



## Lateralization of the parietal old/new effect: An event-related fMRI study comparing recognition memory for words and faces

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### ABSTRACT

Although the parietal cortex is not conventionally thought of as a major component of the neural systems that mediate declarative memory, many fMRI studies of recognition memory have found that correctly identified old items produce greater activation than correctly rejected new items throughout parietal cortex. This effect is usually heavily lateralized to the left. However, the vast majority of previous studies have used verbal materials. Does the left-lateralization of this effect result from the left hemisphere's role in language or does it suggest the possibility of a specialized role for the left hemisphere in recognition memory that applies across stimulus domains? To address this question, we directly compared recognition memory for words and faces in two event-related fMRI experiments with a total of 38 subjects. In the second experiment, we included a manipulation of recognition difficulty. Despite extensive material-specific lateralization in terms of the brain's overall response to stimuli revealed by a direct comparison of words and faces, the parietal old/new effect did not exhibit material-specific lateralization. Rather, the lateralization of the effect depended on the region of parietal cortex in question. In lateral parietal cortex, the effect was left-lateralized. In medial parietal cortex, the effect was bilateral. These findings indicate that the left-lateralization of the parietal old/new effect is unrelated to the left hemisphere's role in language and raises the possibility of a specialized role for the left hemisphere in recognition memory.

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One would be hard pressed to find a textbook on human memory that talks about the parietal cortex extensively. Conventionally, the parietal cortex is not thought to be an important component of the neural systems that produce declarative memory. Nonetheless, interest in the parietal cortex among memory researchers has been growing steadily as an increasing number of fMRI studies of recognition memory are raising the possibility that the parietal cortex may play a role.

Numerous fMRI studies of recognition memory have shown that both lateral and medial regions of the posterior parietal cortex (PPC) are more active when a target is correctly identified as old (hit) than when a distracter is correctly rejected as new (correct rejection), an effect that we will refer to as the *parietal old/new effect*. Clearly, such activation is at least tracking successful recognition, if not directly contributing to it. In a novel voxel-wise meta-analysis, [Wagner et al. \(2005\)](#) showed a stunning consistency in the locus of this effect across seven independent fMRI datasets (for additional reviews, see [Rugg and Henson, 2002](#); [Vilberg and Rugg, 2008](#)). On the lateral surface, the effect is centered on the left angular gyrus, but extends into the supramarginal gyrus and superior parietal lobule. On the medial surface, the effect is seen in the precuneus as well as the posterior cingulate and retrosplenial cortex. The parietal old/new effect is consistently lateralized to the left. On the lateral surface, the

magnitude of the old/new effect is modulated by the memorability of the stimulus ([Wheeler and Buckner, 2003](#); [Shannon and Buckner, 2004](#)) and the rememberer's subjective certainty ([Yonelinas et al., 2005](#)). At the left angular gyrus, the effect is larger if one is remembering the contextual details of an item's occurrence (recollection) rather than a mere vague sense of recency (familiarity; [Henson et al., 1999](#); [Wagner et al., 2005](#); [Yonelinas et al., 2005](#)). Interestingly, the old/new effect appears to track the rememberer's subjective impression that an item is old even if the item is new: new items incorrectly classified as old (false alarms) produce greater activation than old items incorrectly classified as new (misses; [Wagner et al., 2005](#)). An effect with similar functional properties has been observed in event-related potentials obtained from left parietal electrodes ([Rugg and Curran, 2007](#)), though the relationship to the fMRI data is unclear.

Despite an impressive and growing body of data, the functional significance of this effect is essentially unknown. Although it is clear that the old/new effect is tracking the rememberer's subjective decision, it is not at all clear why. Is the PPC somehow involved in the management of retrieved information, perhaps by serving an attentional or working memory role? Or is it instead involved in the decision process, perhaps by representing an abstract decision variable? Or is it an epiphenomenal byproduct of some unknown confound or curious characteristic of neural architecture? (See [Wagner et al. \(2005\)](#), [Vilberg and Rugg \(2008\)](#) for cogent discussions of these possibilities).

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One curious feature of the parietal old/new effect is that it is heavily lateralized to the left. Although widely observed and made note of, little attention has been paid to why the effect is so heavily lateralized and what the functional significance of this observation may be. The vast majority of studies have used verbal or verbalizable materials. It is well-known that the processing of verbal information is heavily lateralized to the left while the processing of other informational domains, such as faces, is lateralized to the right. This material-specific lateralization has been well-documented in the recognition memory domain using a variety of techniques, including fMRI during encoding (Kelley et al., 1998), Wada testing during encoding (Kelley et al., 2002), and studies of split-brain patients (Miller et al., 2002). Given that the vast majority of previous studies have used verbalizable materials, might the left-lateralization of the old/new effect merely be a byproduct of stimulus choice? Some studies with faces have been conducted, with some finding an apparently bilateral old/new effect (Henson et al., 2002; Ishai and Yago, 2006; Simons et al. (2008)) and others finding an apparently left-lateralized old/new effect (Leveroni et al., 2000; Leube et al., 2003; Hofer et al., 2007). Unfortunately, none of these investigations were focused on the issue of laterality, and as a result there were no direct statistical tests of the lateralization of the effect. Further, given the extensive procedural differences across studies, it is difficult to directly compare these results to other studies using words. As a result, the extent to which the parietal old/new effect exhibits material-specific lateralization remains ambiguous.

If the parietal old/new effect exhibits material-specific lateralization, then this would agree with previous results suggesting that neither hemisphere is dominant for recognition memory. However, if the old/new effect is left-lateralized for both words and faces, then this might indicate a special role for the left hemisphere in recognition memory.

We report two event-related fMRI experiments. The first was a straightforward comparison of recognition memory for faces and words. The second experiment was similar except it also included a strong manipulation of the memorability of the items. This was done to determine whether any differences between faces and words obtained in Experiment 1 were actually due to differences in the degree or quality of information retrieved, which could not be easily equated between the two stimulus types. We took a regions of interest approach, using strong a priori information about the likely location of old/new effects in the parietal cortex to guide selection of activation sites for further scrutiny. We compliment this approach with a secondary analysis providing an exploratory search of the whole brain.

## Materials and methods

### Experiment 1

#### Participants

Participants were 22 (10 female) members of the UCSB community. Ages ranged from 21 to 43 (mean=26). All participants reported being right handed. All participants gave informed consent as approved by the UCSB Institutional Review Board. Data from 2 participants were replaced because they were unable to complete the experiment in its entirety. Data from an additional subject were replaced due to a technical error in data acquisition. Data from one of the 12 functional runs from one the subjects included in the final analysis were excluded due to a technical error during acquisition.

#### Stimuli

Stimuli consisted of 408 words and 408 faces. Words were selected using the MRC Psycholinguistic Database ([www.psy.uwa.edu.au/mrcdatabase/uwa\\_mrc.htm](http://www.psy.uwa.edu.au/mrcdatabase/uwa_mrc.htm)). They ranged from 4 to 14 letters in length (mean=7) and 2 to 6 syllables in length (mean=3). The Kucera–Francis written frequency ranged from 50 to 149 (mean=82). For counterbalancing purposes, words were pseudorandomly divided into

two sets of 204 items each. The sets were matched in terms of length and frequency on an item-by-item basis. Faces were drawn from a variety of online face databases (Martinez and Benavente, 1998; CVL Face Database, University of Ljubljana; Weyrauch et al., 2004; Minear and Park, 2004). 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. For counterbalancing purposes, the faces were divided into two sets of 204 items each (128 male). Due to a technical error, the assignment of faces to sets was not completely random, such that items from certain databases were much more likely to be in one set. However, it is unlikely that this systematically affected the results and this error was corrected in Experiment 2, which replicated the major findings of Experiment 1. Items were counterbalanced such that, across participants, each item was equally likely to be a target or a distracter. 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. Words were presented in white 24-point Helvetica font and both words and faces were presented against a black background. Stimuli were controlled by a laptop running the Psychophysics Toolbox 3 ([www.psychtoolbox.org](http://www.psychtoolbox.org)). Stimulus presentation was synchronized to the acquisition of each functional volume.

#### Task

The memory test was divided into a series of 12 study-test cycles. Each cycle consisted of a study session, a distracter task, and a recognition test. The recognition test was the only period in which MRI data was collected, though the subject was inside the scanner bore throughout the entire cycle. Stimuli were randomly assigned to cycles individually for each subject. During the study session, the participant saw 17 faces and 17 words in a random order. Each item was presented for 2 s. To ensure that the subject attended to each item, the participant indicated whether each item was pleasant or unpleasant. All responses were made using an MRI-compatible button box held in the right hand. The filler task consisted of 30 s of simple self-paced arithmetic problems in which the participant discriminated between correct and incorrect solutions to sums of 2 digit numbers. During the recognition test, subjects were presented with all studied items, plus 17 word distracters and 17 face distracters. In order to enable event-related analysis, 34 fixation trials were also included. The ordering of trials was pseudorandomly determined individually for each subject, such that each item type preceded each other item type equally often across the 12 functional runs (Buckner et al., 1998). In addition to the 34 fixation trials, an additional 20 s of fixation occurred at the beginning and end of the recognition test.

#### MRI data acquisition

Subjects were scanned at the UCSB Brain Imaging Center using a 3T 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 122 volumes in each functional run. In addition to the functional data, a high-resolution anatomical image was collected for each subject using a magnetization-prepared rapid acquisition gradient-echo sequence (MPRAGE; TR=2300 ms; TE=2.98 ms; FA=9°; 160 sagittal slices 3-D acquisition; 1.1 mm thick; 1 mm×1 mm in-plane resolution; 256×256 matrix). The entire scanning session was nearly 2 h long.

## MRI data analysis

**Preprocessing.** Standard spatial preprocessing was conducted using SPM5 (<http://www.fil.ion.ucl.ac.uk/spm/>). Images were realigned to the first functional image to correct for minor head motion. No subject 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 3 mm isotropic voxels. All reported stereotaxic coordinates refer to the MNI template and are reported as (x,y,z). Finally, the functional data were smoothed using an isotropic Gaussian kernel (FWHM=8 mm).

**General linear model.** Subsequent analysis was conducted using customized programs. The general linear model was used to model the fMRI time-series (Friston et al., 1995). To model the event-related response, the response at each peri-stimulus time point was modeled by a separate parameter (Ollinger et al., 2001). This approach is very similar to selective averaging (Dale and Buckner, 1997). This method is sometimes referred to as a finite impulse response (FIR) model (Henson et al., 2001). This approach makes minimal assumptions about the shape of the hemodynamic response, thus accommodating the variation in the timing of the response that has been observed across brain regions and individuals (e.g., Schacter et al., 1997) and avoiding the amplitude bias that such variation can introduce (Calhoun et al., 2004). Given a temporal resolution of 2 s., 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. For both words and faces, we modeled three trial types: hits, correct rejections, and errors. Errors included misses, false alarms, missed responses and trials in which multiple responses occurred. Errors were not included in any of the analysis that we report below. This produced a total of 6 trial types. The data were concatenated across the 12 functional runs and stimulus effects were modeled by the same parameters across all runs, though obviously the model did not assume temporal continuity between runs. To correct for linear drift and mean session effects, a constant and a linear drift term were included separately for each

session. The model was estimated separately at each voxel using the standard least-squares solution.

**Contrasts and random-effects analysis.** To test responses against 0, or contrast responses between trial types, we summed the 2nd, 3rd, 4th, and 5th 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. Contrast maps comparing all stimuli to baseline, faces versus words, and hits versus correct rejections (for faces separately, words separately, and faces and words combined) were constructed individually for each subject. The hits versus correct rejections contrast is the critical contrast revealing the old/new effect that is the focus of this paper. These contrast maps were then passed to a second-level random-effects analysis that consisted in testing the contrast against zero using a single-sample *t* test independently at each voxel. For visualization purposes, group *t* maps were transformed to the PALS atlas using multi-fiducial mapping and rendered onto 3D inflated brains using the CARET software (Van Essen, 2005).

**Regions of interest.** The group hits minus correct rejections *t* map was used to define regions within the parietal cortex exhibiting an old/new effect. This method of identifying ROIs is unbiased with respect to detecting differences between words and faces, in the sense that words and faces are weighted equally in the contrast. (Note, however, that the average could disproportionately represent one condition if the effect sizes differ considerably). We anticipated identifying a local maximum within the angular gyrus or intraparietal sulcus. We also anticipated identifying a local maximum along the medial surface of the parietal lobes. Because of these strong a priori hypotheses, we used a threshold of  $p < .01$  with a voxel extent of 10 when identifying these ROIs, although each of the ROIs we analyzed also survives our more conservative whole-brain threshold of  $p < .001$  with an extent of 10. Each ROI consisted of a 12 mm radius sphere centered on a local maximum of interest. Fig. 1 shows the *t* map used to identify the ROIs as well as the ROIs themselves. We identified a local maximum in lateral parietal cortex in both the left hemisphere (−42, −57, 48) and the right hemisphere (42, −57, 48). We also identified a local maximum on the medial surface of the parietal lobes within the

## Old/New Effects & Regions of Interest

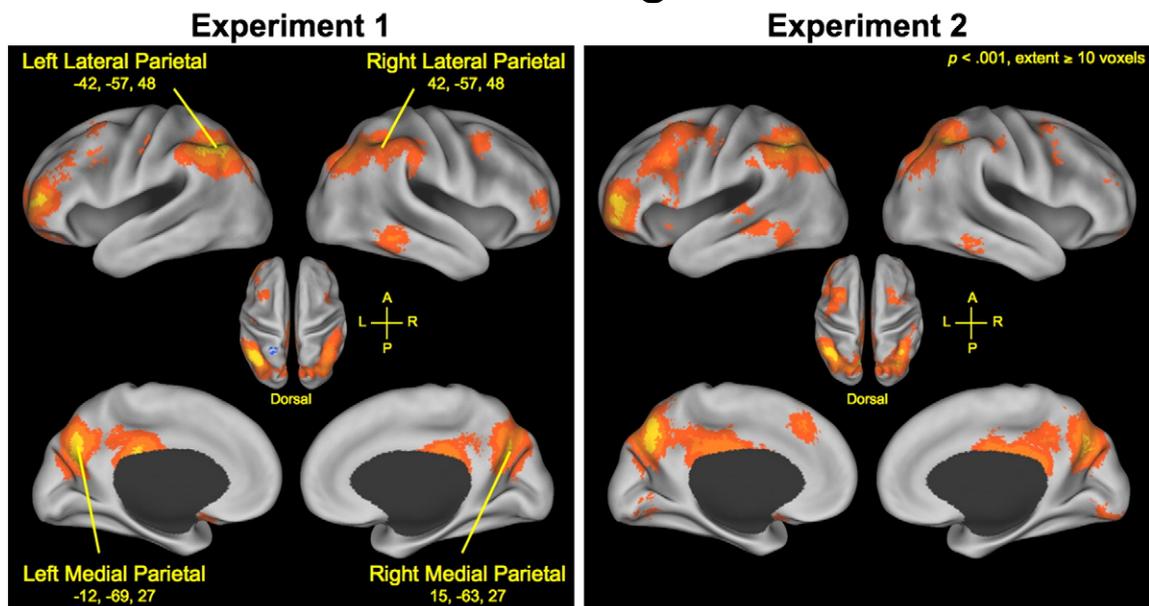
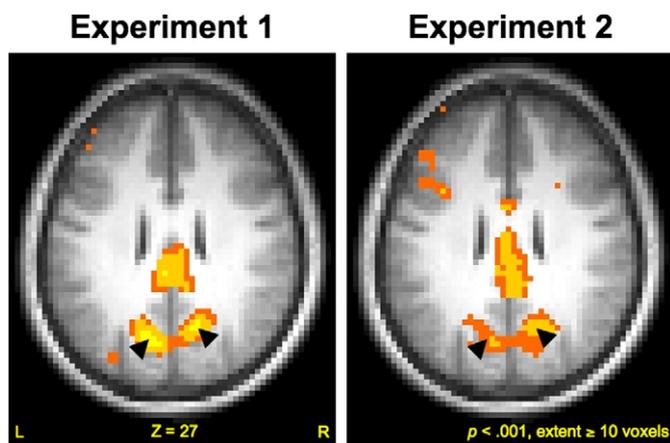


Fig. 1. Old/new effects collapsing across faces, words, and levels of difficulty thresholded at  $p < .001$  with an extent greater than or equal to 10. Locations of the parietal ROIs are shown.



**Fig. 2.** An axial slice of the same data shown in Fig. 1 illustrating that the peaks of the left and right medial parietal clusters are not symmetric. Arrows indicate the peak voxel used to define the ROIs.

precuneus (BA 7) in the left hemisphere ( $-12, -69, 27$ ) and the right hemisphere ( $15, -63, 27$ ). Fig. 2 shows the precuneus ROIs overlaid on an axial slice. It can be seen that the peak in the right hemisphere is more anterior, which is why the two ROIs are not strictly symmetric. Consistent with other studies (e.g., Wagner et al., 2005), there was a distinct medial parietal local maximum in the posterior cingulate. Unfortunately, because this cluster is centered on the midline, it was difficult to unambiguously define a left and right maximum so we did not focus on this region. In addition to our a priori parietal regions, we also decided, after collecting the data, to include an anterior frontal region that showed very robust old/new effects. A local maximum within the anterior frontal cortex (BA 10) was identified in both the left hemisphere ( $-42, 51, 6$ ) and the right hemisphere ( $42, 51, 6$ ). Importantly, both anterior frontal clusters survived our a priori whole-brain threshold of  $p < .001$  with an extent of 10.

For each ROI, parameter estimates were averaged across subjects and a mean event-related response was obtained for each trial type. A peak time point was extracted from the event-related response by averaging the 3rd and 4th time points. Then, the estimated response at peak for each participant and each trial type was entered into an ANOVA with factors for memory (hits versus correct rejections), stimulus type (faces versus words), and hemisphere (left versus right), with participants treated as a random factor. In order to ensure that any observed differences between the left and right ROIs were not due to subtle asymmetries in the signal across regions, a control analysis was done in which each subjects' parameters were divided by the mean of the session constant terms. This analysis produced very similar results.

### Experiment 2

Experiment 2 was very similar to Experiment 1, except that a manipulation of the memorability of the items was included. In the easy condition, 17 faces and 17 words were repeated four times throughout the study session, with the constraint that the repetition of items occurred at least 3 trials apart. In the hard condition, participants studied 51 faces and 51 words and each item was presented only once during the study session. The increase in the number of studied items in the hard condition was created by simply re-ordering the components of Experiment 1: subjects engaged in 3 study sessions, followed by the filler task, followed by 3 test sessions. In the test sessions, participants' memory for all 102 items encountered in the 3 back-to-back study sessions was being tested; targets from all 3 study sessions were randomly assigned to the 3 test sessions individually for each subject. In the easy condition, subjects engaged in three study-test cycles, just as in Experiment 1, with the

**Table 1**  
Recognition responses in Experiment 1

	Faces	Words
Hits	.82 (.02)	.92 (.01)
False alarms	.26 (.03)	.18 (.02)

Note. SEM in parentheses.

exception, of course, that items were now repeated four times in the study session. The entire procedure was then repeated to produce a total of 12 functional runs (6 easy, 6 hard). This design was adopted so that the imaging parameters would be identical across experiments. Further, blocking the manipulation of task difficulty enables one to study the effect of task difficulty on both hits and correct rejections. The order of easy and hard conditions was counterbalanced across subjects. Stimuli were rotated through conditions so that each stimulus occurred equally often in each condition across subjects. There were 16 participants (11 female). Ages ranged from 19 to 51 (mean = 27). All participants reported being right handed; the mean Edinburgh Handedness Inventory score was 96 (range 84 to 100). Data from 3 participants were replaced because they were unable to complete the experiment in its entirety. The analysis was identical to Experiment 1 except that the easy and hard conditions were modeled separately, producing 12 trial types. A contrast comparing the easy and hard conditions was added to the analysis. The ROIs defined from Experiment 1 were used to analyze the data from Experiment 2, providing for a strong test of replication. A factor for task difficulty was added to the ROI ANOVAs. In all other respects, the two experiments were the same.

## Results

### Behavioral results

The proportions of hits and false alarms are shown in Tables 1 and 3 for Experiments 1 and 2, respectively. In Experiment 1, corrected performance (hits minus false alarms) was larger for words than faces [ $t(21) = 7.27, p < .001$ ]. In Experiment 2, corrected performance was entered into an ANOVA with factors for stimulus type (words versus faces) and difficulty. There was a main effect of stimulus type, indicating that words were remembered better than faces [ $F(1,15) = 12.76, p < .01$ ]. There was also a main effect of difficulty, indicating that performance was higher in the easy condition [ $F(1,15) = 331.43, p < .001$ ]. There was also an interaction, indicating that the difficulty manipulation had a larger effect on faces than words [ $F(1,15) = 24.77, p < .001$ ]. The effect of difficulty was significant when words were considered in isolation [ $t(15) = 9.39, p < .001$ ] and also when faces were considered in isolation [ $t(15) = 17.66, p < .001$ ].

To assess response criteria, we calculated the signal detection parameter  $c$  individually for each subject, replacing hit rates of 1 with  $1 - (1/2N)$  as necessary (Macmillan and Creelman, 1991). In Experiment 1, the mean criterion ( $\pm$ SEM) was  $-.13 \pm .07$  for faces and  $-.24 \pm .06$  for words. This difference was not significant [ $t(22) = 1.31, p = .21$ ]. In the Experiment 2, the criterion for faces was more liberal in the easy condition ( $-.21 \pm .10$ ) than the hard condition ( $.05 \pm .10$ ) [ $t(15) =$

**Table 2**  
Recognition reaction times (ms) in Experiment 1

	Faces	Words
Hits	1003 (22)	945 (25)
Misses	1188 (26)	1249 (28)
False alarms	1196 (30)	1207 (29)
Correct rejections	1075 (22)	1063 (24)

Note. SEM in parentheses.

**Table 3**  
Recognition responses in Experiment 2

	Faces		Words	
	Easy	Hard	Easy	Hard
Hits	.92 (.02)	.65 (.04)	.94 (.02)	.82 (.03)
False alarms	.14 (.02)	.31 (.03)	.12 (.03)	.26 (.04)

Note. SEM in parentheses.

4.22,  $p=.001$ ]. For words, the response criteria did not significantly differ between the easy ( $-.26 \pm .11$ ) and the hard ( $-.15 \pm .10$ ) conditions [ $t(15)=1.06$ ,  $p=.31$ ].

Each subjects' median reaction time was calculated for each response type (excluding missed or multiple responses) and was then averaged across subjects. The means for Experiments 1 and 2 are reported in Tables 2 and 4, respectively. We will focus on two critical questions.

First, can the differences in brain activation that we emphasize below be attributed merely to differences in reaction times between conditions? As is generally observed in recognition memory experiments, we found that reaction times were longer for correct rejections than for hits, both in Experiment 1 [ $F(1,21)=29.51$ ,  $p<.001$ ] and in Experiment 2 [ $F(1,15)=5.73$ ,  $p<.05$ ]. Thus, if anything, reaction time effects serve to reduce rather than enhance the old/new effects that we are studying. In Experiment 1, this reaction time difference was significantly larger for words than for faces [ $F(1,21)=4.92$ ,  $p<.05$ ] and there was a corresponding trend in Experiment 2 [ $F(1,15)=4.34$ ,  $p=.06$ ].

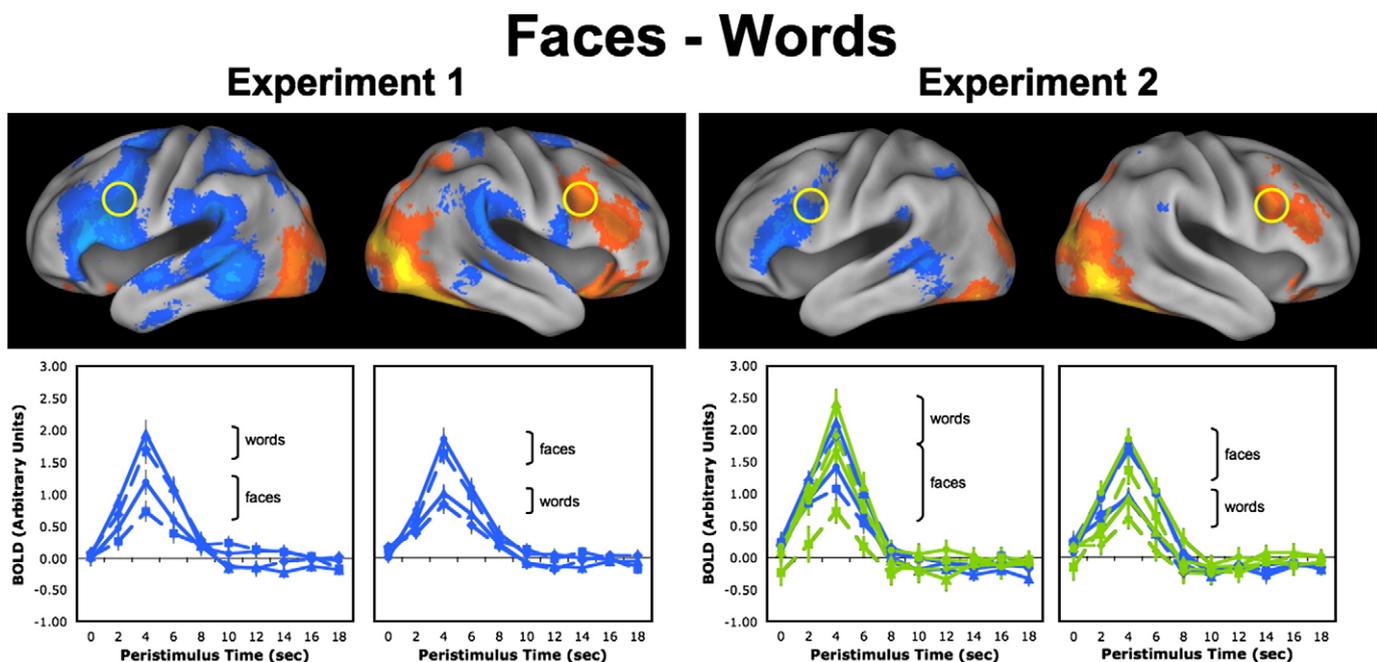
Second, is the effect of difficulty observed in Experiment 2 reflected in reaction times as well as accuracy? Here we continue to restrict our statistical analysis to hits and correct rejections. Reaction times were much slower in the difficult condition [ $F(1,15)=58.21$ ,  $p<.001$ ]. Further, the effect of difficulty on reaction times was larger for faces than for words, thus mirroring the effects on accuracy [ $F(1,15)=7.81$ ,  $p=.01$ ]. Finally, difficulty had a larger effect on hits than correct rejections [ $F(1,15)=6.37$ ,  $p<.05$ ].

### Faces versus words

We first sought to determine whether the classic finding that processing of verbal materials is lateralized to the left hemisphere while processing of faces is lateralized to the right hemisphere – independently of the old/new effect – was replicated in the current dataset. Figure 3 shows a direct comparison of faces and words for both experiments, collapsing across hits and correct rejections and levels of difficulty. Regions in yellow showed a larger response for faces than for words. Regions in blue showed a larger response for words than for faces. A pattern of material-specific lateralization is apparent. Based on the work of Kelley et al. (1998) we decided, prior to an inspection of the data, to define an ROI within dorsolateral prefrontal cortex. The peak within dorsolateral prefrontal cortex was identified using the stimulus versus baseline comparison, which is unbiased with respect to differences between words and faces, in the sense that words and faces are weighted equally in the contrast. (Note, however, that the average could disproportionately represent one condition if the effect sizes differ considerably). The peak is approximately 11 mm from that identified by Kelley et al. (1998) (left:  $-42, 9, 30$ ; right:  $45, 9, 30$ ). The ROI extends across the inferior and middle frontal gyri (BA 6/9/44). The event-related time courses are shown for each ROI below their respective overlays in Fig. 3. A dramatic cross-over interaction was apparent, with greater activation for words than faces in the left hemisphere and vice versa in the right hemisphere. The  $p$  values associated with the ANOVA are shown in Table 5.

### Old/new effects throughout the brain

Fig. 1 shows a direct comparison of hits versus correct rejections collapsing across the two stimulus types and levels of difficulty. The old/new effect was apparent in a number of cortical regions. In lateral parietal cortex, the effect was centered on the inferior parietal lobule (BA 39/40) very close to the intraparietal sulcus and extended dorsally into the superior parietal lobule (BA 7). The effect was also robust in two distinct maxima on the medial surface of parietal



**Fig. 3.** A direct comparison of faces and words, collapsing across hits, correct rejections, and levels of difficulty. Regions more active for faces than words are shown in yellow and regions more active for words than faces are shown in blue. The yellow circle indicates the approximate location of the dorsolateral prefrontal ROI, which was based on the comparison of all trial types (except errors) against baseline (not shown). Event-related time courses are shown for each of the ROIs below their respective overlays. Error bars show  $\pm$  SEM.

cortex: one centered on the precuneus (BA 7/31) and another centered on the posterior cingulate (BA 23/31). There was also a robust effect in anterior prefrontal cortex (BA 10). The effect was also apparent in dorsolateral prefrontal cortex, including premotor areas, particularly in Experiment 2. There were a variety of other clusters exhibiting the old/new effect that are worth noting. The middle temporal gyrus (BA 21/22) showed the effect on the right in Experiment 1 and bilaterally in Experiment 2. The effect was observed bilaterally in the body of the caudate and, in a distinct ventral cluster, in the left caudate and/or putamen. In Experiment 2, the medial aspect of the superior frontal gyrus (BA 6/8) exhibited the effect. In Experiment 2, the effect could also be seen in the right cerebellum, possibly extending into the lingual gyrus. Finally, in Experiment 2, the effect was observed in the left fusiform (BA 19/37) and, more anterior, in the right inferior temporal and fusiform gyri (BA 20/37). The only region to show greater activation for correct rejections than hits was a small perithreshold cluster at the edge of the brain near the post central gyrus, which can be seen in the dorsal view in Fig. 1. This result was not replicated in Experiment 2 and likely reflects a false positive.

Looking at the general patterns in Fig. 1, two things are apparent. First, there is clearly good agreement between the two experiments, with the most prominent loci of activation differing only in magnitude or extent. Second, there is a striking consistency with

the results of other laboratories (see, for instance, Fig. 1 of Wagner et al. (2005)).

Fig. 4 shows the old/new effects observed throughout the cortex separately for faces and words, projected onto a flattened representation of the cortical surface. It can be seen that the pattern of responses in medial and lateral parietal cortex and anterior prefrontal cortex is very similar across the two stimulus types. As a result, we have confidence that the peak average responses used to generate the ROIs are representative of both conditions. Nonetheless, there are subtle variations across the two stimulus types and between experiments. Further, the overall extent of significant activation differs considerably: there is more extensive activation for words than faces in Experiment 1 but more extensive activation for faces than words in Experiment 2. To ensure that subtle variations in the topography of effects for faces and words were not systematically biasing the definitions of our ROIs, we conducted a parallel ROI analysis in which the ROI peaks were identified separately for faces and words, using the data from Experiment 1. This analysis led to very similar conclusions, except as noted below.

#### Lateral parietal cortex

The event-related time courses from the ROI in lateral parietal cortex are shown in panels C–F of Fig. 5. Panels A and B of Fig. 5

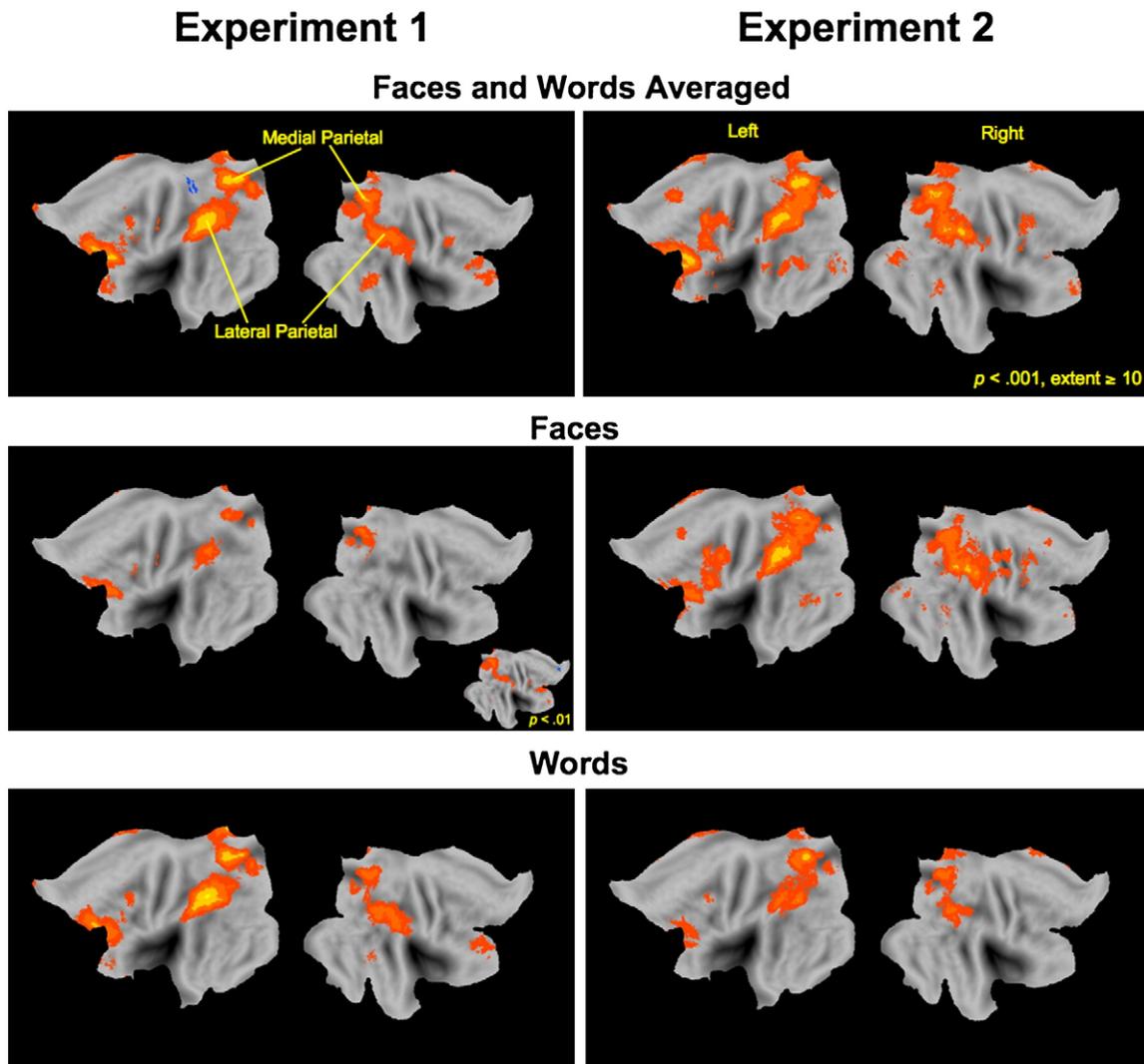


Fig. 4. Old/new effects projected onto a flattened rendering of the cortical surface. The top row shows the old/new effects collapsing across faces and words; this is the same data shown in Fig. 1. The middle and bottom rows show the old/new effects for faces and words, respectively.

# Lateral Parietal Cortex

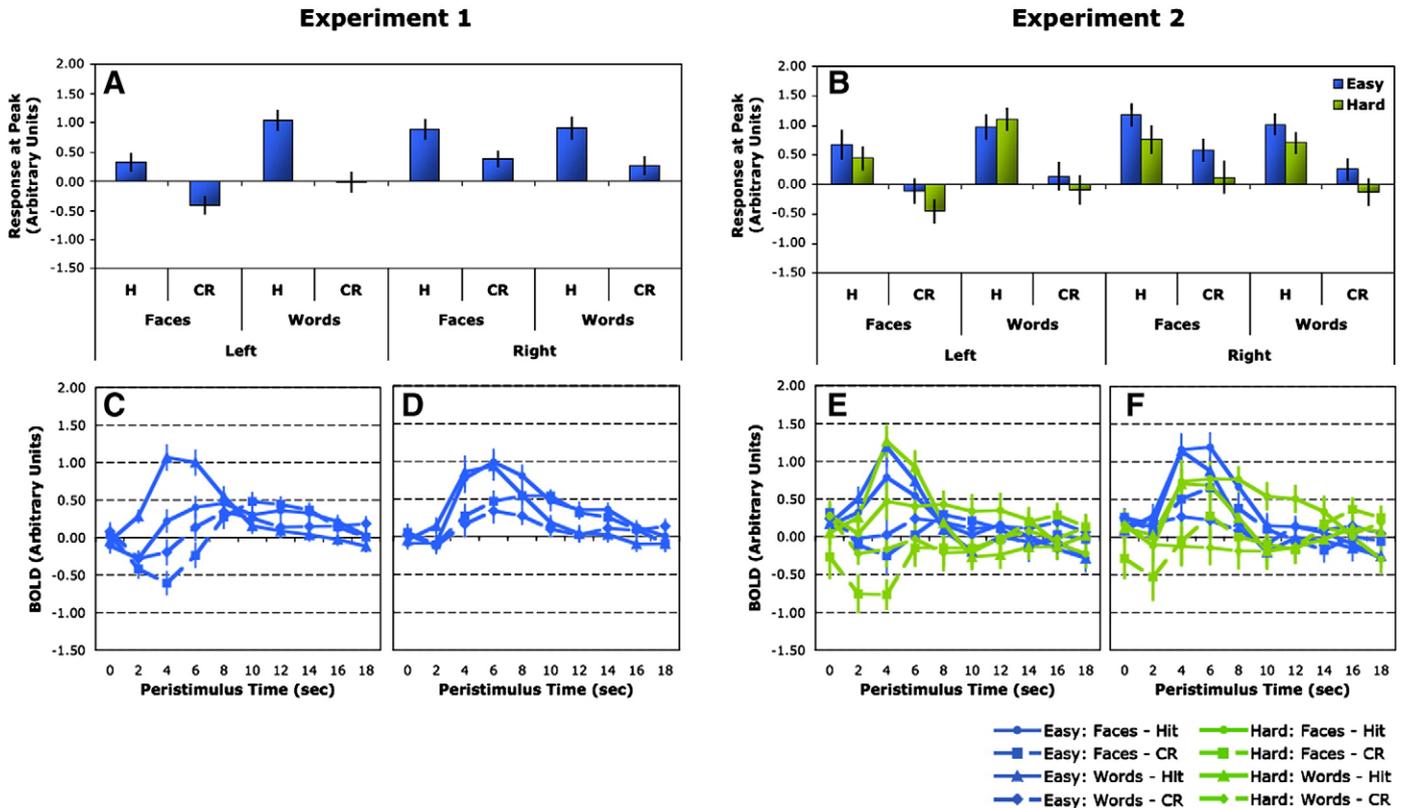


Fig. 5. Data from the lateral parietal ROI. The bar graphs show the average of the 3rd and 4th time points of the event-related response. Error bars show  $\pm$ SEM.

simplify the data by only plotting the response at the peak, which is defined as the mean of the 3rd and 4th time points of the event-related response. Panel A of Fig. 7 simplifies matters further by plotting the magnitude of the old/new effect, which is defined as the difference between hits and correct rejections, averaging across the 3rd and 4th time points of the event-related response. Looking at Fig. 7, it is apparent that there was a robust old/new effect in both left and right parietal cortex for both stimulus types. However, for both words and faces, the effect was heavily lateralized to the left. In Experiment 2, the lateralization is slightly less robust and appears to be driven primarily by the difficult condition, though the interaction is not significant (Table 5).

It should be noted that when the ROIs were defined separately for words and faces, the reliability of the left-lateralization for faces was reduced, even though the peaks were very close to those used in the main analysis (left:  $-45, -57, 48$ ; right:  $42, -57, 48$ ). Using these alternative peaks, the effect was not significantly larger in the left hemisphere in Experiment 1 [ $t(21)=1.55, p=.14$ ] nor in Experiment 2 [ $t(15)=1.66, p=.11$ ], though in both cases there was a trend in the appropriate direction. This suggests that the lateralization of the old/new effect associated with faces may be more subtle than that associated with words. Nonetheless, using these alternative peaks, the old/new effect associated with faces was significantly lateralized to the left when the data was concatenated across the two experiments [ $t(37)=2.35, p<.05$ ], suggesting that the above null result derived merely from a lack of power. We therefore conclude that the old/new effect associated with faces in the lateral parietal cortex is lateralized to the left for both words and faces, though in the case of faces the lateralization may be more subtle.

Unexpectedly, difficulty had no effect on the old/new effect whatsoever (the numerical difference in the left hemisphere for

words is not significant even by an unprotected post-hoc  $t$  test,  $t(15)=1.71, p=.11$ ).

The  $p$  values associated with the various terms of the ANOVAs are shown in Table 5.

## Medial parietal cortex

The data from medial parietal cortex are presented in the same format as before in Figs. 6 and 7 and in Table 5. Looking at Fig. 7, it is apparent that there is again a robust old/new effect in both hemispheres for both stimulus types. However, the pattern of results is quite distinct from lateral parietal cortex. In Experiment 1, the old/new effect was left-lateralized for words [ $t(21)=2.63, p=.02$ ] and was bilateral for faces [ $t(21)=1.70, p=.10$ ]. However, in Experiment 2, the effect was bilateral for both stimulus types. It therefore appears that the old/new effect in medial parietal cortex is bilateral for faces. Although the effect may be left-lateralized for words, the laterality is subtle at best. The observation of a bilateral pattern is not being driven by the spatial proximity of the two ROIs; their centers are 28 mm apart and this is well outside the range of the spatial uncertainty of the data. As in lateral parietal cortex, the old/new effect was unaffected by difficulty.

## Anterior frontal cortex

After inspection of the data, we decided to take a further look at the old/new effect in anterior prefrontal cortex because the old/new effect in this region was very robust and was also heavily lateralized to the left. Data from this ROI is presented in the same format in Fig. 7 and in Table 5. The old/new effect is heavily lateralized to the left for both words and faces. The effect of difficulty on the magnitude of the old/new effect was not significant.

# Medial Parietal Cortex

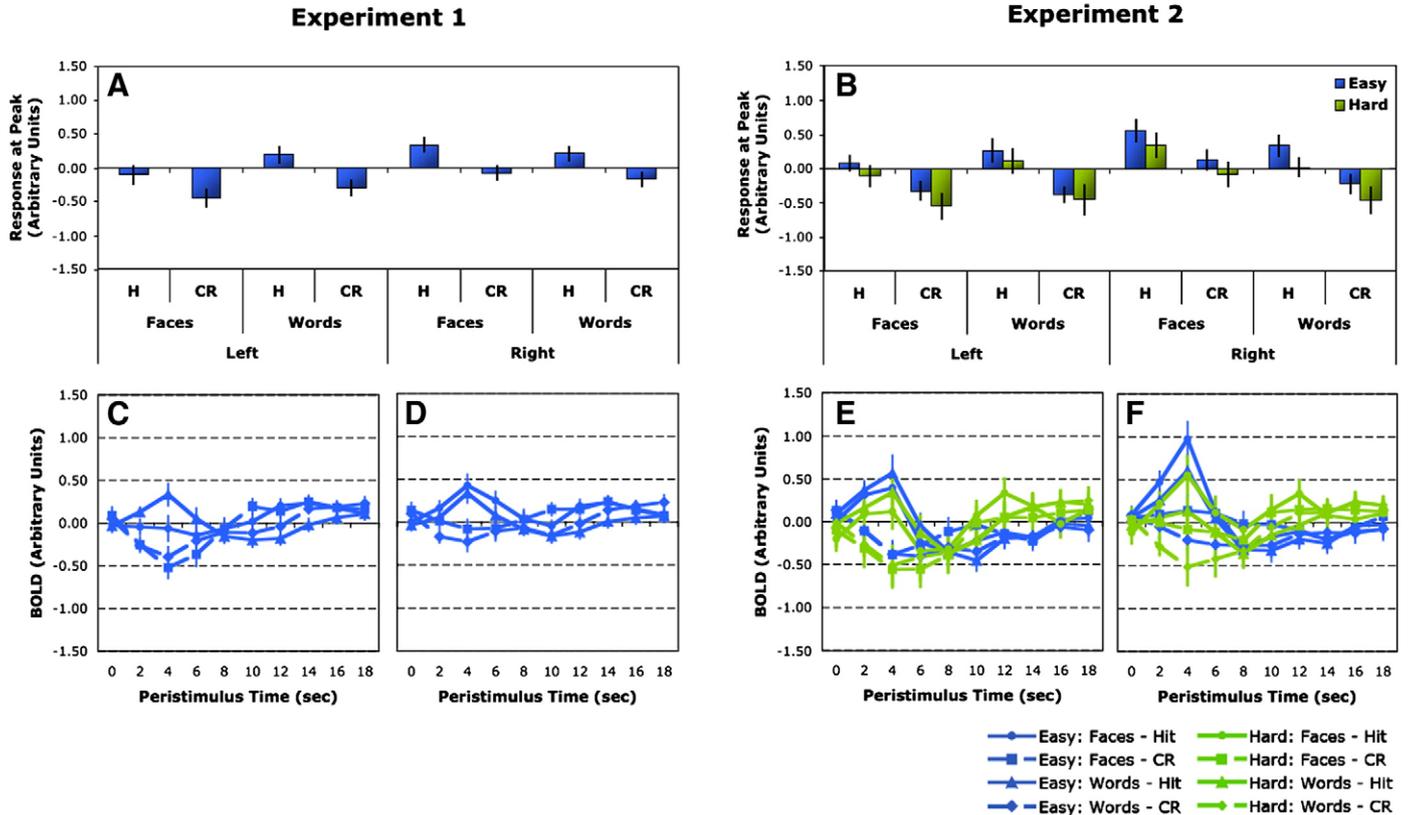


Fig. 6. Data from the medial parietal ROI. The bar graphs show the average of the 3rd and 4th time points of the event-related response. Error bars show  $\pm$ SEM.

## Dorsolateral prefrontal cortex

Our initial interest in the dorsolateral prefrontal cortex that led us to conduct an ROI analysis there was motivated by an effort to replicate previously observed patterns of material-specific lateralization (Fig. 2). In the course of conducting that analysis, we incidentally discovered an interesting pattern in the old/new effects. As can be seen in Fig. 1, the old/new effect had a larger extent in dorsolateral prefrontal cortex in Experiment 2, despite the fact that Experiment 1 had more power. The reason for this result is apparent in panel D of Fig. 7. In Experiment 2, the observed old/new effect is driven almost entirely by the difficult condition. In the difficult condition, there was a dramatic enhancement of the old/new effect. This effect appears to be driven by faces, though the interaction is not significant (Table 5).

## Modulations of old/new effects by difficulty throughout the brain

We directly compared old/new effects in the easy and difficult conditions in a planned whole-brain analysis. Using our a priori whole-brain threshold of  $p < .001$  with an extent of 10, this comparison did not reveal any effects in the parietal cortex in either direction. Thus, our surprising failure to find an enhancement of the parietal old/new effect in the easy condition is not limited to our ROIs but rather generalizes across the extent of parietal cortex. We did find two regions outside the parietal cortex that showed a larger old/new effect for faces in the difficult condition. One region was in the right dorsolateral prefrontal cortex (48, 12, 21) and overlapped with the ROI shown in Figs. 3 and 7. Another region was in the right fusiform gyrus (54, -60, -15). An ROI analysis of this region and its left homolog revealed that this area showed a much larger response to faces than words in the right hemisphere and a slightly larger response to words

than faces in the left hemisphere [ $F(1,15)=40.70, p < .001$ ]. In the easy condition, the old/new effect associated with faces was lateralized to the left [ $t(15)=5.30, p < .001$ ] and did not differ significantly from words. In the difficult condition, the old/new effect associated with faces was greatly enhanced, particularly in the right hemisphere, such that it was not lateralized to the left [ $t(15)=1.28, p = .22$ ]. In the right hemisphere, the old/new effect associated with faces was significant in the difficult condition [ $t(15)=4.30, p = .001$ ] but was not significant in the easy condition [ $t(15)=1.61, p = .13$ ]. In the left hemisphere, the old/new effect associated with faces was significant in both the easy and hard conditions, but the effect was larger in the hard condition [ $t(15)=2.22, p < .05$ ]. For words, a very different pattern was apparent in the fusiform gyrus: none of the old/new effects associated with words approached significance (all  $p \geq 10$ ). It thus appears that the old/new effect in the fusiform gyrus is relatively specific to faces and is enhanced under conditions of uncertainty, particularly in the right hemisphere.

## Discussion

We directly compared recognition memory for words and faces to determine whether previous observations that the parietal old/new effect is lateralized to the left were due to the widespread use of words or otherwise verbalizable materials. Across two experiments, we obtained a pattern of old/new effects throughout the cortex that closely resembles that obtained by other laboratories (compare, for instance, our Fig. 1 to Fig. 1 of Wagner et al. (2005)). Despite extensive material-specific lateralization in terms of the brain's overall response to stimuli revealed by a direct comparison of words and faces (Fig. 3), the parietal old/new effect clearly did not exhibit material-specific lateralization (Fig. 7). Rather, the lateralization of the effect depended

# Old/New Effects

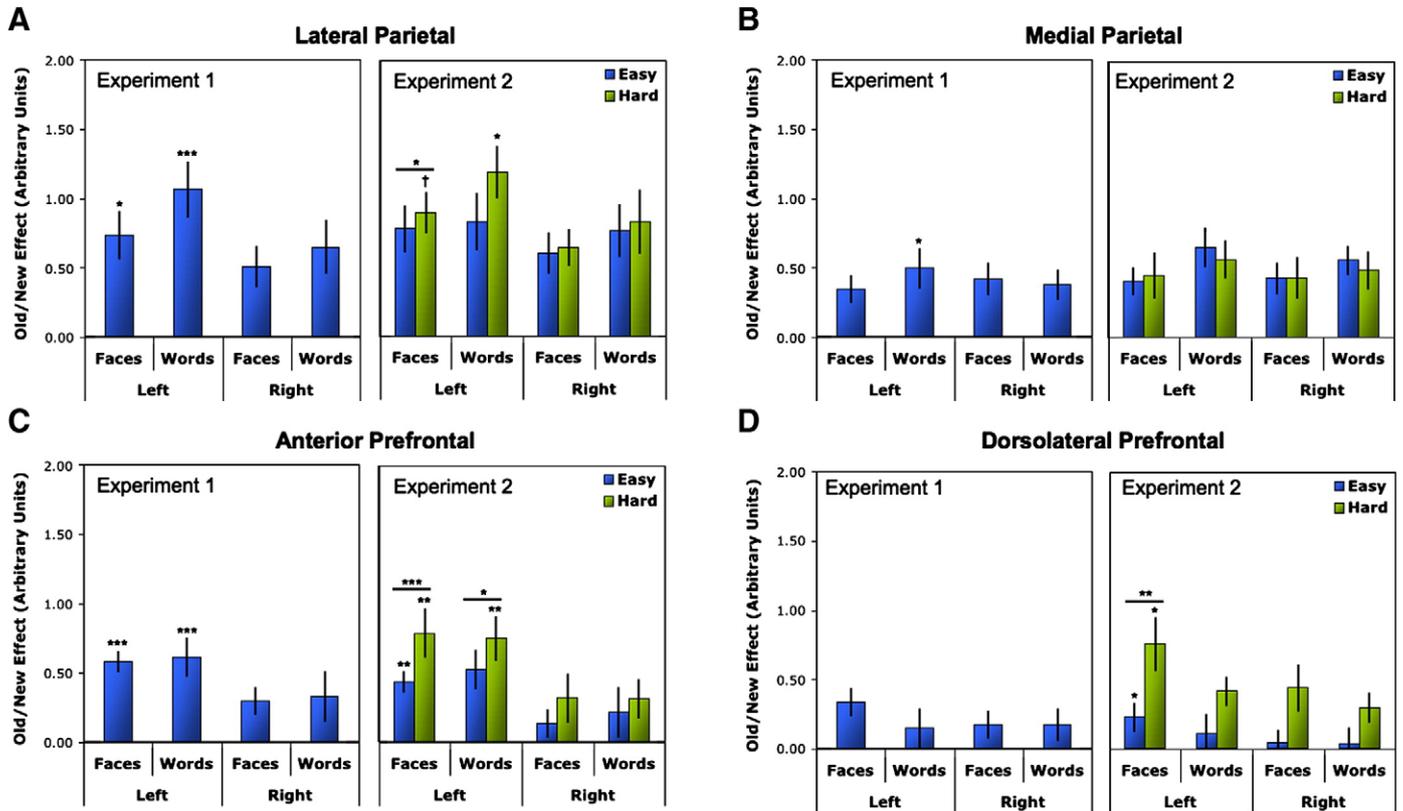


Fig. 7. The magnitude of the old/new effect as a function of difficulty and stimulus type in each of the ROIs. Each bar represents the difference between hits and correct rejections, averaging across the 3rd and 4th time points of the event-related response. Error bars show  $\pm$ SEM.  $\dagger p = .06$ ,  $* p < .05$ ,  $** p < .01$ ,  $*** p < .001$ .  $p$  values represent a direct comparison between the left and right hemispheres for each of the conditions as well as averaged across levels of difficulty (standard paired  $t$  test).

on the region. In lateral parietal cortex, the effect was left-lateralized for both words and faces. In medial parietal cortex, the effect was bilateral for faces with the possibility of a subtle left-lateralization for words. These results suggest that the left-lateralization of the lateral parietal old/new effect is not due to the left hemisphere's role in language and raises the possibility of a specialized role for the left hemisphere in recognition memory that applies across stimulus domains.

Why do we conclude that the left-lateralization is not due to the left hemisphere's role in language? Although there may be some verbal processing of unfamiliar faces, there must certainly be much less verbal processing of these faces than words. Nonetheless, we obtain left-lateralization for both stimulus types. In the anterior prefrontal cortex, the lateralization is unambiguously equal for both stimulus types. In the dorsolateral prefrontal cortex, the lateralization appears to be slightly larger for faces. In the lateral parietal cortex, there is a tendency for the lateralization to be larger for words, but this effect is small. There is thus a dramatic discrepancy between the verbalizability of the material and the magnitude of left-lateralization. Furthermore, there is neuroimaging evidence suggesting that phonological encoding of faces, as indicated by activation of Broca's area, occurs primarily for namable famous faces, not for unfamiliar faces, which were used here (Wig et al., 2004). Indeed, verbal encoding is completely unnecessary for the robust recognition of unfamiliar faces, which occurs in the complete absence of speech in the right hemispheres of callosotomy patients (Miller et al., 2002). For these reasons, we think that verbal processing of these faces was minimal. Further, to the extent that some verbal processing of the faces did occur, this cannot easily explain the magnitude of lateralization, which in many regions was comparable to, or in excess of, that of words.

We were very surprised to find that the lateral parietal old/new effect was not affected by recognition difficulty in Experiment 2,

despite the fact that difficulty had a very large effect on performance (Tables 1 and 3). This is difficult to reconcile with findings that the effect increases with recognition certainty (Yonelinas et al., 2005), is larger for items that received deep encoding rather than shallow encoding (Shannon and Buckner, 2004), and is larger for items that have been studied 20 times as opposed to once (Wheeler and Buckner, 2003). The most obvious difference between our study and these other studies is that whereas we manipulated difficulty across functional runs, the other studies randomly intermixed easy and hard trials. Interestingly, although difficulty did not affect the magnitude of the old/new effect in lateral parietal cortex, the response was larger to both hits and correct rejections in the easy condition (Fig. 5 and Table 5). Although this pattern of results is perplexing, it seems to suggest that modulations of the lateral parietal old/new effect by difficulty are not as straightforward as they first seemed.

In contrast to the lateral parietal cortex, an effect of difficulty was incidentally observed in the dorsolateral prefrontal cortex. In this region, there was a dramatic enhancement of the old/new effect in the

**Table 4**  
Recognition reaction times (ms) in Experiment 2

	Faces		Words	
	Easy	Hard	Easy	Hard
Hits	894 (25)	1048 (38)	863 (27)	966 (32)
Misses	1043 (40)	1103 (58)	1116 (70)	1120 (57)
False alarms	1125 (54)	1127 (44)	1154 (49)	1130 (42)
Correct rejections	962 (44)	1057 (52)	962 (30)	1033 (44)

Note. SEM in parentheses.

**Table 5**  
p Values from the ANOVAs in each ROI

	Lateral parietal		Medial parietal		Anterior prefrontal		Dorsolateral prefrontal	
	Exp 1	Exp 2	Exp 1	Exp 2	Exp 1	Exp 2	Exp 1	Exp 2
Hemi.	<.01	0.21	<b>0.01</b>	<b>0.01</b>	0.05	0.37	0.86	<b>0.04</b>
Diff.	–	<b>0.01</b>	–	0.08	–	0.47	–	0.26
Stim.	<b>0.03</b>	0.47	0.41	0.35	0.25	0.73	0.37	0.76
Memory	<.001	<.001	<.001	<.001	<.001	<.001	<.01	<.001
Hemi. × Diff.	–	<b>0.01</b>	–	0.10	–	0.09	–	0.08
Hemi. × Stim.	<.001	<.001	<.001	<.001	<.01	<.01	<.001	<.001
Diff. × Stim.	–	0.29	–	0.90	–	0.31	–	0.62
Hemi. × Diff. × Stim.	–	0.22	–	0.05	–	0.72	–	0.15
Hemi. × Memory	<.01	<b>0.04</b>	0.56	0.33	<.001	<.01	0.22	<b>0.03</b>
Diff. × Memory	–	0.36	–	0.81	–	0.12	–	<b>0.01</b>
Hemi. × Diff. × Memory	–	0.13	–	0.83	–	0.16	–	0.42
Stim. × Memory	0.09	0.20	0.49	0.22	0.67	0.77	0.37	0.17
Hemi. × Stim. × Memory	0.06	0.98	<.01	0.23	1.00	0.93	0.08	0.25
Diff. × Stim. × Resp.	–	0.60	–	0.69	–	0.68	–	0.51
Hemi. × Diff. × Stim. × Memory	–	0.32	–	0.74	–	0.77	–	0.63

Note. Hemi. = left versus right; Diff. = easy versus hard; Stim. = faces versus words; Memory = hits versus correct rejections. Significant effects are in bold.

difficult condition. We also incidentally observed an enhancement of the old/new effect in the fusiform gyrus that appears to be specific to faces. Speculatively, these data may reflect the influence of an executive or control process that is preferentially engaged under conditions of uncertainty.

Our finding that the old/new effect is left-lateralized for both words and faces in the lateral parietal and anterior prefrontal cortices raises perplexing questions about the functional significance of these effects. Extensive studies of patients that have undergone resection of the corpus callosum, resulting in two hemispheres that operate independently of one another, have not revealed any evidence of amnesic right hemispheres (Gazzaniga, 2000). Rather, the recognition memory performance of the divided cerebral hemispheres depends on the material type, with the left hemisphere showing preferential encoding of words and the right hemisphere showing preferential encoding of faces (Miller et al., 2002). If the neural mechanisms associated with successful retrieval are strongly lateralized to the left regardless of stimulus type, then how is it that the right hemisphere can remember faces so well without any help from the left hemisphere?

These considerations gain force when one considers that patients with damage to the left parietal lobe typically do not exhibit severe memory impairments, certainly nothing close to the impairments associated with damage to the medial temporal lobes or diencephalon (Squire, 1992). As several investigators have pointed out, however, the memory performance of parietal patients has not been studied extensively so these patients may have subtle but theoretically important impairments that have not yet been discovered (Wagner et al., 2005; Vilberg and Rugg, 2008). Nonetheless, this optimism is dampened by the fact that, of the five formal studies of memory in parietal patients, three failed to observe any impairments (Haramati et al., 2008; Simons et al., 2008; Ally et al., 2008; see Berryhill et al. (2007) and Davidson et al. (2008) for exceptions; see Vilberg and Rugg (2008) for review). Clearly, further research on the memory abilities of both callosotomy patients and parietal patients is required. Transcranial magnetic stimulation (TMS) could also be a useful tool for assessing the role of left parietal cortex in memory. Unfortunately, the one study that has used this technique (Rossi et al., 2006) produced ambiguous results (see Vilberg and Rugg, 2008 for discussion). Data bearing on the functional necessity of the parietal lobes for recognition memory is sparse and much more work is required. In the interim, results from fMRI and ERP must be interpreted with restraint, since it is quite possible that these effects are merely epiphenomenal.

Nonetheless, speculations regarding the functional significance of these effects may prove useful since success in research with patients and TMS may very well hinge on theoretical advancements that

develop specific, testable hypotheses. One interesting hypothesis that has been gaining force in the literature is that there is actually a division of labor within lateral parietal cortices: inferior lateral parietal cortex is associated with recollection of memories with specific contextual details and superior lateral parietal cortex is associated with a unidimensional sense of familiarity or recency (Yonelinas et al., 2005; Wagner et al., 2005; Vilberg and Rugg, 2008). Recently, Vilberg and Rugg (2008) completed a meta-analysis of 16 studies supporting this hypothesis. In the current study, we did not attempt to differentiate recollection and familiarity. Given the high level of performance in Experiment 1 and in the easy condition of Experiment 2 (Tables 1 and 2), it seems likely that subjects were recollecting contextual details on a significant proportion of the trials. Our lateral parietal peak is closer to regions that have been associated with familiarity than regions that have been associated with recollection. In this region, the old/new effect is clearly left-lateralized for both stimulus types. We cannot determine conclusively whether this pattern varies across the extent of the cluster.

Speculatively, the fact that the lateral parietal old/new effect does not exhibit material-specific lateralization may indicate that it is relatively removed from the main stimulus processing stream, which tends to exhibit extensive material-specific lateralization (Fig. 3). If the old/new effect is relatively removed from the main stimulus processing stream, then this would be consistent with the hypothesis that the effect represents a relatively abstract decision variable that is accumulating over time (Wagner et al., 2005), a notion that is reminiscent of the classic diffusion model of recognition memory (Ratcliff, 1978) and the work on the role of the intraparietal sulcus in perceptual decision making (Gold and Shadlen, 2007). If lateral parietal cortex does in fact contain a recognition memory accumulator, we would speculate it is most likely in the more dorsal region, since this region shows a graded response to recognition confidence while the ventral region shows a step function consistent with a sensitivity to recollection (Yonelinas et al., 2005).

Although we were particularly interested in the parietal cortex, the old/new effects that we observed were distributed throughout the brain – in both cortical and subcortical structures – and quite prominently in the anterior prefrontal cortex. The relationship between these distinct loci of old/new effects remains rather obscure. Recent advancements in multivariate statistical techniques, such as independent components analysis (McKeown et al., 1998), pattern classification techniques (Mitchell et al., 2004), and analysis of resting state connectivity (Fox et al., 2005), may help us determine whether these distinct regions constitute a unified functional network (e.g., Buckner et al., 2008). Episodic retrieval most likely does not reflect a process occurring at a discrete time in a discrete locus, but rather

likely reflects the continuous flow and evolution of information throughout a distributed cortical network.

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