The Parietal Memory Network Activates Similarly for True and Associative False
Recognition Elicited via the DRM Procedure

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Abstract

Neuroimaging investigations of human memory encoding and retrieval have revealed that multiple regions of parietal cortex contribute to memory. Recently, a sparse network of regions within parietal cortex has been identified using resting state functional connectivity MRI techniques). The regions within this network exhibit consistent task-related responses during memory formation and retrieval, leading to its being called the parietal memory network (PMN). Among its signature patterns are: deactivation during initial experience with an item (e.g., encoding); activation during subsequent repetitions (e.g., at retrieval); greater activation for successfully retrieved familiar words than novel words (e.g., hits relative to correctly-rejected lures). The question of interest here is whether novel words that are subjectively experienced as having been recently studied would elicit PMN activation similar to that of hits. That is, we compared old items correctly recognized to two types of novel items on a recognition test: those correctly identified as new and those incorrectly labeled as old due to their strong associative relation to the studied words (in the DRM false memory protocol). Subjective oldness plays a strong role in driving activation, as hits and false alarms activated similarly (and greater than correctly-rejected lures).

Keywords: fMRI; false memory; DRM; false alarm; retrieval success

Neuroimaging investigations of human memory encoding and retrieval have revealed that multiple regions of parietal cortex contribute to memory. Recently, Gilmore, Nelson, and McDermott (2015) noted that a small set of regions manifests numerous empirical regularities surrounding memory and further that this set of regions forms a functional network. Gilmore et al. referred to this network, which consists of regions within lateral parietal cortex, mid-cingulate, and precuneus, as the parietal memory network (PMN).

One piece of evidence that the PMN reflects memorial processes is its consistent emergence in contrasts involving retrieval success (e.g., comparing hits on a recognition memory test to correctly-rejected lures). Indeed, recent meta-analyses (Kim, 2013; McDermott, Szpunar, & Christ, 2009; Nelson et al., 2010; Spaniol et al., 2009) have demonstrated these regions to be among the regions most consistently reflecting this pattern (Figure 1). Further, the regions tend to demonstrate “negative” subsequent memory effects (i.e., be less active for items subsequently recognized than those not subsequently recognized, Kim, 2011; Otten & Rugg, 2001). They also display an “encoding-retrieval flip” in that they deactivate for novel items (e.g., during an encoding task) and activate for familiar items (e.g., during a retrieval task) (Vannini, O'Brien, O'Keefe, Pihlajamaki, & Sperling, 2011).

Use of the term network is justified by the connectivity-based patterns shown by whole-brain parcellations of the brain using functional connectivity MRI (for a review see Power, Schlaggar, & Petersen, 2014). In short, participants lie awake and still, without direction with respect to cognition. At low frequencies (lower than those evoked by cognitive tasks) activity waxes and wanes, and there is coherent structure to this activity. Specifically, regions that tend to co-activate during directed tasks tend to exhibit synchronicity in these slow-wave, spontaneous fluctuations as well. This feature offers a data-driven way of identifying brain networks, or sets of regions that co-fluctuate spontaneously. Correlation at

rest is thought to emerge over a lifetime of co-activation during cognition (Wig, Schlaggar, & Petersen, 2011).

Using variations of this technique, many labs have begun to classify the network structure of the human brain. The PMN emerges from analyses of resting-state data (Doucet et al., 2011; Power et al., 2011; Smith et al., 2013; Yeo et al., 2011) and from related analyses from task-based connectivity (Shirer, Ryali, Rykhlevskaia, Menon, & Greicius, 2011), as demonstrated in Figure 1 (see also Gilmore et al. 2015). Given enough data, it can readily be identified within a single person (Laumann et al., 2015). Until recently, it was unappreciated as being a coherent network (and can, in coarse network estimates, appear as a part of the default mode network (Power et al., 2011), or frontoparietal control network (Yeo et al., 2011)).

In short, this newly-identified network plays a dynamic role in memory encoding and retrieval. In noting its importance for memory, Gilmore et al (2015) noted several outstanding questions regarding its functional properties. One question is the role that bottom-up and top-down attention play in modulating the activity. Does attention to the degree of oldness influence activity? Another question considered was the role of subjective experience in influencing activity, specifically in the domain of false memory. If participants encounter a lure (new item) on a recognition test but experience it as having been studied, will activity reflect the subjective experience of oldness or the objective situation of novelty (or an intermediate response)? This manuscript addresses these questions of how the network activates during subjectively-compelling false memories.

The method for examining this question was to use a robust method for eliciting false memories through lists of associated words. Specifically, the DRM procedure (Deese, 1959; Roediger & McDermott, 1995) was used; participants encoded a set of words that were highly associated meaningfully (e.g., bed, rest, awake) or through sound (beep, cheap, weep)

to one single, nonpresented word (e.g., sleep), which is highly associated to the presented list words and often referred to as the “critical lure”. This procedure elicits high probabilities of false recognition and false recall (McDermott, 1996), as reviewed by Gallo (2006). Again, the question of interest here centers on activation levels in the PMN for these subjectively-compelling false alarms to critical lures (e.g., sleep).

Method

Subjects

Subjects (N=21, 18 females, mean age 21.6, range 18-32) were recruited from the Washington University community in return for payment. Data from the encoding phase has been reported previously for 17 of the participants (McDermott, Petersen, Watson, & Ojemann, 2003); from that dataset (of N=20), 3 of those subjects did not have useable retrieval data and were replaced, and one additional participant was added.

All subjects reported being right-handed native speakers of English, having normal or corrected-to-normal vision, and lacking reportable neurological problems. Subjects provided informed consent in accordance with the guidelines set by the Washington University Human Studies Committee.

Materials and Presentation Parameters

Lists (72) of 16 words related to one another semantically (e.g., *bed, rest, awake*) or phonologically (e.g., *beep, cheap, weep*) served as stimuli. The phonologically-related words all rhymed. The median word length was 5 for both the semantic and phonological lists, and the median word frequency was 23 per million for the semantic lists and 13.5 per million for the phonological lists (Kucera & Francis, 1967).

The order of runs (or sessions) was as follows. Participants encoded one set of 12 lists in the first run (blocked design), then took a recognition test that spanned 2 runs (event-

related design). This cycle repeated twice, for a total of 3 encoding and 6 retrieval runs. Finally, 3 additional (non-tested) encoding runs took place.

As depicted in **Figure 2**, at the beginning of each block during encoding (i.e., each study list), a cue was displayed in yellow font ("Meaning" or "Rhyme") to inform subjects of the type of list they were about to see, and they were instructed to use the cue to help them focus on the relations among the upcoming words. Words were displayed quickly, such that each 16-word list was displayed in 10 seconds (approximately 560 ms/word with a 50 ms ISI). Following each block of words was a brief period (12.5 s), in which subjects were shown a crosshair and asked to fixate on it and await the next list. Participants were asked to attend closely to the relations among words within each list and were informed that memory tests would occur after some runs.

Data from the 6 runs of recognition test are reported here. Each trial spanned 2 TRs (approximately 5 s): The probe was displayed for 3500 ms, after which the screen was blank until the next trial. The, response deadline was 3800 ms after stimulus onset. Participants were asked to respond via buttonpress while the word was on the screen; after the 3800 ms response deadline, the software awaited the beginning of the subsequent TR, at which point the next trial occurred.

Across the recognition test phases (6 runs), a total of 252 stimuli were presented: 36 critical lures (18 of which corresponded to semantically-related lists and 18 to phonologically-related lists); 72 studied words (36 corresponding to semantic-related and 36 to phonologically-related lists); and 72 unrelated lures (i.e., words not systematically related to the study lists). Ordering of trial types was random and a fixation cross (0-5 s) introduced temporal jitter between trials to enable modeling of the BOLD signal. The studied words appearing on the test were arbitrarily drawn from throughout the lists.

Participants were instructed to respond via buttonpress whether each word shown was recognized from the prior study list (old) or was not studied (new) and to attempt to respond while the word was on the screen.

Scanning Procedures

Scans were obtained on a 1.5 Tesla Siemens Vision System (Erlangen, Germany) with a standard circularly-polarized head coil. A Power Macintosh computer (Apple, Cupertino, CA) and Psyscope software (Cohen, MacWhinney, Flatt, & Provost, 1993) displayed the visual stimuli. An LCD projector shielded with copper wire displayed stimuli on a screen placed at the head of the bore. Subjects viewed the screen via a mirror fastened to the head coil. A pillow and surgical tape minimized head movement. Headphones dampened scanner noise and enabled communication with subjects.

Structural images were acquired using a high-resolution sagittal MPRAGE sequence (1.25x1x1mm voxels). Functional images were collected with an asymmetric spin-echo-planar sequence sensitive to blood-oxygenation-level-dependent (BOLD) contrast (Kwong et al., 1992; Ogawa et al., 1992). In each functional run, 128 sets of 16 contiguous, 8mm-thick axial images (TR=2500 ms, 3.75 x 3.75 mm in-plane resolution) were acquired parallel to the anterior-posterior commissure plane; this procedure offered whole-brain coverage at a high signal-to-noise ratio (Conturo et al., 1996). Approximately 3 min elapsed between runs, during which time instructions were given to subjects over their headphones. The first 4 images of each run were not included in the functional analyses but were used to facilitate alignment of the functional data to the structural images.

Data Preprocessing

Preprocessing of the data for each subject included correction for intensity differences across odd- and even-numbered slices, interpolation to 3 x 3 x 3 mm voxels, temporal alignment to correct for slice-based within-trial differences in acquisition times, movement

correction within and across runs, and transformation into standardized atlas space (Talairach & Tournoux, 1988) via a linear warp (Snyder, 1996). Removal of the linear slope on a voxel-by-voxel basis corrected for frequency drift (Bandettini, Jesmanowicz, Wong, & Hyde, 1993), and whole brain normalization to a common mode of 1000 facilitated comparisons across subjects. Functional data were transformed to stereotaxic atlas space (Talairach and Tournoux 1988) by aligning each subjects' T1-weighted scan to a target T1-weighted template (711-2B) using a series of affine transforms (Michelon et al. 2003; Fox et al. 2005). Although analyses were conducted in 711-2B space, all coordinates reported have been transformed to MNI152 space using software written by Avi Snyder.

General linear model of the fMRI Data

The data were analyzed with general linear models (GLM) (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000) in which a canonical hemodynamic response function (specifically, a gamma function convolved with a boxcar function) was used to estimate the magnitude of response for each condition in each voxel, with an onset delay of 2 s and a duration of 3.5 s (trial length). Variations in onset of the hemodynamic response were accounted for by modeling 3 additional delays of 2 s each for each condition and using each condition's largest obtained parameter estimate.

Each subject's 6 recognition runs (99 MR frames each) were concatenated into a single time series for that subject. The GLMs included 3 regressors of interest: Hits, Critical False Alarms (to associated lures), and Correct Rejections (to unrelated lures)¹. All other trials (misses, trials with no responses, correctly-rejected critical lures, and false alarms to unrelated lures), which occurred too infrequently for reliably modeling, were binned together in a fourth category, which did not enter into subsequent analyses. In addition, a linear trend

¹ A preliminary whole-brain analysis coding hits and false alarms separately for semantically-related and phonologically-related lists showed no difference between the two list types (semantic or phonological) at retrieval, nor did that factor interact with the hit/false alarm dimension. As a result, reported analyses collapse across list type.

term (to account for signal drift) and a constant term (to model the baseline signal) were included as regressors of no interest for each run. Effects are described in terms of percent signal change (i.e., the signal magnitude divided by a constant term). All group-level analyses were performed in 711-2B atlas space, and a spherical smoothing kernel with a 6-mm FWHM was used to accommodate cross-subject variability.

A Priori Region-of-Interest (ROI) definition and statistical contrasts

A priori coordinates for PMN regions were derived from two prior meta-analyses of retrieval success effects. More specifically, the most significant region of left posterior inferior parietal lobule (pIPL), left precuneus (PCU), and left mid-cingulate cortex (MCC) were identified from an activation likelihood estimate of retrieval success effects in 15 recognition memory experiments (McDermott et al., 2009) and a fixed-effects analysis across 8 contrasts from 7 datasets (Nelson et al., 2010). We averaged the coordinates for each region across the two meta-analyses, and drew spherical ROIs (5mm radius) around each. These peak coordinates were converted to MNI152 using the same software that converted all other coordinates reported in this manuscript, described below. A p -value of .05 was adopted here (and for all inferential statistics throughout the manuscript).

Voxelwise Region-of-Interest (ROI) definition and statistical contrasts

For the voxelwise (whole-brain) analysis, an ANOVA was conducted on each 3mm isotropic voxel (one factor, condition, with three levels); the resulting statistical maps were averaged across people to create a group average map, which was multiple-comparison corrected to a whole-brain $p < .05$ by requiring $z > 3.0$ with at least 13 contiguous voxels; these parameters were derived from (McAvoy, Ollinger, & Buckner, 2001). An automated peak-search algorithm (peak_4dfp) written by Avi Snyder searched for the location of peaks in the unthresholded map and created ROIs around each peak. Peaks under 12 mm apart were consolidated via coordinate averaging. ROIs were then obtained by centering a 6-mm radius

sphere, masked by the multiple comparison corrected image, around the coordinates identified by the algorithm.

Analysis and Visualization Software

Image processing was done within FIDL, Washington University's in-house fMRI processing software (<http://www.nil.wustl.edu/~fidl>); this software is written in IDL (Research Systems Inc.). Statistical maps were projected onto the Conte69 surface of the human brain using Connectome Workbench software (Marcus et al., 2011). As there is no 1:1 correspondence between volumetric 711-2B voxels and Conte69 surface vertices, some smoothing of the data occurred on maps presented in Workbench, which reduced activations near the edge of clusters to a value below $z=3$. Z-values displayed in figures therefore are thresholded at a $|z|>1$, as this visually approximates the extent of activations observed in the volume data upon which the analyses were performed.

Results

Behavioral data

The proportion of studied words correctly recognized (i.e., the hit rate) was .69. This value approximated the false alarm rate for critical nonstudied words (.68). Both far exceeded the background false alarm rate to words unrelated to the studied words (.17).

More specifically, as can be seen in **Figure 3**, the hit rate for words presented in the semantically-related lists (.74) exceeded that for the phonologically-related lists (.63), a standard level-of-processing effect (Craik & Tulving, 1975), $t(20)=3.03$, $p<.007$. A similar effect occurred for the false alarm rates such that false alarms to words related to semantic lists (.79) were more likely than those for the phonological lists (.57), $t(20)=3.65$, $p<.001$ (as would be expected, Chan, McDermott, Watson, & Gallo, 2005). Neither hit rate differed significantly from its corresponding false alarm rate, $t(20)=1.39$, $p<.18$ and $t(20)=-1.90$, $p<.07$ for semantic and phonological lists, respectively. The number of trials per participant

per condition ranged from 17-32 and 12-31 for hits to semantic and phonological lists, respectively; from 6-18 and 4-17 for critical false alarms to semantic and phonological lists; and from 30-72 for correctly-rejected unrelated lures. When collapsing across list type (semantic and phonological, as was done for the brain imaging analyses), the range of trial numbers per participant was 17-32 for false alarms to critical lures and 29-61 for hits; in short, there were adequate numbers of trials per person for estimating the BOLD signal for each of the conditions in the general linear models.

On average, correctly-rejected unrelated lures had longer response times (1590 ms) than did hits (1387 ms) or false alarms to critical nonpresented words (1403 ms), which did not differ. Inferential statistics support this conclusion: $t(20)=3.47$, $p<.002$ and $t(20)=2.09$, $p<.02$ for the hit-correct reject and false alarm-correct reject comparisons, respectively, whereas $t(20)=-.5$, $p<.6$ for the hit-false alarm comparison.

A-priori ROIs in the Parietal Memory Network

The *a-priori* ROIs can be seen in **Figure 4** (turquoise spheres, 5 mm radius) along with the corresponding activation magnitudes for the three conditions. The condition (hit, critical FA, correctly-rejected lure) main effect was significant for each ROI. Followup *t*-tests indicated a conclusion that is apparent from Figure 4: Hits and critical false alarms activated similarly in all regions, and in all regions they showed more activation than correctly-rejected unrelated lures (CR), which tended to hover around baseline.

Specifically, the hit-false alarm *t*-tests fell short of significance, $t(20)=.21$, -1.2 , and $-.13$ for IPL PCU and MCC, respectively ($p=.83$, $.24$, and $.89$). Robust differences were seen in the same regions for the hit-correct rejection contrast, $t(20)=4.40$, 3.86 , and 3.15 , respectively ($p=.0003$, $.0010$, and $.0005$) and for the hit-critical false alarm contrast, $t(20)=5.59$, 4.45 , and 3.73 , $p=.00002$, $.0002$, and $.003$.

Voxelwise analysis

Here we consider the whole-brain results of the one-way ANOVA (with 3 levels, corresponding to the activation magnitudes for the three conditions). The resulting statistical map can be seen in **Figure 5** (top left, main effect of condition), where it can be seen that regions throughout the brain exhibited differential activity as a function of the 3 conditions. The peak coordinates for each region emerging from the peak-search algorithm can be seen in **Table 1**. Also reported are the activation magnitudes for each condition for each region (emerging from the peak_4dfp procedure described above) and the follow-up *t*-test values, showing which regions demonstrated which effects.

Table 1 shows the similarities in activation patterns for hits and false alarms and how most of the differences were driven by greater activation for those two conditions than the third (i.e., correct rejections, as can be seen by the magnitudes and by the positive *t*-values for the contrasts). This pattern can also be seen in the maps of *t*-tests (masked by the ANOVA main effect image) appearing in **Figure 5** (lateral and medial surfaces) and **Figure 6** (dorsal surfaces, at the bottom of the figure). Also seen in Figure 6 is the strong correspondence between the *a priori* ROIs (turquoise spheres) and the results of the *t*-contrasts. In addition, the spheres are projected to the contralateral surface to demonstrate the correspondence in activations within right precuneus and right posterior IPL/dorsal angular gyrus.

A final way of demonstrating the strong correspondence of the foci from the ANOVA and the *a priori* regions analyzed above is in **Figure 7**. Specifically, the ANOVA revealed a focus around the precuneus (-4,-67,30), one in the MCC (-3,-31,30), and one in LpIPL/dAG (-40,-59,37). The Euclidean distances from the *a priori* peaks were 6, 6.4, and 5.2 mm, respectively. Further, the response magnitudes underlying the significant ANOVA can be seen in the bar graphs: hits and false alarms activated the network similarly and did so more than correct rejections.

We now consider regions outside the PMN that demonstrated this similarity for hits and false alarms (but differing for correct rejections). Among the activations demonstrating this pattern were regions associated with several control networks (Figures 5 and 6), specifically left insula and medial frontal activations within the cingulo-opercular and salience networks; bilateral inferior parietal sulcus, left middle frontal gyrus, and left anterior frontal cortex (in or near the frontoparietal network). Further, bilateral angular gyrus (more pronounced on the left) and posterior cingulate within the default mode network exhibited this pattern, and (as will be discussed), this network has also been suggested to show properties of control networks.

Turning now to difference outside of networks associated with cognitive control, we see evidence of greater activity for correct rejections than the other two conditions in visual cortex (see Fig 5; Table 1, MNI coordinates -15, -91, -6); further, this visual region demonstrated more activity for hits than for critical false alarms. This region often demonstrates visual priming of words, a point we will consider in the General Discussion.

The direct contrast between Hits and Critical False Alarms is of interest. As is typically seen (Dennis, Bowman, & Turney, 2015), there were not many differences. Of those that did occur (6 ROIs emerging from the ANOVA) all showed greater activity for hits than for false alarms (see Table 1) and were predominantly left-lateralized, except for activations within the intraparietal sulcus (IPS) in the dorsal attention network, which were bilateral. Left supramarginal gyrus (cingulo-opercular network) showed this pattern. Also left ventromedial occipitotemporal cortex, and hand/somatomotor cortex were more active for hits than false alarms. No regions from the main effect ROI creation demonstrated greater activation for false alarms than hits (Table 1), although small clusters of voxels showing this pattern can be seen in the masked *t*-test of this contrast (Figure 5, top right, blue).

Discussion

The data reported here inform understanding of a recently-discovered brain network, the parietal memory network, by showing that some lures on a recognition test activate more than others, depending on the subjective experience of “oldness” accompanying the lure. In the case of compelling false alarms, such as those in the DRM procedure used here, the “oldness” signal can be as great as that for studied words (much like the phenomenological experience for the two types of items is extremely similar, Roediger & McDermott, 1995).

These data also add to the literature showing that false recognition elicited by the DRM paradigm tends to produce activity very similar to hits (e.g., Cabeza, Rao, Wagner, Mayer, & Schacter, 2001; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997; Schacter et al., 1996), as recently reviewed by Dennis et al. (2015).

Differences between True and False Recognition

The differences between hits and false alarms showed patterns opposite of what one might expect. First, visual priming (repetition suppression) occurred such that hits (old words) activated visual cortex less than new words (correctly-rejected lures). This pattern is often attributed to the visual system having an easier time re-reading previously-read words (Schacter & Buckner, 1998) and such perceptual priming is thought to be stimulus-specific (Roediger & McDermott, 1993). In this case, however, even more such priming was seen for the critical false alarms, which demonstrated more attenuation than hits. This finding is curious and impressive. It also conflicts somewhat with the behavioral priming literature on DRM lures, which indicate that although there is some priming on implicit memory tests, it is less than for the actually-studied words (McDermott, 1997; McKone & Murphy, 2000).

A second counterintuitive finding is that regions demonstrating differences between hits and critical false alarms were generally *less* active for false alarms than for hits. Some of these regions appear to be in control networks (e.g., the left dorsal frontal region falls on the border of the frontoparietal and default networks; the bilateral IPS regions bridge

frontoparietal and dorsal attention networks). To the extent that there was any uncertainty about the critical false alarms, one would expect greater cognitive control (and therefore greater activity in control regions) to be manifested during the false memory condition; and although confidence in the false recognition tends to be strong, these false alarms are not held with the same confidence level as hits (Roediger & McDermott, 1995). Again, the behavioral literature might lead one to expect the opposite pattern from what was obtained. Perhaps the associative priming that leads to these robust false memories, elicits such fluency with the nonpresented critical lures that they exhibit this pattern. One would like to know about correctly-rejected critical lures, for which control regions may have been very active (to overcome the strong tendency for false alarms), but there were not enough trials per subject to model these reliably.

The Parietal Memory Network

The primary question addressed here concerns the activity within the newly-identified parietal memory network. This network clearly showed that the stimulus history (objectively old or new) is not the driving feature of activation levels; rather, the subjective status appears to drive activity. In addition to the three left-lateralized ROIs examined here, there was some suggestion that contralateral regions also showed this pattern (e.g., see Figure 6). The conditions under which the network is manifested bilaterally (e.g., the role of stimulus type) is an issue that deserves attention (Gilmore et al., 2015) but cannot be answered with the current dataset.

The behavior of item classes not examined in this analysis is also of interest. The low number of false alarms to unrelated lures in this dataset is typical of most datasets and demonstrates that participants understood the task and followed instructions. If, however, there had been enough items to confidently model the responses it would be nice to know how they might activate the PMN. A speculative answer is that we may see weak activation,

intermediate between strong, confident memories (e.g., hits, critical false alarms) and correct rejections; indeed, a pattern similar to that within the lateral parietal region has been reported by Wheeler and Buckner (2003). A similar question arises for misses (objectively old but subjectively novel) and correctly-rejected critical lures.

The roles of confidence level and recollection (as opposed to familiarity) are also of great interest in understanding the PMN. One common finding in the literature is that the false alarms in the DRM procedure tend to elicit high levels of “remember” responses when the remember/know procedure is used (Gardiner, 1988; Tulving, 1985). Although the procedure was not used in the present experiment (nor does it offer a direct window onto recollection and familiarity) it is safe to assume that many of the false memories would have been classified as remember responses. Does this finding inform the functional role of the PMN? At first glance, it might seem to be in conflict with the suggestion of Gilmore et al that familiarity (or attention to familiarity) drives activation in these regions. Generally, familiarity is thought to underlie “know” responses (not remember). However, familiarity is extremely difficult to isolate (Yonelinas, Otten, Shaw, & Rugg, 2005), and there would seem to be at least a reasonable possibility that familiarity underlies remember responses as much or more than know responses. The contributions of recollection, familiarity, and the salience of both of these processes await further research.

A final unresolved issue that deserves mention is the relation between the PMN, the default mode network, and the frontoparietal control network. The regions of the PMN are adjacent to those within default and frontoparietal networks (Gilmore et al 2015). Specifically, the foci of the PMN tend to lie at the convergence of the frontoparietal and default networks in the inferior parietal lobule and adjacent to default network in mid-cingulate and precuneus. Further, the PMN shares similarities with both networks (e.g. deactivation during initial encounter with novel stimuli like the default mode network and

modulation on the basis of retrieval success like the frontoparietal network). Power et al (2011) note that the default mode demonstrates processing properties much like control networks and that the frontoparietal network appears to have subnetwork structure (e.g., the PMN being highly associated but separable from this network in resting state parcellations). All of this leads to the question of whether the PMN may also be attuned to the degree of attentional focus given to a stimulus (in addition to the perceived novelty or oldness of the stimulus).

Relevance of the Attention to Memory Model

In the neuropsychological literature, lateral parietal cortex has been more the focus of attention research than memory research, leading researchers to theorize about whether the role of parietal cortex in memory retrieval might be underlain by attentional contributions. One prominent framework for considering this question is the Attention to Memory (AtoM) model (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; Ciaramelli, Grady, & Moscovitch, 2008). This model posits that the parietal contribution to memory retrieval can be explained largely in terms of the dichotomy between top-down orientation of attention (which is underlain by dorsal parietal cortex) and by bottom-up attention (underlain by ventral parietal cortex, Corbetta & Shulman, 2002). We find some general agreement with predictions derived from this framework, but our data also suggest a shortcoming.

The relative similarity of hits and critical false alarms in lateral parietal cortex is in general agreement with what the AtoM Model might suggest. That is, if the general recollective experience of hits and critical false alarms is highly similar, as prior research has suggested (e.g., Roediger & McDermott, 1995), then one would expect few differences in regions underlying attentional processing. Specifically, the angular gyrus or other ventral parietal regions contributing to bottom-up processing might exhibit similar activation, as was observed here (Figure 5, top right). With respect to dorsal parietal regions, one would

similarly predict few differences in top-down control. With the exception of IPS, no significant differences between hits and critical false alarms were observed in dorsal parietal regions.

A complication arises in that the AtoM Model explicitly associates the IPS with dorsal parietal regions, and yet the IPS was one of the few locations where activity clearly differed between hits and critical false alarms. This result is difficult to reconcile with the model, because proponents of AtoM have stressed a functional dichotomy in parietal cortex, and argued against the existence of spatially adjacent but functionally distinct regions (i.e., against a “fractionation” view, see Cabeza, Ciaramelli, & Moscovitch 2012a; for further discussion see Nelson, McDermott, & Petersen, 2012; and Cabeza et al., 2012b). That is, if IPS exhibits greater activity for hits, the prediction from the AtoM Model would be that all/most of dorsal parietal cortex should exhibit a similar pattern. If, however, one allows that parietal cortex is more of a functional mosaic than functional dichotomy (Nelson, McDermott, Wig, Schlaggar, & Petersen, 2013), one can continue to accommodate the general lack of differences between hits and critical false alarms (reverting to a region-by-region, rather than dorsal-ventral basis) alongside a difference within IPS, thereby recognizing that regions where differences appear are contribute a dimension of processing that differs hits and critical false alarms. In short, our view is that a dorsal/ventral distinction with respect to the role of parietal cortex in memory retrieval oversimplifies the complex functional landscape of this area of cortex.

Final Considerations and Conclusion

One common concern with fMRI studies, especially those in which there is a prototypical pattern of results across all regions (e.g., hits > correct rejections but not many examples of the reverse) is that reaction time might be driving the effects (e.g., longer responses leading to greater levels of activity). In the present study, the condition with the

least degree of activation (correct rejections) was associated with the longest response latency. In that respect, we can be fairly confident that the data are not simply reflecting response times.

In summary, this report demonstrates that a brain network highly sensitive to the recent prior history with items is more attune with the subjective experience of whether the items *seems* old or familiar, not the objective status of that experience.

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References

- Bandettini, P. A., Jesmanowicz, A., Wong, E. C., & Hyde, J. S. (1993). Processing strategies for time-course data sets in functional MRI of the human brain. *Magnetic Resonance in Medicine*, 30, 161-173.
- Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012a). Cognitive contributions of the ventral parietal cortex: an integrative theoretical account. *Trends In Cognitive Science*, 16(6), 338-352.
- Cabeza, R., Ciaramelli, E., & Moscovitch, M. (2012b). Response to Nelson et al.: ventral parietal subdivisions are not incompatible with an overarching function. *Trends In Cognitive Science*, 16, 400-401.
- Cabeza, R., Ciaramelli, E., Olson, I. R., & Moscovitch, M. (2008). The parietal cortex and episodic memory: An attentional account. *Nature Reviews Neuroscience*, 9, 613-625.
- Cabeza, R., Rao, S. M., Wagner, A. D., Mayer, A. R., & Schacter, D. L. (2001). Can medial temporal lobe regions distinguish true from false? An event-related functional MRI study of veridical and illusory recognition memory. *Proceedings of the National Academy of Science USA*, 98(8), 4805-4810.
- Chan, J. C. K., McDermott, K. B., Watson, J. M., & Gallo, D. A. (2005). The importance of material-processing interactions in inducing false memories. *Memory & Cognition*, 33, 389-395.
- Ciaramelli, E., Grady, C. L., & Moscovitch, M. (2008). Top-down and bottom-up attention to memory: A hypothesis (AtoM) on the role of the posterior parietal cortex in memory retrieval. *Neuropsychologia*, 46, 1828-1851.
- Cohen, J. D., MacWhinney, B., Flatt, M., & Provost, J. (1993). PsyScope: a new graphic interactive environment for designing psychology experiments. *Behavior Research Methods, Instruments, & Computers*, 25, 257-271.
- Conturo, T. E., McKinstry, R. C., Akbudak, E., Snyder, A. Z., Yang, T. Z., & Raichle, M. E. (1996). Sensitivity optimization and experimental design in functional magnetic resonance imaging. *Society for Neuroscience Abstracts*, 22, 7.
- Corbetta, M., & Shulman, G. L. (2002). Control of Goal-directed and Stimulus-driven Attention in the Brain. *Nature Reviews Neuroscience*, 3, 201-216.
- Craik, F. I. M., & Tulving, E. (1975). Depth of processing and the retention of words in episodic memory. *Journal of Experimental Psychology: General*, 104, 268-294.
- Deese, J. (1959). On the prediction of occurrence of particular verbal intrusions in the immediate recall. *Journal of Experimental Psychology*, 58, 17-22.
- Dennis, N. A., Bowman, C. R., & Turney, I. C. (2015). Functional Neuroimaging of False Memories. In D. R. Addis, M. Barense, & A. Duarte (Eds.), *The Wiley Handbook of the Cognitive Neuroscience of Memory*: Wiley.
- Doucet, G., Naveau, M., Petit, L., Delcroix, N., Zago, L., Crivello, F., Jobard, G., Tzourio-Mazoyer, N., Mazoyer, B., Mellet, E., & Joliot, J. (2011). Brain activity at rest: a multiscale hierarchical functional organization. *Journal of Neurophysiology*, 105, 2753-2763.
- Gallo, D. A. (2006). *Associative illusions of memory: False memory research in DRM and related tasks*. NY: Psychology Press.
- Gardiner, J. M. (1988). Functional aspects of recollective experience. *Memory and Cognition*, 16, 309-313.
- Gilmore, A. W., Nelson, D. L., & McDermott, K. B. (2015). A parietal memory network revealed by multiple MRI methods. *Trends in Cognitive Sciences*, 19, 534-543.

- Kim, H. (2011). Neural activity that predicts subsequent memory and forgetting: A meta-analysis of 74 fMRI studies. *Neuroimage*, 54, 2446–2461.
- Kim, H. (2013). Differential neural activity in the recognition of old versus new events: An Activation Likelihood Estimation Meta-Analysis. *Human Brain Mapping*, 34, 814–836.
- Kucera, H., & Francis, W. N. (1967). *Computational analysis of present-day American English*. Providence, RI: Brown University Press.
- Kwong, K. K., Belliveau, J. W., Chesler, D. A., Goldberg, I. E., Weisskoff, R. M., Poncelet, B. P., Kennedy, D. N., Hoppel, B. E., Cohen, M. S., & Turner, R. (1992). Dynamic magnetic resonance imaging of human brain activity during primary sensory stimulation. *Proceedings of the National Academy of Sciences USA*, 89(12), 5675–5679.
- Laumann, T. O., Gordon, E. M., Adeyemo, B., Snyder, A. Z., Joo, S. J., Chen, M.-Y., McDermott, K. B., Nelson, S. M., Dosenbach, N. U. F., Schlaggar, B. L., Mumford, J. A., Poldrack, R. A., & Petersen, S. E. (2015). Functional System and Areal Organization of a Highly Sampled Individual Human Brain. *Neuron*, 87(3), 657–670. doi:doi:10.1016/j.neuron.2015.06.037
- Marcus, D. S., Harwell, J., Olsen, T., Hodge, M., Glasser, M. F., Prior, F., Jenkinson, M., Laumann, T. O., Crutts, S. W., & Van Essen, D. C. (2011). Informatics and data mining: tools and strategies for the Human Connectome Project. *Frontiers in Neuroinformatics*, 5(4). doi:<http://dx.doi.org/10.3389/fninf.2011.00004>
- McAvoy, M. P., Ollinger, J. M., & Buckner, R. L. (2001). Cluster size thresholds for assessment of significant activation in fMRI. *Neuroimage*, 13, 198.
- McDermott, K. B. (1996). The persistence of false memories in list recall. *Journal of Memory and Language*, 35(2), 212–230.
- McDermott, K. B. (1997). Priming on perceptual implicit memory tests can be achieved through presentation of associates. *Psychonomic Bulletin & Review*, 4(4), 582–586.
- McDermott, K. B., Petersen, S. E., Watson, J. M., & Ojemann, J. G. (2003). A method for identifying regions preferentially activated by semantic and phonological processing. *Neuropsychologia*, 41, 293–303.
- McDermott, K. B., Szpunar, K. K., & Christ, S. E. (2009). Laboratory-based and autobiographical retrieval tasks differ substantially in their neural substrates. *Neuropsychologia*, 47, 2290–2298. doi:doi:10.1016/j.neuropsychologia.2008.12.025
- McKone, E., & Murphy, B. (2000). Implicit false memory: Effects of modality and multiple study presentations on long-lived semantic priming. *Journal of Memory & Language*, 43, 89–109.
- Miezin, F. M., Maccotta, L., Ollinger, J. M., Petersen, S. E., & Buckner, R. L. (2000). Characterizing the hemodynamic response: effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. *Neuroimage*, 11, 735–759.
- Nelson, S. M., Cohen, A. L., Power, J. D., Wig, G. S., Miezin, F. M., Wheeler, M. A., Velanova, K., Donaldson, D. I., Phillips, J. S., Schlaggar, B. L., & Petersen, S. E. (2010). A parcellation scheme for human left lateral parietal cortex. *Neuron*, 67, 156–170.
- Nelson, S. M., McDermott, K. B., & Petersen, S. E. (2012). In favor of a ‘fractionation’ view of ventral parietal cortex: comment on Cabeza et al. *Trends In Cognitive Science*, 16(8), 399–400.

- Nelson, S. M., McDermott, K. B., Wig, G. S., Schlaggar, B. L., & Petersen, S. E. (2013). The Critical Roles of Localization and Physiology for Understanding Parietal Contributions to Memory Retrieval. *The Neuroscientist*, 19(6), 578-591.
- Ogawa, S., Tank, D. W., Menon, R., Ellermann, J. M., Kim, S. G., Merkle, H., & Ugurbil, K. (1992). Intrinsic signal changes accompanying sensory stimulation: functional brain mapping with magnetic resonance imaging. *Proceedings of the National Academy of Sciences USA*, 89(13), 5951-5955.
- Otten, L. J., & Rugg, M. D. (2001). When more means less: Neural activity related to unsuccessful memory encoding. *Current Biology*, 11, 1528-1530.
- Power, J. D., Cohen, A. L., Nelson, S. M., Wig, G. S., Barnes, K. A., Church, J. A., Vogel, A. C., Laumann, T. O., Miezin, F. M., Schlaggar, B. L., & Petersen, S. E. (2011). Functional network organization of the human brain. *Neuron*, 72(4), 665-678. doi:10.1016/j.neuron.2011.09.006
- Power, J. D., Schlaggar, B. L., & Petersen, S. E. (2014). Studying brain organization via spontaneous fMRI signal. *Neuron*, 84(4), 681-696. doi:10.1016/j.neuron.2014.09.007
- Roediger, H. L., & McDermott, K. B. (1993). Implicit memory in normal human subjects. In F. Boller & J. Grafman (Eds.), *Handbook of Neuropsychology* (Vol. 8, pp. 63-131). Amsterdam: Elsevier.
- Roediger, H. L., & McDermott, K. B. (1995). Creating false memories: Remembering words not presented in lists. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 21(4), 803-814.
- Schacter, D. L., & Buckner, R. L. (1998). On the relations among priming, conscious recollection, and intentional retrieval: evidence from neuroimaging research. *Neurobiol Learn Mem*, 70(1-2), 284-303.
- Schacter, D. L., Buckner, R. L., Koutstaal, W., Dale, A. M., & Rosen, B. R. (1997). Late onset of anterior prefrontal activity during true and false recognition: An event-related fMRI study. *Neuroimage*, 6, 259-269.
- Schacter, D. L., Reiman, E., Curran, T., Yun, L. S., Bandy, D., McDermott, K. B., & Roediger, H. L. (1996). Neuroanatomical correlates of veridical and illusory recognition memory: evidence from positron emission tomography. *Neuron*, 17(2), 267-274.
- Shirer, W. R., Ryali, S., Rykhlevskaia, E., Menon, V., & Greicius, M. D. (2011). Decoding subject-driven cognitive states with whole-brain connectivity patterns. *Cerebral Cortex*.
- Smith, S. M., Vidaurre, D., Beckmann, C. F., Glasser, M. F., Jenkinson, M., Miller, K. L., Nichols, T. E., Robinson, E. C., Salimi-Khorshidi, G., Wooldrich, M. W., Barch, D. M., Ugurbil, K., & Van Essen, D. C. (2013). Functional connectomics from resting-state fMRI. *Trends in Cognitive Sciences*, 17(12), 666-682.
- Snyder, A. Z. (1996). Difference image versus ratio image error function forms in PET-PET realignment. In D. Bailey & T. Jones (Eds.), *Qualifications of Brain Function Using PET* (pp. 131-137). San Diego, CA: Academic Press.
- Spaniol, J., Davidson, P. S. R., Kim, A. S. N., Han, H., Moscovitch, M., & Grady, C. L. (2009). Event-related fMRI studies of episodic encoding and retrieval: Meta-analyses using activation likelihood estimation. *Neuropsychologia*, 1765-1779.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. NY: Thieme.
- Tulving, E. (1985). Memory and consciousness. *Canadian Psychologist*, 26, 1-12.

- Vannini, P., O'Brien, J., O'Keefe, K., Pihlajamaki, M., & Sperling, R. A. (2011). What Goes Down Must Come Up: Role of the Posteromedial Cortices in Encoding and Retrieval. *Cerebral Cortex*, 22, 22-34.
- Wheeler, M. E., & Buckner, R. L. (2003). Functional dissociation among components of remembering: Control, perceived oldness, and content. *The Journal of Neuroscience*, 23(9), 3869-3880.
- Wig, G. S., Schlaggar, B. L., & Petersen, S. E. (2011). Concepts and principles in the analysis of brain networks. *Annals of the New York Academy of Sciences, Special Issue: The Year in Cognitive Neuroscience*, 1224, 126-146.
- Yeo, B. T., Krienen, F., Sepulcre, J., Sabuncu, M. R., Lashkari, D., Hollinshead, M., Roffman, J. L., Smoller, J. W., Zollei, L., Polimeni, J. R., Fishl, B., Liu, H., & Buckner, R. L. (2011). The organization of the human cerebral cortex estimated by intrinsic functional connectivity. *Journal of Neurophysiology*, 106, 112501165.
- Yonelinas, A. P., Otten, L. J., Shaw, K. N., & Rugg, M. D. (2005). Separating the brain regions involved in recollection and familiarity in recognition memory. *The Journal of Neuroscience*, 25(11), 3002-3008.

Table 1. Peak activation loci resulting from an analysis of variance on the activation magnitudes for hits, critical false alarms, and correctly-rejected unrelated lures. Bold t -values are significant, $p < .05$.

Region label	MNI coordinates			Bold signal change (%)			$t(20)$ -statistic		
	x	y	z	Hit	FA	CR	Hit-CR	FA-CR	Hit-FA
<i><u>Putative PMN ROIs</u></i>									
Left Mid-Cingulate Cortex	-3	-31	30	0.13	0.13	-0.02	4.95	5.31	0.03
Left Inferior Parietal Lobule	-40	-59	37	0.35	0.31	0.13	5.55	5.73	1.33
Right Inferior Parietal Lobule	37	-59	41	0.23	0.20	0.06	4.89	4.48	1.37
Left Precuneus	-4	-67	30	0.09	0.10	-0.08	5.29	6.23	-0.31
<i><u>Other ROIs</u></i>									
Left Anterior Prefrontal Cortex	-30	48	11	0.23	0.23	0.02	4.70	3.60	-0.06
Left Inferior Frontal Gyrus	-36	39	4	0.21	0.24	0.04	5.77	6.54	-1.01
Left Middle Frontal Gyrus	-19	34	38	-0.04	-0.04	-0.16	5.25	5.54	0.02
Left Middle Frontal Gyrus	-32	9	48	0.04	0.04	-.11	4.28	4.30	0.21
Anterior Cingulate Cortex	-4	32	18	0.01	-0.02	-0.13	4.40	4.77	0.93
Anterior Cingulate Cortex	-6	28	37	0.18	0.18	-0.01	4.92	5.64	0.02
Left Pre-Supp. Motor Area	-5	17	44	0.40	0.42	0.22	6.50	5.17	-0.43
Left Anterior Insula	-35	13	0	0.35	0.28	0.16	6.51	2.89	1.32
Left Superior Frontal Sulcus	-26	12	51	-0.02	-0.06	-0.20	5.07	2.93	1.22
Left Putamen	-28	6	-3	0.19	0.20	0.05	5.51	5.16	-0.61
Left Middle Frontal Gyrus	-34	4	42	0.21	0.15	0.03	7.80	5.91	1.85
Left Frontal Eye Fields	-22	3	46	0.13	0.07	0.01	5.27	2.63	2.58
Right Thalamus	8	-2	8	0.36	0.35	0.13	6.23	4.30	0.14
Right Thalamus	5	-10	10	0.34	0.33	0.11	4.60	4.27	0.13
Left Thalamus	-9	-3	10	0.34	0.31	0.13	5.96	4.81	0.63
Left Thalamus	-4	-11	10	0.38	0.39	0.16	4.41	5.60	-0.14
Left Supp. Motor Area	-9	-13	54	0.26	0.21	0.31	-4.22	-5.68	3.60
Left Premotor Cortex	-59	-22	37	0.10	0.07	0.43	-4.58	-3.99	0.44
Left Middle Temporal Gyrus	-53	-42	-3	0.16	0.13	-0.04	6.34	4.14	0.63

Left Posterior Cingulate Cortex	-4	-47	29	-0.12	-0.08	-0.22	3.43	5.01	-1.66
Right Intraparietal Sulcus	39	-50	46	0.15	0.08	0.01	5.15	2.57	3.66
Right Posterior Cingulate Cortex	9	-55	31	-0.15	-0.13	-0.24	4.91	6.05	-0.67
Left Angular Gyrus	44	-60	32	0.00	-0.01	-0.20	6.01	7.17	0.23
Left Intraparietal Sulcus	-34	-64	40	0.52	0.49	0.23	5.85	7.19	0.68
Right Intraparietal Sulcus	32	-66	36	0.23	0.20	0.05	4.95	4.26	1.31
Right Cerebellum	32	-66	-34	0.20	0.21	0.08	6.10	4.31	-0.25
Left Occipital Cortex	-33	-72	-12	0.41	0.29	0.43	-1.04	-4.08	4.06
Left Occipital Cortex	-20	-88	-10	0.40	0.32	0.46	-3.92	-5.66	4.60
Left Occipital Cortex	-15	-91	-6	0.27	0.18	0.34	-3.60	-3.95	2.85
Right Occipital Cortex	20	-91	-6	0.35	0.27	0.42	-2.51	-5.77	2.59
Left Primary Visual Cortex	-9	-100	-8	0.35	0.18	0.42	-1.48	-3.39	2.60

Figure Captions

Figure 1. The parietal memory network emerges from task-based meta-analyses of human memory retrieval (left panel) and connectivity-based network descriptions of the human brain (right panel). Specifically, the network is comprised of regions within the precuneus (PCU), mid-cingulate cortex (MCC) and the posterior inferior parietal lobule/dorsal angular gyrus (pIPL/dAG). . Task-based meta-analyses are adapted from McDermott et al (2009) and Nelson et al (2010), top and bottom, respectively. Connectivity data are from the Human Connectome Project (2013) and Shirer et al (2012), top and bottom, respectively. Figure adapted, with permission, from Gilmore et al (2015).

Figure 2. Schematic of the experimental procedures. During encoding, 16 words/list were presented quickly (560 ms/word) in a blocked design; prior to each list a cue (meaning or rhyme) instructed participants regarding the nature of relations among list members and how to best direct their attention (to the semantic or phonological relations). For the recognition test, words were presented for 3.5 sec each, and participants pressed a button to indicate old or new as a response. An event-related design was used, with with the interstimulus interval (ISI) jittered in time (0-5 sec) between test trials. For study and test, all stimuli were presented as white (or yellow, in the case of the cue) font on black background but are depicted on white background for figure clarity.

Figure 3. Mean probability of an “old” (or “studied”) response on the recognition test as a function of word type. For previously-studied words (i.e., hits, shown in green), participants were slightly more likely to recognize words from the semantically-related lists. A similar pattern was seen for the critical lures, such that false alarms to those items were more common for semantically-related than phonologically-related lists. Critical false alarms were very common, occurring about as often as hits. Participants did not endorse all items as having been

studied, however: False alarms to lures not systematically related to the studied words (unrelated lures, in grey) were infrequent. Error bars represent standard error of the mean.

Figure 4. The Parietal Memory Network responds equivalently for false alarms as for hits on the recognition test. In turquoise are spheres (5mm radius) centered on the 3 *a-priori* ROIs constituting the PMN. The percent signal change of the BOLD response is plotted for hits, for critical false alarms, and for correctly-rejected lures. In all regions, words receiving “yes” (or “old”) responses activated more than “no” (“new”) responses, regardless of the objective status of the word. Error bars represent standard error of the mean.

Figure 5. Analysis of variance (ANOVA) map projected to the surface showing regions that differentially activated for the 3 conditions of interest (top left). Follow-up *t*-tests inform understanding of the main effect and demonstrate which conditions differed and in what direction; all *t*-tests are masked by the main effect of condition.

Figure 6. Whole-brain *t*-tests (masked by the main effect map). The turquoise spheres are the *a priori* ROIs (left hemisphere) and their contralateral projections (right hemisphere) to demonstrate close correspondence in the contrasts and suggestions of bilaterality for two of the three regions.

Figure 7. The main effect of condition and activation magnitudes underlying the map for the closest 3 ROIs to the *a priori* ROIs. Again, the subjective experience of oldness was key to the degree of activation, not the objective oldness; hits and false alarms activated similarly in the positive direction whereas correctly-rejected lures hovered closer to baseline.

Figure1

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