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Neuropsychologia 46 (2008) 1828–1851

NEUROPSYCHOLOGIA

www.elsevier.com/locate/neuropsychologia

Reviews and perspectives

Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval

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Received 22 September 2007; received in revised form 14 March 2008; accepted 21 March 2008
Available online 8 April 2008

Abstract

Recent neuroimaging studies have implicated the posterior parietal cortex in episodic memory retrieval, but there is uncertainty about its specific role. Research in the attentional domain has shown that superior parietal lobe (SPL) regions along the intraparietal sulcus are implicated in the voluntary orienting of attention to relevant aspects of the environment, whereas inferior parietal lobe (IPL) regions at the temporo-parietal junction mediate the automatic allocation of attention to task-relevant information. Here we propose that the SPL and the IPL play conceptually similar roles in episodic memory retrieval. We hypothesize that the SPL allocates top-down attention to memory retrieval, whereas the IPL mediates the automatic, bottom-up attentional capture by retrieved memory contents. By reviewing the existing fMRI literature, we show that the posterior intraparietal sulcus of SPL is consistently active when the need for top-down assistance to memory retrieval is supposedly maximal, e.g., for memories retrieved with low vs. high confidence, for familiar vs. recollected memories, for recognition of high vs. low frequency words. On the other hand, the supramarginal gyrus of IPL is consistently active when the attentional capture by memory contents is supposedly maximal, i.e., for strong vs. weak memories, for vividly recollected vs. familiar memories, for memories retrieved with high vs. low confidence. We introduce a model of episodic memory retrieval that characterizes contributions of posterior parietal cortex.

Keywords: Episodic memory; Retrieval; Parietal cortex; Intraparietal sulcus; Temporo-parietal junction

Contents

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doi:10.1016/j.neuropsychologia.2008.03.022

1. Introduction

Encoding and retrieval are two fundamental memory operations, the former picking up incoming information and binding it into a memory trace, and the latter assuring that appropriate cues interact with the memory trace, so that memory is recovered and, in the case of explicit memory, delivered to consciousness (Moscovitch, 1992). According to dual-process models of recognition and recall (e.g., Atkinson & Juola, 1974; Jacoby, 1991; Mandler, 1980; Tulving, 1985; Yonelinas, 1994), retrieval operations can be carried out by two independent processes, namely recollection and familiarity (Tulving, 1985; Yonelinas, 1994). Recollection is based on memory for contextual details surrounding the original episode (Dudukovic & Knowlton, 2006; Yonelinas, 2002), and accompanied by a vivid, subjective feeling of reliving the original event (Tulving, 1985; Wheeler, Stuss, & Tulving, 1997), whereas familiarity reflects the global strength of the memory trace without additional qualitative information about the context in which it was acquired (Yonelinas, 1994).

Models of memory retrieval have focused on the medial temporal lobe (MTL) and the prefrontal cortex (see Simons & Spiers, 2003). Typically, in those models, the MTL is concerned with representation of the memory trace, which is supported by an ensemble of MTL and neocortical neurons (Moscovitch, 1992; Moscovitch et al., 2005). At retrieval, the MTL, and the memory trace it mediates, may be accessed directly by a retrieval cue or indirectly via strategic operations mediated by the prefrontal cortex. Various retrieval functions, including initiation and maintenance of retrieval mode, cue specification, monitoring and verification are assigned to different regions of prefrontal cortex (Burgess, Dumontheil, & Gilbert, 2007; Dobbins & Han, 2006; Fletcher & Henson, 2001; Moscovitch & Winocur, 1995, 2002; Wheeler & Buckner, 2003).

The role that attention plays in retrieval is not usually considered in many of these models, the Component Process Model (Moscovitch, 1992, 1994; Moscovitch & Umiltà, 1991) being an exception. According to that model, during direct retrieval, a (proximal) cue interacts automatically with information stored in memory systems via the MTL. Direct retrieval is thought to be a relatively automatic process, mediated by the MTL, and requiring few attentional resources. In contrast, during indirect retrieval, the target memory is not automatically elicited by the cue, and, therefore, has to be recovered through a strategic search process. Indirect retrieval is mediated by the PFC, and is attention demanding. Accordingly, performance in memory tasks that make demands on indirect retrieval is easily hindered by a concurrent task (e.g., Jacoby, Woloshyn, & Kelley, 1989; Kane & Engle, 2000; Moscovitch,

1994), whereas performance in memory tasks relying on direct retrieval is not. The only time divided attention can interfere with direct tests of memory is when the distracting task competes for the same neocortical representations as the memory task (Fernandes & Moscovitch, 2000, 2002; but see Carrier & Pashler, 1995). Nevertheless, direct retrieval does inflict costs on the distracting task (e.g., Ciaramelli, Ghetti, & Borsotti, 2008; Craik, Govoni, Naveh-Benjamin, & Anderson, 1996; Fernandes & Moscovitch, 2000). Thus, even when mandatory, episodic memory retrieval usurps attentional resources from ongoing processes.

As this brief summary indicates, studies on attention and memory are concerned with whether memory competes for general or material specific resources, or for output pathways. None of them deals with the different components of attention that figure prominently in the literature (e.g., Corbetta & Shulman, 2002). This is all the more surprising since evidence from electrophysiology (Herron & Wilding, 2005; Rugg & Curran, 2007) and functional neuroimaging (fMRI; e.g., Naghavi & Nyberg, 2005; Wagner, Shannon, Kahn, & Buckner, 2005) consistently shows activity in posterior parietal cortex during memory retrieval. Previous research has shown that the posterior parietal cortex supports distinct attentional systems, which mediate different attentional processes (e.g., Behrmann, Geng, & Shomstein, 2004; Colby & Goldberg, 1999; Corbetta & Shulman, 2002). Thus, its involvement in memory retrieval not only lends support to the notion that attention is needed for episodic memory retrieval, but also raises the question of whether different attentional systems would make separate contributions to this process. Accordingly, a careful examination of the literature suggests that the regions of posterior parietal cortex which are implicated during episodic memory retrieval vary with different retrieval processes and the type of memory that is retrieved (Skinner & Fernandes, 2007).

The aim of the present paper is to advance a hypothesis on the role of posterior parietal cortex during memory retrieval based on the evidence that this brain region supports multiple attentional systems, with distinct attentional functions. According to one prominent theory (Corbetta & Shulman, 2002), the superior attentional system, which involves superior parietal lobe (SPL) regions and is centered on the intraparietal sulcus (IPS), mediates the allocation of top-down attention to specific aspects of the environment, according to the subject's goals. On the other hand, the inferior attentional system, which involves inferior parietal lobe (IPL) regions and is centered on the temporo-parietal junction (TPJ), mediates the automatic capture of attention by salient environmental stimuli (Corbetta & Shulman, 2002; see Fig. 1). In Section 2, we review briefly the literature on the role of SPL and IPL in the attentional domain. We next hypothesize that these two regions play conceptually similar roles in the episodic memory domain as they do in the attentional domain, and formulate predictions derived from our hypothesis (Section 3). In the following sections we test these predictions, by comparing activity in the SPL (BAs 7 and 19) vs. IPL (BAs 39 and 40) in the existing fMRI studies on episodic memory retrieval. Given that recent research on attention has focused specifically on the IPS and TPJ regions (Corbetta & Shulman, 2002), for each condition of interest we will report whether these regions are indeed activated, and, if so, whether the loci of activation correspond to those observed in the attentional literature.

2. Two attentional systems in the brain

Selective attention is the process whereby a subset of the input is selected preferentially for further processing. Such attentional bias can arise either in a top-down fashion, by voluntarily constraining attentional search to stimuli with a specific property, or in a bottom-up fashion, which occurs when stimuli can capture attention relatively automatically (see Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006; Mesulam, 1999; Posner & Petersen, 1990). Voluntary and automatic attention are presumed to be controlled by two partially segregated, yet interacting, neural systems located, respectively, in the SPL and the IPL.

2.1. Top-down attention: the superior parietal lobe and the intraparietal sulcus

It has been shown that human observers are better at detecting an object in a visual scene when they know in advance something about its features, such as its location, motion or color (see Behrmann et al., 2004 and references therein). This facilitation depends on the ability to represent this advance information (i.e., the "attentional set"), and to use it to bias the processing of incoming information. During this top-down attentional signal, SPL regions are maximally engaged (e.g., Giesbrecht,

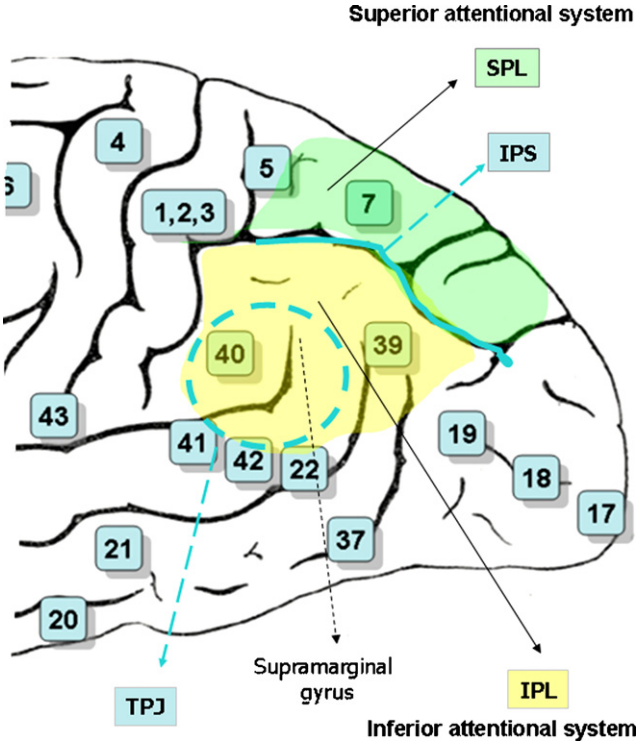

Fig. 1. The inferior and the superior attentional systems. *Note*: SPL: superior parietal lobe; IPL: inferior parietal lobe; IPS: intraparietal sulcus; TPJ: temporo-parietal junction.

Woldorff, Song, & Mangun, 2003; Gottlieb, 2007; Yantis et al., 2002; Yantis & Serences, 2003).

To distinguish the neural sources of the control signals for the generation and maintenance of an attentional set from the top-down effects of that set on the neural activity evoked by the target stimulus, Corbetta and colleagues separated in time the advance information from the target, and investigated brain activity in these two time frames. In a simple detection protocol, they presented a cue in the form of an arrow indicating the most likely location of a subsequent visual target. They found that the IPS of both hemispheres was maximally active during the cue period, i.e., when attention was oriented toward a relevant location (Corbetta, Kincade, Ollinger, McAvoy, & Shulman, 2000). Moreover, when the delay after the cue offset was extended, forcing subjects to maintain attention at the cued location for longer, the IPS was the only brain region that showed a sustained response. These findings strongly implicate the IPS in the voluntary orienting and maintenance of attention to a target location (e.g., T&T coordinates for the IPS: left = −25 −67 48 and right = 27 −59 52 in Corbetta et al., 2000; left = −27 −59 34 and right = 25 −51 49 in Kincade, Abrams, Astafiev, Shulman, & Corbetta, 2005). Other researchers have focused on functions of the posterior parietal cortex that relate to its role in voluntary attention. Platt and Glimcher (1999) demonstrated that in the monkey intraparietal area (LIP), whose proposed homolog in humans is the IPS (Culham & Kanwisher, 2001; Grefkes & Fink, 2005; Orban et al., 2006; Sereno, Pitzalis, & Martinez, 2001), activity is related to the expected reinforcement associated with a cue. A function of the IPS seems therefore to represent the salience of different objects, so to specify the level of priority for directing attention to them (Gottlieb, 2007; see also Colby & Goldberg, 1999).

Activation in the IPS is not apparently restricted to shifts in visuo-spatial attention alone. This region is activated when subjects voluntarily shift their attention between any two dimensions of the input. For example, shifts between two different features of an object (Liu, Slotnick, Serences, & Yantis, 2003), and shifts between two different sensory modalities (Shomstein & Yantis, 2003) activate the IPS. Recent fMRI studies have shown that the IPS is also activated by voluntary orienting to nonperceptual properties of the stimuli, such as their semantic category (Cristescu, Devlin, & Nobre, 2006), their long-term history (Summerfield, Lepsien, Gitelman, Mesulam, & Nobre, 2006), or their representations held in working memory (Lepsien, Griffin, Devlin, & Nobre, 2005).

2.2. *Bottom-up attention: the inferior parietal lobe and the temporo-parietal junction*

A number of fMRI studies have documented that regions in right TPJ, including the supramarginal gyrus, the superior temporal sulcus, and the superior temporal gyrus mediate the bottom-up attentional capture by stimuli that are potentially important for the individual. Downar et al. found that under passive viewing conditions the right TPJ signaled the occurrence of any salient change in sensory stimulation (Downar, Crawley, Mikulis, & Davis, 2000). Accordingly, patients with lesions in the right TPJ may have unilateral neglect, a deficit in detecting contralesional stimuli across diverse sensory modalities (Pavani, Làdavas, & Driver, 2003; Mesulam, 1999). Given that orienting towards unexpected sensory events leads to the interruption the ongoing cognitive activity, TPJ activation has been referred to as a 'circuit-breaker', which causes a shift of attention to behaviourally relevant sensory events previously outside the focus of processing (e.g., T&T coordinates of TPJ: 53 −45 20 in Corbetta et al., 2000; 54 −42 13 in Downar et al., 2000; −47 −40 46 in Bledowski, Prvulovic, Goebel, Zanella, & Linden, 2004).

In the study by Corbetta et al. (2000) which we discussed earlier, the right TPJ was specifically engaged during detection of the target, whereas it showed little if any response to the orienting cue. When the targets occurred at an unexpected location, the activity in this region was further enhanced, and even more lateralized to the right hemisphere. Corbetta et al., therefore, concluded that activation of the right TPJ may mediate automatic attention toward relevant, yet unattended, stimuli (Corbetta et al., 2000; see also McCarthy, Luby, Gore, & Goldman-Rakic, 1997; Indovina & Macaluso, 2007). Accordingly, the right TPJ is also selectively activated when observers monitor the environment for infrequent targets, such as auditory or visual oddball stimuli (e.g., Bledowski et al., 2004; Downar et al., 2000; Stevens, Calhoun, & Kiehl, 2005a). Moreover, TPJ damage reduces the amplitude of P300 scalp electrical potentials that are commonly elicited by the detection of infrequent targets (Knight & Scabini, 1998).

There is evidence that TPJ activity is modulated by task-relevancy, possibly through interactions between the inferior and the superior attentional systems (Corbetta & Shulman, 2002). Thus, when subjects are engaged in a specific task, TPJ is not activated for stimuli that, although physically salient, are not task-relevant (Indovina & Macaluso, 2007). For example, if subjects monitor a change in either a visual or an auditory stimulus presented simultaneously, TPJ activation is enhanced only when the change occurs in the modality that is currently relevant (Downar, Crawley, Mikulis, & Davis, 2001). Moreover, when subjects monitor a central stream of objects for a target, peripheral distracters only activate the TPJ if they share a feature with the target (Serences et al., 2005). Overall, these findings suggest that sensory signals reaching the TPJ have been filtered according to task-relevance, thus ensuring that no attentional capture occurs for salient, yet task-irrelevant, information (Shulman et al., 2003; Shulman, Astafiev, McAvoy, d'Avossa, & Corbetta, 2007).

3. The attention to memory (AtoM) hypothesis

As we have discussed, SPL regions are activated when observers voluntarily orient attention to specific aspects of the stimuli that are consistent with an attentional set, whereas IPL activity is observed when task-relevant information is automatically detected. We propose that the SPL and the IPL would play a conceptually analogous role in episodic memory retrieval.

We hypothesize that the SPL supports indirect retrieval, by allocating top-down attentional resources to strategic retrieval processes (i.e., *top-down attention to memory*). Those pro-

cesses involve directing or constraining memory search, so as to reinstate the target, relative to an irrelevant event (Polyn, Natu, Cohen, & Norman, 2005), as well as post-retrieval processes, such as monitoring and verification of the products of retrieval (Moscovitch & Winocur, 1995). Previous literature has established that strategic pre- and post-retrieval processes are supported by prefrontal cortex (e.g., Addis & McAndrews, 2006; Gilboa et al., 2006; Simons & Spiers, 2003). Here, we are proposing that the SPL also participates in strategic retrieval processes, and, for the purpose of this paper, focus on the parietal component of indirect retrieval. Top-down attention to memory is necessary whenever additional pre- and post-retrieval processing is needed to come up with the memory decision required by the task at hand. Thus, we expected that the SPL would be maximally engaged when individuals are not confident about their memories (Section 4.5), when memories are weak (Section 4.4), when probes have high pre-experimental familiarity (Section 4.7), or share some features with the memory target, yet are not identical to them (Section 4.6). In all of these conditions, discrimination is difficult, and top-down attention will be deployed in the service of making a memorial decision, possibly resulting in long RTs.

On the other hand, we hypothesize that the IPL participates in direct retrieval, by mediating the automatic attentional capture by memory contents retrieved via the MTL (i.e., *bottom-up attention to memory*). A recent study by Vincent et al. (2006) using a seed approach has detected strong functional interconnectivity between the IPL and the hippocampal formation, which makes it reasonable that TPJ activity might be driven by the MTL output. Bottom-up capture of attention by memory contents occurs when a match is perceived between studied and retrieved information. Detection of memory contents should capture attention in much the same way as target detection does in perceptual tasks. Accordingly, episodic retrieval is associated with decrements in performance on concurrent attentional tasks (Ciaramelli et al., 2008; Craik et al., 1996; Fernandes & Moscovitch, 2000). We propose that attentional capture by memory contents, and consequently IPL activity, should vary with the subjective impression that the information is old, namely, with perceived accuracy. Indeed, in fMRI studies the IPL is not only activated for hits, but for false alarms as well (Kahn, Davachi, & Wagner, 2004; Wheeler & Buckner, 2003). Thus, we expected the IPL to be consistently engaged when memory products are strongly experienced as targets, for example, when individuals subjectively feel as if they are reliving their memories (Section 4.2), are confident about their memories (Section 4.5), when memories are strong (Section 4.4), accompanied by rich contextual details (Section 4.3), and match the memory probes perfectly (Section 4.6).

4. Testing the AtoM hypothesis

4.1. Activation in parietal cortex associated with retrieval success

Preliminary to our consideration of parietal retrieval effects, we sought to identify the posterior parietal lobe regions that consistently showed old/new effects. To this end, we reviewed the findings from event-related fMRI studies that (1) used recognition tasks, (2) contained direct comparison of brain activity for hits and correct rejections, and (3) were published by 2006.

4.1.1. Methods

4.1.1.1. Inclusion criteria. We included 19 event-related fMRI studies. We limited our analysis to activations found during test. Because our interest is centered on posterior parietal cortex regions (i.e., BAs 7, 19, 39, and 40), we exclude from our analysis medial parietal cortex regions (i.e., limbic regions of the posterior cingulate and retrosplenial cortex). The latter include phylogenetically old portions of the limbic cortex (Nieuwenhuys, Voogd, & van Huijzen, 1988), and their involvement in memory processes had been established already by patient studies, which document amnesia similar to that following medial temporal damage after lesions in these areas (e.g., Rudge & Warrington, 1991; Valenstein et al., 1987; von Cramon & Schuri, 1992). Also, because retrieval of emotional material may be supported by additional brain regions (Kensinger & Corkin, 2004; Smith, Henson, Dolan, & Rugg, 2004), for those studies that examined both neutral and emotional stimuli (e.g., Maratos, Dolan, Morris, Henson, & Rugg, 2001) we only report peak activations to neutral stimuli. In order to compare directly regions showing brain activation across studies, we transformed all studies using MNI coordinates to Talairach and Tournoux (1988) coordinates, using a non-linear transformation that is available at http://ric.uthscsa.edu/projects/talairachdaemon.html. For studies in which the approximate BA relating to individual coordinates was not reported, we used the Talairach and Tournoux (T&T) atlas to determine the BA.

4.1.1.2. Analyses. In order to establish whether the SPL and the IPL consistently showed retrieval success effects, we calculated the percentage agreement in activation across studies for these brain regions. This measure was calculated by dividing the number of studies that found activation in the IPL (BAs 39 and/or 40) and the SPL (BAs 7 and/or 19) by the number of studies in which activity in that region was investigated, and multiplying this quotient by 100. A value of 50% or greater was considered to indicate a high level of agreement, a value between 30% and 49%, was considered to indicate intermediate agreement, and a value lower than 30% was considered to indicate low agreement (see also Skinner & Fernandes, 2007). Given that some studies were based on regions of interest (e.g., Shannon & Buckner, 2004), in these studies it was not possible to observe any activation for some of the BAs. In such cases, the study was not included in the denominator of the percentage agreement calculation for those BAs. If an activation was bordering two BAs, in the percentage agreement calculation that activation counted as 0.5 for each of the BAs. The same criteria will be adopted in the following sections. Although our analyses focus on the SPL and IPL as a whole, in the Tables we also show the level of agreement for each BA separately.

4.1.2. Results

Table 1 shows the included studies (in rows), BAs of activation and peak coordinates for each study, as well as percentage agreement of activity across studies for SPL and IPL (in parentheses), and for each BA separately. Fig. 2 shows the center of mass for activity in SPL (i.e., in IPS) and in IPL (i.e., separately for TPJ and more posterior regions), together with the coordinates of the superior and inferior attentional systems based on Corbetta et al. (2000).

4.1.2.1. Left hemisphere. We found high agreement in activation in both the SPL (84%) and the IPL (78%). Within the SPL, the posterior part of the IPS showed high consistent activation (57%; median coordinates: −33 −68 44), and so did the precuneus (52%; median coordinates: −6 −62 39). Consistently activated IPL regions included the TPJ (50%; median coordi-

Table 1
Activation peaks for retrieval success effects classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Donaldson, Petersen, and Buckner (2001)	Words	Hit > Cr	−7 −45 30		−37 −69 33	−43 −63 42	10 −66 30			40 −51 54
Donaldson, Petersen, Ollinger, and Buckner (2001)	Words	Hit > Cr	−1 −63 39	−34 −66 42		−40−51 39	34 −63 45			49 −45 48
Henson et al. (2005)	Words	Hit > Cr	−36 −53 52		−36−68 39	−53 −51 33	21 −59 44	33 −65 42		45 −44 52
Herron et al. (2004)	Words	Hit > Cr	−12 −62 39	−33 −68 31					36 −62 36	
Kahn et al. (2004)	Words	Hit > Cr	−30 −70 48	−30 −74 34		−48 −44 49				
Konishi, Wheeler, Donaldson, and Buckner (2000)	Words	Hit > Cr	− 7 −73 34	−29 −69 44		−39 −55 36	9−71 42	35 −73 30		47 −45 50
Lundstrom et al. (2003)	Words	Hit > Cr	−2 −60 42							
Maratos et al. (2005)	Words	Hit > Cr	−36 −62 56		−42 −58 26	−50 −52 40		34 −68 40		36 −64 40
McDermott et al. (2000)	Words	Hit > Cr			−59 −61 24	−37 −51 36	41 −57 48		35 −55 42	47 −49 30
Ragland et al. (2004)	Words	Hit > Cr	−16 −66 48			−56 −34 36	20 −62 56			48 −38 56
Ragland, Valdez, Loughead, Gur, and Gur (2006)	Words	Hit > Cr		−50 −42 40		−40 −56 48				48 −50 48
Shannon and Buckner (2004)	Words	Hit > Cr	−2 −72 30			−44 −61 42				
Tsukiura, Mochizuki-Kawai, and Fujii (2005)	Words	Hit > Cr	−12 −50 39		−51 −62 33	−53 −57 39				
Wheeler and Buckner (2003)	Words	Hit > Cr	−25 −73 44			−55 −43 40		11 −73 42		51 −43 46
von Zerssen et al. (2001)	Words	Hit > Cr	−5 −69 35			−38 −67 43				
Leube, Erb, Grodd, Bartels, and Kircher (2003)	Faces	Hit > Cr				−56 −47 44				
Leveroni et al. (2000)	Faces	Hit > Cr	−5 −51 44	−37 −68 40						
Slotnick, Moo, Segal, and Hart (2003)	Pictures	Hit > Cr					4 −64 44			
Weis, Klaver, Reul, Elger, and Fernandez (2004)	Pictures	Hit > Cr	−32 −64 52			−56 −32 40				36 −40 40

	Left hemisphere				Right hemisphere			
	Superior parietal lobe (84)		Inferior parietal lobe (78)		Superior parietal lobe (47)		Inferior parietal lobe (57)	
	BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement	78	31	26	78	36	21	10	52

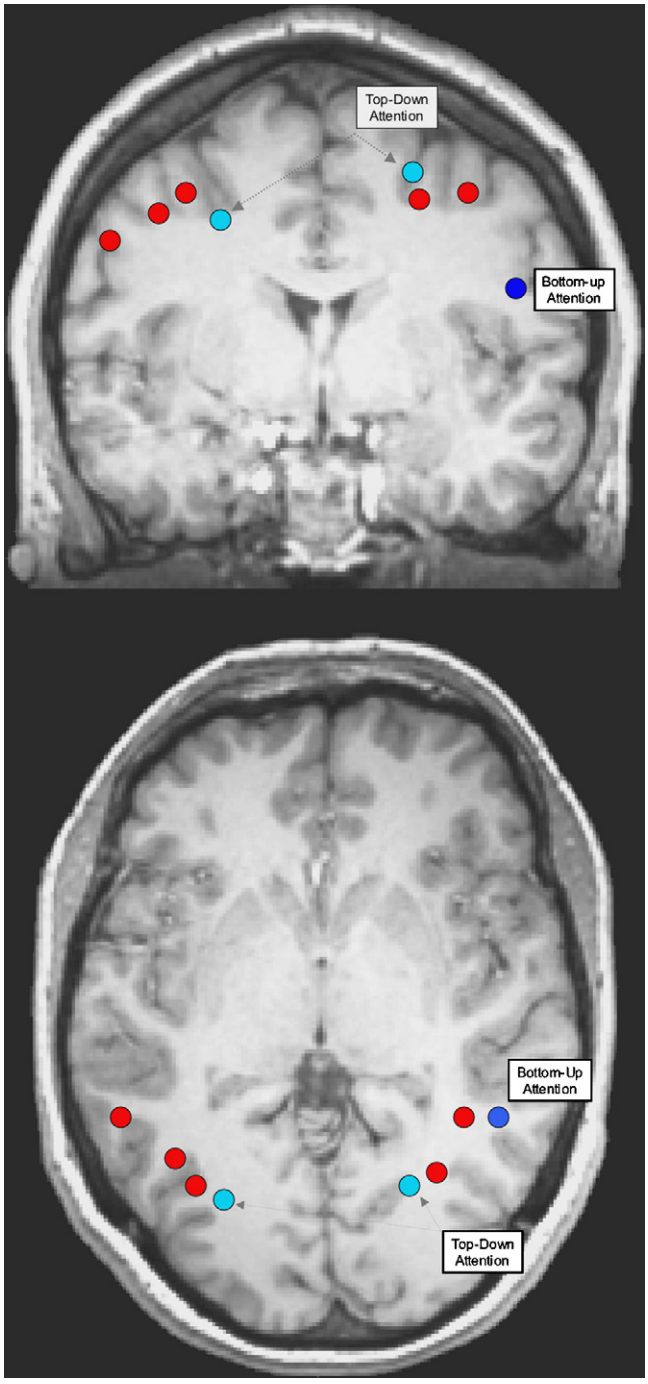

Fig. 2. Center of mass for activity in related to retrieval success effects (in red) in IPS (median coordinates: −33 −68 44 in the left hemisphere; 34 −63 44 in the right hemisphere) and IPL (separately for TPJ, median coordinates: −54 −51 37, and more medial regions, median coordinates: −39 −56 39), together with the coordinates of the superior (in light blue; median coordinates: −26 −67 39 in the left hemisphere; 27 −65 52 in the right hemisphere) and inferior attentional system (in blue; median coordinates: 53 −45 20) based on Corbetta et al. (2000).

nates: −54 −51 37), and more medial and posterior regions in BA 39 (50%; median coordinates: −39 −58 40).

4.1.2.2. Right hemisphere. We found high agreement in IPL (57%) and intermediate agreement in SPL (47%). Activated IPL regions (median coordinates: 47 −45 48; see Table 1) were superior and medial relative to the TPJ loci active in attentional studies (see Table 1). Within the SPL, we observed intermediate levels of agreement in the posterior IPS (37%, median coordinates: 34 −63 44) and low levels of agreement in the precuneus (21%, median coordinates: 9 −68 42).

4.1.3. Discussion

Retrieval success was associated with consistent increase in activity in posterior parietal cortex. As can be seen from Fig. 2, identified regions included a broad left IPL region extending into the TPJ, and a left SPL region involving the posterior IPS (see also Wagner et al., 2005). Activity in these regions was also present in the right hemisphere, but less consistently. These results reveal that the left TPJ and bilateral posterior IPS show consistent retrieval success effects.

4.2. Recollection vs. familiarity

We next examined the relative contribution of the IPL and the SPL to recollection and familiarity. We examined studies that provided estimates of recollection and familiarity using the Remember (R)/Know (K) paradigm (Tulving, 1985) or the ROC procedure (Yonelinas, 2002). In those procedures, memory decisions based on recollection compared to familiarity are accompanied by a sense of reliving the context of items' presentation (for the R/K paradigm) and by high confidence (for the ROC procedure), likely supported by the retrieval of qualitative features of the encoding context (e.g., thoughts, images, and associations) during retrieval. For this reason, retrieval of items judged as recollected as opposed to merely familiar should be associated with higher perceived accuracy. We, therefore, expected recollection to be accompanied by higher IPL activity compared to familiarity.

Decisions made on the basis of familiarity appear more effortful than decisions made on the basis of recollection, at least when recollection and familiarity are assessed with the R/K or the ROC procedure (but see below). In the R/K paradigm, for example, RTs are longer for recognition of items that are subsequently assigned a K compared to a R response (Dewhurst, Holmes, Brandt, & Dean, 2006; see also Yonelinas, Otten, Shaw, & Rugg, 2005). This might reflect the difficulty in making an old/new decision in the absence of contextual information (Henson, Rugg, Shallice, Josephs, & Dolan, 1999): whereas the emergence of contextual details from study (i.e., in the case of R responses) would support a confident and rapid old judgement, in the absence of this information additional pre- or post-retrieval processing might be needed to assess the familiarity of an item relative to other items in the list (Dewhurst et al., 2006). We therefore predict that SPL activity should be greater for familiarity than for recollection.

4.2.1. Methods

4.2.1.1. Included studies. We review the findings of nine studies that investigate brain activity related to recollection and familiarity. A summary of the event-related fMRI studies included in this section can be found in Table 2.

Table 2a
Activation peaks for recollection-based responses classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Subtraction contrasts										
Daselaar, Fleck, and Cabeza (2006)	Words	Recollection			−45 −62 32 (B)	−45 −62 32 (B)				
Eldridge, Knowlton, Furmanski, Bookheimer, and Engel, (2000)	Words	R > K				−50 −41 25				
Fenker et al. (2005)	Words	R > K		−30 −79 43				33 −68 34		
Henson, Rugg, et al. (1999)	Words	R > K		−42 −72 39		−57 −51 39				
Wheeler and Buckner (2004)	Words	R > K	[a]	[a]	−43 −67 40	−51 −51 38	[a]	[a]	[a]	[a]
Yonelinas et al. (2005)	Words	R > K				−53 −25 18			53 −66 12	59 −23 15
Montaldi et al. (2006)	Pictures	R > K			−42 −68 31					
Sharot et al. (2004)	Pictures	R > K, R > N	−10 −68 29		−52 −59 24		10 −68 36			47 −48 30

			Left hemisphere				Right hemisphere			
			Superior parietal lobe (42)		Inferior parietal lobe (88)		Superior parietal lobe (28)		Inferior parietal lobe (28)	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement			14	28	44	56	14	14	14	14
Parametric contrasts										
Daselaar, Fleck, Dobbins, Madden, and Cabeza (2006)	Words	Exponential increase with R				−53 −57 38				

Note: B: the peak is at the border between 2 BAs.
[a] This study is not included in the denominator.

Table 2b
Activation peaks for familiarity-based responses classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA 19	BA 39	BA40
Subtraction contrasts										
Daselaar, Fleck, and Cabeza (2006)	Words	Familiarity	−15 −60 34	−38 −76 33 (B)	−38 −76 33 (B)					
Eldridge et al. (2000)	Words	K > R								
Fenker et al. (2005)	Words	K > N								
Henson, Rugg, Shallice, and Dolan (1999)	Words	K > R, K > N	−12 −60 57	−24 −63 42						
Wheeler and Buckner (2004)	Words	K > N	[a]	[a]	−39 −55 36	[a]	[a]	[a]	[a]	[a]
Montaldi et al. (2006)	Pictures	K > R								
Sharot et al. (2004)	Pictures	K > N	−37 −59 42	−36 −80 33			5 −73 45			38 −48 44

			Left hemisphere				Right hemisphere			
			Superior parietal lobe (50)		Inferior parietal lobe (21)		Superior parietal lobe (16)		Inferior parietal lobe (16)	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement			50	42	21	0	16	0	0	16
Parametric contrasts										
Daselaar, Fleck, Dobbins, et al. (2006)	Words	Increase with familiarity			−38 −76 28					
Yonelinas et al. (2005)	Words	Increase with familiarity	−33 −60 36				36 −62 47			39 −48 36
Montaldi et al. (2006)	Pictures	Increase with familiarity	−3 −76 45			−39 −47 47				

Note: B: the peak is at the border between 2 BAs.
[a] This study is not included in the denominator.

We included studies that (1) used recognition tasks and (2) used the R/K or the ROC procedure to examine recollection and familiarity processes. We did not include studies that assessed recollection and familiarity using the Process Dissociation Procedure (PDP; e.g., Henson, Shallice, et al., 1999). As we stated above, in this section we were interested in sorting out the neural bases of the subjective aspects of recollection (i.e., sense of reliving and confidence), that seem closely related to perceived accuracy, as opposed to the ability to retrieve specific contextual aspects of an episode (but see Section 4.3).

As in Section 2, for those studies that examined both neutral and emotional stimuli (Fenker, Schott, Richardson-Klavehn, Heinze, & Duzel, 2005; Sharot, Delgado, & Phelps, 2004), we report only peak activations relating to neutral stimuli. We limit our analysis to activations found during test (retrieval), in posterior parietal cortex. Only contrasts that specifically examined recollection or familiarity processes were included (i.e., contrasts that examined general recognition memory were not). For recollection-based responding, we included the contrast Remember minus Know and Remember minus New, and ROC recollection estimates. For familiarity-based responding, we included the contrasts Know minus Remember and Know minus New, and ROC familiarity estimates. We examined both subtraction and parametric contrasts.

4.2.2. Results

Tables 2a and 2b show the included studies (in rows), BAs of activation and peak coordinates for each study, as well as percentage agreement of activity across studies for the SPL and the IPL (in parentheses), and for each BA separately, in association with recollection and familiarity.

4.2.2.1. Recollection. In the left hemisphere, we found high level of agreement in IPL (88%) and intermediate levels of agreement in SPL (42%). Activated IPL regions were in TPJ (median coordinates: −51 −57 32), although slightly posterior and superior to the right regions activated in attentional studies (53 −45 26; Corbetta et al., 2000). A parametric contrast showed that a region in TPJ modulated exponentially with recollection (Daselaar, Fleck, Dobbins, et al., 2006). IPL regions were more consistently activated than SPL regions during recollection ($\chi^2 = 7.77$; $p < 0.05$), and more consistently activated for recollection than for familiarity ($\chi^2 = 41.11$; $p < 0.05$). Activated SPL regions involved the precuneus and a region along the posterior IPS (28%; median coordinates: −36 −75 41). In the right hemisphere, we found low levels of agreement in both SPL and IPL (28% in both cases).

4.2.2.2. Familiarity. In the left hemisphere, we found high levels of agreement in SPL (50%), and no consistent activity in IPL (21%). Activated SPL regions were along the posterior IPS (median coordinates: −36 −61 40), although in a region less medial to those mediating attentional cuing. Parametric contrasts revealed that activity in bilateral regions bordering the IPS (median coordinates: −36 −64 37 on the left hemisphere; 37 −55 41 on the right hemisphere) increased with familiarity (see Daselaar, Fleck, Dobbins, et al., 2006; Montaldi, Spencer, Roberts, & Mayes, 2006; Yonelinas et al., 2005). The contribution of SPL regions was comparable between recollection and familiarity ($\chi^2 = 0.48$; $p = 0.48$). However, whereas prominent activity for recollection was in IPL, familiarity was characterized by more consistent activity in SPL than IPL regions ($\chi^2 = 6.11$; $p < 0.05$).

4.2.3. Discussion

Our prediction concerning the IPL was supported: The left IPL was consistently activated for recollection, and activated regions included a region in TPJ. In contrast, the IPL was not consistently activated for familiarity. We did not find the predicted greater activity in SPL for familiarity vs. recollection but did observe that whereas recollection was more consistently associated with activity in IPL than SPL regions, familiarity was more consistently associated with activity in SPL than IPL regions. Thus, in relative terms, the results conformed to our prediction.

4.3. Source memory

The aim of this section was to compare activity in posterior parietal cortex (1) for source vs. item memory and (2) for source memory vs. subjective recollection (i.e., recollection as estimated with the R/K or ROC procedure; see Section 4.2). Source memory involves retrieval of specific details of the encoding context of events (Johnson, Hashtroudi, & Lindsay, 1993). Perceived oldness of an item should be higher when individuals can also reinstate its sources. Thus, retrieval of source compared to item memory should result in higher activity in IPL, similar to what we observed in the comparison of recollection vs. familiarity. We also expected more SPL activity for source compared to item memory, because source information is generally not provided at test whereas item information is, which should increase the need for searching strategically the former compared to the latter.

We next compared activations related to source memory with those associated with recollection as assessed with subjective estimates (i.e., R responses or confidence ratings). It has been proposed that source memory is a more objective estimate of recollection than is the amount of R responses, because it assesses retrieval of context directly, rather than based on subjects' introspection of it. Although objective and subjective estimates of recollection are related in healthy individuals, they are dissociable from each other, for example, as a consequence of insult to prefrontal cortex (e.g., Duarte, Ranganath, & Knight, 2005; Ciaramelli & Ghetti, 2007). We expect that objective and subjective estimates of recollection would be also differentially supported by the posterior parietal cortex. Different from recollection based on R responses, source memory probes the retrieval of specific contextual details that are set by the experimenter, rather than by the participant. These details are likely not to be the first that pop in subjects' mind while recollecting; therefore, there is a need to search for them. For this reason, we predicted that source memory should require a larger contribution from the SPL compared to subjective recollection.

4.3.1. Methods

4.3.1.1. Included studies. A summary of the event-related fMRI studies included in this review can be found in Table 3. We included 11 studies that used source memory tasks, that is, those requiring not only discrimination between studied and unstudied items, but also report of specific aspects of the encoding contexts. We considered the contrasts Source minus Item memory and Correct source minus Incorrect source. We limited our analysis to activations found during test (retrieval), in posterior parietal cortex.

Table 3
Activation peaks for source memory classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Dobbins et al. (2002)	Words	Source > item	−9 −69 33		−39 −66 39	−48 −54 48				
Dobbins, Rice, Wagner, and Schacter (2003)	Words	Source task > recency task	−9 −75 33		−51 −66 39	−45 −57 45				
Kahn et al. (2004)	Words	Source > item	−27 −46 53						36 −45 41	36 −48 42
Kensinger and Schacter (2006)	Words	Correct source > incorrect source				−48 −47 44				
Ragland et al. (2006)	Words	Correct source > incorrect source	−41 −56 50							
Slotnick et al. (2003)	Pictures	Source > item				−53 −61 21	4 −68 44			
Cansino et al. (2002)	Pictures	Correct source > incorrect source								60 −42 26
Dobbins and Han (2006)	Pictures	Source > item	−36 −63 48	−42 48 −6						
Dobbins and Wagner (2005)	Pictures	Source > item	−6 −65 47		−36 −54 33	−48 −41 46				
Fan, Gay Snodgrass, and Bilder (2003)	Pictures	Source > item	−30 −59 49	−34 53 5						
Lundstrom et al. (2003)	Pictures	Source > item	−12 −64 46							

	Left hemisphere				Right hemisphere			
	Superior parietal lobe (72)		Inferior parietal lobe (45)		Superior parietal lobe (9)		Inferior parietal lobe (18)	
	BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement	72	18	27	45	9	0	9	18

4.3.2. Results

Table 3 shows BAs of activation and peak coordinates for each included study, and percentage agreement of activity across studies for the SPL and the IPL (in parentheses), and for each BA separately. The contrast between source and item-memory revealed highly consistent activity in the SPL (72%) and intermediate levels of activity in the IPL (45%). In the SPL, prominent activity was in regions along the middle IPS (50%; median coordinates: −35 −54 48), slightly anterior and less medial to that implicated in attention. In the IPL, activated regions (median coordinates: −48 −56 41) were posterior and superior relative to the right TPJ regions mediating target detection (Corbetta et al., 2000). No consistent pattern of activation was detected in the right hemisphere. In line with the predictions, source memory needed a larger contribution from SPL, compared to subjective recollection ($\chi^2 = 5.07$; $p < 0.05$; see Section 5.1 and Table 2). In contrast, subjective recollection was characterized by a more consistent IPL activity compared to source memory ($\chi^2 = 6.39$; $p < 0.05$).

4.3.3. Discussion

Our predictions were supported: source memory retrieval is accompanied by higher levels of activity in both left IPL and left SPL compared to item memory. Moreover, objective (i.e., source) compared to subjective (i.e., R responses) estimates of recollection resulted in increased contribution from SPL.

4.4. Memory strength

In the laboratory, memory strength can be manipulated by means of encoding conditions that promote deep vs. shallow encoding. Items that had enjoyed deep vs. shallow encoding are typically remembered with higher accuracy (Craik, 2002). Strong, compared to weak, memories should pop out from the memory "background", resulting in high perceived oldness. For this reason, we expect increased IPL activity for strong as compared to weak memories.

4.4.1. Methods

4.4.1.1. Included studies. In reviewing the literature, we found three studies investigating the effect of memory strength on the neural correlates of retrieval (see Table 4). Given the paucity of studies, we consider the findings on a case-by-case basis instead of group analysis. As in the previous sections, we limit our attention to activations found during test (retrieval), and focus on posterior parietal activity.

4.4.2. Results

Table 4 shows BA of activation and peak coordinates for included studies. All the studies compared brain activity related to hits to stimuli that had received deep (e.g., living-nonliving judgment) compared to shallow (e.g., alphabetic judgment) encoding. All the studies report higher left IPL activity for deeply encoded vs. shallowly encoded stimuli (median coordinates: −44 −53 42; Henson, Hornberger, & Rugg, 2005; Iidaka, Matsumoto, Nogawa, Yamamoto, & Sadato, 2006; Shannon & Buckner, 2004), in a region slightly superior relative to the right TPJ sites implicated in target detection. Henson et al. (2005) also report activity in a right IPL region for this comparison.

Table 4
Activation peaks for memory strength effects classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Henson et al. (2005)	Words	Deep hit > shallow hit				−50 −53 44				50 −48 22
Shannon and Buckner (2004)	Words	Retrieval success (deep–shallow)	−2 −72 30		−44 −61 42					
Iidaka et al. (2006)	Pictures	Retrieval success (deep–shallow)				−32 −47 37				

4.4.3. Discussion

Our predictions were supported: Retrieval of strong compared to weak memories results in activity in IPL regions.

4.5. Confidence

Confidence reflects the degree of perceived accuracy, e.g., the degree to which memory products are perceived as old, regardless of whether they truly are. Consequently, in studies investigating confidence associated with memory retrieval, items that are reported as confidently recognized should elicit more IPL activity than those that are less confidently recognized. In contrast, items recognized with low confidence should elicit more SPL activity, because more search attempts and monitoring processes should be needed to come to a memory judgment about these items.

4.5.1. Methods

4.5.1.1. Included studies. In reviewing the literature, we found four studies investigating the neural correlates of memory confidence. As in the previous section, we review them case-by-case, limiting our attention to activations found during test (retrieval) in posterior parietal cortex.

4.5.2. Results

Table 5 shows BAs of activation and peak coordinates for each included study. In the study by Moritz and colleagues, items that received high vs. low confidence judgments, irrespective of accuracy, were characterized by higher activity in left IPL (Moritz, Glascher, Sommer, Buchel, & Braus, 2006). Similar results were obtained by Chua, Schacter, Rand-Giovannetti, and Sperling (2006). In both studies, the region signaling high confidence was in TPJ (median coordinate: −49 −64 25), but, again, posterior to the right TPJ regions sites involved in target detection in the attentional domain. Chua et al. (2006) also showed that a region in left TPJ was specifically dedicated to confidence estimation, rather than recognition judgments.

On the other hand, low confidence judgments appear related to SPL. In the study by Moritz et al. (2006), items that were recognized with low confidence showed increased activity in the right SPL. Similar results were obtained by Fleck, Daselaar, Dobbins, and Cabeza (2006), who demonstrated that a region in the right SPL signaled low confidence associated with memory (as well as perceptual) decisions. In both studies, the SPL region associated to low confidence judgements was in the right posterior IPS (median coordinates: 22 −68 46), quite close to IPS sites involved in cueing attention.

4.5.3. Discussion

Our predictions were supported: memory retrieval accompanied by high vs. low confidence resulted in a left IPL region proximal to TPJ, whereas low vs. high confident retrieval judgments resulted in activity in the right SPL along the IPS. Thus, the SPL was preferentially active when the act of remembering, independent of its result, was experienced as weak, whereas the IPL was preferentially active when the act of remembering, independent of its result, was experienced as strong.

That SPL activity is related to low vs. high confidence decision conflicts with the finding that increasing levels of familiarity are associated with increased SPL activity (Montaldi et al., 2006; Yonelinas et al., 2005), because it is usually assumed that low/high confidence maps onto low/high familiarity. Possibly, what appears as activity related to increased familiarity in these studies reflects a combination of bottom-up attentional processing related to oldness and top-down attentional processing related to the difficulty of using a multi-criterion scale (e.g., to distinguish between confident familiar and R decisions). Note, also, that in Yonelinas et al. (2005), the two highest confidence levels are for items judged as old (sure old, not sure old), whereas the two lowest confidence levels are for items judged as new (not sure new, sure new). Thus, at least for new judgments, Yonelinas et al.'s results show higher SPL activity for unconfident vs. confident decisions, in accordance with the studies reviewed here.

4.6. True vs. false targets

In studies that investigate recognition memory by testing subjects on studied words, lures that are similar/related to the studied words, and lures that are unrelated to the studied words, we expect to find higher IPL activity for studied items than similar/related lures. Studies in the domain of attention have shown that when subjects are required to detect a target (i.e., an object) in an array of objects that can either contain the target, or an object semantically related to the target, or both, the semantically related lure captures subjects' attention when the target is not in the array, but not when it is in the array. In the latter case, subjects' attention – and saccades – are directed at the tar-

Table 5
Activation peaks for confidence effects classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
High confidence										
Moritz et al. (2006)	Words	High > low confidence			−50 −62 39					
Chua et al. (2006)	Faces–names	High > low confidence				−48 −63 14				
Low confidence										
Moritz et al. (2006)	Words	Low > high confidence					21 −65 50			
Fleck et al. (2006)	Words	Low > high confidence		−11 −57 52				23 −72 42		
Confidence judgment										
Chua et al. (2006)	Faces–names	Confidence > recognition				−59 45 23				

get (Moores, Laiti, & Chelazzi, 2003). By analogy, we predict that true targets should pop out from the distracter background more easily than lures that are merely similar to the targets. This prediction should be confirmed at least when comparing hits to correct rejection of similar/related lures, i.e., when the subjects realize that the lure was not actually a memory target. However, it is possible that also similar/related lures which are falsely endorsed as targets would show less IPL activity that true targets. Indeed, even though these items are frequently falsely recognized, in the studies here examined they were endorsed less frequently than true targets, suggesting a lower perceived accuracy (e.g., Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; McDermott, Jones, Petersen, Lageman, & Roediger, 2000; Slotnick & Schacter, 2004; von Zerssen, Mecklinger, Opitz, & von Cramon, 2001).

On the other hand, we expected that activity in SPL should be higher for rejecting similar/related vs. unrelated lures, because the fact that these items are similar to targets should result in the need for increased pre- and post-retrieval processing aimed at verifying their memory status. To answer this question, we will compare activity related to correct rejection of similar/related vs. unrelated lures.

4.6.1. Methods

4.6.1.1. Included studies. A summary of the event-related fMRI studies included in this review can be found in Table 6. We included 6 studies that compared brain activity for recognition of studied items, related\similar lures, and lures unrelated to the studied material. Three studies used the Deese (1959), Roediger and McDermott (1995) paradigm (DRM paradigm), in which individuals study lists of semantically related words which are associated with a non-studied, related word. Participants are later asked to recognize the studied words among semantically related lures and lures that are not related to the studied lists (Cabeza et al., 2001; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; von Zerssen et al., 2001). Two studies used abstract shapes (Slotnick & Schacter, 2004) or paintings (Yago & Ishai, 2006) to be recognized among similar and dissimilar stimuli. The last study involved recognizing studied words (e.g., checklist, needlepoint) among "conjunction" lures (e.g., checkpoint) and unrelated lures (i.e., rabbit; McDermott et al., 2000).

In order to identify brain regions whose activity distinguished targets from related/similar lures, we examined the following contrasts: hits minus false alarms to related/similar lures, hits minus correct rejections for related/similar lures, hits minus correct rejections for (related/similar + unrelated lures). To compare activity related to the rejection of similar/related vs. unrelated lures, we examined the contrast: correct rejections for related/similar lures minus correct rejections of unrelated lures.

4.6.2. Results

Table 6 shows the included studies (in rows), BAs of activation and peak coordinates for each study, and percentage agreement of activity across studies for SPL and IPL (in parentheses), and for each BA separately.

4.6.2.1. Studied-related/similar items. In the left hemisphere, we found high levels of agreement in both IPL (50%) and SPL regions (50%). Activated regions in IPL were in TPJ (50%; median coordinates: −55 −55 32), slightly posterior to the right IPL regions implicated in attention. In the SPL, we observed intermediate levels of activity in bilateral IPS regions (33%).

Table 6
Activation peaks for true, related/similar, and unrelated items classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA 19	BA39	BA40	BA7	BA 19	BA39	BA40
Studied-related/similar items										
Cabeza et al. (2001)	Words	Hit > Fa (related)				−53 −55 32				
McDermott et al. (2000)	Words	Hit > Cr (related + unrelated)				−59 −61 24				47 −49 30
Schacter et al. (1997)	Words	Hit > Fa (related)								
von Zerssen et al. (2001)	Words	Hit > Cr (related + unrelated)	−38 −67 43							
Slotnick and Schacter (2004)	Pictures	Hit > Fa (related)	−16 −53 58			−55 −33 48	14 −66 58			
Yago and Ishai (2006)	Pictures	Hit > Cr (related)	−30 −52 44				32 −50 42			
			Left hemisphere				Right hemisphere			
			Superior parietal lobe (50)		Inferior parietal lobe (50)		Superior parietal lobe (33)		Inferior parietal lobe (16)	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement			50	0	0	50	33	0	0	16
Related/similar–unrelated items										
McDermott et al. (2000)	Words	Cr (related) > Cr (unrelated)					41 −57 48			
von Zerssen et al. (2001)	Words	Cr (related) > Cr (unrelated)								
Yago and Ishai (2006)	Pictures	Cr (related) > Cr (unrelated)	−30 −52 44				32 −50			
			Left hemisphere				Right hemisphere			
			Superior parietal lobe (33)		Inferior parietal lobe (0)		Superior parietal lobe (66)		Inferior parietal lobe (0)	
			BA7	BA19	BA39	BA40	BA7	BA19	BA39	BA40
Percentage agreement			33	0	0	0	66	0	0	0

4.6.2.2. Related/similar–unrelated items. Of the three studies reporting activity related to correct rejection of similar/related–unrelated lures, two found activity in the right IPS (median coordinates: 36 −53 45; McDermott et al., 2000; Yago & Ishai, 2006), and one reported activity in the left IPS (coordinates: −30 −52 44; Yago & Ishai, 2006).

4.6.3. Discussion

Our predictions were supported: retrieval of true targets compared to related/similar lures consistently activated left IPL regions near the TPJ. We also observed intermediate activity in the IPS, bilaterally. When comparing activity related to correct rejection of related/similar vs. unrelated lures, we found highly consistent activity in the IPS, especially on the right.

4.7. Word frequency

Word frequency is an index of our cumulative experience with words. It has been demonstrated widely that low frequency words are recognized faster and more accurately than high frequency words. This phenomenon, termed the "mirror effect" (Glanzer & Adams, 1985), is likely to be due to the more extensive (deep) processing low-frequency words enjoy at encoding compared to high frequency words (Chee, Westphal, Graham, & Song, 2003; Chee, Goh, Lim, Graham, & Lee, 2004). To the extent that low frequency words are recognized more accurately than high frequency words, one should observe more IPL activity in association with recognition of the former compared to the latter. Conversely, more SPL activity should be found for recognition of high frequency words, for which more search attempts and verification are needed in order to assess their episodic memory status.

4.7.1. Methods

4.7.1.1. Included studies. We found two studies investigating the effect of word frequency on the neural bases of episodic memory retrieval. Table 7 shows BAs of activation and peak coordinates for each study.

4.7.2. Results

In the study by de Zubicaray et al., none of the regions that demonstrated old/new item retrieval effects showed a significant modulation according to word frequency (de Zubicaray, McMahon, Eastburn, Finningan, & Humphreys, 2005). There was a trend, however, for a SPL region (T&T: −33 −40 45) to exhibit the largest percent signal change for recognition of high frequency words presented only once at study, which arguably were those with the most ambiguous mnemonic status. The opposite pattern indeed emerged in the right hippocampus, which was the least active for these words. Moreover, in the study by Chee et al. (2004), word frequency modulated brain activity for correct rejections, with larger activity in a left lateral parietal region along the IPS (BA 7/40) for high compared to low-frequency stimuli.

4.7.3. Discussion

Our predictions were partially supported: memory judgments about high frequency words activated regions in the left SPL, but we have no evidence that low frequency words activated IPL regions.

4.8. Target frequency ("targetness")

Studies involving the "oddball paradigm" have detected increased activity in both SPL and IPL for infrequent vs. frequent targets, possibly indicating an increased need for top-down cueing of task-relevance, and increased perceived saliency of the stimuli (e.g., Stevens et al., 2005a; Stevens, Calhoun, & Kiehl, 2005b; Bledowski et al., 2004; Marois, Leung, & Gore, 2000). Analogously, we predict that during episodic recognition, rare targets should increase the need for maintaining top-down attention on the relevant dimensions of the task (i.e., in an episodic retrieval mode). At the same time, these targets may pop out strongly from the background of distracters. For this reason, more activity should be found for infrequent compared to frequent targets in SPL, and possibly in IPL.

4.8.1. Methods

We found one study investigating the effect of target frequency on the neural correlates of memory retrieval (see Table 7).

4.8.2. Results

Herron et al. varied the ratio of old to new items in a recognition task, and found that whereas activity in the left IPL signaled old\new effects independently of target frequency, a region of the left SPL showed higher activity for infrequent compared to frequent targets (T&T: −33 −52 58; Herron, Henson, & Rugg, 2004). The authors investigated the issue further in an ERP study (Herron, Quayle, & Rugg, 2003), in which they analogously documented that whereas the left parietal old\new effect (at 500–800 ms) was not influenced by the relative frequency of targets to lures, target frequency did influence the parietal ERPs to correctly recognized items post-800 ms. Moreover, this effect was found at a qualitatively different scalp distribution than the old/new effect.

4.8.3. Discussion

Our predictions were partially supported: retrieval of low compared to high frequency targets was accompanied by IPS, but not IPL, activity.

4.9. Conclusion

In seven contrasts, we have provided initial evidence that the allocation of top-down attention to memory retrieval is supported by the SPL, whereas the bottom-up attentional capture by retrieved contents is mediated by the IPL. Fig. 3 shows the center of mass for activity across all the examined conditions related to the top-down and bottom-up AtoM systems. For the former, the center of mass was located in the posterior IPS, bilaterally (median coordinates: −36 −57 42 in the left hemisphere; 32 −57 44 in the right hemisphere), and for the latter

Table 7
Activation peaks for word frequency and target frequency effects classified according to Brodmann areas

Study	Stimuli	Contrast	Left hemisphere				Right hemisphere			
			Superior parietal lobe		Inferior parietal lobe		Superior parietal lobe		Inferior parietal lobe	
			BA7	BA 19	BA39	BA40	BA7	BA 19	BA39	BA40
Word frequency										
Chee et al. (2004)	Words	High frequency > low frequency	−41 −62 36 (B)			−41 −62 36 (B)				
de Zubicaray et al. (2005)	Words	High frequency > low frequency	−33 −40 45							
Target frequency										
Herron et al. (2004)	Words	Low frequency > high frequency	−33 −52 58							

Note: B: the peak is at the border between 2 BAs.

in the left supramarginal gyrus (median coordinates: −50 −57 38).

One might ask why we did not find 100% consistency in brain activity across studies in association with top-down and bottom-up attention to memory, although we used broad regions as areas of interest. First, there were no studies on episodic memory designed to examine the effects of bottom-up vs. top-down allocation of attention to memory retrieval. Consequently, we had to infer that the two processes were more likely to occur in some conditions than others. It is possible that the conditions we identified did not distinguish the top-down and bottom-up attentional needs of memory as clearly as we had hoped. Second, studies investigating attentional cuing and target detection all use very similar, basic paradigms. As a result, the activations they found are highly consistent and clustered across studies. In contrast, in the recognition memory domain, many methodological differences exist across studies, e.g., regarding the specific paradigm, the material used, the frequency of targets to lures, etc., which might have weakened the power of our observations. Finally, unlike perceptual search, memory search is not always triggered by stimulus input. Memory search and retrieval are iterative processes, whose initiation and cessation are related to both processes, making it difficult to isolate one process from the other. Given these provisos, we believe that the level of agreement with predictions is encouragingly high.

5. General discussion

Studies in cognitive neuroscience have provided converging evidence that MTL and prefrontal regions of the brain are crucial for episodic memory retrieval (see Baldo & Shimamura, 2002; Moscovitch et al., 2005; Petrides, 2005; Simons & Spiers, 2003). More intriguing is the proposal that the posterior parietal cortex is also implicated in memory retrieval. Rugg and colleagues first reported consistent retrieval success effects in parietal cortex in ERP studies (for review, see Rugg & Curran, 2007). More recently, Wagner et al. (2005) and Naghavi and Nyberg (2005) noted that, in fMRI studies, the posterior parietal cortex shows significantly greater activation for previously studied items that are correctly recognized as old compared to unstudied items that are correctly identified as new (see also Skinner & Fernandes, 2007). Here we support their finding, by showing high levels of agreement for retrieval success effects in left posterior parietal cortex, including a region of the IPL adjacent to the TPJ, and a more focal region in the SPL along the posterior IPS (see Fig. 2). Although less consistent, activity in homologous regions was also present in the right hemisphere.

What might be the role of the posterior parietal cortex during memory retrieval? Following the lead from the behavioural literature that there are two different, but complementary, attentional systems (Behrmann et al., 2004; Nobre et al., 2004; Posner & Petersen, 1990), Corbetta and Shulman proposed that the SPL, and more precisely, the IPS within the SPL, is implicated in directing attention to relevant qualities of the to-be detected information, whereas the IPL, in a region centered on the right TPJ, mediates the automatic allocation of attention to salient changes in the environment (Corbetta & Shulman, 2002; Corbetta et al., 2000). We have proposed that the IPL and the SPL have a conceptually similar function in memory as they do in perception.

5.1. Top-down attention to memory: the superior parietal lobe and the intraparietal sulcus

We hypothesized that the SPL is implicated in allocating top-down attentional resources to memory retrieval, which is necessary under condition in which further retrieval attempts or post-retrieval monitoring operations are necessary to discriminate between what is memory and what is not. In line with our hypothesis, we have found evidence of consistent SPL activity when individuals are not confident in the products of retrieval, regardless of whether they are accurate or not (Fleck et al., 2006; Moritz et al., 2006). The increase in IPS activity for unconfident (compared to confident) memory judgements could be related to participants having engaged in sustained pre- or post-retrieval processing of items near to a decision criterion. Memory judgements about high frequency vs. low frequency words also result in activation of the IPS. This is another situation in which the

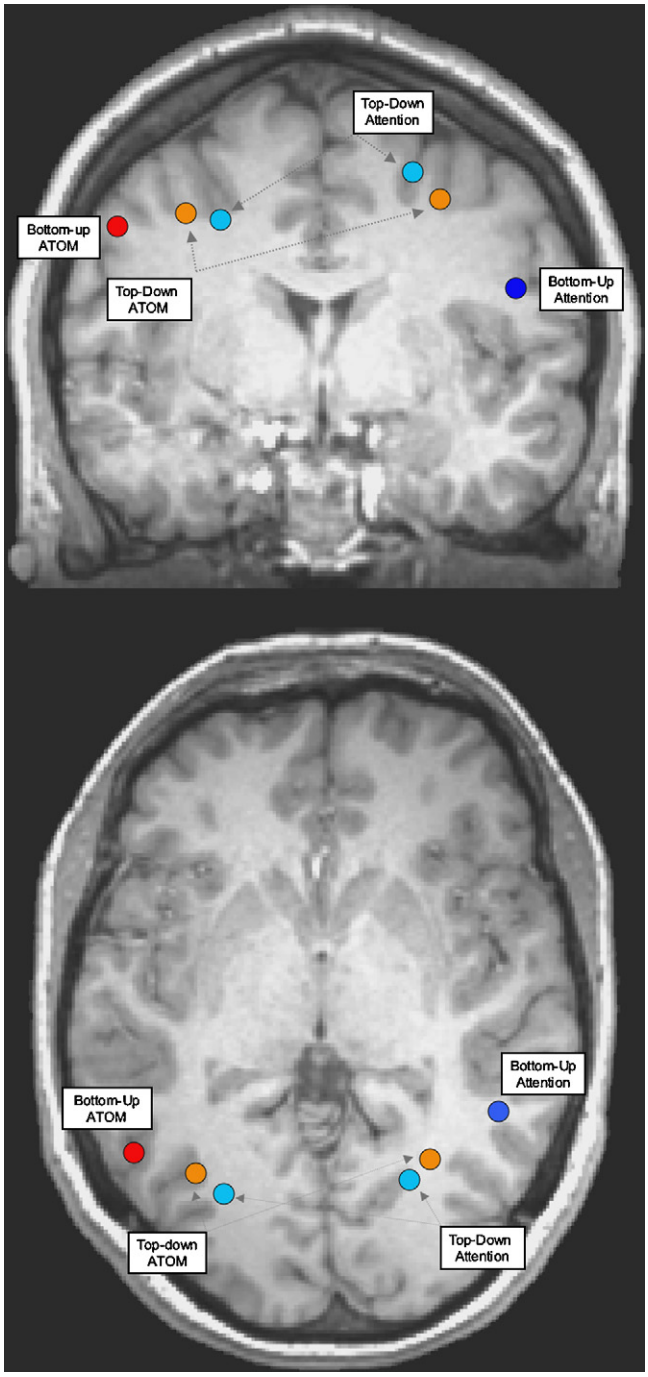

Fig. 3. Center of mass for activity related to top-down (in orange; median coordinates: −36 −57 42 in the left hemisphere; 32 −57 44 in the right hemisphere) and bottom-up attention to memory (in red; median coordinates: −50 −57 38) across all conditions, together with the coordinates of the superior (in light blue; median coordinates: −26 −67 39 in the left hemisphere; 27 −65 52 in the right hemisphere) and inferior attentional system (in blue; median coordinates: 53 −45 20) based on Corbetta et al. (2000).

episodic memory status of items can be perceived as ambiguous: Since high frequency words have been encountered many times, the engagement of costly strategic retrieval processes is needed to decide whether they have also been encountered in the relevant study list (Chee et al., 2004).

Another typical situation of uncertainty in the products of memory retrieval occurs while evaluating lures that are similar to the studied targets in some respect. Because similar/related lures resemble the studied material, they should need more post-retrieval processing to be rejected than lures that do not. Consider, for example, the case of the DRM paradigm: Lures that are unrelated to the studied material are immediately disqualified based on the lack of semantic consistency with the studied material. There is no need to collect additional information about their episodic characteristics. In contrast, rejection of related lures requires collection and monitoring of additional information to make a fine-grained distinction between studied and similar items (von Zerssen et al., 2001). Accordingly, we have found that SPL activity is increased for rejecting lures that were similar/related vs. unrelated to the studied items. Although subject to other interpretations (see below), we believe that the modulation of activity in IPS with the degree of similarity between studied and test items is consistent with a strategic retrieval account of the SPL: the more the commonalities between lures and targets, the higher the demands on memory search and monitoring, the higher the need for top-down attention to memory.

Also consistent with our hypothesis is the evidence that IPS activity is prominent for memory decisions based on familiarity, whereas activity in this brain area is secondary for memories that are vividly recollected. This finding supports our hypothesis that whereas recollected memories "pop out" from the distracter background, memories that are reported as only familiar might have passed through more pre- and post-retrieval processing before being endorsed. Indeed, whereas the recollection of contextual details from the study episode (e.g., which is associated with R responses) is immediate proof of the oldness of the item, this kind of evidence is usually absent (Yonelinas, 2002), or less strong (Wais, Mickes, & Wixted, 2008), for items reported as familiar, which require more information or more monitoring to determine whether they are old or not.

Consistent with our strategic retrieval account of the SPL, this brain region also supports retrieval of source, in addition to item, information. Different from item information, source information is not always available at retrieval and therefore needs to be searched. In line with this proposal, processing in SPL is more consistently observed for retrieval of source information than for emission of Remember responses, despite the latter are deemed to entail retrieval of contextual information as well. It is worth noting, however, that whereas Remember responses are based on the emergence of *whatever* contextual information about the target that the subject recovers, participants are not the arbiters in source memory tasks; they need to search for the information specified by the experimenter, and to monitor information retrieved from MTL structures in the service of making a decision (Dobbins & Han, 2006; Fletcher & Henson, 2001; Simons & Spiers, 2003). Indeed, patients with prefrontal lesions (Ciaramelli & Ghetti, 2007; Duarte et al., 2005), as well as older adults (Duarte, Henson, & Graham, 2008), have poor source memory, yet they can provide a normal amount of *R* responses.

Our finding that source memory is mainly dependent on the SPL whereas subjective estimates of recollection are mainly dependent on the IPL suggests dissociations between objective

and subjective recollection in posterior parietal cortex. Accordingly, Davidson and colleagues have shown that patients with lesions in the IPL have preserved source memory but provide fewer R responses compared normal controls (Davidson et al., 2008). Further, imaging data show that reductions of subjective, but not objective, recollection in older vs. younger adults were related to decreased activity in IPL regions (Duarte et al., 2008). To date, however, there is no evidence that SPL lesions result in impaired source memory: Simons and colleagues required patients with IPL and SPL lesions to make semantic or pleasantness judgments for words and faces and later asked them to determine which of the two judgments they had made about each item at study. Patients performed normally (Simons et al., 2008). Of course, this may relate to the high degree of separation between pleasantness and semantic judgements, which perhaps were retrievable and distinguishable even without engaging in costly strategic processes. Future studies with more subtle source manipulations might reveal deficits in patients with SPL damage.

Also in line with the AtoM hypothesis for the role of the SPL is evidence that activity in this area is sensitive to the frequency of occurrence at test of old to new items. Infrequent targets elicited the highest activity in SPL, whereas IPL was not modulated by frequency of target to lures (Herron et al., 2004). This finding suggests, again, that whereas the IPL automatically detects the products of retrieval, the SPL might be necessary to maintain top-down attention on task-relevant (episodic) features of the target for memory, when much time elapses between targets.

Across all the investigated conditions, we have found that the region of the SPL that mediates top-down attention to memory retrieval is in posterior IPS (median coordinates: −36 −57 42 in the left hemisphere, 32 −57 44 in the right hemisphere). This region is slightly lateral to that implicated in attentional cueing (Corbetta et al., 2000; see Fig. 3). Interestingly, studies investigating the ability to orient attention to semantic categories (Cristescu et al., 2006), or to search for semantic knowledge (Thompson-Shill, D'Esposito, Aguirre, & Farah, 1997), found activity in IPS regions close to ours. This finding suggests that orienting attention to the external space and orienting attention to memory contents may be mediated by adjacent, but distinct, parts of the IPS.

5.2. *Bottom-up attention to memory: the inferior parietal lobe and the temporo-parietal junction*

Analogous to its role in perception, we have hypothesized that the IPL would mediate the automatic attentional capture by the recollected memory, which might be necessary for the memory to enter consciousness, and therefore be experienced as a memory. If this hypothesis is correct, then the IPL should be activated most consistently when memory contents are confidently perceived as old. In line with our predictions, we have found more consistent activity in the left IPL for items that are recognized with high compared to low confidence (Chua et al., 2006; Moritz et al., 2006), for strong compared to weak memories (Shannon & Buckner, 2004), when recognition is accompanied by vivid remembering states (Tulving, 1985; Skinner & Fernandes, 2007; Wagner et al., 2005), or the recollection of contextual details (Cansino, Marquet, Dolan, & Rugg, 2002; Dobbins, Foley, Schacter, & Wagner, 2002), and for true targets compared to lures that are merely similar to the targets (Cabeza et al., 2001; Slotnick & Schacter, 2004).

Although activity during recollection was most prominent in the IPL, it was also noticeable in SPL (Skinner & Fernandes, 2007). Possibly, even though vivid subjective remembering usually imposes its contents upon consciousness, a Remember decision may at times involve post-retrieval monitoring of detected contents, and, possibly, subsequent search and evaluation of additional recollective information. SPL activity during recollection might, therefore, reflect search and monitoring operations that are needed to inform recollective decisions. In line with this proposal, when relatively more objective bases for recollection are probed (e.g., source memory, Section 4.3), activity in SPL is even more consistent. In a recent fMRI investigation, Vilberg and Rugg (2007) compared brain activity for subjective recollection (i.e., *R* responses) to that for objective recollection (i.e., production of the item with which the target had been paired at study). Objective compared to subjective recollection led to an increase in activity in lateral parietal region at the border between the SPL and the IPL (T&T coordinates: −39 −81 39; BA 19/39). This area is posterior and superior to that implicated in subjective recollection (−51 −57 32: see Section 4.2). It seems, then, that the neural bases of recollection are subject to slight movements toward the SPL or the IPL depending on whether objective or subjective indicators are probed. Different from Vilberg and Rugg (2007), however, we do not think that the difference between subjective and objective recollection is in the amount of recovered information: One can re-experience a past event in response to a retrieval cue whether little or much information about the event is retrieved, as the threshold model predicts (Yonelinas, 2002). On the other hand, objective recollection can be (and usually is) satisfied by the retrieval of a bit of information, provided it is the one specified by the experimenter, which may or may not be part of the recollective experience of the subject (see also Yonelinas & Jacoby, 1996). Consequently, it is the need for strategic processes aimed at recovering a specific type of information, not the amount of retrieved information, that varies between the two, and distinguishes them from one another.

Of course, the best evidence in favour of an *essential* role of the IPL during memory retrieval would be to demonstrate that patients with lesions in this brain region show the predicted deficits. It is well-known that patients with lesions in the right IPL, in TPJ, may suffer from unilateral neglect, that is, the unawareness of contralesional stimuli across diverse sensory modalities (Driver & Vuilleumier, 2001; Pavani et al., 2003; Vallar, 1998). As Cabeza (2007) recently argued, if the TPJ has a reflexive attention role in memory retrieval, then one should expect to find some sort of "*memory neglect*" in patients with lesions in that region. We recently tested patients with lesions in the IPL in an associative memory test probing not only for cued recall and recognition, but also for Remember/Know judgments and recall of source information (Davidson et al., 2008). We found that while they were unimpaired in recognition and source memory (see also Simons et al., 2008), parietal patients

were extremely reluctant to judge recognized items as "remembered". A patient from the same study, SM, commented that despite objectively remembering things in real life, she always lacked confidence in her memories, as if she did not know where these had come from. Furthermore, Berryhill et al. have shown that, in a free recall procedure, patients with bilateral parietal lesions produced autobiographical events that were less vivid and contained fewer perceptual, emotional and self-referential details compared to normal controls (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007; see also Davidson et al., 2008). Interestingly, when patients were probed for the same details, they were able to recall them (Berryhill et al., 2007).

Overall, the available studies on patients with IPL lesions show that, if probed appropriately, patients with IPL lesions can access normally item information (Davidson et al., 2008), source information (Davidson et al., 2008; Simons et al., 2008), and even multiple contextual features of complex events (Berryhill et al., 2007). Accordingly, transient disruption of activity in both left and right IPL following transcranial magnetic stimulation (TMS) does not affect recognition memory performance (Rossi et al., 2006). However, memory for contextual details of experienced events does not pop-out automatically (Berryhill et al., 2007) and does not trigger remembering states (Davidson et al., 2008) in these patients. In the TMS study by Rossi et al. (2006), recollection was not examined. It is possible, therefore, that in their study the quality of memories that were retrieved, and the processes by which retrieval occurred, may have been different when TMS was applied than when it was not.

The weak subjective sense of remembering (Davidson et al., 2008), or bottom-up detection of (Berryhill et al., 2007), mnemonic information that is objectively available, could be interpreted as *memory neglect*, namely, the absence of automatic awareness or appreciation of the products of retrieval. Like percepts, memories in parietal patients do not capture attention automatically, leading them to report an absence of memory in severe cases (Berryhill et al., 2007), or diminished recollective experience when the deficit is less severe (Davidson et al., 2008). However, when attention is directed to memory in a top-down fashion, by instructions or cues, its contents are revealed (Berryhill et al., 2007).

Across all the investigated conditions, we have found that the region of the IPL that mediates the bottom-up attentional capture by memory content is in the left supramarginal gyrus (median coordinates: −50 −57 38, see Fig. 3). The lateralization of IPL activity to the left is independent of the type of material (e.g., words vs. faces), as apparent in our Tables (see also Shannon & Buckner, 2004), and conflicts with the evidence that target detection in attentional studies is strongly lateralized to the right (Corbetta et al., 2000). One possibility is that the left hemisphere is involved in controlling attention to internal information, while the right hemisphere directs attention to the external world. However, representational neglect, i.e., neglect for the contralesional side of internally generated images of scenes, is rarely found after left parietal lobe lesions (Bartolomeo, D'Erme, & Gainotti, 1994). Another possibility is that the experience of recollection is closely tied to autobiographical memory, which also is associated with a left-lateralized network of activation (Addis, Moscovitch, Crawley, & McAndrews, 2004; Gilboa, Winocur, Grady, Hevenor, & Moscovitch, 2004; Maguire, 2001; Moscovitch et al., 2005). This may be related to the observation that the left hemisphere is dominant for providing narrative structure or commentary on experiences (Gazzaniga, 1998).

As a final note, we wish to emphasize that, according to an innovative line of research, episodic memory retrieval would allow us not only to remember past events, but also to anticipate future events in the service of decision-making and adaptive behaviour (e.g., Buckner & Carroll, 2007; Schacter, Addis, & Buckner, 2007; Sheldon, Ramos, & Moscovitch, in preparation). Indeed, studies comparing the neural bases of episodic memory retrieval, future imagining, and social problem solving have detected a common network that involves TPJ, in addition to medial-temporal and prefrontal regions (e.g., Addis, Wong, & Schacter, 2007; Saxe & Wexler, 2005). To the extent that this network is needed to conceive and plan future behaviour, it makes sense to us that it is equipped with a 'circuit-breaker' that signals when information of potential relevance for decision-making becomes available from memory.

5.3. Relation to other accounts of the parietal cortex involvement in memory retrieval

To date, three hypotheses have been advanced to account for the role of the posterior parietal cortex in memory retrieval: attention to memory representations, accumulation of sensory signals in the service of memory decisions, and a memory buffer for retrieved information (see Wagner et al., 2005). Given that we have just proposed a specification of the attentional hypothesis (i.e., the AtoM hypothesis; see also Cabeza et al., 2003; Wagner et al., 2005), we now discuss the other two proposals.

According to the *mnemonic accumulator hypothesis*, regions in posterior parietal cortex would play a role in accumulating, or temporally integrating, neural signals related to the target and stored information about it until a criterion is reached that leads to the memory decision required by the task at hand. Such a function is conceptually similar to other proposed forms of information accumulation that are the property of posterior parietal cortex neurons (Colby & Goldberg, 1999; Gottlieb, 2007; Platt & Glimcher, 1999). In the study by Yago and Ishai (2006), the IPS was more active for rejection of lures that were similar vs. dissimilar to the studied material (see also Section 4.6). Arguably, similar lures need more evidence to be rejected compared to unrelated lures. At the moment, there is not enough evidence to determine whether IPS activity is driven by the accumulation of information, as predicted by the mnemonic accumulator hypothesis, or by the search/evaluation of this information, as predicted by the AtoM model. There is a distinction between processes involved in gathering the required information and processes involved in computing the accumulated information to reach a decision. However, these two conceptualizations of IPS functions are related. As we previously said, top-down attentional systems have the capacity to optimize memory search, by implementing retrieval attempts only when more information needs to be gathered to reach a decision (Platt & Glimcher, 1999). Thus, situations of memory uncertainty must drive both detection of

low available information and engagement of strategic retrieval processes (see Colby & Goldberg, 1999 for a related view).

According to the *mnemonic buffer hypothesis,* regions in the IPL would support the representation of recollected information (Vilberg, Moosavi, & Rugg, 2006; Vilberg & Rugg, 2008). In order to influence decision-making, memories must be expressed in active neuronal response patterns, and the IPL could act as the episodic memory buffer proposed by Baddeley (2003). Consistent with this hypothesis, lesion and functional studies implicate left IPL regions in working memory storage (e.g., Paulesu, Frith, & Frackowiak, 1993). Also consistent with this hypothesis is evidence that recollection is characterized by increased IPL activity compared to familiarity, and recollection may be argued to entail the online representation of more information than is familiarity. Also the AtoM hypothesis is able to predict the increased IPL involvement for recollection than for familiarity, but for different reasons: While attempting to explain the specific role of the IPL in recollection, Vilberg and Rugg (2007) focus on the amount of information held in the buffer, whereas we focus on the attentional demands that this recovered information attracts. In a modified Remember/Know recognition test (Vilberg & Rugg, 2007), in which participants could indicate whether they subjectively remembered some contextual details from the study episode, or whether they remembered the item with which the target was paired at study, a left region in BA19/39 was more active for the latter judgment compared to the former. The authors have argued that remembering the specific sources of a memory requires holding a larger amount of information in working memory, and that load effects in IPL supports the mnemonic buffer over the AtoM hypothesis. Although we may agree that load effects would provide evidence in favour of the mnemonic buffer hypothesis, we do not think that Vilberg and Rugg (2007) have presented a convincing case that more information is held in memory when retrieving associative information than during subjective recollection. As we noted earlier, it is not obvious that Remember responses are supported by fewer pieces of information than are associative or source memory decisions. It is hoped that future research will elucidate the relations among the proposed accounts and distinctions between them.

What is most apparent to our reading of the available literature, and that is reflected in the AtoM hypothesis, is the need for a dual-process model of the role of the posterior parietal cortex in memory retrieval, with IPL and SPL making separate contributions. In this respect, one might ask whether the two components of the AtoM model merely map into recollection and familiarity. After all, we have shown that the operation of bottom-up and top-down attentional systems characterizes recollection and familiarity, respectively. As well, the differential involvement of the two systems in supporting strong/confident vs. weak/unconfident memories may reduce to a difference between recollection and familiarity, as high confidence responses/responses to items that received deep encoding are more likely to be associated with recollection, and low confidence responses/responses to items that received shallow encoding with familiarity (Gardiner & Richardson-Klavehn, 2000; Yonelinas, 2002). Also, source memory needs recollection to a greater extent than item-memory. Although the mapping between bottom-up/top-down attentional demands of memory retrieval and recollection/familiarity fits many conditions, it is not completely borne out by the data. For example, the involvement of IPL in recollection varies according to whether subjective or more objective aspects of recollection are probed (Davidson et al., 2008; Duarte et al., 2008). Moreover, the differences are also noted for lures, for which recollection and familiarity do not apply. For this reason, we would argue against reducing the parietal contributions to episodic retrieval to differences between recollection and familiarity. Rather, we suggest that the posterior parietal cortex has attentional functions that *serve* recollection and familiarity, but possibly also non-episodic memory tasks (e.g., Thompson-Shill et al., 1997), as well as non-memory tasks (Corbetta et al., 2000).

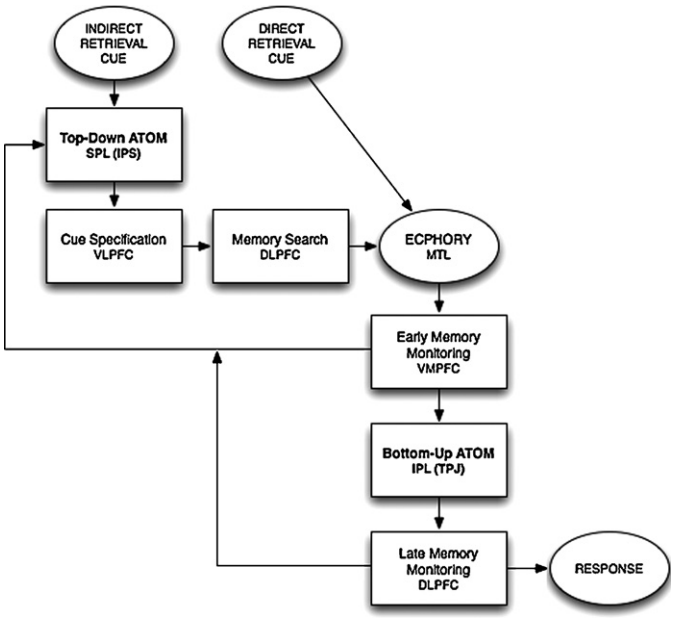

Fig. 4. The attention to memory (AtoM) model. *Note*: VLPFC: ventrolateral prefrontal cortex; DLPFC: dorsolateral prefrontal cortex; VMPFC: ventromedial prefrontal cortex; IPS: intraparietal sulcus; TPJ: temporo-parietal junction.

6. Conclusions and a model

We have introduced a dual-process hypothesis of the role of the posterior parietal cortex in memory retrieval, the AtoM hypothesis. A review of the existing fMRI literature provides initial support for our hypothesis. We end by introducing an extension of the Component Process Model (Moscovitch, 1992, 1994; Moscovitch & Umiltà, 1991; Moscovitch & Winocur, 1995, 2002), that includes the AtoM hypothesis (see Fig. 4).

During direct retrieval, a cue interacts automatically with information stored in memory systems via the MTL (i.e., ecphory). This information is checked for task-relevance by early post-retrieval monitoring systems in ventromedial prefrontal cortex (Gilboa et al., 2006), similar to what happens on search and detection paradigms (Shulman et al., 2003), and TPJ signals detection of task-relevant memory contents. The memory now enters consciousness. If the memory conflicts

with other pieces of information, more strategic monitoring processes, supported by dorsolateral prefrontal cortex, may be triggered to assess whether it is accurate or not. If the memory passes this last prefrontal gate, or there was no conflict in the first place, it triggers behaviour (Schacter et al., 2007), and stops retrieval attempts. Patients with lesions in TPJ are expected to show memory neglect, that is, lack of confidence and diminished remembering states for retrieved information (see Berryhill et al., 2007; Davidson et al., 2008). Conversely, patients with lesions in ventromedial prefrontal cortex, who cannot filter the input to TPJ, may show remembering states and high confidence for task-irrelevant memories (i.e., confabulation; Ciaramelli & Ghetti, 2007; Gilboa et al., 2006). When TPJ is susceptible to detection of task-irrelevant memories, manipulations that reduce attentional resources at retrieval improve memory performance (Ciaramelli et al., 2008).

During indirect retrieval, the target memory is not automatically elicited by the cue, and, therefore, has to be recovered through strategic retrieval processes. The ventrolateral prefrontal cortex selects the cues needed to gain access to the memory (see Badre & Wagner, 2007 for a review), and the dorsolateral prefrontal cortex indicates that a memory search starting from those cues is needed. If retrieved information matches the desired memory, retrieval attempts terminate. If not, the need for further cue specification triggers ventrolateral prefrontal activity, and another cycle of memory search begins. Across this process, the SPL allocates attention to the various components of strategic retrieval, starting from cue specification up to the final memory checking operations. Patients with lesions in SPL are expected to be disproportionately impaired in tasks that load heavily on strategic retrieval processes, e.g., free recall of uncategorized lists, recognition of high frequency words, source memory tasks, etc. These predictions, however, still need to be confirmed.

Acknowledgements

We thank Patrick Davidson and Susanne Ferber for helpful comments on a draft of the paper, Julia Spaniol and Alice Kim for drawing part of the papers to our attention, and Maroquine Aziz for technical support. This research was funded by a Marie Curie individual fellowship to EC and a CIHR (Canada) grant to MM and CG.

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