

Differential Neural Activity in the Recognition of Old Versus New Events: An Activation Likelihood Estimation Meta-Analysis

Hongkeun Kim

Department of Rehabilitation Psychology, Daegu University, Gyeongsan, South Korea

Abstract: This study presents a meta-analysis comparing hit and correct rejection (CR) conditions across 48 fMRI studies. Old/new (hit > CR) effects associated most consistently with (1) components of the default-mode network, including the left angular gyrus, bilateral precuneus, and bilateral posterior cingulate regions, which may support the mental re-experiencing of an old event, or ecphory; (2) components of the cognitive-control network, involving the left dorsolateral and dorsomedial prefrontal cortex and bilateral intraparietal sulcus regions, which may mediate memory and non-memory control functions; and (3) the caudate nucleus, a key part of the brain's reward system that may support the satisfaction tied to target-detection. Direct comparisons of old/new effects between item versus source retrieval and "remember" versus "know" retrieval yielded three main sets of findings. First, default-mode network regions showed greater old/new effects in conditions associated with richer ecphoric processing. Second, cognitive-control network regions showed greater old/new effects in conditions associated with a greater demand for strategic-retrieval processing. Third, the caudate nucleus showed greater old/new effects in conditions tied to greater confidence in target-detection. New/old (CR > hit) effects most strongly associated with the bilateral medial temporal lobe, possibly reflecting greater encoding-related activity for new than for old items, and the right posterior middle temporal regions, possibly reflecting repetition-related neural priming for old items. In conclusion, neural activity distinguishing old from new events comprises an ensemble of multiple memory-specific activities, including encoding, retrieval, and priming, as well as multiple types of more general cognitive activities, including default-mode, cognitive-control, and reward processing. *Hum Brain Mapp* 34:814–836, 2013. © 2011 Wiley Periodicals, Inc.

Key words: fMRI; episodic memory; recognition memory; default-mode network; hippocampus; meta-analysis

Additional Supporting Information may be found in the online version of this article.

This work was supported by a Daegu University research grant in 2011.

*Correspondence to: Hongkeun Kim, Department of Rehabilitation Psychology, Daegu University, Gyeongsan, Gyeongsangbuk-Do 712-714, South Korea. E-mail: hongkn1@gmail.com

Received for publication 15 February 2011; Revised 18 August 2011; Accepted 2 September 2011

DOI: 10.1002/hbm.21474

Published online 23 November 2011 in Wiley Online Library (wileyonlinelibrary.com).

INTRODUCTION

Aim of the Study

The ability to distinguish old from new events is fundamental to episodic memory retrieval. The advent of functional neuroimaging has enabled researchers to compare neural activity during the correct recognition of a studied item (a hit) versus the correct non-recognition of a non-studied, novel item (a correct rejection [CR]). Researchers have shown that these old/new effects (hit > CR), also called "retrieval success" effects, associate with an extensive network of frontal and parietal regions [Spaniol et al.,

2009]. However, these effects have rarely implicated the medial temporal lobe [MTL; Henson, 2005], which plays a critical role in episodic memory. Researchers now generally accept that many retrieval-related activations are not memory-specific but rather mediate more general cognitive operations [Cabeza et al., 2003; Herron et al., 2004; Kim, 2010; O'Connor et al., 2010; Phillips et al., 2009; Sajonz et al., 2010; Vilberg and Rugg, 2009]. The present study aimed to provide a comprehensive meta-analysis of previously reported old/new and new/old (CR > hit) effects. This meta-analysis included only the data concerning visual information retrieval in healthy young adults. In addition to the generic purpose of integrating results across studies, this meta-analysis examined several specific hypotheses regarding old/new and new/old effects.

Old/New Effects

Brain regions associated with old/new effects may be broadly divided into two types: components of the default-mode network [e.g., Buckner et al., 2008; Raichle et al., 2001] and components of the cognitive-control network [e.g., Miller and Cohen, 2001; Vincent et al., 2008]. Both the default-mode and cognitive-control networks are evolving constructs in need of stricter validation, and at best these two networks cover most, but not all, regions implicated in old/new effects. Thus, the dichotomy does not represent a strict categorization of retrieval-related activity, but rather some useful heuristics that can guide further research. The author's motivation for proposing this dichotomy stemmed from the fact that some regions' old/new effects typically emerged as "less deactivations" (default-mode network), whereas other regions' old/new effects typically emerged as "more activations" [cognitive-control network; e.g., Buckner and Carroll, 2007; Fox et al., 2005; Golland et al., 2008; Kim et al., 2010]. This article's later sections review evidence for the two networks' involvement in old/new effects and also describe the author's hypothesis regarding the two networks' involvement in source versus item retrieval and "remember" versus "know" retrieval.

Default-mode network

Originally, researchers defined the default-mode network as the set of regions showing greater activity during the passive resting state than during attention-demanding cognitive tasks [Raichle et al., 2001]. This network's main components comprise the anteromedial prefrontal cortex (PFC), posterior cingulate cortex, precuneus, angular gyrus, and MTL. Recent research [Fox et al., 2005; Fransson, 2005; Golland et al., 2008] on spontaneous fluctuations of low-frequency (<0.1 Hz), blood oxygen level-dependent signals has found intrinsic, correlated activity among these regions, suggesting a distributed functional network. Although old/new effects rarely associate with all members of the default-mode network, the involvement of cer-

tain regions appears to be among the more robust findings. For example, old/new effects in posterior members of the default-mode network (i.e., posterior cingulate cortex, precuneus, and angular gyrus) are typically strong, and they remain robust across manipulations of many experimental variables, including cue modality, motor intentions, and target/non-target (old/new) ratio [Herron et al., 2004; Shannon and Buckner, 2004]. Furthermore, several recent studies [Addis et al., 2007; Hassabis and Maguire, 2007; Kim et al., 2010; Sajonz et al., 2010; Vannini et al., 2011; Vinogradov et al., 2006] have noted that old/new effects include components of the default-mode network.

The functions of the default-mode network are not yet fully understood. However, available evidence has indicated that, at its simplest, it supports internally oriented mentation, such as imagining the future (prospexion), conceiving of others' viewpoints (theory of mind), social cognition, mental navigation, deductive and inductive reasoning, and mind-wandering [Binder et al., 2009; Buckner and Carroll, 2007; Buckner et al., 2008; Gusnard, 2005; Hassabis et al., 2007; LeGrand and Ruby, 2009; Spreng et al., 2009]. Neuroimaging studies of episodic retrieval have provided evidence that vivid memories, such as recollection [Montaldi et al., 2006; Vilberg and Rugg, 2007; Yonelinas et al., 2005], high-confidence recognition [Daselaar et al., 2006; Kim and Cabeza, 2009], source memory [Lundstrom et al., 2005; Smith et al., 2005], and autobiographical remembering [Spreng et al., 2009; Svoboda et al., 2006] occur in association with components of the default-mode network. For example, Yonelinas et al. [2005] showed that recollection activated the anteromedial PFC, posterior cingulate cortex, angular gyrus, and MTL. Combining these two lines of evidence, the author hypothesized that the default-mode network's activity during episodic retrieval supports mental re-experiencing of an old event, or *ecphory* [Tulving, 1983]. Ecphoric experience during a correct "old" decision (hit) and its absence during a correct "new" decision (CR), may directly account for the default-mode network's involvement in old/new effects.

The present study addressed the following three issues regarding the default-mode network's involvement in old/new effects. First, the author investigated which default-mode network regions most consistently associated with old/new effects. Second, the author compared the default-mode network regions' old/new effects in item versus source retrieval. In item-retrieval tasks, participants try to remember items, with no other associated information; whereas, in source-retrieval tasks, they must remember both the item and the context in which it appeared [e.g., color or position; Johnson et al., 1993]. Thus, a source-retrieval task most likely involves richer ecphoric experience (objective recollection) than an item-retrieval task does. Thus, the author predicted that default-mode network regions' old/new effects would be stronger during a source- than during an item-retrieval task. Third, either vividly remembered specific contextual details (*recollection*) or a feeling of oldness, in the absence of contextual details

(*familiarity*), forms the basis of any memory [Yonelinas, 2002]. To distinguish between recollection and familiarity, studies use a Remember-Know procedure, which discriminates between old items that are “remembered” (recollection) and old items that are “known” (familiarity). Since, by definition, recollection implicates a richer ephoric experience than familiarity does, the author predicted that default-mode network regions would associate more strongly with remember/new effects (remember-hit > CR) than with know/new effects (know-hit > CR). In sum, the author’s hypotheses covered both objective recollection (source memory) and subjective recollection (“remember” memory) tasks.

Cognitive-control network

Cognitive-control demand is maximal when a task is novel, prone to interference, taxes working memory, involves conflict resolution, and/or needs strategic processing. Neuropsychological studies have indicated that the PFC is the most crucial site for cognitive control [Miller and Cummings, 1999]. In line with this evidence, functional neuroimaging studies [Badre and Wagner, 2004; Duncan and Owen, 2000; Koechlin et al., 1999; MacDonald et al., 2000; Miller and Cohen, 2001; Ridderinkhof et al., 2004] ascribed cognitive-control functions primarily to several PFC regions, mainly the dorsolateral and dorsomedial PFC. These PFC regions routinely activate during control-demanding cognitive tasks, including shifting attention [Derrfuss et al., 2005; Wager et al., 2004], working memory [Owen et al., 2005; Wager and Smith, 2003], and conflict resolution tasks [Laird et al., 2005b; Nee et al., 2007]. Neuroimaging studies have also provided evidence that cognitive control function is not unique to the PFC and, in fact, involves other regions in the brain, including the dorsal posterior parietal cortex [PPC; Brass et al., 2005; Corbetta and Shulman, 2002; Sohn et al., 2000]. Recent functional connectivity analysis studies [Cole and Schneider, 2007; Dosenbach et al., 2007; Seeley et al., 2007; Spreng et al., 2010; Vincent et al., 2008] have indicated that many cognitive-control regions show correlated activity during task performance, suggesting a distributed control network. Based on broad, qualitative similarities among these studies’ results, the author suggest that the cognitive-control network mainly consists of the dorsolateral PFC, dorsomedial PFC, and dorsal PPC regions.

Although old/new effects rarely associate with all members of the cognitive-control network, the involvement of specific regions have been among the more robust findings [Dobbins et al., 2002; Kahn et al., 2004; Lepage et al., 2000; Spaniol et al., 2009; Velanova et al., 2003; Wagner et al., 2005]. For example, old/new effects typically include activated regions in the dorsolateral PFC and/or intraparietal sulcus (IPS). Cognitive-control network regions’ old/new effects may involve two, broadly different, control functions. First, the regions’ old/new effects may relate to memory control functions. Although basic retrieval opera-

tions, such as cue specification and retrieval attempts, are common to both hits and CRs, more strategic retrieval processes, such as iterative searches and verification of retrieved information, may engage more consistently during a hit than during a CR [Buckner, 2003; Moscovitch, 1992]. Second, the regions’ old/new effects may also relate to non-memory control functions. An influential study by Herron et al. [2004] showed many regions’ old/new effects decreased or even reversed when old/new ratios increased [e.g., 25:75 to 75:25; see also Vilberg and Rugg, 2009]. Their results showed, with remarkably consistency, that cognitive-control regions, but not default-mode regions, were sensitive to old/new ratios. In an analogy to the “oddball paradigm,” O’Connor et al. [2010] supposed that an observer in a recognition memory test might expect to see new items (non-targets) rather than old items (targets). Based on this supposition, they suggested that a correct “old” decision, but not a correct “new” decision, might demand control operations, to countermand a general expectation that items should be new.

The present meta-analysis addressed the following three issues regarding the cognitive-control network’s involvement in old/new effects. First, the author investigated which cognitive-control network regions most consistently associated with old/new effects. Second, source retrieval, which involves the search for experimenter-specified contextual information, likely associates with a greater demand for controlled-retrieval processing relative to item retrieval [Dobbins et al., 2002; Donaldson et al., 2009; Kahn et al., 2004]. Thus, the author predicted that cognitive-control network regions’ old/new effects would be stronger during a source- than during an item-retrieval task. Consistent with this hypothesis, many prior studies [Dobbins and Han, 2006; Dobbins et al., 2003; Fan et al., 2003; Lundstrom et al., 2003] have reported that source retrieval activated components of the cognitive-control network more strongly than item retrieval did. For example, Dobbins and Han [2006] showed that multiple left PFC and parietal regions showed greater activity during attempted context retrieval, as compared with during item retrieval. Third, controlled-retrieval processing should engage strongly when memories are weak or familiarity-based; whereas there should be little need for controlled retrieval when the memory signal is maximal or recollection-based [Kim and Caneza, 2009; Moscovitch, 1992; Yonelinas et al., 2005]. Thus, the author predicted that cognitive-control network regions would associate more strongly with know/new effects than with remember/new effects. Consistent with this hypothesis, a recent meta-analysis of know/remember (know > remember) contrasts [Kim, 2010] found these associated mainly with the dorsal frontoparietal regions.

In sum, as with the author’s hypotheses relating to the default-mode network, the author’s hypotheses for the cognitive-control network covered both objective and subjective recollection tasks. Many prior investigations have explicitly or implicitly addressed hypotheses similar to the

present ones relating to item versus source memory or “remember” versus “know” memory. However, these studies have rarely entertained such hypotheses in terms of network affiliations, instead focusing on a few specific regions of interest, such as the MTL [Daselaar et al., 2006; Eldridge et al., 2000], PFC [Achim and Lepage, 2005; Dobbins et al., 2002], and parietal regions [Ciaramelli et al., 2008; Lundstrom et al., 2005]. Thus, the present approach’s main strength lies in its emphasis on a more global, system-wide model, as well as on the meta-analytic integration of convergent findings across studies.

Material-type effects

The majority of prior studies on old/new effects [Chee et al., 2004; de Zubicaray et al., 2005; Henson et al., 2000] used verbal materials (i.e., words) as memoranda and found that old/new effects were predominantly left-lateralized. The hemispheric specialization principle indicates the processing of verbal materials depends more on left- than on right-hemispheric processing; whereas the processing of nonverbal, pictorial materials involves more right- than left-hemispheric processing [Springer and Deutsch, 1997]. Thus, the predominant left-lateralization of old/new effects found in prior studies may be due to the widespread use of verbal materials, rather than to retrieval-related processing having any greater intrinsic association with the left-hemisphere than with the right-hemisphere. On the other hand, Guerin and Miller [2009; see also Leube et al., 2003; Leveroni et al., 2000] reported a predominance of left-lateralization for parietal and other old/new effects, irrespective of stimulus type, suggesting that the left hemisphere plays a specialized role in retrieval processing. To address this issue, the author compared the old/new effects found by studies using verbal versus those using pictorial materials (e.g., pictures of common objects or faces).

New/Old Effects

A study by Tulving et al. [1996] was one of the first to describe brain regions that responded to new items to a greater degree than they did to old items. Their findings indicated that the “novelty” activations occurred in the right MTL region and bilaterally, in the temporal and parietal regions. Though relatively few neuroimaging studies have focused on new/old (CR > hit) effects, researchers have generally accepted these effects’ relevance to understanding memory and other cognitive functions [Donaldson et al., 2001; Kahn et al., 2004]. However, two competing hypotheses for new/old effects exist [Habib, 2001]. First, Tulving et al. [1996] suggested the encoding system is biased to process novel, as opposed to familiar, information, because the system evolved to register information having high survival value. According to this “novelty-encoding” hypothesis, new/old effects may reflect greater encoding-related activity for new than for

old items. Supporting the hypothesis, new items presented during a recognition memory test lead to “incidental” memory formation and subsequent memory effects [Buckner et al., 2001; Stark and Okado, 2003]. Second, studies of implicit memory tasks have shown repetition-related “deactivations” for old items, or *neural priming*, which may support behavioral priming effects [Henson and Rugg, 2003]. Neural priming may also play a role in explicit memory tasks, by providing a familiarity signal [Daselaar et al., 2006; Gonsalves et al., 2005; Henson et al., 2003]. Most likely, new/old effects reflect both novelty-encoding (activations for new items) and neural priming (deactivations for old items) effects, although one factor may be more important than the other is in a given region.

The present meta-analysis addressed the following two issues regarding new/old effects. First, the author investigated which brain regions most consistently associated with new/old effects. This investigation was crucial, since studies have elucidated relatively little about such regions. The author was particularly interested in whether the effects included an MTL region. As noted before, old/new effects have rarely implicated an MTL region, despite its well-established role in episodic memory [Squire et al., 2004]. Regarding this negative finding, certain studies [Buckner et al., 2001; Stark and Okado, 2003] proposed that retrieval-related MTL activity (old > new) occurs, but encoding-related MTL activity (new > old) offsets or even reverses it. A finding of MTL new/old effects in the current study would be consistent with this view and would also suggest that a low signal-to-noise ratio, susceptibility to MRI artifacts, or other nuisance factors play relatively minor roles in the MTL’s lack of involvement in old/new effects. Finally, to address possible effects of material-type on new/old effects, the author compared new/old effects in the studies using verbal versus those using pictorial materials. A limited number of available studies precluded meta-analysis of other variables of potential interest (e.g., item vs. source retrieval).

Meta-Analysis

The present study’s principal methodology was a quantitative (i.e., statistical) meta-analysis of the relevant literature. Meta-analysis has played an increasingly important role in identifying significant concordances in brain activity patterns across many neuroimaging studies [Wager et al., 2007]. As the number of neuroimaging studies continues to grow, at a rapidly accelerating pace, discerning convergent and divergent findings among studies becomes increasingly important, as well as increasingly harder [Laird et al., 2009]. A quantitative meta-analysis is a uniquely valuable tool for accomplishing this goal. The results of the present meta-analyses identified the brain regions associating most reliably with old/new or new/old effects, as well as those most consistently exhibiting modulation of these effects by some commonly used

experimental variables (source versus item retrieval, recollection vs. familiarity, and verbal vs. pictorial). Although several meta-analysis studies on old/new effects emerged recently, most used a tabular method [Skinner and Fernandes, 2007], often focusing exclusively on specific regions of interest, such as the MTL [Diana et al., 2007; Henson, 2005] or PPC [Ciaramelli et al., 2008; Hutchinson et al., 2009; Vilberg and Rugg, 2008]. Those that used a quantitative as well as a whole-brain approach [Kim, 2010; Spaniol et al., 2009] only partially addressed issues that overlap the current study. The author discusses some relevant findings from these studies later, in the context of the current study's findings.

MATERIALS AND METHODS

Study/Contrast Selection

To isolate all fMRI studies reporting an old/new (hit > CR), remember/new (remember-hit > CR), know/new (know-hit > CR), or new/old (CR > hit) contrast, the author completed multiple literature searches via PubMed. Additionally, the author performed a reference list check of recent neuroimaging memory study reviews [Ciaramelli et al., 2008; Diana et al., 2007; Spaniol et al., 2009; Uncapher and Wagner, 2009; Vilberg and Rugg, 2008], to identify relevant studies the online database search did not reveal. These search results were filtered to include only studies that (1) tested healthy, young participants; (2) presented retrieval cues via a visual modality; (3) performed whole-brain analyses; and (4) reported coordinate-based data analyses. Ultimately, the author selected a set of 48 independent studies, involving 767 participants, for inclusion in the meta-analyses. The meta-analyses examined 38 old/new, 8 remember/new, 5 know/new, and 19 new/old contrasts. For each contrast type, Appendix lists the selected studies, along with the number of participants, the retrieval-cue material, the type of retrieval (item vs. source), the encoding task, the retention interval, and the number of reported foci for each study.

Additional criteria for selecting a study/contrast were as follows. First, in selecting subjective recollection studies, the author included studies using a standard remember-know procedure as well as those using its slight variant, i.e., a response classification in terms of high-confidence (HC) versus low-confidence (LC). Although they lack a one-to-one correspondence, HC versus LC recognition, on average, aligns rather closely with "remember" versus "know" recognition, respectively [Dunn, 2004; Wixted and Stretch, 2004]. Second, in selecting contrasts from subjective recollection studies, the author included remember/new and know/new contrasts but excluded any remember/know or know/remember contrasts, both because the author's previous study [Kim, 2010] included a meta-analysis of these contrasts and because the current study focused primarily on distinguishing "old" versus "new" recognition, rather than the two types of "old" recognition.

Third, in selecting contrasts from objective recollection studies, the author included source-correct (SC)-hit/new contrasts but excluded source-incorrect (SI)-hit/new and (SC + SI)-hit/new contrasts, both because relatively few studies reported them and because the current study focused on *successful* source retrieval (see below). Fourth, a minor subset of the selected studies included both young and old participants and reported common, but not separate, contrasts for the two age groups. In such cases, the author selected the common contrasts for meta-analysis. Finally, another minor subset of the selected studies reported contrasts by using a regular statistical threshold, as well as a similar contrast using a more lenient threshold. The author excluded the activation foci from the latter contrasts, which usually targeted specific regions of interest. One example of such is the study by de Zubicaray et al. [2005], who used a statistical threshold of 0.001 for their whole-brain analysis but used .005 for their a priori regions of interest.

Data Analyses

Old/new effects

The author performed the following three types of meta-analyses on old/new (hit > CR) contrasts. The first analyzed all 38 included studies together. The second was a set of *subgroup* meta-analyses, each involving a subset of included studies. Few dimensions by which one might distinguish the selected studies to ensure a meaningful analysis were available. One such was whether the retrieval cue was verbal (words) or pictorial (e.g., face photos). Another dimension was whether the retrieval task was an item- or a source-memory task. Crossing these two dimensions classified the selected studies into four subgroups: verbal-item ($n = 22$), pictorial-item ($n = 9$), verbal-source ($n = 5$), and pictorial-source ($n = 2$). This portion of the study comprised three subgroup meta-analyses, one each for the verbal-item, pictorial-item, and verbal-source subgroups. The pictorial-source subgroup could not accommodate this analysis, due to the limited number of available studies. The third meta-analysis type, a *subtraction* meta-analysis, directly compared pairs of study subgroups. Testing the effects of the material's nature (verbal vs. pictorial) required a subtraction meta-analysis on the verbal-item subgroup versus the pictorial-item subgroup. Testing the effects of retrieval type (item vs. source) required a subtraction meta-analysis on the verbal-item subgroup versus the versus-source subgroup.

Remember-HC/new and know-LC/new effects

In this category, the author also performed three meta-analyses. The first meta-analysis examined all eight remember-HC/new (remember-HC hit > CR) studies together. The second analyzed all five know-LC/new (know-LC hit > CR) studies together. The third, a

subtraction meta-analysis, directly compared remember-HC/new and know-LC/new effects. The remember-HC/new or know-LC/new effects could not accommodate a subgroup analysis, due the limited number of available studies.

New/old effects

Most of the selected studies reported a CR > hit contrast, but a minor subset reported a CR > remember-hit contrast or CR > know-hit contrast. A meta-analysis of new/old effects examined the three types of contrasts together, because the limited number of available studies did not require separate analyses. The author performed three types of meta-analyses on new/old contrasts. The first analyzed all 19 studies together. The second was a set of *subgroup* meta-analyses, each involving a subset of the included studies. To perform these, the author divided the selected new/old studies into four subgroups: verbal-item ($n = 10$), pictorial-item ($n = 6$), verbal-source ($n = 1$), and pictorial-source ($n = 2$). This portion of the study comprised two subgroup meta-analyses, one each for the verbal-item and pictorial-item subgroups. The third type of meta-analysis was a subtraction meta-analysis on the verbal-item subgroup versus the pictorial-item subgroup, to address how material-type affected new/old effects.

A subtraction meta-analysis between groups of unequal size could bias the results, because a larger group of studies would have greater statistical power to detect activation [Owen et al., 2005]. To address this issue, the author randomly selected a subsample of the larger group and thus made the comparison between two equal-sized groups. For example, to compare old/new effects between the verbal-item subgroup ($n = 22$) and the pictorial-item subgroup ($n = 9$), the author randomly selected nine studies from the verbal-item subgroup for the comparison. Random selection was applied in a flexible manner, so the selection would be unbiased with regard to the proportions of studies reporting relatively high versus relatively low numbers of activation foci. Random selection for the subtraction analysis between remember/new and know/new effects also balanced the proportions of studies using verbal versus pictorial materials.

Meta-Analysis Techniques

In this study, the author performed activation likelihood estimation (ALE) meta-analyses, as described by Laird et al. [2005a], performing all data processing via the GingerALE program, Version 1.1 (available at: www.brainmap.org). The author determined the spatial normalization space for each study and converted all activation foci reported in Montreal Neurological Institute (MNI) coordinates, into Talairach coordinates [Talairach and Tournoux, 1988]. Individual studies' activation foci were modeled as peaks of three-dimensional Gaussian probability distributions, with a full-width half-maximum (FWHM) of 10 mm.

Then, the author summed the three-dimensional Gaussian distributions to create an ALE map estimating each voxel's activation likelihood across the entire set of studies. To determine the ALE map's statistical significance, the author employed a permutation test of randomly generated foci, computing 5,000 permutations using the same FWHM value and the same number of foci as in the ALE map. For each subtraction meta-analysis, the author carried out a permutation test of the difference between the two subgroups. The author thresholded all permutation tests, with a false-discovery rate (FDR) value of $P < 0.05$ [Genovese et al., 2002] and with clusters of suprathreshold voxels exceeding 400 mm^3 . For visualizing the meta-analytic results, the author projected the thresholded ALE maps onto either an inflated population average landmark surface (PALS), via CARET software [Van Essen, 2005], or an International Consortium for Brain Mapping (ICBM) template, via MANGO software (available at: <http://ric.uthscsa.edu/mango>).

The present study includes the caveat that some subgroup meta-analyses contained relatively few studies. A meta-analysis based on a small number of studies can potentially yield unreliable results, reducing the meta-analysis's statistical power to detect significant activation concordances while increasing the risk of outliers biasing the results. To reduce the risk of such, the author ensured that all meta-analyses involved at least five independent studies (in the case of subtraction analyses, at least five studies in each subgroup) and had a relatively conservative spatial extent threshold (400 mm^3). However, one should still take with caution the results of those subgroup meta-analyses involving few studies; they need further confirmation in future meta-analyses that include a larger number of studies.

RESULTS

Old/New Effects

All included studies

Table I and Figure 1 show the ALE meta-analysis results for all included studies ($n = 38$). Old/new effects associated most consistently with seven neural regions: the left angular gyrus (Brodmann area [BA] 39, 40), bilateral precuneus (BA 7), bilateral posterior cingulate cortex (BA 23, 31), left dorsolateral PFC (BA 6, 8, 9, 46, 10), left dorsomedial PFC (BA 6, 8), bilateral dorsal PPC (BA 7, 19), and bilateral caudate nucleus. Most bilateral clusters were predominantly left-lateralized. The left dorsolateral PFC cluster, which was the largest, included both the anterior and posterior extent of the middle frontal gyrus and extended into the inferior frontal gyrus's dorsal extent. The broad, qualitative similarity to prior descriptions of the default-mode network indicated three of the seven clusters (left angular gyrus, bilateral precuneus, and bilateral posterior cingulate cortex) were components of the default-mode

TABLE I. Old/new effects: Results from an ALE meta-analysis of all included studies

Lobe	Region	H	BA	Talairach			Volume (mm ³)	ALE (×10 ³)
				x	y	z		
Frontal	Dorsolateral PFC, insula	L	6, 8, 9, 46, 10	-32	18	2	21,648	42.2
	Dorsolateral PFC	R	10	28	52	12	504	18.3
	Dorsomedial PFC	L	6, 8	-6	24	44	3,752	40.8
	Insula	R	—	28	18	8	496	19.3
Temporal	MTG	L	21	-60	-40	-8	936	22.3
Parietal	Angular gyrus, dorsal PPC	L	39, 40, 7, 19	-36	-64	42	13,640	57.3
	Dorsal PPC	R	7, 19	32	-70	34	5,256	43.5
	Posterior cingulate cortex	B	23, 31	-4	-40	32	5,288	37.5
	Precuneus	B	7, 31	-6	-70	30	10,152	66.5
Sublobar	Caudate nucleus	L	—	-10	2	10	4,992	31.7
	Caudate nucleus	R	—	10	2	16	4,504	36.7

ALE, activation likelihood estimation; BA, Brodmann area; H, hemisphere; MTG, middle temporal gyrus; PFC, prefrontal cortex; PPC, posterior parietal cortex.

network. Similarly, three other clusters (left dorsolateral PFC, left dorsomedial PFC, and bilateral dorsal PPC) were

components of the cognitive-control network. More minor clusters occurred in the left anterior insula, left middle temporal cortex (BA 21), and right anterior dorsolateral PFC (BA 10).

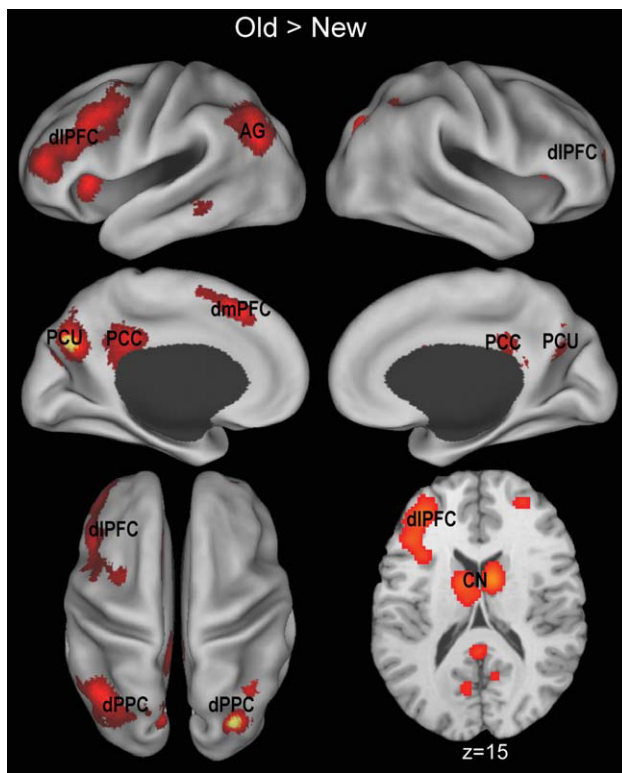


Figure 1.

Brain regions associated with old/new effects in a meta-analysis involving all included studies. AG, angular gyrus; CN, caudate nucleus; dIPFC, dorsolateral prefrontal cortex; dmPFC, dorsomedial prefrontal cortex; dPPC, dorsal posterior parietal cortex; PCC, posterior cingulate cortex; PCU, precuneus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

Item versus source retrieval

Table II and Figure 2 show the meta-analysis results for the verbal-item subgroup ($n = 22$), the verbal-source subgroup ($n = 5$), and the subtraction analysis between the two subgroups. In both subgroups, major old/new effects occurred within a seven-region network, identified via the meta-analysis of the whole group. Each involved the left angular gyrus, left precuneus, bilateral posterior cingulate cortex, left dorsolateral PFC, left dorsomedial PFC, left IPS, and bilateral caudate nucleus (see Fig. 2A,B). Though the verbal-item subgroup clusters were generally larger than the verbal-source subgroup clusters were, interpretation of these differences requires caution, given that statistical power to detect activations was greater in the verbal-item subgroup. The subtraction meta-analyses below circumvented this problem by comparing two equal-sized subgroups. The subtraction analyses showed that the default-mode network regions (the left precuneus and bilateral posterior cingulate cortex), cognitive-control network regions (left dorsolateral PFC, left dorsomedial PFC, and left IPS), and the caudate nucleus each associated with greater old/new effects during a source-retrieval task than they did during an item-retrieval task (see Fig. 2C). No regions significantly associated with the reverse effects: i.e., greater old/new effects during an item- than during a source-retrieval task.

Verbal versus pictorial material

Table III and Figure 3 show the meta-analysis results for the pictorial-item subgroup ($n = 9$) and the subtraction analysis between the verbal-item and the pictorial-item

TABLE II. Old/new effects in the verbal-item and verbal-source subgroups and variable old/new effects between the two subgroups

Lobe	Region	H	BA	Talairach			Volume (mm ³)	ALE ($\times 10^3$)
				x	y	z		
Verbal-item: old > new								
Frontal	Dorsolateral PFC	L	10, 46	-38	44	12	3,984	22.0
	Dorsolateral PFC	L	9, 6	-42	10	40	4,512	24.2
	Insula	L	—	-32	16	4	2,120	26.0
	Insula	R	—	28	18	6	480	14.4
	Dorsomedial PFC	L	8	-6	20	46	1,296	20.3
	Dorsomedial PFC	L	9	-6	32	30	776	16.8
Parietal	Angular gyrus, intraparietal sulcus	L	39, 40, 7, 19	-44	-62	42	9,456	32.1
	Intraparietal sulcus	R	19	32	-70	34	5,360	33.2
	Posterior cingulate cortex	B	31, 23	-4	-36	32	3,960	23.8
Sublobar	Precuneus	L	7, 31	-6	-70	30	4,944	40.7
	Caudate nucleus	L	—	-10	0	10	7,360	21.1
	Caudate nucleus	R	—	8	12	2	6,80	17.5
	Thalamus	L	—	-10	-36	4	1,144	14.0
	Midbrain	L	—	-14	-30	-10	688	16.0
Verbal-source: old > new								
Frontal	Dorsolateral PFC, insula	L	9, 46	-42	22	24	5,784	19.0
	Dorsolateral PFC	L	6	-32	-2	58	488	10.0
	Dorsomedial PFC	L	6	-6	16	48	1,992	15.9
Parietal	Angular gyrus, intraparietal sulcus	L	39, 7	-36	-64	44	2,544	14.3
	Posterior cingulate cortex	B	23	2	-34	30	1,832	12.3
	Precuneus	L	7, 31	-6	-70	30	2,056	18.0
Sublobar	Caudate nucleus	R	—	10	0	18	992	12.6
	Caudate nucleus	L	—	-12	2	10	592	12.0
	Thalamus	L	—	-6	-16	12	416	8.3
	Cerebellum	R	—	34	-66	-30	528	10.3
Verbal-source old/new > verbal-item old/new								
Frontal	Dorsolateral PFC	L	46, 9	-42	22	24	3,352	17.9
	Dorsomedial PFC	L	8	-8	16	46	1,072	12.3
Parietal	Intraparietal sulcus	L	7	-36	-62	46	1,064	10.7
	Posterior cingulate cortex	B	31	4	-34	28	608	10.9
	Precuneus	L	7	-8	-68	28	808	11.8
Sublobar	Caudate nucleus	R	—	10	0	20	456	10.8
	Cerebellum	R	—	34	-66	-30	504	10.3
Verbal-item old/new > verbal-source old/new								
No significant activation								

For abbreviations, see Table I.

subgroups. The pictorial-item subgroup also mainly showed old/new effects within a seven-region network that involved the left angular gyrus, left posterior cingulate cortex, bilateral precuneus, bilateral dorsolateral PFC, left dorsomedial PFC, left IPS, and right caudate nucleus (see Fig. 3A). The subtraction analyses showed that the regions associated with greater old/new effects for verbal than for pictorial materials (the red regions in Fig. 3B), being the left dorsolateral PFC, left insula, left angular gyrus, and left precuneus regions, were larger than the regions associated with the reverse, i.e., greater old/new effects for pictorial than for verbal materials (the blue regions in Fig. 3B), which comprised a right dorsolateral PFC region.

Remember-HC/New and Know-LC/New Effects

Table IV and Figure 4 show the meta-analysis results for remember-HC/new effects ($n = 8$), know-LC/new effects ($n = 5$), and the subtraction analysis between the two effects. First, remember-HC/new effects associated most consistently with the left angular gyrus (BA 39), left precuneus (BA 7, 31), left posterior cingulate cortex (BA 23, 31), left posterior dorsolateral PFC (BA 6), left dorsomedial PFC (BA 6, 8), left IPS (BA 7), and right caudate nucleus (see Fig. 4A). Second, know-LC/new effects associated most consistently with the left dorsolateral PFC (BA 9, 46, 10), left IPS (BA 7), and bilateral superior PPC/precuneus (BA 7; see Fig. 4B). Third, the subtraction analyses showed

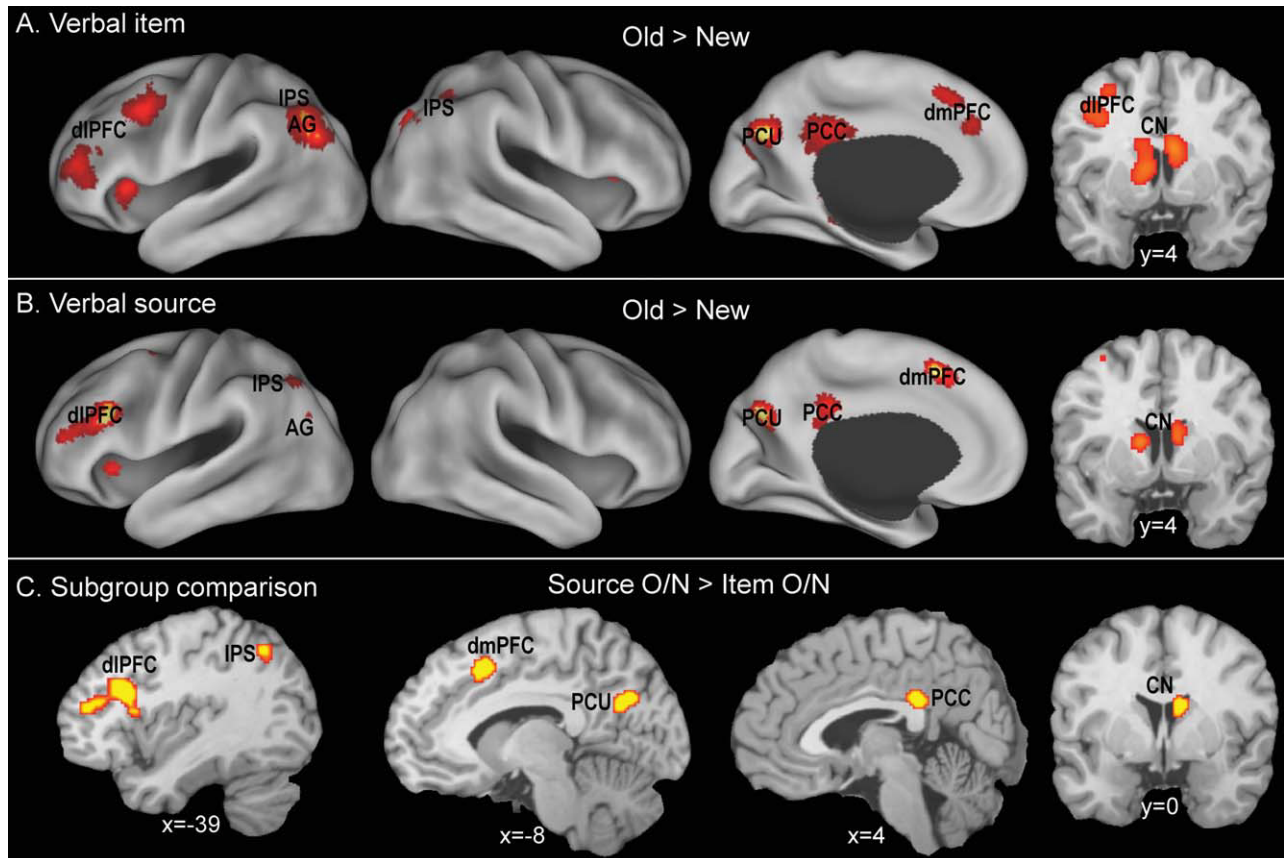


Figure 2.

Brain regions associated with old/new effects in the verbal-item (A) and verbal-source (B) subgroups and with greater old/new effects for the verbal-source subgroup than for the verbal-item subgroup (C). IPS, intraparietal sulcus. For other abbreviations, see Figure 1. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

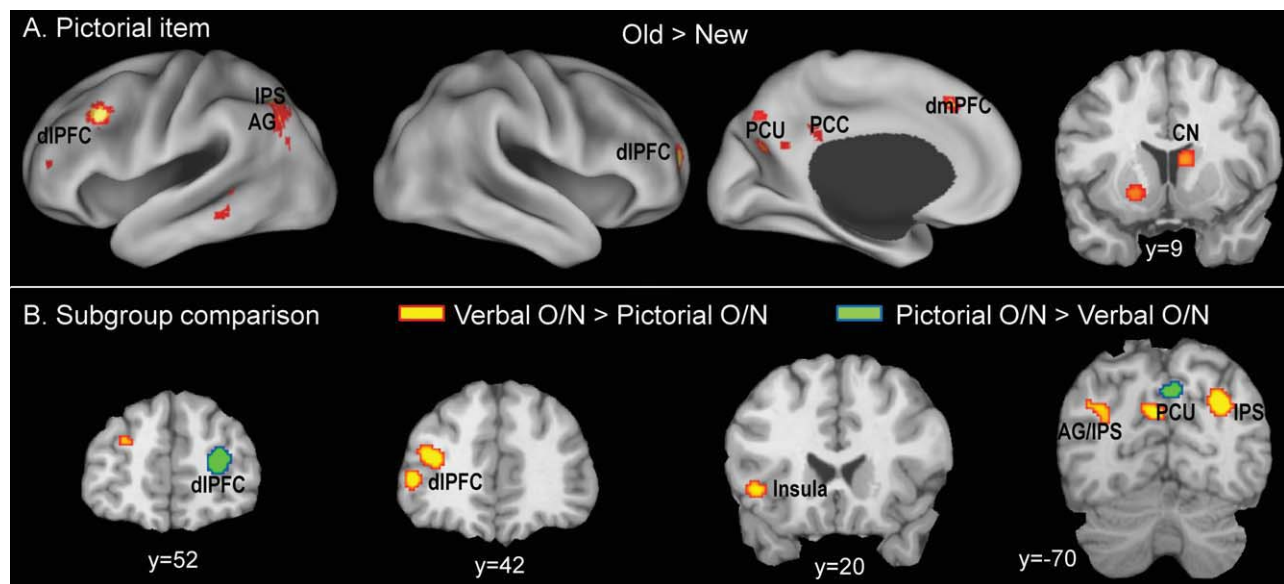


Figure 3.

Brain regions associated with old/new effects in the pictorial-item subgroup (A), and variable old/new effects in a comparison of verbal-item and pictorial-item subgroups (B). IPS, intraparietal sulcus. For other abbreviations, see Figure 1. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE III. Old/new effects in the pictorial-item subgroup and variable old/new effects between the verbal-item and pictorial-item subgroup

Lobe	Region	H	BA	Talairach			Volume (mm ³)	ALE (×10 ³)
				<i>x</i>	<i>y</i>	<i>z</i>		
Pictorial-item: old > new								
Frontal	Dorsolateral PFC	R	10	26	52	12	1,136	15.3
	Dorsolateral PFC	L	46	-34	46	8	584	10.4
	Dorsolateral PFC	L	9	-42	18	34	1,120	14.6
	Dorsolateral PFC	R	6	26	16	48	488	10.4
	Dorsomedial PFC	L	8	-6	26	40	712	10.2
Temporal	MTG	L	21	-60	-38	-10	584	10.1
Parietal	Angular gyrus, intraparietal sulcus	L	39, 7, 19	-40	-60	38	3,600	15.6
	Intraparietal sulcus	L	7	-46	-42	36	536	10.0
	Posterior cingulate cortex	L	31	-8	-44	28	456	8.4
	Posterior cingulate cortex	L	31	-12	-64	26	928	11.8
	Precuneus	B	7	2	-74	38	1,432	14.0
Sublobar	Caudate nucleus	R	—	10	10	12	480	10.0
	Putamen	L	—	-18	8	-8	440	9.4
Verbal-item old/new > pictorial-item old/new								
Frontal	Dorsolateral PFC	L	10	-20	58	22	672	11.4
	Dorsolateral PFC	L	46	-34	42	16	800	13.8
	Dorsolateral PFC	L	46	-46	40	4	880	12.9
	Dorsolateral PFC	L	6, 9	-40	10	42	1,640	15.6
	Insula	L	—	-44	18	-4	472	11.3
Parietal	Angular gyrus, intraparietal sulcus	L	39, 7	-32	-62	38	816	12.1
	Intraparietal sulcus	R	7	30	-70	34	1,208	17.4
	Precuneus	L	7	-6	-64	32	960	13.0
Pictorial-item old/new > verbal-item old/new								
Frontal	Dorsolateral PFC	R	10	26	52	12	936	-15.3
Parietal	Precuneus	B	7	2	-72	40	480	-10.3

For abbreviations, see Table I.

that default-mode network regions (left angular gyrus, left precuneus, and left posterior cingulate cortex) showed a greater association with remember-HC/new than with know-LC/new effects; whereas cognitive-control network regions (left anterior dorsolateral PFC and bilateral superior PPC/precuneus) associated with the reverse effects, i.e., greater know-LC/new than remember-HC/new effects (see Fig. 4C). Though the caudate nucleus associated with remember-HC/new effects and not with know-LC/new effects, the subtraction analysis did not detect this difference.

New/Old Effects

Table V and Figure 5A show the ALE meta-analysis results for all included studies ($n = 19$). There were only two major clusters associated with new/old effects, one involving the MTL and the other involving a right posterior middle temporal gyrus (MTG) region and its transition to the occipital cortex (BA 37, 19). The MTL cluster bilaterally involved both the hippocampus and amygdala. Further minor clusters occurred in the right dorsomedial PFC (BA 9, 6) and right postcentral cortex (BA 2). Table V

and Figure 5B–D show the meta-analysis results for the verbal-item subgroup ($n = 10$), the pictorial-item subgroup ($n = 6$), and the subtraction analysis between the two subgroups. Focusing on the two major “new/old” clusters, identified by the meta-analysis of the whole group, the author found new/old effects for the verbal-item subgroup associated with the bilateral amygdala and right posterior MTG (see Fig. 5B) and those for the pictorial-item subgroup associated with the bilateral hippocampus and right posterior MTG (see Fig. 5C). The subtraction analysis indicated that the bilateral hippocampus and right posterior MTL regions associated with greater new/old effects for pictorial than for verbal materials (see Fig. 5D).

Additional Analyses

The subtraction meta-analyses reported above considered a random selection of studies within a larger group of studies, to equalize the number of studies within each group. One limitation of this approach is that the results could be idiosyncratic to a particular random selection. To address this issue, for each subtraction meta-analysis, the author performed two additional analyses, each using a

different random selection of studies. The Supporting Information, available online, shows these results. The additional subtraction analyses between verbal-source versus verbal-item old/new effects (see Supporting Information Table S1), remember-HC/new versus know-LC/new effects (see Supporting Information Table S3), and verbal-item versus pictorial-item new/old effects (see Supporting Information Table S4) yielded results generally consistent with the original results, with a few minor exceptions. For example, both of the additional subtraction analyses involving verbal-source and verbal-item old/new effects indicated that default-mode network regions (left precuneus and bilateral posterior cingulate cortex), cognitive-control network regions (left dorsolateral PFC, left dorsomedial PFC, and left IPS), and the caudate nucleus each associated with greater old/new effects during source-retrieval than they did during item-retrieval tasks. However, the additional subtraction analyses involving verbal-item versus pictorial-item old/new effects yielded results showing greater variability (see Supporting Information Table S2), indicating a particular random selection drove certain effects. In this subtraction analysis, consistent findings across all three analyses were limited to the left dorsolateral PFC (BA 46), left insula, and left angular gyrus (BA 39), each associated with greater old/new effects for verbal than for pictorial materials, and to a right dorsolateral PFC region (BA 10), which associated with greater old/new effects for pictorial than for verbal materials.

DISCUSSION

Old/New Effects

These results reveal that old/new effects associated most consistently with seven neural regions: the left angular gyrus, bilateral precuneus, bilateral posterior cingulate cortex, left dorsolateral PFC, left dorsomedial PFC, bilateral IPS, and bilateral caudate nucleus. These regions largely show consistency with those regions one previous meta-analysis of old/new effects found [Spaniol et al., 2009]. These regions may be broadly categorized into three types: (1) default-mode network regions, involving the first three of the seven regions; (2) cognitive-control network regions, involving the next three regions; and (3) the caudate nucleus. The author discusses each of these categories separately below.

Default-mode network: Ecphory

The regions most consistently associating with old/new effects include three default-mode network regions: the left angular gyrus, bilateral precuneus, and bilateral posterior cingulate cortex. Combining evidence showing the default-mode network supports internally oriented mentation [Fox et al., 2005; Fransson, 2005; Golland et al., 2008] with evidence showing vivid memories, such as recollection [Montaldi et al., 2006; Vilberg and Rugg, 2007; Yoneli-

nas et al., 2005], high-confidence recognition [Daselaar et al., 2006; Kim and Cabeza, 2009], source memory [Lundstrom et al., 2005; Smith et al., 2005], and autobiographical remembering [Spreng et al., 2009; Svoboda et al., 2006], involve components of the default-mode network, the author hypothesize that, during episodic retrieval, the network supports mental re-experiencing of the old event, or *ecphory*. The current comparisons between old/new effects for item- versus source-retrieval and for remember-HC versus know-LC provide supporting evidence for this hypothesis. First, default-mode network regions, involving the left precuneus and bilateral posterior cingulate cortex, show greater old/new effects during a source-retrieval task than they show during an item-retrieval task (see Fig. 2C), likely reflecting richer ecphoric processing during source than item retrieval. Second, default-mode network regions, including the left angular gyrus, left posterior cingulate cortex, and bilateral precuneus, associate more strongly with remember-HC/new than with know-LC/new effects (Fig. 4C), likely reflecting greater ecphoric processing during “remember” retrieval than during “know” retrieval.

Subcomponents of the default-mode network most likely mediate different subcomponents of ecphoric processing. Researchers are currently debating the role of the ventral PPC (angular gyrus) in episodic memory retrieval [Hutchinson et al., 2009; Wagner et al., 2005]. Extending the attention model of Corbetta and Shulman [2002] to the domain of memory, the *Attention to Memory (AtoM) model* [Cabeza et al., 2008; Ciaramelli et al., 2010] indicates ventral PPC activity mediates the bottom-up attentional processes captured by salient retrieval output. Alternatively, the *output buffer hypothesis* indicates the ventral PPC supports the maintenance of retrieved content in “something like the episodic buffer proposed by Baddeley [2000]” [Vilberg and Rugg, 2008; see also Guerin and Miller, 2011]. Both views are compatible with the ecphory hypothesis, and further studies are needed to adjudicate between these two views. The precuneus/posterior cingulate cortex’s roles in episodic retrieval have received relatively little attention. Functional connectivity analysis studies [Andrews-Hanna et al., 2010; Buckner et al., 2009; Cole et al., 2010; Fransson and Marrelec, 2008] indicate the precuneus/posterior cingulate cortex is among the more globally connected regions within the default-mode network. Thus, these regions may act as a central, convergence node integrating retrieved information with other components of internally oriented mentation, such as self-referential [Buckner and Carroll, 2007; Gusnard, 2005], semantic/conceptual [Binder et al., 1999, 2009], and social/emotional [Amodio and Frith, 2006; Saxe, 2006] processing.

Old/new effects do not associate significantly with other major components of the default-mode network, such as the MTL and anteromedial PFC. This “null” finding requires comment, since it potentially goes against the ecphory hypothesis. First, the present meta-analysis of new/old effects shows the MTL’s strong involvement,

TABLE IV. Remember-HC/new and know-LC/new effects and the subtraction results between them

Lobe	Region	H	BA	Talairach			Volume (mm ³)	ALE (×10 ³)
				x	y	z		
Remember-HC > new								
Frontal	Dorsolateral PFC	L	6	-40	4	44	2,800	13.2
	Dorsomedial PFC	L	6	-12	16	58	552	11.3
	Dorsomedial PFC	L	6, 8	-6	30	36	568	12.1
Temporal	MTG	L	21	-58	-24	-4	808	10.3
Parietal	Angular gyrus, intraparietal sulcus	L	39, 7	-48	-60	24	2,944	14.5
	Posterior cingulate cortex	L	23	-6	-26	30	680	10.2
	Posterior cingulate cortex	L	31	-8	-44	32	912	12.7
	Precuneus	L	31, 7	-4	-70	28	2,264	13.6
Sublobar	Caudate nucleus	R	—	8	8	-2	432	9.9
	Thalamus	L	—	-12	-34	4	464	8.2
Know-LC > new								
Frontal	Dorsolateral PFC	L	10	-32	48	18	744	11.0
	Dorsolateral PFC	L	46	-40	24	22	488	7.0
	Dorsolateral PFC	R	9	46	32	30	472	7.1
	Insula	L	—	-52	16	8	448	6.9
Parietal	Superior PPC/precuneus	L	7	-12	-70	46	632	8.5
	Superior PPC/precuneus	R	7	6	-74	46	728	10.7
	Intraparietal sulcus	L	7	-22	-68	34	576	7.5
	Intraparietal sulcus	L	7	-36	-58	42	456	7.1
Remember-HC/new > know-LC/new								
Parietal	Angular gyrus	L	39	-50	-60	24	984	11.1
	Posterior cingulate cortex	L	31	-8	-44	34	496	9.7
	Posterior cingulate cortex	L	23	-8	-28	30	536	9.9
	Precuneus	B	31	0	-68	26	1,232	11.2
Sublobar	Thalamus	L	—	-12	-34	4	664	8.2
Know-LC/new > remember-HC/new								
Frontal	Dorsolateral PFC	L	10	-32	48	18	584	-10.9
Parietal	Superior PPC/precuneus	L	7	-12	-70	46	448	-8.5
	Superior PPC/precuneus	R	7	6	-74	46	528	-10.6

For abbreviations, see Table I.

likely reflecting greater encoding-related activity for new than for old items (see below). Thus, the lack of MTL involvement in old/new effects may reflect, at least in part, the “masking” of retrieval-related activity (old > new) by stronger encoding-related activity (new > old), rather than a true absence of retrieval-related activity in the MTL [Buckner et al., 2001; Stark and Okado, 2003]. Second, researchers [D’Argembeau et al., 2007; Gusnard and Raichle, 2001; Johnson et al., 2006] had thought the anteromedial PFC played a pivotal role in self-referential processing. Studies [Spreng et al., 2009; Svoboda et al., 2006] had shown that autobiographical memory retrieval typically involved strong self-referential processing, as well as strong activation of the anteromedial PFC. However, laboratory-based episodic retrieval, given its impoverished encoding environment [Cabeza and St Jacques, 2007], may typically involve weak self-referential processing, as well as weak activation of the anteromedial PFC. Finally, the author’s previous meta-analysis study [Kim, 2010] shows that remember/know (remember > know)

effects include both the MTL and anteromedial PFC regions, along with other default-mode network regions, providing positive evidence for both regions’ involvement in “remember” retrieval.

Cognitive-control network: Memory and non-memory control

The regions most consistently associating with old/new effects also include the left dorsolateral PFC, left dorsomedial PFC, and bilateral dorsal PPC. As mentioned previously, these three regions show correlated activity during control-demanding cognitive tasks [Cole and Schneider, 2007; Dosenbach et al., 2007; Seeley et al., 2007; Vincent et al., 2008], suggesting a distributed control network. During episodic retrieval, these regions may support memory as well as non-memory control functions. The current comparisons between old/new effects for item- versus source-retrieval and for remember-HC versus know-LC retrieval provide evidence for the network’s involvement in

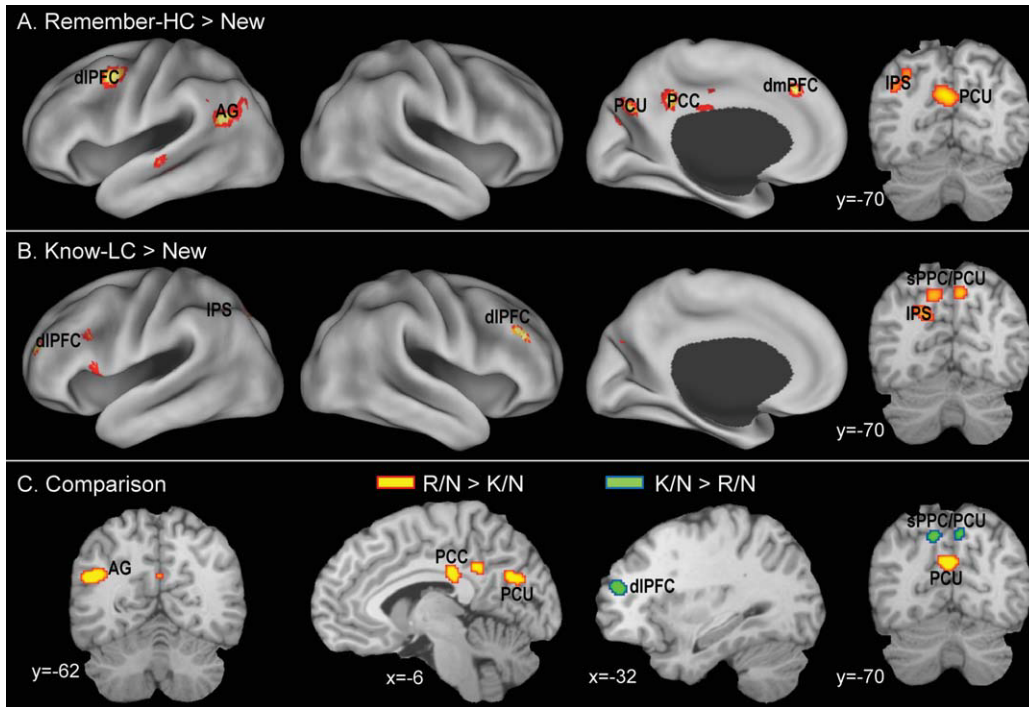


Figure 4.

Brain regions associated with remember-HC/new (A) and know-LC/new effects (B), and the significant differences between the two effects (C). IPS, intraparietal sulcus; sPPC, superior posterior parietal cortex. For other abbreviations, see Figure 1. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

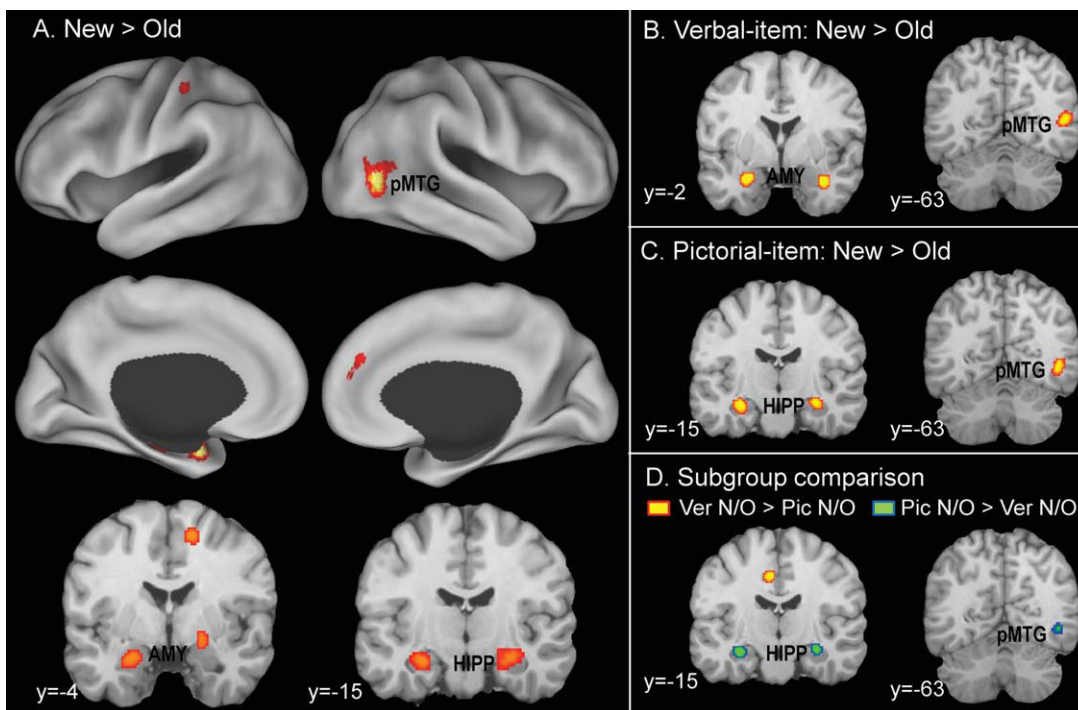


Figure 5.

Brain regions associated with new/old effects in the whole group (A), in the verbal-item subgroup (B), and in the pictorial-item subgroup (C), as well as variable new/old effects in a comparison of the two subgroups (D). AMY, amygdala; HIPP, hippocampus; pMTG, posterior middle temporal gyrus. [Color figure can be viewed in the online issue, which is available at wileyonlinelibrary.com.]

TABLE V. New/old effects in the whole group, verbal-item and pictorial-item subgroups, and variable new/old effects between the two subgroups

Lobe	Region	H	BA	Talairach			Volume (mm ³)	ALE ($\times 10^3$)
				x	y	z		
All studies: new > old								
Frontal	Dorsomedial PFC	R	9	6	48	16	648	9.9
	Dorsomedial PFC	R	6	16	-4	56	472	12.5
Temporal	Amygdala	L	—	-28	2	-24	1,592	19
	Hippocampus	L	—	-28	-18	-18	912	14.8
Parietal	Hippocampus, amygdala	R	—	30	-12	-16	1,936	14.1
	Posterior MTG	R	37, 19	46	-62	8	2,824	16
	Postcentral cortex	L	2	-44	-30	54	440	11.6
	White matter	R	—	22	-48	48	768	11.5
Verbal-item: new > old								
Frontal	Dorsomedial PFC	L	6, 24	-6	-12	44	664	11.4
	Dorsomedial PFC	R	6	6	6	52	504	8.7
Temporal	Amygdala	L	—	-28	2	-24	1,136	12.6
	Amygdala	R	—	36	-4	-26	808	10.1
Parietal	Posterior MTG	R	37, 19	50	-64	10	536	7.9
	Superior temporal gyrus	L	41	-48	-18	12	448	7.7
	White matter	R	—	20	-50	48	568	9.7
Pictorial-item: new > old								
Frontal	Dorsomedial PFC	R	9	8	44	18	424	7.3
Temporal	Hippocampus	L	—	-30	-18	-18	608	10.2
	Hippocampus	R	—	30	-12	-14	1,712	12.1
Sublobar	Posterior MTG	R	37, 19	40	-54	-4	1,328	9.0
	Putamen	R	—	28	-24	0	472	7.3
Verbal-item new/old > pictorial-item new/old								
Frontal	Dorsomedial PFC	L	31	-6	-14	44	536	11.2
Temporal	White matter	R	—	36	-4	-26	776	10.0
Pictorial-item new/old > verbal-item new/old								
Temporal	Hippocampus	L	—	-30	-18	-18	536	-10.2
	Hippocampus	R	—	20	2	0	1,024	-7.0
	Posterior MTG	R	37, 19	40	-54	-4	840	-8.9

For abbreviations, see Table I.

controlled-retrieval functions. First, the left dorsolateral PFC, left dorsomedial PFC, and left IPS regions show greater old/new effects during a source-retrieval task than they show during an item-retrieval task (see Fig. 2C). As previous studies [Dobbins et al., 2006; Fan et al., 2003; Kahn et al., 2004; Lundstrom et al., 2003] that directly compare memory for item versus source reveal, these findings likely reflect greater demand for controlled-retrieval processing during source than during item retrieval. Second, the left anterior dorsolateral PFC and bilateral superior PPC/precuneus regions associate more strongly with know-LC/new than they do with remember-HC/new effects (Fig. 4C), likely reflecting that “know” retrieval demands controlled-retrieval processing to a greater degree than “remember” retrieval does.

Subcomponents of the cognitive-control network most likely mediate differential subcomponents of controlled-retrieval operations. A body of neuroimaging data on the PFC [MacDonald et al., 2000; Miller and Cohen, 2001; Rid-

derinkhof et al., 2004; Rushworth et al., 2007] indicates a dissociation between the dorsomedial PFC, which monitors performance and signals during any need for control adjustments, and the dorsolateral PFC, which implements control operations. Retrieval-related activity in the PFC may dissociate similarly between the dorsomedial PFC, where activity may support the monitoring of controlled-retrieval demand, and the dorsolateral PFC, where activity may support controlled-retrieval operations [Badre and Wagner, 2004; Fleck et al., 2006; Velanova et al., 2003; Wheeler and Buckner, 2003]. One influential hypothesis regarding lateral PFC organization suggests a rostrocaudal control hierarchy, whereby the posterior-to-anterior lateral PFC supports progressively more abstract control-operations [Badre, 2008; Christoff and Gabrieli, 2000; Koechlin et al., 1999]. Thus, the anterior dorsolateral PFC may engage in more abstract-level control of retrieval operations, such as keeping a main goal in mind during iterative retrieval searches; whereas the more posterior

dorsolateral PFC may more specifically reflect controlled search processes. In contrast, and based on distinct response patterns in the left PFC during source memory, Dobbins et al. [2002] propose a tripartite model of lateral PFC organization, in which the anterior ventrolateral PFC mediates semantic analysis/cue specification, the posterior ventrolateral PFC subserves phonological maintenance/rehearsal, and the posterior dorsolateral and frontopolar PFC support recollective monitoring.

With respect to the dorsal PPC, the present study indicates a dissociation between more inferior regions (the IPS), which are common to remember-HC/new and know-LC/new effects, and more superior regions, which are specific to know-LC/new effects (see Fig. 4). The author's previous meta-analysis study [Kim, 2010] report similar dissociations within the dorsal PPC. The aforementioned AtoM model [Cabeza et al., 2008] proposes an additional hypothesis, whereby dorsal PPC activity mediates top-down attentional control, guided by retrieval goals. This hypothesis fits with data on the superior subregion of the dorsal PPC, which are specific to know-LC/new effects, but not with data on the inferior subregion involving the IPS. The latter may mainly support non-memory control functions (see below). The present data also indicate a functional dissociation within the posterior precuneus. While inferior portions of the posterior precuneus ($xyz = 0, -68, 26$) associate more strongly with remember-HC/new effects than with know-LC/new effects, suggesting a default-mode network region, superior portions ($xyz = -12, -70, 46$) associate more strongly with know-LC/new effects than with remember-HC/new effects, suggesting a functional connection with the cognitive-control network (see rightmost illustration in Fig. 4C). This functional dissociation between superior and inferior subregions is broadly consistent with recent evidence suggesting connectivity-based subdivisions within the precuneus [Cauda et al., 2010; Margulies et al., 2009; Vincent et al., 2008]. For example, a functional connectivity study by Vincent et al. [2008] indicates that the superior precuneus is part of the task-positive/dorsal attention system. Thus, although researchers have postulated that the precuneus is a core region in the default-mode network, the present study (and recent connectivity studies) implicates distinct functional subdivisions.

An unresolved issue concerns whether, and to what extent, the cognitive-control network regions' association with old/new effects may reflect non-memory control operations. A promising approach to this issue is to subdivide the "old/new" regions into those that are sensitive to old/new ratios (i.e., the relative probability of old and new items during a recognition test) and others that are not sensitive to old/new ratios. Using this approach, Herron et al. [2004; see also Vilberg and Rugg, 2009] show that old/new effects in most cognitive-control network regions decrease or even reverse when old/new ratios increase (e.g., from 25:75 to 75:25). Herron et al. [2004] propose that these regions' activities "reflect processes that

are contingent upon, rather than in support of, successful recognition." Related to this, Vilberg and Rugg [2008] suggest activity in the vicinity of the IPS reflects "something akin to the salience or 'target-value' of the eliciting stimulus event." Based on the hypothesis that an observer in a recognition memory test may expect to see new items (non-targets) rather than old items (targets), O'Connor et al. [2010] suggest an "observer must countermand a general expectation that items are new to successfully execute a correct 'old' decision." Using a memory analog of the Posner "attention-cueing" paradigm, they also provide evidence that most retrieval-success (old > new) regions also track what they call "expectancy violation" (invalid cueing > valid cueing). Thus, most cognitive-control regions may support operations that countermand an expectation that items are new, as well as having memory-specific control operations.

Caudate nucleus: Reward

Old/new effects also associate strongly with bilateral caudate nucleus regions. The caudate nucleus's involvement in old/new effects, despite occurring frequently in findings, has received little attention until quite recently. Animal studies provide a rich body of evidence that the caudate nucleus and adjacent striatal regions play a key role in the brain's reward system [Schultz, 2000]. In line with this evidence, functional neuroimaging studies in humans [de Greck et al., 2008; Delgado, 2007; Delgado et al., 2000] find that performance-related positive and negative feedback (e.g., monetary rewards) modulates caudate activity. Recent studies [Han et al., 2010; Tricomi and Fiez, 2008] have proposed that human subjects in a recognition memory test may value detection of "old" items (targets) more than they value "new" items (non-targets). Based on this supposition, these studies suggest that caudate nucleus activity during episodic retrieval may reflect the reward or satisfaction of successful target detection. Supporting this hypothesis, Han et al. [2010] report that the caudate nucleus shows old/new effects when the study paradigm provides incentive to hits, but it shows new/old effects when the paradigm provides incentive to CRs. In the present study, the caudate nucleus regions show greater old/new effects during a source-retrieval task than they show during an item-retrieval task, likely reflecting the greater reward or satisfaction associated with more confident target-detection (objective recollection; see Fig. 2C). Though the caudate nucleus associates with remember-HC/new effects but not with know-LC/new effects, this difference is not significant in the subtraction analysis. However, the author's previous meta-analysis study [Kim, 2010] shows that remember/know (remember > know) effects include a caudate nucleus region, also likely reflecting the greater satisfaction associated with more confident target-detection (subjective recollection). Recent studies using resting-state functional connectivity MRI [Barnes et al., 2010; Di Martino et al.,

2008] find subregional differences within the striatum. For example, the dorsal caudate connects functionally to the lateral PFC, whereas the ventral striatum activity connects functionally to the anteromedial PFC. Thus, distinct caudate subregions may coactivate with either the default-mode or cognitive-control network, depending on task requirements.

Material-type effects

The studies using verbal materials as well as pictorial materials report predominantly left-lateralized old/new effects (see Figs. 2A and 3A). A direct comparison between the studies using verbal versus pictorial materials yields rather variable results, depending on the particular random selection of studies. This comparison shows greater reliability with regard to stronger old/new effects for verbal versus pictorial materials in the left dorsolateral PFC, left insula, and the left angular gyrus regions. Such a comparison also yields greater old/new effects for pictorial versus verbal materials in the right dorsolateral PFC region. Although future meta-analysis studies, using a larger sample of studies, need to address the issue of reliable material-type effects, the current results clearly show predominant left-lateralization of old/new effects, even for pictorial materials. Thus, the widespread research using verbal materials is unlikely to adequately account for the common, predominant left-lateralization of old/new effects. Rather, the left hemisphere appears dominant for recognition memory across stimulus domains [Guerin and Miller, 2009; Leube et al., 2003; Leveroni et al., 2000]. For example, upon directly comparing memory for words versus faces, Guerin and Miller [2009] report that the parietal old/new effects did not exhibit material-specific lateralization but rather strong left hemisphere lateralization. Alternatively, the predominant left-lateralization of old/new effects for pictorial materials in the current analysis may reflect, at least in part, the use of verbalizable pictorial materials (e.g., pictures of common objects) in many included studies. In line with this view, Klostermann et al. [2009] report that the parietal old/new effects for nonlinguistic auditory stimuli lateralized to the right hemisphere. Future studies might address whether certain classes of visual, nonverbal materials may yield predominantly right-lateralized old/new effects in the parietal and other regions.

New/Old Effects

The meta-analyses of new/old effects indicate only two major clusters, one involving the bilateral MTL and the other involving a right posterior MTG region and its transition to the occipital cortex (see Fig. 5A). The MTL cluster bilaterally involves the hippocampus and amygdala. According to one novelty-encoding hypothesis [Tulving et al., 1996], the MTL regions' new/old effects may reflect greater encoding-related activity for new than for old

items [Kirchhoff et al., 2000; Law et al., 2005; Stark and Okado, 2003]. Though the effects may also reflect repetition-related "deactivations" for old items, or neural priming [Daselaar et al., 2006; Gonsalves et al., 2005; Henson et al., 2003], a "pure" priming hypothesis does not account for "incidental" memory formation for new items and subsequent memory effects [Buckner et al., 2001; Stark and Okado, 2003]. Consistent with the novelty-encoding hypothesis, Kumaran and Maguire [2006] show that hippocampal responses reflect mismatches between what is expected (based on past associations) and current sensory input. Poppenk et al. [2010] provide evidence of a functional dissociation along the hippocampus's longitudinal axis: the encoding of novel materials mainly involved the anterior hippocampus and amygdala, whereas the encoding of previously experienced materials mainly involved the posterior hippocampus. The current new/old effects fall mostly within the anterior half of the hippocampus and amygdala, consistent with these regions' specialization for encoding novel information.

As discussed, the current study shows the MTL's lack of involvement in old/new effects. The finding of strong MTL involvement in new/old effects has critical implications for interpreting the lack of MTL involvement in old/new effects. First, the MTL's non-involvement in old/new effects may reflect, at least in part, a "masking" of retrieval-related activity (old > new) by stronger, encoding-related activity (new > old), rather than reflecting a true absence of retrieval-related MTL activity. Second, a low signal-to-noise ratio, susceptibility to MRI artifacts, or other nuisance factors may play a rather minor role in the MTL's lack of involvement in old/new effects.

The analyses of material-types indicate that new/old effects for verbal materials in MTL regions mainly involve the bilateral amygdala; whereas those for pictorial materials mainly involve the bilateral hippocampus. A direct comparison between new/old effects regarding studies that use verbal versus pictorial materials reveals greater new/old effects for pictorial than for verbal materials in MTL regions, mostly involving the bilateral hippocampus (see Fig. 5D). This material-dependent MTL effect may relate to the widespread use of common words, which participants had encountered numerous times before the studies, as memoranda. Thus, participants have high pre-experimental familiarity with the verbal materials, but not with the pictorial materials used in memory studies. Because of this, the greater MTL new/old effects for pictorial than for verbal materials may reflect greater encoding-related activity for more novel than for familiar information. The author's previous meta-analysis of subsequent memory effects [remembered > forgotten; Kim, 2011] indicates similar material-dependent effects in MTL regions. Incidentally, this parallel finding with subsequent memory effects provides evidence that current new/old effects in the MTL reflect greater encoding-related activity for new than for old items, rather than neural priming for old items.

The right posterior MTG cluster is not near any regions showing significant subsequent memory effects in the aforementioned meta-analysis. Rather, this and adjacent regions frequently associate with repetition-related priming effects [Henson and Rugg, 2003; Schacter and Buckner, 1998]. Thus, this region's new/old effects may mainly reflect priming-related "deactivations" for old items. This priming effect may be perceptual in nature, given that (1) the cluster is in the visual association area (BA 19, 37); (2) it lateralizes to the right-hemisphere, even for verbal materials; and (3) the effects are stronger for pictorial than for verbal materials (see Fig. 5D).

Conclusions

This meta-analysis of old/new effects (hit > CR) indicated that such effects associated most strongly with: (1) components of the default-mode network, including the left angular gyrus, bilateral precuneus, and bilateral posterior cingulate cortex regions, which may support mental re-experiencing of an old event, or ecphory; (2) components of the cognitive-control network, involving the left dorsolateral PFC, left dorsomedial PFC, and bilateral IPS regions, which may mediate memory and non-memory control functions; and (3) the caudate nucleus, which is a key part of the brain's reward system and may support the reward or satisfaction tied to target-detection. Direct comparisons of old/new effects between item versus source retrieval and "remember" versus "know" retrieval yielded three main sets of findings. First, default-mode network regions exhibited greater activation in conditions associated with greater ecphoric processing, i.e., with source than with item retrieval and with "remember" than with "know" retrieval. Second, cognitive-control network regions showed greater activation in conditions associated with greater demand for controlled-retrieval processing, i.e., with source than with item retrieval and with "know" than with "remember" retrieval. Third, the caudate nucleus showed greater activation during source retrieval than it showed during item retrieval, likely reflecting the greater satisfaction associated with more confident target-detection. The meta-analysis of new/old effects (CR > hit) indicated that such effects associated most strongly with the bilateral MTL and right posterior MTG/occipital regions. The MTL's new/old effects may primarily reflect greater encoding-related activity for new than for old items. This encoding-related MTL activity (new > old) may mask retrieval-related MTL activity (old > new), yielding an apparent lack of MTL involvement in old/new effects. The right posterior MTGs new/old effects may mainly reflect repetition-related neural priming effects. Taken together, these findings suggest that differential neural activity for old versus new events is an ensemble of multiple memory-specific activities, including encoding, retrieval, and priming, as well as of multiple types of

more general cognitive activity, including default-mode, cognitive-control, and reward processing.

REFERENCES

- Achim AM, Lepage M (2005): Dorsolateral prefrontal cortex involvement in memory post-retrieval monitoring revealed in both item and associative recognition tests. *Neuroimage* 24:1113–1121.
- Addis D, Wong A, Schacter D (2007): Remembering the past and imagining the future: common and distinct neural substrates during event construction and elaboration. *Neuropsychologia* 45:1363–1377.
- Amodio D, Frith C (2006): Meeting of minds: The medial frontal cortex and social cognition. *Nat Rev Neurosci* 7:268–277.
- Andrews-Hanna JR, Reidler JS, Sepulcre J, Poulin R, Buckner RL (2010): Functional-anatomic fractionation of the brain's default network. *Neuron* 65:550–562.
- Baddeley A (2000): The episodic buffer: A new component of working memory? *Trends Cogn Sci* 4:417–423.
- Badre D (2008): Cognitive control hierarchy and the rostro-caudal organization of the frontal lobes. *Trends Cogn Sci* 12:193–200.
- Badre D, Wagner A (2004): Selection integration and conflict monitoring: Assessing the nature and generality of prefrontal cognitive control mechanisms. *Neuron* 41:473–487.
- Barnes KA, Cohen AL, Power JD, Nelson SM, Dosenbach YBL, Miezin FM, Petersen SE, Schlaggar BL (2010): Identifying basal ganglia divisions in individuals using resting-state functional connectivity MRI. *Front Syst Neurosci*, 4:18.
- Binder J, Frost J, Hammeke T, Bellgowan P, Rao S, Cox R (1999): Conceptual processing during the conscious resting state: a functional MRI study. *J Cogn Neurosci* 11:80–93.
- Binder JR, Desai RH, Graves WW, Conant LL (2009): Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cereb Cortex* 19:2767–2796.
- Brass M, Ullsperger M, Knoesche T, Cramon D, Phillips N (2005): Who comes first? The role of the prefrontal and parietal cortex in cognitive control. *J Cogn Neurosci* 17:1367–1375.
- Buckner R (2003): Functional-anatomic correlates of control processes in memory. *J Neurosci* 23:3999–4004.
- Buckner R, Andrews-Hanna J, Schacter D (2008): The brain's default network. *Ann NY Acad Sci* 1124:1–38.
- Buckner R, Carroll D (2007): Self-projection and the brain. *Trends Cogn Sci* 11:49–57.
- Buckner R, Sepulcre J, Talukdar T, Krienen F, Liu H, Hedden T, Andrews-Hanna J, Sperling R, Johnson K (2009): Cortical hubs revealed by intrinsic functional connectivity: Mapping assessment of stability and relation to Alzheimer's disease. *J Neurosci* 29:1860–1873.
- Buckner RL, Wheeler ME, Sheridan MA (2001): Encoding processes during retrieval tasks. *J Cogn Neurosci* 13:406–415.
- Cabeza R, Ciaramelli E, Olson I, Moscovitch M (2008): The parietal cortex and episodic memory: An attentional account. *Nat Rev Neurosci* 9:613–625.
- Cabeza R, Dolcos F, Prince S, Rice H, Weissman D, Nyberg L (2003): Attention-related activity during episodic memory retrieval: A cross-function fMRI study. *Neuropsychologia* 41:390–399.
- Cabeza R, St Jacques P (2007): Functional neuroimaging of autobiographical memory. *Trends Cogn Sci* 11:219–227.
- Cauda F, Geminiani G, D'Agata F, Sacco K, Duca S, Bagshaw AP, Cavanna AE (2010): Functional connectivity of the posteromedial cortex. *PLoS One* 5:e13107.

- Chee MWL, Goh JOS, 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.
- Christoff K, Gabrieli J (2000): The frontopolar cortex and human cognition: Evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology* 28:168–186.
- Ciaramelli E, Grady C, Levine B, Ween J, Moscovitch M (2010): Top-down and bottom-up attention to memory are dissociated in posterior parietal cortex: Neuroimaging and neuropsychological evidence. *J Neurosci* 30:4943–4956.
- Ciaramelli E, Grady C, Moscovitch M (2008): Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia* 46:1828–1851.
- Cole M, Schneider W (2007): The cognitive control network: Integrated cortical regions with dissociable functions. *Neuroimage* 37:343–360.
- Cole MW, Pathak S, Schneider W (2010): Identifying the brain's most globally connected regions. *Neuroimage* 49:3132–3148.
- Corbetta M, Shulman G (2002): Control of goal-directed and stimulus-driven attention in the brain. *Nat Rev Neurosci* 3:201–215.
- D'Argembeau A, Ruby P, Collette F, Degueldre C, Baeteeu E, Luxen A, Maquet P, Salmon E (2007): Distinct regions of the medial prefrontal cortex are associated with self-referential processing and perspective taking. *J Cogn Neurosci* 19:935–944.
- Daselaar SM, Fleck MS, Cabeza R (2006): Triple dissociation in the medial temporal lobes: Recollection familiarity and novelty. *J Neurophysiol* 96:1902–1911.
- Daselaar SM, Rombouts SARB, Veltman DJ, Raaijmakers JGW, Lazeron RHC, Jonker C (2001): Parahippocampal activation during successful recognition of words: A self-paced event-related fMRI study. *Neuroimage* 13:1113–1120.
- Daselaar SM, Veltman DJ, Rombouts SARB, Raaijmakers JGW, Jonker C (2003): Neuroanatomical correlates of episodic encoding and retrieval in young and elderly subjects. *Brain* 126:43–56.
- de Greck M, Rotte M, Paus R, Moritz D, Thiemann R, Proesch U, Bruer U, Moerth S, Tempelmann C, Bogerts B (2008): Is our self based on reward? Self-relatedness recruits neural activity in the reward system. *Neuroimage* 39:2066–2075.
- de Zubicaray GI, McMahon KL, Eastburn MM, Finnigan S, Humphreys MS (2005): fMRI evidence of word frequency and strength effects in recognition memory. *Cogn Brain Res* 24:587–598.
- Delgado M (2007): Reward-related responses in the human striatum. *Ann NY Acad Sci* 1104:70–88.
- Delgado M, Nystrom L, Fissell C, Noll D, Fiez J (2000): Tracking the hemodynamic responses to reward and punishment in the striatum. *J Neurophysiol* 84:3072–3077.
- Derrfuss J, Brass M, Neumann J, Von Cramon D (2005): Involvement of the inferior frontal junction in cognitive control: Meta-analyses of switching and Stroop studies. *Hum Brain Mapp* 25:22–34.
- Di Martino A, Scheres A, Margulies DS, Kelly AMC, Uddin LQ, Shehzad Z, Biswal B, Walters JR, Castellanos FX, Milham MP (2008): Functional connectivity of human striatum: A resting state fMRI study. *Cereb Cortex* 18:2735–2747.
- 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.
- Dobbins IG, Foley H, Schacter DL, Wagner AD (2002): Executive control during episodic retrieval: multiple prefrontal processes subserved source memory. *Neuron* 35:989–996.
- Dobbins IG, Han S (2006): Cue- versus probe-dependent prefrontal cortex activity during contextual remembering. *J Cogn Neurosci* 18:1439–1452.
- Dobbins IG, Rice H, Wagner A, Schacter D (2003): Memory orientation and success: Separable neurocognitive components underlying episodic recognition. *Neuropsychologia* 41:318–333.
- Donaldson DI, Petersen SE, Buckner RL (2001): Dissociating memory retrieval processes using fMRI: Evidence that priming does not support recognition memory. *Neuron* 31:1047–1059.
- Donaldson D, Wheeler M, Petersen S (2009): Remember the source: Dissociating frontal and parietal contributions to episodic memory. *J Cogn Neurosci* 22:377–391.
- Dosenbach N, Fair D, Miezin F, Cohen A, Wenger K, Dosenbach R, Fox M, Snyder A, Vincent J, Raichle M (2007): Distinct brain networks for adaptive and stable task control in humans. *Proc Natl Acad Sci USA* 104:11073–11078.
- Duarte A, Graham KS, Henson RN (2010): Age-related changes in neural activity associated with familiarity recollection and false recognition. *Neurobiol Aging* 31:1814–1830.
- Duncan J, Owen A (2000): Common regions of the human frontal lobe recruited by diverse cognitive demands. *Trends Neurosci* 23:475–483.
- Dunn J (2004): Remember-know: A matter of confidence. *Psychol Rev* 111:524–542.
- Eldridge LL, Knowlton BJ, Furmanski CS, Bookheimer SY, Engel SA (2000): Remembering episodes: A selective role for the hippocampus during retrieval. *Nat Neurosci* 3:1149–1152.
- Fan J, Snodgrass JG, Bilder RM (2003): Functional magnetic resonance imaging of source versus item memory. *Neuroreport* 14:2275–2281.
- Fenker DB, Schott BH, Richardson-Klavehn A, Heinze H-J, Düzel E (2005): Recapitulating emotional context: Activity of amygdala hippocampus and fusiform cortex during recollection and familiarity. *Eur J Neurosci* 21:1993–1999.
- Fleck M, Daselaar S, Dobbins I, Cabeza R (2006): Role of prefrontal and anterior cingulate regions in decision-making processes shared by memory and nonmemory tasks. *Cereb Cortex* 16:1623–1630.
- Fliessbach K, Weis S, Klaver P, Elger CE, Weber B (2006): The effect of word concreteness on recognition memory. *Neuroimage* 32:1413–1421.
- 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 USA* 102:9673–9678.
- Fransson P (2005): Spontaneous low-frequency BOLD signal fluctuations: An fMRI investigation of the resting-state default mode of brain function hypothesis. *Hum Brain Mapp* 26:15–29.
- Fransson P, Marrelec G (2008): The precuneus/posterior cingulate cortex plays a pivotal role in the default mode network: Evidence from a partial correlation network analysis. *Neuroimage* 42:1178–1184.
- Genovese C, Lazar N, Nichols T (2002): Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *Neuroimage* 15:870–878.
- 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, 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.

- Guerin SA, Miller MB (2011): Parietal cortex tracks the amount of information retrieved even when it is not the basis of a memory decision. *Neuroimage* 55:801–807.
- Guerin SA, Miller MB (2009): Lateralization of the parietal old/new effect: An event-related fMRI study comparing recognition memory for words and faces. *Neuroimage* 44:232–242.
- Gusnard D (2005): Being a self: Considerations from functional imaging. *Conscious Cogn* 14:679–697.
- Gusnard D, Raichle M (2001): Searching for a baseline: Functional imaging and the resting human brain. *Nat Rev Neurosci* 2:685–694.
- Habib R (2001): On the relation between conceptual priming neural priming and novelty assessment. *Scand J Psychol* 42:187–195.
- Han S, Huettel S, Raposo A, Adcock R, Dobbins I (2010): Functional significance of striatal responses during episodic decisions: Recovery or goal attainment? *J Neurosci* 30:4767–4775.
- Hassabis D, Kumaran D, Maguire E (2007): Using imagination to understand the neural basis of episodic memory. *J Neurosci* 27:14365–14374.
- Hassabis D, Maguire E (2007): Deconstructing episodic memory with construction. *Trends Cogn Sci* 11:299–306.
- 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, Cansino S, Herron J, Robb W, Rugg M (2003): A familiarity signal in human anterior medial temporal cortex? *Hippocampus* 13:301–304.
- Henson R, Hornberger M, Rugg MD (2005): Further dissociating the processes involved in recognition memory: An fMRI study. *J Cogn Neurosci* 17:1058–1073.
- Henson R, Rugg M (2003): Neural response suppression haemodynamic repetition effects and behavioural priming. *Neuropsychologia* 41:263–270.
- Henson R, Rugg M, Shallice T, Dolan R (2000): Confidence in recognition memory for words: dissociating right prefrontal roles in episodic retrieval. *J Cogn Neurosci* 12:913–923.
- Henson R, Shallice T, Dolan R (1999): Right prefrontal cortex and episodic memory retrieval: A functional MRI test of the monitoring hypothesis. *Brain* 122:1367–1381.
- Herron JE, Henson RNA, Rugg MD (2004): Probability effects on the neural correlates of retrieval success: An fMRI study. *Neuroimage* 21:302–310.
- Hornberger M, Rugg MD, Henson RNA (2006): fMRI correlates of retrieval orientation. *Neuropsychologia* 44:1425–1436.
- Hutchinson J, Uncapher M, Wagner A (2009): Posterior parietal cortex and episodic retrieval: Convergent and divergent effects of attention and memory. *Learn Mem* 16:343–356.
- Iidaka T, Matsumoto A, Nogawa J, Yamamoto Y, Sadato N (2006): Frontoparietal network involved in successful retrieval from episodic memory spatial and temporal analyses using fMRI and ERP. *Cereb Cortex* 16:1349–1360.
- Jessen F, Flacke S, Granath D, Manka C, Scheef L, Papassotiropoulos A, Schild H, Heun R (2001): Encoding and retrieval related cerebral activation in continuous verbal recognition. *Cogn Brain Res* 12:199–206.
- Johnson M, Hashtroudi S, Lindsay D (1993): Source monitoring. *Psychol Bull* 114:3–28.
- Johnson M, Raye C, Mitchell K, Touryan S, Greene E, Nolen-Hoeksema S (2006): Dissociating medial frontal and posterior cingulate activity during self-reflection. *Soc Cogn Affect Neurosci* 1:56–64.
- Kahn I, Davachi L, Wagner AD (2004): Functional-neuroanatomic correlates of recollection: Implications for models of recognition memory. *J Neurosci* 24:4172–4180.
- Kim H (2011): Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *Neuroimage* 54:2446–2461.
- Kim H (2010): Dissociating the roles of the default-mode dorsal and ventral networks in episodic memory retrieval. *Neuroimage* 50:1648–1657.
- Kim H, Cabeza R (2009): Common and specific brain regions in high- versus low-confidence recognition memory. *Brain Res* 1282:103–113.
- 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 BA, Wagner AD, Maril A, Stern CE (2000): Prefrontal-temporal circuitry for episodic encoding and subsequent memory. *J Neurosci* 20:6173–6180.
- Klostermann EC, Loui P, Shimamura AP (2009): Activation of right parietal cortex during memory retrieval of nonlinguistic auditory stimuli. *Cogn Affect Behav Neurosci* 9:242–248.
- Koechlin E, Basso G, Pietrini P, Panzer S, Grafman J (1999): The role of the anterior prefrontal cortex in human cognition. *Nature* 399:148–151.
- Konishi S, Wheeler ME, Donaldson DI, Buckner RL (2000): Neural correlates of episodic retrieval success. *Neuroimage* 12:276–286.
- Kumaran D, Maguire EA (2006): An unexpected sequence of events: mismatch detection in the human hippocampus. *PLoS Biol* 4:2372–2382.
- Laird A, Fox P, Price C, Glahn D, Uecker A, Lancaster J, Turkeltaub P, Kochunov P, Fox P (2005a): ALE meta-analysis: Controlling the false discovery rate and performing statistical contrasts. *Hum Brain Mapp* 25:155–164.
- Laird A, McMillan K, Lancaster J, Kochunov P, Turkeltaub P, Pardo J, Fox P (2005b): A comparison of label-based review and ALE meta-analysis in the Stroop task. *Hum Brain Mapp* 25:6–21.
- Laird AR, Lancaster JL, Fox PT (2009): Lost in localization? The focus is meta-analysis. *Neuroimage* 48:18–20.
- Law J, Flanery M, Wirth S, Yanike M, Smith A, Frank L, Suzuki W, Brown E, Stark C (2005): Functional magnetic resonance imaging activity during the gradual acquisition and expression of paired-associate memory. *J Neurosci* 25:5720–5729.
- Legrand D, Ruby P (2009): What is self-specific? Theoretical investigation and critical review of neuroimaging results. *Psychol Rev* 116:252–282.
- Lepage M, Ghaffar O, Nyberg L, Tulving E (2000): Prefrontal cortex and episodic memory retrieval mode. *Proc Natl Acad Sci USA* 97:506–511.
- Lepage M, Pelletier M, Achim A, Montoya A, Menear M, Lal S (2010): Parietal cortex and episodic memory retrieval in schizophrenia. *Psychiatry Res* 182:191–199.
- Leube D, Erb M, Grodd W, Bartels M, Kircher T (2003): Successful episodic memory retrieval of newly learned faces activates a left fronto-parietal network. *Cogn Brain Res* 18:97–101.
- Leveroni CL, Seidenberg M, Mayer AR, Mead LA, Binder JR, Rao SM (2000): Neural systems underlying the recognition of familiar and newly learned faces. *J Neurosci* 20:878–886.
- Lundstrom BN, Ingvar M, Petersson KM (2005): The role of precuneus and left inferior frontal cortex during source memory episodic retrieval. *Neuroimage* 27:824–834.
- Lundstrom BN, Petersson KM, Andersson J, Johansson M, Fransson P, Ingvar M (2003): Isolating the retrieval of imagined pictures during episodic memory: Activation of the left precuneus and left prefrontal cortex. *Neuroimage* 20:1934–1943.

- MacDonald A, Cohen J, Stenger V, Carter C (2000): Dissociating the role of the dorsolateral prefrontal and anterior cingulate cortex in cognitive control. *Science* 288:1835–1838.
- Maratos EJ, Dolan RJ, Morris JS, Henson RNA, Rugg MD (2001): Neural activity associated with episodic memory for emotional context. *Neuropsychologia* 39:910–920.
- Margulies DS, Vincent JL, Kelly C, Lohmann G, Uddin LQ, Biswal BB, Villringer A, Castellanos FX, Milham MP, Petrides M (2009): Precuneus shares intrinsic functional architecture in humans and monkeys. *Proc Natl Acad Sci USA* 106:20069–20074.
- McDermott KB, Jones TC, Petersen SE, Lageman SK, Roediger HL (2000): Retrieval success is accompanied by enhanced activation in anterior prefrontal cortex during recognition memory: An event-related fMRI study. *J Cogn Neurosci* 12:965–976.
- Miller B, Cummings J (1999): *The Human Frontal Lobes*. New York: Guilford Press.
- Miller E, Cohen J (2001): An integrative theory of prefrontal cortex function. *Annu Rev Neurosci* 24:167–202.
- Montaldi D, Spencer TJ, Roberts N, Mayes AR (2006): The neural system that mediates familiarity memory. *Hippocampus* 16: 504–520.
- Morcom AM, Li J, Rugg MD (2007): Age effects on the neural correlates of episodic retrieval: Increased cortical recruitment with matched performance. *Cereb Cortex* 17:2491–2506.
- Moscovitch M (1992): Memory and working-with-memory: A component process model based on modules and central systems. *J Cogn Neurosci* 4:257–267.
- Nee D, Wager T, Jonides J (2007): Interference resolution: Insights from a meta-analysis of neuroimaging tasks. *Cogn Affect Behav Neurosci* 7:1–17.
- O'Connor A, Han S, Dobbins I (2010): The inferior parietal lobule and recognition memory: Expectancy violation or successful retrieval? *J Neurosci* 30:2924–2934.
- 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.
- Phillips JS, Velanova K, Wolk DA, Wheeler ME (2009): Left posterior parietal cortex participates in both task preparation and episodic retrieval. *Neuroimage* 46:1209–1221.
- Poppenk J, McIntosh AR, Craik FIM, Moscovitch M (2010): Past experience modulates the neural mechanisms of episodic memory formation. *J Neurosci* 30:4707–4716.
- Ragland JD, Gur RC, Valdez J, Turetsky BI, Elliott M, Kohler C, Siegel S, Kanes S, Gur RE (2004): Event-related fMRI of fronto-temporal activity during word encoding and recognition in schizophrenia. *Am J Psychiatry* 161:1004–1015.
- Ragland JD, Valdez JN, Loughhead J, Gur RC, Gur RE (2006): Functional magnetic resonance imaging of internal source monitoring in schizophrenia: Recognition with and without recollection. *Schizophr Res* 87:160–171.
- Raichle M, MacLeod A, Snyder A, Powers W, Gusnard D, Shulman G (2001): A default mode of brain function. *Proc Natl Acad Sci USA* 98:676–682.
- Raposo A, Han S, Dobbins IG (2009): Ventrolateral prefrontal cortex and self-initiated semantic elaboration during memory retrieval. *Neuropsychologia* 47:2261–2271.
- Ridderinkhof K, Ullsperger M, Crone E, Nieuwenhuis S (2004): The role of the medial frontal cortex in cognitive control. *Science* 306:443–447.
- Rombouts S, Barkhof F, Witter M, Machielsen W, Scheltens P (2001): Anterior medial temporal lobe activation during attempted retrieval of encoded visuospatial scenes: An event-related fMRI study. *Neuroimage* 14:67–76.
- Rushworth M, Buckley M, Behrens T, Walton M, Bannerman D (2007): Functional organization of the medial frontal cortex. *Curr Opin Neurobiol* 17:220–227.
- Sajonz B, Kahnt T, Margulies DS, Park SQ, Wittmann A, Stoy M, Ströhle A, Heinz A, Northoff G, Bermpohl F (2010): Delineating self-referential processing from episodic memory retrieval: Common and dissociable networks. *Neuroimage* 50:1606–1617.
- Saxe R (2006): Uniquely human social cognition. *Curr Opin Neurobiol* 16:235–239.
- Schacter D, Buckner R (1998): Priming and the brain. *Neuron* 20:185–195.
- Schultz W (2000): Multiple reward signals in the brain. *Nat Rev Neurosci* 1:199–207.
- Seeley W, Menon V, Schatzberg A, Keller J, Glover G, Kenna H, Reiss A, Greicius M (2007): Dissociable intrinsic connectivity networks for salience processing and executive control. *J Neurosci* 27:2349–2356.
- Shannon BJ, Buckner RL (2004): Functional-anatomic correlates of memory retrieval that suggest nontraditional processing roles for multiple distinct regions within posterior parietal cortex. *J Neurosci* 24:10084–10092.
- Sharot T, Delgado MR, Phelps EA (2004): How emotion enhances the feeling of remembering. *Nat Neurosci* 7:1376–1380.
- Skinner E, Fernandes M (2007): Neural correlates of recollection and familiarity: A review of neuroimaging and patient data. *Neuropsychologia* 45:2163–2179.
- Slotnick S, Moo L, Segal J, Hart J (2003): Distinct prefrontal cortex activity associated with item memory and source memory for visual shapes. *Cogn Brain Res* 17:75–82.
- Smith APR, Henson RNA, Dolan RJ, Rugg MD (2004): fMRI correlates of the episodic retrieval of emotional contexts. *Neuroimage* 22:868–878.
- Smith APR, Henson RNA, Rugg MD, Dolan RJ (2005): Modulation of retrieval processing reflects accuracy of emotional source memory. *Learn Mem* 12:472–479.
- Sohn M, Ursu S, Anderson J, Stenger V, Carter C (2000): The role of prefrontal cortex and posterior parietal cortex in task switching. *Proc Natl Acad Sci USA* 97:13448–13453.
- 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.
- 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.
- Spreng RN, Stevens WD, Chamberlain JP, Gilmore AW, Schacter DL (2010): Default network activity coupled with the frontoparietal control network supports goal-directed cognition. *Neuroimage* 53:303–317.
- Springer S, Deutsch G (1997): *Left Brain Right Brain: Perspectives from Cognitive Neuroscience*. New York: Freeman.
- Squire L, Stark C, Clark R (2004): The medial temporal lobe. *Annu Rev Neurosci* 27:279–306.
- Stark C, Okado Y (2003): Making memories without trying: Medial temporal lobe activity associated with incidental memory formation during recognition. *J Neurosci* 23:6748–6753.
- Svoboda E, McKinnon M, Levine B (2006): The functional neuroanatomy of autobiographical memory: a meta-analysis. *Neuropsychologia* 44:2189–2208.

- Talairach J, Tournoux P (1988): Co-planar Stereotaxic Atlas of the Human Brain. New York: Thieme.
- Tricomi E, Fiez J (2008): Feedback signals in the caudate reflect goal achievement on a declarative memory task. *Neuroimage* 41:1154–1167.
- Trinkler I, King JA, Doeller CF, Rugg MD, Burgess N (2009): Neural bases of autobiographical support for episodic recollection of faces. *Hippocampus* 19:718–730.
- Tsukiura T, Mochizuki-Kawai H, Fujii T (2005): The effect of encoding strategies on medial temporal lobe activations during the recognition of words: An event-related fMRI study. *Neuroimage* 25:452–461.
- Tulving E (1983): *Elements of Episodic Memory*. Oxford: Clarendon Press.
- 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.
- 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.
- van der Veen FM, Nijhuis FAP, Tisserand DJ, Backes WH, Jolles J (2006): Effects of aging on recognition of intentionally and incidentally stored words: An fMRI study. *Neuropsychologia* 44:2477–2486.
- Van Essen D (2005): A population-average landmark-and surface-based (PALS) atlas of human cerebral cortex. *Neuroimage* 28:635–662.
- Vannini P, O'Brien J, O'Keefe K, Pihlajamaki M, LaViolette P, Sperling RA (2011): What goes down must come up: Role of the posteromedial cortices in encoding and retrieval. *Cereb Cortex* 21:22–34.
- Velanova K, Jacoby L, Wheeler M, McAvoy M, Petersen S, Buckner R (2003): Functional-anatomic correlates of sustained and transient processing components engaged during controlled retrieval. *J Neurosci* 23:8460–8470.
- Vilberg KL, Rugg MD (2007): Dissociation of the neural correlates of recognition memory according to familiarity, recollection, and amount of recollected information. *Neuropsychologia* 45:2216–2225.
- Vilberg K, Rugg M (2008): Memory retrieval and the parietal cortex: A review of evidence from a dual-process perspective. *Neuropsychologia* 46:1787–1799.
- Vilberg KL, Rugg MD (2009): An investigation of the effects of relative probability of old and new test items on the neural correlates of successful and unsuccessful source memory. *Neuroimage* 45:562–571.
- Vincent J, Kahn I, Snyder A, Raichle M, Buckner R (2008): Evidence for a frontoparietal control system revealed by intrinsic functional connectivity. *J Neurophysiol* 100:3328–3342.
- Vinogradov S, Luks T, Simpson G, Schulman B, Glenn S, Wong A (2006): Brain activation patterns during memory of cognitive agency. *Neuroimage* 31:896–905.
- 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.
- Wager T, Smith E (2003): Neuroimaging studies of working memory: A meta-analysis. *Cogn Affect Behav Neurosci* 3:255–274.
- Wagner A, Shannon B, Kahn I, Buckner R (2005): Parietal lobe contributions to episodic memory retrieval. *Trends Cogn Sci* 9:445–453.
- Weis S, Klaver P, Reul J, Elger CE, Fernandez G (2004): Temporal and cerebellar brain regions that support both declarative memory formation and retrieval. *Cereb Cortex* 14:256–267.
- Wheeler M, Buckner R (2003): Functional dissociation among components of remembering: control perceived oldness and content. *J Neurosci* 23:3869–3880.
- Wixted J, Stretch V (2004): In defense of the signal detection interpretation of remember/know judgments. *Psychon Bull Rev* 11:616–641.
- Woodruff C, Johnson J, Uncapher M, Rugg M (2005): Content-specificity of the neural correlates of recollection. *Neuropsychologia* 43:1022–1032.
- Yonelinas A (2002): The nature of recollection and familiarity: A review of 30 years of research. *J Mem Lang* 46:441–517.
- Yonelinas AP, Otten LJ, Shaw KN, Rugg MD (2005): Separating the brain regions involved in recollection and familiarity in recognition memory. *J Neurosci* 25:3002–3008.
- Zerssen GC, Mecklinger A, Opitz B, Cramon DY (2001): Conscious recollection and illusory recognition: An event-related fMRI study. *Eur J Neurosci* 13:2148–2156.

APPENDIX: DETAILS OF INDIVIDUAL STUDIES

Reference	Number of participants	Retrieval-cue material	Type of retrieval	Encoding task	Retention interval ^a	Number of foci
Old > new						
Achim and Lepage, 2005	18	Clipart images	Item	Item/pair judgments	Short	25
Chee et al., 2004	16	Words	Item	Living/non-living judgments	Long	8
Chee et al., 2004	13	Words	Item	Living/non-living judgments	Long	3
Ciarra et al., 2010	14	Words	Item	Forming a sentence including the item	Short	10
Daselaar et al., 2001	13	Words	Item	Intentional encoding	Short	4
Daselaar et al., 2003	17	Words	Item	Pleasant/unpleasant judgments	Short	9
de Zubicaray et al., 2005	14	Words	Item	Intentional encoding	Short	12
Donaldson et al., 2001	22	Words	Item	Abstract/concrete judgments	Short	22
Donaldson et al., 2009	26	Words	Source	Forming a sentence including the item	Short	28
Han et al., 2010	19	Words	Item	Syllable judgments	Short	40
Henson et al., 2000	12	Words	Item	Pleasant/unpleasant judgments	Short	4
Henson et al., 2005	22	Words	Item	Living/non-living and alphabetical-order judgments	Short	24
Herron et al., 2004	12	Words	Item	Living/non-living judgments	Short	5
Hornberger et al., 2006	17	Words	Item	Size judgments	Short	18
Iidaka et al., 2006	16	Line drawings	Item	Natural/man-made and left/right judgments	Short	20
Jessen et al., 2001	17	Words	Item	Continuous recognition	Short	10
Konishi et al., 2000	13	Words	Item	Intentional encoding	Short	30
Lepage et al., 2010	18	Clipart images	Item	Item/pair judgments	Short	4
Leube et al., 2003	12	Face photos	Item	Male/female judgments	Short	2
Leveroni et al., 2000	11	Face photos	Item	Pleasant/unpleasant judgments	Short	3
Lundstrom et al., 2003	21	Words	Item	Emotion rating on a 3-point scale	Short	1
Lundstrom et al., 2003	21	Words	Source	Emotion rating on a 3-point scale	Short	12
Lundstrom et al., 2005	16	Words	Source	Emotion rating on a 3-point scale	Long	19
Maratos et al., 2001	12	Words	Item	Emotion rating on a 7-point scale	Short	32
McDermott et al., 2000	24	Words	Item	Intentional encoding	Short	8
Morcom et al., 2007	16	Object photos	Source	Size and living/non-living judgments	Short	25
O'Connor et al., 2010	19	Words	Item	Syllable judgments	Short	24
Ragland et al., 2004	15	Words	Item	Intentional encoding	Short	5
Ragland et al., 2006	13	Words	Source	Uppercase/lowercase and concrete/abstract judgments	Short	11
Raposo et al., 2009	16	Words	Source	Pleasant/unpleasant and concrete/abstract judgments	Short	15
Rombouts et al., 2001	9	Color pictures	Item	Building-presence judgments	Short	1
Sajonz et al., 2010	29	Affective pictures	Item	Indoor/outdoor situation judgments	Long	18
Slotnick et al., 2003	8	Abstract shapes	Item	Intentional encoding	Short	6
Smith et al., 2004	15	Object pictures	Item	Emotion rating on a 3-point scale	Short	10
Smith et al., 2005	18	Object pictures	Source	Imagining a connection between item and background	Short	16
Tsukiura et al., 2005	18	Words	Item	Forming a sentence, reading, and copying	Short	10
van der Veen et al., 2006	12	Words	Item	Physical, phonological, and semantic judgments	Short	5
Zerseen et al., 2001	12	Words	Item	Intentional encoding	Short	16
Remember-HC > new						
Fenker et al., 2005	20	Words	Item	Intentional encoding	Short	24
Fliessbach et al., 2006	21	Words	Item	Intentional encoding	Short	11
Henson et al., 1999	12	Words	Item	Word/non-word judgments	Short	12

APPENDIX: (Continued)

Reference	Number of participants	Retrieval-cue material	Type of retrieval	Encoding task	Retention interval ^a	Number of foci
Kim et al., 2010	12	Words	Item	Semantic category judgments	Short	6
Sharot et al., 2004	13	Affective pictures	Item	Visual complexity rating	Short	15
Trinkler et al., 2009	14	Face photos	Item	Personally-known/famous/unknown judgments	Short	7
Weis et al., 2004	16	Scene photos	Item	Building/landscape judgments	Short	17
Woodruff et al., 2005	16	Words	Item	Living/non-living judgments	Short	15
Know-LC > new						
Duarte et al., 2010	13	Line drawings	Item	Size judgments	Short	11
Fenker et al., 2005	20	Words	Item	Intentional encoding	Short	2
Henson et al., 1999	12	Words	Item	Word/non-word judgments	Short	7
Kim et al., 2010	12	Words	Item	Semantic category judgments	Short	4 ^b
Sharot et al., 2004	13	Affective pictures	Item	Visual complexity rating	Short	19
New > old						
Achim and Lepage, 2005	18	Clipart images	Item	Item/pair judgments	Short	3
Daselaar et al., 2003	17	Words	Item	Pleasant/unpleasant judgments	Short	4
de Zubicaray et al., 2005	14	Words	Item	Intentional encoding	Short	13
Donaldson et al., 2001	22	Words	Item	Abstract/concrete judgments	Short	2
Duarte et al., 2010	13	Line drawings	Item	Size judgments	Short	15
Henson et al., 1999	12	Words	Item	Word/non-word judgments	Short	24
Henson et al., 2005	22	Words	Item	Living/non-living and alphabetical-order judgments	Short	1
Hornberger et al., 2006	17	Words	Item	Size judgments	Short	6
Jessen et al., 2001	17	Words	Item	Continuous recognition	Short	10
Kahn et al., 2004	17	Words	Source	Mental imagining and backward reading	Long	15
Kim et al., 2010	12	Words	Item	Semantic category judgments	Short	7
Leveroni et al., 2000	11	Face photos	Item	Pleasant/unpleasant judgments	Short	7
McDermott et al., 2000	24	Words	Item	Intentional encoding	Short	1
Morcom et al., 2007	16	Object photos	Source	Size and living/non-living judgments	Short	5
Rombouts et al., 2001	9	Color pictures	Item	Building-presence judgments	Short	35
Sharot et al., 2004	13	Affective pictures	Item	Visual complexity rating	Short	1
Slotnick et al., 2003	8	Abstract shapes	Item	Intentional encoding	Short	4
van der Veen et al., 2006	12	Words	Item	Physical, phonological, and semantic judgments	Short	1
Vilberg and Rugg, 2009	18	Object photos	Source	Soft/hard and big/small judgments	Short	17

^aShort = 1 h or less; long = 1 day or more.^bObtained from a re-analysis of the original data.