Neuroimaging Evidence for Agenda-Dependent Monitoring of Different Features During Short-Term Source Memory Tests

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A short-term source monitoring procedure with functional magnetic resonance imaging assessed neural activity when participants made judgments about the format of 1 of 4 studied items (picture, word), the encoding task performed (cost, place), or whether an item was old or new. The results support findings from long-term memory studies showing that left anterior ventrolateral prefrontal cortex (PFC) is engaged when people make source attributions about reflectively generated information (cognitive operations, conceptual features). The findings also point to a role for right lateral PFC in attention to perceptual features and/or familiarity in making source decisions. Activity in posterior regions also differed depending on what was evaluated. These results provide neuroimaging evidence for theoretical approaches emphasizing that agendas influence which features are monitored during remembering (e.g., M. K. Johnson, S. Hashtroudi, & D. S. Lindsay, 1993). They also support the hypothesis that some of the activity in left lateral PFC and posterior regions associated with remembering specific information is not unique to long-term memory but rather is associated with agenda-driven source monitoring processes common to working memory and long-term memory.

Keywords: source memory, source monitoring, fMRI, ventrolateral prefrontal cortex

Event memories are composites of features that collectively make up the *content* and the *context* of an event. Such details help differentiate one event from another and make a memory *episodic*. That is, the features of our mental experiences are a basis for attributing them to memory for a particular past episode—they provide evidence for the *source* of a mental experience (Johnson, 2006; Johnson et al., 1993). Such source details may derive from perception or thought (e.g., imagination, inference) and may include sensory details (e.g., format, pitch), spatio–temporal details (e.g., location, time of day), semantic information (e.g., category membership, associated items), emotional information (e.g., how we felt), cognitive operations (e.g., records of processes engaged), and so on. In contrast, less vivid (i.e., less rich, differentiated, or embellished) remembering may yield only feelings of familiarity or recency. Although some memories may have little source information, they nevertheless may yield a strong feeling of familiarity; thus, high confidence in a memory and recollection can be dissociable (Rajaram, 1993; Yonelinas, Otten, Shaw, & Rugg, 2005).

The distinction between more and less detailed or differentiated subjective experiences (e.g., Mandler, 1980) has figured into many theoretical characterizations of memory, for example, the source monitoring framework (SMF; Johnson et al., 1993; Johnson & Raye, 1981), dual process models (e.g., Jacoby, 1991; Yonelinas, 1999), and states of consciousness theories (e.g., Gardiner & Richardson-Klavehn, 2000; Tulving, 1985). One difference between the SMF and these other theoretical approaches is that the SMF has been more concerned with the specific types and amounts of various memory features that contribute to recollection (e.g., Conway, Collins, Gathercole, & Anderson, 1996; Durso & Johnson, 1980; Johnson, Foley, & Leach, 1988; McGinnis & Roberts, 1996; Suengas & Johnson, 1988; see also, e.g., Gardiner, Ramponi, & Richardson-Klavehn, 1998).

The SMF also emphasizes the idea that which features are activated and used during remembering depends on one's agendas (e.g., goals) at the time that remembering takes place. That is, a memory attribution is only partly dependent on what has been encoded; it also depends to a large part on what the rememberer later looks for and uses. There is considerable behavioral data supporting this proposition (e.g., Dodson & Johnson, 1993; Dodson & Schacter, 2001; Lindsay & Johnson, 1989; Marsh & Hicks, 1998; Mather, Henkel, & Johnson, 1997; Rahhal, May, & Hasher, 2002; Zaragoza & Koshmider, 1989). Concepts more recently developed in the context of the neuroimaging domain, such as *retrieval orientation* (e.g., Rugg & Wilding, 2000), *domain-sensitive biasing* (e.g., Dobbins & Wagner, 2005), or *cue-based planning* (e.g., Dobbins & Han, 2006), generally express ideas similar to that of the SMF: Remembering is affected by agendas. So far, these concepts have been invoked in the context of studies investigating the neural correlates of processes engaged in controlled retrieval of information from long-term memory (LTM),

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and they tend to emphasize the importance of encoding specificity in LTM, that is, the match between a cue and what has been encoded (e.g., Morris, Bransford, & Franks, 1977; Tulving & Thomson, 1973).

The SMF idea of agenda-dependent remembering assumes the importance of encoding specificity as well, but it also highlights that source monitoring involves a number of component processes that may interact in an iterative manner (e.g., Johnson & Raye, 2000). For example, focusing on a specific type of information can be relatively automatic (i.e., in response to a cue, e.g., reactivation) or more strategic (controlled; i.e., via self-generated cues, e.g., retrieval). Furthermore, the processes that evaluate activated information involve criteria setting (e.g., weighting the importance of features according to an active agenda) and attributional decision processes (e.g., comparing activated features to expected features). From the SMF perspective, we would expect some of these processes to be engaged both when information is currently active and when it must be revived from LTM and others (e.g., retrieval) to be engaged primarily when information needs to be revived from LTM. Thus, in the former case, we would expect similarities in the brain regions engaged, on the basis of the assumption that working memory (WM) and LTM draw on a common set of component processes (e.g., Johnson & Hirst, 1993; see also, e.g., Dobbins & Han, 2006; Ranganath & Blumenfeld, 2005).

Studies of the brain areas associated with agenda-dependent remembering have primarily focused on LTM and on the prefrontal cortex (PFC) as a region of particular interest, in part because of neuropsychological evidence that damage to PFC disrupts source memory more than old–new recognition memory in LTM paradigms (e.g., Shimamura, Janowsky, & Squire, 1990). A number of functional magnetic resonance imaging (fMRI) studies have reported greater activity in left lateral PFC (and sometimes right as well) during LTM source tasks than during old–new recognition (e.g., Cansino, Maquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins & Han, 2006; Dobbins & Wagner, 2005; Dudukovic & Wagner, 2007; Henson, Shallice, & Dolan, 1999; Konishi et al., 2002; Nolde, Johnson, & D'Esposito, 1998; Ranganath, Johnson, & D'Esposito, 2000; Raye, Johnson, Mitchell, Nolde, & D'Esposito, 2000; Rugg, Fletcher, Chua, & Dolan, 1999; Slotnick, Moo, Segal, & Hart, 2003; among others). Activity during old–new tasks in which familiarity may be sufficient (and other memory tasks that rely on more undifferentiated information such as recency), on the other hand, tends to be right lateralized (e.g., Dobbins, Simons, & Schacter, 2004; Kensinger, Clarke, & Corkin, 2003; Raye et al., 2000). The pattern of findings across these LTM studies suggests that left and right PFC are differentially involved in memory attributions depending on the specificity of the information sought and evaluated and on the need for strategic revival and evaluation processes (Nolde, Johnson, & Raye, 1998).

To more directly address the question of how different source-specifying features (e.g., perceptual, semantic, spatiotemporal, affective) are differentially accessed and weighted depending on agendas active at the time of remembering (Dodson & Schacter, 2001; Johnson et al., 1997; Marsh & Hicks, 1998; Mather et al., 1997), a logical next step is to more completely characterize how specific features and processes are reflected in neural activity during agenda-driven remembering. Recent neuroimaging studies

that compare two LTM source tasks have begun to provide evidence bearing on this important issue.

The monitoring of reflectively or internally generated information is especially interesting because of its presumed central role in source and reality monitoring (e.g., Johnson et al., 1993; Johnson & Raye, 1981). According to the SMF, our thoughts and the processes by which we generate them leave records that can be accessed later to help identify (and misidentify) the origin of information (e.g., Finke, Johnson, & Shyi, 1988; Roediger & McDermott, 1995). Thus, we might especially expect features that are perceptually derived and those that are reflectively generated to show different functional distributions of activity in PFC and/or other areas (e.g., posterior representational areas). Consistent with this hypothesis about such functional specificity in PFC, recent evidence from long-term source memory studies suggests that left anterior ventrolateral PFC is more active during source monitoring of internally generated information, such as the task performed during encoding (or the conceptual information generated), than during source monitoring of perceptually derived information, such as stimulus size, position on the screen (left–right), or list membership (e.g., Dobbins & Wagner, 2005; Simons, Gilbert, Owen, Fletcher, & Burgess, 2005; Simons, Owen, Fletcher, & Burgess, 2005). Several studies show that lateral PFC and medial anterior PFC are also sensitive to internally generated information, such as what task (e.g., read or generated) had been performed at encoding (e.g., Simons, Davis, Gilbert, Frith, & Burgess, 2006; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; see also, Dobbins & Wagner, 2005). In addition, within medial anterior PFC, a more posterior region may be especially sensitive to self-versus other-generated information (Simons, Henson, Gilbert, & Fletcher, 2008; Vinogradov et al., 2006). Thus, there is increasing evidence for differentiation of PFC by feature type during long-term source memory tasks.

The current study asked if these function–brain area relations extend to short-term source memory (STSM), in which participants make source judgments about information that is currently being maintained in WM (e.g., Mitchell, Johnson, Raye, & Greene, 2004; Mitchell, Raye, Johnson, & Greene, 2006). One reason such information should be informative is that LTM tasks involve both revival and evaluation processes. That is, an LTM probe by definition cues information that is not currently active. A WM task, on the other hand, minimizes the need for revival of information in LTM. Thus neural activity at the time of the probe should be relatively more likely to be associated with setting, holding, and carrying out an agenda for *evaluation* processes involved in source monitoring than with LTM retrieval. Of course, information that is not currently within the focus of reflective attention, even if it has some residual activation, may require controlled processing (e.g., *refreshing*, Johnson et al., 2005; Raye, Johnson, Mitchell, Reeder, & Greene, 2002; see also Cowan, 1999) to make it the focus of attention, and relatively automatic *reactivation* or more controlled *retrieval* (e.g., Johnson, 1992) from LTM can occur during a WM task as well. Nevertheless, compared with the typical LTM source memory task, in an STSM task with an immediate test, the relative contribution of agenda-driven evaluation processes to the fMRI signal should be greater than that of revival processes, which are in turn likely to contribute relatively more during an LTM task. Thus, if the left-lateralized activity typically found in long-term source memory tasks reflects primarily retrieval of feature infor-

mation (or attempts to retrieve feature information) from LTM, we would not expect to see such activity when source judgments are made about information being currently maintained in a WM task. Initial evidence that left-lateralized PFC activity associated with source memory does not depend on retrieving feature information from LTM was provided by Mitchell et al. (2004) for format (picture–word) and location (left–right) source tasks.

Here we used the STSM procedure to compare neural activity associated with source attributions about reflectively generated *encoding task* information (cost or place judgments) versus source attributions about perceptually derived *format* information (whether an item had been seen as a picture or a word). We compared these two source decisions to old–new decisions. On each trial, two line drawings of common objects and two concrete words were presented in random sequence. For two of these study items (one picture and one word), participants decided whether it would cost more or less than $20 (*cost* judgment) and for the other two items (a picture and a word), they decided whether it would be more likely to be found indoors or outdoors (*place* judgment). Randomly, on each trial, old–new, picture–word (format), or cost–place (task) information was immediately probed for a single item from that trial. This procedure holds encoding conditions constant across test conditions, encourages active maintenance of the information, and minimizes the retention interval between encoding and test. We expected to replicate our previous finding of greater left lateralized PFC activity for source than for old–new tests, but of primary interest here were differences in the neural activity associated with the type of source information tested (format vs. task). The findings should help clarify the role of several brain regions in agenda-dependent monitoring of externally derived (format) and internally generated (task) source information.

Method

Participants

Participants (*N* = 16, 9 women and 7 men; *M* age = 22, *SD* = 2.4 years) were right-handed, native-English speaking students who reported being in good health, with no history of serious head trauma or primary degenerative neurological disorder; they had normal or corrected-to-normal vision, and none were taking psychotropic medications. All participants were paid. The Human Investigation Committee of Yale University Medical School approved the protocol, and informed consent was obtained from all participants.

Task and Design

During scanning, stimuli were projected onto a screen at the foot of the scanner, and participants viewed them via a mirror mounted on the head coil. Each trial was 20 s (see Figure 1). Participants saw four study items presented sequentially. Two of the items were concrete nouns printed in lowercase (words); two were black-and-white line drawings of common objects (pictures). For one of each item type, participants made a cost judgment ("Would this item cost less or more than $20?") and for the other item of each type they made a place judgment ("Would this item more likely be found indoors or outdoors?"). Format (picture–word) and task type (cost–place) were pseudo-randomly presented and counterbalanced across participants so that, across runs, each format–encoding task combination appeared equally often in each ordinal position in each testing condition. A cue was presented 150 ms before each stimulus onset to let participants know which judgment task they were to perform for that item, and the cue remained on the screen while the stimulus was shown for 1,700 ms (with a 150-ms interstimulus interval). Participants made their response via a left-handed (less, indoors) or right-handed (more, outdoors) button press.

After 1 s of unfilled time, test response cues were presented to let participants know which test decision (old–new, picture–word, cost–place) they would have to make, and 1 s later the test probe (always a word in capital letters) appeared below the cues, in the middle of the screen, for 3,000 ms. The test types, which were explained in advance to participants, were as follows: *format* (picture–word), in which the probe always represented an old item
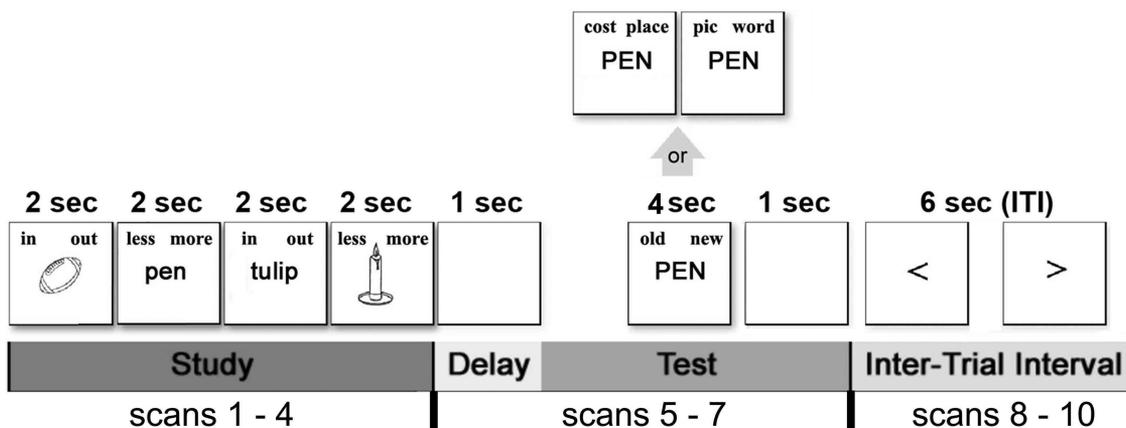

Figure 1. Procedure and trial timeline. Note that during the test period, the cues were presented 1 s before the probe item was displayed, and they stayed on while the probe was on the screen; there was a 1-s blank before the intertrial interval (ITI) began. One full brain scan was acquired every 2 s; thus, there were 10 scans (images) per trial. The test types were random. See the text for full details.

and participants were to indicate whether the item originally appeared as a picture (left-hand button press) or a word (right-hand button press); *encoding task* (cost–place), in which the probe always represented an old item and participants were to indicate whether they originally made a cost decision (left-hand button press) or place decision (right-hand button press) for that item; or *old–new*, in which the probe equally often represented an old (previously presented) item or a new item and participants indicated old (left-hand button press) or new (right-hand button press). Study items were not repeated across trials and only one of the four items was tested on each trial. Across trials, there were an equal number of probes of each test type, and targets were chosen equally often from each ordinal study position, format, and judgment type. Analyses reported in Mitchell et al. (2004, Footnote 2) showed that the greater match between study and test format for word items than for picture items does not disproportionately affect the picture–word tests in this procedure (e.g., by advantaging the word vs. picture trials on picture–word tests), perhaps because with so much specific detail active, fluency becomes a less diagnostic cue.

One second of blank time after the offset of the test probe was followed by a 6-s intertrial interval that included two arrows, each randomly pointing left or right, presented sequentially for 1,400 ms each, randomly pointing to the left or to the right. Participants were told that when they saw an arrow, while it was still on the screen, they should push a button with their left hand if the arrow pointed left and with their right hand if it pointed right. The intertrial interval was not used as a baseline in the analyses, but rather, the arrows provided a task common to all conditions to allow time for the hemodynamic response associated with remembering and to decrease variability among participants from uncontrolled mental activity between trials (Raye et al., 2002).

Stimuli were common objects whose names were one to three syllables in length (e.g., *bell*, *strawberry*). Pictures were chosen from the Snodgrass and Vanderwart (1980) corpus and similar drawings provided by Friedman (see, Cycowicz, Friedman, Rothstein, & Snodgrass, 1997). Words were chosen from among the remaining picture labels and similar concrete nouns. For the test probes, names of the pictures were either the original labels or single-word names reached by agreement among the experimenters. Items were equated on various dimensions between conditions on the basis of published norms (Cycowicz et al., 1997; Kucera & Francis, 1967; Snodgrass & Vanderwart, 1980; see Mitchell et al., 2004, for details). Across participants, each item appeared equally often for each type of test.

The design thus had a single factor (condition) with three levels (test type: picture–word, cost–place, old–new). Each of six runs had six trials of each test type (picture–word, cost–place, old–new), presented in a pseudo-random fashion, with a different trial order for each participant.

Imaging Details

The study was run on a 1.5-T SONATA scanner (Siemens Corporation, New York NY), at the Magnetic Resonance Research Center at Yale University. T1-weighted anatomical images were acquired for each participant. Functional scans were acquired with a single-shot echoplanar gradient-echo pulse sequence (TR = 2,000 ms, TE = 35 ms, flip angle = 80°, FOV 24). The 24 axial

slices (slice thickness = 3.8 mm, resolution = 3.75 × 3.75 mm in plane) were aligned with the AC-PC line. Each run began with 12 blank seconds to allow tissue to reach steady state magnetization and was followed by a 1-min rest interval. One volume was collected every 2 s, or 10 full brain scans for each trial; thus there were, for each person, a total of 360 images in each test condition.

Analyses of Behavioral Data

Accuracy is expressed as d' scores. Responses that required a left-handed response (old, picture, cost) were coded as targets and those requiring a right-handed response (new, word, place) were coded as lures so d' scores could be calculated. Perfect scores were adjusted as follows: $p(\text{hits}) = 1$ was recalculated as $1 - 1/(2N)$; $p(\text{false alarms}) = 0$ was recalculated as $1/(2N)$, where $N =$ the maximum number of hits or false alarms possible (Macmillan & Creelman, 1991).

Analyses of fMRI Data

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

The fMRI data were analyzed using an analysis of variance (ANOVA; NIS software, Laboratory for Clinical Cognitive Neuroscience, University of Pittsburgh, and the Neuroscience of Cognitive Control Laboratory, Princeton University) in which test conditions (picture–word, cost–place, old–new) were directly compared to identify brain regions that had 6 contiguous voxels each showing a significant Condition × Time Within Trial interaction at $p < .00001$ (Forman et al., 1995). This approach does not require predefining the shape of the hemodynamic response, and the regions were not identified by using the intertrial interval as a baseline. Participant was a random factor, and run (1–6), condition (picture–word, cost–place, old–new), and time within trial (Scans 1–10) were fixed factors. The hemodynamic response that indexes brain activity in fMRI responds slowly, rising to a peak 4–6 s after the critical event (Huettel et al., 2004). Because encoding conditions were held constant, differences between the conditions should be seen as differences in the fMRI signal 16–20 s after the start of the trial (Scans 8–10), corresponding to the test period in each trial. Thus, for each region of activation identified in the ANOVA, planned comparisons were conducted on the mean percent signal change within trials (from Time 1) for Scans 8, 9, and 10 to determine which conditions significantly differed ($p < .05$) at test; that is, subsequent analyses were conducted only on clusters identified in the initial ANOVA for the time period associated with the test.

The F maps resulting from the ANOVA were transformed to Talairach space using AFNI (Cox, 1996), and areas of activation were localized using Talairach Daemon software (Lancaster, Summerlin, Rainey, Freitas, & Fox, 1997) as well as manually checked with the Talairach and Tournoux (1988) and/or Duvernoy (1999) atlases. All regions of activation are reported in Talairach coordinates.

Results and Discussion

Behavioral Results

Table 1 shows accuracy, measured as d', and response times (RTs) on correct trials for each test type. As expected, there was a main effect of condition for accuracy, $F(2, 30) = 48.78$, $MSE = 0.23$, $p < .00001$, with participants performing best on the old–new test, followed by the picture–word and then the cost–place tests ($ps < .0001$). There was also a main effect of condition for RTs, $F(2, 30) = 40.46$, $MSE = 11,402$, $p < .00001$. The pattern (old–new $<$ picture–word $<$ cost–place, $ps < .001$) suggests that even with memorial features recently activated and participants motivated to keep them active in WM, monitoring more specific features takes time, and information about the encoding task performed appears to be less salient or more difficult to evaluate than is perceptual format information (see also, e.g., Dobbins & Wagner, 2005).

fMRI Results

Table 2 lists all regions of activation identified as showing a Condition × Time interaction, as described in the Method section. As shown in Part A of Table 2, there were four regions with the activity pattern cost–place $>$ picture–word $>$ old–new: a large area of the left lateral PFC that included middle frontal, precentral, and inferior frontal gyri; an area of medial frontal gyrus, extending into anterior cingulate cortex (ACC); an area of left middle and inferior temporal gyri; and an area of left inferior parietal lobule. Mitchell et al. (2004) reported a similar large region of left PFC where activity in a STSM study was greater on a format (picture vs. word) test than on a location (left vs. right) test, which was in turn greater than an old–new test. In fact, although Mitchell et al. focused on frontal regions and did not report other areas, two independent experiments found areas quite similar to all four of those in Part A of Table 2, and they showed the pattern picture–word $>$ left–right $>$ old–new.

There were no areas in which activity was greater in picture–word than in both old–new and cost–place, but as shown in Part B of Table 2, there were posterior regions where picture–word did not differ from old–new but did evoke more activity than cost–place: an area of right superior temporal gyrus, an area of right middle and inferior temporal gyri extending into middle occipital gyrus, an area of right cuneus/precuneus extending into superior occipital gyrus, and a medial area of the precuneus extending into posterior cingulate cortex. Consistent with other findings (e.g.,

Table 1
Mean Short-Term Source Memory Accuracy (d') and Mean Response Times (RTs) for Correct Responses

	d'		RT (ms)	
Test type	M	SEM	M	SEM
CP	1.60	0.18	1,613	52
PW	2.45	0.22	1,466	59
ON	3.29	0.20	1,275	44

Note. CP = cost–place (encoding task); PW = picture–word (format); ON = old–new.

Dobbins & Wagner, 2005), when the threshold was dropped to 6 contiguous voxels each at $p < .0001$, an area (8 voxels) of right lateral PFC was identified that showed picture–word = old–new $>$ cost–place (Brodmann area [BA] 46[45]; Talairach coordinates = 45, 29, 19; middle and inferior frontal gyri; max $F = 3.24$).

The fact that this area of right PFC showing picture–word $>$ cost–place required a lower threshold to detect suggests that right PFC activity was engaged more in picture–word than in cost–place only on some trials, perhaps when source evidence was less differentiated or less vivid. Evidence consistent with this possibility was provided by an analysis in which we coded each trial for whether a correct or incorrect response had been given ($N = 14$ for this analysis because 2 participants made no errors in the old–new condition and thus had to be excluded). This analysis (with 6 contiguous voxels each at $p < .001$) identified an area (see Figure 2) of right lateral PFC that showed no significant differences among conditions for correct responses but showed greater activity for picture–word than for both cost–place and old–new ($p < .10$ for the picture–word $>$ old–new comparison) for incorrect responses. For comparison, Figure 2 also shows an area of left lateral PFC where activity for correct responses showed the pattern cost–place $>$ picture–word (.06) $>$ old–new, and for incorrect responses, the pattern of activity was cost–place = picture–word $>$ old–new.

Areas that showed greater activity for old–new than both source tests are shown in Part C of Table 2. They included right and left superior and middle temporal gyri, right precentral gyrus, and right inferior parietal lobule. LTM studies have found right prefrontal activity associated with old–new recognition (e.g., Dobbins et al., 2004; Kensinger et al., 2003; Raye et al., 2000) compared with source tests. Given the short retention interval in the current study, and the fact that two thirds of the trials in our study involved source judgments, we were not necessarily expecting to see areas of PFC where old–new $>$ source tests because participants may have evaluated specific details on some old–new trials (e.g., Mitchell et al., 2004).

To further probe for differences related to specific source information, we also conducted an analysis that included only correct cost–place and picture–word trials ($p < .001$, 6 continuous voxels). The regions (see Table 3) showing cost–place $>$ picture–word and picture–word $>$ cost–place were similar to those identified in the analysis that included all trials (see Table 2). Three regions of left lateral PFC, all showing cost–place $>$ picture–word, are shown in Figure 3: an area of anterior ventrolateral PFC (see Figure 3A), an area of mid-ventrolateral PFC (see Figure 3B), and an area of dorsolateral PFC (see Figure 3C). Not surprisingly, the pattern of activity was similar for similar subregions of the corresponding large left lateral PFC area in Table 2.

General Discussion

We used a STSM procedure to identify areas sensitive to the evaluation of specific features during agenda-dependent remembering. Holding encoding constant, we asked people about either the encoding task they performed (cost estimate or indoor–outdoor judgment) or the format of an item (picture or word) presented up to a few seconds before, and we compared activity during those two source memory tests to that during old–new discriminations.

Table 2
Regions of Activation Showing a Condition × Time Interaction in Analyses Including All Trials

Hemisphere	BA area	Anatomical area	Talairach coordinates (x, y, z)	No. of voxels	Max F
		A: CP > PW > ON			
L	9/6, 46, 47, 45	MFG, PrCG/IFG	−36, 3, 35	247	8.81
M	32, 6, 8, 24	MdFG, ACC	−6, 16, 43	54	6.54
L	21 (37)	MTG, (ITG)	−54, −43, −2	32	5.66
L	40, 39, 7	IPL, AG, PCu, SPL, SMG (follows intraparietal sulcus)	−30, −57, 35	128	8.08
		B: ON = PW > CP			
R	38	STG (claustrum)	34, 2, −12	6	4.14
R	37, 21, 19	MTG, ITG, MOG	48, −62, −1	36	4.83
R/M	19/7, 18	Cu/PCu, SOG	18, −78, 35	16	4.13
M	7 (31)	PCu, (PCC)	5, −45, 39	16	3.93*
		C: ON > CP = PW			
R	38, 22 (21)	STG, (MTG)	53, 3, −5	24	4.55
L	22, 21, 6	STG, (MTG)	−55, −4, −2	12	4.13**
R	6	PrCG	46, 2, 15	6	3.60
R	40	IPL, (SMG)	51, −36, 35	9	4.09
		D: CP = PW > ON			
L		claustrum (putamen)	−29, 15, −2	15	5.09
M		thalamus (caudate, lentiform nucleus)	7, 1, 2	18	4.34

Note. Talairach coordinates are for the local maximum for each region of activation. Brodmann area (BA) and anatomical areas are listed in order of approximate size, with approximately equal areas of activation indicated by a slash and areas with only a relatively small extent included in parentheses. Significant differences between the test conditions were determined using planned comparisons conducted on the percent signal change within trials (from Time 1) for Scans 8-10, averaged across all trials of that type and all voxels in that region ($p < .05$). CP = cost–place; PW = picture–word; ON = old–new; L = left; MFG = middle frontal gyrus; PrCG = precentral gyrus; IFG = inferior frontal gyrus; M = medial; MdFG = medial frontal gyrus; ACC = anterior cingulate cortex; IPL = inferior parietal lobule; AG = angular gyrus; PCu = precuneus; SPL = superior parietal lobule; SMG = supramarginal gyrus; R = right; STG = superior temporal gyrus; MTG = middle temporal gyrus; ITG = inferior temporal gyrus; MOG = middle occipital gyrus; Cu = cuneus; SOG = superior occipital gyrus; PCC = posterior cingulate cortex.
* ON > PW, $p = .05$; ** ON > PW, $p = .08$.

The finding of greater left dorsolateral and ventrolateral PFC activity for source than for old–new tests (see Part A of Table 2) extends previous findings for format and location source information using this STSM procedure (Mitchell et al., 2004, 2006) to source memory for judgments about internally generated task information. The current findings thus provide further support for the conclusion that regions of left lateral PFC are likely to be recruited when a memory task requires evaluation of specific
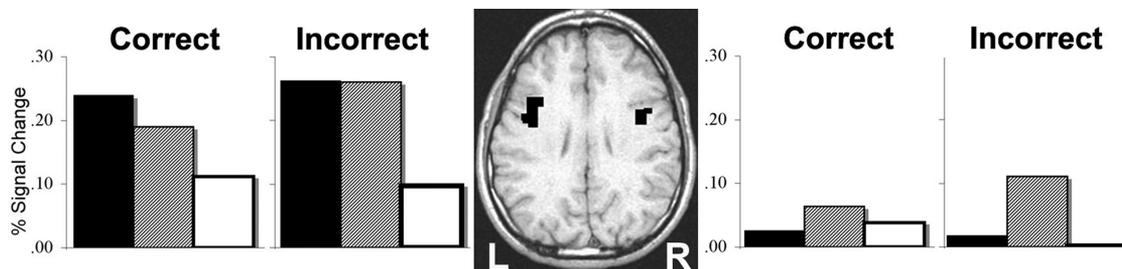

Figure 2. Regions of left ($x = −40$, $y = −1$, $z = 26$; middle frontal–precentral gyri and inferior frontal gyrus, BA 9/6, 44; max $F = 4.27$) and right ($x = 42$, $y = 2$, $z = 27$; precentral and inferior and middle frontal gyri, BA 6, 44[9]; max $F = 3.91$) lateral prefrontal cortex identified as showing a significant Condition × Time interaction ($p < .001$, 6 contiguous voxels) in an analysis that examined activity on correct and incorrect trials separately. The bar graphs show the mean percent signal change during Scans 8–10 (test period activity, assuming a 4- to 6-s lag in the hemodynamic response), averaged across all trials of that type and all voxels in that region. Solid bars represent cost–place trials, hatched bars represent picture–word trials, and open bars represent old–new trials.

Table 3

Regions of Activation Showing a Condition × Time Interaction in Analyses Including Only Correct Trials in the Cost–Place (CP) and Picture–Word (PW) Conditions

Hemisphere	BA area	Anatomical area	Talairach Coordinates (x, y, z)	No. of voxels	Max F
		A: CP > PW			
L	**47**	**IFG, OFG**	**−45, 45, −5**	**20**	**5.71**
L	**45**	**IFG**	**−52, 18, 6**	**16**	**4.62**
L	**9**	**MFG**	**−48, 10, 35**	**8**	**3.83**
M	**6,32**	**MdFG, ACC**	**−5, 8, 47**	**10**	**4.51**
L	21	MTG	−54, −43, −2	19	5.22
L	39, 22	MTG, STG	−42, −54, 10	6	4.16
L	19, 39/40/7	IPL (IPS, PCu)	−34, −69, 39	65	6.36
		B: PW > CP			
R		amygdala putamen	27, −2, −8	7	5.01
R	19, 18 (17)	Cu, SPL, IOS, POS	22, −78, 23	47	5.29
L	19, 18	MOG, Cu	−25, −84, 18	13	5.68
L	6/4	PrCG/PoCG	−39, −17, 31	6	4.53

Note. Talairach coordinates are for the local maximum for each region of activation. Brodmann area (BA) and anatomical areas are listed in order of approximate size, with approximately equal areas of activation indicated by a slash and areas with only a relatively small extent included in parentheses. Significant differences between the test conditions were determined using planned comparisons conducted on the percent signal change within trials (from Time 1) for Scans 8-10, averaged across all trials of that type and voxels in that region ($p < .05$). Areas in bold are shown in Figures 3 and 4. CP = cost–place; PW = picture–word; L = left; IFG = inferior frontal gyrus; OFG = orbitofrontal gyrus; MFG = middle frontal gyrus; M = medial; MdFG = medial frontal gyrus; ACC = anterior cingulate cortex; MTG = middle temporal gyrus; STG = superior temporal gyrus; IPL = inferior parietal lobule; IPS = intraparietal sulcus; PCu = precuneus; R = right; Cu = cuneus; SPL = superior parietal lobule; IOS = intra occipital sulcus; POS = parietal occipital sulcus; MOG = middle occipital gyrus; PrCG = precentral gyrus; PoCG = postcentral gyrus.

features. Moreover, these results converge with those of Mitchell et al. (2004) to strengthen the proposal that at least some of the left-lateralized dorsolateral and ventrolateral PFC activity found in studies of long-term source memory is not unique to LTM but rather is associated with agenda-driven source monitoring processes (e.g., what features are salient and how information will be weighted or evaluated) common to WM and LTM (see also, e.g., Dobbins & Han, 2006, for a similar conclusion). Further specifying the brain areas and neural networks associated with different memorial features and component processes (e.g., refreshing, reactivating, retrieving; Johnson, 1992) involved in making source attributions during remembering under various agenda conditions is one of the current challenges of cognitive neuroimaging (e.g., Dobbins & Han, 2006; Dobbins & Wagner, 2005).

Along these lines, consistent with recent long-term source memory studies (e.g., Dobbins et al., 2002; Dobbins & Wagner, 2005; Simons, Gilbert, et al., 2005; Simons et al, 2008; Simons, Owen, et al., 2005), our finding that cost–place > picture–word in left anterior ventrolateral PFC (BA 47, see Table 3 and Figure 3A) provides further evidence of a role for this area in source memory for reflectively generated information. Dobbins et al. (2002, Experiment 2) showed that an area of left anterior ventrolateral PFC (Montreal Neurological Institute coordinates −45, 45, −6) very close to ours was more active when participants were remembering the encoding task compared to recency information. Dobbins and Wagner (2005) compared source memory for encoding task to source memory for size and to recognition of a novel item and found that a left anterior ventrolateral region (BA 47; MNI coordinates −48, 33, −9) was more active during task judgments than during size or novelty judgments.

As noted in the introduction, in addition to left anterior ventrolateral PFC, LTM studies provide evidence for the involvement of anterior PFC (BA 10) in memory for reflectively generated information (e.g., Dobbins & Wagner, 2005; Simons et al., 2006; Simons et al., 2008; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; Vinogradov et al., 2006), and there may be functional differences between subregions of anterior medial PFC associated with different types of self-relevant features associated with reality monitoring (Simons et al., in press). We did not observe activity in anterior PFC associated with our cost–place task. One possibility is that activity at test in anterior ventrolateral PFC, which we did observe, is associated with processing the conceptual–semantic features of what was generated during the encoding task (e.g., an item's cost or its usual location; e.g., Dobbins & Wagner, 2005) and activity in anterior PFC is associated with processing information about the cognitive operations that were engaged (e.g., to make a cost or place judgment), and our participants focused on semantic features rather than cognitive operations. Another possibility is that anterior PFC is engaged during the active retrieval of information from LTM. For example, perhaps it is involved in initiating strategic retrieval searches (e.g., Dobbins & Han, 2006); the need for such retrieval was minimized in our procedure. Both of these hypotheses deserve further investigation.

Dobbins and Wagner (2005) also reported activity in several regions of right posterior ventrolateral and right dorsolateral PFC associated with their size judgment task and emphasized the role of these regions in memory tasks in which participants focus on perceptual details. Consistent with this, we saw activity in the right lateral PFC for picture–word source judgments. Dobbins and Wagner's study and test items were all pictures, and their perceptual
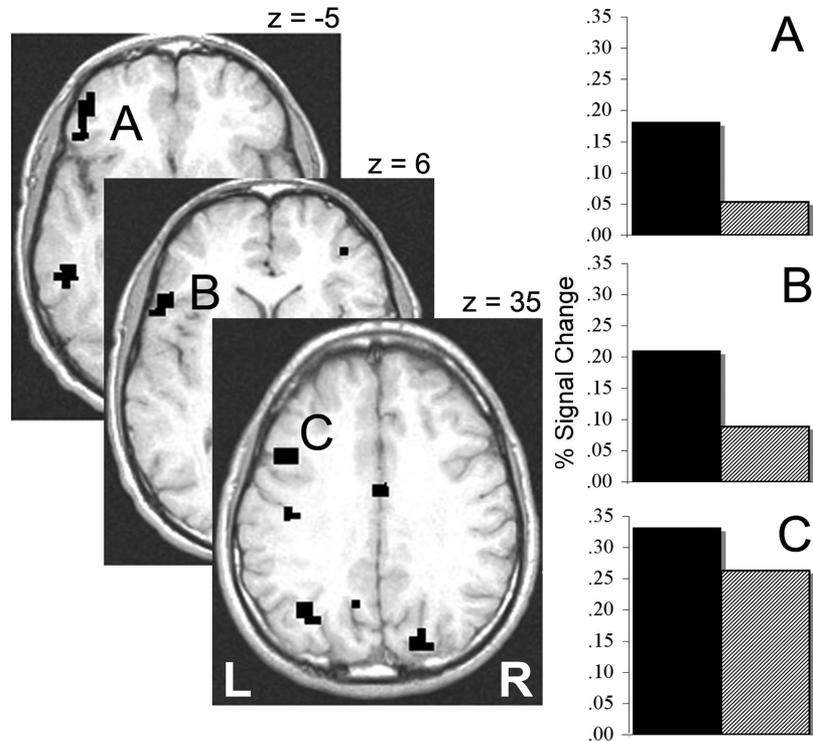
Figure 3. Three areas of the left lateral prefrontal cortex (PFC) identified as showing a significant Condition $\times$ Time interaction ($p < .001$, 6 contiguous voxels; Forman et al., 1995) in an analysis that examined activity on correct trials in the cost–place and picture–word conditions only. All areas showed greater activity in cost–place than in picture–word trials, as indicated in the bar graphs (solid = cost–place, hatched = picture–word). A: An area of anterior ventrolateral PFC ($x = -45$, $y = 45$, $z = -5$; inferior frontal gyrus and orbitofrontal cortex, BA 47; max $F = 5.71$). B: An area of mid-ventrolateral PFC ($x = -52$, $y = 18$, $z = 6$; inferior frontal gyrus, BA 45; max $F = 4.62$). C: An area of dorsolateral PFC ($x = -48$, $y = 10$, $z = 35$; middle frontal gyrus, BA 9; max $F = 3.83$). The bar graphs show the mean percent signal change during Scans 8–10 (test period activity, assuming a 4- to 6-s lag in the hemodynamic response), averaged across all trials of that type and all voxels in that region.

source task was a size judgment. They suggested the activity they observed reflected allocation of attention to the perceptual details of the test probes. The fact that our probes were all words yet we also observed greater activity in right PFC in our picture–word than cost–place test suggests that right lateral PFC is engaged not only when participants inspect *perceptually* present details (e.g., of test probes, as in Dobbins & Wagner, 2005) but also when participants *reflectively* attend to perceptual qualities of active mental representations (as in our study). The fact that we saw picture–word > cost–place in an area of right lateral PFC only on incorrect trials (see Figure 2) suggests that when perceptual information is poor, participants may be more likely to engage right lateral PFC either in an effort to evaluate whatever perceptual information they do have and/or to evaluate familiarity (see, e.g., Nolde, Johnson, and Raye, 1998; Mitchell et al., 2004, Experiment 3, for evidence consistent with this latter possibility). More analytic manipulations are needed to further specify the roles of various right lateral PFC regions in attending to perceptual features of test probes versus attending to features of perceptual mental representations versus attending to more global information, such as familiarity.

Our WM task was designed to produce several active multifeatured representations from which participants would need to select

relevant features for source monitoring. The shorter RTs on picture–word than on cost–place trials suggest that format information was more readily available than task information. We also found greater activity in the cost–place compared with the picture–word condition (see Table 3) in left dorsolateral PFC (BA 9), left mid-ventrolateral PFC (BA 45), and medial PFC, ACC (BA 6,32). These areas from the current study were within 1.9, 2.8, and 1.5 voxels, respectively, of corresponding areas identified in a study in which participants were shown three words and cued immediately to refresh one of these three active representations compared with refreshing a single active representation (Johnson et al., 2005, Experiment 5). Consistent with other findings in the literature, the pattern of activity in Johnson et al.'s (2005) study supported the conclusion that refreshing one of several active representations involves a network of regions sensitive to conflict among active representations (ACC; e.g., Botvinick, Cohen, & Carter, 2004), selection of a relevant item (ventrolateral PFC; e.g., Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997), and refreshing (fore-grounding) the target item (dorsolateral PFC; e.g., Raye et al., 2002; see also, Dobbins & Han, 2006). Thus, one interpretation of the greater activity in these areas for the cost–place than for the
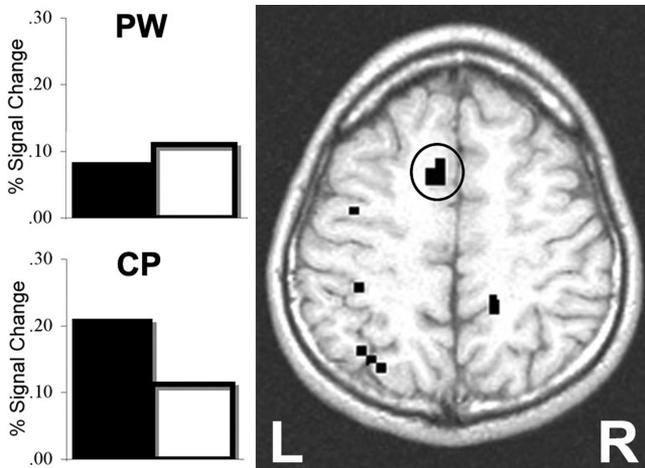
Figure 4. A region of medial frontal gyrus and anterior cingulate cortex ($x = -5$, $y = -8$, $z = 47$; BA, 6, 32; max $F = 4.51$) identified as showing a significant Condition × Time interaction ($p < .001$, 6 contiguous voxels) in an analysis that examined activity on correct trials in the cost–place (CP) and picture–word (PW) conditions as a function of whether the target item had been presented as a picture (solid) or a word (open) during study. The bar graphs show the mean percent signal change during Scans 8–10 (test period activity, assuming a 4- to 6-s lag in the hemodynamic response), averaged across all trials of that type and all voxels in the region.

picture–word condition in the present study is that evaluating source features at test involved selectively refreshing the target feature from among multiple active features, and that there was greater competition from active but irrelevant picture–word features on cost–place trials than vice versa.

Consistent with this interpretation, Figure 4 shows that for correct items during the picture–word test, activity in a region including ACC did not differ for picture and word items. In contrast, during the cost–place test it did: Activity was greater for picture than for word items. Anterior cingulate activity is associated with cognitive competition in a broad range of tasks (e.g., Botvinick et al., 2004), and a meta-analysis suggests it is engaged during WM tasks in selective attention processes used to maintain focus on task-relevant stimulus dimensions (Wager & Smith, 2003). These findings are consistent with the hypothesis that participants in our procedure experienced some competition from salient pictorial information when they were monitoring for task information during the cost–place test.

As would be expected, activity in posterior regions also differed depending on what was being evaluated (see Table 2). Activity was greater for cost–place than for picture–word trials in left middle temporal gyrus and left inferior parietal lobule and greater for picture–word than cost–place trials in right middle temporal gyrus and right cuneus/precuneus. Both source tasks showed greater activity than the old–new task in left temporal and parietal regions; we found a similar pattern in previous STSM studies (Mitchell et al., 2004, unpublished data). Left parietal cortex is active in many long-term source memory studies (e.g., Dobbins et al., 2002; Dobbins & Wagner, 2005; Kahn, Davachi, & Wagner, 2004; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005; Vilberg & Rugg, 2007), as well as other kinds of LTM tasks (e.g., Wheeler & Buckner, 2004), and has been associated with recol-

lection (see, e.g., Wagner, Shannon, Kahn, & Buckner, 2005, for a recent review). The findings from our STSM studies suggest that some of the parietal activity during LTM studies reflects processes involved in selectively focusing on and evaluating activated information.

In summary, the present findings provide converging evidence for the importance of left anterior ventrolateral PFC in the monitoring of self-generated information (Dobbins & Wagner, 2005; Simons, Gilbert, et al., 2005; Simons, Owen, et al., 2005). In addition, they provide further evidence suggesting that at least some of the left-lateralized PFC activity in long-term source memory studies, and perhaps activity in posterior regions such as parietal cortex as well, is associated with maintenance and evaluation of active information during the monitoring of features (e.g., Mitchell et al., 2004). Of course, our conclusion that the PFC activity we observe with this procedure primarily reflects focusing on and evaluating (weighting) specific types of active features requires further corroboration because although our STSM procedure may reduce the need for active retrieval from LTM, the procedure does not preclude it. In any event, the substantial similarities between results of short-term memory and LTM source monitoring fMRI studies is consistent with the emerging view that there is a common set of component processes underlying WM and LTM (Johnson & Hirst, 1993; see also, e.g., Dobbins & Han, 2006; Ranganath & Blumenfeld, 2005), with varying combinations of processes engaged and types of information considered depending on the circumstances. The present results, along with the related studies from other labs cited here, illustrate that a cognitive neuroscience approach provides useful converging tools for clarifying and testing theoretical characterizations of qualitative features and processes of human memory such as represented in the source monitoring framework (Johnson et al., 1993), and that such theoretical characterizations can inform and guide neuroimaging investigations.

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