than incorrect source judgments (e.g., Cansino, Maquet, Dolan, and Rugg (2002), see Ciaramelli et al. (2008), Mitchell and Johnson, 2009, Olson and Berryhill (2009), Wagner, Shannon, Kahn, and Buckner (2005), for reviews). More generally, there is increasing evidence that parietal cortex is important in reflectively attending to activated information (internal representations), perhaps serving to represent multiple features, integrate features, or select among them based on agenda-relevance (e.g., Cabeza (2008), Chun and Johnson (2011), Shimamura (2011), Vilberg and Rugg (2008), Wagner et al. (2005)).

"Attention-based" theories of the role of lateral parietal cortex in memory (Cabeza, 2008; Ciaramelli et al., 2008) suggest that ventral posterior parietal regions are involved in bottom-up attention to active information during remembering, and dorsal posterior parietal cortex is involved in top-down control of attention. The area in Fig. 6A is similar to two regions ($-40,-66,24$; $-34,-66,26$) shown to be involved in bottom-up attention to information revived in response to a memory probe (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010). Based partly on lesion patient data, Berryhill and colleagues (Berryhill, 2012) have argued that posterior parietal cortex is specifically involved in attention to details of activated internal representations of past events which gives rise to the subjective sense of remembering and/or being confident in a memory. Lateral temporoparietal, in addition to posterior medial, regions similar to ours have been shown to be involved in autobiographical memory (McDermott, Szpunar, & Christ, 2009), as well as both remembering past and imagining future events with familiar contexts (Szpunar, Chan, & McDermott, 2009). The MS > PW pattern shown in the region in Fig. 6A is consistent with a focus on more personal/autobiographical information (i.e., self-relevant information) for the me–Sarah than picture–word decisions. Although speculative, the fact that older adults showed significantly more activity in this region on MS trials than did young adults suggests that older adults were attending to more (e.g., a broader range of) personally relevant and/or autobiographical information, especially in making their me–Sarah source decisions (e.g., thoughts, feelings; Hashtroudi, Johnson, & Chrosniak, 1990).

The pattern of activity in the area shown in Fig. 6D is consistent with this idea. The region shown in Fig. 6D is close to two regions that were part of a posterior inferior parietal–superior frontal gyrus module that Nelson et al. (2010) argue is involved in post-retrieval monitoring, including communicating the outcome of that monitoring to the angular gyrus-medial PFC module. Assuming ventrolateral parietal cortex reflects bottom-up activation and/or attention to bottom-up activation of source features (Cabeza et al., 2012; Cabeza, 2008; Ciaramelli et al., 2008), greater activation in this area in older than young adults during both types of source tests suggests older adults were considering more (or more different kinds) of information, providing further evidence that older adults may have had a harder time focusing on the most diagnostic, source-specifying information (McDonough et al., 2012).

One possibility is that the test probes generated more, or more types, of information for older than young adults. Alternatively, older adults' relatively greater activity in this area on the source tasks compared to young might reflect not that more information was generated, but that selective focus was less successful. These are not mutually exclusive options. The fact that older adults performed worse than young adults behaviorally on the source tasks is consistent with either hypothesis. Indeed, the pattern of correlations between parietal and frontal areas seems to support these possibilities over the alternative idea that older adults monitored (revived, evaluated) *less* information. The correlational analyses showed greater connectivity between parietal seeds and frontal areas for young than older adults.

Of course, we cannot tell from the current data whether older adults' greater parietal activity involves only the manipulated features, or also involves attention to other information, such as feelings, related thoughts, etc. Nevertheless, that the activity was seen on correct trials invites the speculation that older adults may have been considering at least partially different information than young adults in making their source memory decisions, perhaps especially on MS trials, and this information may have been helpful to some extent. In any event, together, the pattern of regional activations and correlations between parietal seeds and frontal regions are generally consistent with an age-related disruption in a reflective fronto-parietal attentional network.

A common idea implicit in much of the episodic memory literature is that changes in activity of control regions of PFC associated with agenda-directed retrieval should have a *direct* impact on activity in one or more specific posterior region (i.e., the target of the retrieval attempt). But, most fMRI studies with older adults do not separately consider processes associated with "looking for" information (e.g., set effects, cue-biased retrieval, etc.) and those associated with "looking at" the (relevant and non-relevant) information that gets activated (i.e., evaluation: weighting/prioritizing features, comparing them to expectations/standards, etc.). Together, the current pattern of frontal and lateral parietal regional activity and correlations between representational areas and between parietal and frontal regions seems to suggest that, under circumstances that tax agenda-driven source memory processing, older adults may have more difficulty with selection/inhibition processes than with search processes involved in initially directing retrieval to appropriate representational areas. This possibility requires more systematic investigation.

In sum, the current findings highlight a situation where older adults' representational regions show clear *differential* activity to features during encoding, and appropriate *differential* activity at test depending on the category of targeted source information (in this case task vs. format). Yet, under these circumstances, older adults also showed evidence consistent with disrupted source monitoring of activated information: (1) less trial-by-trial reciprocal relations between activity in representational regions and (2) differences in frontal and parietal function presumably associated with selective reflective attention directed at activated information. The current findings converge with other recent evidence that older adults may be more disrupted on reflective

than perceptual attention (Mitchell et al., 2010). They also are consistent with the idea that older adults do not necessarily have less information active during remembering than young adults (Campbell et al., 2012), but what is being monitored may sometimes not be the most diagnostic information. Older adults may know where to "look for" certain types of agenda-appropriate information, but they also appear to be less able to constrain their reflective attention to the most relevant active information, that is, to control what activated information they "look at" (Hasher & Zacks, 1988).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.neuropsychologia.2013.01.012.

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