Effects of task orientation on subsequent source memory as revealed by functional MRI

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Research Highlights
(1) Source memory effects in the prefrontal cortex and hippocampus were modulated by task orientation.
(2) Item memory effects in the prefrontal cortex were modulated by task orientation.
(3) The hippocampus contributes to the intentional encoding of item-source associations.
(4) The prefrontal cortex is biased toward encoding and storing information to which attention is directed.
(5) The neuromechanisms underlying task orientation effects on source memory depend on various activation modes in the right prefrontal cortex and hippocampus.

Abstract
Episodic memories are composed of various interrelated elements, including those specific to items of central interest and those pertaining to related features, such as the color, shape, size, spatial location, temporal order, and media or modalities of presentation. Memory about a core item (such as a word, object, or picture) is called item memory while memory about the context or related features of a core item is defined as source memory. What determines which sources within an episode are successfully remembered is of particular interest to researchers. Behavioral evidence suggests that the orientation of a memory task influences whether the related source of the item will be remembered later. This study explored changes in the hippocampus and prefrontal cortex while participants completed two tasks: an item-oriented task and a source-oriented task. We used functional MRI to investigate the neural mechanisms by which task orientation influences source encoding. We found that subsequent source memory effects in the right prefrontal cortex and hippocampus were modulated by task orientation, whereas task orientation modulated item memory effects in the prefrontal cortex. These findings highlight the possibility that the hippocampus contributes to the intentional encoding of item-source associations, whereas the prefrontal cortex is biased toward processing information to which attention is directed.

Key Words
neural regeneration; neuropsychology; learning; source memory; task orientation; hippocampus; prefrontal cortex; functional MRI; grants-supported paper; neuroregeneration

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INTRODUCTION

Episodic memories are composed of various interrelated elements, including those specific to items of central interest and those pertaining to related features, such as the color, shape, size, spatial location, temporal order, and media or modalities of presentation\(^1\text{-}^3\). Memory about a core item (such as a word, object, or picture) is called item memory while memory about the context or related features of a core item is defined as source memory.

What factors influence the successful retrieval of various sources within an episodic memory? Several neuroimaging studies have reported that during encoding, neural activity in the frontal, occipital, and medial temporal regions differs according to whether the related source of the item was remembered in a subsequent memory test\(^3\text{-}^{13}\). These differences in neural activity are often described as "subsequent source memory effects"\(^14\). New findings about subsequent source memory effects may have implications for understanding the process of memory formation and the causes of various memory disorders.

Precisely how subsequent source memory effects are modulated by the cognitive operations engaged during a memory task has not yet been established. For instance, although behavioral studies have found improved source memory when emphasizing the relevant relationships between a source and item\(^15\text{-}^{18}\), the neural mechanism underlying this phenomenon is unknown. Kuo and Van Petten\(^18\) described the effects of study task orientation on source memory. In their experiment, participants were required to perform two tasks: an item-oriented task and an integrative task (source-oriented task). In the item-oriented task, participants judged whether items depicted in drawings were larger or smaller than those on a computer monitor. Source-item conjunctions were not part of the task requirements. In the integrative task, participants judged whether item-color conjunctions were appropriate (red stop sign) or inappropriate (blue apple). The researchers found that source memory was enhanced by 14% in the source-oriented task. Thus, it appears that after initial encoding, subsequent memory for a source is directly modulated by the orientation (item or source) of the task.

Although this link has yet to be firmly established, recent investigations have uncovered new information about the neural substrates of attentional control as well as the modulatory effect of attention on subsequent item memory effects\(^19\text{-}^{24}\). For instance, the prefrontal cortex is known to be critically involved in memory encoding\(^19\text{-}^{22}\). Specifically, activity in the dorsolateral prefrontal cortex during a study task is attenuated by the conditions of a secondary task (hard, easy, or no secondary task)\(^24\). Also, subsequent item memory effects (the differences in neural activity between recognized items and forgotten items) in the left prefrontal cortex and the left anterior hippocampus is evident in the easy secondary task condition, but not in the hard secondary task condition\(^23\). Given that task orientation determines how one should focus their attention on upcoming events (i.e., attend to items or item-source conjunctions\(^18\)), it is possible that the subsequent source memory effects in the above-mentioned brain regions are modulated by task orientation.

This event-related functional MRI study was designed to investigate the neural mechanisms by which task orientation influences source encoding, i.e., whether subsequent source memory effects are modulated by task orientation. Participants were first scanned while they studied a list of colored objects under two task conditions. In the item-oriented task, participants judged whether the items depicted in pictures could be animate in reality. In the source-oriented task, participants judged whether the item-color conjunctions were plausible (red hat) or not (blue apple) in reality. After scanning, participants took a subsequent memory test where they first made a decision about whether they had seen the item previously, and then, for familiar items, they gave a source (color) judgment. We predict that the subsequent source memory effects in the
prefrontal cortex and hippocampus (neural activity elicited by recognized items with accurate versus inaccurate source judgments) will be modulated by task orientation.

RESULTS

Quantitative analysis of participants
All 15 participants were included in the final analysis.

Behavioral results
In the memory test, the learning items were recognized at a rate of 76 ± 10% for the source-oriented task and 68 ± 13% for the item-oriented task. The hit rates in the source-oriented task were significantly higher than those in the item-oriented task (t(14) = 3.98, P < 0.01). Lures were correctly rejected at a rate of 85 ± 14%. The source memory accuracy (number of correct source trials as a proportion of correctly recognized trials) in the source-oriented task (0.54 ± 0.16) was significantly higher than that in the item-oriented task (0.45 ± 0.14) (t(14) = 3.49, P < 0.01). However, the source memory accuracy in both tasks was significantly above the chance level of 33% (source-oriented: t(14) = 4.95, P < 0.01; item-oriented: t(14) = 3.53, P < 0.01). Therefore, there were 20 ± 8 Miss, 29 ± 10 Item Only, and 35 ± 13 Source Correct encoding trials in the source-oriented condition and 27 ± 11 Miss, 30 ± 6 Item Only, and 27 ± 12 Source Correct encoding trials in the item-oriented condition (Table 1). The source accuracy for implausible items was not significantly different from that of plausible items (t(14) = 1.04, P > 0.05).

| Table 1 | Judgment of previously learned objects in the memory test |
|---------|----------------------------------------------------------|
| Item    | SM | IO | Miss | FA | CJ |
| Item-oriented task | 27±12 | 30±6 | 27±11 |
| Source-oriented task | 35±13 | 29±10 | 20±8 | 13±12 | 71±14 |
| New items | A total of 15 participants completed the memory test; each task contained 84 items. The results are expressed as mean ± SD. SM: Appeared, correct color; IO: appeared, wrong color; Miss: did not appear; FA: appeared; CJ: did not appear. |

Functional MRI indicators of subsequent memory effects
Source memory
We first identified regions showing subsequent source memory effects by collapsing the data across tasks and contrasting Source Correct with Item Only trials. Consistent with previous studies, several regions, including the left superior frontal gyrus/middle frontal gyrus and the inferior frontal gyrus, exhibited subsequent source memory effects (Table 2, Figure 1).

Item memory
Regions demonstrating subsequent item memory effects were identified by contrasting Item Only with Miss trial data. Consistent with previous studies, several regions, including the bilateral fusiform cortex, exhibited subsequent item memory effects (Table 2).

Subsequent source memory effects modulated by task orientation
To examine regions showing enhanced source memory effects during the source-oriented task relative to the item-oriented task, we computed an interaction contrast [(Source Correct – Item Only)source-oriented – (Source Correct – Item Only)item-oriented]. This analysis revealed activity in several regions, including the right superior frontal gyrus, right hippocampus, and right superior orbital gyrus (Table 3, Figure 2). These results supported our prediction that item memory effects in the dorsolateral and ventral prefrontal cortex and the hippocampus were attenuated in the item-oriented task versus the source-oriented task. The beta estimates of the Source Correct and Item Only trials in the two tasks were further extracted from the right superior frontal gyrus, right hippocampus, and right superior orbital gyrus region of interest data to calculate the contrast values of Source Correct versus Item Only trials (Figure 2). A follow-up analysis of the contrast values demonstrated that the subsequent source memory effects in the above three clusters were significantly larger than zero for the source-oriented task (ts < 2.14, Ps < 0.05), but were smaller than zero for the item-oriented task. Moreover, the subsequent source memory effects in these regions were significantly larger in the source-oriented task than in the item-oriented task (ts < 2.83, Ps < 0.02). The reverse contrast revealed no significant activation.

Subsequent item memory effects modulated by task orientation
In contrast to the source-oriented task, attention was directed toward the item in the item-oriented task. We investigated whether item-orientation, compared with source-orientation, would promote subsequent item memory effects in the prefrontal cortex. To this end, we conducted an interaction contrast [(Item Only – Miss)item-oriented – (Item Only – Miss)source-oriented]. This analysis revealed activity in several regions, including the left middle frontal gyrus, indicating a critical role for the prefrontal cortex in attentional control during memory encoding (Table 3, Figure 3). The reverse contrast re-
vealed no significant activation.

Table 2  Brain regions showing subsequent memory effects

| Region                      | Brodmann area | Peak activation | t value | Voxels |
|-----------------------------|----------------|-----------------|---------|--------|
| Source memory               |                |                |         |        |
| L Superior frontal gyrus    | 8              | −20             | 24      | 62     | 4.13  | 120   |
| L Middle frontal gyrus      | 8              | −28             | 30      | 54     | 4.00  | 30    |
| L Inferior frontal gyrus    | 48             | −36             | 34      | 8      | 3.67  | 30    |
| Item memory                 |                |                |         |        |
| L Fusiform gyrus            | 20             | −42             | −38     | −22    | 6.21  | 753   |
| R Fusiform gyrus            | 20             | 40              | −38     | −22    | 4.44  | 597   |
| L Paracentral lobule        | 4              | −10             | −30     | 70     | 4.42  | 251   |
| R Supramarginal gyrus       | 1              | 62              | −24     | 48     | 4.23  | 96    |
| R Middle occipital gyrus    | 19             | 34              | −70     | 34     | 4.21  | 252   |
| L Superior parietal lobule  | 7              | −16             | −60     | 46     | 4.12  | 56    |
| L Middle occipital gyrus    | 19             | −26             | −72     | 28     | 3.78  | 47    |
| R Inferior parietal lobule  | 7              | 32              | −50     | 52     | 3.63  | 28    |

A voxel-wise threshold P < 0.001 (uncorrected) was used in the whole brain volume search. Clusters with 20 or more significant re-sampled voxels are reported. L: Left hemisphere; R: right hemisphere. Italics represent LOCAL MAXIMUM in the same CLUSTER.

DISCUSSION

The aim of the present study was to elucidate the neural mechanisms by which task orientation influences the probability that source information is encoded into an integrated memory trace. Consistent with previous studies[18], our behavioral results indicate that source memory performance was greater in a source-oriented task. Our functional MRI findings show that subsequent source memory effects in the right prefrontal cortex and hippocampus were modulated by task orientation.

Subsequent source memory effects were evident in the hippocampus following the source-oriented task, but not the item-oriented task. However, this findings stands in marked contrast to much literature on the general role of the hippocampus in source encoding, regardless of study task[45, 78, 25]. This raises the question of why, in the present study, the right hippocampus showed subsequent source memory effects that were limited to the source-oriented task. A plausible explanation is that, like in the source-oriented condition in the present study, item-source associations were deeply encoded in nearly all the studies in the literature. These studies, which generally include a source-oriented condition similar to that used in the present study, either directly used the study task (such as a size task) as the source, used an oriented study task as the source (such as the item-source color conjunction judgment task used in the present study), or explicitly instructed participants to remember the source. Our findings highlight the possibility that subsequent source memory effects in the hippocampus are present only when item-source associations are well learned. Although previous studies repeatedly demonstrate the role of the hippocampus in binding items to their related source, we extended these results by restricting the contribution of the hippocampus to the intentional encoding of item-source associations (the definition of intentional encoding[26]). It should be noted that we used an intrinsic aspect of an item, i.e., color, as the source[27]. Further investigation is needed to examine the effects of task orientation on the encoding of external sources, such as location or temporal order.

Although prefrontal subsequent source memory effects were attenuated in the item-oriented task, subsequent item memory effects in the prefrontal cortex were enhanced. This evidence of a tradeoff of prefrontal activities could have implications for understanding the role of the
prefrontal cortex during task-orientation modulation of memory encoding.

Table 3  Regions showing subsequent memory effects modulated by task orientation

| Region | Brodmann area | Peak activation | t value | Voxel |
|--------|---------------|-----------------|---------|-------|
| (Source Correct – Item Only) source-oriented – (Source Correct – Item Only) item-oriented | | X | Y | Z | |
| L Calcarine gyrus | 17 | –8 | –60 | 6 | 5.14 | 561 |
| R Fuss | 17 | 20 | –35 | 16 | 4.10 | 295 |
| R Superior frontal gyrus | 6 | 20 | –14 | 72 | 4.94 | 58 |
| R Middle temporal gyrus | 21 | 60 | 2 | –20 | 4.64 | 32 |
| L Rolandic operculum | 48 | –48 | –18 | 16 | 4.57 | 93 |
| L Temporal pole | 38 | –54 | 14 | –16 | 4.52 | 56 |
| R Hippocampus | 20 | 36 | –24 | –20 | 4.17 | 25 |
| R Superior orbital gyrus | 11 | 26 | 36 | –14 | 4.16 | 58 |
| L Lingual gyrus | 37 | –22 | –48 | –4 | 4.07 | 59 |
| (Source Correct – Item Only) item-oriented – (Source Correct – Item Only) source-oriented | No regions |
| (Item Only – Miss) source-oriented – (Item Only – Miss) item-oriented | No regions |
| (Item Only – Miss) item-oriented – (Item Only – Miss) source-oriented | L Middle occipital gyrus | 18 | –18 | –94 | 2 | 4.35 | 167 |
| L Temporal pole | 36 | –52 | 16 | –16 | 4.08 | 28 |
| R Middle frontal gyrus | 9 | –34 | 12 | 50 | 3.75 | 23 |
| R Inferior occipital gyrus | 19 | 38 | –74 | –4 | 3.69 | 23 |

A voxel-wise threshold $P < 0.001$ (uncorrected) was used in the whole brain volume search. Clusters with 20 or more significant re-sampled voxels are reported. L: Left hemisphere; R: right hemisphere. Italics represent LOCAL MAXIMUM in the same CLUSTER.

Figure 2  Brain regions showing subsequent source memory effects modulated by task orientation.

(A) The analysis revealed clusters located in the right superior frontal gyrus (R.SFG), right hippocampus (R.HIPP), and right superior orbital gyrus (R.SOG).

(B) Average contrast values of Source Correct versus Item Only trials across the above three clusters in the two tasks. Subsequent source memory effects were evident in the dorsolateral and ventral prefrontal cortex and the right hippocampus for the source-oriented task, but were absent in these regions during the item-oriented task. Data are expressed as mean ± SD. $^aP < 0.05$, $^bP < 0.001$ indicates the difference between the contrast values (Source Correct – Item Only) in the source-oriented task, whereas $^cP < 0.05$, $^dP < 0.001$ indicates the distance of the contrast values from zero for the source-oriented task. These analyses were done using a t-test.

Figure 3  Brain regions showing subsequent item memory effects modulated by task orientation.

The analysis revealed clusters (circle) located in the left middle frontal gyrus (L.MFG). Based on this pattern of prefrontal activities, we propose that the prefrontal cortex is biased to process the information to which attention is directed. Indeed, a previous study demonstrated that as the difficulty of a secondary task increased, activity related to the study task declined and activity corresponding to the secondary task increased in the prefrontal cortex. This was likely due to attention being directed away from the first task and toward the second. Extending the attentional control perspective of the prefrontal cortex, enhanced prefrontal activity modulated by attention may further support the formation of memories about the attended information. By this argument, subsequent memory effects in the prefrontal cortex should be enhanced for
whatever information is attended to. Although the prefrontal cortex has generally been implicated in attentional control during encoding, we suggest that these results can be extended by relating prefrontal cortex activity to the attentional modulation of memory formation.

One previous neuroimaging study investigated whether subsequent source memory effects were sensitive to the cognitive operations engaged during study. Consistent with the higher memory performance associated with a semantic vs. nonsemantic encoding task,[28-30] Park and colleagues[14] revealed that subsequent source memory effects were influenced by whether the encoding task was semantic. Thus, we chose to assess the modulation of subsequent source memory effects by other cognitive operations engaged during study, i.e., task orientation. Our investigation of the effects of task orientation on subsequent source memory effects may provide further evidence for the notion that subsequent source memory effects are sensitive to the cognitive operations engaged during study.

In summary, the results of the present study suggest that: (1) the hippocampus contributes to intentional encoding of item-source associations; (2) the prefrontal cortex is biased to encode and store the information to which attention is directed; (3) subsequent source memory effects are sensitive to the cognitive operations engaged during study.

SUBJECTS AND METHODS

Design
A functional MRI event related design.

Time and setting
Experiments were conducted in 2010 at the Shanghai Key Laboratory of Functional Magnetic Resonance, China.

Subjects
Fifteen right-handed volunteers from the Fudan University and East China Normal University communities participated in this study (seven males and eight females, 20–30 years of age, mean age 23.00 ± 2.59 years). All participants had normal or corrected-to-normal vision and none reported a significant abnormal neurological history. All participants gave informed consent before scanning and were paid ¥50 RMB for their involvement. The study was conducted in accordance with the Declaration of Helsinki.

Methods

Materials
252 grayscale pictures of common objects were randomly selected from the revised Snodgrass and Vanderwart’s object pictorial set[31]. Of these, 168 were randomly selected to serve as learning items, with 84 in each task condition, and 84 served as lures during the memory test. The learning items in each condition were randomly colored one of three different colors (red [RGB: 255, 0, 0], green [RGB: 0, 150, 0] or blue [RGB: 0, 0, 255]), with 28 items in each color. Half of the learning items were assigned an appropriate color for the object depicted in the image, 42 for each task. The complexity, agreement, imagery, and familiarity of the items were counterbalanced across the different conditions and different colors.

Procedure
Before initiating the experiment, all participants were told that their memory for each item and its color would be tested at a later time, and that their main task during the encoding phase was to make the requested judgments according to task cues. They were asked not to do anything after each judgment, such as try to remember the item and its color or complete the other task. After the encoding phase, all participants indicated that they did not have enough time to perform another task within the available 3 seconds, and all reported that they had followed our instructions. During the encoding phase, 168 learning items were presented sequentially to each participant who were in the functional MRI scanner. For each encoding trial, a 1-second task cue was presented, followed by a 3-second colored item (Figure 4).

Figure 4 Experimental design.
(A) Scanned encoding phase. The task cues were varied between trials, and participants were instructed to complete a source-oriented task or an item-oriented task according to the task cue.
(B) Subsequent memory test. For items judged to be “old” in the item memory test, source memory for color was further assessed.

s: Second.
The task cues were varied between trials. Participants were asked to judge whether the given color of an item was plausible in reality when they saw “PLAUSIBLE?” displayed on the screen (source-oriented task). Similarly, they were asked to judge whether an item would be animate in reality when they saw “ANIMATE?” (item-oriented task). Responses were given via a magnet-compatible button box placed below each participant’s right hand. The encoding trials were intermixed with 4-second null trials (42 trials in all), during which a black fixation cross was presented. The trials were separated by a jittered inter-stimulus interval (a fixation cross) that was 0–1 second long. Approximately 10 minutes after the encoding phase, participants were given a self-paced memory test outside the scanner. 252 gray objects were presented sequentially in a random order. Participants were asked to indicate whether each object was old (presented during the encoding phase) or new (not presented during the encoding phase). If they responded “old”, they were then asked to indicate the original color of the object.

**Functional MRI scan**

Imaging was carried out using a 3.0 T Siemens scanner (Siemens, Malvern, PA, USA). Functional imaging was acquired using a gradient-echo echo-planar imaging sequence (repetition time = 2 200 ms, echo time = 30 ms, field of view = 220 mm², matrix size = 64 x 64). We acquired thirty-five slices that were parallel to the AC-PC line (slice thickness = 3 mm, gap = 0.3 mm). The first five volumes were discarded to allow for T1 equilibration. Before the functional run, a high-resolution structural image was acquired using a T1-weighted, multiplanar reconstruction sequence (repetition time = 1 900 ms, echo time = 3.42 ms, 192 slices, slice thickness = 1 mm, field of view = 256 mm², matrix size = 256 x 256).

**Functional MRI data analysis**

Data preprocessing was performed using Statistical Parametric Mapping software (SPM5, Wellcome Department of Cognitive Neurology, London, UK). During data preprocessing, all volumes were realigned spatially to the first volume of the first time series. The resulting images were re-sampled to 2 x 2 x 2 mm³ voxel size, spatially normalized to a standard echo-planar imaging template by using the “unified segmentation” function in SPM5 (based on the Montreal Neurological Institute reference brain), and smoothed with an 8 mm full-width, half-maximum isotropic Gaussian kernel.

**Statistical analysis**

Statistical analyses were performed using the general linear model implemented in SPM5. Encoding trials were first classified into three memory conditions according to each participant’s performance on the subsequent memory test: (1) learned items later judged to be new (Miss); (2) learned items later recognized without correct source judgment (Item Only); (3) learned items later recognized with correct source judgment (Source Correct). Then, the three types of encoding trials were modeled separately for each task (item-oriented task and source-oriented task). Thus, each encoding trial was modeled using a canonical hemodynamic response function and its temporal derivative, according to 3 x 2 conditions. All the encoding trials were modeled as 4-second long events using the onset time of the task cues. We used six regressors to model movement-related variance and one to model the overall mean during the entire encoding phase. Parameter estimates (beta estimates, see figures) for each regressor of interest at the single subject level were included in the flexible factorial group analysis. The beta estimates for each participant in the six conditions were entered into a flexible factorial analysis of variance. The relevant contrasts of interest between the two conditions were conducted using this analysis of variance model, while assigning weights of 0 to the remaining conditions.

**Contrasts**

Brain activation related to subsequent source memory effects was defined using (Source Correct – Item Only) contrast. Brain activation related to subsequent item memory effects was defined using (Item Only – Miss) contrast. Furthermore, the [(Source Correct – Item Only)source-oriented – (Source Correct – Item Only)item-oriented] contrast was computed to identify regions showing enhanced subsequent source memory effects in the source-oriented task relative to the item-oriented task. We set the voxel-wise P threshold at P < 0.001 (uncorrected) for the resulting statistical map and used a spatial-extent threshold of 20 contiguous re-sampled voxels. Anatomic labeling of activation clusters was performed using the Anatomy Toolbox[26]. Peak voxels were reported using Montreal Neurological Institute coordinates.

**Region of interest analyses**

To further test how task orientation affected subsequent source memory effects, specific activation clusters identified by [(Source Correct – Item Only)source-oriented – (Source Correct – Item Only)item-oriented] contrast were used to compute regions of interest. Regions of interest were defined as the activated clusters, and their parameter estimates were extracted to calculate the contrast...
values of Source Correct versus Item Only trials. This was done using the MarsBaR toolbox in SPM5.

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