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Posterior parietal cortex and episodic encoding: Insights from fMRI subsequent memory effects and dual-attention theory

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ABSTRACT

The formation of episodic memories—memories for life events—is affected by attention during event processing. A leading neurobiological model of attention posits two separate yet interacting systems that depend on distinct regions in lateral posterior parietal cortex (PPC). From this dual-attention perspective, dorsal PPC is thought to support the goal-directed allocation of attention, whereas ventral PPC is thought to support reflexive orienting to information that automatically captures attention. To advance understanding of how parietal mechanisms may impact event encoding, we review functional MRI studies that document the relationship between lateral PPC activation during encoding and subsequent memory performance (e.g., later remembering or forgetting). This review reveals that (a) encoding-related activity is frequently observed in human lateral PPC, (b) increased activation in dorsal PPC is associated with later memory success, and (c) increased activation in ventral PPC predominantly correlates with later memory failure. From a dual-attention perspective, these findings suggest that allocating goal-directed attention during event processing increases the probability that the event will be remembered later, whereas the capture of reflexive attention during event processing may have negative consequences for event encoding. The prevalence of encoding-related activation in parietal cortex suggests that neurobiological models of episodic memory should consider how parietal-mediated attentional mechanisms regulate encoding.

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1. Introduction

Episodic memory—conscious memory for life events—enables organisms to bridge the temporal gap between past and present (Tulving, 1985), allowing the past to inform present thought, decisions, and actions. During the last few decades, efforts to characterize the neural architecture of episodic memory have traditionally focused on mechanisms of the medial temporal lobe (MTL)—the hippocampus and adjacent medial temporal cortex—as well as those of the prefrontal cortex (PFC). While this focus is grounded in a rich literature documenting the negative consequences of MTL and PFC lesions on episodic memory (Scoville & Milner, 1957; reviewed in Eichenbaum, 2004; Ranganath & Knight, 2003; Shimamura, 1995; Squire, 1992), recent neuroimaging studies suggest that a complete story of the functional neurobiology of episodic memory may require appreciation of possible contributions from parietal cortex. This rapidly emerging neuroimaging literature indicates that dorsal and ventral regions of lateral posterior parietal cortex (PPC; Fig. 1) are consistently active during episodic *retrieval*. Now established functional dissociations between dorsal and ventral PPC during episodic remembering are beginning to

shed new light on the neural and cognitive mechanisms underlying episodic retrieval (reviewed in Cabeza, 2008; Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005; for detailed anatomical boundaries, landmarks, and connectivity of PPC, see Olson and Berryhill, this issue).

At the same time, a growing body of evidence suggests that dorsal and ventral regions in lateral PPC are components of two dissociable, yet interacting, fronto-parietal attentional systems (e.g., Behrmann, Geng, & Shomstein, 2004; Corbetta, Patel, & Shulman, 2008; Corbetta & Shulman, 2002). From this dual-attention perspective, dorsal PPC regions—superior parietal lobule (SPL) and intraparietal sulcus (IPS)—mediate goal-directed or 'top-down' attention, whereas ventral PPC regions—inferior parietal lobule (IPL; comprised of supramarginal and angular gyri) and temporoparietal junction (TPJ)[1]—mediate stimulus-driven, reflexive, or 'bottom-up' attention. Anatomically, this dorsal/ventral PPC dissociation in the domain of attention qualitatively parallels the dorsal/ventral dissociation in PPC responses during episodic retrieval, motivating recent proposals articulating the role of goal-directed and reflexive 'attention to memory' during epi-

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[1] For the sake of consistency, here we hold to the definition of TPJ as defined by Corbetta, Patel, and Shulman (2008) as encompassing the area identified in Fig. 1 as the ventral portion of SMG.
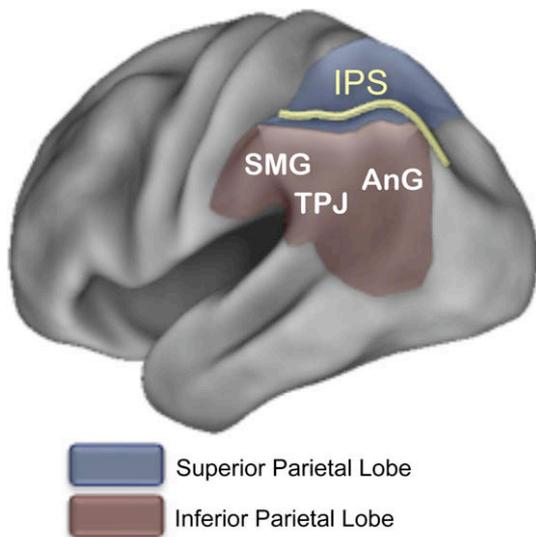
Fig. 1. Posterior parietal anatomy. Lateral posterior parietal cortex (PPC) is segregated into dorsal and ventral regions by the intraparietal sulcus (IPS). Dorsal regions include superior parietal lobe (SPL) and IPS, and ventral regions include aspects of inferior parietal lobe (IPL), namely supramarginal gyrus (SMG), temporoparietal junction (TPJ), and angular gyrus (AnG). Borders are drawn from projected borders of PALS-B12 fiducial atlas (Caret; Van Essen, 2005).

sodic retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008). While it remains possible that the correspondence between attention and episodic retrieval effects in PPC is more apparent than real (Hutchinson, Uncapher, & Wagner, submitted for publication), we view this cross-domain integrative theorizing as an important development for understanding the neural bases of episodic memory.

The ability to remember a past event is not only influenced by processes at retrieval, but also is predicated on processes engaged at the time of event encoding. While extensive behavioral evidence indicates that attention is a critical factor affecting episodic memory formation (Anderson & Craik, 1974; Baddeley, Lewis, Eldridge, & Thomson, 1984; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Kellogg, Bourne, & Cocklin, 1982; Moscovitch, 1992; Murdock, 1965; Park, Smith, Dudley, & Lafronza, 1989; for reviews see Chun & Turk-Browne, 2007; Craik, 2001), the neuroimaging literature examining the neural correlates of encoding has predominantly focused on the PFC and MTL. Given the dual-attention perspective on lateral PPC function and its possible implications for understanding episodic retrieval, here we take a parallel approach to explore the possibility that lateral PPC mechanisms may be more central to episodic *encoding* than previously assumed. In particular, we report a meta-analysis of lateral PPC findings from event-related functional magnetic resonance imaging (fMRI) studies investigating episodic encoding, focusing on studies that used the *subsequent memory paradigm* (Brewer, Zhao, Desmond, Glover, & Gabrieli, 1998; Wagner et al., 1998; for review see Paller & Wagner, 2002) to relate encoding-stage neural activity with the subsequent mnemonic fate of an event (e.g., later remembered or forgotten). We first report the findings from this meta-analysis, and then propose a theoretical framework that describes possible contributions of lateral PPC mechanisms to episodic encoding. Throughout, we aim to connect this largely overlooked neuroimaging literature on lateral PPC activation during episodic encoding with that on lateral PPC mechanisms of goal-directed and reflexive attention.

2. Functional neuroimaging studies of encoding

Since the introduction of functional neuroimaging methods, study of the neural mechanisms of episodic encoding has advanced

by means of various experimental paradigms. Early designs relied on comparing positron emission tomography (PET) or fMRI signals integrated across extended periods or 'blocks' of specific mental tasks. These blocked designs often varied the encoding tasks while holding constant the nature of the stimuli, or vice versa (for reviews see Buckner & Wheeler, 2001; Cabeza & Nyberg, 2000; Wagner, Koutstaal, & Schacter, 1999). For instance, candidate neural correlates of encoding were identified by contrasting the activity elicited by stimulus processing tasks yielding superior later memory with those yielding poorer later memory (i.e., 'levels of processing' manipulations; Craik & Lockhart, 1972; Craik & Tulving, 1975). Incidental encoding tasks that lead to superior memory generally include those where attention to stimulus meaning is required (e.g., semantic classification or self-reference judgments), whereas memory is typically poorer when more superficial aspects of stimuli are attended (e.g., judgments of phonology or, even more superficial attributes such as color, shape, or size). While studies employing levels-of-processing designs have predominantly emphasized that ventrolateral PFC activation is greater during meaningful vs. superficial orienting tasks (e.g. Demb et al., 1995; Gabrieli, Poldrack, & Desmond, 1998; Kapur et al., 1994), some studies have revealed the reverse pattern in PPC. For example, Wagner et al. (1998) observed greater activation in bilateral ventral and dorsal PPC during superficial vs. meaningful word processing (unpublished observations).

Another blocked-design approach is to directly vary the availability of stimulus-directed attention during encoding. It is well established that memory suffers when an encoding task is performed concurrently with a distracting task (e.g., Anderson & Craik, 1974; Baddeley, Scott, Drynan, & Smith, 1969; Baddeley et al., 1984; Murdock, 1965; for reviews see Craik, 2001; Yonelinas, 2002). This impairment may reflect the negative consequence of having fewer attentional resources to direct toward the to-be-encoded information. Given the importance of lateral PPC in theories of attention, it is surprising that, of the few blocked-design studies investigating the impact of divided-attention on neural correlates of encoding (e.g., Anderson et al., 2000; Fletcher, Shallice, & Dolan, 1998; Fletcher et al., 1995; Iidaka, Anderson, Kapur, Cabeza, & Craik, 2000; Shallice et al., 1994), only one reported an effect in lateral PPC. Specifically, Iidaka and colleagues (2000) observed increased activation in ventral PPC [~Brodmann's area (BA) 40] when volunteers intentionally encoded word pairs while performing a demanding vs. an easy secondary task.

The preceding between-condition comparisons in blocked-design studies provide a relatively indirect measure of encoding-related processing. A more direct blocked-design approach is to relate encoding activity during a block of study items to later memory performance, averaged across all of the items in the block. This approach has been implemented using both across- and within-subject analyses (Alkire, Haier, Fallon, & Cahill, 1998; Cahill et al., 1996; Fernandez et al., 1998, 1999). Notably, Alkire and colleagues (1998) reported that across-subject variability in ventral PPC activation (supramarginal and angular gyri, ~BAs 40 and 39, respectively) during encoding blocks positively correlated with the number of items later recalled from the blocks. This finding, when taken together with the levels-of-processing and divided-attention blocked-design literatures, provides limited but suggestive evidence for a role of lateral PPC in event encoding.

3. Subsequent memory methodology

Central to understanding episodic memory is delineation of the neurobiological processes that influence whether an individual event will be memorable or forgotten. Because blocked functional imaging designs provide measures of *average* activity over blocks

of events, such studies do not afford leverage on this important issue. Rather, event-related designs are required to relate activity elicited by individual experimental events to later memory for the events (Paller & Wagner, 2002; Rugg, 1995; Sommer, Schweinberger, & Matt, 1991). During the past decade, over 100 fMRI studies have used an event-related 'subsequent memory' approach—adapted from electroencephalography (EEG) methods (for reviews of EEG studies, see Rugg, 1995; Wagner et al., 1999)—to delineate the neural processes that differentiate events that will be later remembered or forgotten.

FMRI studies employing the subsequent memory procedure circumvent the need to vary processing demands at encoding in order to influence later memory performance. Instead, in these studies the individual hemodynamic responses elicited by discrete study items are recorded and classified according to the subsequent mnemonic fate of each stimulus, as assessed in a post-encoding memory test (Fig. 2). By holding constant the nature of the encoding task and the stimulus materials, variability in the magnitude of activity during encoding can be directly correlated with variability in later memory performance. Differences in activity elicited by items later remembered versus forgotten ('subsequent memory effects') are interpreted as candidate neural correlates of successful encoding.

Reassuringly, many of the regions associated with encoding in blocked-design studies converge with those identified with the subsequent memory procedure. For example, subsequent memory studies have consistently reported effects in ventrolateral PFC (inferior frontal gyrus; IFG) and MTL (hippocampus and MTL cortex) (for reviews see Blumenfeld & Ranganath, 2006; Davachi, 2006; Paller & Wagner, 2002; Rugg, Otten, & Henson, 2002). When combined with the rich neuropsychological literatures documenting global amnesia following MTL insult (Cohen & Eichenbaum, 1995; Squire, 1992) and modest but significant episodic memory impairments following lateral PFC lesions (Wheeler, Stuss, & Tulving, 1995), the ubiquity of subsequent memory effects in PFC and MTL may have overshadowed lateral parietal encoding effects, despite their being reported in dozens of event-related fMRI studies. The aim of the present review is to draw attention to these lateral PPC subsequent memory effects, and to begin to consider possible mechanistic contributions of parietal cortex to episodic encoding.

4. Meta-analysis of fMRI subsequent memory effects in lateral PPC

In reviewing the subsequent memory literature, we constrained our search space to studies identified in PubMed and the ISI Web of Science, using the search terms 'fMRI' and either 'subsequent memory', 'episodic encoding', 'encoding', or 'learning'. We additionally searched the ISI Web of Science cited reference database for articles citing the original fMRI subsequent memory studies (Brewer et al., 1998; Wagner et al., 1998), refining the 500+ results using the aforementioned search terms. We included only studies that investigated healthy young adults, excluding studies that employed pharmacological manipulations or special populations such as minors, older adults, or patients diagnosed with amnesia, Alzheimer's disease, mild cognitive impairment, schizophrenia, or depression.

We restricted analyses to studies that conducted within-subjects, event-related analyses of items that were submitted to a traditional subsequent memory contrast, as described above. These criteria excluded studies that relied only on connectivity analyses, tested only non-veridical (false) memory, only contrasted study tasks against baseline, or performed contrasts within a mnemonic category (e.g., subsequently remembered items that were studied in one condition vs. another, without comparing to the relevant subsequently forgotten items). The motivation behind this latter exclusion criterion is predicated on the idea that the objective of the meta-analysis is to assess the distribution of effects of encoding success or failure, as defined by contrasts that compare different subsequent memory outcomes. Thus, 'simple effects' (within a mnemonic category) or 'main effects' (collapsing across mnemonic categories) of additional factors are beyond the scope of this review. By the same token, parametric contrasts were included when the contributing cells varied along a mnemonic dimension, for example increasing memory confidence or number of items remembered from a multi-item study event.

Identified subsequent memory foci were included in the analysis if the effects fell within lateral PPC, defined broadly (posterior, lateral, superior or inferior parietal cortex), regionally (supramarginal gyrus, SMG; angular gyrus, AnG; intraparietal sulcus, IPS; superior parietal lobule, SPL; inferior parietal lobule, IPL; temporoparietal junction, TPJ), or according to reported approximate Brod-
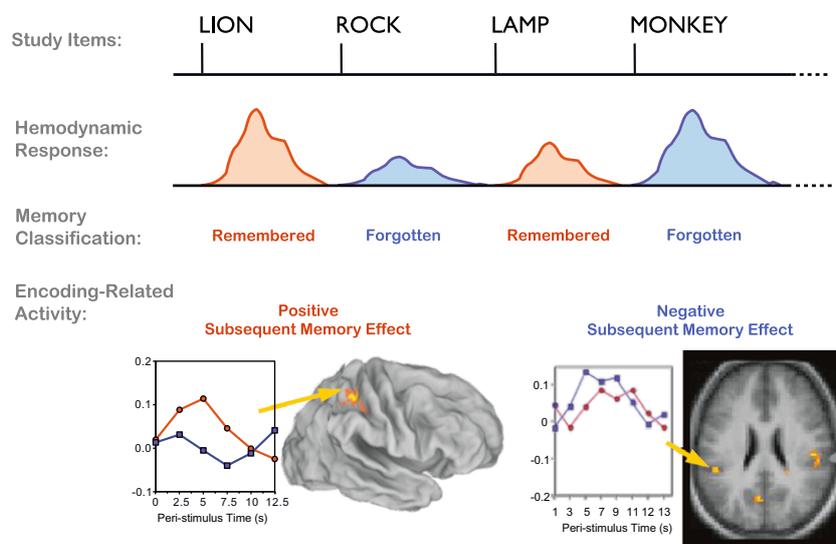
Fig. 2. Subsequent memory procedure. Neural correlates of memory formation are investigated by recording the hemodynamic response (using event-related fMRI) elicited by individual study items, and classifying each response according to the mnemonic fate of the eliciting item (remembered or forgotten). Responses can correlate positively (remembered > forgotten; positive subsequent memory effects) or negatively (forgotten > remembered; negative subsequent memory effects) with later memory. Positive subsequent memory effect depicted from Uncapher, Otten, and Rugg (2006), negative effect depicted from Wagner and Davachi (2001).

mann's area (~BA 7, 40, 39, or the superior aspect of 19). The foci of the reported peak voxels were required to project to the lateral (and not medial) surface of a fiducial brain, within the aforementioned BAs comprising lateral PPC, using a surface-rendering algorithm that accounted for differing stereotaxic spaces (Van Essen, 2005; see below). All foci listed as demonstrating significant subsequent memory effects—according to study-specific statistical thresholds—were included.

Each subsequent memory effect that fulfilled the above criteria was classified along the following dimensions: (1) *positive vs. negative effects*—effects were considered 'positive' if the directional contrast was *subsequently remembered > forgotten*, and 'negative' for the opposite contrast; (2) *retention interval*—effects were classified according to the duration of the interval between study and test, as either short (up to 45 min after study) or long (from 24 h to 3 week); (3) *study material*—effects were segregated according to whether the studied stimuli were words (words, word pairs, or sentences) or images (objects, scenes, or photographs); (4) *study task*—the orienting tasks under which items were studied were classified as semantic (requiring some meaning-based classification of the study items; e.g., animacy or pleasantness judgments, or imagining the meaning of study items), verbal (requiring some judgment of phonology), or spatial (item-location associative encoding); due to low Ns, studies not falling into these three categories were not considered when assessing the effect of study task; (5) *memory classification*—effects were segregated according to how later memory was assessed, including recognition only (tasks requiring only old/new recognition decisions), high confidence (tasks segregating different levels of recognition confidence, with effects comparing high confidence hits with low confidence hits and/or misses), source (tests of memory for contextual 'source' information, such as the task, location, or color in which an item was studied), recollection/recall (effects assessing 'Remember' responses from a 'Remember/Know' paradigm, or cued or free recall), or familiarity (effects assessing 'Know' responses, parametric contrasts across multiple levels of recognition confidence, or item memory when source information was not successfully retrieved).

Foci were surface-rendered onto a fiducial brain (PALS-B12) using Caret Software (http://brainmap.wustl.edu/caret; Van Essen, 2005). The Caret surface-rendering algorithm maps stereotaxic coordinates—including those in Talairach and MNI spaces—onto a standardized PALS-B12 atlas surface using a 'surface atlas mediation' strategy (Van Essen & Dierker, 2007). This strategy affords a method of visualizing foci from multiple studies on a common atlas, accounting for different stereotaxic spaces. We overlaid the boundaries of relevant BAs (as delineated in Caret) onto the fiducial brain in order to classify the surface-projected subsequent memory foci according to approximate BAs in an unbiased and consistent manner. Table 1 lists the foci from all studies contributing to the meta-analysis, with the corresponding classifications for the five factors of interest and approximate BAs.

5. PPC Subsequent memory effects

A total of 93 studies fit the above inclusion criteria of which 37 studies (40%) reported lateral PPC subsequent memory effects (Table 1; studies not reporting effects in lateral PPC listed in Appendix), yielding 137 peak foci (Table 1 and Fig. 3). While fairly common, the frequency of PPC encoding effects nevertheless appears lower than the ubiquitously observed PPC effects during episodic retrieval (for reviews see Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008; Vilberg & Rugg, 2008; Wagner et al., 2005). Furthermore, no obvious laterality exists in PPC subsequent memory effects (Fig. 3; 56% of foci were localized to the left hemi-

sphere), whereas a recent meta-analysis of fMRI retrieval effects in PPC reported twice as many foci in the left hemisphere as in the right (Vilberg & Rugg, 2008). Thus, PPC functional contributions during encoding may be only partially overlapping with those during retrieval. We next characterize the patterns of PPC subsequent memory effects along five classification dimensions.

5.1. Positive vs. negative subsequent memory effects

Mechanistic interpretations of lateral PPC function may be informed by considering encoding responses that positively (remembered > forgotten) and negatively (forgotten > remembered) correlate with an event's later mnemonic fate (Otten & Rugg, 2001a; Wagner & Davachi, 2001). However, it is worth noting that, of the 93 studies considered here, the overwhelming majority (96.8%) reported positive subsequent memory effects, while only 9.3% reported negative effects. At present, it is unclear whether this imbalance of positive and negative effects reflects a differential frequency of such effects or a reporting bias in favor of positive encoding correlates.

Of the 90 studies reporting positive subsequent memory effects anywhere in the brain, 33 studies (36.7%) reported one or more positive effects in lateral PPC. By contrast, of the 10 studies reporting negative subsequent memory effects anywhere in the brain, eight (80%) reported one or more negative subsequent memory effects in lateral PPC. Moreover, while we do not focus on medial PPC here, the two other studies reported negative effects in medial parietal regions (Reynolds, Donaldson, Wagner, & Braver, 2004; Turk-Browne, Yi, & Chun, 2006).

The distribution of positive and negative effects across lateral PPC subregions (Fig. 3) reveals a striking regional dissociation. While positive effects are predominantly found in dorsal regions (SPL and IPS), negative effects are confined exclusively to ventral regions (IPL and TPJ). To quantify this dorsal/ventral dissociation, we calculated the percentage of positive and negative foci falling in each subregion. As reported in Table 2, 85% of positive effects fall within or dorsal to IPS, while none of the negative subsequent memory foci are found in these dorsal regions.

The positive effects are distributed fairly evenly along the (anterior–posterior) length of IPS and adjacent SPL, with 45% of positive effects found in the more anterior regions [sometimes referred to as BA 7a (Brodmann, 1914) or 7A and 7PC (Scheperjans, Grefkes, Palomero-Gallagher, Schleicher, & Zilles, 2005; Scheperjans, Palomero-Gallagher, Grefkes, Schleicher, & Zilles, 2005, Scheperjans et al., 2007, 2008); defined here as the ascending and horizontal segments of IPS and/or adjacent SPL], and 41% in more posterior regions [BA 7b (Brodmann, 1914) or 7P (Scheperjans, Grefkes, et al., 2005; Scheperjans, Palomero-Gallagher, et al., 2005, Scheperjans et al., 2007, 2008); here defined as the descending segment of IPS and/or adjacent SPL]. The remaining 14% of positive effects are found in ventral regions and—like the dorsal effects—fall fairly evenly in anterior and posterior regions, with eight foci observed in SMG (BA 40) and nine in AnG (BA 39).

5.2. Retention interval and subsequent memory effects

We next segregated subsequent memory foci according to whether the interval between study and test was short or long. Of the 93 studies exhibiting subsequent memory effects, all but two explicitly indicated the retention interval. Of these 91 studies, the majority (85.7%) used short intervals (arbitrarily defined here as 45 min or less, whereas long intervals were defined as 24 h or longer).

Lateral PPC subsequent memory effects were observed in 42.3% (33 of 78) of short interval studies and in 30.8% (4 of 13) of long interval studies, yielding 113 foci from short interval studies (89

Table 1
Coordinates of peak voxels of clusters exhibiting subsequent memory effects in lateral PPC.

Reference	X	Y	Z	~BA	Pos/neg	Retention interval	Study material	Study task	Memory classification
Buckner, Wheeler, and Sheridan (2001)	−35	−63	24	39	pos	short	words	sem	recog
	−43	−75	18	19/39	pos	short	words	sem	recog
	−37	−79	30	19	pos	short	words	sem	recog
Cansino, Maquet, Dolan, and Rugg (2002)	−44	−42	32	40	pos	short	pics	sem (& spatial)	source (loc)
Chee, Goh, Lim, Graham, and Lee (2004)	−28	−74	41	7p/19	pos	long	words	sem	recog
Chua, Schacter, Rand-Giovannetti, and Sperling (2007)	−54	−50	36	40	neg[us]	short	both	sem	neg
	60	−46	46	40	neg[us]	short	both	sem	neg
	56	−52	22	39	neg[us]	short	both	sem	neg
	58	−34	34	40	neg[us]	short	both	sem	neg
	−64	−46	16	40	neg[us]	short	both	sem	neg
	−64	−40	32	40	neg[us]	short	both	sem	neg
	60	−38	48	40	neg[us]	short	both	sem	neg
	−60	−38	36	40	neg[us]	short	both	sem	neg
Clark and Wagner (2003)	−27	−72	54	7p	pos	short	words	verbal	hi conf
	−27	−69	30	7p/19	pos	short	words	verbal	hi conf
	30	−75	51	7p	pos	short	words	verbal	hi conf
	60	−45	36	40	neg[b]	short	words	verbal	neg
	51	−51	39	39	neg[b]	short	words	verbal	neg
	48	−57	18	39	neg[b]	short	words	verbal	neg
Daselaar, Prince, Cabeza (2004)	60	−43	30	39/40	neg[b]	short	words	sem	neg
	49	−49	48	39/40	neg[b]	short	words	sem	neg
Davachi, Maril, and Wagner (2001)	−24	−57	45	7a	pos	short	words	verbal	recog
	30	−63	45	7p	pos	short	words	verbal	recog
Dickerson et al. (2007)	−27	−60	39	7a	pos	short	pics	sem	recall (free)
	−51	−51	42	40	pos	short	pics	sem	recall (free)
Garoff, Slotnick, and Schacter (2005)	−52	−25	33	7a	pos	long	pics	sem	—
	22	−56	61	7p	pos	long	pics	sem	—
	−21	−56	60	7a	pos	long	pics	sem	famil (source inc > miss)
	−48	−39	54	7a	pos	long	pics	sem	famil (source inc > miss)
	−27	−56	43	7a	pos	long	pics	sem	famil (source inc > miss)
	−50	−29	44	7a	pos	long	pics	sem	famil (source inc > miss)
	27	−56	49	7p	pos	long	pics	sem	famil (source inc > miss)
	−49	−39	53	7a	pos	long	pics	sem	recog
	26	−58	47	7p	pos	long	pics	sem	recog
	−37	−54	54	7a	pos	long	pics	sem	recog
Gonsalves et al. (2004)	43	−49	17	39	neg[us]	short	pics	sem	neg
Heinze et al. (2006)	−28	−72	42	7p	pos	short	words	mem only	recall (free)
	−44	−48	50	7a	pos	short	words	mem only	recall (free)
	−42	−46	50	7a	pos	short	words	mem only	recall (free)
	−60	−54	34	40	pos	short	words	mem only	recall (free)
	36	−78	40	19	pos	short	words	mem only	recall (free)
Henson, Rugg, Shallice, Josephs, and Dolan (1999)	−27	−60	60	7a	pos	short	words	verbal	recoll (R > K)
Kao, Davis, and Gabrieli (2005)	34	−48	49	7a	pos	short	pics	JOL	hi conf
	30	−54	34	7p/19	pos	short	pics	JOL	hi conf
	−22	−72	41	7p/19	pos	short	pics	JOL	hi conf
Kensinger and Schacter (2006)	22	−47	60	7a	pos	short	words	sem	source (task)
	24	−47	55	7a	pos	short	words	sem	source (task)
	−27	−63	28		pos	short	words	sem	famil (source inc > miss)
Kensinger, Garoff-Eaton, and Schacter (2007)	30	−37	25	41/40	pos	short	pics	sem	recog
	29	−65	35	19/7p	pos	short	pics	sem	source (item details)
	−51	−30	46	7a	pos	short	pics	sem	source (item details)

(continued on next page)

Table 1 (continued)

Reference	X	Y	Z	~BA	Pos/neg	Retention interval	Study material	Study task	Memory classification
	−48	−28	46	7a	pos	short	pics	sem	source (task)
Kim and Cabeza (2006)	−30	−72	31	19	pos	short	words	sem	hi conf
Kirchhoff et al. (2000)	31	−80	31	19	pos	short	pics	sem	hi conf
	46	−71	28	39/19	pos	short	pics	sem	hi conf
	−25	−77	28	19	pos	short	pics	sem	hi conf
	−40	−77	21	19/39	pos	short	pics	sem	hi conf
	−25	−87	34	7p/19	pos	short	pics	sem	hi conf
	50	−52	43	39/40	neg[us]	short	pics	sem	neg
Otten (2007)	48	−54	27	39/40	neg[us]	long	words	sem	neg
	36	−48	54	7a	pos	long	words	sem	recoll (R > M)
	39	−24	30	40	neg[a/b]	long	words	sem	neg
	−39	−57	24	39	neg[b]	long	words	sem	neg
	−57	−30	51	7a	pos	long	words	sem	famil (K > M)
	30	−51	54	7a	pos	long	words	sem	famil (K > M)
	−39	−48	63	7a	pos	long	words	sem	famil (K > M)
	42	−42	48	7a	pos	long	words	sem	famil (K > M)
	−39	−60	33	39	neg[us]	long	words	sem	neg
	−21	−54	51	7a	pos	long	words	sem	famil (K > M)
	−30	−72	24	19	pos	long	words	sem	famil (K > M)
Otten, Henson, and Rugg (2001)	−45	−39	33	41/40	pos	short	words	sem	hi conf
Otten, Henson, and Rugg (2002)	−27	−51	63	7a	pos	short	words	verbal	hi conf
	−24	−63	45	7p	pos	short	words	verbal	hi conf
Otten and Rugg (2001a)	−54	−54	36	40	neg[us]	short	words	sem	neg
	−54	−42	48	40	neg[us]	short	words	sem	neg
	63	−45	27	40	neg[us]	short	words	sem	neg
	63	−33	42	40	neg[us]	short	words	sem	neg
Otten and Rugg (2001b)	−39	−45	51	7a	pos	short	words	verbal	hi conf
	39	−45	45	7a	pos	short	words	verbal	hi conf
	−39	−45	51	7a	pos	short	words	verbal	hi conf
	39	−45	45	7a	pos	short	words	verbal	hi conf
	−42	−39	42	7a	pos	short	words	verbal	hi conf
	39	−42	45	7a	pos	short	words	verbal	hi conf
	−39	−45	51	7a	pos	short	words	verbal	hi conf
	39	−45	45	7a	pos	short	words	verbal	hi conf
	−39	−45	51	7a	pos	short	words	verbal	hi conf
	39	−45	45	7a	pos	short	words	verbal	hi conf
Ranganath et al. (2004)	−52	−30	34	7a	pos	short	words	sem	source (col/task)
	−40	−40	48	7a	pos	short	words	sem	source (col/task)
	48	−38	40	7a	pos	short	words	sem	source (col/task)
	36	−58	44	7p	pos	short	words	sem	source (col/task)
	−44	−36	36	40	pos	short	words	sem	famil (conf)
	−46	−44	38	7a	pos	short	words	sem	famil (conf)
	−56	−30	38	7a	pos	short	words	sem	famil (conf)
	−44	−40	56	7a	pos	short	words	sem	famil (conf)
	−22	−68	54	7p	pos	short	words	sem	famil (conf)
	−28	−58	52	7a	pos	short	words	sem	famil (conf)
Reber et al. (2002)	29	−61	46	7p	pos	short	words	DF	recog
	32	−62	45	7p	pos	short	words	DF	recog
Reynolds et al. (2004)	−32	−72	48	7p	pos	short	words	sem	source (task)
	34	−60	45	7p	pos	short	words	sem	source (task)
Schott et al. (2006a)	−30	−68	45	7p	pos	short	words	verbal	recall (cued)
	−39	−59	53	7a	pos	short	words	verbal	recall (cued)
	−33	−62	50	7a	pos	short	words	verbal	recall (cued)
	−21	−73	56	7p	pos	short	words	verbal	recall (cued)
Sommer, Rose, Gläscher, Wolbers, and Büchel (2005a)	33	−63	48	7p	pos	short	pics	spatial (& sem)	source (loc)

Study	x	y	z	BA					
	−9	−81	48	7p	pos	short	pics	spatial (& sem)	source (loc)
	−30	−57	45	7a	pos	short	pics	spatial (& sem)	source (loc)
	27	−69	57	7p	pos	short	pics	spatial (& sem)	source (loc)
	−15	−75	57	7p	pos	short	pics	spatial (& sem)	source (loc)
	−30	−57	33	7a	pos	short	pics	spatial (& sem)	source (loc)
Sommer, Rose, Weiller, and Büchel (2005b)	27	−60	54	7p	pos	short	pics	spatial (& sem)	source (loc)
	−15	−78	54	7p	pos	short	pics	spatial (& sem)	source (loc)
	−33	−60	36	7a	pos	short	pics	spatial (& sem)	source (loc)
Sommer, Rose, and Büchel (2006)	54	−51	15	39	pos	short	pics	spatial (& sem)	source (loc-primacy)
	54	−66	39	39	pos	short	pics	spatial (& sem)	source (loc-primacy)
	57	−21	30	40	pos	short	pics	spatial (& sem)	source (loc-primacy)
	33	−63	48	7p	pos	short	pics	spatial (& sem)	source (loc)
	−27	−78	21	19	pos	short	pics	spatial (& sem)	source (loc)
Staresina and Davachi (2006)	−39	−54	57	7a	pos	short	words	sem	recall (free)
	−39	−54	57	7a	pos	short	words	sem	recall (free)
	−57	−54	30	40	pos	short	words	sem	recall (free)
	−36	−69	42	39	pos	short	words	sem	recall (free)
	54	−60	39	39	pos	short	words	sem	recall (free)
	39	−57	42	7a	pos	short	words	sem	recall (free)
Tendolkar et al. (2007)	28	−66	55	7p	pos	short	pics	sem	recog
Uncapher, Otten, Rugg (2006)	21	−42	48	7a	pos	short	words	spatial (& sem)	source (loc and col)
Uncapher and Rugg (2005a)	30	−63	57	7p	pos	short and long	words	sem	recoll (R > M)
Uncapher and Rugg (2008)	36	−75	45	7p/19	pos	short	words	sem	recoll (R > M)
Wagner and Davachi (2001)	50	−49	34	40	neg[us]	short	words	sem	neg
	56	−43	34	40	neg[us]	short	words	sem	neg
	50	−43	46	40	neg[us]	short	words	sem	neg
	57	−30	21	40	neg[b]	short	words	verbal	neg
	−54	−39	24	40	neg[a]	short	words	verbal	neg
Weis, Klaver, Reul, Elger, and Fernandez (2004)	−28	−72	40	7p/19	pos	short	pics	mem only	hi conf
Wittman et al. (2005)	−30	−73	45	7p	pos	short	pics	sem	recog
	18	−70	59	7p	pos	long	pics	sem	recog

Coordinates are listed in study-specific space (e.g., MNI, Talairach). Reported BA designation approximated by identifying where each focus projected on the PALS-B12 atlas (see Meta-Analysis of fMRI Subsequent Memory Effects in Lateral PPC).

7a, anterior aspect of BA 7; 7p, posterior aspect of BA 7; pos, positive subsequent memory effect (remembered > forgotten), neg, negative subsequent memory effect (forgotten > remembered), neg[a], negative subsequent memory effects *above* baseline, neg[b], negative subsequent memory effects *below* baseline, neg[a/b], negative subsequent memory effects *above and below* baseline (i.e., forgotten above baseline, remembered below baseline), neg[us], unspecified relationship between negative subsequent memory effects and baseline; pics, pictures; sem, semantically-oriented study task; JOL, judgment of learning task; DF, directed forgetting task; mem only, memorization only task; recog, recognition classification (hits > miss); famil, familiarity classification; famil (conf), familiarity classification based on parametric contrast of confidence judgments; famil (K > M), familiarity classification based on 'know' > miss; famil (source inc > miss), familiarity classification based on incorrect source judgments (accurate item judgment) > miss; hi conf, high confidence recognition (vs. low confidence recognition or miss); source (loc), accurate item-location judgment; source (loc and col), accurate item-location and item-color judgment; source (col/task), accurate item-color and/or item-task judgment; recoll (R > M), recollection classification based on 'remember' > miss.
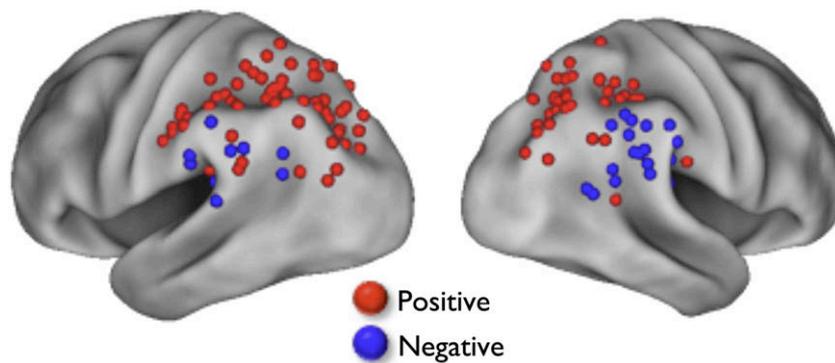
Fig. 3. Positive and negative subsequent memory effects. Effects are segregated according to whether they correlate positively or negatively with later memory success.

positive, 24 negative), 23 from long interval studies (19 positive, 4 negative), and one from a study employing both intervals (the effect positively predicted later memory for both intervals).

As was noted in the previous section, dorsal PPC regions exclusively demonstrate positive subsequent memory effects and ventral PPC regions demonstrate mostly negative effects. Further segregating these effects according to retention interval seems to account for the positive effects that fall in ventral PPC, as every such focus comes from a study in which memory was tested after a short delay (Fig. 4). In fact, while we arbitrarily defined the short retention interval classification to include studies with delays of 45 min or less, all positive subsequent memory effects in ventral PPC come from studies using a retention interval of 15 min or less. This finding, while based on a limited number of observations, suggests that retention interval differentially impacts subsequent memory effects in dorsal and ventral PPC: positive effects associated with successful memory days or weeks later fall exclusively in dorsal regions, whereas positive effects following a short retention interval span both dorsal and ventral regions.

Although the relatively small sample size suggests interpretative caution is warranted at this point, we tentatively propose this distribution—if real—suggests that different PPC mechanisms may give rise to memories that are differentially durable, with dorsal mechanisms supporting longer lasting memories (thus correlating positively with memory success at both short and long intervals) and ventral mechanisms supporting more transient memories (correlating positively only at shorter intervals or negatively at both intervals).

5.3. Effects of study material, study task, and memory classification

Dissociable patterns of encoding activity in PFC and MTL have been observed as a function of the nature of the study material and task, as well as the manner in which later memory is assessed (e.g., Davachi, Mitchell, & Wagner, 2003; Kirchhoff, Wagner, Maril, & Stern, 2000; Otten & Rugg, 2001b; Ranganath et al., 2004). To determine their effect on parietal encoding activation, we classified the positive subsequent memory foci considered herein according to these three factors (there were too few negative foci to permit similar analyses).

In striking contrast to PFC and MTL, these dimensions appear to have little to no impact on the pattern of PPC subsequent memory effects (Figs. 5 and 6). For instance, word and picture stimuli exhibit seemingly overlapping effects throughout PPC (Fig. 5A). Similarly, whereas classic accounts of PPC function prominently feature a spatial attention component (reviewed in Husain & Nachev, 2007), here we report no obvious regional dissociations between spatial and non-spatial encoding tasks (Fig. 5B). What did emerge from this task analysis is the suggestion that foci from verbally oriented encoding tasks are confined to (predominantly left-

lateralized) dorsal regions, particularly concentrating along the horizontal segment of left IPS and adjacent SPL. Analysis of test type revealed that IPS and adjacent SPL demonstrate effects for every memory classification (Fig. 6), with several classes localized exclusively to these dorsal regions (effects associated with item familiarity, cued recall and 'remember' judgments).

6. Theoretical implications of parietal encoding effects

Two dissociations are suggested by the present meta-analysis, with both showing regional distinctions along the dorsal/ventral axis of PPC: (1) the vast majority of positive subsequent memory effects are observed in dorsal PPC, while all negative subsequent memory effects localize to ventral PPC; and (2) the positive effects that do fall in ventral regions all derive from studies that used a short retention interval. We discuss possible interpretations of these findings in the context of theoretical accounts of dorsal and ventral PPC mechanisms.

6.1. Dorsal PPC contributions to encoding

Encoding activation in dorsal regions of lateral PPC is associated with subsequent memory (a) tested after short and long intervals, (b) for all types of study material, (c) following various types of study tasks, and (d) using memory probes for conjunctive memory (e.g., recollection) and item memory (e.g., familiarity). Increases in dorsal PPC encoding activation are consistently associated with successful remembering, as dorsal PPC regions do not demonstrate negative subsequent memory effects. Taken together, these findings suggest that dorsal PPC mechanisms play a broad role in the successful formation of episodic memories.

6.1.1. Positive subsequent memory effects

As a whole, neocortical activation during stimulus or event processing is commonly held to reflect ongoing processes engaged in service of performing the task at hand (Konorski, 1967). An episodic representation of the event is thought to be created when the products of this distributed pattern of neocortical activity are encoded via mechanisms of the MTL (e.g., Aggleton & Brown, 2006; Brown & Aggleton, 2001; Norman & O'Reilly, 2003; Squire et al., 2004). By this account, subsequent memory effects in the hippocampus and surrounding MTL cortices are thought to reflect increased or more effective engagement of MTL encoding mechanisms, leading to an increased probability that the eliciting event will be later remembered.

What, then, do positive subsequent memory effects in neocortex reflect? The answer to this question will of course depend on the neocortical mechanisms exhibiting such signals. In the case of dorsal PPC, positive subsequent memory effects likely tell an attentional story, given how frequently this region is implicated

Table 2
Distribution of effects in lateral PPC.

	Pos/neg		Retention interval				Study material			Study task			Memory classification					
	Pos	Neg	Short-pos	Long-pos	Short-neg	Long-neg	Words	Pictures	Verbal	Sem	Spatial	Mem only	Other	Recog	Famil	Hi Conf	Source	Recoll/Recall
IPS/SPL:																		
~BA7a	50	0	37	13	0	0	36	14	15	32	4	2	1	3	14	12	11	9
~BA7p/BA19	45	0	39	7	0	0	22	23	7	30	8	3	4	10	4	13	12	6
IPL/TPJ:																		
~BA40	8	18	8	0	17	1	4	4	0	7	2	1	0	1	1	1	2	3
~BA39	8	10	8	0	7	3	4	4	0	8	2	2	0	2	0	2	2	2

BA 7a, anterior aspect of BA7; BA7p, posterior aspect of BA7; Pos, positive subsequent memory effect; Neg, negative subsequent memory effect; Sem, semantic study task; Mem only, memorization only study task; Recog, only recognition judgment reported; Famil, familiarity classification; Hi Conf, high confident recognition; Recoll, recollection (as indexed by 'remember' judgments).
Effects from Table 1 quantified by region and dimension.

in tasks requiring goal-directed or 'executive' attentional resources. Indeed, a recent meta-analysis of 60 neuroimaging studies of attention and working memory reported dorsal PPC to be consistently implicated in executive processing (Wager & Smith, 2003), a finding that aligns with the aforementioned dual-attention hypothesis that posits that dorsal PPC mechanisms support the allocation of goal-directed attention (Corbetta & Shulman, 2002; Corbetta et al., 2008; see also Hutchinson et al., submitted for publication). Importantly, 'top-down' attention is thought to facilitate the processing of attended sensory signals and internally generated representations (spatial attention: Bichot, Rossi, & Desimone, 2005; Brefczynski & DeYoe, 1999; Luck, Chelazzi, Hillyard, & Desimone, 1997; Moran & Desimone, 1985; Tootell et al, 1998; Treue & Maunsell, 1996; feature-based attention: Bichot et al., 2005; Liu, Larsson, & Carrasco, 2007; McAdams & Maunsell, 2000; Saenz, Buracas, & Boynton, 2002; Serences & Boynton, 2007; Treue & Martinez-Trujillo, 1999), which may, in turn, increase the probability that the attended information is encoded into episodic memory via the MTL. As such, positive subsequent memory effects may reflect this influence of goal-directed attention on event encoding.

6.1.2. Study material and study task

Proponents of the dual-attention hypothesis posit that dorsal PPC mechanisms are engaged in a broad range of tasks, encompassing a wide variety of informational domains and modalities (reviewed in Corbetta et al., 2008). Thus, from this perspective, goal-directed attention can be engaged to facilitate the processing of both words and pictures, and can be engaged during goal-directed task performance regardless of the representational domain central to the task. Compatible with this hypothesis, our meta-analysis revealed that dorsal PPC activation demonstrates subsequent memory effects for all types of study material and following a wide variety of orienting tasks.

On the other hand, an extensive literature points to a more specialized role of dorsal PPC in spatial attention (reviewed in Husain & Nachev, 2007). For example, fMRI data indicate that multiple IPS subregions demonstrate topographic representations of attended space (Saygin & Sereno, 2008; Silver, Ress, & Heeger, 2005), as revealed using covert attentional orienting (Silver et al., 2005), memory-guided saccade (Hagler, Riecke, & Sereno, 2007; Konen & Kastner, 2008a; Konen & Kastner, 2008b; Levy, Schluppeck, Heeger, & Glimcher 2007; Schluppeck, Curtis, Glimcher, & Heeger, 2006; Schluppeck, Glimcher, & Heeger, 2005; Sereno, Pitzalis, & Martinez, 2001) or reach (Hagler et al., 2007; Levy et al. 2007), and passive viewing paradigms (Swisher, Halko, Merabet, McMains, & Somers, 2007). From this perspective, we might expect dorsal PPC to be differentially associated with subsequent memory effects when the encoding task requires attention to the location of the study item. However, while many spatial effects did localize to dorsal regions (both IPS and SPL), some were also observed in ventral PPC; furthermore, many non-spatial (verbal and semantic) encoding tasks yielded subsequent memory effects localized to dorsal PPC. This broad distribution of task effects could be a consequence of all surveyed tasks requiring at least some degree of dorsal PPC-mediated spatial attention. For example, attending to object-location associations may recruit similar visuospatial attention processes as those that allow subjects (in verbal or semantic tasks) to localize the study item in extrapersonal space, or to attend to different features of a stimulus that necessarily occupy (albeit only slightly) different spatial locations. Interestingly, a recent study observed that directing attention towards object-location vs. object-color enhanced the magnitude of subsequent memory effects for these different associations in different dorsal PPC regions, right SPL and IPS, respectively (Uncapher & Rugg, submitted for publication). This finding seems to argue against the idea that dorsal PPC mechanisms operate in a more domain-general manner, though additional within-
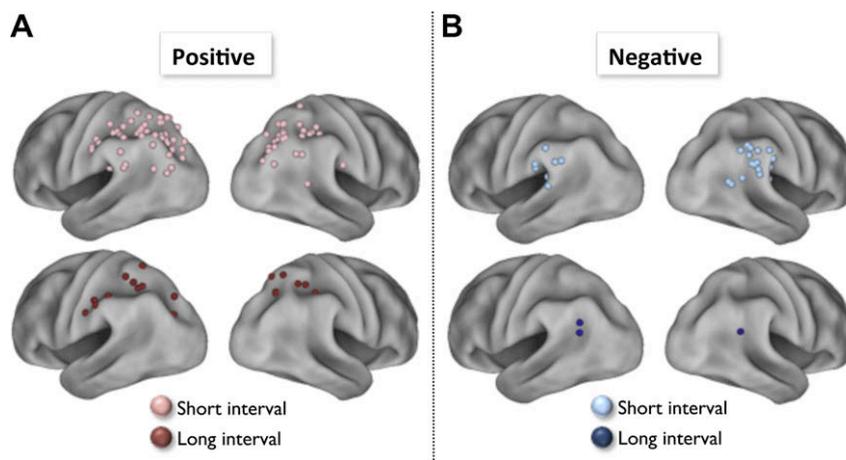
Fig. 4. Retention interval. Positive and negative subsequent memory effects segregated according to whether the interval between study and test was short or long.
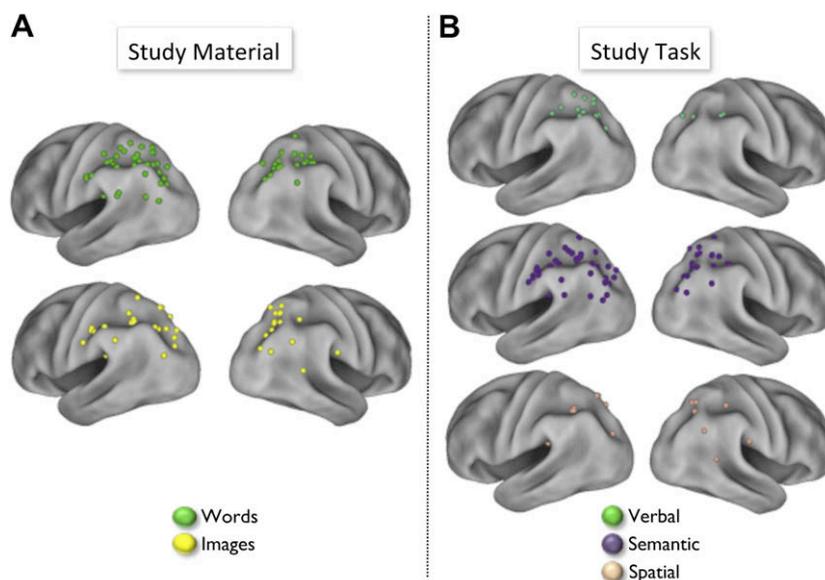

Fig. 5. Study material and task. Subsequent memory effects segregated according to whether (A) study items were words or images, and (B) items were studied under a verbal, semantic, or spatial orienting task. Given low sample sizes for negative effects, only positive effects are displayed.

subject direct comparisons of subsequent memory following spatial and non-spatial orienting are required to determine whether a goal-directed spatial attention mechanism is a component of the dorsal PPC processes that positively impact episodic encoding.

Also arguing against the notion of domain-general dorsal PPC mechanisms is a finding from a recent review of the dual attention and episodic *retrieval* literatures (Hutchinson et al., submitted for publication). This review demonstrated that goal-directed attention and episodic retrieval effects appear to localize to predominantly non-overlapping regions in dorsal PPC. Specifically, goal-directed attention effects appear to fall most consistently along the medial bank of IPS and in SPL, whereas retrieval effects appear to fall more consistently in the lateral bank of IPS. Importantly, because the present meta-analysis reveals positive encoding effects in medial IPS and SPL, as well as in lateral IPS, it would appear that multiple dorsal PPC mechanisms are differentially recruited during the encoding of events that are subsequently remembered. Open issues for future study include specification of the functional mechanisms mediated by lateral IPS and how they impact episodic learning and remembering, as

well as confirmation that medial IPS and SPL encoding effects reflect the consequences of goal-directed attention.

6.1.3. Memory classification

Previous reviews of the subsequent memory literature focused on PFC and MTL (Blumenfeld & Ranganath, 2006; Buckner & Wheeler, 2001; Cabeza & Nyberg, 2000; Paller & Wagner, 2002; Wagner et al., 1999) have revealed functional segregation of encoding-related activity in these regions according to the manner in which later memory is assessed. Functional dissociations within the MTL circuit, in particular, have been observed based on whether the subsequent memory test probes for conjunctive knowledge (e.g., recollection judgments, source memory decisions, and associative recognition) or item knowledge (e.g., item recognition or graded familiarity judgments) (reviewed in Davachi, 2006; Henson, 2005; but see, Squire, Wixted, & Clark, 2007).

In contrast, the present meta-analysis did not reveal a dissociation in dorsal PPC as a function of conjunctive memory (indexed by recall/recollection or source tests) vs. item memory (indexed by familiarity and, perhaps, undifferentiated recognition tests).
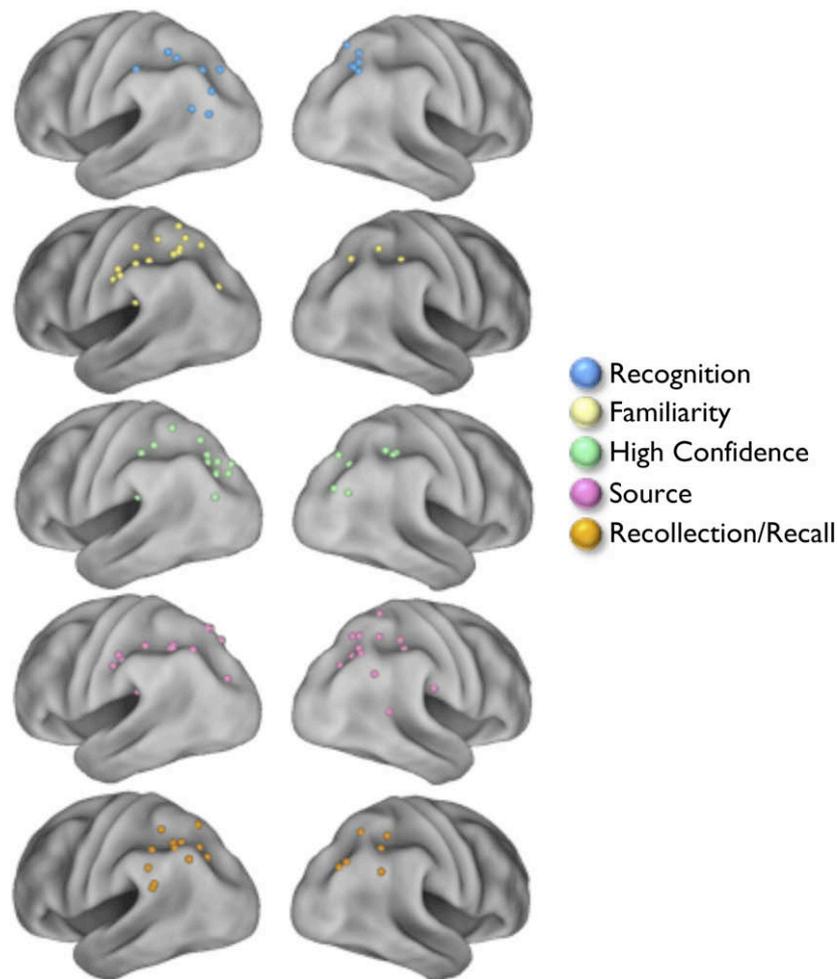
Fig. 6. Memory classification. Subsequent memory effects segregated according to the associated memory classification: undifferentiated recognition, familiarity, high confidence recognition, source retrieval, recollection or recall. Given low sample sizes for negative effects, only positive effects are displayed.

This finding suggests that dorsal PPC mediates the online processing of experiences—rather than directly subserving episodic memory formation—such that PPC mechanisms modulate the information that eventually projects to and gets encoded by the MTL. This account suggests at least two mechanistic alternatives. On the one hand, the mechanisms that determine whether an event will result in item memory encoding, conjunctive memory encoding, or both may be principally MTL dependent. Alternatively, it may be that goal-directed attention during event processing impacts both item and conjunctive memory formation (hence the findings in Fig. 6), while at the same time being differentially more important for the latter (e.g., Moscovitch, 1992; Yonelinas, 2002). Critically, any differential role of goal-directed attention for conjunctive encoding may only be apparent when directly considering the impact of varying the availability of goal-directed attention during event processing on item vs. conjunctive memory.

With respect to this latter possibility, the behavioral and neuroimaging literatures offer a mixed pattern of results. At the behavioral level, extensive data indicate that when attention is divided between a study task and a secondary, distracting task, both item and conjunctive memory are negatively impacted, with the divided-attention (DA) cost often being greater for conjunctive memory (DA sometimes even has no effect on item memory; see Craik, 2001; Yonelinas 2002 for reviews). At the neural level, only a few fMRI studies have investigated the impact of DA on subsequent memory effects (Kensinger, Clarke, & Corkin, 2003; Uncapher & Rugg, 2005b, 2008), with only one having examined the effect of DA on subsequent memory effects for item vs. conjunctive knowledge (using a remember/know paradigm; Uncapher & Rugg, 2008) [Note: Kensinger et al., 2003 conducted a companion behavioral study using a remember/know paradigm, but did not have these measures of item vs. conjunctive memory for subsequent memory effects]. Uncapher and Rugg (2008) replicated previous behavioral findings, as subsequent recollection (which depends on conjunctive encoding) was harmed by difficult DA tasks, while subsequent familiarity (which depends on item encoding) was left intact. Neurally, subsequent memory effects associated with recollection were reported in posterior IPS, and these effects were attenuated in the difficult DA condition. This same region of posterior IPS also showed a similar pattern of attenuated subsequent memory effects for familiarity under difficult DA (though this effect was slightly less robust; unpublished observations). Collectively, Uncapher & Rugg's (2008) findings are consistent with the present meta-analysis, as they indicate that item and conjunctive encoding are both modulated by dorsal PPC mechanisms, with no clear evidence that conjunctive encoding differentially depends on dorsal PPC-mediated goal-directed attention.

Given these findings, we revisited a set of recent studies investigating how different item features are bound into conjunctive memories (Uncapher, Otten, & Rugg, 2006; Uncapher & Rugg, submitted for publication). The first study reported a selective con-

junctive (item-color-location) encoding effect in right anterior IPS (Uncapher et al., 2006), and a selective item encoding effect in a nearby lateral portion IPS (unpublished observation). In the second study (Uncapher & Rugg, submitted for publication), right SPL and IPS exhibited selective item-location and item-color effects, respectively, whereas left IPS exhibited item-only effects. These findings are broadly consistent with the present meta-analysis, as they reveal dorsal PPC subsequent memory effects for both conjunctive and item memory. At the same time, they indicate that within-study functional dissociations along the conjunction/item dimension can be obtained in dorsal PPC, raising open questions for future investigation. One possibility is that these dissociations reflect the encoding consequences of distinct dorsal PPC goal-directed attention mechanisms that facilitate the processing of different kinds of event content (items, item-location or item-color associations, and multi-feature associations).

6.2. Ventral PPC contributions to encoding

The present meta-analysis revealed that (a) negative subsequent memory effects are exclusively localized to ventral PPC, and (b) the minority of positive subsequent memory effects that fall in ventral PPC are observed in studies with short retention intervals. Each of these findings has implications for understanding ventral PPC contributions to encoding.

6.2.1. Negative subsequent memory effects

Accounts of negative subsequent memory effects have proposed a form of attentional competition, wherein such effects might reflect a shift away from mechanisms that promote successful encoding or a shift of processing away from the to-be-encoded event information (Otten & Rugg, 2001a; Wagner & Davachi, 2001). For example, event encoding may suffer if item-level processing is diminished in favor of implementing a task switch (Otten & Rugg, 2001a; Reynolds et al., 2004), selecting response representations or processing the task set (Otten & Rugg, 2001a), or processing task-irrelevant thoughts or stimulus features (Wagner & Davachi, 2001; but see, Daselaar, Prince, & Cabeza, 2004). Motivated by the dual-attention hypothesis that posits a role for ventral PPC in reflexive attention, Cabeza (2008) has proposed that the processing of such irrelevant information may occur when the information captures bottom-up, reflexive attention. To the extent that this information is not the information about which memory will be tested, then such attentional capture may be negatively associated with later event remembering.

The present meta-analysis revealed that all reported negative subsequent memory effects in lateral PPC are confined to ventral PPC, with the majority being observed in TPJ (~BA 40). Compatible with Cabeza's proposal, TPJ is hypothesized to be a key node in the ventral attention network and is thought to mediate attentional reorienting in a domain-general manner, including reorienting between different spatial locations, stimulus features, or even reorienting between internally and externally generated representations (Corbetta et al., 2008). For instance, negative effects could reflect a disengagement from the external visual input in favor of introspective thoughts (in line with proposals of Cabeza, 2008; Wagner & Davachi, 2001).

The present meta-analysis reveals that negative subsequent memory effects are not only found in TPJ, but also in the more posterior AnG (~BA 39). Recent evidence suggests that TPJ and AnG reflect separate nodes of two functionally dissociable networks, namely the ventral attention and 'default' networks, respectively (reviewed in Corbetta et al., 2008). The default network is posited to mediate internally directed cognitive operations (Buckner, Andrews-Hanna, & Schacter, 2008; Mazoyer et al., 2001; Raichle et al., 2001; Shulman et al., 1997; but see Morcom & Fletcher, 2007), as evidenced by the dual findings that activity in the regions putatively comprising the default network (1) functionally correlates with activity of other nodes of the network during passive ('resting-state') conditions (Fox et al., 2005; Greicius, Krasnow, Reiss, & Menon, 2003), and (2) is enhanced during passive (or 'baseline') conditions relative to when volunteers engage in active cognitive tasks (e.g., Binder et al., 1999; Mazoyer et al., 2001; Shulman et al., 1997; see Buckner et al., 2008 for review).

We sought to exploit this latter finding that default network nodes show 'task-induced deactivations' in order to explore whether negative subsequent memory effects arise from engagement of the default network. To this end, we classified each negative focus as being associated with activation above, below, or straddling baseline, or as unspecified (see Table 1). Unfortunately, because most papers reporting negative foci did not specify the direction of activation relative to baseline — only nine of the 28 negative foci were explicitly reported in relation to baseline — strong conclusions cannot yet be drawn. Nevertheless, of the nine, it is interesting to note that the majority indeed fell below baseline, with only one effect above and one straddling baseline. In contrast to the recent demonstration that ventral PPC activations during episodic retrieval predominantly localize to AnG, rather than TPJ (Hutchinson et al., submitted for publication), no obvious regional dissociations emerge from these nine foci regarding their distribution in TPJ and AnG. Thus, while it is premature to interpret the relation between these negative subsequent memory effects and the default network, these initial observations suggest that future investigations should consider the relationship between negative effects and baseline. Such investigations may bear on whether negative effects arise from reflexive orienting to irrelevant representations or from engaging internally directed 'default' processing (see also Daselaar et al., 2004; Shrager, Kirwan, & Squire, 2008 for discussion of below-baseline negative effects).

6.2.2. Retention interval

Does the dual-attention interpretation of encoding-related PPC activity offer an account for our finding that positive subsequent memory effects are sometimes observed in ventral PPC? Interpretative leverage may come from the finding that positive subsequent memory effects in ventral PPC only seem to arise when memory is assessed immediately or minutes after study. Given this finding, we speculatively propose that under some conditions the information capturing the reflexive attentional system may be features of the study item itself—such as when there is a salient item feature due to incongruency (e.g., an object presented in a peculiar color) or infrequency (e.g., a word containing a low bigram frequency, such as two ZZs). To the extent that the attention-capturing information is superficial in nature, it may only be available for retrieval over a short period of time, either due to greater susceptibility to interference or a more rapid decay rate (Alba & Hasher, 1983; Brainerd & Reyna, 1993; Dudai, 2004; Kintsch, Welsch, Schmalhofer, & Zimny, 1990; Koriat, Goldsmith, & Pansky, 2000; Reyna & Brainerd, 1995; Wixted, 2004). In addition, because the strategies used to retrieve information change with time, with an increased emphasis on event meaning rather than event details over time (Goldsmith & Koriat, 1999; Goldsmith, Koriat, Weinberg-Eliezer, & Pansky, 1998; Koriat et al., 2000; Rugg, Johnson, Park, & Uncapher, 2008; Schacter, Norman, & Koutstaal, 1998; Uncapher & Rugg, 2005a), a shift in retrieval orientation may result in a decreased reliance on memory for superficial aspects of study items as the retention interval increases. Thus, while speculative, ventral PPC mechanisms may contribute to successful episodic memory by fostering the encoding of atypical or surface event details that impact retrieval only over short retention intervals.

7. Conclusion

The goal of the present review was to highlight the presence of subsequent memory effects in lateral PPC and to consider the relation between these effects and attentional theories of PPC function. When considered in light of the dual-attention model of PPC (Corbetta et al., 2008), the present data tell a parsimonious—but under-specified—story. First, dorsal PPC mechanisms that mediate goal-directed attention appear to promote the successful encoding of stimuli, and thus these regions demonstrate positive subsequent memory effects. Second, ventral PPC mechanisms that mediate reflexive reorienting appear to reflect an attentional shift from the to-be-encoded information to memory-irrelevant information, and thus these regions demonstrate negative subsequent memory effects. Finally, we suggest that when ventral PPC mechanisms reflexively orient attention to information about the study item itself, these mechanisms may promote memory that enables retrieval only over the short term. Collectively, these findings add to an emerging appreciation that fully-specified neurobiological models of episodic memory may require a broader focus of attention that includes specification of how parietal cortex interacts with the MTL and PFC to enable remembering. While it is unclear at present whether parietal contributions to episodic retrieval reflect the consequences of attentional mechanisms (e.g., Hutchinson et al., submitted for publication; Vilberg & Rugg, 2008; see also Cabeza 2008; Cabeza et al., 2008; Ciaramelli et al., 2008), the present review suggests that multiple parietal attentional mechanisms modulate episodic encoding.

Acknowledgments

Appendix

Subsequent memory studies that do not report effects in lateral PPC: Achim et al. (2007), Adcock et al. (2006), Addis and McAndrews (2006), Baker et al. (2001), Brassen et al. (2006), Buckner et al. (2000), Canli et al. (2002, 2000), Chee et al. (2003), Davachi & Wagner (2002), De Zubicaray et al. (2005), Dolcos et al. (2004a, 2004b, 2007), Erk et al. (2005, 2003), Fischer et al. (2007), Fletcher et al. (2003), Fliessbach et al. (2007), Harvey et al. (2007), Hasson et al. (2007), Hayes et al. (2007), Jackson and Schacter (2004), Kensinger and Corkin (2004), Kensinger and Schacter (2005), Kirchhoff and Buckner (2006), Kirwan and Stark (2004), Lehmann, 2004, Macrae et al. (2004), Maril et al. (2003), Mitchell et al. (2005, 2004), Murray and Ranganath (2007), Okado and Stark (2005), Park et al. (2008), Powell et al. (2005), Prince et al. (2007), Qin et al. (2007), Rypma and D'Esposito (2003), Schon et al. (2004), Schott et al. (2006b), Sperling et al. (2003), Staresina and Davachi (2008), Stark and Okado (2003), Strange et al. (2002), Summerfield et al. (2006), Talmi et al. (2008), Wittmann et al. 2008, Yoo et al. (2007).

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