

Parietal cortex tracks the amount of information retrieved even when it is not the basis of a memory decision

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ABSTRACT

Although the parietal cortex is not conventionally associated with memory, a large number of recent fMRI studies have suggested that the parietal cortex may play a role in recognition memory. Activity in the lateral parietal cortex is correlated with the subjective impression that an item is old. It has therefore been proposed that the parietal cortex may be determining the outcome of the decision process. For instance, parietal cortex may be temporally integrating mnemonic information in favor of an “old” response until a decision criterion is reached (mnemonic accumulator hypothesis). Activity in the lateral parietal cortex also increases with the amount of information retrieved. It has thus been proposed that lateral parietal cortex may be acting as a working memory buffer into which retrieved information is transferred (output buffer hypothesis). In previous studies, confidence in an “old” decision and the amount of information retrieved have been confounded, thus making these competing hypotheses difficult to differentiate. We used a frequency discrimination paradigm to dissociate the amount of information retrieved from memory and decision certainty. We found that lateral and medial regions of parietal cortex previously implicated in recognition memory track the absolute amount of information retrieved even when this is not the basis of the recognition decision. Our results present a serious challenge to proposals that the parietal cortex contributes directly to the recognition decision process.

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In recent years, interest in the parietal cortex among memory researchers has been growing as a steadily increasing number of neuroimaging studies of recognition memory implicate the parietal cortex. Activity in the left lateral parietal cortex is greater for old items correctly classified as old than new items correctly classified as new (see Cabeza et al., 2008; Rugg and Henson, 2002; Vilberg and Rugg, 2008; Wagner et al., 2005 for reviews). Activity in the left lateral parietal cortex is larger when items are well-remembered because they have been elaborately encoded (Shannon and Buckner, 2004) or because they have been studied repetitively (Wheeler and Buckner, 2003). Activity in left lateral parietal cortex increases with the rated confidence that an item is old (Yonelinas et al., 2005). Interestingly, activity in left lateral parietal cortex tracks the subjective impression that an item is old, regardless of whether the item is in fact old: new items incorrectly classified as old are associated with greater activity than old items incorrectly classified as new (Kahn et al., 2004; Wagner et al., 2005; Wheeler and Buckner, 2003). These properties of the left lateral parietal cortex generalize across several material types, including visual and non-visual stimuli (Shannon and Buckner,

2004) and verbal and non-verbal stimuli (Guerin and Miller, 2009). These effects also persist across changes in response mapping, such as responding only to old items versus responding only to new items (Shannon and Buckner, 2004). As a result, the apparent mnemonic properties of the parietal cortex do not appear to be a byproduct of some low-level feature of the recognition task, such as sensory or motor processes. Rather, these patterns of activity in the parietal cortex appear to be tracking a more abstract cognitive operation that is somehow systematically correlated with the retrieval of information from memory.

Wagner et al. (2005) outlined three proposals to account for these findings. Each of these hypotheses takes a previously hypothesized function of the posterior parietal cortex and applies it to the memory phenomena.

The *attention to internal representations hypothesis* builds on the role of the parietal cortex in perceptual attention (Corbetta and Shulman, 2002). It posits that in addition to its role in directing attention towards behaviorally relevant external stimuli, regions of posterior parietal cortex may also enable one to direct attention towards behaviorally relevant *internal* representations, such as mnemonic information dependent upon the medial temporal lobes (Rugg and Henson, 2002; Wagner et al., 2005). This proposal has been extended by Cabeza (2008) and Ciaramelli et al. (2008). Building on

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the dual system framework of Corbetta and Shulman (2002), these researchers have proposed an additional distinction between a dorsal region that supports top down attention to internal representations and a ventral region that supports bottom up attention to internal representations.

The *output buffer hypothesis* builds on the ideas of Baddeley (2000) and proposes that regions of parietal cortex may serve as a working memory buffer that maintains retrieved information in active neural firing patterns that are available to decision making processes. Vilberg and Rugg (2008) elaborated this proposal further by specifically emphasizing the potential role of the left lateral parietal cortex in enabling an integrated, multi-modal episodic representation, drawing a close parallel to Baddeley's (2000) concept of an "episodic buffer". They suggest that "by contributing to the generation and maintenance of an integrated representation of retrieved information, inferior parietal cortex acts as an interface between episodic memory and the executive systems that monitor and control on-line processing." (pg. 1794). As pointed out by both Wagner et al. (2005) and Vilberg and Rugg (2008), it is unlikely that the parietal cortex serves this function entirely on its own. Rather, it is likely that the parietal cortex enables a working memory buffer through its interaction with other cortical systems involved in the storage of information, such as the medial temporal lobe and sensory cortex.

The *mnemonic accumulator hypothesis* is motivated first and foremost by the observation that activity in lateral parietal cortex tracks the subjective impression that an item is old. If parietal cortex is tracking the outcome of the decision process, then it is possible that it is *determining* the outcome of the decision. Regions of the posterior parietal cortex have been shown to play such a role in the context of perceptual decision making: Gold and Shadlen (2007) have shown that neurons in area LIP accumulate conflicting sensory signals from area MT over time until a decision criterion is reached. According to the mnemonic accumulator hypothesis, regions of the posterior parietal cortex may play an analogous role in the context of recognition decision making, perhaps accumulating information originating from medial temporal regions. Cognitive psychologists have long suspected that recognition memory relies on a decision making process that entails the temporal integration of evidence. Indeed, the influential model of Ratcliff (1978), which so nicely accounts for the decision making properties of LIP neurons (Gold and Shadlen, 2007), was first proposed as a theory of recognition memory, not as a theory of perceptual decision making per se.

The extant research is primarily based on variants of yes/no recognition. One limitation of this task is that it confounds the amount of information retrieved from memory with the certainty with which an old response is made. This is because, as one retrieves more information from memory regarding the previous occurrence of the test item, one obtains more evidence that an item is old, and is thus more likely to respond "old" with high certainty. This is particularly problematic when attempting to distinguish between the output buffer hypothesis and the mnemonic accumulator hypothesis. Both models will predict that activity in left lateral parietal cortex will be larger when a person responds "old" and, furthermore, will be larger when a person responds "old" with high confidence rather than low confidence. However, the two models make this prediction for very different reasons. The output buffer hypothesis states that activity is larger in these circumstances because more retrieved information is being maintained in working memory. The mnemonic accumulator model states that activity is larger in these circumstances because there is more accumulated evidence in favor of an old response. Does left lateral parietal cortex track the retrieval of information per se or does it track the amount of evidence in favor of the current memory decision? As long as these two psychological variables are conflated, it will be difficult to distinguish between these two hypotheses.

We used a frequency discrimination task to dissociate the amount of information retrieved and decision certainty. In this task, the

participant studies a series of stimuli that repeat a variable number of times. Then, in the memory test, the participant is presented with two items, one of which was presented more frequently than the other during the study session. The participant's task is to choose the stimulus that was presented more frequently.

Memory for frequency and standard recognition memory appear to rely on very similar memory systems. Judgments of frequency are impaired in Korsakoff's patients (Huppert and Piercy, 1978; Meudell et al., 1985; Strauss et al., 1985). Frequency discrimination was severely impaired in the famous patient H.M. (Sagar et al., 1990, Table 4), though some unilateral medial temporal lobe patients do not show statistically significant impairments (Smith and Milner, 1988). There is some evidence that memory for frequency is also dependent on the right frontal lobe. An fMRI study found increased activity in the right dorsolateral prefrontal cortex during judgments of frequency, relative to standard recognition (Dobbins et al., 2004). Further, patients with right frontal damage were found to be impaired on a frequency discrimination task (Smith and Milner, 1988). Judgments of frequency and frequency discrimination are impaired in older adults, even when older adults show intact implicit memory for the same information (Wiggs et al., 1994).

Recognition memory is widely believed to rely on two distinct processes: familiarity and recollection. Familiarity is the impression that an item has been encountered recently without the retrieval of further details. Recollection is the retrieval of specific contextual details, such as what you were thinking at the time the item was encountered (Yonelinas, 2002). Like standard recognition memory, memory for frequency appears to depend on both familiarity and recollection. The partial reliance of frequency judgments on familiarity can be seen in the tendency of study duration (Hintzman, 2004) and the similarity of a test item to the studied items (Hintzman et al., 1992) to bias judgments of frequency. On the other hand, recollection also appears to make a contribution to memory for frequency. Judgments of frequency are superior following "deep" encoding conditions (e.g., Hintzman and Hartry, 1990), which is generally viewed as a property of recollection (Yonelinas et al., 2005). Furthermore, when participants report that they remember details of the context in which an item was encountered (a "remember" response), their judgments of frequency are high and reasonably accurate. However, if they say they cannot remember details of the context, their judgments of frequency are low and far less accurate (Hintzman, 2001).

We assume that items that were studied more frequently are, on average, associated with the retrieval of more information during the memory test, though we do not explicitly test this in the current study. However – in contrast to yes/no recognition – in frequency discrimination, the decision is based on the *relative* amount of information retrieved (Hintzman and Gold, 1983; Hintzman and Stern, 1984). When the difference in frequency between the two items is large, participants do well. When the difference is small, participants do poorly. Reaction time data strongly suggest that participants explicitly compare their memory for the two items: reaction times are inversely related to the difference in frequency between the two items, regardless of the absolute frequency of the items (Hintzman and Gold, 1983; Hintzman et al., 1981).

If left lateral parietal cortex tracks the absolute amount of information retrieved from memory, regardless of the specific nature of the memory decision required by the task, as the output buffer hypothesis predicts, then activity in this region should increase with the absolute frequency of the test items, regardless of the difference in frequency between the test items. However, if left lateral parietal cortex tracks the certainty of the memory decision, perhaps because it is a component of the decision making mechanism, then activity in this region should be large when the difference in frequency between the test items is large, regardless of the absolute frequency of the test items.

Materials and methods

Participants

16 participants (8 male) between 19 and 30 years old (mean = 24) participated after giving informed consent, as approved by the UCSB Human Subjects Committee. Data from one participant was replaced because she failed to complete the experiment in its entirety. All participants were right handed. Edinburgh Handedness Inventory scores ranged between 54 and 100 (mean = 91).

Stimuli

576 faces drawn from the FERET database served as stimuli. The faces were selected to be front facing against a white background with a neutral expression and without glasses. They were cropped at the boundaries of the face, converted to grayscale, normalized for size and resolution, and roughly normalized for brightness and contrast. Stimuli were randomly assigned to conditions individually for each participant. Stimuli were back projected onto a screen at the head of the scanner bore and were visible to the participant by a mirror mounted on the head coil. Stimuli were controlled by a laptop running the Psychophysics Toolbox 3 (www.psychtoolbox.org). Stimulus presentation was synchronized to the acquisition of each functional volume.

Task

The memory test was divided into a series of 8 study-test cycles. To avoid fatigue, the experiment was further divided into two sessions of 4 study-test cycles each, spaced 24 h apart. During the study phase, the participant was presented with 18 faces presented only once, 18 faces presented twice, 18 faces presented 5 times, and 18 faces presented 6 times. This produced a total of 72 faces and 252 study trials. The trials were ordered randomly, with the constraint that the same item could not be presented in two consecutive trials. On each trial, the face was presented for 1.5 s and the participant was instructed to press the left button if the face was “pleasant” and the right button if the face was “unpleasant”, using an MRI compatible button box held in the right hand. fMRI data was not collected during the study phase, though the participant was inside the scanner bore.

The test phase immediately followed the study phase. fMRI data was collected during the test phase. The participant was presented with two faces from the immediately preceding study phase, on either side of a cross hair. The frequency of the items was varied to produce three trial types: low–low, low–high, and high–high. A low–low trial is a pairing of a low frequency item (1 or 2) with another low frequency item (1 or 2). A low–high trial is a pairing of a low frequency item (1 or 2) with a high-frequency item (5 or 6). A high–high trial is a pairing of a high-frequency item (5 or 6) with another high-frequency item (5 or 6). Half the time, the lower frequency item was presented on the left side, as determined by a random ordering. The participant was presented with 12 trials of each type, 36 total. Each trial lasted 4 s. In addition to the frequency discrimination trials, there were 18 fixation baseline trials in each test session, each 4 s long. Furthermore, each functional run began and ended with 12 s of fixation. The ordering of all trials was determined randomly individually for each participant. Across the 8 study-test cycles, there were a total of 96 test trials per condition.

MRI data acquisition

Participants were scanned at the UCSB Brain Imaging Center using a 3 T Siemens TIM Trio scanner with a standard 12-channel head coil. Cushions were placed around the head to minimize head motion. Functional runs consisted in a T2*-weighted single shot gradient-

echo, echo-planar sequence sensitive to BOLD contrast (TR = 2 s; TE = 30 ms; FA = 90°) with generalized autocalibrating partially parallel acquisitions (GRAPPA). Each volume consisted of 33 slices acquired parallel to the AC–PC plane (interleaved acquisition; 3 mm thick with .5 mm gap; 3 mm × 3 mm in-plane resolution; 64 × 64 matrix). Four volumes were discarded prior to task onset to allow for tissue magnetization, followed by the collection of 120 volumes in each functional run. In addition to the functional data, a high-resolution anatomical image was collected for each participant using a FLASH sequence (TR = 15 ms; TE = 4.2 ms; FA = 20°; 256 × 256 matrix; FOV 240–260 mm; 192 sagittal slices 3D acquisition; .89 mm thick).

MRI data analysis

Preprocessing

Standard preprocessing was conducted using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). Images were realigned to correct for minor head motion. No participant moved by more than 3 mm or 2° within a functional run. The functional images were coregistered to the anatomical image. The anatomical image was normalized (using combined segmentation and normalization) to conform to the MNI-152 template and the parameters of this transformation were applied to the functional images, which were re-sampled to 2 mm isotropic voxels. All reported stereotaxic coordinates refer to the MNI template and are reported as (x,y,z). The functional data were smoothed using an isotropic Gaussian kernel (FWHM = 8 mm).

General linear model

Subsequent analysis was conducted using customized programs implementing a standard least-squares voxel-wise general linear model, as described in Guerin and Miller (2009). Briefly, to model the event-related response, the response at each peri-stimulus time point was modeled by a separate parameter (Ollinger et al., 2001). We used 10 parameters to model a total window length of 20 s. Each trial type of interest was modeled by a unique set of 10 parameters. We modeled 4 trial types: low–low, low–high correct, low–high incorrect, and high–high. We distinguished between correct and incorrect only for the low–high condition because in the other conditions participants' responses were dominated by guesses. The low–high correct trial type is of particular interest because we expect that on these trials the perceived difference in frequency between the items is large. The low–high incorrect trial type is of less interest and is based on a much smaller number of trials, since participants made relatively few errors in this condition. As a result, we only included the low–high correct trial type in our whole-brain analyses. Nonetheless, we include the low–high incorrect trial type in our figures to provide a complete representation of the results. A constant and a linear drift term were included separately for each functional run.

Contrasts and random effects analysis

To contrast responses between trial types, we summed the 2nd, 3rd, and 4th time points of the estimated event-related response. This captures the peak of the response while avoiding the undershoots that are sometimes observed at the very beginning or end of the response. Two critical contrast maps were constructed. The first compared the low–high correct trials to the average of the low–low and high–high trials. Regions revealed by this contrast are correlated with the basis of the decision: the difference in frequency between the items. The second contrast tested for a linear increase, such that high–high > low–high > low–low. Mathematically, this is equivalent to a direct subtraction of the low–low condition from the high–high condition (contrast vector = [−1 0 1]). Regions revealed by this contrast are correlated with the absolute amount of information retrieved from memory. These contrast maps were then passed to a second-level random-effects analysis that consisted in testing the contrast against

zero using a voxel-wise single-sample *t* test. The resulting *t* maps were thresholded at $p < .001$, extent $\geq 30 \text{ mm}^3$. For each reported activation, we also indicate whether the activation survives a false discovery rate (FDR) correction at $p < .05$ (Benjamini and Hochberg, 1995). For visualization purposes, group *t* maps were rendered onto 3D inflated brains using the CARET software (Van Essen, 2005).

Results

Behavioral data

Fig. 1 shows the mean percent correct and reaction time for each of the three conditions. The main effect of condition on accuracy was significant [$F(2,30) = 95.05$, $p < .001$]. Accuracy was greater in the low–high condition than the low–low condition [$t(15) = 8.77$, $p < .001$] and the high–high condition [$t(15) = 12.69$, $p < .001$]. Accuracy was also larger in the low–low condition than the high–high condition, though this difference was much smaller [$t(15) = 3.89$, $p = .001$].

In the low–low and high–high conditions, participants performed very poorly. It is important to emphasize that this was by design. Nonetheless, one may be concerned that in these conditions participants are simply not performing the task. However, given that participants are performing very well in the low–high condition and the conditions are randomly intermixed, this is an implausible explanation of the results.

The mean reaction time was obtained by first calculating each participant's median reaction time and then averaging across participants. The reaction time data is reported separately for correct and incorrect responses. The main effect of condition on reaction time for correct responses was significant [$F(2,30) = 15.50$, $p < .001$]. Reaction times for correct responses were longer in the low–low condition than in the low–high condition [$t(15) = 4.69$, $p < .001$] and the high–high condition [$t(15) = 4.07$, $p = .001$]. Reaction times for correct responses did not differ significantly between the low–high and the high–high conditions [$t(15) = .85$, $p = .41$]. There was a main effect of condition on reaction time for incorrect responses [$F(2,30) = 13.14$, $p < .001$]. Reaction times for incorrect responses in the low–low condition were longer than reaction times for incorrect responses in the high–high condition [$t(15) = 5.33$, $p < .001$]. Reaction times for incorrect responses in the low–high condition were longer than reaction times for incorrect responses in the high–high condition [$t(15) = 3.92$, $p = .001$]. Reaction times for incorrect responses did not differ between the low–low and low–high conditions [$t(15) = 1.02$, $p = .32$].

One might have expected the plots of reaction times to be U-shaped, with faster reaction times in the low–high condition reflecting the fact that this is the easiest condition. However, previous work on the frequency discrimination task has shown that reaction times exhibit a “congruency effect” (Hintzman and Gold, 1983). When participants are asked to select the most frequently studied item, they respond more quickly to frequently presented items, over and beyond the effects of discrimination difficulty. If participants are asked to select the least frequently presented item, the reaction time pattern is reversed. Thus, the reaction time data obtained in this experiment had been anticipated based on this previous work.

fMRI data

We interrogated the neuroimaging data with two contrasts. The first contrast compared the low–high condition to the average of the other conditions. Regions revealed by this contrast are correlated with the basis of the decision: the difference in frequency between the two items. No region was more active in the low–high condition at our statistical criteria ($p < .001$, extent $\geq 30 \text{ mm}^3$). To aid the reader in determining the role of statistical power in this outcome, Supplementary Fig. 1 provides the same data at a much more lenient threshold ($p < .05$, extent $\geq 30 \text{ mm}^3$). We caution the reader that this map is likely to include a large number of false positives and that over interpretation of data falling outside regions predicted *a priori* is likely to lead to erroneous conclusions. Nonetheless, the anterior intraparietal sulcus and anterior supramarginal gyrus activations, which are anterior to the typical parietal memory effects, should be interrogated in future work.

One region in the anterior cingulate was less active in the low–high condition ($-8, 22, 46$; Fig. 2). This result does not survive an FDR correction ($p < .05$). We also incidentally observed that, within the low–high condition, the anterior cingulate response was larger on incorrect trials than correct trials, $t(15) = 3.52$, $p = .003$.

The second contrast tested a linear increase across the conditions, such that high–high > low–high > low–low. Regions revealed by this contrast track the absolute amount of information retrieved. This contrast revealed activity in numerous parietal areas, most prominently in the angular gyrus and precuneus (Fig. 3). All voxels classified as significant for this contrast also survive an FDR correction ($p < .05$). The pattern of results closely resembles that obtained in other experiments (e.g., Wagner et al., 2005).

To complement this analysis, we also conducted an analysis in which incorrect responses were excluded for all three trial types (in the subject-level analysis, errors were coded as a fourth condition of no interest). Supplementary Fig. 2 shows the results of this analysis in

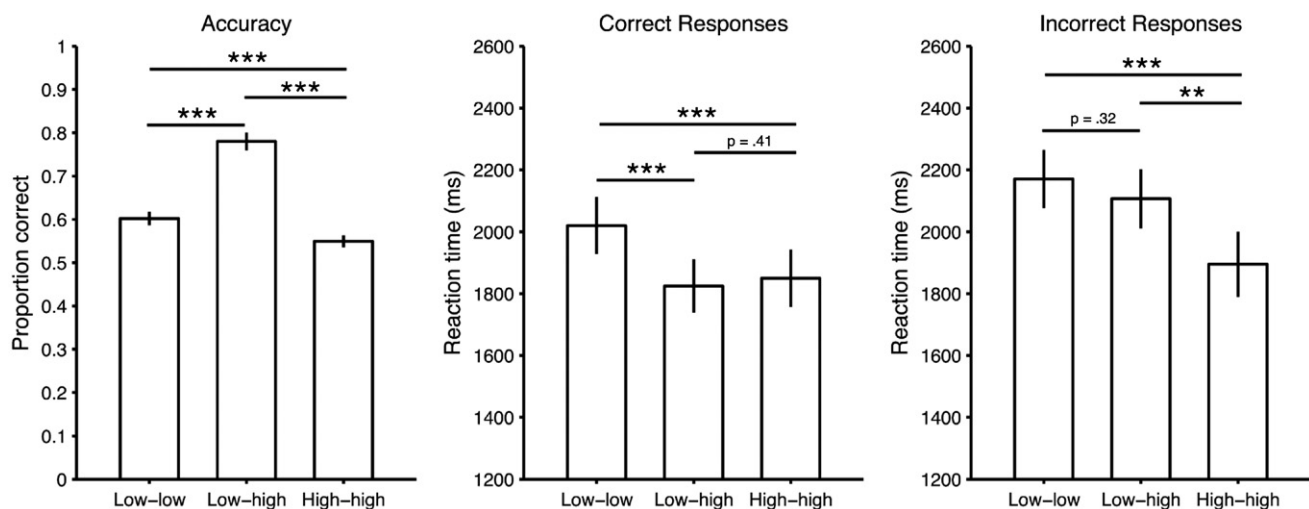


Fig. 1. Accuracy and reaction time. Error bars = $\pm$ s.e.m. *** $p \leq .001$. ** $p < .01$.

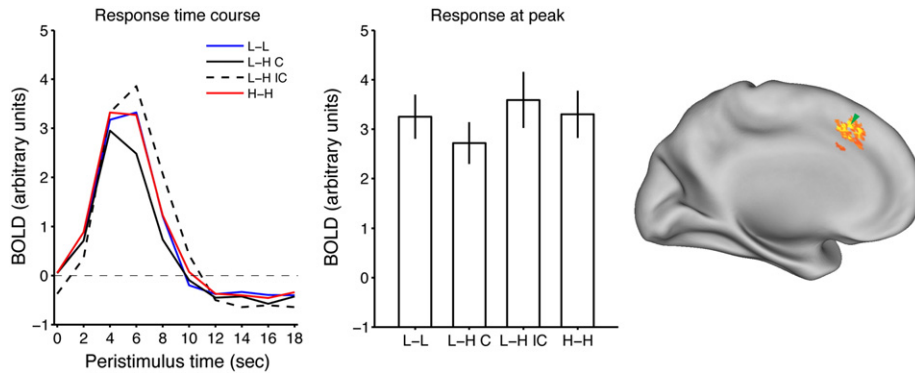


Fig. 2. Anterior cingulate region tracking decision uncertainty ($-8, 22, 46$). Plots are based on an average of all significant voxels within 12 mm of the peak. Response at peak is the average of the 3rd and 4th response time points (4 and 6 s). The far right panel shows the medial wall of the left hemisphere. The approximate location of the peak is indicated by the green arrow. L-L = low-low; L-H C = low-high correct response; L-H IC = low-high incorrect response; H-H = high-high. Error bars = $\pm$ s.e.m.

the same form as Fig. 3. Because this analysis has much less power, the threshold has been lowered to $p < .01$ extent ≥ 30 mm³ to aid visual comparison of the topography of activations to those shown in Fig. 3. The two topographies closely resemble one another. Supplementary Fig. 3 shows this data at the same threshold as Fig. 3 ($p < .001$, extent ≥ 30 mm³). Although an analysis restricted to correct responses for all three trial types has reduced power, it produces a qualitatively similar pattern of results.

It should be cautioned that the contrast shown in Fig. 3 and Supplementary Figs. 2 and 3 is based on the high-high and low-low trial types. This is an efficient and powerful statistical test for detecting a linear increase across conditions. However, this test does not strictly require that the low-high condition is numerically intermediate between the low-low and high-high conditions. To establish this, further confirmatory tests are required. Therefore, pairwise comparisons were conducted in each ROI. The results of these comparisons are indicated in Fig. 3 and Supplementary Fig. 2.

The patterns of laterality in lateral parietal cortex are worth noting. Previous work has shown that lateral parietal memory effects are lateralized to the left for both words and nonfamous faces (Guerin and Miller, 2009; cf. Klostermann et al., 2009). The largest effect on the lateral surface is in the left angular gyrus, where the effect is larger on the left (e in Fig. 3; $-44, -64, 22$) than on the right ($(44, -64, 22)$; $t(15) = 2.95$, $p = .01$). However, in a distinct region in the intraparietal sulcus, the effect is larger on the right (h in Fig. 3; $40, -46, 40$) than on the left ($(-40, -46, 40)$ $t(15) = 2.58$, $p = .02$). The patterns of laterality in these two regions differ significantly, as indicated by a region $\times$ hemisphere interaction [$F(1,15) = 17.73$, $p < .001$]. These results raise the possibility that the tendency of parietal memory effects to be lateralized to the left does not generalize across the full extent of the parietal cortex.

In addition to the parietal effects, more modest effects were observed in the left thalamus ($-14, -12, 10$), the left superior/middle frontal gyrus ($-16, 34, 42$), the left anterior prefrontal cortex ($-18, 60, 10$), the right superior/middle frontal gyrus ($20, 32, 36$), and the right superior/middle temporal gyrus ($64, -32, -10$).

Discussion

Using a frequency discrimination task, we found that regions of parietal cortex previously implicated in recognition memory did not track the certainty of the decision. Rather, parietal cortex tracked the amount of information retrieved from memory. These data present a serious challenge to any model that posits that parietal cortex is directly involved in the decision process. Rather, parietal activity appears to be intimately related to the retrieval of information per se, regardless of the specific nature of the decision required by the task.

The only brain region that we found to be correlated with decision certainty was the anterior cingulate, which was more active on low-low trials and high-high trials than on low-high trials. In other words, activity within this region was negatively correlated with decision certainty. Within the low-high condition, this region was more active on incorrect trials than correct trials. Previous research has implicated this region of the anterior cingulate in response conflict and error monitoring (Barch et al., 2001), so the present finding is not particularly surprising. Given these previous findings, it is likely that the effects in the anterior cingulate are not distinctly mnemonic in nature but rather reflect processes relating to making a decision under conditions of uncertainty. What is perhaps more surprising is that other regions associated with “cognitive control” were not also revealed in this contrast. For instance, previous observations suggest that the lateral inferior prefrontal cortex is more active when retrieval is effortful, regardless of whether an item is old or new (Velanova et al., 2003; see also Wheeler and Buckner, 2003). However, in a recent study, we failed to observe this effect (Guerin and Miller, 2009). Thus, even across yes/no recognition experiments manipulating difficulty, engagement of the lateral inferior prefrontal cortex has been inconsistent and may depend on the procedural details of the study. With this in mind, our failure to observe modulations of lateral prefrontal cortex in the current task seems less surprising.

Although we did not attempt to specifically measure the accumulation of evidence over time, the current data does bear on the accumulator model of parietal memory effects reviewed in the introduction. This is because the accumulator model is not merely a statement about the role of the parietal cortex in the integration of evidence over time, but also the role of the parietal cortex in the decision process. Specifically, the model proposes that the left lateral parietal cortex encodes the basis of the decision, such that if activity in this region exceeds a certain threshold, the subject responds “old”. In the current task, the basis of the decision is the relative frequency between items, which is highest in the low-high condition. Because lateral parietal cortex tracks the absolute frequency of items, rather than the relative frequency of items, it does not appear to encode the basis of the decision in a frequency discrimination task. If the left lateral parietal cortex does indeed encode the basis of the recognition decision, then it must be a relatively inflexible decision mechanism that does not generalize to discrimination tasks. As it stands, such an explanation of parietal memory effects would appear to have limited applicability. It seems reasonable to search for more general accounts that explain why we obtain parietal memory effects not only in standard recognition tasks, but also in tasks such as the frequency discrimination task.

Because reaction times tend to be faster at higher frequencies, reflecting a “congruity effect” (Hintzman and Gold, 1983), one might be tempted to argue that evidence is accumulating more

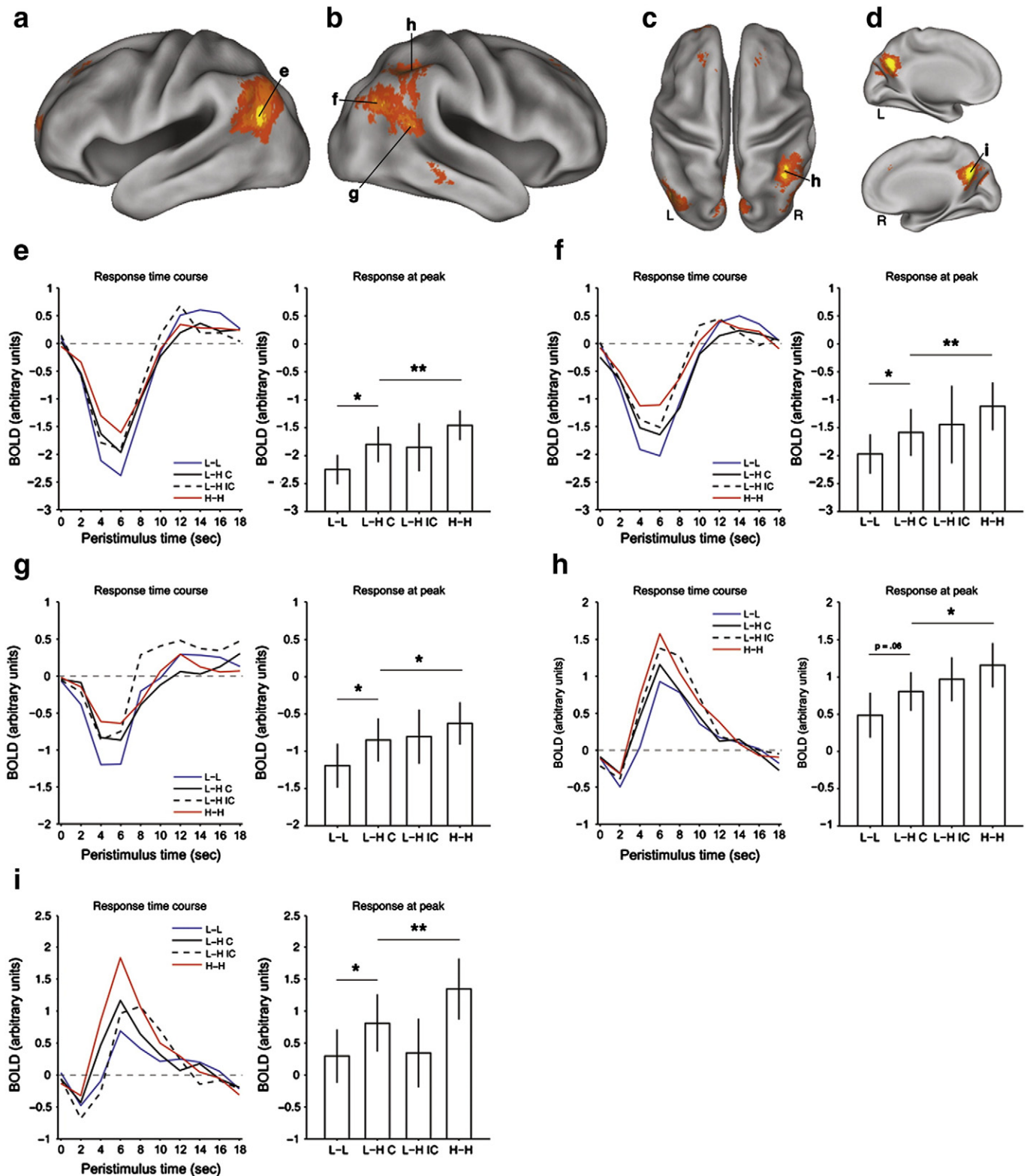


Fig. 3. Regions tracking the absolute amount of information retrieved. Contrast: high–high > low–low. Threshold: $p < .001$, extent ≥ 30 mm³. (a) Left lateral view. (b) Right lateral view. (c) Dorsal view looking down on the brain; anterior on top. (d) Medial view. (e) Left angular gyrus (−44, −64, 22). (f) Right angular gyrus (48, −68, 32). (g) Right supramarginal gyrus/temporal–parietal junction (48, −46, 20). (h) Right intraparietal sulcus (40, −46, 40). (i) Right precuneus (4, −64, 34); ROI includes left precuneus. Plots are based on an average of all significant voxels within 12 mm of the peak. Response at peak is the average of the 3rd and 4th response time points (4 and 6 s). L–L = low–low; L–H C = low–high correct response; L–H IC = low–high incorrect response; H–H = high–high. Error bars = $\pm$ s.e.m. * $p < .05$; ** $p < .01$. Confirmatory pairwise comparisons were not conducted for high–high > low–low because these regions were defined by that comparison.

rapidly in this condition. Given the large differences in accuracy across conditions, and the strong *a priori* basis for predicting this pattern in the accuracy data, it is difficult to argue that participants had a greater

evidentiary basis for their decision in the high–high condition. Indeed, the observed pattern in the reaction time data was predicted based on previous research on the “congruency effect” which supported the

conclusion that frequency discrimination is based on a comparison of the estimated frequencies of the two items, such that performance improves with increases in the difference in frequency between items (Hintzman and Gold, 1983). Additionally, the data from this experiment also casts doubt on this interpretation. Specifically, correct responses are associated with closely equated reaction times in the low–high and high–high conditions (in fact, they are numerically larger in the high–high condition; see Fig. 1). Given that reaction times are equated, the large discrepancy in accuracy must be taken to indicate a greater evidentiary basis for the decision in the low–high condition. Nonetheless, the analysis based on these very same trials indicates that activity in the critical parietal regions of interest is greater in the high–high condition than the low–high condition (see Supplementary Figs. 1 and 2). It is very difficult to see how this could be interpreted as a neural correlate of the accumulation of evidence.

Nonetheless, these issues do point to the importance of further investigating the temporal dynamics of recognition decisions. In the current study, we focused on large differences in the basis of the decision across trials. It will also be important to study the temporal evolution of activity associated with recognition decisions, using complementary neuroimaging techniques such as MEG and EEG, which will provide superior temporal resolution at the cost of poor spatial resolution. The present results make it unlikely that the parietal regions reported here will exhibit an accumulation pattern in the final moments of a decision. However, our data cannot conclusively speak to the functions of regions that were not implicated in the primary analysis. Other regions – including parietal regions distinct from those reported here – may serve as a mnemonic accumulator. It is possible that we have failed to detect these additional regions in the current study due to a lack of sufficient sensitivity, owing to either the nature of the experimental task, the poor temporal resolution of fMRI, insufficient power, or some combination thereof.

The implications of the present results for the attention to internal representations hypothesis are more ambiguous. The predictions of this model in the context of the current experiment are unclear.

The finding that activity in the ventral lateral parietal region increases with the amount of information retrieved from memory is consistent with the proposal that this region may be a component of a working memory buffer that maintains retrieved content. As we discussed earlier, the memory effects obtained in lateral parietal cortex appear to generalize across a variety of domains, including verbal and nonverbal information (Guerin and Miller, 2009) as well as visual and auditory information (Shannon and Buckner, 2004). Thus, if this region is a component of a working memory buffer for retrieved information, then this buffer appears to be multi-modal in nature. It has thus been proposed that this region may be at least part of the neural basis for the “episodic buffer” proposed by Baddeley (2000). According to this proposal, the left angular gyrus interacts with other regions, perhaps building heavily on its connectivity with the medial temporal lobe (Vincent et al., 2006), to help orchestrate a high level, multi-modal representation of retrieved content (Vilberg and Rugg, 2008; see also Wagner et al., 2005).

Supplementary materials related to this article can be found online at doi:10.1016/j.neuroimage.2010.11.066.

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