Published in final edited form as:

Neuropsychologia. 2013 May ; 51(6): 1061–1076. doi:10.1016/j.neuropsychologia.2013.02.018.

Unexpected novelty and familiarity orienting responses in lateral parietal cortex during recognition judgment

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Abstract

The role of lateral parietal cortex during recognition memory is heavily debated. We examined parietal activation during an Explicit Memory Cueing recognition paradigm that biases participants towards expecting novel or familiar stimuli on a trial-by-trial basis using anticipatory cues (“Likely Old”, “Likely New”), compared to trials with neutral cues (“????”). Three qualitatively distinct patterns were observed in the left lateral parietal cortex. An unexpected novelty response occurred in left anterior intraparietal cortex (IPS)/post-central gyrus (PoCG) in which greater activation was observed for new versus old materials following the “Likely Old” cue, but not following the “Likely New” cue. In contrast, anterior angular gyrus demonstrated an unexpected familiarity response with greater activation for old versus new materials following the “Likely New” cue, but not the “Likely Old” cue. Thus these two regions demonstrated increased responses that were selective for either new or old materials respectively, but only when they were unexpected. In contrast, a mid IPS area demonstrated greater response for whichever class of memoranda was unanticipated given the cue condition (an unexpected memory response). Analogous response patterns in regions outside of parietal cortex, and the results of a resting state connectivity analysis, suggested these three response patterns were associated with visuo-spatial orienting following unexpected novelty, source monitoring operations following unexpected familiarity, and general executive control processes following violated expectations. These findings support a Memory Orienting Model of the left lateral parietal cortex in which the region is linked to the investigation of unexpected novelty or familiarity in the environment.

Keywords

episodic memory; parietal cortex; prefrontal cortex; decision biasing; external cues

Introduction

The parietal lobe, particularly the posterior parietal cortex (PPC) has recently become the focus of a great deal of attention from memory researchers. This interest arose because the PPC is frequently activated in neuroimaging studies of recognition memory despite its more

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established role in visuo-spatial attention. However, parietal lesions are not historically linked with recognition memory impairment nor do recent neuropsychological investigations specifically examining basic recognition memory following parietal lesion suggest a discernible accuracy impairment memory, despite using tasks quite similar to those shown to activate lateral parietal areas during fMRI research (Ally, Simons, McKeever, Peers, & Budson, 2008; Ciaramelli, Grady, Levine, Ween, & Moscovitch, 2010; Dobbins, Jaeger, Studer, & Simons, 2012; Simons, Peers, Mazuz, Berryhill, & Olson, 2010). The inconsistency between the brain imaging and neuropsychological findings has continued to pique interest in the functional significance (if any) of the prominent activations seen in this region during recognition memory judgments.

In considering putative functional roles for the PPC, Wagner, Shannon, Kahn and Buckner(2005) reviewed neuroimaging studies that found PPC activation and noted that while the PPC tends to show an old-new effect (greater activity at retrieval for previously studied materials than previously unstudied materials), it was also sensitive to the subjective feeling of oldness (false alarms evoked more activity than misses), introspective indications of recollection versus familiarity, and the goals or retrieval orientation of the participant. Following these observations and consideration of the role of the PPC in other research, they suggested three potential functions. First, the PPC could be involved in maintaining or shifting attention to “internal, mnemonic representations”. Under this account, when a participant retrieves information (presumably within another region, such as the medial temporal lobes (MTL)), the parietal lobe would be needed to move attention from external stimuli, or other memory representations, to this new memory content. Second, the PPC could be a “mnemonic accumulator”, gathering episodic memory evidence from other regions in service of making an eventual memory decision. The portions of PPC connected to the MTL, for example, could integrate its retrieval activity over time, triggering a judgment of recognition when information levels reached a decision bound. Finally, the PPC could be an episodic memory output buffer that stores recovered long-term representations in a form rapidly accessible to decision making. Under this framework, raw memory representations are assumed inaccessible or too distributed for decision making systems to act upon and instead require an intermediate term store or buffer for conscious access during choice or reasoning (Baddeley, 2000). Thus the PPC would act as a temporary buffer similar to those proposed to operate in verbal or visual working memory in order to make retrieved episodic memory contents rapidly available for ongoing reasoning or executive operations. Wagner et al (2005) noted that each of these hypotheses accounts for different aspects of the data, that they may not be exclusive, and that different regions within the PPC may perform different functions (see also Naghavi & Nyberg, 2005).

A somewhat different perspective has arisen from the research of Cabeza, Ciaramelli and colleagues, who have proposed a close functional parallel between parietal activations during recognition, and those observed during research on visuo-spatial attention (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008). Cabeza et al (2008) connected work on the PPC and attention to the memory literature, emphasizing that that dorsal and ventral PPC regions are thought to have dissociable roles in visuo-spatial attention, such that the dorsal parietal cortex (DPC) appears more responsive to top-down attentional demands while the ventral parietal cortex (VPC) appears to be involved in bottom-up attentional capture. Turning to memory, this potentially explains why dorsal PPC regions show increased activation for low confidence memory judgments, when top down monitoring for diagnostic memory content is presumably maximal, whereas ventral parietal regions appear to demonstrate the greatest activation when recovered memory contents are presumably vivid and/or salient, for example, during recognition accompanied by contextual recollection. This framework had been dubbed the attention to memory model and asserts that dorsal parietal regions in the superior parietal lobule (SPL) are critical for the guided or top down search for episodic

memory content, whereas ventral parietal regions in the inferior parietal lobule (IPL) are critical for the capture of attention when salient memory content is suddenly recovered.

In the current report we use a modified version of the Explicit Memory Cueing task developed by O'Connor et al. (2010) to probe the functional significance of parietal responses during recognition judgment (for a blocked manipulation of recognition memory expectations see Herron, Henson, & Rugg, 2004). During the Explicit Memory Cueing task, anticipatory cues preceded each recognition memory probe indicating whether each upcoming memory item was likely to have been studied ("Likely Old") or not ("Likely New"). One key finding of the report was that activation was highest in the lateral parietal region whenever the subjects' expectations were violated by the upcoming memoranda, regardless of whether these items were correctly judged old or new. This invalid memory cueing effect was present in left supramarginal gyrus and because it demonstrated that activation differed as a function of violated expectations for correctly judged new materials (viz., correct rejections), this led O'Connor et al. to reject the idea that lateral parietal cortex played a direct role in the successful recovery or storage of episodic information because such information should be largely absent during correct rejection of new materials (O'Connor, Han, & Dobbins, 2010).

Although the O'Connor et al. (2010) study linked lateral parietal responses with the violation of memorial expectations, there were several potential drawbacks to the design. First, uncued or neutral trials were not intermixed among the cued trials making it difficult to compare the cued responses to responses that should be analogous to those observed in standard recognition paradigms. Second, the validity of the cues was not explicitly provided to the subjects and was instead learned via feedback. Finally, both highly valid and random cues were used in different blocks in an attempt to examine carryover learning effects. These latter two manipulations likely added considerable individual variability in the extent to which participants consciously believed the cues to be predictive and generally lowered the power of the cues to drive decision biases. Here we eliminated these potentially problematic aspects by fully intermixing cued and uncued trials, and by explicitly and correctly informing subjects that all predictive cues were 75% accurate, and hence should be actively used to bolster recognition performance. As shown below, this procedure allowed us to isolate functionally distinct patterns of response in the left lateral parietal cortex, suggesting separate regions specialized for the orienting of attention following unexpectedly familiar versus unexpectedly novel items. A third pattern was also present, similar to that identified in O'Connor et al. (2010) in which memory content that violated expectations (regardless of whether old or new) elicited increased activation.

Before turning to the procedure, we outline a putative model of memory orienting (Memory Orienting Model) and make a key distinction between functional interpretations of PPC that assume the region plays a direct causal role in accurate recognition (causal models) versus interpretations that instead assume the region supports a functional role that is a consequence of recognition retrieval processes, but that does not directly support those retrieval processes (consequential models). The causal/consequential distinction is important because the two perspectives lead to divergent predictions about patterns of activations across conditions and about the link between brain activation and individual differences in recognition ability. For example, the episodic retrieval buffer model is a causal model. Under this framework, conscious access to episodic knowledge during reasoning and choice is directly mediated by and hence causally dependent upon PPC. Hence, an individual with a severely damaged episodic buffer cannot reliably evince accurate recognition and should be functionally amnesic. Furthermore, the level of activation of the buffer in a healthy individual should be a reliable index of the amount of episodic information currently available to decision making operations (Yu, Johnson, & Rugg, 2012). With all other things

being equal, individuals who demonstrate a greater activation difference for studied versus new items during testing should be more accurate because they are buffering more diagnostic episodic information in a form accessible to conscious recognition judgment. Overall, the episodic buffer, mnemonic accumulator, and VPC attentional capture component of the attention to memory model are all causal models. In each case, the function ascribed to the relevant portion of PPC is logically essential for, and indicative of, accurate recognition judgment.

Consequential models lead to a different set of predictions. Under these frameworks, activation in PPC, while dependent on retrieval processes, does not directly support those retrieval processes. Instead the activation represents a consequence that follows retrieval under certain contexts or task demands. The top down attention component of the attention to memory framework is potentially consistent with a consequential model. Under the model, Cabeza and colleagues assume that weak or ambiguous memory signals lead to the increased engagement of top down monitoring for memory content in SPL region(s). Such top down engagement would also presumably arise even without ambiguous signals, if instead the observers were simply forewarned that an upcoming recognition demand would be quite difficult. In terms of individual differences in recognition skill, observers who are highly skilled would presumably require engagement of this region less often than those who were unskilled because the latter would be much more likely to encounter ambiguous memory signals. Critically, if the monitoring operation did not noticeably improve or directly interact with retrieval processes, then the top down attention component of the attention to memory model would be consequential in that damage to the region would not lead to any gross impairment in basic recognition ability. Currently, however, the degree to which this component is thought to directly facilitate retrieval is somewhat unclear in the discussions of the model.

Based on the work of O'Connor et al. (2010) and the large literature linking PPC with visuo-spatial and other forms of attentional orienting we hypothesize that its role during recognition is also linked to orienting behavior. Thus PPC activation is a marker of the degree to which a memory signal is unexpected in a given context. As in other orienting domains, the primary purpose of this orienting response is investigatory. That is, the response is assumed to signal and eventually aid in the resolution of a perceived ambiguity. We discuss the evolutionary importance of resolving unexpected novelty and familiarity signals more in the discussion section, but here we note that the idea of memory orienting is not new among memory researchers. For example, in the dual process recognition theory of Mandler, item familiarity can play a key orienting role as exemplified by the oft-cited 'Butcher-on-the-bus' anecdote presented in that influential paper (Mandler, 1980). The anecdote describes a situation where upon boarding a bus, one's attention is captured by a fellow passenger who is oddly familiar, but whose familiarity initially defies explanation. Finally, following a deliberate source monitoring attempt involving several considered possible sources (e.g., is he from work?, the milkman?, etc.) one generates the appropriate cue and recollects that the individual is in fact the butcher from the local supermarket (for a more elaborate illustration see chapter 11 Baddeley, 1998).

This anecdote is not really one of recognition memory per se, but one highlighting how recognition signals can lead to an initial orienting response (the original attentional capture by the unexpectedly familiar passenger) and to subsequent deliberative attempts to explain the environmental ambiguity detected by the initial orienting response (deliberative memory search). Here the potentially more controlled retrieval behavior (source monitoring) is a consequence of an initial uncontrolled detection of an anomalous familiarity signal, but critically, neither the orienting response nor the deliberative attempts to explain that orienting response are causal with respect to the initial recognition process that begun the

sequence. Thus, while the ability to discriminate the novel from the familiar is a prerequisite to the orienting phenomenon, it does not explain that phenomenon. More formally, recognition discrimination ability is necessary but not sufficient for the orienting phenomenon. The dependency of orienting on early discrimination ability is a characteristic of all orienting models. For example, in the Posner spatial cueing paradigm, small central arrows are used to forecast the spatial position of subsequent targets of either detection or discrimination (Posner & Petersen, 1990). These cues are generally valid and hence observers shift their covert spatial attention to the cued regions to facilitate or ease future judgments. Critically, when stimuli instead appear in the unexpected/uncued location it is assumed that parietal orienting mechanisms disengage attention from the expected region and drive attention towards the discrepancy. What is perhaps less appreciated, because the locations used are perfectly discriminable, is that this orienting mechanism necessarily depends on a core ability of the observer to discriminate between the left and right side of space in the absence of spatial cueing. Thus spatial orienting presumes spatial discrimination ability (which in the typical paradigm is presumably at ceiling for all subjects given the eccentricities typically used), and the observer's spatial discrimination ability will contribute to how salient violations of cued expectations are. Thus, we propose a Memory Orienting Model of PPC activation that is in line with these broad characteristics. Activation is presumed to reflect the degree to which initial recognition signals confirm versus contradict expectations, and the ability of observers to discriminate the novel from the familiar in the absence of cues will contribute to the salience of the detected violations of expectation (and hence size of the orienting response) under cueing. The model is strictly consequential in that the PPC orienting responses are a reaction to initial unexpected recognition signals, but they do not causally contribute to the initial retrieval process itself. The adaptive function of the responses is to investigate and potentially resolve the perceived memory discrepancy, and as we demonstrate in the results, it appears that different mechanisms are recruited for orienting to unexpected novelty compared to orienting to unexpected familiarity in the environment.

Materials and Methods

Participants-Main Study

Eighteen individuals aged 19 to 35 years (8 female, mean age, 24.8; SD, 3.54) participated in the study. Written informed consent was obtained in accordance with the Institutional Review Board of Washington University in St. Louis. Two participants were excluded due to reporting nausea, and one due to falling asleep during scanning, leaving fifteen individuals for analysis. One of the fifteen participants failed to finish the final experimental block, but the completed blocks were included for analysis. Participants were right handed native English speakers with no history of neurological and psychiatric problems, and were paid \$25 per hour for their participation. Vision was normal or corrected to normal using contact lenses or magnet compatible glasses.

Stimuli

A total of 480 words were randomly sampled for each participant from a pool of 1216 words. From each sampled list, four lists of 120 words were used in each study-test cycle (60 words were assigned as old and 60 as new). The items in the pool had an average of 7.09 letters, 2.34 syllables, and Kucera-Francis corpus frequency of 8.85.

Task and procedures

Participants entered the scanner and completed 2 structural scanning sessions followed by 8 functional scans examining study and test (4 scans each). For the present report, only the 4 test scans examining retrieval were analyzed. For both the study and test sessions, a genetic

algorithm that optimized the design efficiency for the contrasts of interest (Wager & Nichols, 2003) determined the order of the conditions. During each study session, 60 items were presented intermixed with 15 additional fixation trials. Participants were required to indicate whether each word had one or more syllables, having 2.3 seconds to perform each judgment using a magnet compatible key pad. A task prompt illustrating the correct key mappings was presented below each study item (“1 or 2 or more syllables”), and a fixation crosshair was presented for 200 ms before each item presentation, yielding a stimulus onset asynchrony (SOA) of 2.5 seconds.

Immediately following each study session, a scanned recognition test was administered in which the 60 studied words were intermixed with 60 new words and presented along with an additional 28 fixation trials of equal duration. Probabilistic cues “Likely Old” or “Likely New” described as “hints” to the participants preceded each of the recognition memory probes by 1.5 seconds. Following the cue’s appearance, both cue and recognition probe were presented for an additional 3.3 seconds, followed by a 200 ms fixation period before the next trial (SOA = 5 seconds). During each test session, there were 48 trials in which cues preceded old items (36 valid trials = “Likely Old” cue, and 12 invalid trials = “Likely New” cue), and 48 trials in which cues preceded a new items (36 valid trials = “Likely New” cue, and 12 invalid trials = “Likely Old” cue). The remaining 12 old and 12 new items (uncued items) at each scanned test cycle were preceded by question marks (“????”) and hence subjects were not cued towards either familiarity or novelty. Participants were correctly informed that when present, 75% of the cues were valid and should be used to bolster performance. A basic recognition judgment was indicated using two buttons on the response box (*Old*, *New*), followed by a confidence rating of their recognition response using four buttons on the response box (*Guessing*, *Low confident*, *Moderately confident*, and *Highly confident*). They were required to make both judgments while the probe was visible (i.e., 3.3 seconds), and a reminder prompt indicating the key mapping for each response was presented below each test probe.

fMRI acquisition and preprocessing

Data acquisition was conducted using a 3T Siemens Trio whole-body MRI scanner (Siemens Medical Solutions, Erlanger, Germany) and a standard whole-head coil. The acquisition of functional data was performed utilizing an interleaved ascending echo-planar pulse sequence (TR = 2500ms, TE = 27ms, 42 axial slices parallel to the anterior-commissure and posterior-commissure plane with isotropic 4mm voxels, and no inter-slice gap). Foam pillows were utilized to minimize head motion. For each run, 296 volumes were acquired, and the first two volumes of each run were discarded to allow T1 stabilization. High-resolution T1-weighted and T2-weighted scans were acquired prior to the active-task data acquisition. BOLD data were preprocessed using SPM8 (Wellcome Department of Imaging Neuroscience, London). Rigid body motion correction was conducted by aligning all volumes with the first collected volume, following correction for slice acquisition time using sinc interpolation. Functional data were spatially normalized to a canonical MNI echo-planar template using 12-parameter affine and cosine basis transformations, and resampled to 3mm isotropic voxels. Volumes were spatially smoothed with a 6mm Gaussian kernel.

fMRI data modeling

Initial analyses were carried out using SPM8 (Wellcome Trust Centre for Neuroimaging, <http://www.fil.ion.ucl.ac.uk/spm/software/spm8/>). Functional data were modeled by convolving a canonical hemodynamic response function (HRF) with a series of delta functions set to the onset of the test probe (1.5 seconds into each trial). Prior analyses (such as in O’Connor et al, 2010) suggested that the parietal response is drawn out over time, so the response duration was modeled at 3 seconds. Modeled events included hits from each of

the three cue conditions (uncued, likely old', and likely new'), correct rejections from each cue condition, false alarms following a likely old' cue, and misses following a likely new' cue. All other errors occurred too infrequently to be analyzed and were combined into a single variable of no interest. Model estimates for each condition were fit for each participant and then used at the second level to create the analyses described below.

To initially investigate the effect of the cues, the flexible factorial module was used to conduct a within-subjects analysis. Non-directional F contrasts were created for both the main effects of cue type and item type as well as their interaction. T contrasts were also created to conduct follow-up tests as described in the results section. Results were thresholded at an uncorrected p value of .001 with at least five contiguous voxels. Additional T and F contrasts were created for the purposes of isolating 3 separate responses patterns as described in the results section. These contrasts were also used to create the parietal lobe regions of interest (ROIs) (see table 1). Beta weights and timecourse data for each participant were extracted from each ROI using MarsBaR (Brett et al., 2002; <http://marsbar.sourceforge.net/>). Visualizations were created using Caret (Van Essen et al., 2001; <http://www.nitrc.org/projects/caret/>) and MRIcroGL (<http://www.cabiatl.com/mricrogl/>).

Resting state fMRI analysis

For the resting state analysis, a secondary data set of BOLD data was collected from 16 young adults aged 20–22 years (7 female, mean age, 21; *SD*, 0.73) in two scanning sessions in which participants fixated a cross-hair for 6 minutes with instructions to stay awake and remain still. The resting state data acquisition and preprocessing was similar to the active task except for the TR (2200ms), the number of volumes acquired (164), the number of axial slices per run (36), and for the software in which the preprocessing was performed (SPM5, Wellcome Department of Imaging Neuroscience, London, <http://www.fil.ion.ucl.ac.uk/spm/software/spm5/>). The data analysis was conducted by extracting the time course of three parietal ROIs which were entered as covariates of interest in conjunction with 8 mm diameter seed regions or covariates entered as sources of nonspecific variance (6 parameters resulting from the rigid body correction of head motion, and signals from the averaged whole brain, seed within left lateral ventricle, seed within left hemisphere white matter, and the 9 first derivatives of these covariates) in an SPM5 general linear model (Fox et al., 2005). The ROIs entered as covariates of interest were the parietal lobe regions demonstrating selective novelty orienting, selective familiarity orienting, or general invalid cueing effects as defined below in the results section. (see also Figure 2).

Results

Behavior-Analysis

Accuracy was initially considered using a mixed ANOVA with factors of Outcome (Hit vs. Correct Rejection - CR) and Cue Type (Likely Old – LO, Likely New – LN, or Uncued – UC). There was no main effect of Outcome ($F < 1$) indicating that overall hits and correct rejection rates were similar. The main effect of Cue Type also failed to reach significance ($F(2,28) = 2.43$, $MSe = .003$, $p = .106$) suggesting that the average correct response rates were similar across the three cueing conditions. Finally, there was a strong Cue Type by Outcome interaction ($F(2,28) = 27.00$, $MSe = .025$, $p < .001$). As Figure 1a demonstrates, this interaction occurred because while the hit and correct rejection rates were similar during Uncued trials ($p = .88$), hits were more frequent than correct rejections under the Likely Old cue condition ($p < .001$) whereas the reverse was true under the Likely New cue condition ($p < .001$) (Fisher's LSD). As we document using signal detection measures below, this pattern is completely consistent with a shifting familiarity criterion and a fixed accuracy across the three cue conditions.

The analysis of mean response confidence was restricted to correct reports and again considered using a mixed ANOVA with factors of Outcome (Hit vs. CR) and Cue Type (Likely Old – LO, Likely New – LN, or Uncued – UC). There was a main effect of Outcome with generally higher confidence for hits than correct rejections ($F(1,14) = 23.86$, $MSe = .183$, $p < .001$). There was no main effect of Cue Type ($F(2,28) = 1.82$, $MSe = .052$, $p = .181$). However, there was a Cue Type by Outcome interaction ($F(2,28) = 7.21$, $MSe = .049$, $p = .002$). The primary cause of the interaction was the differential effect of the Likely Old and Likely New cues on confidence for hits versus correct rejections. More specifically, for correct rejections, invalid (Likely Old) versus valid (Likely New) cueing reduced mean confidence (2.78 vs. 3.09, $p < .001$) whereas confidence during hits remained uniformly high and unaffected by the validity of the external cues (3.31 vs. 3.42, $p = .147$) (Figure 1b).

The above pattern of accuracy and mean confidence across the Likely Old and Likely New cues replicates a dissociation of accuracy and confidence first documented by Jaeger, Cox, and Dobbins (2012) and successfully simulated via a dual process model of recognition. Under the model, the Likely Old and Likely New cues are assumed to influence the use of familiarity via a shifting familiarity decision criterion. Thus, the use of familiarity to endorse an item as recognized is reduced under the Likely New cue condition compared to the Likely Old cue condition. In contrast, the model assumes that the cues have no influence on trials in which the studied recognition probes evoke contextual recollection. During these trials it is assumed the observers identify the recognition probes as “old” regardless of the form of the external cue, and it is also assumed that they do so with high confidence. Despite the simplicity of the model, it successfully anticipates the pattern of accuracy and confidence shown in the “Likely Old” and “Likely New” cue conditions of Figure 1. Both hits and correct rejection rates fall in response to invalid cueing because of shifts in the familiarity criterion. However, confidence in hits is generally higher than that of correct rejections because of the contribution of recollection. Moreover, the mean confidence of hits is unaffected by the shifts of criterion. Although the conservative criterion under the Likely New cue serves to lower the confidence of familiarity based hits during Likely New cued trials, it also serves to render more of the overall hit trials dependent upon recollection based responses, which again are highly confident. These counteracting processes result in little to no change in the averaged confidence of hits across the Likely Old and Likely New cues, despite the fact that the hit rate itself changes considerably as a function of the cueing procedure (for more detail see Jaeger, Cox, & Dobbins, 2012).

A final consequence of the dual process model of the Explicit Memory Cueing effect is that hit rates during invalidly cued trials (Likely New cue) are expected to be more heavily saturated with recollection than during validly cued trials (Likely Old cue). That is, the increasingly strict criterion induced by the invalid Likely New cues serves to restrict the contribution of familiarity to the overall hit rate under this cue condition. The simulations used in Jaeger, Cox and Dobbins were based on similar encoding operations as this paper and the recollection estimate for this type of encoding was approximately .29. Assuming a similar rate here, the conditional probability of recollection under the Likely Old cue is this rate divided by the hit rate under that condition, $.29/.84$ or 34%. In contrast, the conditional probability of recollection under the Likely New cue condition is $.29/.55$ or 53%. Thus, under the model, the invalid cueing manipulation has the effect of increasing the likelihood that hits are determined by recollection, which again buoys the confidence of those hits despite the fact that the overall hit rate decreases because observers are increasingly unwilling to use familiarity during Likely New cue trials.

Finally, under both the dual and single process models of recognition, the criterion shifts are expected to have little effect on the overall summary measure of accuracy, d' . We confirmed this using a one way repeated measures ANOVA on d' calculated separately from the three

cueing conditions. There was no effect of cues on d' ($F < 1$). In contrast the cues greatly influenced the estimate of decision bias (C) ($F(2,28) = 24.17$, $MSe = .17$, $p < .001$). As expected, the “Likely New” cue resulted in more conservative responding compared to the uncued condition (.56 (.35) vs. .01 (.31); $t(14) = 4.95$, $p < .001$), whereas the “Likely Old” cue yielded more liberal responding compared to the uncued condition (−.48 (.51) vs. .01 (.31); $t(14) = 3.92$, $p < .001$). Thus, the behavioral data suggest that cueing altered the decision criterion on a trial-by-trial basis, but did not influence the relative discriminability of studied and new materials.

fMRI - Analyses

Condition Level Effects-Whole Brain

Analysis began with a two factor within-subjects ANOVA with factors of Cue Type (Uncued-UC, “Likely Old”-LO, and “Likely New”-LN) and Response Type (hits or correct rejections). As Figure 2 illustrates, there was a robust interaction between Cue Type and Response Type (red areas) implicating anterior, lateral, and dorsal prefrontal areas, along with lateral parietal regions. This pattern replicates O’Connor, Han, and Dobbins (2010) demonstrating that the response to old and new materials is heavily dependent upon the trial-wise expectations of the observers. Additionally, the main effect of Item Type also implicated prefrontal and parietal regions (green areas), proximal to those demonstrating an interaction pattern. The main effect of Cue Type implicated a single small region of right anterior prefrontal cortex (not shown).

Closer analysis of the main effect of Response Type in left lateral parietal cortex suggested functional heterogeneity in the activation patterns. As the plots in Figure 2 demonstrate, the left anterior parietal Response Type effect reached significance because there was greater activation during correct rejections than hits under the LO cue condition (graph A). Notably however, the differential response was muted the LN and uncued trials. A largely reverse pattern occurred in the posterior parietal main effect of Response Type activation (graph B). Here, there was greater activation during hits versus correct rejections under the LN and UC cue conditions. However, there was little evidence for a Response Type difference under the LO cue condition. Thus, these regions differ both in terms of which type of item they responded maximally to, and under which cue condition this differential response occurred. In the case of the anterior region it responded more strongly to new than old items during correct responding, but this difference was most prominent when subjects incorrectly expected familiar items during the trial (“Likely Old” cue condition). In contrast, the posterior region responded more strongly to old than new items during correct responding, but this difference was most prominent when the subject incorrectly expected new items (“Likely New” cue condition). We refer to these two patterns as the unexpected novelty and unexpected familiarity responses respectively. It is important to note that the above responses suggest that not only are the two regions differentially sensitive to novelty and familiarity, but that this differential sensitivity is also strongly, if not entirely dependent on the observer’s expectations. Hence the anterior region is sensitive to novelty under the “Likely Old” cue condition but not under the “Likely New” cue condition. In contrast, the posterior region is sensitive to familiarity under the “Likely New” cue condition, but not under the “Likely Old” cue condition.

Finally, there were also regions that showed increased response whenever the memory probe was unexpected, regardless of whether the item was novel or familiar. For example, the intermediate left IPS region demonstrated a full crossover pattern such that hits yielded greater activation than correct rejections during the “Likely New” cue condition, but correct rejections yielded greater activation than hits during the “Likely Old” cue condition (bar graphs not shown). Thus the region demonstrated an elevated response whenever memory

content violated the cued expectation, regardless of the nature of that violation, unexpected novelty or familiarity. We refer to this more general pattern as the unexpected memory response.

Although the ANOVA demonstrated important functional differences in left parietal cortex, it was not tailored to isolate selective orienting effects, and indeed these were fortuitously detected by the main effect of Response Type simply because the direction of response tended to converge in two of the three cueing conditions used (Figure 2). In order to directly isolate these newly observed patterns we conducted three new targeted contrasts in combination with exclusive masking, focusing exclusively on the actively cued (LO or LN) conditions in which expectations were directly manipulated and presumably maximized. Unexpected novelty responses were identified by looking for regions demonstrating greater activation during correct rejections than for hits, but only under the cue condition where new items were unexpected, namely the “Likely Old” cue condition. Thus, the contrast identifies regions demonstrating correct rejections greater than hits during the “Likely Old” cue (thresholded at .001, 5 voxels), but that show little evidence for any item type effect under the “Likely New” cue when novel materials are expected (exclusive masking using F contrast of Item Type under the “Likely New” cue, $p = .25$). Note that the liberal threshold applied to the exclusion mask ensures that surviving voxels do **not** differentiate correct rejections versus hits when the subject received the “Likely New” cue. Thus, the contrast isolates responses to novelty that occur only when it is unexpectedly encountered. As Figure 3 green regions show, this contrast isolates anterior parietal regions bilaterally (anterior intra-parietal sulcus-IPS and post-central gyrus - PoCG) along with the frontal eye fields and middle frontal gyri (Table 1).

To isolate the unexpected familiarity response, we identified regions demonstrating greater activation for hits than correct rejections under the “Likely New” cue, exclusively masking any regions demonstrating response type effects under the “Likely Old” cue condition via an F contrast. As Figure 3 blue regions show, this response was predominantly left lateralized implicating left posterior parietal cortex (anterior angular gyrus - aAG), left lateral premotor and anterior prefrontal regions (Table 1).

Finally, to identify general unexpected memory responses we performed a conjunction analysis looking for regions demonstrating both greater activation during hits than correct rejections under the “Likely new” cue and correct rejections greater than hits under the “Likely Old” cue. As Figure 3, red regions show, the contrast isolated bilateral mid-lateral parietal regions, midline presupplementary motor cortex, bilateral anterior insulae, and bilateral dorsolateral PFC (Table 1).

The above analyses isolate three qualitatively different response patterns all within left lateral parietal cortex during this paradigm; unexpected novelty response, unexpected familiarity response, and a general unexpected memory effect, nestled between the two. The anterior and posterior selective orienting responses represent a full double dissociation of function within the parietal cortex during recognition judgment. As expected given the contrast and masking procedures, the anterior region demonstrates a significantly greater response to correct rejections than hits under the “Likely Old” cue ($t(14)=4.54$, $p < .001$) but no differential response under the “Likely New” cue ($t < 1$). In contrast, the posterior region demonstrates a significantly greater response to hits than correct rejections under the “Likely New” cue ($t(14)=5.01$, $p < .001$) but no differential response under the “Likely Old” cue ($t < 1$). Thus the t statistics confirm the contrast and masking procedures demonstrating that the two regions are both differentially sensitive to item types and cue conditions.

The general unexpected memory response that is nestled between the two areas in Figure 3 represents a third potential process; however, there is some concern that at least in the left hemisphere, this pattern may simply reflect a smoothing or averaging artifact. That is, the response could reflect a smearing of the two selective orienting responses. This seems unlikely for two reasons. First, the response does not appear attenuated as would be expected if it were simply the average across the two selective orienting responses. That is, both the hits greater than correct rejection response (under the “Likely New” cue) and the correct rejection versus hit response (under the “Likely Old” cue) are robust in this region and do not appear to be the average of the anterior and posterior, proximal effects which would arguably mute their size. Second, the general unexpected memory response is also present in the right parietal lobe even though there is not an unexpected familiarity response present in the right parietal lobe. Thus the general unexpected memory response in the right parietal lobe cannot reflect an artifact of averaging two selective orienting effects, since only one of these selective orienting effects is present in this hemisphere. This in turn suggests that the effect in the left parietal cortex is likewise not an averaging or smoothing artifact since it occurs in a roughly homologous area.

Condition-Level Effects – Comparisons within Left PPC

The above analysis identified three functionally distinct patterns in left PPC. Here we further consider whether these patterns, at the condition level, are compatible with a causal role in recognition judgment as outlined in the introduction. More specifically, we examine whether the pattern of activation response makes sense in light of either accumulation or episodic buffer accounts of left PPC during recognition. Beginning with the PoCG unexpected novelty response, this activation can clearly be ruled out since it demonstrates the greatest activation for novel, not familiar materials and hence cannot be accumulating or buffering episodic content for old items (Figure 3). The mid IPS response can also be easily ruled out as a causal recognition process in line with episodic accumulation or buffering because of the complete crossover interaction. While the region does display greater activation for hits than correct rejections under the Likely New cue, this pattern completely and reliably reverses under the Likely Old cue. Hence it is clear that the region is demonstrating heightened activation for whichever class of memoranda is unexpected, regardless of study status. Thus the role of this region cannot be the accumulation or buffering of episodic evidence. This leaves the aAG region, whose pattern is more equivocal. Figure 4 again displays the mean activations of the region under the four conditions representing the crossing of Cue Type (Likely Old and Likely New) and Response Type (Hit or Correct Rejection). Additionally, the figure displays the mean strength of evidence values for each response outcome determined from a basic signal detection model. These values represent the average strength of evidence underlying each of the four response outcomes given the d' and criterion values calculated from the Likely Old and Likely New response proportions in the behavioral data. One can use these mean strength values, in conjunction with the pairwise comparison of the four activation conditions to see if the pattern of differences makes sense under the strength based signal detection account. Under accumulation or buffering accounts, one would expect that activation and strength of evidence values should be concordant. If hypothetical condition A yields greater activation than hypothetical condition B, then the strength of episodic evidence should be higher under condition A than condition B.

Two of the four theoretically meaningful contrasts fit with the idea that the aAG is buffering or signaling episodic strength of evidence. First, there is reliably greater activation for hits than correct rejections under the Likely New cue condition with a concordant pattern of strength values (strength 2.12 vs -0.19 ; activation - $t(15) = 5.01$, $p < .001$). Second, when one compares the activation of hits under the Likely New cue to that of hits under the Likely Old

cue there is reliably greater activation under the former, which is again concordant with signal detection strength estimates (strength 2.12 vs. 1.56; activation $-t(15) = 3.20$, $p = .006$). This also makes sense under the strength account because the shifted criterion across the conditions means that the average strength of hits under the Likely New condition should be higher than the more watered down strength of the hits under the Likely Old cue condition. That is, only the strongest old items survive the stringent criterion induced by the Likely New cue. However, despite these two consistent findings, there are two qualitatively inconsistent findings present. First, the activation to correct rejections under the Likely Old cue is reliably higher than the activation of correct rejections under the Likely New cue ($t(15) = 2.96$, $p = .010$). As the strength values show, this is qualitatively reversed from what should occur under the strength model in which the strength of correct rejections under the Likely Old cue ($-.67$) is lower than the strength of evidence under the Likely New cue ($-.19$). This occurs because the criterion under the Likely Old cue condition should render new items under this condition far less familiar (i.e., more clearly novel) than new items under the Likely New cue condition. That is, the former contain only the least familiar items compared to the latter, and under an episodic accumulation or buffering account there cannot be greater activation for the least familiar class of responses. The final comparison that also weighs against a strength based interpretation of the aAG response is the contrast of hits and correct rejections under the Likely Old cue condition. This contrast yielded no evidence for an activation difference ($t < 1$) despite the fact that the strength values are clearly different and much higher for the hits (1.56) than the correct rejections $-.67$. Additionally, the null effect of the activation comparison was not due to low power because the activation means are actually numerically reversed compared to the expectation of the strength model. Thus, two of the four comparisons of aAG activation not only fail to support a strength-of-evidence interpretation, they directly contradict that interpretation, at least under a simple signal detection model of strength/familiarity. It is also important to re-emphasize the fact that the behavioral accuracy of the subjects under these two cue conditions is equivalent. Despite the fact that there is no evidence for an activation difference for hits and correct rejections under the Likely Old cue, the average d' is virtually identical to that observed under the Likely New cue condition, in which the aAG activation difference is prominent. If these aAG signals were the basis of accurate recognition judgment, this should not occur.

Despite the evidence weighing against the strength model above, concerns may still arise that somehow the different criteria, perhaps in conjunction with recollection possibly playing a more prevalent role in hit rates under the Likely New cue condition, may still somehow salvage a strength of episodic evidence based account of the aAG response. To further examine this issue, we re-modeled the data in the anterior angular gyrus ROI, ignoring the actual response of the subjects. Thus we examined the pattern of response to old and new items strictly as a function of cue condition. Critically, under extant dual and single process models, the evidence supporting recognition judgments is assumed stationary in light of the external cues, which only serve to shift a decision criterion; an assumption bolstered by the fact that the measured behavioral d' did not differ across the cueing conditions (see behavioral results above). Because observers are working with the same evidence under the two active cueing conditions (Likely Old and Likely New), the expectation for a region strictly representing strength of episodic evidence (either familiarity and/or recollection) is that the overall signal for old items should exceed that for new items (collapsed across responses), and that this difference should be similar for the two cue conditions. In other words, if the signal differences observed in anterior angular gyrus in Figure 3 and Figure 4 were an artifact of the different response criteria adopted under the Likely Old and Likely New cue conditions, then considering the data irrespective of response should reliably reveal greater activation for old than new items under both cueing conditions because evidence is necessarily generally higher for the old than the new materials.

In contradiction to this expectation, the extracted aAG ROI data yielded a Cue Condition (Likely Old vs. Likely New) $\times$ Item Type (All Old vs. All New trials) interaction ($F(1,14) = 5.33$, $MSe = .053$, $p = .037$) (Figure 5). As with the correct response data, this occurred because old materials only yielded greater activation than new materials under the Likely New cueing condition (.53 vs. .29, $t(15) = 2.36$, $p = .033$), not under the Likely Old cueing condition (.37 vs. .41, $t < 1$). Indeed the overall activation for old items under the Likely Old cue was lower than that of new items. This further suggests that the aAG region is signaling an orienting response, not an evidentiary response; it reliably signals differences between old and new materials, but only when old materials are unexpected given the cueing condition; its activation conveys no information about the classes of memoranda when the observer is instead anticipating familiarity.

Subject Level Effects – Individual Variation in Accuracy

The above data challenge an account of the aAG region as generally signaling the recovery of episodic content and instead suggest that this region only responds when episodic content is unexpected. Thus its response seems to be a marker of unexpected familiarity, not familiarity in general and in light of the introduction we would characterize it as a marker of orienting. As noted in the introduction, orienting models are consequential models that depend upon the ability of observers to discriminate old and new materials in order for orienting to occur. That is, one cannot orient to unexpected familiarity unless novel and familiar materials are initially discriminable in the absence of strong expectations. This leads to a prediction about the relationship between individual variation in basic recognition skill and the size of the orienting response in the anterior angular gyrus. Namely, individuals with greater recognition skill should show more prominent orienting responses because the violations of their expectations will be more salient. This can be formalized using a multiple regression framework and looking at the relationship between aAG responses and d' across the observers. Under the Memory Orienting Model, aAG activation during the Likely New cue condition (the unexpected familiarity response) should be associated with individual variation in d' across all three cue conditions (Figure 6 bottom). That is, the size of the unexpected familiarity response should reflect subject differences in core discrimination skill which should be reliably reflected in each of the three separate cueing conditions. Critically the use of both hit and correct rejection activation as independent variables in the model ensures that the differential response (regardless of overall differences in general activation across subjects) is used to predict d' differences across the subjects (Figure 6).

In contrast to the Memory Orienting Model, an evidence based/causal model of aAG such as accumulation or buffer models predict that the aAG response within all three cueing conditions should track subject variation in d' within those same conditions (Figure 6 top). If the region signals the accumulation of episodic evidence then under similar conditions (e.g., the Likely Old cueing condition) observers with higher activation for hits and lower activation for correct rejections should generate more accurate recognition responses within that condition. It is important to note that this prediction might hold even if the overall level of activation for hits and correct rejections was similar when collapsed across observers, as was the case for hits and correct rejections under the Likely Old cue condition (Figure 3 and Figure 4). This is because correlation-based measures are not dependent upon mean activation levels (i.e., scale invariant).

As shown in Figure 6 and Table 2, the findings support the Memory Orienting Model. The differential activation for hits and correct rejections under the Likely New cueing condition (viz. the unexpected familiarity response), **and only that cueing condition**, reliably predicts the variation in subject discrimination skill under all three cueing conditions. In contrast, activations in neither the Likely Old nor Uncued conditions predict subject accuracy within

those same conditions, which in light of the strong predictive strength under the Likely New cue condition, strongly challenges the notion that this region directly stores or accumulates episodic evidence, and instead supports the hypothesis that the region signals orienting to unexpectedly familiar materials. Critically, the degree of orienting appears linked to the salience of the expectation violation, which is a function of individual differences in basic recognition skill. In short, the aAG response is a consequence that follows the ability to discriminate the novel and familiar, it is not the cause of that ability.

Finally, it is perhaps important to comment on the effect size linking the aAG unexpected familiarity response to behavioral differences in accuracy. The regression indicated that more than 71% of the variation in subject d' s during the Likely New cue condition was accounted for by the aAG activations within that condition. Although not as large, the effect sizes in the remaining two predictions, where aAG activation during the Likely New cue condition were used to predict relative subject accuracy in the remaining two cue conditions, were also quite large. Thus even though the aAG unexpected familiarity ROI was defined wholly independent of observer accuracy, it nonetheless remarkably reliably predicts individual variation in discrimination skill; a pattern wholly consistent with the idea that the salience of unexpected familiarity is reflected in the size of the aAG response.

Although the aAG response was the primary focus of the individual differences brain-behavior analysis, we also examined the left PoCG response shown in Figure 3 using the same methods. Unlike the aAG unexpected familiarity response, the PoCG unexpected novelty response (Likely Old cueing condition) was not generally predictive of performance failing account for a significant proportion of behavioral variance in accuracy during all three cueing conditions (p 's for all model R-square values $> .093$). Furthermore, the activation response within the remaining Likely New and Uncued cueing conditions also failed to track behavioral accuracy within those same conditions ($p = .161$ & $p = .224$ for model R-squares respectively). This generally poor predictive ability may represent a true null, however, it is important to note that the unexpected novelty response is considerably more distributed in parietal cortex than the unexpected familiarity response, occurring bilaterally and in more than one region (PoCG and dorsal parietal area ~BA7 in both hemispheres). This distributed pattern may weaken any brain-behavior correspondence at the level of subjects since individuals may have different peak response locations within the regions implicated in the condition contrast.

The Unexpected Familiarity Network – Resting State and Event-related correspondence

Here we focus on the regions displaying the unexpected familiarity response given its clear relevance for prior recognition findings. The regions demonstrating responses to unexpectedly familiar stimuli in Figure 3 are unique in that they are highly left lateralized and potentially form a functional network linked to attentional orienting towards mnemonic familiarity. Aside from the common manner in which these regions responded to the combination of cueing conditions and memoranda, another way to further define functionally linked regions is through analysis of resting state BOLD data. We examined an independent sample of subjects who passively viewed a fixation cross during resting scans as outlined in the methods section. For this group we entered all three left lateral parietal regions of interest from Figure 3 into the design matrix and searched for regions showing greater functional connectivity to the anterior angular gyrus region than the other two regions combined (contrast $[1, -.5, -.5]$). Following this we searched for regions that were significant in both this resting state data contrast (.001, 5 voxels), and the selective familiarity orienting contrast in the current experiment (.001). The resulting conjunction map in Figure 8a unsurprisingly captures left anterior angular gyrus, but more importantly it captures the same left lateral premotor, anterior PFC and posterior cingulate areas that were originally demonstrated via the unexpected familiarity response contrast in Figure 3.

Because these findings are drawn from two separate experimental data sets, each thresholded at .001, the detected overlapping regions constitute a highly robust finding linking patterns of spontaneous slow waves of activity at rest, to the event-related patterns discovered via the Explicit Memory Cueing manipulation. This strengthens the claim that the regions form a functional network. Below, in the discussion section we also note that these same regions also have been implicated in source memory monitoring studies and thus at least three different techniques/paradigms appear to isolate these same areas, providing convergent evidence on their functional significance.

Relation to prior Angular Gyrus findings

As noted during an initial review of this manuscript, the anterior angular gyrus response documented here does not look spatially coincident with prior angular gyrus activations argued to support recollection during recognition (e.g. Yonelinas, Otten, Shaw, & Rugg, 2005). The latter are usually more inferior and as indicated by a recent meta-analysis are centered on MNI coordinates $-40, -74, 24$ in contrast to the current aAG response which is located at $-33, -70, 49$ (Kim, 2011). There is likely also an additional important difference in these regions. The current aAG response is clearly an activation. That is, unexpectedly familiar materials activate the region relative to baseline. In contrast, most of the prior studies linking the AG to recollection are relative deactivations. That is, trials in which recollection is presumed to occur yield activation at or slightly below baseline, whereas trials in which recollection is assumed absent (viz. familiarity responses) yield activation reliably below baseline. This general activation difference between anterior/dorsal and posterior/ventral angular gyrus is potentially consistent with the known cytoarchitectural differences in the two regions (Caspers, et al., 2006) and with recent resting connectivity fMRI research suggesting different functional connections for the two angular gyrus regions (Uddin, et al., 2010). To more directly investigate this issue, we took the reported center of mass for putative recollection effects from Kim (2011) and created a 6 mm radius ROI. This ROI was then used to extract the response during the current paradigm. As shown in Figure 7, the angular gyrus ROI from the meta-analysis, unlike the aAG response linked to the unexpected familiarity response, yields a deactivation pattern. Additionally, the pattern does not seem consistent with a recollection account in that the lowest level of activation occurs for the condition that is most likely linked with prevalent recollection, namely, hits under the Likely New cueing condition (Jaeger, Cox & Dobbins 2012). As noted in the behavioral results, hits during Likely New trials are presumably more heavily dependent upon successful recollection than hits during Likely Old trials, in which observers use a more lax criterion for familiarity-based endorsement. These activation data were submitted to a Cue Type (Likely Old or Likely New) by Response Type (Hit or Correct Rejection) ANOVA. There were no significant main effects. However there was an interaction of Cue Type and Response Type ($F(1,14) = 5.43$, $MSe = .954$, $p = .035$). Post hoc comparisons suggested that the interaction resulted because of greater deactivation for hits than correct rejections under the Likely New cue but greater deactivation for correct rejections versus hits under the Likely Old Cue. However, only the former comparison approached significance ($p = .068$) (Fisher's LSD). Despite the noisier pattern of data in this region, it is clear that the activations are being influence by the cues because of the significant interaction F value, and because the hit rate activation was reliably modulated by whether the cue was Likely New, versus Likely Old ($p = .023$). We also used the activations for hits and correct rejections in this more ventral AG region in an attempt to predict subject accuracy (d') separately within the Likely Old and Likely New cueing conditions. Neither regression approached significance.

The ventral AG response taken from the meta-analysis of Kim (2011) does not yield a pattern that is easy to interpret as a marker of recollection in this paradigm. The clearest

observed difference occurred for hits when validly cued versus hits when invalidly cued (Figure 7 grey bars); a finding at odds with the idea that hits under invalid cueing are increasingly confined to recollection trials. Also, the region does not reliably predict individual variation in recognition accuracy (in contrast to the aAG unexpected familiarity response in the current study which strongly tracked accuracy). However, given the differences in the paradigms that report this region and the cueing procedure used here, and the noisiness of the response, we do not interpret it further.

Discussion

The current study demonstrates considerable functional heterogeneity in the left lateral parietal cortex response during recognition judgment, and furthermore, that this heterogeneity is linked to the discordance between memory expectations and memory evidence. Three separate patterns were discovered. An unexpected familiarity response was observed in the anterior angular gyrus, which demonstrated greater activation for hits than correct rejections during the “Likely New” cue condition, when familiar materials were unexpected, but no differential response during the “Likely Old” cue condition when these materials were strongly anticipated (Figure 3 and Figure 4). The response in the more anterior PoCG region was qualitatively different (unexpected novelty response), favoring novelty, but again, only when it was unanticipated given the “Likely Old” cue; there was no differential response in PoCG when subjects anticipated new materials following the “Likely New” cue (Figure 3). More generally, these two regions reflect differences in the confirmation versus disconfirmation of two types of memory expectation. The intermediate region, located in mid IPS, demonstrated a full cross-over pattern across cue conditions, yielding a greater response to whichever class of memoranda (old or new) was currently unexpected (unexpected memory response). In the case of the right lateral parietal response, only the unexpected novelty and unexpected memory responses occurred. Thus overall, there was evidence for dissociations within lateral parietal areas, and across the cerebral hemispheres.

Differences During Uncued Trials

The condition contrasts and individual differences analysis heavily focused on the actively cued conditions (Likely Old and Likely New). However, as Figure 2 demonstrates, the PoCG and aAG regions yield more muted patterns of differential response under the uncued trials that are analogous to the unexpected familiarity and unexpected novelty responses seen during cueing. This presumably reflects the fact that when the external cue is ambiguous “????”, the observers expectations will vary from trial-to-trial as a function of uncontrolled factors such as random response and/or stimulus clustering during the serial presentation of the materials, and this would be consistent with recent behavioral work noting that there are sequential dependencies of the responses of observers during more standard recognition paradigms (Malmberg & Annis, 2012). However, it is the fact that these uncued responses can either be amplified or completely eliminated via the active cues that is important, since it is only under this situation that the experimenter is actively controlling the expectations of the observers. In contrast, the responses during the uncued trials presumably represent the averaging across trials in which expectations were varying towards either novelty or familiarity, which in turn would explain why the response looks like a muted version of that seen during the active cue conditions.

Extant Models of Parietal Activation

As noted in the introduction there are numerous competing theories with respect to the role of lateral parietal cortex during recognition memory. One potentially useful way to parse these theories is by whether their functional characterizations would be essential for

translating memory evidence into accurate recognition judgment (causal models) or instead whether they posit a process that depends upon recognition signals, but does not directly support their retrieval or the explicit judgment accuracy of stimuli as novel or familiar (consequential models). One example of a consequential model is the Memory Orienting Model we propose here. In contrast, models that assume that the PPC accumulates or buffers episodic content, and that this function is vital for judgment of stimuli as recognized, are causal models. As detailed in the results section, none of the three regions we examined in left lateral parietal cortex is consistent with a causal role in accurate recognition judgment. The PoCG responds to maximally to novel, not familiar materials, and the mid IPS region shows a response that is entirely dependent upon the expectations of the observer.

This then leaves the aAG, a region more broadly linked to episodic retrieval in the recent functional imaging literature. However, there are at least four reasons that this particular area, as opposed to perhaps more ventral AG areas, is more clearly linked to orienting and not a causal role in recognition such as buffering or accumulating episodic content. First, the condition level contrasts did not support a causal role. Under a causal account activation should be concordant with memory strength since the region is storing recovered episodic content. However, two of the four direct contrasts directly contradicted this notion because the strength values were discordant with the activation values (Figure 4). Second, and related to the condition level effects, the activation patterns remained inconsistent with a causal role when we collapsed across response outcome. Thus even when the potential for criterion shifts to alter the average strength of evidence in the considered bins is eliminated, the pattern in aAG remained inconsistent with a causal account. The region only differentiated old and new materials (regardless of accuracy of response) under the “Likely New” cueing condition, not the “Likely Old” cueing condition (Figure 5). Because observers are discriminating the materials equally well across these two conditions (d' values are statistically equivalent) this again weighs against a causal role and favors the region as supporting an orienting response. Third, the pattern of multiple regression outcomes linking aAG activation and individual variation in accuracy (d') favored the Memory Orienting Model, not a causal model (Figure 6). Although the unexpected familiarity response (hit versus correct rejection activation following a “Likely New” cue) strongly predicted behavioral differences in accuracy in all three cueing conditions, the response of aAG under neither “Likely Old” cue nor the uncued condition reliably predicted accuracy within those same conditions. Thus the region only responds differentially following a “Likely New” cue and does so to the extent that violations of expectation are salient to the observers given their skill level. Fourth and finally, the aAG response observed in the current report is not spatially overlapping with the AG responses linked to subjective reports of recollection in the prior literature (see Kim 2011). As Figure 7 demonstrates, the center of mass of the region previously linked to subjective recollection is considerably ventral and somewhat posterior to the anterior AG response documented here. Furthermore, that region typically shows a deactivation, not an activation in response to memoranda and that finding was replicated here. The extracted betas from the more ventral region in the current research do not seem to easily translate into a recollection specific account, but they should not be over interpreted given that they are noisy and that this design was not targeted specifically towards evoking rich temporally extended recollections. Thus, while we present considerable evidence that recollection specific or causal recognition interpretations of the lateral parietal areas shown in Figure 3 are inappropriate, the current data do not strongly challenge or support claims that left ventral AG shown in other reports may support the buffering or accumulation of recovered episodic information (e.g., Yu, Johnson & Rugg 2012).

Convergence of Findings (Subjects, Conditions, Patient Populations)

The above empirical results argue in favor of an orienting framework for interpreting the role of lateral parietal cortex during recognition based on condition level and subject by condition level effects. However, it is also important to seek convergence across the fMRI and neuropsychological literatures, and here again, the Memory Orienting Model seems to fare better than accounts positing a causal role in recognition for the simple reason that damage to large portions of lateral parietal cortex does not seem to disrupt recognition accuracy. Thus while some reports do suggest alteration in the expression of confidence during memory judgment (e.g. Simons, et al., 2010), the clear consensus in this new research area is that these patients do not suffer from any impairment in the accuracy of recognition memory (Ciaramelli, et al., 2010; Simons, et al., 2010) (but see Davidson, et al., 2008). This was also the case in a recent report by Dobbins, Jaeger, Studer, and Simons (2012) who contrasted parietal patients, frontal patients and healthy controls on a version of the Explicit Memory Cueing task. Critically, the parietal patient group was unable to use the “Likely New” cues to appropriately bias their performance whereas both the frontal lobe patients and controls used these cues similarly. However, the performance of the parietal patients and control patients when uncued was statistically indistinguishable, underscoring the fact that standard recognition accuracy is not compromised in this group. Instead, their deficit seems to manifest in the inability to appropriately incorporate externally signaled biases into their recognition decisions.

Interestingly, the parietal patient and control groups did not differ in response to the “Likely Old” cue condition. These cues were not vigorously used by any of the three groups but nonetheless one can speculate why the “Likely New” cue condition should better differentiate the groups than the “Likely Old” condition given the fMRI findings here. As we further discuss below and as demonstrated in Figure 8, the unexpected familiarity response is extremely left lateralized. Indeed, in parietal cortex there is only a single lateral parietal region demonstrating that response and that is in left aAG. In contrast, in the right lateral parietal cortex there were only unexpected novelty and unexpected memory responses. Thus overall, there is less hemispheric redundancy observed for the unexpected familiarity response in comparison to the other two types of orienting-linked responses. Since the unexpected familiarity response is linked to the “Likely New” cueing condition, this may explain why orienting behavior linked to this cueing condition may be more easily disrupted following parietal lesion. It is also worth noting that the parietal lesions in Dobbins et al. (2012) were also somewhat left lateralized, which means that not only is the unexpected familiarity response localized to left lateral parietal cortex, but that this patient group was quite likely to have damage to this left lateralized region. Again, however, this is highly speculative at this point, particularly since as noted above, the use of the “Likely Old” cues in Dobbins et al. was moderate by all groups. Nonetheless, that patient study fits with the broader notion that the parietal response during recognition is likely the consequence, not the cause of recognition abilities and it, along with the current findings, suggests that parietal patients would be impaired in recognition memory orienting or biasing behavior.

Aside from our Memory Orienting Model, another potentially consequential model of parietal response during recognition is the attention to memory model of Cabeza, Ciaramelli, and colleagues (Cabeza, Ciaramelli, & Moscovitch, 2012; Cabeza, et al., 2008; Cabeza, et al., 2011). As noted in the introduction, this model makes a fundamental distinction between dorsal SPL and ventral parietal IPL responses during recognition with the dorsal parietal response linked to the monitoring or search for episodic content in effortful situations (so-called top down attention) and the ventral parietal cortex (supramarginal and angular gyri) supporting attentional capture by rich or vivid memory content (so-called bottom up attention). However, there are several potential problems in applying this model to the

current data. First and foremost, there is nothing within current attention to memory framework that would have predicted the three separate classes of orienting responses documented here. This is not to say that the framework might not be expanded post hoc to try to fit the findings within either top down or bottom up mechanisms. For example, during an initial review of this manuscript it was suggested that the left PoCG unexpected novelty response might reflect the exertion of greater top down monitoring when one unexpectedly encounters a novel stimulus. Thus perhaps novelty is rechecked or revalidated through increased monitoring of episodic content to make sure there is none actually available. The problem with this explanation however, is that it should apply to all unexpected memoranda; that is, increased monitoring should occur for unexpectedly familiar items in PoCG as well. However, as the dissociation in Figure 3 demonstrates, this does not occur and the PoCG does not differentiate memoranda following the “Likely New” cues even though old materials are unexpected in this condition and performance consequently declines. Instead, the mid-IPS region shown in Figure 3 shows such a general response, demonstrating increased activation to whichever class of memoranda is unexpected given the initial cue. More generally then, we suspect that the basic top down monitoring construct may prove to be too broad given the functional specialization the current data suggest in lateral parietal cortex.

A second set of challenges for the attention to memory model in light of the current data has to do with the spatial location of the responses. Within the framework a distinction is made between SPL for top down monitoring (typically BA 7) and IPL (supramarginal gyrus and angular gyrus) for bottom up attention. However, the unexpected novelty PoCG response is neither in the superior parietal lobule (or BA 7) nor is it in either of the IPL regions mentioned in the framework. Of course, one could expand the set of regions considered in the framework, but as with the post hoc explanation of the unexpected novelty response itself, doing so eliminates the simplicity and possibly the falsifiability of the original model.

Despite our reservations about trying to shoehorn the current data into the original attention to memory model, it is important to stress that the current data are consistent with the broad theme of that framework in that they suggest the lateral parietal response more likely reflects attentional mechanisms rather than memory processes per se. However, the current Memory Orienting Model account of these data, strictly assumes that these responses are consequential and not causal with respect to basic recognition ability, and the model assumes the responses reflect processes tied to orienting and investigation of discrepant memory signals. In contrast, the attention to memory model assumes an SPL top down monitoring process that seems to be theorized as important for recovering weak recognition evidence (i.e., potentially causal). It also assumes an IPL bottom up process that is clearly causal in nature since it is critical for recollections to capture the attention of the observer. Thus these two explanatory frameworks differ in important ways.

Functional Importance of Memory Orienting

In isolation, the qualitatively different patterns of response in left lateral parietal cortex support a functional interpretation linked to attentional orienting. However, aside from noting the pattern is consistent with orienting following violated memory expectations, understanding the potentially adaptive nature of that orienting requires consideration of the extra-parietal regions also demonstrating analogous response patterns. The most unique and left lateralized response pattern is the unexpected familiarity response in aAG. Aside from anterior angular gyrus, this contrast map also included left lateral premotor cortex and left anterior PFC (Figure 3). In a series of studies contrasting memory judgments that required identifying items from a specific prior task context (source memory judgment) versus those that could be identified on the basis of simple feelings of relative familiarity (item based memory judgment), Dobbins, Wagner and colleagues repeatedly identified the above three

areas as linked to source memory attempt (Dobbins, Foley, Schacter, & Wagner, 2002; Dobbins, Rice, Wagner, & Schacter, 2003; Dobbins & Wagner, 2005; Han, O'Connor, Eslick, & Dobbins, 2012). Figure 8b shows an overlay from these studies using spheres for tabled maxima closest to those shown here. It is clear that there is considerable correspondence despite the fact that those paradigms differed in materials and procedures. Additionally, the source versus item memory contrasts in those four studies were all highly left lateralized, just as is the selective familiarity orienting pattern here. These correspondences strongly suggest that the selective familiarity orienting response is linked to the engagement of regions critical for source memory monitoring when observers encounter unexpectedly familiar memoranda. As with the anterior angular gyrus response, it is important to note that characterizing the remaining regions as involved in source monitoring processes does not mean that their activation directly signals successful retrieval of episodic content. For example, Dobbins et al. (2003) directly contrasted activation in these regions during successful and unsuccessful source memory judgments. Although the activity was generally higher during source versus item memory judgments, accuracy did not differ across source hits versus source misses. This led to the general conclusion that the regions support source monitoring attempts, but that these attempts do not guarantee successful retrieval. Regardless, the key idea is that the unexpected familiarity response reflects an investigatory reaction to unexpected familiarity in the environment. The overlap of the current response with those in deliberate source monitoring studies suggests that following the initial orienting, observers engage in source monitoring in an attempt to resolve the discrepancy.

Taking the same general approach to understanding the unexpected novelty response, the most notable regions implicated outside the lateral parietal areas were what appear to be the frontal eye fields and medial SPL regions (Figure 3 green regions). Both regions are routinely implicated in visuo-spatial attention research and thought important for endogenous spatial orienting and planned eye movement respectively (e.g., Awh, Armstrong, & Moore, 2006; Corbetta, 1998; Kelley, Serences, Giesbrecht, & Yantis, 2008). Co-recruitment of these regions makes sense when an observer encounters an expectedly novel stimulus as further attention to, and visual inspection of, such stimuli is warranted and adaptive. Thus the unexpected novelty and familiarity responses represent two fundamentally different responses to a recognition anomaly given an observer's a priori expectations. Unexpectedly novel items do not lead to source monitoring but instead mobilize resources linked to visual inspection of the environment. In contrast, unexpectedly familiar items do not lead to heightened visuo-spatial processing resources linked to environmental exploration, but instead to an internally directed source memory monitoring processes that support source attribution.

Finally, numerous regions outside of lateral parietal cortex demonstrated more general invalid memory cueing effects, including midline pre-supplementary motor cortex, bilateral dLPFC and bilateral anterior insula (Figure 3 red areas). These areas are routinely implicated in controlled judgments across a host of domains and are assumed vital for overriding planned or automatic actions when they are contextually inappropriate (for review see Vincent, Kahn, Snyder, Raichle, & Buckner, 2008). Thus the fact that these regions display a general invalid cueing effect for both old and new memoranda, and that they are recruited when expectations linked to a generally valid cue are violated, makes sense. Thus the Explicit Memory Cueing paradigm appears to effectively isolate systems or networks involved in source memory monitoring, visuo-spatial orienting, and general cognitive or executive control. Critically, it is the strong expectations instilled in the observers via the generally valid cueing that presumably affords this pattern isolation. However, it is also the case that these systems are presumably also engaged when

expectations are not quite so strong and this in turn explains the frequent observation of these areas in prior recognition research.

More broadly, the patterns seen in Figure 3 make sense if one assumes that a key role of episodic memory is that of alerting observers for the need to investigate stimuli or situations that elicit unexpected memory signals. Thus unexpected novelty in the environment clearly should be investigated and since the signal is one of novelty, consulting long term memory for its disambiguation does not make adaptive sense. Instead, visual orienting and perceptual exploration are called for in such situations and in this light engagement of medial SPL and the frontal eye fields presumably prepares the observer to investigate the source of the novelty signal. In contrast, unexpectedly perceived familiarity also should be thoroughly investigated, particularly since stimuli can be familiar but nonetheless potentially threatening (or deceptive, etc.). Thus engaging a broader system linked to source memory monitoring, and conversely not orienting attention outwards, is an adaptive response to unexpected familiarity in the environment. Of course, it is important to keep in mind that the typical recognition memory experiment constitutes a highly unusual situation from an orienting perspective since the trials are randomized. That is, if one orients to, say, unexpected novelty in the actual environment it is unlikely that the evoking stimulus (or stimuli) will be subsequently immediately replaced in several seconds by a stimulus whose memory properties are randomly determined. Thus even though these robust orienting responses are likely highly adaptive, there is no reason to expect that they would benefit the observer in an environment that is specifically designed to not have any temporal continuity in the memory status of serially encountered objects; namely, a typical recognition experiment.

Conclusion

In conclusion, the left lateral parietal cortex appears to support functionally distinct attentional orienting processes triggered by early episodic recognition signals. We view the role of these responses as investigatory processes that are triggered by recognition signals when they are discordant with expectations. Because the orienting is the consequence of discrepant recognition signals we refer to this Memory Orienting Model as consequential and not causal with respect to recognition ability. A series of analyses supports this interpretation and the data demonstrate that individuals who are highly skilled at recognition also demonstrate the most robust orienting responses to familiar materials when they violate cued expectations. Additionally, the clear functional dissociations observed in left parietal cortex are consistent with the idea that the region likely subserves highly distinct cognitive processes, a finding which corresponds well with graph analytic techniques also suggesting considerable functional heterogeneity in parietal cortex (Nelson, et al., 2010; Ploran, et al., 2007).

Acknowledgments

This research was supported by National Institutes of Health grant R01 NIMH073982 to I.G.D.

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Figure 1.

Confidence and Accuracy During the Explicit Memory Cueing paradigm. Panel a) summarizes hit and correct rejection rates as a function of cueing conditions. Panel b) illustrates changes in mean expressed confidence as a function of the cueing conditions. Box is 1 standard error of the mean, Box plus whiskers is two standard errors of the mean. Filled boxes are hit trials whereas open boxes are correct rejection trials. The data demonstrate a dissociation of response accuracy and response confidence that has been successfully simulated by the dual process model of recognition.

Figure 2.

Initial ANOVA results with factors of Cue Condition (Likely Old, Likely New, Uncued [????]) and Response Type (Hit or Correct Rejection [CR]). Areas in red illustrate regions demonstrating a significant interaction of the factors (.001, 5 voxel threshold). Areas in green demonstrated main effect of Response Type at same threshold. Bar plots show the extracted average betas from the two regions of interest denoted by the orange circles, namely, post-central gyrus (PoCG) and anterior angular gyrus (aAG).

Memory Orienting Patterns

Figure 3.

Targeted contrasts and masking procedures isolated three different patterns of response in left lateral parietal cortex. The left anterior IPS/PoCG region in green illustrated an unexpected novelty response pattern with bar plot a) illustrating the pattern across Cue Conditions and Item Types. The posterior anterior angular gyrus region in blue demonstrated an unexpected familiarity response with bar plot b) illustrating the pattern of response across Cue Conditions and Item Types. The mid IPS region in red demonstrated a general unexpected memory effect with bar plot c) illustrating the pattern of response across Cue Conditions and Item Types.

Figure 4.

Comparison of mean activation and mean implied evidence strength in anterior angular gyrus. The bottom distributions illustrate the relative location of the decision criteria and evidence distributions for the "Likely New" and "Likely Old" cue conditions under a basic signal detection model. Triangles within the distributions help illustrate the fact that under the model, the criterion determines how extreme the strength values are that contribute to the reports. Numeric values indicate the average strength in the truncated sections of the distributions with these values listed alongside the distributions and the activation bars in the plot above. See text for more detail.

aAG Activation – Collapsed Across Response Outcome

Figure 5.

Anterior angular gyrus activation regardless of response outcome. Data were extracted from the aAG ROI under a model that ignored response outcomes. Thus the model shows the average activation to items under the two active cue conditions, regardless of observer responses. These data replicate the patterns seen when instead using only correct reports in Figure 3.

Figure 6.

Contrasting brain-behavior (subject level) predictions of causal versus consequential accounts of aAG activation. Under a causal account such as the episodic buffer or accumulation models, aAG signal corresponds to the amount or fidelity of retrieved memory evidence. Hence, within each cueing condition, the relative activation for hits and correct rejections should predict individual variation in subject accuracy within each of those conditions. The top panel illustrates the three regressions testing this prediction. The thickness of arrows corresponds the size of the R-squared values of each model. The bottom panel illustrates the predictions of the Memory Orienting Model, a consequential account of aAG activation. The sizes of the unexpected familiarity differential response (Likely New cue condition) is assumed to reflect the salience of the discrepancy between memory signals and expectations. Thus the model predicts that an reliable behavioral indicator of relative subject accuracy should be associated with the differential activation response observed under the Likely New cue.

Figure 7.

Extraction of activation betas from ventral angular gyrus center of mass identified by Kim 2012. This region is associated with subjective reports of remembering and high confidence recognition. Unlike the anterior angular gyrus response implicated in the current study, the ventral region shows a pattern of deactivation.

Figure 8.

Panel a) demonstrates that there was a high degree of overlap in the parietal and frontal regions isolated via the selective familiarity response in the Explicit Memory Cueing paradigm and resting state functional connectivity in a separate group of subjects. In the latter group, the three left parietal ROIs were taken from the current cueing study and used to create three resting state seeds that were simultaneously present in the design matrix. A map was then created using the contrast of the anterior angular gyrus seed (1) versus the mid IPS and anterior IPS/PoCG seeds ($-.5$ $-.5$). This map was thresholded at .001 with a 5 voxel extent, within the mask identified by the unexpected familiarity response in the current cueing study (inclusive masking with a .001 threshold). Thus the two methods provide convergent evidence that the three regions are functionally integrated. Panel b) demonstrates overlap between the current selective familiarity orienting response and four prior studies contrasting source memory with item memory judgments (see text for further description and citations). White spheres represent maxima within those studies that were deemed proximal to the current selective familiarity orienting response by visual inspection.

Table 1

Unexpected familiarity, unexpected novelty, and unexpected memory response regions. (see table on next page).

Unexpected Familiarity: Hit>CR under LN cue ($p<.001$, 5 contiguous voxels) exclusively masked with non-directional Hit-CR F test under LO cue ($p>.25$)					
Number of Voxels	T value	X	Y	Z	Region
133	5.13	-33	-70	49	L. Inferior Parietal Lobule, Angular Gyrus
123	4.88	-6	-85	-35	L. Cerebellum
98	5.90	-36	56	-5	L. Middle Orbital Gyrus
86	4.67	-36	23	49	L. Middle Frontal Gyrus
63	4.99	0	-40	28	L. Posterior Cingulate Cortex
63	4.91	-6	-55	-41	L. Cerebellum
31	4.57	-9	11	4	L. Caudate Nucleus
20	4.91	-3	35	58	L. Superior Medial Gyrus
18	4.28	18	-103	1	Area 17, R. Calcarine Gyrus
16	4.36	39	-70	-50	R. Cerebellum
7	4.68	-9	38	40	L. Superior Medial Gyrus
7	3.83	12	2	16	R. Thalamus
6	3.48	-39	-70	-29	L. Cerebellum
5	3.72	-15	-100	-14	Area 17/18, L. Lingual Gyrus

Unexpected Familiarity: CR>Hit under LO cue ($p<.001$, 5 contiguous voxels) exclusively masked with non-directional Hit-CR F test under LN cue ($p>.25$)					
Number of Voxels	T value	X	Y	Z	Region
524	5.19	33	5	61	Area 6/2, R. Frontal/Postcentral Gyrus
157	5.42	-45	-34	43	L. Inferior Parietal Lobule
116	5.20	-27	-4	55	L. Precentral Gyrus
106	4.58	30	56	13	R. Superior/Middle Frontal Gyrus
44	3.87	21	-67	58	R. Superior Parietal Lobule/Precuneus
37	4.40	-54	11	16	L. Inferior Frontal Gyrus

Unexpected Familiarity: CR>Hit under LO cue (p<.001, 5 contiguous voxels) exclusively masked with non-directional Hit-CR F test under LN cue(p>.25)					
Number of Voxels	T value	X	Y	Z	Region
23	4.10	-36	44	25	L. Middle Frontal Gyrus
10	3.83	-21	-64	55	L. Superior Parietal Lobule
6	4.12	9	26	31	R. Middle Cingulate Cortex
6	3.65	-3	-16	-5	Thalamus
5	3.76	-12	14	67	Area 6, L. SMA

Unexpected Memory: Hit>CR under LN cue (p<.001, 5 contiguous voxels) inclusively masked with CR>Hit under LO cue (p<.001)					
Number of Voxels	T value	X	Y	Z	Region
353	6.71	0	26	52	L. Superior Medial Gyrus
257	6.74	-51	20	34	L. Inferior Frontal Gyrus
189	5.48	48	20	43	R. Middle/Inferior Frontal Gyrus
153	6.32	36	26	-8	R. Inferior Frontal Gyrus
89	5.18	45	-58	46	R. Inferior Parietal Lobule/Angular Gyrus
62	7.23	-30	23	-8	L. Insula/Temporal Pole
27	4.34	-33	-52	43	L. Inferior Parietal Lobule
13	4.49	33	62	1	R. Middle Frontal Gyrus
6	3.78	-24	-100	-2	L. Middle Occipital Gyrus

Table 2

Multiple regression results predicting subject accuracy (d') using aAG activation during hits and correct rejections under the three cueing conditions. Regressions correspond to the five separate regressions illustrated in Figure 6. Note that paths labeled 1 and 4 in that figure constitute the same multiple regression.

Behavioral (DV)	Activation Predictors	Activation	Estimate	Std. Error	t value	Pr(> t)	R-square
d' ("Likely New")	aAG during "Likely New"	(Intercept)	1.16378	0.19934	5.838	7.98E-05	
	paths 1 and 4 Figure 6	Hit	0.31543	0.08755	3.603	0.003626	
		CR	-0.62741	0.11644	-5.388	0.000163	0.714
d' ("Likely Old")	aAG during "Likely New"	(Intercept)	1.13224	0.20906	5.416	0.000156	
	path 5 Figure 6	Hit	0.19222	0.09182	2.094	0.058203	
		CR	-0.32705	0.12212	-2.678	0.020106	0.395
d' (Uncued)	aAG during "Likely New"	(Intercept)	0.90689	0.20694	4.382	0.000893	
	path 6 Figure 6	Hit	0.32087	0.09089	3.53	0.004143	
		CR	-0.35493	0.12088	-2.936	0.01246	0.54
d' ("Likely Old")	aAG during "Likely Old"	(Intercept)	1.50498	0.2431	6.191	4.65E-05	
	path 2 Figure 6	LOhit	-0.10657	0.16289	-0.654	0.525	
		LOCR	-0.03622	0.1186	-0.305	0.765	0.059
d' (Uncued)	aAG during Uncued (???)	(Intercept)	1.5381	0.34663	4.437	0.000811	
	path 6 Figure 6	UChit	-0.05599	0.15411	-0.363	0.722678	
		UCCR	-0.03729	0.1014	-0.368	0.719476	0.024