NeuroImage xxx (2013) xxx–xxx

Contents lists available at SciVerse ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/ynimg

# Dynamic changes in parietal activation during encoding: Implications for human learning and memory

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ARTICLE INFO

*Article history:*
Accepted 26 May 2013
Available online xxxx

*Keywords:*
Posterior parietal cortex
Episodic memory
Encoding
fMRI

ABSTRACT

The ventral posterior parietal cortex (vPPC) monitors successful memory retrieval, yet its role during learning remains unclear. Indeed, increased vPPC activation during stimulus encoding is often negatively correlated with subsequent memory performance, suggesting that this region is suppressed during learning. Alternatively, the vPPC may engage in learning-related processes immediately after stimulus encoding thus facilitating retrieval at a later time. To investigate this possibility, we assessed vPPC activity during item presentation and immediately following its offset when a cue to remember was presented. We observed a dynamic change in vPPC response such that activity was negatively correlated with subsequent memory during stimulus presentation but positively correlated immediately following the stimulus during the cue phase. Furthermore, regional differences in this effect suggest a degree of functional heterogeneity within the vPPC. These findings demonstrate that the vPPC is engaged during learning and acts to facilitate post-encoding memory processes that establish long-term cortical representations.



## Introduction

Advances in our understanding of the neural bases of human memory have implicated a broad cortical network involved in the encoding, retention, and ultimate retrieval of recently learned information. While early investigations focused on the medial temporal lobe (MTL) and prefrontal cortex (PFC; Scoville and Milner, 1957; Shimamura, 1995; Squire and Alvarez, 1995), recent neuroimaging investigations have identified regions in the posterior parietal cortex (PPC) that are particularly active when an item has been successfully retrieved (Cabeza et al., 2012; Konishi et al., 2000; Shimamura, 2011; Wagner et al., 2005). Retrieval-related activations within the PPC are functionally dissociable such that activity related to low confidence, familiarity based responses are clustered within the dorsal PPC (dPPC), and activity related to high confidence, recollective responses are clustered within the ventral PPC (vPPC) regions (Kim and Cabeza, 2009; Wheeler and Buckner, 2004). Furthermore, these retrieval-related activations appear to be dissociable from attention-related activity such that memory tasks generally elicit left-lateralized activity in the angular gyrus (AnG), whereas activations occurring during attention tasks are clustered in right temporo-parietal junction (TPJ) and supra-marginal gyrus (SMG; Hutchinson et al., 2009).

Although neuroimaging findings suggest an important contribution of the vPPC to successful retrieval, its role during memory encoding is unclear. In some studies, the vPPC was *negatively* correlated with subsequent memory, such that items later remembered elicit greater vPPC deactivation during encoding compared to items later remembered, a phenomenon referred to as a negative subsequent memory effect (SME; see Uncapher and Wagner, 2009). Extant theories of PPC contributions to memory have struggled to explain this apparent conflict between the negative impact during encoding and positive influence during recognition tests, a pattern described as the *encoding/retrieval flip* (Daselaar et al., 2009). One possibility is that the negative influence of vPPC activity during encoding is related to its role as part of the *default mode network* (DMN), which also includes regions within the PFC, MTL, and medial PPC. Initially, the DMN was found to be more active during rest periods and inter-trial intervals compared to moments when participants were engaged in task-relevant activity (Buckner et al., 2008; Raichle et al., 2001). Recent findings suggest that this network is suppressed during perceptually-driven/externally attended conditions and engaged during conceptually-driven/internally attended situations (Guerin et al., 2012; Sestieri et al., 2010). Thus, findings of increased vPPC (i.e., DMN) activity at encoding for subsequently forgotten items suggest that participants during such encoding trials may have been sacrificing stimulus-driven encoding for irrelevant conceptually-driven processing (e.g., mind wandering).

The role of functionally distinct sub-regions within the vPPC may also help explain differential effects associated with the encoding/

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1053-8119/$ – see front matter © 2013 Published by Elsevier Inc.
http://dx.doi.org/10.1016/j.neuroimage.2013.05.113

retrieval flip. The anterior portion of the vPPC, including the TPJ and SMG, are thought to be a part of the *ventral attention network* involved in attentional reorienting (Corbetta et al., 2008; Shulman et al., 2007) and task-switching (Otten and Rugg, 2001; Wagner and Davachi, 2001). During perceptual search, activity within the TPJ/SMG is often suppressed, a phenomenon proposed to reflect filtering (down-regulating) of task-irrelevant stimuli (Shulman et al., 2007). Activation of these areas at encoding is thought to reflect inadvertent bottom–up capture by irrelevant stimulus features or shifts of attention away from task-relevant features (Otten and Rugg, 2001; Uncapher et al., 2011). Either of these possibilities would serve to divert resources away from processes such as elaborative encoding, which would contribute to successful memory formation.

To the extent that vPPC activity is involved in internally mediated mnemonic processes, it is possible that this region is suppressed during stimulus presentations, but becomes engaged immediately thereafter. This possibility is consistent with a recent theory of episodic memory which suggests that the vPPC is critical for the *cortical binding of relational activity* (*CoBRA*; Shimamura, 2011). According to CoBRA, the vPPC acts as a convergence zone that enables the binding of event features as an encapsulated episodic representation. Initial binding of event features is established by the MTL, which is also involved in post-encoding strengthening of episodic representations (i.e. consolidation) through reactivation or replay of event features (Eichenbaum et al., 1992; Shimamura and Wickens, 2009). The vPPC participates in cortical binding by establishing more direct links between event features during reactivation (e.g., rehearsal, elaborative encoding). We addressed the role of the vPPC in facilitating memory processes during learning by assessing neural correlates of SME immediately following stimulus presentation. In order to differentially emphasize memory processing during this time period, we presented one of two cues just after stimulus presentation which instructed subjects to either remember the item or ignore it. Later, subjects were given a recognition memory test and the SME was assessed for activity during both stimulus presentation and the cue phase.

## Methods

### Participants

Nineteen healthy subjects were included in this study (mean age 22.05 years, range 18 to 34 years; 13 females). Recruitment was conducted via advertisement on the UC Berkeley Department of Psychology website (http://psychology.berkeley.edu/rsvp). All subjects were native English speakers and were right-handed. None of the subjects reported a history of neuropsychiatric disorders or brain injury or having recently taken psychoactive medication. Subjects were paid for their participation and gave informed consent according to guidelines approved by the UC Berkeley Office for the Protection of Human Subjects. One subject was excluded from analysis due to below chance performance on the memory test.

### Stimuli

Three-hundred and twenty photographs of outdoor scenes were used in this study. Half of the scenes included people and half did not. A total of 160 pictures were used during the encoding session, with the remaining pictures used as new items during the test session. The pictures used in each condition were rotated across subjects such that each picture occurred in all conditions with equal frequency.

### Behavioral procedure

All trials were presented using *E-Prime 2 Professional* software (http://www.pstnet.com/eprime.cfm). The encoding session took place in the fMRI scanner and was presented in four functional runs (see Fig. 1). During each run, subjects were presented pictures that they were told would be on a later memory test (Remember items) and pictures that they were told would not be included in the memory test (Ignore items). Trials began with a stimulus presentation slide displaying a photograph of a scene (3 s), during which time subjects

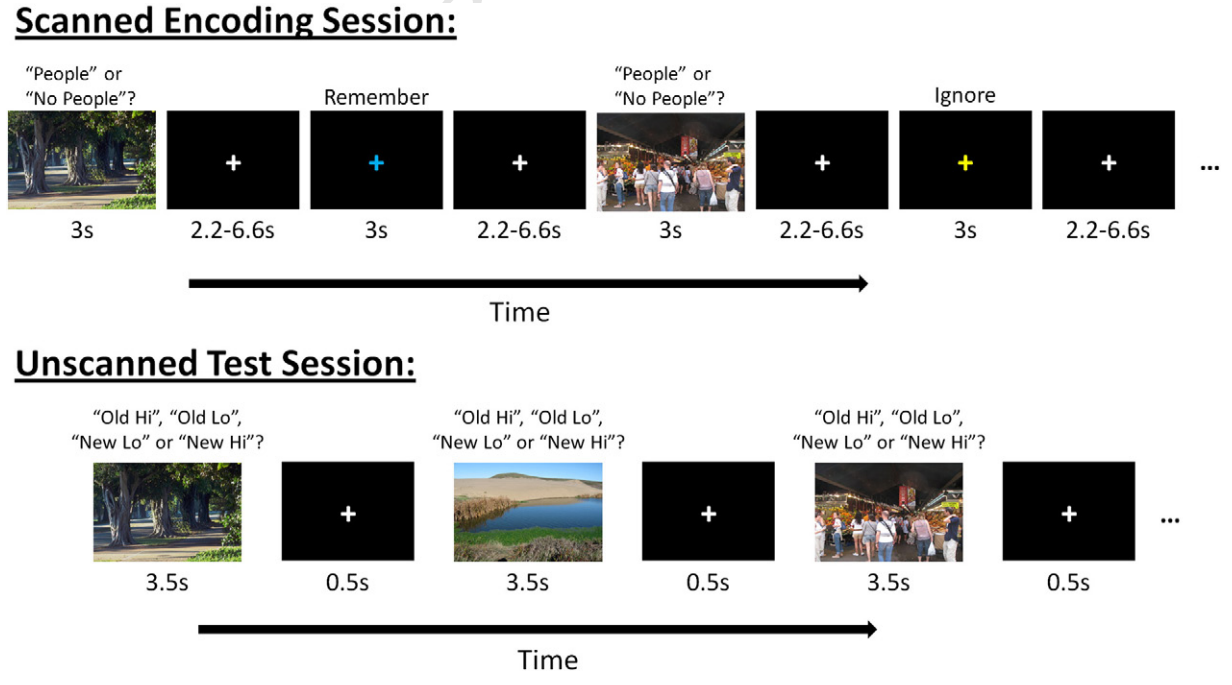


**Fig. 1.** Behavioral task: During scanned encoding trials, subjects were presented with a picture and responded whether there were people or no people. A cue (represented by colored fixation cross) then indicated whether the previous picture should be remembered for a later memory test or could be ignored. At test, subjects were presented with all pictures from the encoding session (regardless of cue type) along with new items. Subjects responded whether each item was old or new and rated their confidence.

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responded whether there were people or no people in the scene with a button press using a 4-button response box using either thumbs (response mappings were counterbalanced across subjects). A jittered white fixation cross then appeared in the center of the screen (2.2–6.6 s, mean = 3.3 s), and thereafter changed in color (blue or yellow) for 3 s to indicate whether the preceding picture should be remembered for a later memory test or could be ignored (cue color counterbalanced across subjects). Finally, another jittered white fixation cross appeared (2.2–6.6 s, mean = 3.3 s). For each of the four functional runs, 20 Remember trials were intermixed with 20 Ignore trials.

The subsequent recognition test phase took place outside of the scanner using a desktop computer and was presented in 4 blocks (see Fig. 1). Each block consisted of 40 old pictures (20 Remembered and 20 Ignored) and 40 new pictures for a total of 160 old items (80 Remembered and 80 Ignored) and 160 new items. Trials consisted of a picture displayed for 3.5 s followed by a 0.5 s centrally presented fixation cross. During the stimulus presentation slide, subjects were given a four-choice forced response as to whether they had seen the picture during the scanned encoding session or if it was new to the experiment. Additionally, they were asked to judge their response confidence as high or low, resulting in four response options ("Old-High", "Old-Low", "New-Low", "New-High"). Responses of whether there were people or no people were not modeled in this analysis. Subjects were instructed to make their best guess if unsure of an item's mnemonic status. Responses were made with key-presses and the button mappings were counter-balanced across subjects.

### *fMRI acquisition*

Subjects were scanned with a 3T Siemens (Erlangen, Germany) Trio scanner housed at the UC Berkeley Brain Imaging Center. For each of the four functional runs, we used a T2*-weighted echo-planar imaging (EPI) sequence [TR = 2278 ms; TE = 26 ms; flip angle = 60°; matrix = 90 × 90; FOV = 210 mm; 3 mm slice thickness]. Thirty-four axial slices oriented to the AC–PC were acquired in a sequential descending order giving whole brain coverage. A total of 216 volumes were collected during each of the functional imaging runs. The first nine volumes of each run were discarded to allow for magnetization preparation. A high resolution magnetization-prepared rapid-acquisition gradient echo (MPRAGE) [TR = 2300 ms; TE = 2.98; matrix = 256 × 256; FOV = 256; sagittal plane; slice thickness = 1 mm; 160 slices] and a gradient-echo multislice (GEMS) [TR = 250 ms; TE = 22; matrix = 256 × 256; FOV = 256; 3 mm slice thickness, 34 slices] were collected for registration purposes.

### *fMRI data analysis*

Data were preprocessed and analyzed with the FSL toolbox v4.1.9 (http://www.fmrib.ox.ac.uk/fsl; Smith et al., 2004). Motion correction was performed with MCFLIRT, aligning all images to the middle slice with rigid body transformation. BET (brain extraction tool) was then used to create a mask of the brain from the first volume of each time series and used to separate brain from surrounding skull and tissue in each volume. All images were spatially smoothed with a 5 mm FWHM Gaussian kernel to reduce noise and allow group analysis. High-pass temporal filtering was performed using the local Gaussian-weighted fit of a running line to remove low frequency artifacts. Subject data was registered to standard space in a two-step process using FLIRT (FMRIB's Linear Image Registration Tool). First, EPIs were registered to each subject's skull-stripped high resolution T1-weighted image. Second, subject's T1-weighted images were registered to standard (MNI) space (FSL's MNI152 template). The two registrations were then combined to take the subject's EPI images and run-level statistical maps into standard space.

A multi-level, mixed effects general linear model was run using FILM (FMRIB's Improved Linear Model) which treated subjects as random effects. Individual runs from the test phase were modeled in subject space and resulting statistical maps were registered to standard space for higher level analysis. Regressors of interest were obtained by convolving onset times with FSL's double-gamma hemodynamic response function and the temporal derivative. The stimulus and cue phases of each encoding trial were modeled separately based on the encoding condition and subsequent memory accuracy from the test phase. This resulted in 3 factors, each with 2 levels (Phase: Stimulus/Cue, Cue type: Remember/Ignore, Accuracy: Correct/Incorrect). The responses of whether pictures contained people were not modeled in the current analysis. Motion parameters were included as additional confound variables and temporal autocorrelation was removed through pre-whitening. To assess subsequent memory effects, whole brain contrasts were entered to compare Stimulus and cue phase activity for items remembered correctly and incorrectly on the later memory test.

A second level analysis combined the runs for each subject using a one-sample *t*-test, treating runs as fixed effects. Third-level group statistical maps were created for each contrast using FLAME (FMRIB's Local Analysis of Mixed Effects). FLAME implements a Bayesian two-stage model, the first being a fast approach to the posterior probabilities of activation for each voxel and the second uses a slower Markov Chain Monte Carlo (MCMC) based analysis for all voxels identified as being near threshold in the first stage. The whole brain family-wise error was corrected to $p < .05$ using Gaussian Random Field theory with a cluster forming threshold of $z > 2.3$.

Two ROI analyses were conducted to obtain more detailed measures of subsequent memory effects (SME). The first analysis used functionally derived ROIs reflecting regions that exhibited SMEs during the stimulus phase. We conducted a split-half analysis in order to avoid potential bias in our functionally-defined ROIs (Kriegeskorte et al., 2009). Subjects were randomly split into two groups and statistical maps resulting from the stimulus phase contrasts of correct vs. incorrect items on the memory test were generated from the first group. These maps were thresholded at $z > 2.3$ and the resulting clusters were used as ROIs to query activation in the second group. The mean z-scores of all conditions were extracted from each of these ROIs. We conducted three repeated measure ANOVAs. The first two considered either stimulus or cue phase activity only and used Cue type (Remember/Ignore) and Accuracy (Correct/Incorrect) as factors. The third was restricted to remember items in order to isolate trials during which memory processes that may otherwise occur over an extended period of time were likely to be most prominent. Phase (Stimulus/Cue) and Accuracy (Correct/Incorrect) were entered as factors in these analyses. Direct comparisons between conditions were also made for a priori contrasts of interest. Significance for all reported t-statistics is two-tailed (Table 1). Q2

In order to assess regional effects within the vPPC, we also conducted a second analysis using structurally-defined ROIs. While anterior/posterior dissociations appear to exist at retrieval (Elman et al., 2012, 2013; Hutchinson et al., 2009), subsequent memory effects appear to occur more broadly throughout the vPPC (Uncapher and Wagner, 2009). Therefore, we chose to explore regional differences within three sub-divisions of the vPPC. The regions chosen were bilateral AnG, SMG, and inferior parietal lobule (IPL) as defined by the AAL atlas (Tzourio-Mazoyer et al., 2002). Mean z-scores for Remember trials only were extracted from each of these ROIs for each run. We conducted repeated measures ANOVAs with a Greenhouse–Geiser correction for both the stimulus and cue phases and within each hemisphere using Region (AnG, SMG, IPL) and Accuracy (Correct/Incorrect) as factors. Post-hoc tests using Bonferroni correction were run to examine pairwise differences between regions. All reported t-tests are two-tailed.

Results from the whole brain analysis and both sets of ROIs investigated are presented on inflated surfaces of the PALS-B12 atlas using Caret software (Van Essen, 2005). Volumes in FLIRT stereotaxic space were mapped to the surface using the metric enclosing voxel mapping algorithm.



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**Table 1**
Subsequent memory effects as indicated by the contrast of stimulus phase activity for items later remembered correctly versus incorrectly. Coordinates of local maxima within significant clusters are reported in MNI-space and regional labels were derived from the Harvard–Oxford Cortical Atlas.

| Region | Hemisphere | X (mm) | Y (mm) | Z (mm) | Z-score |
|---|---|---|---|---|---|
| *Correct > incorrect* | | | | | |
| Amygdala | L | −18 | −8 | −18 | 3.35 |
| Hippocampus | L | −24 | −14 | −22 | 3.3 |
| Intracalcarine cortex | R | 6 | −82 | 0 | 3.28 |
| Lateral occipital cortex | L | −38 | −86 | 14 | 4.14 |
| | L | −20 | −68 | 52 | 3.64 |
| | L | −26 | −66 | 26 | 3.21 |
| | R | 24 | −64 | 54 | 3.66 |
| Lingual gyrus | R | 18 | −38 | −12 | 3.27 |
| Occipital fusiform gyrus | R | 34 | −66 | −12 | 3.11 |
| Occipital pole | L | −12 | −102 | −4 | 3.31 |
| | L | −22 | −96 | −4 | 3.14 |
| | L | −22 | −96 | 2 | 3.14 |
| | R | 10 | −102 | 2 | 4.09 |
| | R | 30 | −90 | −8 | 3.13 |
| Parahippocampal gyrus | R | 30 | −26 | −24 | 3.42 |
| Temporal fusiform cortex | L | −32 | −38 | −18 | 4.82 |
| | L | −38 | −10 | −28 | 3.68 |
| | R | 38 | −2 | −34 | 3.68 |
| | R | 42 | −16 | −26 | 3.26 |
| Temporal occipital fusiform cortex | R | 30 | −44 | −10 | 4.56 |
| *Incorrect > correct* | | | | | |
| Angular gyrus | L | −50 | −56 | 36 | 3.89 |
| | R | 54 | −52 | 36 | 4.7 |
| Anterior cingulate gyrus | L | −10 | 40 | 12 | 3.23 |
| | R | 6 | 38 | −2 | 3.3 |
| Frontal pole | L | −40 | 42 | 20 | 3.73 |
| | R | 18 | 50 | 36 | 3.94 |
| | R | 36 | 62 | 6 | 3.54 |
| | R | 6 | 56 | 0 | 3.46 |
| | R | 44 | 58 | −4 | 3.4 |
| Middle frontal gyrus | L | −38 | 24 | 42 | 3.37 |
| | R | 42 | 16 | 46 | 4.07 |
| | R | 30 | 30 | 30 | 3.13 |
| Middle temporal gyrus | R | 60 | −34 | −4 | 3.84 |
| | R | 66 | −14 | −10 | 3.42 |
| Paracingulate gyrus | R | 4 | 32 | 34 | 4.98 |
| Planum temporale | R | 62 | −6 | 4 | 3.11 |
| Posterior cingulate gyrus | L | −12 | −48 | 32 | 3.37 |
| | R | 2 | −26 | 40 | 4.15 |
| | R | 10 | −50 | 34 | 3.85 |
| | R | 2 | −42 | 18 | 3.56 |
| | R | 6 | −50 | 26 | 3.13 |
| | L | −8 | −44 | 22 | 3.22 |
| Precuneus cortex | R | 10 | −68 | 32 | 4.09 |
| Superior frontal gyrus | L | −12 | 32 | 56 | 3.2 |
| | R | 6 | 40 | 50 | 3.53 |
| | R | 18 | 22 | 60 | 3.24 |
| | R | 14 | 24 | 54 | 3.18 |
| | R | 8 | 28 | 48 | 3.13 |
| Superior temporal gyrus | L | −62 | −26 | −4 | 3.25 |
| | R | 66 | −14 | 6 | 3.44 |
| | R | 58 | −12 | −8 | 3.14 |
| Supramarginal gyrus | L | −58 | −42 | 18 | 3.15 |
| | R | 52 | −22 | 28 | 3.16 |

## Results

### Behavioral results

Subsequent memory performance for items cued as Remember (71.3% correct) was significantly better than for items cued as Ignore (66.3% correct), [$t(17) = 2.35$, $p = 0.03$]. Memory for both conditions was well above chance performance (50%). Response latencies for the People/No People decision were similar between conditions (Remember = 1415.83, Ignore = 1410.61 ms), [$t(17) = 0.220$, $p = 0.83$].

### fMRI results

We first performed a standard subsequent memory effect (SME) analysis in which item encoding (i.e., stimulus phase) activity was contrasted between subsequently remembered and subsequently forgotten items (hits > misses). For these SMEs, we collapsed items across levels of confidence as subjects gave very few low confidence responses at test. The whole-brain SME analysis showed areas of increased activity within bilateral medial temporal lobes including the hippocampus and parahippocampal gyrus. Additionally, SMEs were found in bilateral dPPC and lateral occipital cortices (see Fig. 2). Other regions, particularly those corresponding to the DMN, showed reduced or negative SMEs. Stimulus phase activity in these regions was significantly greater for subsequently forgotten than remembered items. These areas included bilateral vPPC (extending across both TPJ and AnG), mPPC, mPFC, lateral temporal cortices and lateral PFC (lPFC). No above threshold regions resulted from the whole brain comparison of SMEs during the cue phase.

### Functional ROI results

Dynamic changes across stimulus and cue phases were assessed by keying on functionally active regions during the stimulus phase and determining their status during the cue phase. To prevent potential bias in our comparisons, we conducted a split-half analysis in which activity from half of our subjects was queried using ROIs defined by the other half. Mean z statistics of all conditions were extracted for every run (Fig. 3). Both left and right vPPC ROIs showed negative SMEs during the stimulus phase as evidenced by a significant main effect of Accuracy [Left: $F(1,9) = 12.6$, $p = 0.006$; Right: $F(1,9) = 21.0$, $p < 0.001$] (see Fig. 3). That is, there was significant deactivation of the vPPC for correctly remembered items. During the cue phase, the left vPPC showed a significant main effect of Cue type (Remember vs Ignore) [$F(1,9) = 5.00$, $p = 0.05$]. Furthermore, there was a significant Phase × Accuracy interaction [$F(1,9) = 6.15$, $p = 0.04$] driven by an above baseline positive SME during Remember trials [$t(9) = 2.46$, $p = 0.04$] with no significant difference during Ignore trials [$t(9) = 1.56$, $p = 0.15$]. In contrast, there were no memory-based differences during the cue phase in the right vPPC.

Interestingly, dramatic changes in activations occurred between stimulus and cue phases for Remember items, reflected by a Phase × Accuracy interaction for Remember items in the left vPPC [$F(1,9) = 18.6$, $p = 0.002$]. Whereas this region exhibited a below baseline negative subsequent memory effect (SME) during the stimulus phase [$t(9) = 2.38$, $p = 0.04$], it exhibited an above baseline positive SME during the cue phase [$t(9) = 2.46$, $p = 0.04$]. Thus, not only was there an overall shift from deactivation to activation within the region, but the pattern of activity between correct and incorrect responses was doubly dissociated across trial phases. The right vPPC likewise demonstrated a Phase × Accuracy interaction [$F(1,9) = 22.8$, $p < 0.001$], yet this was primarily driven by the presence of a significant negative SME during the stimulus phase [$t(9) = 4.15$, $p = 0.003$] and the absence of any SME during the cue phase [$t(9) = 1.01$, $p = 0.34$].

The dPPC displayed similar patterns of activity bilaterally (see Fig. 3). During the stimulus phase, above baseline positive SMEs were present as indicated by a main effect of Accuracy in each hemisphere [Left: $F(1,9) = 56.2$, $p < 0.001$; Right: $F(1,9) = 79.3$, $p < 0.001$]. There were significant Cue × Accuracy interactions bilaterally during the cue phase [Left: $F(1,9) = 13.8$, $p = 0.005$; Right: $F(1,9) = 10.5$, $p = 0.01$]. This interaction is the results of above baseline positive SMEs continuing through the cue phase during Remember items [$t(9) = 4.79$, $p = 0.001$; Right: $t(9) = 3.29$, $p = 0.01$], but a lack of any such differences during Ignore trials [$t(9) = 1.49$, $p = 0.17$; Right: $t(9) = 1.69$, $p = 0.13$]. In assessing changes across trial phase for Remember trials only, we found significant Phase × Accuracy interactions bilaterally [Left: $F(1,9) = 41.9$, $p < 0.001$; Right: $F(1,9) = 17.4$, $p = 0.002$]. However, unlike the shift from negative to positive SME over the course of the

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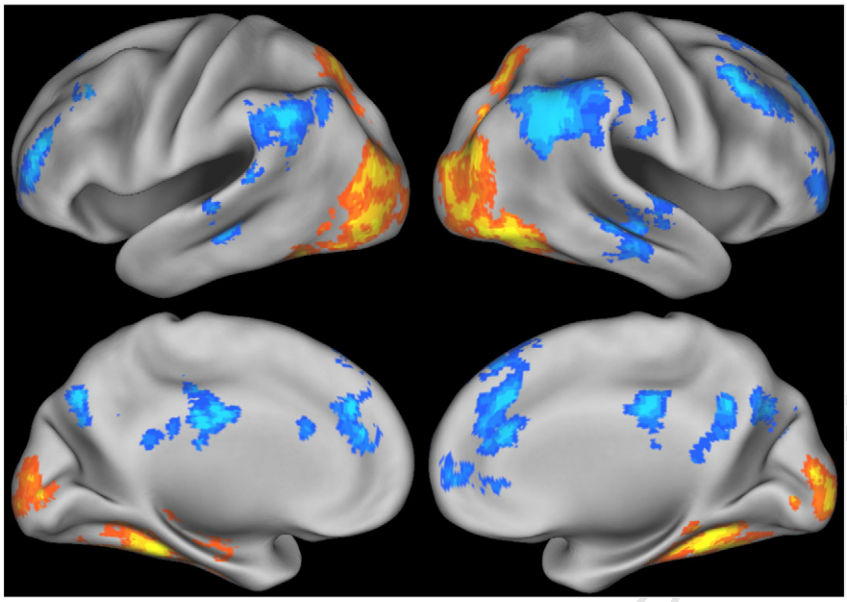

**Fig. 2.** Whole-brain analysis showing regional subsequent memory effects during the encoding session. Activity from the stimulus phase was compared between items subsequently remembered (correct) on a later memory test versus those that were forgotten (incorrect). Warm colors represent regions in which there was greater activity for correct compared to incorrect and the opposite contrast is represented by cool colors. All clusters survived correction for multiple comparisons and results are displayed on inflated surfaces of the PALS-B12 atlas using Caret software (Van Essen, 2005).

trial that occurred in the vPPC, these dPPC regions demonstrated consistently above baseline positive SMEs, albeit to a greater extent during the stimulus phase.

Although our primary interest was in the lateral parietal cortex, we also assessed functionally derived clusters falling within the memory network more broadly, including bilateral medial posterior parietal cortex (mPPC), bilateral medial and lateral prefrontal cortex (mPFC and lPFC, respectively) and left hippocampus. Results from these analyses are reported in the Supplementary Results (see also Supplementary Fig. S1). Briefly, all regions demonstrated stimulus phase SMEs consistent with those found in the whole brain analysis (positive SME: left hippocampus; negative SME: bilateral mPPC, mPFC and lPFC). Additionally, when assessing only Remember trials, all regions demonstrated significant Phase × Accuracy interactions except for the left hippocampus (which showed a trend for an interaction). However, these interactions were driven primarily by the significant stimulus phase SME's—no significant memory-based differences were present during the cue phase in any of these regions. Therefore, we found that the only regions in which cue phase SMEs occurred were the left vPPC and bilateral dPPC. Furthermore, only the left vPPC appeared to display the dynamic shift from deactivation-driven negative SMEs to activation-driven positive SMEs over the course of Remember trials.

*Structural ROI results*

Although there is evidence for regional dissociation of activity within the vPPC at retrieval (Elman et al., 2012, 2013; Hutchinson et al., 2009), encoding-related activity appears to be distributed somewhat more broadly (Uncapher and Wagner, 2009). To further explore possible regional differences, we conducted an ROI analysis of three anatomically-defined regions including the AnG, SMG and IPL as defined by the AAL atlas (Tzourio-Mazoyer et al., 2002; see Fig. 4). Mean z-scores extracted from these ROIs during the stimulus and cue phases were submitted to repeated measures ANOVAs using Greenhouse–Geiser correction for non-sphericity and pairwise differences between regions were explored using post-hoc tests with Bonferroni correction.

In the left hemisphere, there were significant main effects of Accuracy [$F(1,17) = 39.3$, $p = 0.020$] and Region [$F(1.62,27.59) = 6.65$, $p < 0.001$] as well as a significant Accuracy × Region interaction [$F(1.62,27.47) = 11.47$, $p < 0.001$] during the stimulus phase. Overall activity in the AnG was reduced below baseline significantly more than in the SMG ($p < 0.001$) and IPL ($p < 0.001$), and activity in the SMG was lower than in the IPL ($p < 0.001$). More specifically, a deactivation-driven negative SME emerged in the AnG [$t(17) = 3.48$, $p = 0.003$], whereas activity levels producing a significant negative SME in the SMG [$t(17) = 2.87$, $p = 0.01$] fell on either side of baseline. There was no SME in the left IPL [$t(17) = 0.47$, $p = 0.65$].

Also during the stimulus phase, significant main effects of Accuracy [$F(1,17) = 20.145$, $p < 0.001$] and Region [$F(1.84,31.3)$, $p = 0.008$] emerged in the right hemisphere. Significant negative SMEs occurred in all regions and overall deactivation in the AnG (for both correct and incorrect items) was significantly stronger than in the IPL, which straddled baseline levels of activation ($p = 0.004$). The SMG showed intermediate levels of overall activity in relation to the other regions, but was not significantly different from either (AnG: $p = 0.234$; SMG: $p = 0.588$).

Shifts in these patterns of activity occurred as trials progressed to the post-stimulus cue phase. There were significant regional differences [main effect of Region: $F(1.51,25.61) = 8.18$, $p = 0.004$] such that there was a trend for overall activity in the AnG being higher than in the SMG ($p = 0.088$), and there was significantly higher activity in the IPL than in the SMG ($p < 0.001$). Interestingly, a main effect of Accuracy [$F(1,17) = 6.256$, $p = 0.023$], driven by elevated levels of activity for correct compared to incorrect items, emerged in the left hemisphere and the Region × Accuracy interaction was borderline significant [$F(1.81,30.81) = 3.077$, $p = 0.059$]. More precisely, there were significant positive SMEs present in the AnG [$t(17) = 2.09$, $p = 0.05$] and IPL [$t(17) = 3.35$, $p = 0.004$], although the effect in the SMG was at the non-significant trend level [$t(17) = 1.64$, $p = 0.12$].

The right hemisphere did not show such robust memory effects during the cue phase as there was no significant main effect of Accuracy [$F(1,17) = 2.11$, $p = 0.16$]. However, there was a significant main effect of Region [$F(1.4,23.77) = 3.71$, $p = 0.05$] driven by higher overall levels of activity in the IPL compared to the SMG ($p = 0.002$). Only the IPL displayed a marginal positive SME [$t(17) = 1.97$, $p = 0.07$]. The Accuracy × Region interaction was not significant.

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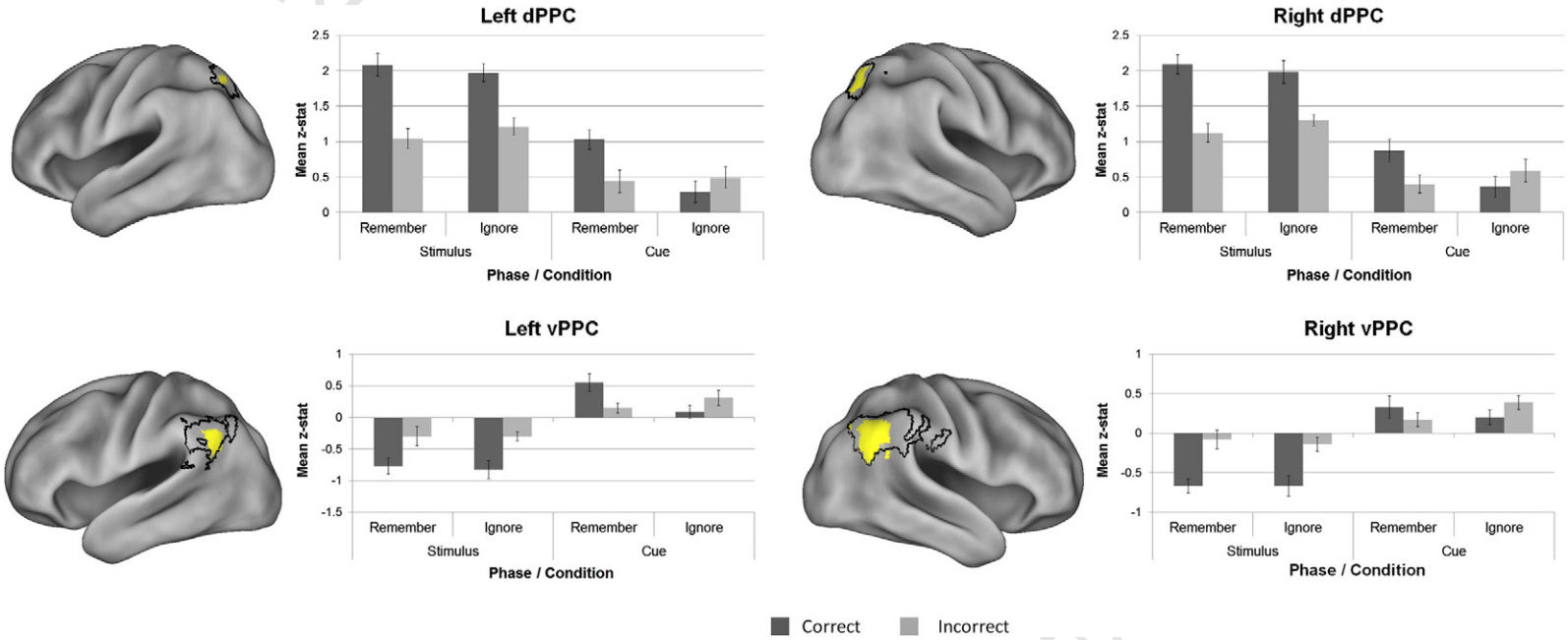


**Fig. 3.** Split-half ROI analysis of activity during stimulus and cue phases within lateral parietal regions displaying subsequent memory effects during the stimulus phase. Subjects were randomly split into two groups, and stimulus phase subsequent memory effects (SMEs; Correct vs Incorrect) within the first group were thresholded at $z > \pm 2.3$. The resultant clusters from the first group formed the ROIs used to query condition-specific activity within the second group, thus avoiding potential bias. Clusters generated by the first group within the ventral posterior parietal cortex (left: $x = 52.1$, $y = -58.5$, $z = 33.0$; right: $x = 53.7$, $y = -54.4$, $z = 35.8$) and dorsal posterior parietal cortex (left: $x = -21.9$, $y = -59.4$, $z = 51.8$; right: $x = 23.8$, $y = -60.8$, $z = 50.6$) are displayed with black outlines representing clusters from the whole group stimulus phase contrasts for purposes of comparison. Mean z-scores were extracted from each ROI in order to assess patterns of activity within stimulus and cue phases. The left ventral posterior parietal cortex exhibits a flip of activity, driven by a negative SME during stimulus phase and positive SME during cue phase. ROIs are displayed on inflated surfaces of the PALS-B12 atlas using Caret software (Van Essen, 2005). Error bars represent standard error of the mean.

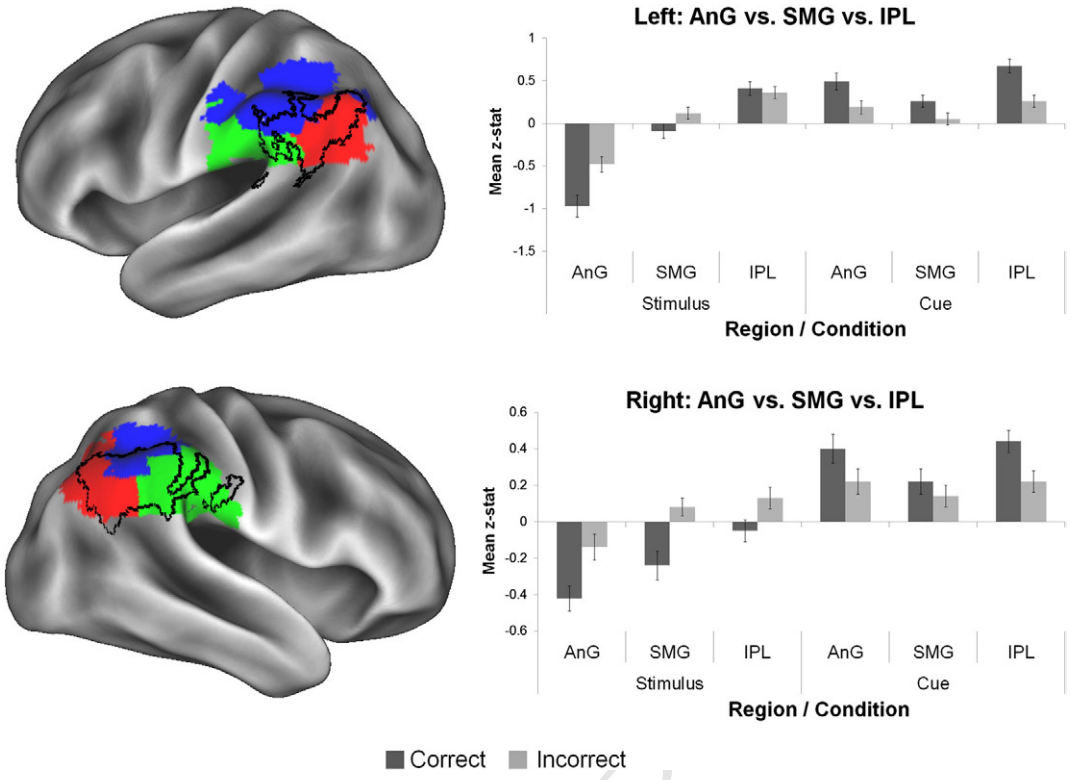


**Fig. 4.** ROI analysis of regional differences within the ventral posterior parietal cortex. Anatomically-defined ROIS corresponding to the angular gyrus (AnG; red), supramarginal gyrus (SMG; green), and inferior parietal lobule (IPL; blue) were derived from the AAL atlas (Tzourio-Mazoyer et al., 2002). Areas demonstrating subsequent memory effects (as defined by the whole group stimulus phase contrast of Correct vs. Incorrect) are outlined in black for purposes of comparison. Mean z-scores were extracted from each ROI in order to compare Stimulus and cue phase activity in order to assess regional differences during encoding. ROIs are displayed on inflated surfaces of the PALS-B12 atlas using Caret software (Van Essen, 2005). Error bars represent standard error of the mean. Regional differences within the functionally derived ROI suggest that the vPPC may be composed of multiple sub-divisions, each providing unique contributions to learning.

## Discussion

Consistent with previous findings, vPPC activity during stimulus encoding was negatively correlated with subsequent memory (Buckner et al., 2008; Daselaar et al., 2004; Otten and Rugg, 2001). Yet immediately after stimulus presentation, when subjects were presented a cue to remember the item, positive SMEs were observed in the vPPC. This study is the first to demonstrate a dynamic interplay in which both negative and positive SMEs in the vPPC occur during learning. Thus, these regions are not always suppressed during the learning phase. As soon as stimulus-driven encoding is terminated and elaborative encoding is engaged (via a cue to remember), vPPC activity is positively correlated with subsequent memory performance.

Other regions, such as the hippocampus, parahippocampal gyrus, dPPC and lateral occipital cortex, exhibited positive SMEs during stimulus presentations. Previous findings have shown that these regions drive memory-related processing during stimulus encoding (Davachi and Wagner, 2002; Eichenbaum and Cohen, 1993; Epstein, 2005; Köhler et al., 2002; Shimamura and Wickens, 2009; Squire and Zola, 1998). It has been suggested that the dPPC engages top–down attentional processes that enhance or select visuospatial representations stored along the dorsal visual pathway and in the lateral occipital cortex, as well as increasing the gain of input to the hippocampus in order to support elaborative processing of relevant stimuli (Corbetta et al., 2000; Guerin et al., 2012; Uncapher and Rugg, 2009; Uncapher et al., 2011). Consistent with consolidation theory (Davachi and Wagner, 2002; Eichenbaum and Cohen, 1993; Epstein, 2005; Köhler et al., 2002; Shimamura and Wickens, 2009; Squire and Zola, 1998), the MTL facilitates rapid binding of co-active representations as episodic memories. We did not find significant hippocampal SMEs in the period immediately following stimulus offset, as has been reported previously (Ben-Yakov and Dudai, 2011). However, the previous study employed movie clips rather than disparate photographs as stimuli, which may have extended elaborative binding processes over time, a process known to be dependent on hippocampal function (Staresina and Davachi, 2009).

Regions outside the vPPC that showed negative SMEs during stimulus presentations included the mPPC, mPFC and lPFC. As mentioned above, these regions are part of the DMN, which may be specifically engaged during internally driven tasks and suppressed by perceptually driven tasks (Nakao et al., 2012; Wagner et al., 2005, but see Huijbers et al., 2011). An extension of the attention to memory hypothesis (Cabeza et al., 2012; Uncapher and Rugg, 2009) ascribes vPPC SMEs during encoding to the modulatory effects of perceptual processing that are apparent in studies of selective attention. Negative SMEs during stimulus encoding may suggest that these regions were inadvertently activated (e.g., mind wandering, unfocused attention) when attention should have been focused on stimulus encoding (Cabeza et al., 2012; Otten and Rugg, 2001; Uncapher et al., 2011). Active suppression of these regions during encoding may also represent more efficient reallocation of resources to areas mediating successful memory formation (Daselaar et al., 2004; Shulman et al., 2007). Whereas all of these regions exhibited negative SMEs during the stimulus phase, the vPPC was the only region that also showed a reliable positive SME during the cue phase. Thus, as part of the DMN, the vPPC may be suppressed during sensory-driven processing, but it becomes engaged to serve memory processing immediately thereafter. This finding offers an explanation of the so-called encoding/retrieval flip (Daselaar et al., 2009) which, during learning, may be better characterized as a dynamic effect in which the vPPC is suppressed during stimulus presentation but



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becomes functionally important immediately after to support post-encoding memory processes.

Theoretical models of vPPC function have focused on retrieval-phase processes, as it has been difficult to account for negative SMEs during learning (Cabeza et al., 2008; Shimamura, 2011; Vilberg and Rugg, 2008; Wagner et al., 2005). We have shown, however, that immediately following stimulus presentation, vPPC activity is positively correlated with successful memory. Another complicating factor concerns functionally dissociable sub-regions that exist within the vPPC (Elman et al., 2012, 2013; Hutchinson et al., 2009, 2012; Nelson et al., 2010; Sestieri et al., 2010). What appears to be a singular cluster emerging within the vPPC from our whole-brain analysis of stimulus phase activity actually extends across multiple anatomical sub-divisions. In the present study, the dynamic flip between stimulus and cue phase activity was most apparent in the AnG and IPL compared to the SMG/TPJ (see Fig. 4). It may be that regions displaying similar patterns of activity in a given trial phase may be driven by separate processes.

When given an intentional cue to remember, elaborative encoding strategies are engaged to facilitate subsequent memory. Such strategies likely involve executive control processes that initiate the selection, maintenance, and manipulation of information in working memory (Badre and Wagner, 2007; Shimamura, 2008). PFC–PPC networks have been implicated in such processes (Buchsbaum et al., 2011; Henson et al., 2000). During cues to remember, it is likely that memory retrieval was engaged as subjects were trying to rehearse or study the item. Our vPPC findings could not, however, be attributed simply to engaging in a retrieval strategy or "mode". If that were the case, then all Remember trials should reflect such effects. In the SMG, we did observe such an effect, which is consistent with this region being implicated in phonological rehearsal, though it has been demonstrated that such processes are functionally dissociated from other vPPC regions proximal to our AnG and IPL regions (Buchsbaum et al., 2011). It may be that the role of the SMG in such rehearsal processes is related to an episodic buffer (Baddeley, 2000; Vilberg and Rugg, 2008) or attention to memory (Cabeza et al., 2008; Ciaramelli et al., 2008). Therefore, these particular accounts of parietal contributions during retrieval may also provide a useful description on SMG mechanisms during encoding that serve to maintain on-line representations of stimuli following their offset.

One could argue that vPPC activity during learning actually reflects the same retrieval processes that are engaged during test phases (e.g., yes/no recognition). We would not disagree with this point, but when "retrieval" is used in this manner, the distinction between retrieval and encoding processes becomes blurred and the term must be described functionally with respect to how such processes contribute to learning. With respect to CoBRA theory (Shimamura, 2011), we suggest that the vPPC acts as a convergence zone for cortical bindings of episodic features, and these bindings become established through post-encoding replay or retrieval. During stimulus presentations, the MTL initially binds active event features, particularly those enhanced or selected by PFC executive control processes. The vPPC operates with MTL bindings to establish long-lasting episodic representations and can thus be viewed as the final stage of neocortical consolidation (see Shimamura, 2011). CoBRA is consistent with analyses of resting-state activity, in which hippocampal and vPPC regions sensitive to retrieval success are co-active in the absence of task demands (Vincent et al., 2006). Also, in a directed forgetting EEG study, the frequency of parietal sleep spindles during a nap between study and test phases was correlated with subsequent recognition performance (Saletin and Walker, 2012). Thus, activation of this parietal network during sleep, perhaps indicative of re-activation of recently established memories, facilitated memory.

The present findings demonstrated that memory-related vPPC activity is not restricted to test phases and can be correlated with subsequent memory during the learning phase. Specifically, AG activity was negatively correlated with subsequent memory when items were presented, but it became positively correlated with memory immediately after presentations when cued to remember. Positive SMEs during the cue phase suggests that the AG is involved in elaborative encoding, such as self-generation or retrieval practice, which are known to enhance subsequent memory (Rosner et al., 2012). Although we observed positive SMEs in the AG immediately following stimulus presentations, we suggest that anytime after perceptual processing when a prior experience is retrieved, replayed, or re-analyzed, vPPC regions are involved in consolidating or cortically binding features of that experience. Our use of cues indicating that an item should be remembered was intended to emphasize such processes that may otherwise occur over much longer time periods. That the post-encoding activity within the AnG and IPL is predictive of subsequent memory success indicates that their contributions are beneficial to memory formation in addition to their role in supporting retrieval. The decision to characterize these processes as solely encoding or retrieval-based may therefore depend more on experimental context than any inherent boundary between the two.

In summary, we observed dynamic interactions in neural activity during the learning phase that is involved in successfully encoding and storing information. Whereas some regions showed positive SMEs during stimulus encoding (e.g., lateral occipital cortex, medial temporal lobe, dPPC) other regions showed negative SMEs (e.g., mPFC, vPPC, mPPC). During cues to remember, positive SMEs were observed in the vPPC and IPL. Interestingly, the vPPC was the only region that showed significant negative SMEs during stimulus presentation and positive SMEs during cues to remember. These findings advance our understanding of the neural basis of memory processes, and in particular extend the importance of the vPPC to post-encoding processes during learning.

## Acknowledgments

This research was supported by the NSF Grant BCS-0745835 and NIH Grant NS040813.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.neuroimage.2013.05.113.

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