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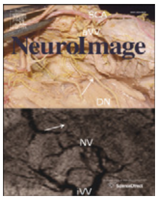

Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies

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ABSTRACT

The present study performed a quantitative meta-analysis of functional MRI studies that used a subsequent memory approach. The meta-analysis considered both subsequent memory (SM; remembered>forgotten) and subsequent forgetting (SF; forgotten>remembered) effects, restricting the data used to that concerning visual information encoding in healthy young adults. The meta-analysis of SM effects indicated that they most consistently associated with five neural regions: left inferior frontal cortex (IFC), bilateral fusiform cortex, bilateral hippocampal formation, bilateral premotor cortex (PMC), and bilateral posterior parietal cortex (PPC). Direct comparisons of the SM effects between the studies using verbal versus pictorial material and item-memory versus associative-memory tasks yielded three main sets of findings. First, the left IFC exhibited greater SM effects during verbal material than pictorial material encoding, whereas the fusiform cortex exhibited greater SM effects during pictorial material rather than verbal material encoding. Second, bilateral hippocampal regions showed greater SM effects during pictorial material encoding compared to verbal material encoding. Furthermore, the left hippocampal region showed greater SM effects during pictorial-associative versus pictorial-item encoding. Third, bilateral PMC and PPC regions, which may support attention during encoding, exhibited greater SM effects during item encoding than during associative encoding. The meta-analysis of SF effects indicated they associated mostly with default-mode network regions, including the anterior and posterior midline cortex, the bilateral temporoparietal junction, and the bilateral superior frontal cortex. Recurrent activity oscillations between the task-positive and task-negative/default-mode networks may account for trial-to-trial variability in participants' encoding performances, which is a fundamental source of both SM and SF effects. Taken together, these findings clarify the neural activity that supports successful encoding, as well as the neural activity that leads to encoding failure.

Introduction

The aim of the study

On any given day, we encounter and experience many events. Only some of these experiences are transformed into memories and can be subsequently remembered. A key line of inquiry for students of memory concerns the neural activity predicting events that will be remembered, as opposed to those that will be forgotten. The advent of event-related functional magnetic resonance imaging (fMRI) made an extremely powerful paradigm for addressing this question possible (Brewer et al., 1998; A. Wagner et al., 1998; A.D. Wagner et al., 1998). In this paradigm, participants are presented with a series of encoding stimuli (trials), and encoding stimuli are sorted into those that would be remembered versus those that would be forgotten, based on participants' performances on a subsequent memory test. The fMRI signal that is greater for the stimuli later remembered than for those later forgotten (called a *subsequent memory* [SM] effect) indicates the presence of neural activity that supports successful encoding. The reverse situation, i.e., greater fMRI signal for the stimuli later forgotten than for those later remembered (called a *subsequent forgetting* (SF) effect), indicates neural activity that interferes with successful encoding. The SM paradigm, with its "compelling" operational definition of successful encoding activity, was very popular throughout the past decade. To date, over 100 fMRI studies have used the SM approach (Uncapher and Wagner, 2009). The present study aimed to provide the first comprehensive meta-analysis of such literature. This meta-analysis, though restricted to the literature examining visual information encoding in healthy young adults, considered both SM and SF effects.

Abbreviations: ACC, anterior cingulate cortex; ALE, activation likelihood estimation; IFC, inferior frontal cortex; MTL, medial temporal lobe; PCC, posterior cingulate cortex; PFC, prefrontal cortex; PMC, premotor cortex; PPC, posterior parietal cortex; SF, subsequent forgetting; SM, subsequent memory; TPJ, temporoparietal junction.

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SM effects

In addition to the generic purpose of integrating results across studies, the present meta-analysis investigated several specific hypotheses regarding SM effects. After reviewing the relevant literature, comprising all published fMRI studies using an SM approach, we observed the emergence of two major study divisions. In one group of studies, the to-be-remembered material was verbal (e.g., words), while in the other group, it was pictorial (e.g., pictures, scenes, or faces). Further, one group of studies used *item-memory* tasks, while the other group used *associative-memory* tasks. In an item-memory task, participants try to remember an item with no other associated information, whereas in an associative-memory task, they must remember both an item and some information associated with that item, e.g., the context in which the item was presented (*item–context association*) or the fact that two items were presented as a pair (*item–item association*). Based on the reviewed studies' two divisions, the present meta-analysis compared (*i*) the SM effects of those studies using verbal versus pictorial material and (*ii*) the SM effects of those studies using item-memory versus associative-memory tasks. These comparisons cut across several critical issues relating to episodic encoding activity (see below).

Neuroimaging studies examining SM effects have traditionally focused on the prefrontal cortex (PFC) and the medial temporal lobe (MTL; Buckner et al., 2001; Fernandez and Tendolkar, 2001; Simons and Spiers, 2003). However, other brain regions, such as the fusiform cortex (Dickerson et al., 2007; Garoff et al., 2005; Kim and Cabeza, 2007), posterior parietal cortex (PPC; Sommer et al., 2005a,b; Uncapher and Rugg, 2009), and premotor cortex (PMC; Kao et al., 2005; Morcom et al., 2003) have been associated with SM effects. The multiple brain regions associated with SM effects may be broadly divided into three types, (*i*) content processing, (*ii*) storage, and (*iii*) attention. First, content processing regions mediate “the transformation of sensory input into internal representations that are interpreted or comprehended” (Paller and Wagner, 2002). The PFC, particularly the left inferior frontal cortex (IFC) and fusiform cortex are canonical examples of such regions (Kirchhoff et al., 2000). Second, storage regions bind the content representations into a durable memory representation, which the individual can access and retrieve into consciousness later. The MTL, and, in particular, the hippocampal formation, is widely recognized as the key structure in this function (Diana et al., 2007; Squire et al., 2004). Finally, attention during encoding selects an event among competing inputs and biases its “online” processing. A leading model of visual attention (Corbetta et al., 2002; Corbetta et al., 2008) has implicated a frontoparietal network, which includes the PMC and PPC, as a critical attention-coding structure. This three-component model does not represent a strict categorization of encoding-related activity, but rather some useful heuristics that can guide further research. For example, all regions displaying SM effects may have at least some relevance to storage.

As stated above, the present meta-analysis also compared SM effects between studies using verbal versus pictorial material. Historically, researchers have framed such comparisons and associated results in terms of hemispheric specialization or *laterality effects* (Golby et al., 2001; Kelley et al., 1998). This presupposes that verbal material encoding depends more on left- than right-hemispheric processing, whereas pictorial material encoding involves more right- than left-hemispheric processing. However, in the present meta-analysis, the primary purposes for this comparison were to address the following two hypotheses.

The first hypothesis states processing and successfully encoding either verbal or pictorial materials, which are canonically different in content, will emphasize different content-processing regions. Specifically, the left IFC, known to support controlled semantic/phonological retrieval and analysis (Badre and Wagner, 2007; Buckner et al., 1999), may be critical for successfully encoding verbal material, whereas the fusiform cortex, known to mediate visuoperceptual analysis and differentiation (Garoff et al., 2005; Kanwisher et al., 2001), may be critical for successfully encoding pictorial material.

Second, many SM studies have failed to find significant effects in the MTL (for a review, see Henson, 2005), despite the MTL's widely accepted critical role in storage operations. This failure remains largely unexplained, though researchers have attributed it to a low signal-to-noise ratio, susceptibility to MRI artifacts, or other nuisance factors. One relevant factor may be the widespread use of high frequency words, which participants had encountered numerous times prior to the studies, as encoding stimuli. Thus, participants had high pre-experimental familiarity with the verbal material, but not the pictorial material, used in SM studies. One influential view of the encoding process, known as the novelty-encoding hypothesis (Tulving et al., 1996), suggested the encoding system is biased toward processing novel, as opposed to familiar, information, because the system evolved to register information having high survival value. Thus, the second hypothesis addressed in this comparison is a novelty-encoding hypothesis predicting greater SM effects in the MTL during the encoding of pictorial material as compared to verbal material.

The present meta-analysis also compared SM effects between those studies using an item-memory task versus those with an associative-memory task. Historically, the distinction between item- versus associative-memory related to the distinction between *familiarity* (i.e., a feeling of “oldness” in the absence of contextual details) and *recollection* (i.e., vividly remembering specific contextual details). For example, a dual-process model of recognition memory suggested that associative recognition reflects recollection-based responses, whereas item recognition reflects both recollection- and familiarity-based responses (Yonelinas, 1997). The primary purposes for the present comparison of item- versus recognition-memory were to test the following two hypotheses.

First, prior discussions of the neural substrates for item- versus associative-memory predominantly focused on the MTL (Brown and Aggleton, 2001; Eichenbaum et al., 2007). A critical MTL function in episodic encoding is *binding* or *associating* multiple internal representations linked to an event, so the individual can retrieve the resultant representation as a whole (Davachi, 2006; Diana et al., 2007; Squire et al., 2004). Even though an item-memory task implicitly involves associating an item with spatiotemporal characteristics of the study episode, an associative-memory task makes stronger demands on associations, by requiring explicit item-context or item-item associations. Thus, the first hypothesis states MTL regions will show more robust SM effects during an associative-encoding task than during an item-encoding task.

Second, the distinction between item- and associative-memory, though traditionally focused on the MTL, may also involve differential SM effects in other brain regions (Kirwan et al., 2008). An associative-encoding task, as compared to an item-encoding task, typically makes greater content-processing demands, presenting multiple pieces of information and requiring relational processing among them. For example, an item–item association task may ask participants to rate how well two members of a pair (e.g., word–word) fit together (e.g., Qin et al., 2007) or to form a mental image incorporating both members of a pair and rate the quality of the image (e.g., Jackson and Schacter, 2004). By contrast, an item encoding task typically involves a relatively simple semantic (e.g., Is the word concrete or abstract?) or visual judgment (e.g., Is the face male or female?). Thus, the second hypothesis states content processing regions, such as left IFC and fusiform cortex, will exhibit stronger SM effects during associative versus item encoding.

Finally, encoding makes demands on attention, as shown by extensive behavioral evidence demonstrating that divided attention had negative effects on encoding (e.g., Craik et al., 1996). However, SM studies' explicit documentation of attention-related effects are relatively recent (Kensinger et al., 2003; Uncapher and Rugg, 2009;

Uncapher and Rugg, 2008). A recent meta-analysis (Uncapher and Wagner, 2009) of relevant literature focused on the PPC as mediating attention during encoding. However, mounting evidence suggests attention does not depend on a single region but rather on a network of regions that interact with each other (for a review, see Raz and Buhle, 2006). Thus, attention during encoding is unlikely to involve a single region, but rather multiple regions, which include the frontal as well as the parietal cortex. Both a leading visual attention model (Corbetta et al., 2002; Corbetta et al., 2008) and meta-analyses of attention and working memory studies (Owen et al., 2005; Wager et al., 2004) suggest perhaps a frontoparietal network, including both the PMC and PPC, supports attention during encoding. Thus, the present meta-analysis investigated whether the PMC and PPC regions showed significant SM effects, and, if so, whether the nature of the material (verbal versus pictorial) and/or the type of encoding (item versus associative) modulated these SM effects.

SF effects

Otten and Rugg (2001b) were the first to describe regions that showed SF effects, also called “reversed” or “negative” SM effects (Duverne et al., 2009; Weis et al., 2004). Their findings indicated SF effects were associated with widespread cortical regions, including the inferior parietal, medial parietal, posterior cingulate, and superior frontal cortices. At a minimum, these findings indicated that, to understand encoding, researchers must pay attention, not only to the positive correlates of remembering (SM effects), but also to the negative correlates of remembering (SF effects). Though relatively few fMRI studies have focused on SF effects, researchers generally accept the existence of cortical regions associated with SF effects (Park and Rugg, 2008; Shrager et al., 2008). Given the relatively limited number of available studies, the present meta-analysis focused mainly on *general* SF effects, involving the whole group, rather than *specific* SF effects restricted to a subgroup.

Multiple prior studies (Daselaar et al., 2004; Kim et al., 2010; Park and Rugg, 2008; Shrager et al., 2008; Turk-Browne et al., 2006) noted that the regions associated with SF effects tended to be components of what has been termed the *default-mode network*, which consists of the anterior and posterior midline cortex, the temporoparietal junction (TPJ), and the superior frontal cortex (Raichle et al., 2001). Based on this evidence, the present study examined whether, and to what extent, SF effects associate with default-mode network regions. The default-mode network was originally defined as the set of regions that are more active during the passive resting state than during attention-demanding cognitive tasks (Raichle et al., 2001; Shulman et al., 1997; Laird et al., 2009a). Researchers are currently debating these regions' functions, but increasing evidence suggests they mediate self-referential processing, or, more generally, internally oriented processing, as indicated by higher activations (or less deactivations) of these regions during imagining the future, conceiving the viewpoint of others (theory of mind), and autobiographical memory (for reviews, see Buckner and Carroll, 2007; Gusnard and Raichle, 2001; Spreng et al., 2009). Of greater direct relevance to SF effects, activation of these regions during an exogenous task may signal a wandering mind or momentary lapse of attention (Christoff et al., 2009; Mason et al., 2007; McKiernan et al., 2006; Weissman et al., 2006). For example, Christoff et al. (2009), using experience sampling during an fMRI task, found direct evidence for an association between activation of default-mode network regions and mind-wandering. Thus, activation of these regions during encoding may take neural resources away from the processes that lead to effective remembering.

Meta-analysis

The present study's principal methodology was a quantitative (i.e., statistical) meta-analysis of the relevant literature. A primary use for meta-analyses in neuroimaging is identifying significant concordances in brain activity patterns across a set of independent studies using a specific paradigm (Wager et al., 2007). The discernment of findings' convergences and divergences among studies is becoming increasingly important, albeit more difficult, as neuroimaging data continue to accumulate at a rapidly accelerating pace (Laird et al., 2009b). A quantitative meta-analysis provides an efficient and bias-free means of accomplishing this. The results of the present meta-analysis identify the brain regions most reliably associated with SM or SF effects and those most consistently exhibiting modulation of SM effects by the nature of the material and/or by the type of encoding. Of four recent meta-analyses of neuroimaging data that included SM studies, only one (Spaniol et al., 2009) used a quantitative approach; however, it employed a limited database (26 studies). The other three used a tabular method and focused exclusively on the MTL (Diana et al., 2007), PFC (Blumenfeld and Ranganath, 2007), or PPC (Uncapher and Wagner, 2009). Thus, the present study is the first quantitative meta-analysis of SM studies based on a comprehensive database and a whole-brain approach.

Materials and methods

Study selection

Multiple literature searches via Pubmed were completed in order to isolate all fMRI studies reporting SM or SF effects. Additionally, a reference list check of recent neuroimaging memory study reviews (Diana et al., 2007; Spaniol et al., 2009; Uncapher and Wagner, 2009) was done to identify relevant studies not found by the online database search. These search results were filtered to include only studies that (*i*) included healthy, young participants, (*ii*) presented encoding material via visual modality, (*iii*) performed whole-brain analyses, and (*iv*) reported coordinate-based data analyses. This search retrieved 74 studies. Of these, 15 reported both SM and SF effects, 57 reported only SM effects, and 2 reported only SF effects. Thus, the meta-analysis of SM effects covered 72 studies, and the meta-analysis of SF effects covered 17 studies. Appendix A lists the included studies, along with the number of participants, the nature of materials (verbal versus pictorial), the type of encoding (item versus associative), the study task, the retention interval, and the number of reported foci for each study.

Study groupings

Few dimensions by which to distinguish the selected studies, in order to ensure a meaningful analysis, were available. One such was whether the to-be-remembered material was verbal (e.g., words) or pictorial (e.g., pictures, scenes, or faces). Another dimension was whether the study task was an item- or an associative-memory task. In an item-memory task, participants try to remember an item with no other associated information. However, in one type of associative-memory task, they must remember both an item and its context, as initially presented (e.g., color, location), while in the other type, participants need to remember that two items previously appeared together (e.g., word–word). Crossing these two dimensions classified the selected SM studies into four subgroups: (*i*) the verbal-item subgroup ($n=31$), (*ii*) the pictorial-item subgroup ($n=16$), (*iii*) the verbal-associative subgroup ($n=12$), and (*iv*) the pictorial-associative subgroup ($n=13$). The selected studies for SF effects divided similarly into four subgroups: (*i*) verbal-item ($n=11$), (*ii*) pictorial-item ($n=2$), (*iii*) verbal-associative ($n=3$), and (*iv*) pictorial-associative ($n=1$). Within either SM or SF effects, this grouping was exclusive, so that no study belonged to more than one subgroup (see below). For each subgroup, Table 1 lists the number of studies, the number of participants, and the number of foci in the meta-analysis. A minor subset of the studies using an associative-encoding task (e.g., Sperling et al., 2003) presented both verbal and pictorial material within one trial (e.g., face–name). Both because a dichotomous grouping was advantageous in terms of statistical power, given the relatively limited number of available studies, and because a pictorial component of "mixed" material ought to yield richer stimulus encoding relative to a verbal component (e.g., Mintzer and Snodgrass, 1999; Nelson et al., 1976), we categorized this subset as part of the pictorial-associative subgroup.

Contrast selection

A subset of the selected studies reported multiple contrasts that could reflect different subgroups. Most such cases came from associative-memory studies (e.g., Kensinger and Schacter, 2006; Ranganath et al., 2004) reporting a contrast that probed associative SM (e.g., item-and-source SM>item-not-source SM) as well as item SM (e.g., item-not-source SM>forgotten). We excluded any contrast probing item SM from such studies, because (*i*) encoding tasks in these studies differed appreciably from those used in item SM studies, (*ii*) the distinction between associative- and item-memory in these studies tended to be conflated with the distinction between strong and weak memory (Kirwan et al., 2008; Squire et al., 2007), and (*iii*) including such contrasts would result in statistical dependencies (i.e., partially overlapping participants) between some subgroups. Another subset of the selected studies (e.g., Fliessbach et al., 2007; Otten and Rugg, 2001a) reported multiple contrasts reflecting the same subgroup, such as one for semantically encoded words and one for phonologically encoded words. If such multiple contrasts were statistically independent (i.e., based on completely different trials), they were included. If they were statistically dependent (i.e., based on overlapping trials), we selected the contrast associated with the largest number of reported foci. Yet another minor subset of the selected studies (e.g., Morcom et al., 2003) included both young and old participants and reported common, but not separate, contrasts for the two age groups. In such cases, we selected the common contrasts for meta-analysis. A final minor subset of the selected studies (e.g., Staresina and Davachi, 2006) reported a contrast using a regular statistical threshold and a similar contrast using a lower threshold; we excluded these latter contrasts, which usually targeted the MTL regions.

Data analyses

This study included three types of meta-analyses on SM effects. The first meta-analysis analyzed all studies together. The second was a *subgroup* meta-analysis examining each subgroup of studies separately: one each for the verbal-item, pictorial-item, verbal-associative, and pictorial-associative subgroups. The third, a *subtraction* meta-analysis, directly compared pairs of study subgroups. Testing the effects of the material's nature (verbal versus pictorial) unconfounded by the effects of encoding type (item versus associative) required two separate subtraction meta-analyses, one on the verbal-item subgroup versus the pictorial-item subgroup and the other on the verbal-associative subgroup versus the pictorial-associative subgroup. Likewise, investigating the encoding-type effects unconfounded by the material's nature required two more such meta-analyses, one on the verbal-item subgroup versus the verbal-associative subgroup and the other on the pictorial-item subgroup versus the pictorial-associative subgroup. The SF effects required only two meta-analyses, due to the limited number of available studies: one involving the whole group and the other restricted to the verbal item subgroup.

The higher statistical power to detect activation within a larger group of studies could have confounded these subtraction meta-analyses between groups of unequal size (Owen et al., 2005). To address this issue, we randomly selected a subsample of the larger group, thus making the comparison between two equally sized groups. For example, to compare SM effects between the verbal-item subgroup ($n=31$) and the verbal-associative subgroup ($n=12$), we randomly selected 12 studies for the comparison from the verbal-item subgroup. An alternative to such a random selection would be to select studies by *matching* on some variables, such as subject number and statistical threshold. We chose a random selection approach for the present study because it was more directly applicable, given the relatively limited number of studies available in most subgroups. The present subtraction analyses emphasized *simple* effects between the subgroups. Alternatively, one could emphasize *main* effects by collapsing across some subgroups. However, we chose to emphasize simple effects in the present study because this allows stricter control of the confounding between the two encoding variables (encoding material and encoding type) and informal observation of *interaction* effects via comparing sets of simple effects. The last point is important because meta-analytic techniques for fMRI data do not yet extend to formal analyses of interaction effects.

Table 1
Classification of studies included in the meta-analysis.

Subgroup	Number of studies	Number of participants	Number of foci
SM effects			
Verbal item	31	499	321
Pictorial item	16	264	237
Verbal associative	12	190	82
Pictorial associative	13	224	136
SF effects			
Verbal item	11	192	88
Pictorial item	2	32	5
Verbal associative	3	45	28
Pictorial associative	1	17	11

Meta-analytic techniques

For the activation likelihood estimation (ALE) meta-analysis (Laird et al., 2005), data processing was carried out via the GingerALE 1.2 program (www.brainmap.org). The "icbm2tal" transform (Lancaster et al., 2007) converted the Montreal Neurological Institute (MNI) coordinates to Talairach coordinates (Talairach and Tournoux, 1988). Individual studies' reported foci of maximal activation were modeled as peaks of 3D Gaussian probability distributions, with a full-width half-maximum (FWHM) of 10 mm. The 3D Gaussian distributions were then summed to create an ALE map estimating each voxel's activation likelihood across the entire set of studies. The ALE map's statistical significance was determined via a permutation test of randomly generated foci. Five thousand permutations were computed using the same FWHM value and the same number of foci as was used in computing the ALE map. For a subtraction meta-analysis, we carried out a permutation test of the difference between two equally sized groups. All permutation tests were thresholded by a false discovery rate (FDR) value of $p<0.05$ (Genovese et al., 2002) and by clusters of suprathreshold voxels exceeding 300 mm^3. The ALE maps in Figs. 1–5 are projected either onto an inflated population average landmark surface (PALS) via CARET software (Van Essen, 2005) or onto an International Consortium for Brain Mapping (ICBM) template (Mazziotta et al., 2001).

Results

SM effects

Table 2 and Fig. 1 show the ALE meta-analysis results for all included studies (see supplementary material available online (Supplementary Fig. 1) for a series of coronal views). The results indicated SM effects were mainly associated with five regions: the left

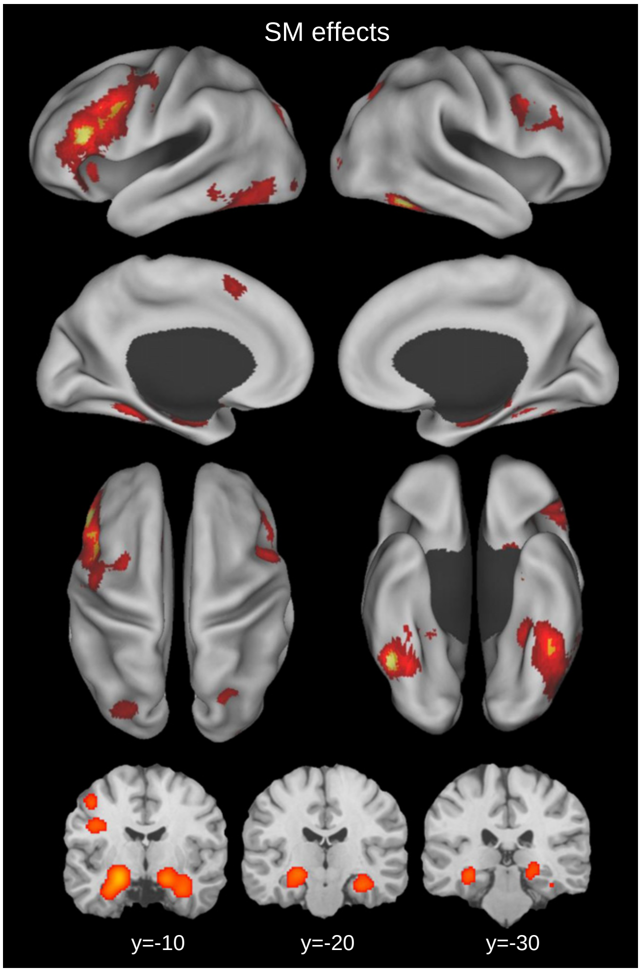

Fig. 1. Brain regions associated with significant SM effects in a meta-analysis involving all studies.

IFC, bilateral fusiform cortex, bilateral MTL, bilateral PMC, and bilateral PPC, in approximate order of decreasing spatial extent. The left IFC cluster (Brodmann area [BA] 44, 45, 46, 47) included both the anterior and posterior extent of the inferior frontal gyrus and extended into the middle frontal gyrus's ventral extent. The fusiform cortex clusters (BA 37) included both the anterior and posterior extent of the fusiform gyrus. The MTL clusters centered on the anterior hippocampal formation and extended into the amygdala. The PMC clusters (BA 6) centered on the junction of the precentral sulcus with the middle frontal gyrus. The PPC clusters (BA 7) centered on the intraparietal sulcus.

Table 3 and Fig. 2 present the results from the ALE meta-analysis for each subgroup of studies (see supplementary material available online (Supplementary Figs. 2–5) for a series of coronal views). First, the verbal-item subgroup mainly exhibited SM effects in the left IFC, left fusiform cortex, left PMC, left PPC, and left MTL (see Fig. 2A), in approximate order of decreasing spatial extent. Most clusters were predominantly left-sided. Second, the pictorial-item subgroup mainly exhibited SM effects in the fusiform cortex, hippocampal formation, PMC, PPC, and IFC regions (Fig. 2B), in approximate order of decreasing spatial extent. These clusters were nearly bilaterally symmetrical, except for the predominantly left-sided PMC clusters. Third, the verbal-associative subgroup mainly exhibited SM effects in the left posterior IFC/insula, bilateral fusiform cortex, and left hippocampal formation (Fig. 2C), in approximate order of decreasing spatial extent. There were no significant SM effects within the PMC or PPC regions. Finally, the pictorial-associative subgroup mainly exhibited SM effects in the hippocampal formation, fusiform cortex, PMC, left IFC, and right PPC (Fig. 2D), in approximate order of decreasing spatial extent. Thus, in each subgroup, the major SM effects occurred within a five-region network, identified by the meta-analysis of all studies; however, the relative magnitudes of the five regions' SM effects among the four subgroups showed rather large differences. Yet, interpretation of these differences requires care, given that the statistical power to detect activation differed among these subgroups. The subtraction meta-analyses below circumvented this problem by comparing two equal-size subgroups.

Table 4 and Fig. 3 show comparison results for the verbal-item and pictorial-item subgroups and for the verbal-associative and pictorial-associative subgroups. There were three main sets of findings. First, in both comparisons, the left IFC regions, extending into the ventral extent of the middle frontal gyrus (BA, 44, 45, 46), showed greater SM effects during verbal material encoding as compared to pictorial material encoding (see Fig. 3A and E). Second, in both comparisons, the bilateral fusiform/occipital cortex (Fig. 3B and F), bilateral hippocampal formation (Fig. 3C and G), and bilateral PPC regions (Fig. 3D and H) exhibited greater SM effects during pictorial material encoding as compared to verbal material encoding. Finally, the bilateral PMC (Fig. 3A) and left anterior fusiform regions (Fig. 3B) showed greater SM effects during verbal item encoding than pictorial item encoding. The peak coordinates ($xyz = -46, -50, -24$) in the left anterior fusiform region were virtually identical to those previously described as the “visual word form” region (for a review, see McCandliss et al., 2003).

Table 5 and Fig. 4 show the comparison between the verbal-associative and verbal-item subgroups and the comparison between the pictorial-associative and pictorial-item subgroups. There were three main sets of findings. First, in both comparisons, the left PMC (Fig. 4A and D) and bilateral PPC regions (Fig. 4B, C, and F) exhibited greater SM effects during the encoding of item information relative to associative information. Second, the left hippocampal region showed greater SM effects during pictorial-associative than during pictorial-item encoding (Fig. 4E). Finally, the left posterior IFC (BA 45)/insular region showed greater SM effects during verbal-associative than during verbal-item encoding (Fig. 4A).

SF effects

Table 6 and Fig. 5 show the whole group ALE meta-analysis results and the ALE meta-analysis for the verbal item subgroup alone (see supplementary material available online (Supplementary Figs. 6 and 7) for a series of coronal views). In the meta-analyses of the whole group (see Fig. 5A), SF effects associated mostly with default-mode network regions, including the posterior cingulate cortex (PCC)/precuneus (BA 31, 23, 7), the TPJ (BA 40, 39), the superior frontal cortex (BA 8), the anterior cingulate cortex (ACC)/ventromedial PFC (BA 32, 24), and the frontal pole (BA 10), in approximate order of decreasing spatial extent. Though most clusters were somewhat bilaterally symmetrical, the TPJ cluster was larger in the right than in the left hemisphere. The verbal-item subgroup results (see Fig. 5B) were highly comparable to those for the whole group, except that each cluster was slightly smaller in the subgroup analysis.

Discussion

SM effects

These results revealed that SM effects associated most consistently with five neural regions: left IFC, bilateral fusiform cortex, bilateral hippocampal formation, bilateral PMC, and bilateral PPC. Moreover, the SM effects' magnitude in these regions showed reliable modulation by the nature of the material (verbal or pictorial) and/or by encoding

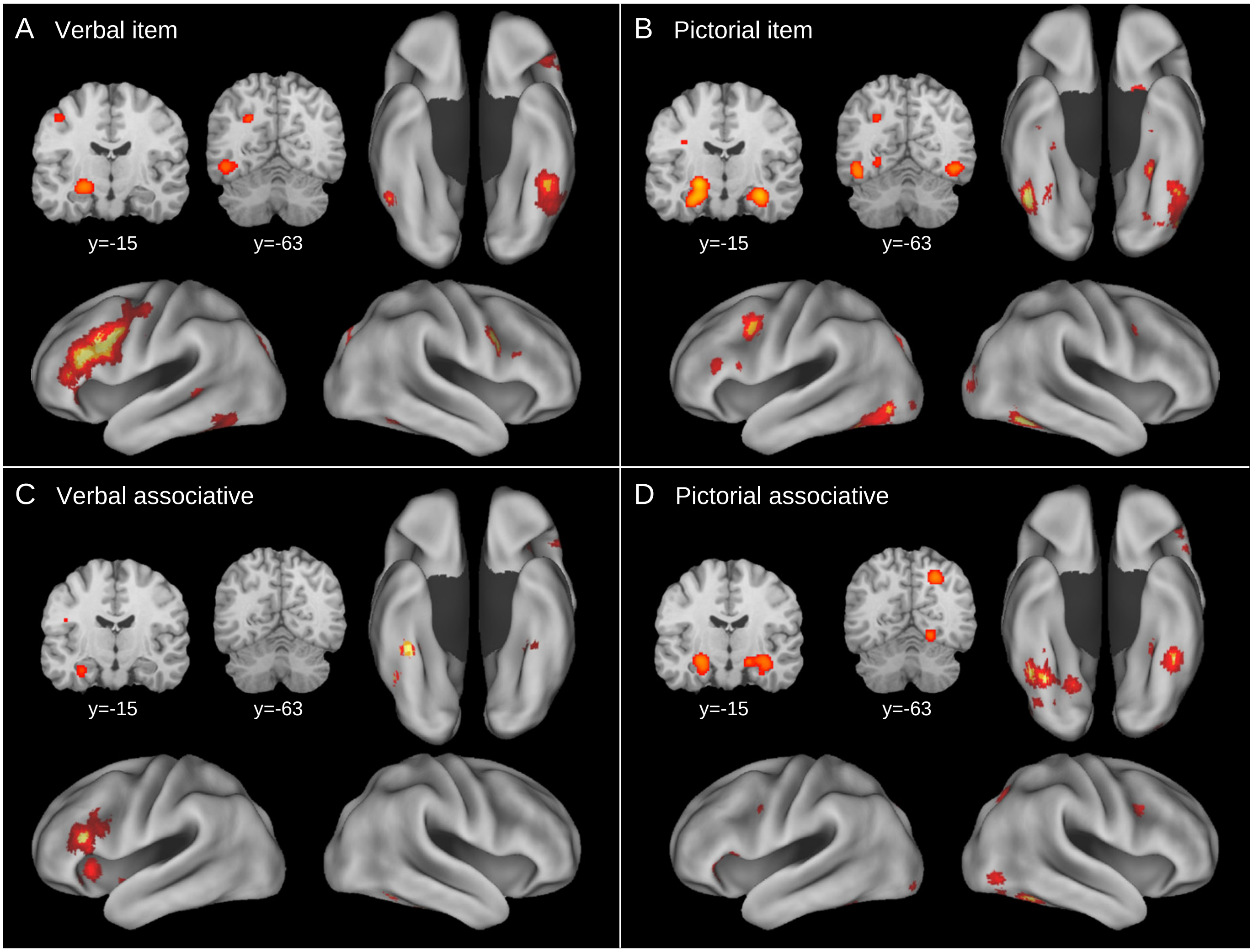

Fig. 2. Brain regions associated with significant SM effects in separate meta-analyses of the verbal-item (A), pictorial-item (B), verbal-associative (C), and pictorial-associative (D) subgroups.

type (item or associative). As per the three-component model outlined in Introduction section, activation of the left IFC and fusiform cortex regions may mediate content processing, activation of the hippocampal formation may support storage operations, and activation of the PMC and PPC regions may reflect attention during encoding. Separate sections below discuss findings regarding the three component regions.

Content processing: Left IFC and fusiform cortex

The left IFC is one of the regions most widely recognized as exhibiting SM effects. Several encoding models have implicated PFC–MTL interaction as the critical component of successful encoding (Buckner et al., 1999; Fernandez and Tendolkar, 2001; Simons and Spiers, 2003). In the present meta-analysis, the left IFC showed the greatest SM effects by far, across all studies. The fusiform cortex, which prior SM studies relatively neglected, showed the second-greatest SM effects. Even though both of these regions showed strong modulation of SM effects by the nature of the material, the two regions' modulation directions were diametrically opposed. The left IFC's SM effects were strong during verbal material encoding but relatively weak during pictorial material encoding. In contrast, the fusiform cortex's SM effects were robust during pictorial material encoding but relatively modest (and predominantly lateralized to the left) during verbal material encoding. Direct comparisons of equal-sized groups of studies confirmed both the greater SM effects in the left IFC during verbal material encoding and the greater SM effects in the fusiform/occipital cortex during pictorial material encoding. Thus, verbal material encoding strongly engaged the left IFC, known to support controlled semantic/phonological retrieval and analysis (Badre and Wagner, 2007; Dobbins and Wagner, 2005), whereas pictorial material encoding strongly engaged the fusiform/occipital cortex, known to mediate visuoperceptual analysis and differentiation (Garoff et al., 2005; Kanwisher et al., 2001). This pattern of findings is in accordance with the “task-dependency” principle (Otten and Rugg, 2001a; Rugg et al., 2002), which suggests successful encoding does not depend on a set of fixed brain regions. Rather, a task's processing requirements determine which brain regions will be functionally critical for successful encoding.

This study had two other main findings involving content-processing regions. First, the left posterior IFC/insular region exhibited greater SM effects during verbal-associative than verbal-item encoding (see Fig. 4A). Relative to an item-memory task, an associative-memory task typically presents more information and requires more elaborative information encoding. Thus, greater SM effects in the left posterior IFC/insular region may reflect increased demands on controlled semantic processing during verbal-associative encoding

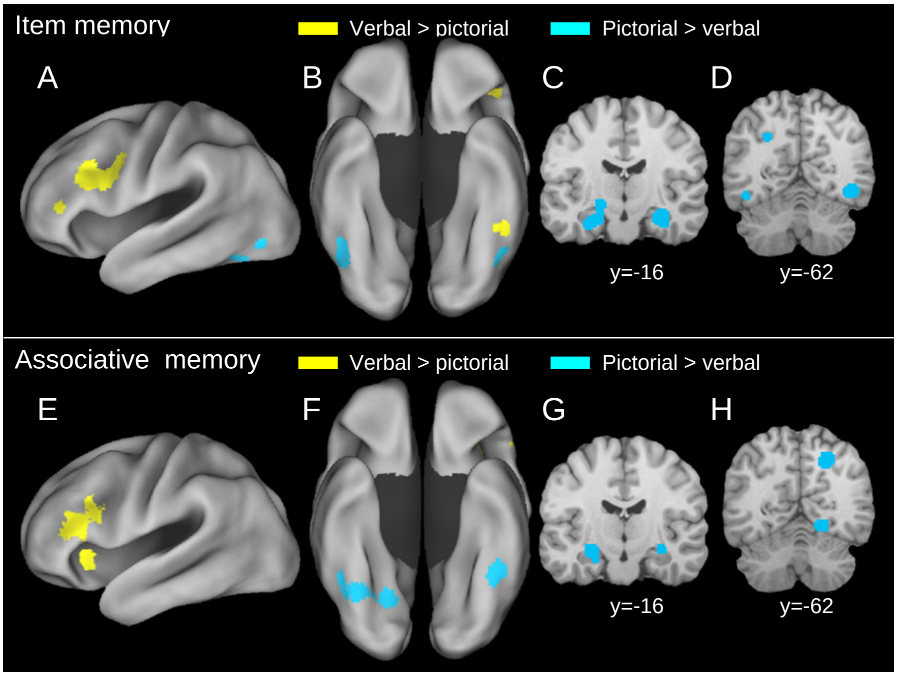

Fig. 3. Brain regions associated with variable SM effects in a comparison of the verbal-item and pictorial-item subgroups (*upper panel*), and a comparison of the verbal-associative and pictorial-associative subgroups (*lower panel*).

(Kirwan et al., 2008). Some evidence also suggests the lateral PFC may be involved in organizing multiple pieces of information in working memory, thereby building associations among items (Blumenfeld and Ranganath, 2007). Thus, greater SM effects in the left posterior IFC region may also reflect increased demands on organizational processing during verbal-associative encoding.

Second, the left anterior fusiform region showed greater SM effects during verbal-item than pictorial-item encoding (see Fig. 3B). The left anterior fusiform region, which corresponded closely to previously described "visual word form" region, is particularly responsive to visual words and, according to some studies, is specialized for processing orthography (Kirchhoff et al., 2000; McCandliss et al., 2003). Thus, the SM effects in this region may contribute to orthographic information encoding. However, this requires cautious interpretation because the contrast between the pictorial-associative subgroup and the verbal-associative subgroup showed the reverse effect in a similar region (see Fig. 3F). The classification of associative-memory tasks with verbal and pictorial stimuli into the pictorial-associative subgroup may have biased the contrast. Further investigation is required to more fully understand the nature of SM effects subserved by the left anterior fusiform region.

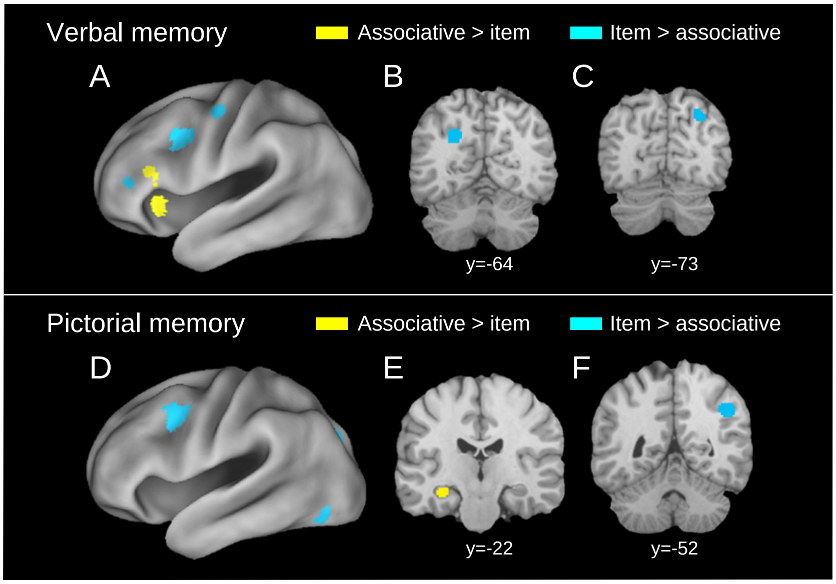

Fig. 4. Brain regions associated with variable SM effects in a comparison of the verbal-associative and verbal-item subgroups (*upper panel*), and a comparison of the pictorial-associative and pictorial-item subgroups (*lower panel*).

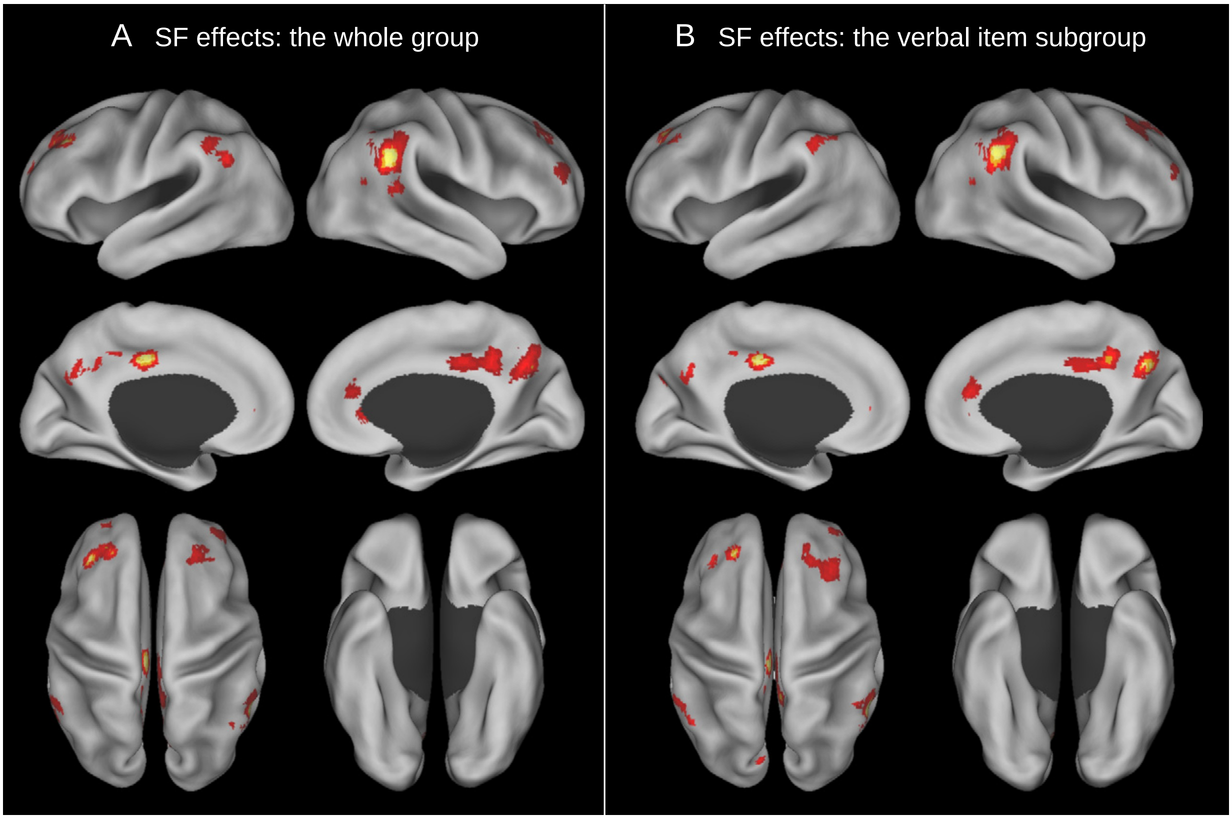

Fig. 5. Brain regions associated with significant SF effects in a meta-analysis involving the whole group (A) and one restricted to the verbal-item subgroup (B).

Storage function: MTL

The MTL is widely recognized as the key structure in storage operations (for a review, see Squire et al., 2004). The present meta-analysis of all included studies indicated robust SM effects in this region. The MTL clusters were centered at the anterior hippocampal formation, suggesting that among the MTL subregions, this region plays a critical role (Lepage et al., 1998). The MTL clusters included the amygdala, possibly reflecting the presentation of emotional stimuli in some studies (e.g., Erk et al., 2003; Kensinger and Schacter, 2006). The SM effects in the hippocampal formation showed strong modulation by the nature of the material. Hippocampal SM effects were robust and bilateral during pictorial material encoding but relatively weak (and left-lateralized) during verbal material encoding. Direct comparisons of equal-sized groups of studies confirmed that both the left and right hippocampal formation showed greater SM effects during pictorial material encoding. This indicates an important neural basis for why humans remember pictures better than they remember words, a phenomenon confirmed in countless behavioral experiments and called the “picture superiority effect” (e.g., Mintzer and Snodgrass, 1999; Nelson et al., 1976). This finding also provides moderate support for the novelty-encoding hypothesis (Tulving et al., 1996), given that the SM studies' participants had high pre-experimental familiarity with the verbal material used, but not with the pictorial material. Though the support was moderate, due to the confounding of novelty with stimulus type, available evidence (e.g., Gonsalves et al., 2005; Martin, 1999; O'Kane et al., 2005; Stern et al., 1996) indicates that MTL activation magnitude depends on novelty, even when it is more strictly controlled.

The present meta-analyses indicated that the SM effects on associative- as well as item-memory centered on the hippocampal formation. To investigate whether the analyses' use of a 10 mm kernel may have blurred some distinctions in the MTL, we performed an

Table 2
SM effects: results from an ALE meta-analysis of all studies.

Lobe	Region	H	BA	Talairach			Volume (mm^3)	ALE ($\times 10^3$)
				x	y	z		
Frontal	IFC, PMC, precentral gyrus	L	44, 45, 46, 47, 6, 4	−46	26	16	29632	66.5
	IFC, PMC	R	44, 46, 6	48	8	30	4560	31.6
	PreSMA	L	8	−6	16	48	880	20.2
Temporal	Hippocampus, PHG, amygdala	L	28, 34, 36	−22	−10	−16	8736	50.0
	Hippocampus, PHG, amygdala	R	28, 34, 36	18	−8	−16	5976	38.0
	Fusiform gyrus	L	37, 20	−42	−46	−22	14648	47.5
	Fusiform gyrus	R	37	44	−52	−14	7712	53.8
Parietal	Intraparietal sulcus	L	7, 19	−28	−76	36	3152	32.9
	Intraparietal sulcus	R	7	26	−62	46	1224	24.4
Occipital	Middle occipital gyrus	R	18	28	−86	6	576	21.0
	Inferior occipital gyrus	L	18	−32	−90	−6	304	18.2

H, hemisphere; BA, Brodmann area; ALE, activation likelihood estimation; IFC, inferior frontal cortex; PMC, premotor cortex; SMA, supplementary motor area; PHG, parahippocampal gyrus.

Table 3
SM effects: results from separate ALE meta-analyses of four subgroups of studies.

Lobe	Region	H	BA	Talairach			Volume (mm^3)	ALE ($\times 10^3$)
				x	y	z		
Verbal item subgroup								
Frontal	IFC, PMC, precentral gyrus	L	44, 45, 46, 47, 6, 4	−42	12	28	23024	36.9
	IFC	R	44	50	26	28	312	11.3
	PMC	R	6	50	6	30	2152	23.7
	PreSMA	L	8	−6	16	54	608	12.9
	SMA	L	6	−4	0	58	416	14.4
Temporal	Hippocampus, amygdala	L	–	−22	−14	−12	1688	20.5
	Fusiform gyrus	R	37	50	−52	−16	496	16.6
	Fusiform gyrus, middle temporal gyrus	L	37, 22	−44	−48	−22	6568	28.1
Parietal	Intraparietal sulcus	L	7, 19	−30	−76	36	2392	19.7
	Intraparietal sulcus	R	7, 19	30	−74	34	496	12.2
Pictorial item subgroup								
Frontal	IFC	L	45	−48	30	14	1008	12.7
	IFC	L	44	−54	12	16	448	11.5
	PMC	L	6	−34	0	42	4280	16.9
	PMC	R	6	42	4	32	536	12.5
	PreSMA	L	8	−8	12	48	456	11.2
Temporal	Hippocampus, PHG, amygdala	L	28, 34	−22	−16	−10	5968	21.1
	Hippocampus, PHG	R	36	32	−18	−20	2472	20.5
	PHG, amygdala	R	34	16	−8	−16	544	13.7
	Fusiform gyrus	L	37	−30	−38	−12	1048	15.4
	Fusiform gyrus	L	37	−44	−72	−8	4208	14.9
	Fusiform gyrus	R	37	44	−54	−12	4384	24.2
Parietal	Intraparietal sulcus	L	7	−26	−60	34	440	12.0
	Intraparietal sulcus	R	40	46	−52	38	568	15.3
	Intraparietal sulcus	L	19	−26	−76	32	744	14.0
Occipital	Middle occipital gyrus	R	18	28	−86	6	1480	16.6
Verbal associative subgroup								
Frontal	IFC	L	44, 45	−48	24	16	6424	28.0
	IFC	L	47	−32	20	−2	3008	18.1
	Insula	L	13	−44	4	−6	632	8.2
	White matter	L	–	−44	−6	28	848	9.3
Temporal	Hippocampus	L	–	−32	−12	−24	568	10.0
	Amygdala	L	–	−18	−6	−16	672	12.2
	Amygdala	R	–	18	−2	−18	472	9.3
	Fusiform gyrus	R	37	44	−50	−10	856	10.9
	Fusiform gyrus	R	37	38	−34	−22	680	11.6
	Fusiform gyrus	L	20	−34	−38	−16	352	7.7
	Fusiform gyrus	L	37	−44	−50	−10	352	8.0
Pictorial associative subgroup								
Frontal	IFC	L	47, 45	−42	30	−2	1344	10.8
	PMC	L	6	−44	0	26	1152	10.0
	PMC	L	6	−28	2	56	496	8.2
	PMC	R	6	42	8	30	528	10.9
Temporal	Hippocampus, amygdala	R	–	20	−10	−14	3400	16.1
	Hippocampus, amygdala, fusiform gyrus	L	37	−20	−6	−14	6952	17.8
	Fusiform gyrus	R	37	40	−52	−16	4824	23.5
	Fusiform gyrus	R	19	42	−74	−4	1792	13.2
Parietal	Intraparietal sulcus	R	7	24	−62	46	1184	13.0
	Intraparietal sulcus	L	7	−14	−80	44	384	8.4
Occipital	Inferior occipital gyrus	L	18	−32	−90	−8	448	9.5
Sub-lobar	Thalamus	R	–	22	−26	−6	320	10.6

For abbreviations, see Table 2.

additional set of meta-analyses with a smaller kernel (5 mm). These results were similar to the original ones, suggesting that the findings do not reflect kernel size. The fact that the SM effects centered on the hippocampus for both item- and associative-memory does not support the view that the hippocampal formation and the adjacent cortex (i.e., perirhinal/parahippocampal cortex) are functionally dichotomized along the lines of associative-encoding versus item-encoding (Brown and Aggleton, 2001; Davachi, 2006). Instead, this finding suggests the hippocampal formation plays a central role and the adjacent cortex plays a less essential, supplementary role in both item- and associative-encoding (Squire et al., 2007). The left hippocampal region showed greater SM effects during pictorial-associative information encoding relative to pictorial-item information (see Fig. 4E). This may reflect a greater demand for hippocampal *binding* mechanisms during associative encoding (Kirwan et al., 2008). However, one should interpret this with caution, given the lack of differences in hippocampal SM effects for verbal-associative compared to verbal-item encoding. This null effect may be attributable, in part, to weak MTL involvement in both verbal-item and verbal-associative tasks and to associated low statistical power.

Attention during encoding: PMC and PPC

Few prior studies of SM effects have focused on PMC or PPC regions; however, the present meta-analysis indicated significant SM effects in these regions. The PMC clusters' center was at the junction of the precentral sulcus and the middle frontal gyrus, while the PPC clusters' centered at the intraparietal sulcus. Given that both PMC and PPC regions are prominent components of a frontoparietal attention system (Corbetta et al., 2008; Raz and Buhle, 2006), both may play important roles in regulating attention during encoding. Both PMC

Table 4
Brain regions associated with variable SM effects for encoding verbal versus pictorial material.

Lobe	Region	H	BA	Talairach			Volume (mm^3)	ALE (x10^3)
				x	*y*	*z*		
Item memory: verbal>pictorial								
Frontal	IFC, PMC	L	44, 6	−48	10	24	3792	20.1
	IFC	L	46	−40	26	2	1720	20.0
	PMC	R	6	52	6	26	1088	19.6
Temporal	Fusiform gyrus	L	37	−46	−50	−24	632	16.5
Item memory: pictorial>verbal								
Frontal	Precentral gyrus	L	4	−32	−2	40	480	−14.7
Temporal	Hippocampus. PHG	L	28, 34, 36	−20	−16	−8	2064	−13.7
	Hippocampus. PHG	R	28, 34, 36	32	−10	−26	1840	−12.7
	Fusiform gyrus	L	37	−42	−64	−16	416	−10.4
	Fusiform gyrus	R	37	44	−54	−12	3536	−22.4
Parietal	Intraparietal sulcus	L	7	−26	−60	34	304	−12.0
	Intraparietal sulcus	R	40	46	−52	38	480	−15.2
Occipital	Inferior occipital gyrus	L	19	−44	−74	−6	352	−12.6
	Middle occipital gyrus	R	18	28	−86	4	1352	−16.5
Sub-lobar	Putamen	L	–	−24	10	−8	1032	−15.3
Associative memory: verbal>pictorial								
Frontal	IFC	L	44, 45	−48	24	16	4384	24.9
	Insula	L	13	−32	18	0	1208	16.8
Associative memory: pictorial>verbal								
Frontal	PMC	L	6	−26	−10	44	392	−7.6
	White matter	L	–	−36	−2	18	344	−8.7
Temporal	Hippocampus	L	–	−24	−10	−22	2344	−10.0
	Hippocampus	R	–	40	−20	−18	1368	−7.3
	Fusiform gyrus	R	37	18	−60	−10	3440	−13.9
	Fusiform gyrus	R	19	26	−70	−16	1152	−7.1
	Fusiform gyrus	L	37	−42	−46	−22	1288	−14.1
Parietal	Intraparietal sulcus	R	7	24	−62	46	1024	−12.7
	Precuneus	L	7	−14	−80	44	392	−8.4

For abbreviations, see Table 2.

and PPC regions showed greater SM effects during item-encoding tasks than during associative-encoding tasks (see Fig. 4A and D). Associative-encoding tasks present multiple pieces of information simultaneously or successively within a trial (e.g., Prince et al., 2007; Qin et al., 2007). Relatively weak SM effects in the PMC and PPC regions during associative-encoding tasks may reflect a variable attentional focus, in terms of both space and time, associated with such presentations. The SM effects in PMC regions were greater during verbal-item than pictorial-item encoding (Fig. 3A), whereas the SM effects in PPC regions were greater during pictorial material

Table 5
Brain regions associated with variable SM effects for associative encoding versus item encoding.

Lobe	Region	H	BA	Talairach			Volume (mm^3)	ALE ($\times 10^3$)
				x	*y*	*z*		
Verbal memory: associative>item								
Frontal	IFC	L	45	−46	22	14	1008	17.7
	Insula	L	13	−32	18	−2	1040	16.6
Temporal	Fusiform gyrus	R	37	38	−34	−22	424	11.4
Verbal memory: item>associative								
Frontal	IFC	L	46	−42	38	8	1048	−8.8
	PMC	L	6	−40	6	32	1400	−15.4
	PMC	R	6	52	6	24	664	−10.7
	Precentral gyrus	L	4	−44	−12	50	424	−10.7
Temporal	Fusiform gyrus	L	37	−38	−60	−10	440	−9.3
	Fusiform gyrus	L	37	−42	−44	−22	328	−10.4
Parietal	Intraparietal sulcus	R	19	28	−76	42	304	−8.6
	Intraparietal sulcus	L	7	−24	−64	32	728	−12.4
Pictorial memory: associative>item								
Temporal	Hippocampus, amygdala	L	–	−20	−6	−12	536	14.5
	Hippocampus	L	–	−32	−30	−12	760	12.0
	Fusiform gyrus	R	19	18	−60	−10	416	13.6
Parietal	Intraparietal sulcus	R	7	22	−62	46	648	12.3
Occipital	Inferior occipital gyrus	R	19	42	−74	−4	648	12.8
Pictorial memory: item>associative								
Frontal	PMC	L	6	−34	−10	28	3576	−11.0
Temporal	Fusiform gyrus	R	37	44	−58	−10	608	−13.2
	Fusiform gyrus	L	19	−44	−72	−10	376	−10.2
Parietal	Intraparietal sulcus	L	19	−26	−76	32	736	−13.7
	Intraparietal sulcus	R	40	46	−52	38	696	−15.3
Occipital	Middle occipital gyrus	R	18	30	−84	6	424	−10.3
Sub-lobar	Globus pallidus	L	–	−22	−16	−8	752	−16.8

For abbreviations, see Table 2.

Table 6
SF effects: results from ALE meta-analyses of all studies and of the verbal-item subgroup.

Lobe	Region	H	BA	Talairach			Volume (mm^3)	ALE ($\times 10^3$)
				x	y	z		
All studies								
Frontal	Frontal pole	L	10	−26	54	22	368	9.9
	Frontal pole	R	10	38	46	18	704	8.8
	Superior frontal cortex	L	8	−36	30	38	2632	16.2
	Superior frontal cortex	R	8	24	36	36	880	13.4
	Superior frontal cortex	R	8	34	32	42	400	7.8
	ACC, ventromedial PFC	B	32, 24	0	44	2	2176	13.2
Temporal	Superior temporal gyrus	L	22	−48	−14	−8	720	10.5
Parietal	PCC, precuneus	B	31, 23, 7	0	−26	38	9992	19.0
	TPJ	L	40	−52	−56	32	1136	11.8
	TPJ	R	40, 39	54	−46	30	6448	21.9
Verbal item subgroup								
Frontal	Frontal pole	R	10	36	50	20	304	7.3
	Superior frontal cortex	L	8	−36	30	40	584	10.9
	Superior frontal cortex	L	8	−22	34	38	1000	12.5
	Superior frontal cortex	R	8	34	24	44	2056	9.9
	ACC, ventromedial PFC	B	32, 24	0	44	2	2232	13.1
Parietal	PCC	B	31, 23	−2	−26	38	3432	13.1
	Precuneus	B	7	8	−64	34	2696	14.2
	TPJ	L	40	−54	−48	42	616	8.3
	TPJ	R	40, 39	52	−48	34	5160	16.1
Occipital	Cuneus	L	19	−8	−80	32	408	8.8

ACC, anterior cingulate cortex; PFC, prefrontal cortex; PCC, posterior cingulate cortex; TPJ, temporoparietal junction. For other abbreviations, see Table 2.

than verbal material encoding (see Fig. 3D and H). These findings suggest the PMC region may mainly support attention to conceptual representations, whereas the PPC region may mainly mediate attention to perceptual representations. This hypothesis is consistent with the findings that (*i*) divided attention during the encoding of words attenuates SM effects in the posterior frontal cortex and other regions (Uncapher and Rugg, 2008) and (*ii*) selective attention to perceptual features enhances the SM effects in the PPC and other regions (Uncapher and Rugg, 2009).

Laterality effects

Prior studies (Golby et al., 2001; Kelley et al., 1998) comparing encoding activities for verbal and pictorial material predominantly focused on laterality effects. In the present meta-analysis, the studies using verbal material exhibited predominantly left-lateralized SM effects, whereas the studies using pictorial material showed slightly *left-lateralized* SM effects in the IFC and more bilaterally balanced SM effects in other regions. While certain classes of pictorial material may predominantly engage right-hemispheric processing, most pictorial material is, at least in part, dually (i.e., verbally and visually) codable and may involve both left- and right-hemispheric processing. For example, pictures of common objects, which were among the most commonly used pictorial materials in prior SM studies (e.g., Dickerson et al., 2007; Garoff et al., 2005), are particularly amenable to dual encoding. Future meta-analyses may address whether different types of pictorial material (e.g., objects, scenes, faces) are associated with differential laterality effects. The SM effects in the left IFC during pictorial material encoding may reflect involvement of semantic/conceptual information.

SF effects

This meta-analysis's results revealed SF effects associated mostly with default-mode network regions, including the PCC/precuneus, ACC/ventromedial PFC, TPJ, superior frontal cortex, and frontal pole. Though previous researchers noted an association between the default-mode network and SF effects (Daselaar et al., 2004; Kim et al., 2010; Park and Rugg, 2008; Shrager et al., 2008; Turk-Browne et al., 2006), the evidence was equivocal, with most studies suggesting only parts of the network were involved. The present meta-analysis provided more definitive evidence, by correlating most of the network's key components and by integrating results across studies. As noted in Introduction section, increased activity in the default-mode network during an attention-demanding task likely signals mind-wandering or brief lapses in attention (Christoff et al., 2009; Mason et al., 2007; McKiernan et al., 2006; Weissman et al., 2006). The SF effects' association with the default-mode network may reflect this factor. However, the association may not be “compulsory” but rather tied to encoding “exogenous” information, which is the case in most SM studies. When encoding “endogenous” information, such as episodes of imagining the future or the viewpoint of another person, some default-mode network regions may be associated with SM rather than SF effects. Consistent with this view, research has shown increased activity in the medial PFC, a key component of the default-mode network, is not detrimental, but beneficial, to encoding self-referential information (Macrae et al., 2004) or episodes of social cognition (Harvey et al., 2007; Mitchell et al., 2004).

This study did not include a formal analysis of encoding variables (e.g., verbal versus pictorial) due to the limited number of available studies. However, the analysis confined to the verbal-item subgroup yielded results that were highly comparable to those involving the whole group. Thus, SF effects seem to be relatively consistent across various encoding variables; a few prior studies have also suggested this conclusion (Daselaar et al., 2004; Park and Rugg, 2008). Though most clusters were bilaterally comparable regarding magnitude, the TPJ cluster was stronger in the right than in the left hemisphere, possibly suggesting the right TPJ's more critical role in mind-wandering. Consistent with this finding, evidence suggests the right TPJ is more critically involved in reorienting attention, and, possibly, in self-referential processing, than the left TPJ is (for reviews, see Corbetta et al., 2008; Decety and Lamm, 2007). Alternatively, if the effect is specific to verbal stimuli, the finding may suggest more critical involvement of the TPJ contralateral to the “specialized” hemisphere in mind-wandering. Further studies are needed to differentiate between these two possibilities.

A fundamental source of SF as well as SM effects is trial-to-trial variability in participants' encoding performances. Though researchers commonly view this intertrial variability as “noise” in the data and rarely interpret it, it may also reflect a systematic factor. Recent research (Fox et al., 2005; Fransson, 2006; Golland et al., 2008) based on intrinsic low-frequency (<0.1 Hz) blood-oxygen-level-dependent signal fluctuations indicated that the brain recurrently oscillates between an externally oriented processing mode, which reflects increased activity in the task-positive network and decreased activity in the task-negative/default-mode network, and an internally oriented processing mode, which correlates with increased activity in the task-negative network and decreased activity in the task-positive network (for a review, see Fox and Raichle, 2007). Increasing evidence also indicates these ongoing activity fluctuations contribute to intertrial variability in many aspects of perception and behavior (Boly et al., 2007; Fox et al., 2007; Li et al., 2007; for a review, see Northoff et al., 2010). The present findings on SF and SM effects are in line with this evidence. Specifically, the findings indicate that the stimuli presented at the externally oriented processing phase (i.e., increased activity in the task-positive network and decreased activity in the task-negative network) tend to be effectively encoded, whereas the stimuli presented at the internally oriented processing phase (i.e., increased activity in the task-negative network and decreased activity in the task-positive network) tend to be poorly encoded (compare Figs. 1 and 5). More generally, these findings support the view that "measured neuronal responses represent an approximately linear superposition of task-evoked neuronal activity and ongoing spontaneous activity" (Fox and Raichle, 2007).

Conclusions

The present study performed a meta-analysis of functional MRI studies using an SM approach. The meta-analysis of SM effects indicated they most consistently associated with five neural regions: the left IFC, bilateral fusiform cortex, bilateral hippocampal formation, bilateral PMC, and bilateral PPC. Comparisons of SM effects among the four subgroups of studies, formed by crossing two major study divisions (verbal versus pictorial material and item versus associative encoding), yielded three main sets of findings. First, the left IFC and bilateral fusiform cortex, which are canonical content-processing regions, showed "mirror-imaged" modulation of SM effects by the nature of the material. The left IFC showed greater SM effects during verbal material encoding than during pictorial material encoding, whereas the fusiform cortex showed greater SM effects during pictorial material encoding than verbal material encoding. Second, the bilateral hippocampal regions, which are critical for storage operations, showed greater SM effects during pictorial material encoding compared to verbal material encoding, possibly reflecting greater hippocampal involvement in processing novel, rather than familiar, information. The left hippocampal region showed greater SM effects during pictorial-associative than pictorial-item encoding, possibly reflecting a greater demand on hippocampal binding mechanisms during associative encoding. Third, both PMC and PPC regions, which may support attention during encoding, showed greater SM effects during item encoding relative to associative encoding, possibly reflecting a constant attentional focus that is higher during item encoding. The meta-analysis of SF effects indicated they associated mostly with default-mode network regions, including the anterior and posterior medial cortex, the bilateral TPJ, and the bilateral superior frontal cortex. Recurrent activity oscillations between the task-positive and task-negative/default-mode networks may account for trial-to-trial variability in participants' encoding performances, which is a fundamental source of both SM and SF effects. Taken together, the present findings clarify the neural activity supporting successful encoding, as well as the neural activity leading to encoding failure.

Acknowledgments

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Appendix A. Details of individual studies

1st Author	Year	Number of participants	Nature of material	Type of encoding	Study task	Retention interval[a]	Number of foci
Subsequent memory effects (remembered>forgotten)							
Axmacher	2008	30	Verbal	Item	Semantic, orthographic	Short	17
Baker	2001	18	Verbal	Item	Semantic, orthographic	Short	10
Brassen	2006	13	Verbal	Item	Semantic	Short	7
Buckner	2001	14	Verbal	Item	Recognition	Short	13
Canli	2002	24	Pictorial	Item	Subjective judgment	Long	36
Cansino	2002	17	Pictorial	Associative	Spatial	Short	16
Chee	2004	16	Verbal	Item	Semantic	Long	5
Chee	2003	16	Verbal	Item	Semantic	Long	2
Clark	2003	17	Verbal	Item	Phonological	Short	15
de Zubicaray	2005	14	Verbal	Item	Intentional encoding	Short	6
Dennis	2008	14	Pictorial	Item	N-back	Short	17
Dennis	2007	12	Verbal	Item	Semantic	Short	7
Dickerson	2007	15	Pictorial	Item	Spatial	Short	7
Duverne	2009	16	Verbal	Item	Semantic	Short	10
Erk	2003	10	Verbal	Item	Semantic	Short	6
Erk	2005	10	Verbal	Item	Semantic	Short	3
Fischer	2007	24	Pictorial	Item	Spatial	Short	2
Fletcher	2003	9	Verbal	Item	Semantic, orthographic	Short	5
Fliessbach	2007	19	Verbal	Item	Semantic, orthographic	Short	13
Fliessbach	2006	21	Verbal	Item	Intentional encoding	Short	4
Garoff	2005	12	Pictorial	Item	Visualizing	Long	37
Gold	2006	15	Verbal	Associative	Visualizing	Short	4
Gonsalves	2004	11	Verbal	Associative	Visualizing	Short	2
Gottlieb	2010	20	Pictorial	Associative	Spatial	Short	8
Gutchess	2005	14	Pictorial	Item	Spatial	Short	17
Habib	2008	20	Verbal	Associative	Intentional encoding	Short	4
Harvey	2007	12	Pictorial	Item	Spatial	Short	12
Haskins	2008	14	Verbal	Associative	Semantic	Short	9
Heinze	2006	15	Verbal	Item	Intentional encoding	Short	7

(continued on next page)

Appendix A (*continued*)

1st Author	Year	Number of participants	Nature of material	Type of encoding	Study task	Retention interval[a]	Number of foci
Henson	2005	22	Verbal	Item	Orthographic	Short	19
Jackson	2004	12	Verbal	Associative	Visualizing	Short	9
Kao	2005	16	Pictorial	Item	Judgment of learning	Short	9
Kensinger	2007	20	Pictorial	Item	Spatial, visualizing	Short	14
Kensinger	2006	21	Pictorial	Associative	Spatial	Short	9
Kim	2007	16	Verbal	Item	Semantic	Short	11
Kirwan	2008	14	Verbal	Associative	Semantic, visualizing	Short	2
Macrae	2004	22	Verbal	Item	Semantic	Short	4
Maril	2003	17	Verbal	Associative	Visualizing	Short	10
Miller	2008	17	Pictorial	Associative	Subjective judgment	Short	19
Mitchell	2004	17	Pictorial	Associative	Sequencing	Short	2
Morcom	2003	14	Verbal	Item	Semantic	Short	42
Nichols	2006	16	Pictorial	Item	Spatial	Short	8
Otten	2007	18	Verbal	Item	Visualizing	Long	3
Otten	2001	15	Verbal	Item	Semantic	Short	19
Otten	2002	16	Verbal	Item	Semantic, phonological	Short	13
Otten	2001	17	Verbal	Item	Semantic, phonological	Short	9
Park	2008	20	Verbal	Associative	Semantic, phonological	Short	1
Park	2008	17	Verbal	Associative	Semantic, phonological	Short	6
Prince	2007	12	Verbal	Associative	Semantic	Short	4
Qin	2007	20	Pictorial	Associative	Subjective judgment	Short	20
Qin	2009	20	Pictorial	Associative	Intentional encoding	3 hrs	2
Ranganath	2005	15	Pictorial	Item	Spatial	Short	25
Ranganath	2004	13	Verbal	Associative	Semantic, visualizing	Short	21
Raye	2002	12	Verbal	Item	Reading	Short	5
Reber	2002	12	Verbal	Item	Directed forgetting	Short	4
Schott	2006	25	Verbal	Item	Phonological	Short	26
Sergerie	2005	18	Pictorial	Item	Spatial	Short	25
Shrager	2008	14	Verbal	Item	Semantic	Short	4
Sommer	2005	15	Pictorial	Associative	Spatial	Short	20
Sommer	2005	15	Pictorial	Associative	Spatial	Short	17
Spencer	2009	12	Pictorial	Item	Spatial	Long	3
Sperling	2003	16	Pictorial	Associative	Subjective judgment	Short	5
Staresina	2006	16	Verbal	Associative	Visualizing	Short	6
Tendolkar	2007	20	Pictorial	Item	Spatial	Short	5
Tsukiura	2010	20	Pictorial	Associative	Spatial	Short	5
Uncapher	2009	15	Pictorial	Associative	Spatial, visualizing	Short	11
Uncapher	2006	20	Verbal	Associative	Semantic	Short	6
Uncapher	2005	18	Verbal	Item	Semantic	Long	14
Uncapher	2008	15	Verbal	Item	Semantic	Short	9
Wagner	1998	13	Verbal	Item	Semantic	Short	9
Weis	2004	16	Pictorial	Item	Spatial	Short	7
Wittmann	2005	16	Pictorial	Item	Judgment of reward	Short	13
Subsequent forgetting effects (forgotten>remembered)							
Axmacher	2008	30	Verbal	Item	Semantic, orthographic	Short	7
Clark	2003	20	Verbal	Item	Phonological	Short	15
Daselaar	2004	14	Verbal	Associative	Subjective judgment	Short	14
Duverne	2009	16	Verbal	Item	Semantic	Short	2
Gonsalves	2004	11	Verbal	Associative	Visualizing	Short	2
Kim	2010	12	Verbal	Item	Semantic	Short	8
Miller	2008	17	Pictorial	Associative	Subjective judgment	Short	11
Otten	2007	18	Verbal	Item	Visualizing	Long	4
Otten	2001	15	Verbal	Item	Semantic	Short	6
Otten	2001	17	Verbal	Item	Semantic, phonological	Short	6
Park	2008	20	Verbal	Associative	Semantic, phonological	Short	12
Raye	2002	12	Verbal	Item	Reading	Short	4
Schott	2006	25	Verbal	Item	Phonological	Short	10
Shrager	2008	14	Verbal	Item	Semantic	Short	14
Turk-Browne	2006	16	Pictorial	Item	Spatial	Short	3
Wagner	2001	13	Verbal	Item	Semantic	Short	12
Weis	2004	16	Pictorial	Item	Spatial	Short	2

Descriptions of details are limited to the experimental conditions included in the meta-analysis. [a]Short = 30 min or less; Long = 24 h or more.

Appendix B. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2010.09.045.

References

Axmacher, N., Schmitz, D.P., Weinreich, I., Elger, C.E., Fell, J., 2008. Interaction of working memory and long-term memory in the medial temporal lobe. Cereb. Cortex 18, 2868–2878.

Badre, D., Wagner, A., 2007. Left ventrolateral prefrontal cortex and the cognitive control of memory. Neuropsychologia 45, 2883–2901.

Baker, J.T., Sanders, A.L., Maccotta, L., Buckner, R.L., 2001. Neural correlates of verbal memory encoding during semantic and structural processing tasks. NeuroReport 12, 1251–1256.

Blumenfeld, R., Ranganath, C., 2007. Prefrontal cortex and long-term memory encoding: an integrative review of findings from neuropsychology and neuroimaging. Neuroscientist 13, 280–291.

Boly, M., Balteau, E., Schnakers, C., Degueldre, C., Moonen, G., Luxen, A., Phillips, C., Peigneux, P., Maquet, P., Laureys, S., 2007. Baseline brain activity fluctuations predict somatosensory perception in humans. Proc. Natl. Acad. Sci. U. S. A. 104, 12187–12192.

Brassen, S., Weber-Fahr, W., Sommer, T., Lehmbeck, J.T., Braus, D.F., 2006. Hippocampal-prefrontal encoding activation predicts whether words can be successfully recalled or only recognized. Behav. Brain Res. 171, 271–278.

Brewer, J., Zhao, Z., Desmond, J., Glover, G., Gabrieli, J., 1998. Making memories: brain activity that predicts how well visual experience will be remembered. Science 281, 1185–1187.

Brown, M., Aggleton, J., 2001. Recognition memory: what are the roles of the perirhinal cortex and hippocampus? Nat. Rev. Neurosci. 2, 61–62.

Buckner, R., Carroll, D., 2007. Self-projection and the brain. Trends Cogn. Sci. 11, 49–57.

Buckner, R., Kelley, W., Petersen, S., 1999. Frontal cortex contributes to human memory formation. Nat. Neurosci. 2, 311–314.

Buckner, R.L., Wheeler, M.E., Sheridan, M.A., 2001. Encoding processes during retrieval tasks. J. Cogn. Neurosci. 13, 406–415.

Canli, T., Desmond, J.E., Zhao, Z., Gabrieli, J.D.E., 2002. Sex differences in the neural basis of emotional memories. Proc. Natl. Acad. Sci. U. S. A. 99, 10789–10794.

Cansino, S., Maquet, P., Dolan, R.J., Rugg, M.D., 2002. Brain activity underlying encoding and retrieval of source memory. Cereb. Cortex 12, 1048–1056.

Chee, M.W.L., Goh, J.O.S., Lim, Y., Graham, S., Lee, K., 2004. Recognition memory for studied words is determined by cortical activation differences at encoding but not during retrieval. NeuroImage 22, 1456–1465.

Chee, M.W.L., Westphal, C., Goh, J., Graham, S., Song, A.W., 2003. Word frequency and subsequent memory effects studied using event-related fMRI. NeuroImage 20, 1042–1051.

Christoff, K., Gordon, A., Smallwood, J., Smith, R., Schooler, J., 2009. Experience sampling during fMRI reveals default network and executive system contributions to mind wandering. Proc. Natl. Acad. Sci. U. S. A. 106, 8719–8724.

Clark, D., Wagner, A.D., 2003. Assembling and encoding word representations: fMRI subsequent memory effects implicate a role for phonological control. Neuropsychologia 41, 304–317.

Corbetta, M., Kincade, J., Shulman, G., 2002. Neural systems for visual orienting and their relationships to spatial working memory. J. Cogn. Neurosci. 14, 508–523.

Corbetta, M., Patel, G., Shulman, G., 2008. The reorienting system of the human brain: from environment to theory of mind. Neuron 58, 306–324.

Craik, F., Govoni, R., Naveh-Benjamin, M., Anderson, N., 1996. The effects of divided attention on encoding and retrieval processes in human memory. J. Exp. Psychol. Gen. 125, 159–180.

Daselaar, S.M., Prince, S.E., Cabeza, R., 2004. When less means more: deactivations during encoding that predict subsequent memory. NeuroImage 23, 921–927.

Davachi, L., 2006. Item, context and relational episodic encoding in humans. Curr. Opin. Neurobiol. 16, 693–700.

De Zubicaray, G.I., McMahon, K.L., Eastburn, M.M., Finnigan, S., Humphreys, M.S., 2005. fMRI evidence of word frequency and strength effects during episodic memory encoding. Cogn. Brain Res. 22, 439–450.

Decety, J., Lamm, C., 2007. The role of the right temporoparietal junction in social interaction: how low-level computational processes contribute to meta-cognition. Neuroscientist 13, 580–593.

Dennis, N.A., Daselaar, S., Cabeza, R., 2007. Effects of aging on transient and sustained successful memory encoding activity. Neurobiol. Aging 28, 1749–1758.

Dennis, N., Hayes, S., Prince, S., Madden, D., Huettel, S., Cabeza, R., 2008. Effects of aging on the neural correlates of successful item and source memory encoding. J. Exp. Psychol. Learn. Mem. Cogn. 34, 791–808.

Diana, R., Yonelinas, A., Ranganath, C., 2007. Imaging recollection and familiarity in the medial temporal lobe: a three-component model. Trends Cogn. Sci. 11, 379–386.

Dickerson, B.C., Miller, S.L., Greve, D.N., Dale, A.M., Albert, M.S., Schacter, D.L., Sperling, R.A., 2007. Prefrontal-hippocampal-fusiform activity during encoding predicts intraindividual differences in free recall ability: an event-related functional-anatomic MRI study. Hippocampus 17, 1060–1070.

Dobbins, I.G., Wagner, A.D., 2005. Domain-general and domain-sensitive prefrontal mechanisms for recollecting events and detecting novelty. Cereb. Cortex 15, 1768–1778.

Duverne, S., Motamedinia, S., Rugg, M.D., 2009. The relationship between aging, performance, and the neural correlates of successful memory encoding. Cereb. Cortex 19, 733–744.

Eichenbaum, H., Yonelinas, A., Ranganath, C., 2007. The medial temporal lobe and recognition memory. Annu. Rev. Neurosci. 30, 123–152.

Erk, S., Kiefer, M., Grothe, J., Wunderlich, A.P., Spitzer, M., Walter, H., 2003. Emotional context modulates subsequent memory effect. NeuroImage 18, 439–447.

Erk, S., Martin, S., Walter, H., 2005. Emotional context during encoding of neutral items modulates brain activation not only during encoding but also during recognition. NeuroImage 26, 829–838.

Fernandez, G., Tendolkar, I., 2001. Integrated brain activity in medial temporal and prefrontal areas predicts subsequent memory performance: human declarative memory formation at the system level. Brain Res. Bull. 55, 1–9.

Fischer, H., Sandblom, J., Nyberg, L., Herlitz, A., Backman, L., 2007. Brain activation while forming memories of fearful and neutral faces in women and men. Emotion 7, 767–773.

Fletcher, P.C., Stephenson, C.M.E., Carpenter, T.A., Donovan, T., Bullmore, E.T., 2003. Regional brain activations predicting subsequent memory success: an event-related fMRI study of the influence of encoding tasks. Cortex 39, 1009–1026.

Fliessbach, K., Weis, S., Klaver, P., Elger, C.E., Weber, B., 2006. The effect of word concreteness on recognition memory. NeuroImage 32, 1413–1421.

Fliessbach, K., Trautner, P., Quesada, C.M., Elger, C.E., Weber, B., 2007. Cerebellar contributions to episodic memory encoding as revealed by fMRI. NeuroImage 35, 1330–1337.

Fox, M., Raichle, M., 2007. Spontaneous fluctuations in brain activity observed with functional magnetic resonance imaging. Nat. Rev. Neurosci. 8, 700–711.

Fox, M., Snyder, A., Vincent, J., Corbetta, M., Van Essen, D., Raichle, M., 2005. The human brain is intrinsically organized into dynamic, anticorrelated functional networks. Proc. Natl. Acad. Sci. U. S. A. 102, 9673–9678.

Fox, M., Snyder, A., Vincent, J., Raichle, M., 2007. Intrinsic fluctuations within cortical systems account for intertrial variability in human behavior. Neuron 56, 171–184.

Fransson, P., 2006. How default is the default mode of brain function?: further evidence from intrinsic BOLD signal fluctuations. Neuropsychologia 44, 2836–2845.

Garoff, R.J., Slotnick, S.D., Schacter, D.L., 2005. The neural origins of specific and general memory: the role of the fusiform cortex. Neuropsychologia 43, 847–859.

Genovese, C., Lazar, N., Nichols, T., 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. NeuroImage 15, 870–878.

Golby, A., Poldrack, R., Brewer, J., Spencer, D., Desmond, J., Aron, A., Gabrieli, J., 2001. Material-specific lateralization in the medial temporal lobe and prefrontal cortex during memory encoding. Brain 124, 1841.

Gold, J.J., Smith, C.N., Bayley, P.J., Shrager, Y., Brewer, J.B., Stark, C.E.L., Hopkins, R.O., Squire, L.R., 2006. Item memory, source memory, and the medial temporal lobe: concordant findings from fMRI and memory-impaired patients. Proc. Natl. Acad. Sci. U. S. A. 103, 9351–9356.

Golland, Y., Golland, P., Bentin, S., Malach, R., 2008. Data-driven clustering reveals a fundamental subdivision of the human cortex into two global systems. Neuropsychologia 46, 540–553.

Gonsalves, B., Reber, P., Gitelman, D., Parrish, T., Mesulam, M., Paller, K., 2004. Neural evidence that vivid imagining can lead to false remembering. Psychol. Sci. 15, 655–660.

Gonsalves, B., Kahn, I., Curran, T., Norman, K., Wagner, A., 2005. Memory strength and repetition suppression: multimodal imaging of medial temporal cortical contributions to recognition. Neuron 47, 751–761.

Gottlieb, L.J., Uncapher, M.R., Rugg, M.D., 2010. Dissociation of the neural correlates of visual and auditory contextual encoding. Neuropsychologia 48, 137–144.

Gusnard, D., Raichle, M., 2001. Searching for a baseline: functional imaging and the resting human brain. Nat. Rev. Neurosci. 2, 685–694.

Gutchess, A.H., Welsh, R.C., Hedden, T., Bangert, A., Minear, M., Liu, L.L., Park, D.C., 2005. Aging and the neural correlates of successful picture encoding: frontal activations compensate for decreased medial-temporal activity. J. Cogn. Neurosci. 17, 84–96.

Habib, R., Nyberg, L., 2008. Neural correlates of availability and accessibility in memory. Cereb. Cortex 18, 1720–1726.

Harvey, P.-O., Fossati, P., Lepage, M., 2007. Modulation of memory formation by stimulus content: specific role of the medial prefrontal cortex in the successful encoding of social pictures. J. Cogn. Neurosci. 19, 351–362.

Haskins, A.L., Yonelinas, A.P., Quamme, J.R., Ranganath, C., 2008. Perirhinal cortex supports encoding and familiarity-based recognition of novel associations. Neuron 59, 554–560.

Heinze, S., Sartory, G., Muller, B., de Greiff, A., Forsting, M., Juptner, M., 2006. Neural encoding correlates of high and low verbal memory performance. J. Psychophysiol. 20, 68–78.

Henson, R., 2005. A mini-review of fMRI studies of human medial temporal lobe activity associated with recognition memory. Q. J. Exp. Psychol. B 58, 340–360.

Henson, R.N.A., Hornberger, M., Rugg, M.D., 2005. Further dissociating the processes involved in recognition memory: an fMRI Study. J. Cogn. Neurosci. 17, 1058–1073.

Jackson, O., Schacter, D.L., 2004. Encoding activity in anterior medial temporal lobe supports subsequent associative recognition. NeuroImage 21, 456–462.

Kanwisher, N., Downing, P., Epstein, R., Kourtzi, Z., 2001. Functional neuroimaging of visual recognition. In: Cabeza, R., Kingstone, A. (Eds.), Handbook of Functional Neuroimaging of Cognition. The MIT Press, Cambridge, Massachusetts, pp. 109–151.

Kao, Y.-C., Davis, E.S., Gabrieli, J.D.E., 2005. Neural correlates of actual and predicted memory formation. Nat. Neurosci. 8, 1776–1783.

Kelley, W., Miezin, F., McDermott, K., Buckner, R., Raichle, M., Cohen, N., Ollinger, J., Akbudak, E., Conturo, T., Snyder, A., 1998. Hemispheric specialization in human dorsal frontal cortex and medial temporal lobe for verbal and nonverbal memory encoding. Neuron 20, 927–936.

Kensinger, E.A., Schacter, D.L., 2006. Amygdala activity is associated with the successful encoding of item, but not source, information for positive and negative stimuli. J. Neurosci. 26, 2564–2570.

Kensinger, E., Clarke, R., Corkin, S., 2003. What neural correlates underlie successful encoding and retrieval? A functional magnetic resonance imaging study using a divided attention paradigm. J. Neurosci. 23, 2407–2415.

Kensinger, E.A., Garoff-Eaton, R.J., Schacter, D.L., 2007. How negative emotion enhances the visual specificity of a memory. J. Cogn. Neurosci. 19, 1872–1887.

Kim, H., Cabeza, R., 2007. Differential contributions of prefrontal, medial temporal, and sensory-perceptual regions to true and false memory formation. Cereb. Cortex 17, 2143–2150.

Kim, H., Daselaar, S., Cabeza, R., 2010. Overlapping brain activity between episodic memory encoding and retrieval: roles of the task-positive and task-negative networks. NeuroImage 49, 1045–1054.

Kirchhoff, B.A., Wagner, A.D., Maril, A., Stern, C.E., 2000. Prefrontal-temporal circuitry for episodic encoding and subsequent memory. J. Neurosci. 20, 6173–6180.

Kirwan, C., Wixted, J., Squire, L., 2008. Activity in the medial temporal lobe predicts memory strength, whereas activity in the prefrontal cortex predicts recollection. J. Neurosci. 28, 10541–10548.

Laird, A., Fox, P., Price, C., Glahn, D., Uecker, A., Lancaster, J., Turkeltaub, P., Kochunov, P., Fox, P., 2005. ALE meta-analysis: controlling the false discovery rate and performing statistical contrasts. Hum. Brain Mapp. 25, 155–164.

Laird, A., Eickhoff, S., Li, K., Robin, D., Glahn, D., Fox, P., 2009a. Investigating the functional heterogeneity of the default mode network using coordinate-based meta-analytic modeling. J. Neurosci. 29, 14496–14505.

Laird, A.R., Lancaster, J.L., Fox, P.T., 2009b. Lost in localization? The focus is meta-analysis. NeuroImage 48, 18–20.

Lancaster, J., Tordesillas-Gutierrez, D., Martinez, M., Salinas, F., Evans, A., Zilles, K., Mazziotta, J., Fox, P., 2007. Bias between MNI and Talairach coordinates analyzed using the ICBM-152 brain template. Hum. Brain Mapp. 28, 1194–1205.

Lepage, M., Habib, R., Tulving, E., 1998. Hippocampal PET activations of memory encoding and retrieval: the HIPER model. Hippocampus 8, 313–322.

Li, C., Yan, P., Bergquist, K., Sinha, R., 2007. Greater activation of the "default" brain regions predicts stop signal errors. NeuroImage 38, 640–648.

Macrae, C.N., Moran, J.M., Heatherton, T.F., Banfield, J.F., Kelley, W.M., 2004. Medial prefrontal activity predicts memory for self. Cereb. Cortex 14, 647–654.

Maril, A., Simons, J.S., Mitchell, J.P., Schwartz, B.L., Schacter, D.L., 2003. Feeling-of-knowing in episodic memory: an event-related fMRI study. NeuroImage 18, 827–836.

Martin, A., 1999. Automatic activation of the medial temporal lobe during encoding: lateralized influences of meaning and novelty. Hippocampus 9, 62–70.

Mason, M., Norton, M., Van Horn, J., Wegner, D., Grafton, S., Macrae, C., 2007. Wandering minds: the default network and stimulus-independent thought. Science 315, 393–395.

Mazziotta, J., Toga, A., Evans, A., Fox, P., Lancaster, J., Zilles, K., Woods, R., Paus, T., Simpson, G., Pike, B., 2001. A probabilistic atlas and reference system for the human brain: International Consortium for Brain Mapping (ICBM). Philos. Trans. R. Soc. Lond. B Biol. 356, 1293–1322.

McCandliss, B., Cohen, L., Dehaene, S., 2003. The visual word form area: expertise for reading in the fusiform gyrus. Trends Cogn. Sci. 7, 293–299.

McKiernan, K., D'Angelo, B., Kaufman, J., Binder, J., 2006. Interrupting the "stream of consciousness": an fMRI investigation. NeuroImage 29, 1185–1191.

Miller, S.L., Celone, K., DePeau, K., Diamond, E., Dickerson, B.C., Rentz, D., Pihlajamäki, M., Sperling, R.A., 2008. Age-related memory impairment associated with loss of parietal deactivation but preserved hippocampal activation. Proc. Natl. Acad. Sci. U. S. A. 105, 2181–2186.

Mintzer, M., Snodgrass, J., 1999. The picture superiority effect: support for the distinctiveness model. Am. J. Psychol. 112, 113–146.

Mitchell, J.P., Macrae, C.N., Banaji, M.R., 2004. Encoding-specific effects of social cognition on the neural correlates of subsequent memory. J. Neurosci. 24, 4912–4917.

Morcom, A.M., Good, C.D., Frackowiak, R.S.J., Rugg, M.D., 2003. Age effects on the neural correlates of successful memory encoding. Brain 126, 213–229.

Nelson, D., Reed, V., Walling, J., 1976. Pictorial superiority effect. J. Exp. Psychol. Hum. Learn. 2, 523–528.

Nichols, E.A., Kao, Y.-C., Verfaellie, M., Gabrieli, J.D.E., 2006. Working memory and long-term memory for faces: evidence from fMRI and global amnesia for involvement of the medial temporal lobes. Hippocampus 16, 604–616.

Northoff, G., Qin, P., Nakao, T., 2010. Rest–stimulus interaction in the brain: a review. Trends Neurosci. 33, 277–284.

O'Kane, G., Insler, R., Wagner, A., 2005. Conceptual and perceptual novelty effects in human medial temporal cortex. Hippocampus 15, 326–332.

Otten, L., 2007. Fragments of a larger whole: retrieval cues constrain observed neural correlates of memory encoding. Cereb. Cortex 17, 2030–2038.

Otten, L.J., Rugg, M.D., 2001a. Task-dependency of the neural correlates of episodic encoding as measured by fMRI. Cereb. Cortex 11, 1150–1160.

Otten, L.J., Rugg, M.D., 2001b. When more means less: neural activity related to unsuccessful memory encoding. Curr. Biol. 11, 1528–1530.

Otten, L.J., Henson, R.N.A., Rugg, M.D., 2001. Depth of processing effects on neural correlates of memory encoding: relationship between findings from across- and within-task comparisons. Brain 124, 399–412.

Otten, L.J., Henson, R.N.A., Rugg, M.D., 2002. State-related and item-related neural correlates of successful memory encoding. Nat. Neurosci. 5, 1339.

Owen, A., McMillan, K., Laird, A., Bullmore, E., 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. Hum. Brain Mapp. 25, 46–59.

Paller, K., Wagner, A., 2002. Observing the transformation of experience into memory. Trends Cogn. Sci. 6, 93–102.

Park, H., Rugg, M., 2008. Neural correlates of successful encoding of semantically and phonologically mediated inter-item associations. NeuroImage 43, 165–172.

Park, H., Uncapher, M.R., Rugg, M.D., 2008. Effects of study task on the neural correlates of source encoding. Learn. Mem. 15, 417–425.

Prince, S.E., Tsukiura, T., Cabeza, R., 2007. Distinguishing the neural correlates of episodic memory encoding and semantic memory retrieval. Psychol. Sci. 18, 144–151.

Qin, S., Piekema, C., Petersson, K., Han, B., Luo, J., Fernandez, G., 2007. Probing the transformation of discontinuous associations into episodic memory: an event-related fMRI study. NeuroImage 38, 212–222.

Qin, S., Rijpkema, M., Tendolkar, I., Piekema, C., Hermans, E., Binder, M., Petersson, K., Luo, J., Fernandez, G., 2009. Dissecting medial temporal lobe contributions to item and associative memory formation. NeuroImage 46, 874–881.

Raichle, M., MacLeod, A., Snyder, A., Powers, W., Gusnard, D., Shulman, G., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. U. S. A. 98, 676–682.

Ranganath, C., Yonelinas, A.P., Cohen, M.X., Dy, C.J., Tom, S.M., D'Esposito, M., 2004. Dissociable correlates of recollection and familiarity within the medial temporal lobes. Neuropsychologia 42, 2–13.

Ranganath, C., Cohen, M.X., Brozinsky, C.J., 2005. Working memory maintenance contributes to long-term memory formation: neural and behavioral evidence. J. Cogn. Neurosci. 17, 994–1010.

Raye, C.L., Johnson, M.K., Mitchell, K.J., Reeder, J.A., Greene, E.J., 2002. Neuroimaging a single thought: dorsolateral PFC activity associated with refreshing just-activated information. NeuroImage 15, 447–453.

Raz, A., Buhle, J., 2006. Typologies of attentional networks. Nat. Rev. Neurosci. 7, 367–379.

Reber, P.J., Siwiec, R.M., Gitleman, D.R., Parrish, T.B., Mesulam, M.-M., Paller, K.A., 2002. Neural correlates of successful encoding identified using functional magnetic resonance imaging. J. Neurosci. 22, 9541–9548.

Rugg, M., Otten, L., Henson, R., 2002. The neural basis of episodic memory: evidence from functional neuroimaging. Philos. Trans. R. Soc. Lond. B Biol. 357, 1097–1110.

Schott, B.H., Richardson-Klavehn, A., Henson, R.N.A., Becker, C., Heinze, H.-J., Düzel, E., 2006. Neuroanatomical dissociation of encoding processes related to priming and explicit memory. J. Neurosci. 26, 792–800.

Sergerie, K., Lepage, M., Armony, J.L., 2005. A face to remember: emotional expression modulates prefrontal activity during memory formation. NeuroImage 24, 580–585.

Shrager, Y., Kirwan, C., Squire, L., 2008. Activity in both hippocampus and perirhinal cortex predicts the memory strength of subsequently remembered information. Neuron 59, 547–553.

Shulman, G.L., Fiez, J.A., Corbetta, M., Buckner, R.L., Miezin, F.M., Raichle, M.E., Petersen, S.E., 1997. Common blood flow changes across visual tasks: II. Decreases in cerebral cortex. J. Cogn. Neurosci. 9, 648–663.

Simons, J., Spiers, H., 2003. Prefrontal and medial temporal lobe interactions in long-term memory. Nat. Rev. Neurosci. 4, 637–648.

Sommer, T., Rose, M., Glascher, J., Wolbers, T., Büchel, C., 2005a. Dissociable contributions within the medial temporal lobe to encoding of object–location associations. Learn. Mem. 12, 343–351.

Sommer, T., Rose, M., Weiller, C., Büchel, C., 2005b. Contributions of occipital, parietal and parahippocampal cortex to encoding of object–location associations. Neuropsychologia 43, 732–743.

Spaniol, J., Davidson, P., Kim, A., Han, H., Moscovitch, M., Grady, C., 2009. Event-related fMRI studies of episodic encoding and retrieval: meta-analyses using activation likelihood estimation. Neuropsychologia 47, 1765–1779.

Spencer, T., Montaldi, D., Gong, Q., Roberts, N., Mayes, A., 2009. Object priming and recognition memory: dissociable effects in left frontal cortex at encoding. Neuropsychologia 47, 2942–2947.

Sperling, R., Chua, E., Cocchiarella, A., Rand-Giovannetti, E., Poldrack, R., Schacter, D.L., Albert, M., 2003. Putting names to faces: successful encoding of associative memories activates the anterior hippocampal formation. NeuroImage 20, 1400–1410.

Spreng, R., Mar, R., Kim, A., 2009. The common neural basis of autobiographical memory, prospection, navigation, theory of mind, and the default mode: a quantitative meta-analysis. J. Cogn. Neurosci. 21, 489–510.

Squire, L., Stark, C., Clark, R., 2004. The medial temporal lobe. Annu. Rev. Neurosci. 27, 279–306.

Squire, L., Wixted, J., Clark, R., 2007. Recognition memory and the medial temporal lobe: a new perspective. Nat. Rev. Neurosci. 8, 872.

Staresina, B.P., Davachi, L., 2006. Differential encoding mechanisms for subsequent associative recognition and free recall. J. Neurosci. 26, 9162–9172.

Stern, C., Corkin, S., Gonzalez, R., Guimaraes, A., Baker, J., Jennings, P.J., Carr, C.A., Sugiura, R.M., Vedantham, V., Rosen, B.R., 1996. The hippocampal formation participates in novel picture encoding: evidence from functional magnetic resonance imaging. Proc. Natl. Acad. Sci. U. S. A. 93, 8660–8665.

Talairach, J., Tournoux, P., 1988. Co-planar Stereotaxic Atlas of the Human Brain. Thieme, New York.

Tendolkar, I., Arnold, J., Petersson, K.M., Weis, S., Anke, B.-D., van Eijndhoven, P., Buitelaar, J., Fernández, G., 2007. Probing the neural correlates of associative memory formation: a parametrically analyzed event-related functional MRI study. Brain Res. 1142, 159–168.

Tsukiura, T., Mano, Y., Sekiguchi, A., Yomogida, Y., Hoshi, K., Kambara, T., Takeuchi, H., Sugiura, M., Kawashima, R., 2010. Dissociable roles of the anterior temporal regions in successful encoding of memory for person identity information. J. Cogn. Neurosci. 22, 2226–2237.

Tulving, E., Markowitsch, H., Craik, F., Habib, R., Houle, S., 1996. Novelty and familiarity activations in PET studies of memory encoding and retrieval. Cereb. Cortex 6, 71–79.

Turk-Browne, N.B., Yi, D.-J., Chun, M.M., 2006. Linking implicit and explicit memory: common encoding factors and shared representations. Neuron 49, 917–927.

Uncapher, M.R., Rugg, M.D., 2005. Encoding and the durability of episodic memory: a functional magnetic resonance imaging study. J. Neurosci. 25, 7260–7267.

Uncapher, M.R., Rugg, M.D., 2008. Fractionation of the component processes underlying successful episodic encoding: a combined fMRI and divided-attention study. J. Cogn. Neurosci. 20, 240–254.

Uncapher, M., Rugg, M., 2009. Selecting for memory? The influence of selective attention on the mnemonic binding of contextual information. J. Neurosci. 29, 8270–8279.

Uncapher, M., Wagner, A., 2009. Posterior parietal cortex and episodic encoding: insights from fMRI subsequent memory effects and dual-attention theory. Neurobiol. Learn. Mem. 91, 139–154.

Uncapher, M.R., Otten, L.J., Rugg, M.D., 2006. Episodic encoding is more than the sum of its parts: an fMRI investigation of multifeatural contextual encoding. Neuron 52, 547–556.

Van Essen, D., 2005. A population-average, landmark-and surface-based (PALS) atlas of human cerebral cortex. NeuroImage 28, 635–662.

Wager, T., Jonides, J., Reading, S., 2004. Neuroimaging studies of shifting attention: a meta-analysis. NeuroImage 22, 1679–1693.

Wager, T., Lindquist, M., Kaplan, L., 2007. Meta-analysis of functional neuroimaging data: current and future directions. Soc. Cogn. Affect. Neurosci. 2, 150–158.

Wagner, A.D., Davachi, L., 2001. Cognitive neuroscience: forgetting of things past. Curr. Biol. 11, R964–R967.

Wagner, A., Poldrack, R., Eldridge, L., Desmond, J., Glover, G., 1998. Material-specific lateralization of prefrontal activation during episodic encoding and retrieval. NeuroReport 9, 3711–3717.

Wagner, A.D., Schacter, D.L., Rotte, M., Koutstaal, W., Maril, A., Dale, A.M., Rosen, B.R., Buckner, R.L., 1998. Building memories: remembering and forgetting of verbal experiences as predicted by brain activity. Science 281, 1188–1191.

Weis, S., Klaver, P., Reul, J., Elger, C.E., Fernandez, G., 2004. Temporal and cerebellar brain regions that support both declarative memory formation and retrieval. Cereb. Cortex 14, 256–267.

Weissman, D., Roberts, K., Visscher, K., Woldorff, M., 2006. The neural bases of momentary lapses in attention. Nat. Neurosci. 9, 971–978.

Wittmann, B.C., Schott, B.H., Guderian, S., Frey, J.U., Heinze, H.-J., Düzel, E., 2005. Reward-related fMRI activation of dopaminergic midbrain is associated with enhanced hippocampus-dependent long-term memory formation. Neuron 45, 459–467.

Yonelinas, A., 1997. Recognition memory ROCs for item and associative information: the contribution of recollection and familiarity. Mem. Cogn. 25, 747–763.