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Research report

Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes

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Abstract

In contrast to item memory, which refers to recognition or recall of previously presented information, source memory refers to memory for the context of previously presented information. The relatively few functional MRI (fMRI) source memory studies conducted to date have provided evidence that item memory and source memory are associated with differential activity in right and left prefrontal cortex, respectively. To both confirm this distinction in prefrontal cortex and to determine whether other differences in the neural substrates associated with these cognitive functions exist, an event-related fMRI study was conducted. In this study, item memory and source memory encoding phases were identical; participants viewed a series of abstract visual shapes presented on the left or right side of the screen and were instructed to remember each shape and its spatial location. During the item memory retrieval phase, shapes from the encoding phase were intermixed with new shapes and participants made an old–new judgment. During the source memory retrieval phase, all shapes were from the encoding phase and participants made a left–right judgment. An event-related analysis of item memory and source memory revealed a right and left prefrontal cortex distinction. Moreover, only item memory was associated with activity in the medial temporal lobes. These results confirm and extend previous findings that item memory and source memory are associated with distinct neural substrates.

Theme: Neural basis of behavior

Topic: Cognition

Keywords: Shape; Object; Nonverbal; Spatial; Memory; Source memory; Prefrontal cortex; Medial temporal lobe; Parahippocampal gyrus; Functional magnetic resonance imaging

1. Introduction

One can determine whether a person remembers a previously presented item by showing them the item and asking ‘‘Have you seen this before?’’ Alternatively, one can inquire as to the context in which the item was previously presented, e.g. ‘‘Where did you see this before?’’ Here, the term *item memory* will be used to refer to memory of previous exposure to a specific item[1] while the term *source memory* will be used to refer to the context in which that item was presented [20,49]. Source memory can

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[1] The term ‘item’ is used broadly to refer to any unitary form that can be uniquely identified by its features and/or meaningfulness (e.g. words, faces, objects, scenes, and shapes). When the phrase ‘item memory’ is used, it refers to either recognition memory or memory recall. In the present experiment, the phrase refers to recognition memory only. Lastly, unless otherwise specified, the term *memory* throughout the paper refers only to the cognitive process of memory retrieval, as opposed to memory encoding or both retrieval and encoding.

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refer to the time at which information was presented (e.g. words from list 1 vs. list 2), a feature of the information (e.g. red vs. green shapes), or the spatial location of previously presented information (e.g. objects on the left vs. right side of the screen). In the last decade, a growing body of convergent evidence has been amassed regarding the neural substrates associated with item memory; however, much less is known about the neural substrates associated with source memory.

Using functional magnetic resonance imaging (fMRI) and positron emission tomography (PET), item memory has been shown to consistently activate right prefrontal cortex [2–4,14–16,26,27,32,33,38,51,57], consistent with Tulving's hemispheric encoding/retrieval asymmetry model (HERA) [31,55], the medial parietal cortex [2,3,5,14–16,19,21,27,41,45,51,56], and the medial temporal lobes, which include the hippocampus and parahippocampal gyri [4–6,9,13,24,37,39–46,51].

Findings from event-related potential (ERP) studies of item memory are highly consistent with the functional imaging results. In particular, item memory elicits a right frontal [1,7,8,34,53,58,59] and parietal scalp response [1,7,8,34,58,59]. To date, medial temporal lobe activation during item memory has not been reported using ERPs, presumably due to the depth of medial temporal sources relative to recording electrodes on the scalp.

In contrast to item memory, the source memory ERP literature is less consistent. Some researchers have argued that source memory and item memory have similar scalp distributions, differing only quantitatively, rather than qualitatively, and thus rely on the same neural substrates [1,7,59]. In these studies, participants were instructed to make an item memory judgment immediately followed by a source memory judgment for each stimulus thus requiring a dual judgment; the concomitant item memory *and* source memory retrieval processes on each trial may have masked a true distinction between item memory and source memory. Indeed, neuropsychological evidence of source memory deficits with spared item memory [18,48] indicates there are distinct neural substrates for item memory and source memory. In ERP studies where item and source memory decisions have been isolated, source memory has been associated with unique prefrontal activation [47,53], specifically in the left prefrontal cortex [34]. Although ERPs provide excellent temporal resolution, their spatial resolution is poor relative to fMRI (i.e. centimeters vs. millimeters); thus, fMRI results should provide a more spatially precise measure of neural activity associated with item memory and source memory.

Though few in number, fMRI studies of item memory and source memory have produced very consistent results. Two studies used words [32,38] and one study used objects [33]. Across studies, item memory was associated with activity in the right prefrontal cortex and source memory was associated with activity in the left prefrontal cortex. Of note, fMRI studies of either item memory or source memory have not generally isolated the processes associated with successful memory retrieval from those associated with memory retrieval effort. In the present study, this issue was addressed by only reporting results of comparisons between correct responses (e.g. correct item memory trials compared to correct rejection trials). This type of analysis has been conducted in a remember/know paradigm [17], where remember judgments, compared to know judgments, were associated with left prefrontal activity. The similarity between these results and source memory results might be expected, as remember judgments have been associated with memory for specific contextual details [54].

The purpose of the present investigation was to better delineate the neural distinction between item memory and source memory. To more purely assess aspects of memory, without the neural activity associated with the processing of meaningful stimuli (e.g. words or objects), abstract visual shapes were used. We found distinct neural substrates associated with item memory and source memory in both the prefrontal cortex and the medial temporal lobe.

2. Materials and methods

2.1. Participants

Eight right-handed adults (six females), ranging in age from 25 to 45 years, took part in the experiment. All participants had normal or corrected to normal visual acuity. After the nature of the experiment, which had been approved by the Johns Hopkins internal review board, was fully comprehended by each participant, written consent was obtained before the experiment commenced.

2.2. Stimuli and tasks

Abstract visual shapes, similar to those used to study visuospatial processing [22,23,50], were selected as stimuli in an effort to minimize the potential confounds of semantic processing or differences in familiarity during memory encoding and retrieval.

Each participant completed one item memory run and two source memory runs. During the encoding phase of all runs, 10 shapes were serially presented in a pseudorandom sequence on either the left or right side of the screen for 4.5 s, with an inter-trial interval of 5 s (Fig. 1). At the beginning of each encoding phase, participants were visually presented with the instructions ‘‘Remember each shape and which side of the screen it is on’’ for 10 s. Participants were not informed as to the type of retrieval task that would follow the encoding task to ensure that similar encoding strategies would be used across runs thus eliminating encoding differences as a potential confound during memory retrieval. Shapes were not repeated across runs.

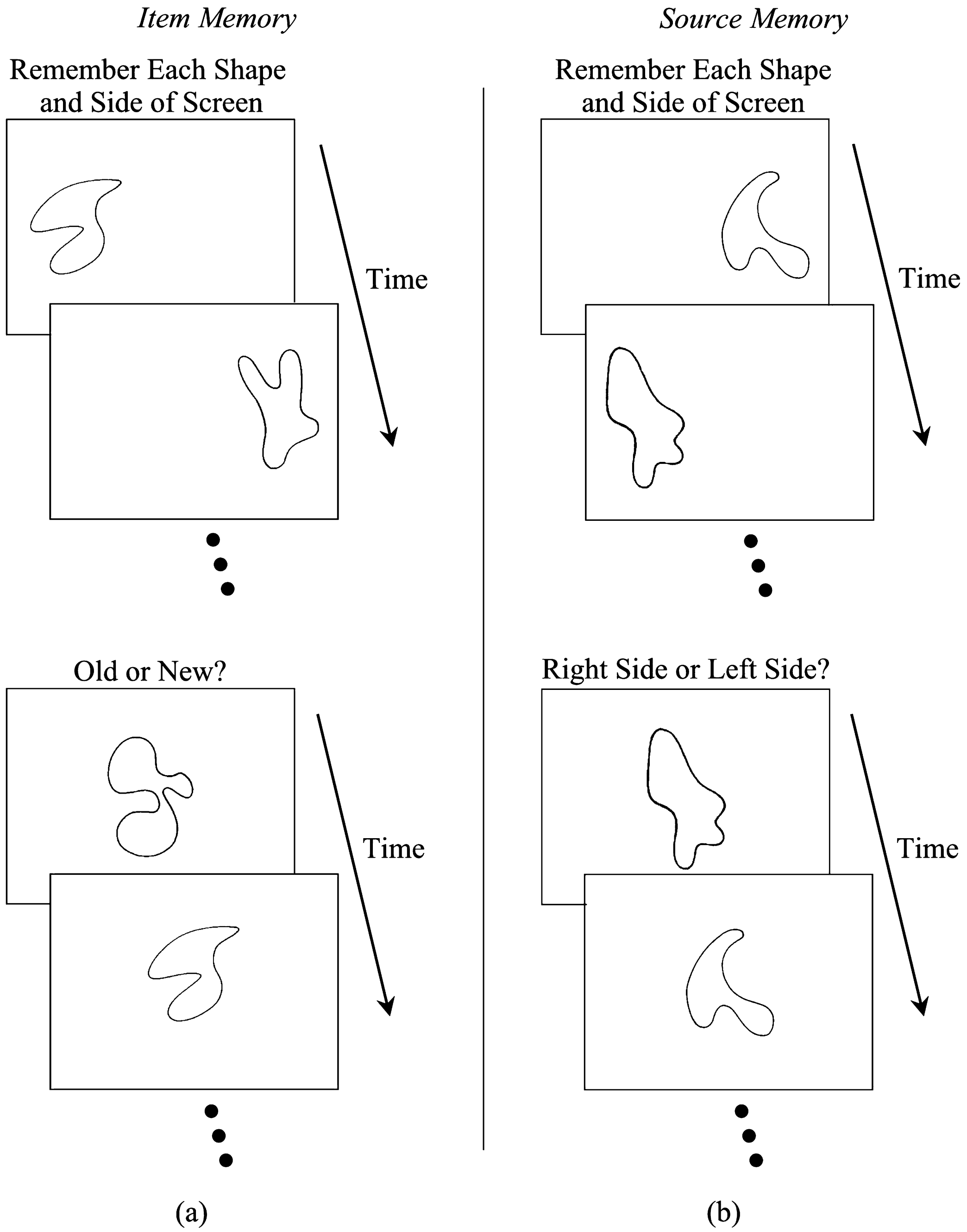

Fig. 1. Prototypical stimuli and tasks used in the present study. Depiction of the encoding phases, in the top half of the figure, and the retrieval phases, in the bottom half of the figure. Besides using unique stimuli for each set, the encoding procedure was identical for item memory and source memory runs; participants were presented with abstract shapes on either the left or right side of the screen. (a) During the retrieval phase of an item memory run, shapes from the encoding phase and new shapes were presented in the center of the screen. Participants indicated whether each shape was previously presented or new. (b) During the retrieval phase of a source memory run, only shapes from the encoding phase were presented. Participants indicated the side of the screen on which each shape had been presented.

During the retrieval phase of an item memory run, participants were first visually presented with instructions, for 10 s, to press a button in their right hand if they had seen the shape previously and press a button in their left hand if the shape was new. The 10 shapes presented during encoding in addition to 10 new shapes were serially presented in the center of the screen, in pseudorandom order, for 4.5 s with an inter-trial interval of 8.2 s (Fig. 1a). During the retrieval phase of a source memory run, only the 10 shapes presented during the preceding encoding phase were presented using the protocol just described (Fig. 1b). Participants were visually instructed, for 10 s, to press a button in their right hand if the shape was previously presented on the right and their left hand if the shape was previously presented on the left.

2.3. fMRI

2.3.1. Data acquisition

All images were acquired using a Phillips 1.5-Tesla ACS-NT scanner with a receive-only end-capped quadrature birdcage head coil. T1-weighted high-resolution anatomic images were acquired using an SPGR sequence (TR=20 ms; TE=4.6 ms; flip angle=30°; phase encoding=right to left; matrix=256×256; field of view=240 mm; slice orientation=axial; number of slices=100; slice thickness=1.4 mm, no gap). T2*-weighted functional images were acquired using an EPI sequence (TR=1000 ms; TE=50 ms; flip angle=70°; phase encoding=right to left; matrix=64×64; field of view=240 mm; slice orientation=axial oblique; number of slices=15; slice thickness=7 mm, no gap).

2.3.2. Pre-processing

Data pre-processing and analysis were conducted using SPM99 (Wellcome Department of Cognitive Neurology).

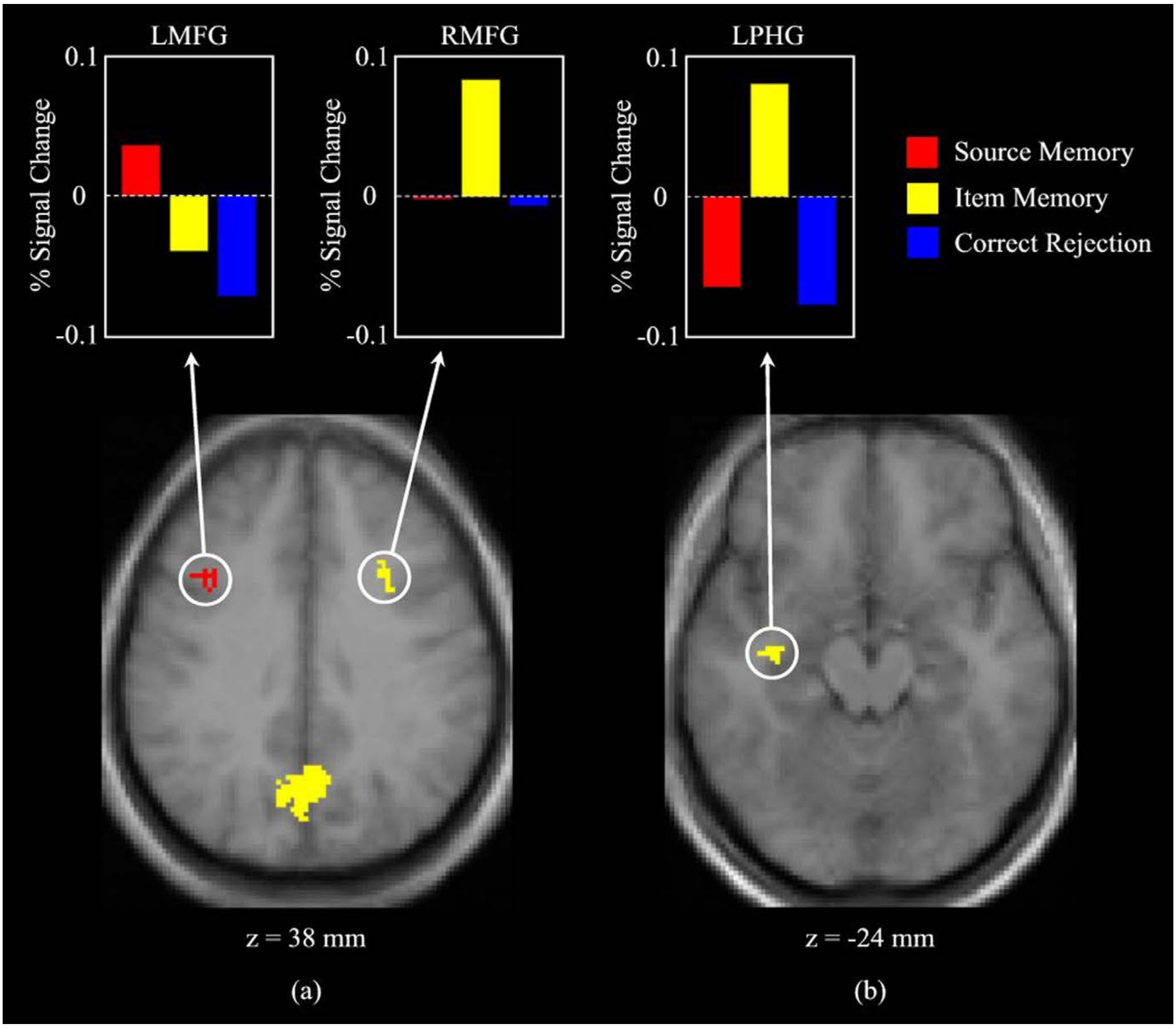

Fig. 2. Item memory and source memory activation results. Selected axial slices through group anatomic volume with overlay of functional activation associated with item memory, shown in yellow, and source memory, shown in red (anterior is toward the top and the left hemisphere is on the left). Within selected regions of interest, event-related activity associated with source memory, item memory, and correct rejection trials is shown in the upper part of the figure (color key to upper right). (a) The source memory vs. item memory contrast was associated with activity in the left middle frontal gyrus (LMFG, BA 9) and the item memory vs. correct rejection contrast was associated with activity in the right middle frontal gyrus (RMFG, BA 9) and the precuneous (BA 7). (b) The item memory vs. correct rejection contrast was associated with activity in the left parahippocampal gyrus (LPHG, BA 36).

Functional data were slice-time corrected, motion corrected, normalized to a standard template (which included resampling at 2 mm isotropic resolution), and spatially smoothed with a 7.5 mm full-width half maximum (FWHM) Gaussian kernel. Event-dependent high-pass filtering was used whereby the cutoff period, in seconds, was twice the longest interval between successive occurrences of the most frequent event. No low-pass filtering was used.

Anatomic data were normalized to a standard template and then averaged over all participants using custom software written in MATLAB (The MathWorks Inc., Natick, MA, USA). All results of the functional analysis were overlaid onto this average anatomic image for display.

2.3.3. Analysis

Only data from the retrieval phase of the task were analyzed. To ensure the results would be representative of all participants, a random-effect analysis was conducted [10–12]. Specifically, individual participant analyses were conducted first, and only those results that were statistically consistent across participants are reported.

An event-related approach was used where all occurrences of a particular event type were modeled using a standard hemodynamic response function. During the item memory retrieval phase, a shape from the encoding phase could be remembered (hit) or not remembered (miss) while a new shape could be recognized as new (correct rejection) or falsely recognized as old (false alarm). During the source memory retrieval phase, the spatial location could be remembered (hit) or not remembered (miss/false alarm). For each participant, the hemodynamic response model for the six event types were entered into a general linear model. In addition, the mean activity for each run was modeled.

Contrasts were restricted to those of theoretical interest. To assess the neural regions associated with item memory, item memory hits were contrasted with correct rejections (the reverse contrast was also used to ascertain item memory related deactivations). As source memory involves both item recognition and memory for spatial context, source memory related activity was obtained by contrasting source memory hits with item memory hits (the reverse contrast was also used to characterize item memory-specific activity).

After obtaining the contrasts of parameter estimates for all participants, a one-sample t-test was used to assess the consistency of the result across participants at each voxel. An individual voxel threshold of $P=0.01$ ($t=3$) was used, uncorrected for multiple comparisons. To enforce an a priori threshold of $P=0.05$, corrected for multiple comparisons, a cluster extent threshold was used in all statistical contrasts reported. The cluster extent threshold was obtained by simulating whole-brain fMRI activation using custom software written in MATLAB. In a single simulation, by modeling the entire functional image matrix ($64\times64\times15$ voxels), assuming a type I error voxel activation probability of 0.01, and smoothing the activation map by convolution with a 3-dimensional 7.5-mm FWHM Gaussian kernel, the size of each contiguous cluster of voxels was determined. After 10,000 simulations, the probability of each cluster size was determined and the cluster extent that yielded $P<0.05$, i.e. 98 contiguous resampled voxels, was selected for use in voxel extent thresholding.

3. Results

Behavioral accuracies for item memory hits (79±6%, one standard error reported), correct rejections (79±6%), and source memory hits (77±3%) indicate that the task was not too easy, nor too difficult. In addition, the similarity in accuracy across trial types argues against difficulty related differences that could potentially contaminate the results.

Fig. 2 illustrates the activity associated with item memory and source memory. Consistent with a large body of experimental evidence, item memory was associated with activity in the right middle frontal gyrus, precuneous, and left parahippocampal gyrus. A complete set of activations associated with each contrast, including the Talairach coordinates [52] of maximal activation is shown in Table 1. Item memory was also associated with left pre-central gyrus activity, which can be attributed to motor response,[2] left extrastriate activity, and left middle temporal gyrus activity. There were no substantial item memory deactivations, as the correct rejection vs. item memory contrast yielded only motor related activity (i.e. right pre-central gyrus, left caudate, and right putamen).

In comparison to item memory, source memory was associated with activity in the left middle frontal gyrus (Fig. 2). Moreover, source memory elicited activity in the left superior frontal gyrus, the left inferior frontal gyrus, right superior frontal gyrus, and bilateral superior temporal cortex. The item memory vs. source memory contrast revealed activity in the medial superior frontal gyrus (BA 6) and left pre-and post-central gyrus, which can be attributed to motor response, and left superior parietal

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[2] One caveat that deserves mention is the difference in motor response between event types that was inherent in the experimental design. Certain events were associated with the response of one hand while other events were associated with the response of the other hand. For example, correct item memory trials were associated with right-hand responses while correct rejections were associated with left-hand responses. As such, a statistical contrast between item memory vs. correct rejection will not only yield neural regions associated with item memory but also produce neural regions associated with right-hand motor response. Fortunately, the neural regions associated with motor response are well known [25,28,29,35,36] including the basal ganglia, motor cortex, pre-motor cortex, and the supplementary motor area (in BA 4 and BA6), and these regions are distinct from those associated with memory retrieval.

Table 1
Neural activations associated with item memory and source memory

Region	BA	x	y	z	Z
Item memory vs. correct rejection					
Right middle frontal gyrus	9	32	23	41	3.63
Left pre-central gyrus	4	−30	−19	49	4.72
Right precuneous	7	4	−68	44	4.02
Left extrastriate cortex	18	−8	−52	6	3.89
Left middle temporal gyrus	21	−48	−18	−13	4.14
Left parahippocampal gyrus	36	−40	−17	−24	2.80
Correct rejection vs. item memory					
Right pre-central gyrus	6	40	−7	59	4.81
Right pre-central gyrus	4	36	−25	53	4.45
Left caudate	–	−12	4	7	5.05
Right putamen	–	22	4	−4	4.52
Source memory vs. item memory					
Right superior frontal gyrus	9	20	46	20	3.96
Left superior frontal gyrus	9	−22	45	9	3.96
Left middle frontal gyrus	9	−42	21	38	3.37
Left inferior frontal gyrus	47	−28	21	−4	3.73
Right superor temporal sulcus	41	28	−23	10	3.82
Left superior temporal gyrus	39	−53	−61	21	3.95
Item memory vs. source memory					
Right superior frontal gyrus	6	2	2	46	3.61
Left pre-central gyrus	4	−20	−16	67	4.53
Left post-central gyrus	40	−63	−9	17	4.06
Left superior parietal lobule	7	−12	−69	55	4.53

BA refers to Brodmann Area and coordinates (*x*, *y*, *z*) are reported in Talairach space. Regions and coordinates reported refer to the most statistically significant voxel within a cluster.

lobule. Thus, besides the differences in motor activations, source memory involves bilateral prefrontal cortex activation, albeit more extensively left than right, and bilateral temporal cortex activation.

To delineate the pattern of activity within each selected region-of-interest, the mean event-related activity 4–5 s following stimulus onset is also reported (Fig. 2). Within the left middle frontal gyrus (LMFG), source memory was associated with an event-related increase in activity while item memory and correct rejection were associated with an event-related decrease in activity. This general pattern was consistent across all source memory activations in prefrontal cortex. Within the right middle frontal gyrus (RMFG), there was an item memory related increase in activity, but no source memory or correct rejection related decreases in activity. In the left parahippocampal gyrus (LPHG), there was an item memory related increase in activity in addition to source memory and correct rejection related decreases in activity. Thus, source memory and item memory were associated with event-related activity increases in their respective regions of activation, within which other event types produced either no change or event-related activity decreases.

4. Discussion

In the present study, item memory, as assessed by the item memory vs. correct rejection contrast, was associated with activity in right prefrontal cortex, parietal cortex, and the medial temporal lobe consistent with a large body of neuroimaging research [2–6,9,13–16,19,21,24,26,27,32,33,37,39–46,51,55–57]. Source memory, as assessed by the source memory vs. item memory contrast, was associated with left prefrontal cortex activity, which is consistent with previous neuroimaging results [17,30,32,33,38], and right prefrontal cortex activity, similar to one report [38]. Thus, across studies, the left prefrontal cortex appears to be most consistently active during source memory. Therefore, one distinction between item memory and source memory appears to be primary reliance on the right and left prefrontal cortex, respectively.

However, one reason to question the item memory hemispheric laterality effect in prefrontal cortex is based upon the direct statistical contrasts (Table 1). Specifically, the direct contrast between item memory and source memory yielded no prefrontal areas, indicating similar levels of activity in right prefrontal cortex, while the reverse contrast showed numerous prefrontal activations. These results indicate that source memory relies to some degree on similar regions in the right prefrontal cortex as item memory, but also involves additional prefrontal regions, most extensively in the left.

Of most importance, the direct statistical contrast between item memory and source memory, and vice versa, resulted in distinct neural regions associated with each of these cognitive functions. If item memory and source memory relied on similar activity within the same neural regions, no significant differences would have emerged. The distinction was further evidenced by the pattern of event-related activity within the regions of interest, showing item memory-specific activity in the right prefrontal cortex and left medial temporal lobe and source memory-specific activity in the left prefrontal cortex. If, for example, left middle frontal gyrus activity were associated with source memory and item memory, both event types would have resulted in an event-related increase in activity (in actuality, item memory evoked an event-related decrease in activity). Thus, the notion that item memory and source memory are qualitatively the same, and only quantitatively different is highly unlikely. Similar to others, right prefrontal cortex was found to be associated with item memory and left prefrontal cortex with source memory (Fig. 2). Moreover, only item memory was associated with activity in the medial temporal lobe.

The present results replicate and extend previous source memory results. First, using abstract visual shapes, we replicated the distinction between right prefrontal cortex specific activity associated with item memory and left prefrontal cortex specific activity associated with source memory. In addition, we found that only item memory was associated with activity in the medial temporal lobe. Taken together, these results provide strong evidence that item memory and source memory rely on distinct neural substrates.

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