# Overlapping Parietal Activity in Memory and Perception: Evidence for the Attention to Memory Model

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## Abstract

■ The specific role of different parietal regions to episodic retrieval is a topic of intense debate. According to the Attention to Memory (AtoM) model, dorsal parietal cortex (DPC) mediates top–down attention processes guided by retrieval goals, whereas ventral parietal cortex (VPC) mediates bottom–up attention processes captured by the retrieval output or the retrieval cue. This model also hypothesizes that the attentional functions of DPC and VPC are similar for memory and perception. To investigate this last hypothesis, we scanned participants with event-related fMRI whereas they performed memory and perception tasks, each comprising an *orienting* phase (top–down attention) and a *detection* phase (bottom–up attention). The study yielded two main findings. First, consistent with the AtoM model, orienting-related activity for memory and percep-

tion overlapped in DPC, whereas detection-related activity for memory and perception overlapped in VPC. The DPC overlap was greater in the left intraparietal sulcus, and the VPC overlap in the left TPJ. Around overlapping areas, there were differences in the spatial distribution of memory and perception activations, which were consistent with trends reported in the literature. Second, both DPC and VPC showed stronger connectivity with medial-temporal lobe during the memory task and with visual cortex during the perception task. These findings suggest that, during memory tasks, some parietal regions mediate similar attentional control processes to those involved in perception tasks (orienting in DPC vs. detection in VPC), although on different types of information (mnemonic vs. sensory). ■

## INTRODUCTION

The role of posterior parietal cortex in episodic memory retrieval is a conundrum; on the one hand, this region is one of the most frequently activated in functional neuroimaging studies of episodic retrieval, but on the other hand, damage to this area does not yield severe memory deficits, such as the ones that follow medial-temporal lobe (MTL) damage. Several hypotheses have been advanced to account for the contributions of posterior parietal regions to episodic retrieval (for reviews, see Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008; Vilberg & Rugg, 2008; Wagner, Shannon, Kahn, & Buckner, 2005). One hypothesis is that these contributions are related to attentional processes that differ for dorsal parietal cortex (DPC; intraparietal sulcus [IPS] and superior parietal lobule, lateral and medial) and ventral parietal cortex (VPC; supramarginal gyrus, including the TPJ and the angular gyrus). According to this view, known as the Attention to Memory (AtoM) model, DPC mediates top–down attention processes guided by retrieval goals, whereas VPC mediates bottom–up attention processes captured by

the retrieval output or the retrieval cue (Cabeza et al., 2008; Ciaramelli et al., 2008).

The AtoM model is supported by both functional neuroimaging and lesion data. Functional neuroimaging evidence has linked DPC to top–down attention and VPC to bottom–up attention in both perception and memory domains. In the perception domain, fMRI studies using oddball and Posner-type paradigms have associated DPC to voluntary orienting of visual attention to locations or targets in space and VPC to the detection of such targets (for a review, see Corbetta & Shulman, 2002). In the memory domain, conditions involving demanding memory search or monitoring processes tend to show greater DPC activity, whereas conditions involving rich, attention-grabbing memories tend to show greater VPC activity (Cabeza et al., 2008). For example, in a "Posner-like" recognition memory experiment, DPC was activated when subjects oriented toward a memory target upon presentation of a relevant cue, whereas VPC was activated when memory targets were detected in the absence of cues or after invalid memory cueing (Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; for VPC sensitivity to invalid memory cueing, see also O'Connor, Han, & Dobbins, 2010). Thus, DPC is associated with orienting and VPC with detection, in both the memory and perception domains.

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Turning to lesion data, patients with parietal lesions show subtle memory difficulties that suggest a deficit in attention to retrieved memories rather than in retrieval per se. For example, patients with VPC lesions have difficulty spontaneously reporting retrieved memories about themselves, but these memories are available and can be accessed by specific questions that guide top–down attention toward these memories (Berryhill, Phuong, Picasso, Cabeza, & Olson, 2007). Such patients also have problems subjectively evaluating their retrieved memories (Drowos, Berryhill, Andre, & Olson, 2010; Simons, Peers, Mazuz, Berryhill, & Olson, 2010; Davidson et al., 2008), possibly because their memory retrieval is less spontaneous, so the patients' sense of re-experience is diminished.

The current study focuses on a recent issue regarding the functional neuroimaging evidence for the AtoM model. Although DPC and VPC have been associated, respectively, with top–down and bottom–up attention in both perception (Corbetta & Shulman, 2002) and memory tasks (Cabeza et al., 2008; Ciaramelli et al., 2008), a recent fMRI meta-analysis suggested that the exact locations of top–down and bottom–up activations peaks in the left hemisphere are not identical for perception and memory (Hutchinson, Uncapher, & Wagner, 2009). For example, top–down attention peaks within DPC tend to be more superior in perception studies, falling mostly on the *medial bank* of IPS and the superior parietal lobule, but more inferior in memory studies, falling mostly on the *lateral bank* of IPS. As for bottom–up attention peaks within VPC, they tend to be more anterior in the perception studies, falling mostly in TPJ and supramarginal gyrus, but more posterior in the memory studies, extending toward the angular gyrus. Similar differences in localization for perception and memory were reported in the recent fMRI study by Sestieri, Shulman, and Corbetta (2010), which compared activity while participants searched for an object in a movie clip or remembered the script of a movie watched before scanning.

Although the differences in localization found in the meta-analysis by Hutchinson et al. (2009) and in the fMRI study by Sestieri et al. (2010) are interesting, they are not necessarily inconsistent with the AtoM model. The AtoM model assumes that DPC and VPC play similar attentional roles in perception and memory, but it does not assume that the location of parietal activations must be identical in these two domains. Moreover, the AtoM model assumes that top–down vs. bottom–up attention is only one of several factors determining the localization of parietal activations. Other important factors include the spatial versus nonspatial nature of the task and the verbal versus nonverbal nature of the stimuli (Cabeza, 2008). Both of these factors may have contributed to the localization differences found by Sestieri et al. (2010) and Hutchinson et al. (2009). For example, Sestieri et al. (2010) compared a perception task that emphasized spatial processing to a memory task that emphasized nonspatial meaning-based processing. Although the AtoM model applies to both spatial and nonspatial attention and to both verbal and nonverbal domains, overlaps between memory and perception would be less likely to be detected when memory and perception tasks differ in one or more of these dimensions. Thus, the present study compared memory and perception tasks that were matched in both dimensions.

In the present study, both memory and perception tasks were verbal and nonspatial. Both tasks distinguished between orienting-related and detection-related activations, and cross-task overlaps were identified using conjunction analyses. In both tasks, participants oriented toward a series of items in which a target was embedded and pressed a key when they detected it (see Figure 1). The two tasks
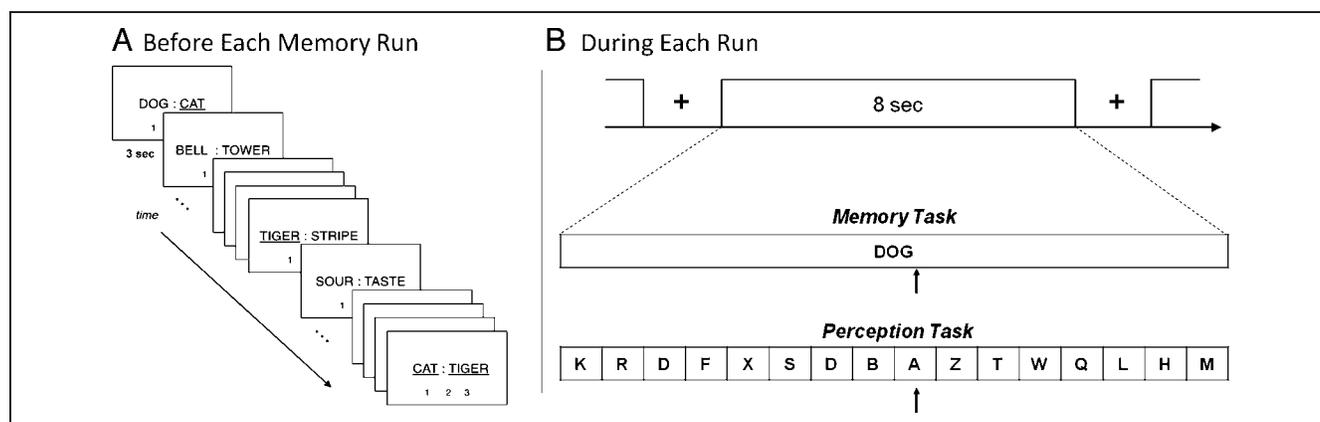
**Figure 1.** (A) Before each memory retrieval run, participants viewed pairs of words and gave an association rating for each pair. Each pair overlapped with either one or two other pairs, such that three pairs formed a chain to be recalled later. The entire list of words was repeated twice. Underlines are used here to highlight overlaps and were not seen onscreen. (B) The memory and perception task runs shared similar timing, with 8-sec trials and responses (indicated with arrows) coming around halfway through. In the memory task, participants viewed the first word of each four-word chain and covertly recalled the remaining words in order, pressing a button upon recalling the fourth. In the perception task, participants viewed a stream of sequentially presented letters at 2 letters/sec and pressed a button when a vowel appeared.

differed in whether orienting and detection were applied to internally retrieved memories or to externally presented stimuli. Memory-orienting started with the presentation of a word (e.g., *dog*), which participants used as a cue to recall three overlapping word pairs that they previously studied (e.g., *dog–cat*; *cat–tiger*; *tiger–stripe*). The three pairs, which had been previously studied, were randomly mixed with many other pairs; hence, given the limited time between stimuli at study, participants needed to re-construct the links during the retrieval scan. When participants retrieved the last word of the chain (e.g., *stripe*), they pressed the key to indicate that the target memory had been detected. In the perception task, participants viewed a stream of consonants (2/sec) and when they detected a vowel, which was the target of the visual orienting in this case, they pressed the key.

In both tasks, *orienting-related activity* was measured as activity from the presentation of the stimulus that triggered the orienting (i.e., the first word of the chain for the memory task, the first consonant of the stream for the perception task) until the key press and *detection-related activity* as transient activity calculated as being triggered just before the key press. To be able to subtract out simple motor-related activity, participants also performed a simple tapping task in a separate condition. On the basis of the AtoM model, we expected that some DPC regions would show orienting-related activity for both memory and perception and that some VPC regions would show detection-related activity for both memory and perception. It is worth noting that, given our goal of finding overlaps in activation, differences in stimuli between perception tasks (e.g., one word vs. many consonants) is an advantage rather than a disadvantage, because if activation overlaps are found, they are more likely to reflect similarity in processes rather than similarity in stimuli. At the same time, similarity in processes does not imply that the localization of activations must be identical because precise localization seems likely to be determined by multiple factors, and top–down versus bottom–up attention is only one of them.

A secondary goal of the study was to investigate the AtoM model's prediction that the functional connectivity of DPC and VPC should differ for memory versus perception tasks. Although the attentional contributions of these regions are assumed to be similar for memory and perception tasks, the source of information being processed in the two tasks is different. According to the model, during memory tasks, parietal regions would be searching and detecting memory information coming from the MTL regions, whereas during perception tasks, they would be searching and detecting perceptual information coming from sensory regions, such as the visual cortex in the current study. Thus, we predicted that, despite overlapping activations, DPC and VPC would show stronger connectivity with MTL during the memory task and stronger connectivity with visual cortex during the perception task.

## METHODS

### Participants

Eighteen adults (10 women) with an average age of 22.5 years (*SD* = 2.8 years) were scanned and paid for participation in the study. Participants were recruited from the Durham, North Carolina, community. Written informed consent was obtained from all participants for a protocol approved by the Duke University Institutional Review Board.

### Behavioral Methods

As illustrated by Figure 1, both memory and perception trials consisted of 8-sec blocks followed by a jittered inter-trial interval with a mean duration of 4.4 sec. During the block, participants made a single response when they found the memory or perception target. Memory and perception trials were grouped in separate runs (three memory runs, three perception runs).

Before each memory run, participants studied 60 word pairs (e.g., *dog–cat; penguin–tuxedo*). The pairs were selected from free association norms (Nelson, McEvoy, & Schreiber, 2004) so that groups of three pairs formed four-word "chains" (e.g., *dog–cat–tiger–stripe; penguin–tuxedo–prom–date; malt–shake–rattle–snake*). To promote sequential recall within each chain, words were chosen such that only the presented pairs (e.g., *dog–cat*) had listed association strengths (mean = 0.14, *SD* = 0.17). No normed association strength was found between noncontiguous words of the same chain (e.g., *dog–tiger*) or between words in different chains (e.g., *dog–penguin*). During study, each pair was presented for 3 sec while participants rated the relatedness between the words (medium, strong, very strong). The pairs of one chain were intermixed with the pairs of other chains (e.g., *dog–cat, penguin–tuxedo, malt–shake*), and each pair was presented twice. It is worth noting that the overlapping word pair learning task is different than typical transitive inference tasks (e.g., Shohamy & Wagner, 2008), because it does not fulfill the transitive property (e.g., *dog* is associated with *cat* and *cat* is associated with *tiger*, but *dog* is not associated with *tiger*), and because the pairs are based on pre-existing semantic associations, rather than newly formed episodic associations, such as, e.g., in the Shohamy and Wagner study.

During memory runs, each trial consisted of the first word of a quartet (e.g., *dog*), which remained on the screen during the 8-sec block. During this period, participants covertly recalled the three overlapping pairs (*dog → cat → tiger → stripe*) and pressed a key when they recalled the last word (e.g., *stripe*). Participants were instructed to recall the four words of the chain sequentially before pressing the key, and they practiced this task out loud before the scan session. The main reason for using overlapping word pairs rather than single words or pairs was to slow down retrieval so that orienting and

detection processes could be dissociated in time. Given that participants never saw the four-word chain as a unit but only the component pairs intermixed with other unrelated pairs and that the retrieval cue (e.g., *dog*) was not semantically associated to the target (e.g., *stripe*), the easiest method for recalling the target was to follow the associations in the chain (*dog → cat → tiger → stripe*). As reported in the behavioral results, this took longer than 4 sec on average, making it highly unlikely that these connections would have been made spontaneously at encoding. Behavioral piloting and practice sessions revealed that participants understood and correctly performed the recall task.

During perception runs, each trial consisted of 15 consonants and 1 vowel presented at a rate of 500 msec per letter (300-msec presentation plus 200-msec blank). Participants' task was to press a key when they saw the vowel. About three "catch trials" in each run contained no vowel. Letter sequences were generated randomly for each trial, but the serial position of the vowel was yoked to the participant's RT in the previous memory scan, ensuring a comparable RT mean and distribution for memory and perception tasks.

In addition to memory and perception scans, the session included also a finger tapping run, which was used as a control for simple motor-related activity. Participants pressed a key once per second in time in response to a beep and continued to approximate the same timing after beeping ceased. The finger-tapping task was expected to subtract out the simple motor-related neural component of key pressing in the memory and perception tasks but not other associated processes, such as response preparation. The session included also an autobiographical memory scan, whose results are not reported here. Participants performed a shorter practice version of each task outside the scanner before the scanning session.

After scanning, participants completed an overt version of the memory task. The recall tests displayed the same words presented during the memory (retrieval) runs (e.g., *dog*), in the same order as during these runs, and participants recalled all words in the chain aloud (e.g., *cat, tiger, stripe*) and pressed a key when they retrieved the last word of the chain (e.g., stripe). The goal of this test was to confirm successful recall of the words in each chain. The intertrial interval of the posttest was constant at 2 sec. Verbal responses were recorded using a digital voice recorder.

## fMRI Methods

### Scanning

Images were collected from a 4-T GE scanner. Acoustic scanner noise was reduced with earplugs, and head motion was reduced with foam pads and headbands. Stimuli were presented with LCD goggles (Resonance Technology, Inc., Northridge, CA), and behavioral responses were recorded with a four-key fiber-optic response box (Resonance Technology, Inc., Northridge, CA). Anatomical scanning started with a T1-weighted sagittal localizer series. The anterior (AC) and posterior commissures (PC) were identified in the midsagittal slice, and 34 contiguous oblique slices were prescribed parallel to the AC–PC plane. High-resolution T1-weighted structural images were acquired with a 450-msec repetition time, a 9-msec echo time, a 24-cm field of view, a $256^2$ matrix, and a slice thickness of 1.9 mm. Functional scanning employed an inverse spiral sequence with a 2-s repetition time, a 27-msec echo time, a 24-cm field of view, a $64^2$ image matrix, and a 60° flip angle. Thirty-four contiguous slices were acquired with the same slice prescription as the anatomical images. Slice thickness was 3.75 mm, resulting in 3.75-mm$^3$ isotropic voxels.

Data were processed using SPM5 (Wellcome Department of Cognitive Neurology, www.fil.ion.ucl.ac.uk/spm). The first six volumes were discarded to allow for scanner equilibration. The acquired images were then corrected for differences in slice acquisition times and realigned. Functional images were spatially normalized to a standard stereotactic space, using the Montreal Neurological Institute templates implemented in SPM5 and resliced to a resolution of 3.75 mm$^3$. Finally, the volumes were spatially smoothed using an 8-mm isotropic Gaussian kernel and grand mean scaled to the whole-brain signal.

### General Linear Model

For each participant, orienting and detection phases in both tasks were modeled for all trials with responses, except for any catch trials responded to in error. A general linear model was created using SPM5 software to define regressors related to top–down and bottom–up attentional activity in each task. Orienting activity was modeled by convolving a canonical hemodynamic response (HDR) function with a boxcar function beginning at trial onset and ending at the button press, whereas detection activity was modeled by convolving the canonical HDR function with a delta (stick) function placed 150 msec before the key press. The hemodynamic peak of this canonical HDR occurred several seconds after the response.

Primary analyses of interest related to neural activity common to mnemonic and perceptual attention tasks in the two phases—top–down orienting and bottom–up detection—of each trial. Thus, for each phase, a conjunction analysis was performed using the random effects group contrasts of memory > baseline and perception > baseline, each thresholded at $p < .001$, uncorrected. Because the experimental hypothesis concerned the role of posterior parietal regions, analyses were performed in ROIs restricted to the parietal lobes minus the sensorimotor cortex, anatomically defined using WFU Pickatlas tools (Maldjian, Laurienti, Kraft, & Burdette, 2003). To control for motor-related activity, the conjunction results were

exclusively masked with regions activated during the key press motor task.

### Functional Connectivity

To test the hypothesis that parietal regions from the conjunction analysis were differentially coactive with MTL and visual cortex depending on task, we conducted an analysis based on individual trial activity. ROIs selected for this analysis included the largest memory perception overlap in orienting-related activity within DPC (−26, −67, 45; see Table 1) and in detection-related activity within VPC (−59, −28, 26; see Table 1), as well as anatomical ROIs corresponding to the hypothetical input regions for memory and perception tasks, namely MTL and visual cortex. Given that the strongest parietal overlaps were found in the left hemisphere, the anatomical ROIs for MTL and visual cortex were also identified within the left hemisphere. The MTL ROI was derived using the left hippocampus label of the AAL atlas (Tzourio-Mazoyer et al., 2002) in the WFU Pickatlas tool, whereas the visual cortex ROI was created by selecting left BA 17 from Pickatlas's Brodmann's area labels and dilating the volume by four voxels in three dimensions.

To examine individual trial activity, we created an additional general linear model. Each trial eliciting a button press was modeled by two covariates, one for orienting and one for detection activity. This yielded two parameter estimates ("betas") for each individual trial and each individual participant. For each phase—orienting and detection—analysis focused on the corresponding parietal ROI and the corresponding MTL and visual cortex ROIs. Thus, for each phase, trials were sorted by task, and for every participant, trial-to-trial correlations were calculated between betas from the relevant parietal region and each of the other two regions. Individual subject correlations were Fisher-transformed and compared in separate repeated measures ANOVAs with Task (memory, perception) and ROI (MTL, visual) as within-subject factors.

## RESULTS

### Behavioral Results

In the memory task, mean RT was 4.14 sec (SD = 0.69). In the perception task, RT relative to vowel target onset was 0.56 sec (SD = 0.18), resulting in a total RT—relative to trial onset (i.e., initial letter onset)—of 4.44 sec (SD = 0.70). The RT difference between tasks, although relatively small, was significant ($p < .005$). Only trials with RTs under 8 sec were included in fMRI analyses, resulting in somewhat more trials in the perception task (46 trials, SD = 5.7) than in the memory task (41.3, SD = 9.9). To assess whether the key press in the memory task was a valid measure of covert recall, we calculated Goodman and Kruskal's gamma value (Goodman & Kruskal, 1954), linking presence/absence of a key press in the scanner with success/failure of overt recall (entire word chain) outside the scanner across trials for each participant. The average gamma of 0.91 (SD = 0.082) was very strong and significant ($p < .05$), supporting the use of the key press as a measure of recall success in the scanner.

### fMRI Results

#### Conjunction Analyses

Table 1 lists parietal regions showing overlaps in activation between memory and perception tasks during the orienting block and during the detection event. Consistent with the AtoM model, memory–perception overlaps in orienting-related activity were found within DPC, whereas memory–perception overlaps in detection-related activity were found within VPC. These overlaps occurred in both hemispheres but were largest and strongest in left parietal regions. As illustrated by the rendering in Figure 2, in the left hemisphere, the memory–perception overlap in orienting-related activity (in blue) was maximal in the IPS, and memory–perception overlap in detection-related activity (in yellow) was maximal in the supramarginal gyrus, near the TPJ. Supporting the contributions of

**Table 1.** Regions Showing Orienting- and Detection-related Activity During Both Perception and Memory Tasks

| | | Hemisphere | BA | Talairach Coordinates | | | t Score | Voxels |
|---|---|---|---|---|---|---|---|---|
| | | | | x | y | z | | |
| *Orienting-related activity* | | | | | | | | |
| DPC | Superior parietal lobule | Left | BA 7 | −26 | −67 | 45 | 6.89 | 385 |
| DPC | Superior parietal lobule | Right | BA 7 | 30 | −52 | 45 | 4.62 | 18 |
| DPC | Precuneus | Right | BA 7 | 11 | −71 | 39 | 4.14 | 20 |
| *Detection-related Activity* | | | | | | | | |
| VPC | Inferior parietal lobule | Left | BA 40 | −59 | −28 | 26 | 5.91 | 250 |
| VPC | Inferior parietal lobule | Right | BA 40 | 41 | −52 | 48 | 5.15 | 128 |

top–down attention to successful recall, orienting-related activity in the memory task was significantly greater ($p <$ .001) for trials in which recall was successful (indicated by key press within time limit) than unsuccessful (no key press).

Although the study was not designed to identify differences between the two tasks, it is worth noting that perception- and memory-specific activations extended in different directions from the overlapping areas (see purple and green activations in the slices in Figure 2). Within DPC, orienting-related activity in the perception task extended dorsally toward the medial bank of IPS (in purple), whereas orienting-related activity in the memory task extended ventrally toward the lateral bank of IPS (in green). Within VPC, detection-related activity in the perception task was more anterior (in purple), whereas detection-related activity in the memory task extended posteriorly toward the angular gyrus (in green). These differences in the distribution of perception and memory activations are globally consistent with the results of Sestieri et al. (2010) and Hutchinson et al. (2009).

Although the current study focuses on parietal activations, to confirm that orienting-related activity in the memory task varied as a function of retrieval success, we conducted an exploratory whole-brain contrast ($p <$ .001, $k > 5$ voxels) between successful recall trials (with responses) versus unsuccessful trials (no responses). As expected, this contrast yielded regions typically associated with successful episodic retrieval including the left hippocampus ($-26, -40, 2, t = 5.22$), the posterior cin-

gulate ($-11, -50, 20, t = 9.00$), and frontal lobe regions ($-4, -1, 60, t = 6.74$; $xyz = 21, 26, 18, t = 6.27$). The finding that hippocampus showed greater activity for response versus no-response trials confirms the assumption that these responses tracked memory recovery.

### Functional Connectivity

Figure 3 shows the strength of functional connectivity between two parietal ROIs (the DPC region showing memory–perception overlaps in orienting-related activity and the VPC region showing memory–perception overlaps in detection-related activity) with hypothetical input regions in MTL and visual cortex (anatomically defined ROI). Consistent with the AtoM model, parietal connectivity was stronger with the MTL during the memory task but with visual cortex during the perception task. Separate ANOVAs yielded significant Task (memory, perception) × ROI (MTL, visual cortex) interactions for both orienting-related activity in DPC [$F(1, 17) = 5.65, p < .03$] and detection-related activity in VPC [$F(1, 17) = 7.2, p < .02$]. Collapsing over parietal ROIs and forms of attention, parietal connectivity with visual cortex was stronger during the perception task than during the memory task, $t(18) = 2.27, p < .05$, whereas parietal connectivity with MTL was stronger during the memory task than during the perception task, $t(18) = 1.75, p < .05$. Thus, perception and memory tasks recruited similar parietal regions, but their functional connectivity with hypothetical input regions,

**Figure 2.** (A) Memory–perception conjunctions in orienting-related activity (in blue) and in detection-related activity (in yellow/orange) within left parietal cortex. Both memory and perception showed orienting-related activity in IPS and detection-related activity in TPJ. (B) Distribution of perception-specific (purple) and memory-specific (green) activity around shared activations identified by conjunction analyses. Within DPC, orienting-related activity extended toward the medial (superior) bank of IPS in the perception task but toward the lateral (inferior) bank in the memory task. Within VPC, detection-related activity was localized anteriorly in the perception task, but it extended posteriorly toward the angular gyrus in the memory task.
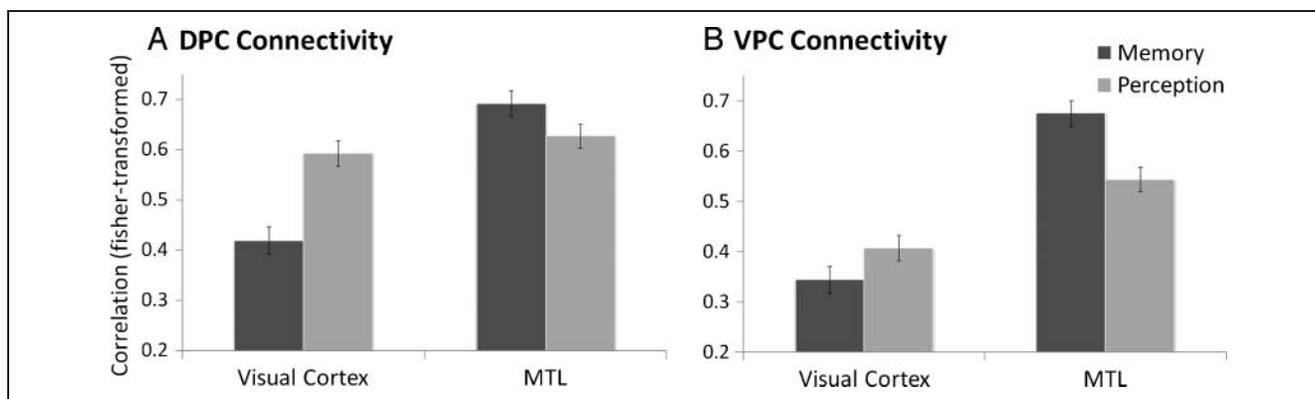


A Memory–perception conjunctions

B Task-specific activity around overlaps

Orienting-related activity

$Y = -60$

Perception   Memory

Detection-related activity

$Z = 27$

■ Orienting-related activity: Perception ∩ Memory
■ Detection-related activity: Perception ∩ Memory
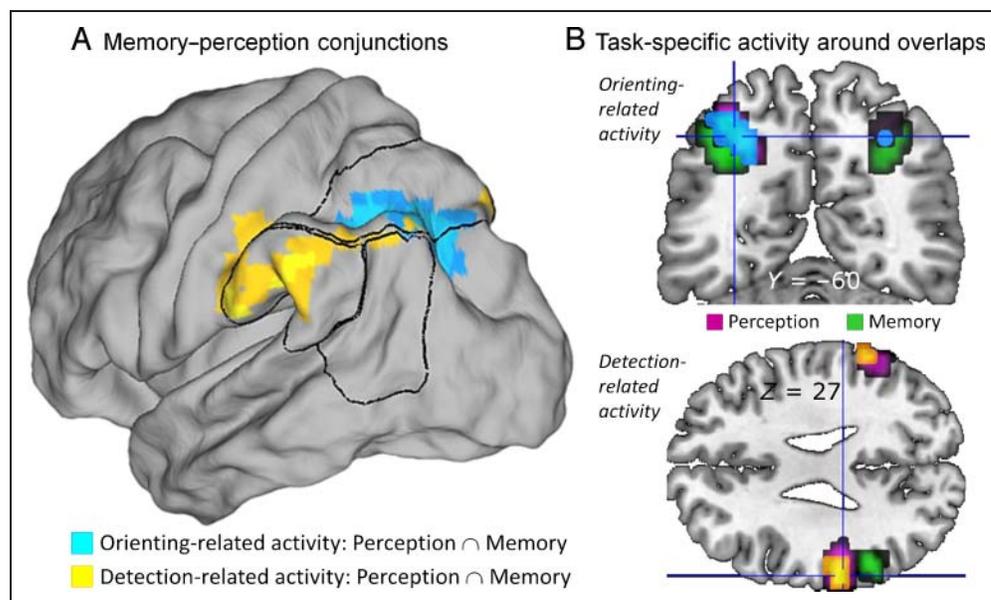
**Figure 3.** Functional connectivity of parietal regions showing perception–memory overlaps (A, orienting-related DPC region: −26, −67, 45; B, detection-related VPC region: −59, −28, 26) with hypothetical left hemisphere input regions for perception (visual cortex) and memory (MTL). Connectivity with visual cortex was stronger for perception than memory, whereas connectivity with MTL was stronger for memory than perception.

visual cortex and MTL, differed for sensory versus mnemonic information.

## DISCUSSION

This study yielded two main findings. First, consistent with the AtoM model, DPC showed orienting-related activity during both memory and perception tasks, whereas VPC showed detection-related activity during both tasks (see Figure 2). Second, and also consistent with the AtoM model, these parietal lobe regions showed stronger connectivity with the MTL during the memory task but with visual cortex during the perception task (see Figure 3). Taken together, these findings suggest that, during memory and perception tasks, parietal regions mediate similar attentional processes (orienting in DPC vs. detection in VPC) but on different types of information (mnemonic information in memory tasks vs. sensory information in perceptual tasks).

The finding that orienting-related activity for perception and memory overlapped in DPC (mainly in IPS) and that detection-related activity for perception and memory overlapped in VPC (mainly in TPJ) is not inconsistent with differences in localization between perception and memory found by Sestieri et al. (2010) and Hutchinson et al. (2009). As mentioned before, the meta-analysis by Hutchinson et al. (2009) found that DPC activations tended to be more superior for perception (e.g., medial bank of IPS) but more inferior for memory (lateral bank of IPS) and that VPC activations tended to be more anterior for perception (TPJ) but more posterior for memory (angular gyrus). As illustrated by the slices in Figure 2, the non-overlapping portions of perception and memory activations showed similar trends in the current study: a superior–inferior difference around IPS and an anterior–posterior difference around TPJ. At the same time, our results clearly show that attention-related memory and perception activations overlap in IPS (top–down attention) and in TPJ

(bottom–up attention). Thus, the present findings show that differences in parietal localization between perception and memory (Sestieri et al., 2010; Hutchinson et al., 2009) are not necessarily incompatible with the AtoM model: The precise distribution of memory-related and perception-related activations may differ, but they can still overlap as predicted by the AtoM model. Even when the distribution of areas of activation diverge, orienting and detecting in both tasks still are associated, respectively, with DPC and VPC activation.

It is worth noting that, although we found a significant overlap between memory and perception, the AtoM model does not require a perfect overlap, and it would be also consistent with perception–attention and memory–attention activations being in proximity to one another. The assumption that DPC and VPC contribute differently to top–down versus bottom–up attention does not imply that this is the only factor accounting for the spatial distribution of activations within parietal cortex. Other important factors seem likely to include the spatial versus nonspatial nature of the task, the modality of the stimuli, etc. As an example of this last factor, for example, there is evidence that regions mediating similar attentional processes for audition versus vision are close to each other but not overlapping (Wu, Weissman, Roberts, & Woldorff, 2007; Woldorff et al., 2004).

Another important factor modulating the spatial distribution on brain activations is the verbal versus nonverbal nature of the stimuli. This factor could explain why memory–perception overlaps in the current study were found primarily in the left hemisphere. Although parietal activations in episodic retrieval and attention fMRI studies have been reported in both hemispheres (Cabeza et al., 2008; Corbetta & Shulman, 2002), they tend to be more frequent in the left hemisphere in episodic retrieval studies and in the right hemisphere in attention studies (Hutchinson et al., 2009). We have previously speculated that this difference may reflect the fact that most retrieval studies use verbal/meaningful stimuli, such

as words, whereas most attention studies use nonverbal/meaningless stimuli, such as flashes and sounds (Cabeza et al., 2008). Consistent with this account, an episodic retrieval fMRI study that used abstract musical stimuli found old–new effects only in the right parietal cortex (Klostermann, Loui, & Shimamura, 2009). The stimuli-type account can explain the left lateralization of parietal overlaps in the current study because the stimuli were verbal in both tasks (words vs. letters). Also their verbal nature, memory, and perception stimuli were quite different (meaningful vs. meaningless, constant vs. stream), making it unlikely that parietal overlaps reflected similarities in stimuli rather than (attentional) processes engaged in the two tasks.

Turning to the second main finding, parietal regions showed stronger interactions with MTL during the memory task and with visual cortex during the perception task. These differences should be treated with caution, because the two tasks were not perfectly matched in stimulus and presentation format. The difference in connectivity evinced by DPC and VPC in the memory versus perception task provides further support for the AtoM model. Parietal regions deemed to mediate top–down and bottom–up attention for both memory and perceptual tasks did target brain regions providing the relevant information on which to operate in the two tasks: MTL for memory traces and visual cortex for percepts.

Although the current study was not designed to compare different hypotheses regarding parietal contributions to episodic retrieval (for a review, see Wagner et al., 2005), the results are more consistent with the AtoM model than with alternative accounts. These alternative accounts include the output buffer hypothesis (parietal regions hold retrieved information), the mnemonic accumulator hypothesis (parietal regions temporally integrate a strength signal), and internal attention hypothesis (parietal regions focus attention on internally generated representations). Given that these hypotheses do not assume functional differences between DPC and VPC, the AtoM model provides a better account for the dissociation found in the current study. One instantiation of the output buffer hypothesis, the episodic buffer hypothesis (Vilberg & Rugg, 2008) does distinguish between VPC and DPC functions, linking VPC to recollection and DPC to familiarity. It is unclear, however, how the recollection–familiarity distinction explains the detection-orienting dissociation between VPC and DPC and the overlap of perception–memory activations in these regions. The internal attention hypothesis cannot easily explain why TPJ and central IPS were recruited by both internal and external information, but it could explain the differential involvement of the angular gyrus and lateral IPS in the memory task. Finally, the mnemonic accumulator hypothesis could explain memory–perception overlaps in VPC under the assumption that the accumulator accrues not only mnemonic, but also sensory, signals. However, if the accumulator reaches threshold just before the response, the current study would link this mechanism to

VPC, whereas accumulator theorists have linked it to IPS in DPC (e.g., Donaldson, Wheeler, & Petersen, 2010).

In summary, the current study found (1) that, for both memory and perception tasks, DPC showed orienting-related activity and VPC showed detection-related activity and (2) that the same parietal regions showed stronger connectivity with visual cortex during the perception task but with the MTL during the memory task. These findings are consistent with the AtoM model's assumptions that DPC and VPC, respectively, mediates top–down versus bottom–up attention and that these attentional processes apply both to perceptual inputs from sensory cortices and to mnemonic inputs from MTL.

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