Brain Networks Related to Beta Oscillatory Activity during Episodic Memory Retrieval

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Abstract

■ Evidence from fMRI has consistently located a widespread network of frontal, parietal, and temporal lobe regions during episodic retrieval. However, the temporal limitations of the fMRI methodology have made it difficult to assess the transient network dynamics by which these distributed regions coordinate activity. Recent evidence suggests that beta oscillations (17–20 Hz) are important for top–down control for memory suppression. However, the spatial limitations of the EEG methodology make it difficult to assess the relationship between these oscillatory signals and the distributed networks identified with fMRI. This study used simultaneous EEG/fMRI to identify networks related to beta oscillations during episodic retrieval. Participants studied adjectives and either imagined a scene (Place Task) or judged its pleasantness (Pleasant Task). During the recognition test, participants decided which task was performed with each word ("Old Place Task" or "Old Pleasant Task") or "New." EEG results revealed that posterior beta power was greater for new than old words. fMRI results revealed activity in a frontal, parietal network that was greater for old than new words, consistent with prior studies. Although overall beta power increases correlated with decreased activity within a predominantly parietal network, within the right dorsolateral and ventrolateral pFC, beta power correlated with BOLD activity more under conditions requiring more cognitive control and EEG/fMRI effects in the right frontal cortex correlated with BOLD activity in a frontoparietal network. Therefore, using simultaneous EEG and fMRI, the present results suggest that beta oscillations are related to postretrieval control operations in the right frontal cortex and act within a broader postretrieval control network. ■

INTRODUCTION

Evidence from neuroimaging (PET and fMRI) studies has consistently located a widespread network of frontal, parietal, and temporal lobe regions during episodic retrieval (Spaniol et al., 2009). Some functional specificity for controlled episodic retrieval has been identified within pFC (reviewed in Nyhus & Badre, 2015). According to the two-process model (Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005), the left anterior ventrolateral pFC (VLPFC) and the mid-VLPFC participate in distinct networks that respectively support control over access to memory versus control over how retrieved information influences decision and action. The more dorsal frontoparietal network including mid-VLPFC, dorsolateral pFC (DLPFC), inferior parietal cortex, and BG acts postretrieval to align what has been retrieved with task goals by selecting appropriate representations, setting decision criteria, and monitoring the outcome of retrieval. Consistent with this idea, neuroimaging studies have provided evidence that the right DLPFC is involved in postretrieval monitoring (Rugg, Henson, & Robb, 2003; Henson, Rugg, Shallice, & Dolan, 2000; Henson, Shallice, & Dolan, 1999; Rugg, Fletcher, Chua, & Dolan, 1999; Fletcher, Shallice, Frith, Frackowiak, & Dolan, 1998; Rugg, Fletcher, Frith, Frackowiak, & Dolan, 1996; Schacter, Alpert, Savage, Rauch, & Albert, 1996) and the right VLPFC and DLPFC have been implicated in inhibition of memory retrieval leading to later forgetting (Anderson & Hanslmayr, 2014; Butler & James, 2010; Kuhl, Kahn, Dudukovic, & Wagner, 2008; Depue, Curran, & Banich, 2007; Anderson et al., 2004).

However, the temporal limitations of the fMRI methodology have made it difficult to assess the transient network dynamics by which these distributed regions coordinate activity. Neural oscillations play an important role in communication among neurons within a network. Neural oscillations in different frequencies have been studied extensively in humans and animals and have been shown to be important for episodic memory. Multiple EEG studies have shown positive theta (4–8 Hz) and gamma (25–100 Hz) effects during episodic memory encoding and retrieval. Many studies have shown greater gamma and theta power for subsequently remembered than forgotten items as well as greater gamma and theta power for correctly remembered items than new items (reviewed in Nyhus & Curran, 2010). In addition, theta oscillations over frontal electrodes have been shown to be greater under conditions requiring control of episodic retrieval, including the retrieval of source information (reviewed in Nyhus & Curran, 2010). Based on this

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evidence, it has been proposed that theta oscillations allow for top–down control in episodic memory (Klimesch, Freunberger, & Sauseng, 2010; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Klimesch, Freunberger, Sauseng, & Gruber, 2008; Kahana, Seelig, & Madsen, 2001; Klimesch, 1996, 1999).

In contrast to theta and gamma, alpha (8–12 Hz) and beta (17–20 Hz) frequencies often show negative effects during episodic memory encoding and retrieval. Power decreases in the alpha and beta band predict subsequent recall (Hanslmayr, Spitzer, & Bauml, 2009; Fell, Ludowig, Rosburg, Axmacher, & Elger, 2008; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Weiss & Rappelsberger, 2000; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Klimesch et al., 1996). In addition, power decreases in alpha and beta frequencies are greater for correctly remembered items than new items (Khader & Rosler, 2011; Zion-Golumbic, Kutas, & Bentin, 2010; Spitzer, Hanslmayr, Opitz, Mecklinger, & Bauml, 2009; Düzel et al., 2003; Klimesch et al., 2001; Klimesch, 1999; Burgess & Gruzelier, 1997). The alpha rhythm has been related to semantic memory because it consistently desynchronizes with the presentation of semantically related items (Klimesch et al., 1997, 2004, 2008; Mölle, Marshall, Fehm, & Born, 2002; Klimesch, 1996, 1999; Klimesch, Vogt, & Doppelmayr, 1999; Klimesch, Schimke, & Schwaiger, 1994). But little is known about the functional role of beta oscillations in episodic memory.

Recent research has begun to explore the role of beta oscillations in episodic encoding and retrieval. A recent study using multi-unit recording in monkeys showed that both theta and beta frequency are important for frontal cortex–hippocampal interactions during associative memory (Brincat & Miller, 2015). In humans, beta oscillations have been related to semantic encoding (Hanslmayr et al., 2009, 2011) and control operations, and interference resolution and memory suppression (Waldhauser, Bauml, & Hanslmayr, 2015; Ketz, O'Reilly, & Curran, 2014; Hanslmayr et al., 2012; Waldhauser, Johansson, & Hanslmayr, 2012; Khader & Rosler, 2011).

For example, to examine whether changes in alpha and beta oscillations lead to selective memory retrieval, Waldhauser et al. (2012) studied the EEG correlates of retrieval-induced forgetting. In a memory design adapted from a visual half-field manipulation, participants studied associations between abstract shapes and colors that either reinforced or competed with the target memory representation. Alpha and beta power increased over the posterior ipsilateral hemisphere for competing memory representations and correlated with later forgetting. In addition, alpha and beta power decreased over the posterior contralateral hemisphere for target memory representations. These results suggest that beta oscillations represent inhibition of competing memory representations.

Two studies have localized beta oscillatory activity during directed forgetting to frontal cortex. Hanslmayr et al.

(2012) simultaneously recorded EEG and fMRI while participants studied two lists of words. After presentation of the first list, participants were told to remember the list or forget the list. Following the forget cue, beta long-range synchronization decreased. Furthermore, this decrease in beta synchronization correlated with increased BOLD in the left DLPFC. rTMS to the left DLPFC led to a reduction of beta synchronization and to greater forgetting. In addition, a recent study using the Think/No-Think task showed decreased alpha and beta power for No-Think items relative to the Think items (Waldhauser et al., 2015). Importantly, using source localization of the EEG data, the posterior beta power effects were localized to the right frontal cortex. These results are consistent with previous fMRI studies showing greater activity in the right frontal cortex for memory suppression (Anderson & Hanslmayr, 2014; Butler & James, 2010; Kuhl et al., 2008; Depue et al., 2007; Anderson et al., 2004). Therefore, beta oscillations may relate to memory suppression mechanisms in the right frontal cortex.

Outside the memory domain, beta oscillations have long been associated with motor processing. Recently, there has been convincing evidence that beta oscillations in the right inferior pFC are related to response inhibition. Patients with Parkinson's disease on and off medication showed greater beta power over right frontal channels for successful stop trials compared with unsuccessful stop trials in the stop signal task on medication (George et al., 2013; Swann et al., 2009, 2011, 2012). In addition, intracranial recordings confirm the localization of increased beta power for successful stop trials compared with unsuccessful stop trials to the right inferior frontal cortex (Swann et al., 2009, 2012). These results are consistent with fMRI studies of inhibitory control in the right inferior frontal gyrus (Aron, Robbins, & Poldrack, 2004). Taken together, these results suggest that beta oscillations provide a means of communication in an inhibitory control network including right inferior frontal cortex for response inhibition.

Therefore, previous studies have shown that the right pFC is involved in postretrieval control operations, such as postretrieval monitoring and inhibition of memory retrieval (Anderson & Hanslmayr, 2014; Butler & James, 2010; Kuhl et al., 2008; Depue et al., 2007; Anderson et al., 2004; Rugg et al., 1996, 1999, 2003; Henson et al., 1999, 2000; Fletcher et al., 1998; Schacter et al., 1996). In addition, previous research has shown that beta oscillations are involved in inhibitory control. Beta oscillations have been related to inhibition of task-irrelevant information and directed memory suppression (Waldhauser et al., 2012, 2015; Ketz et al., 2014; Hanslmayr et al., 2012; Khader & Rosler, 2011) and response inhibition (George et al., 2013; Swann et al., 2009, 2011, 2012). In addition, beta oscillations may be related to inhibitory control mechanisms of the right frontal cortex as beta effects in memory suppression and response inhibition localize to the right frontal cortex

(Waldhauser et al., 2015; Swann et al., 2009, 2012), but the source of beta effects during episodic retrieval have not been confirmed with fMRI. Although neural oscillations have been studied with simultaneous EEG and fMRI during episodic memory encoding (Hanslmayr et al., 2011, 2012), no study has examined the relationship between neural oscillations and the BOLD response during episodic retrieval.

To address this gap, we simultaneously recorded EEG and fMRI during a source memory retrieval task (adapted from Kahn, Davachi, & Wagner, 2004) to examine the relationship between beta oscillations and BOLD activity during episodic memory retrieval. We predicted that beta power would correlate with activity in the right frontal cortex more in conditions requiring more cognitive control and would act within a broader postretrieval control network. The temporal limitations of the fMRI methodology have made it difficult to assess the transient network dynamics by which distributed brain regions coordinate activity. And the spatial limitations of the EEG methodology make it difficult to assess the relationship between these oscillatory signals and the distributed networks identified with fMRI. Combining EEG and fMRI allows us to capitalize on the strengths of each approach (Jorge, van der Zwaag, & Figueiredo, 2014). Whereas EEG allows us to examine beta oscillations, fMRI provides insight into the neural correlates of beta oscillations. By combining the two approaches, we can gain insight into the relationship between beta oscillations and neural activity during episodic memory retrieval.

METHODS

Participants

Twenty-four people participated in the experiment for payment. All participants gave informed consent. There were 14 male and 10 female participants with ages of 18–29 years. All participants were right-handed, with normal or corrected-to-normal vision, native English speakers, and screened for the use of psychiatric and neurological medications and conditions, as well as for contraindications for MRI.

Stimuli

Experimental stimuli consisted of 800 adjectives (e.g., dirty, happy). Fifteen additional adjectives were used for practice. The words were common English adjectives roughly equated for word frequency ($M = 34.86$, $SD = 86.96$, range 0–1171) according to the Kucera and Francis (1967) word norms. All adjectives were presented in upper case in white on a black background.

Design

Memory status (old, new) and encoding task (place, pleasantness) were manipulated within participants.

Word lists were randomized across encoding task. In each session, participants were presented with both encoding tasks randomly intermixed. The order of trials and duration of jittered intertrial intervals within a block was determined by optimizing the efficiency of the design matrix so as to permit estimation of the event-related MRI response (Dale, 1999). Test key assignments were counterbalanced across participants.

Procedure

In each session, participants were given instructions and then presented with a short practice study block. Practice study blocks consisted of 10 study words. After completing the practice study block, participants began the study block.

For each study block, participants viewed 400 words. For half of the trials, the cue "Place" preceded the word, and participants created a mental image of a spatial scene described by the adjective (place task—e.g., for "DIRTY," the participant might imagine a messy room). For the other half of the trials, the cue "Pleasant" preceded the word, and participants thought about the meaning of the word and rated its pleasantness (pleasantness task—e.g., for "HAPPY," the participant might think that the word was pleasant; see Figure 1). After performing the encoding task for each word, participants were asked to rate how successfully they performed each encoding task. Using their index and middle fingers of both hands, participants pressed one of four buttons: 1 = *unsuccessful*; 2 = *partially*; 3 = *with effort*; 4 = *with ease*. Each word was preceded by a 500-msec cue (Place/Pleasant), indicating which encoding task to perform followed by a 200-msec blank screen. The adjective was then presented for 500 msec followed by a 4000-msec fixation during
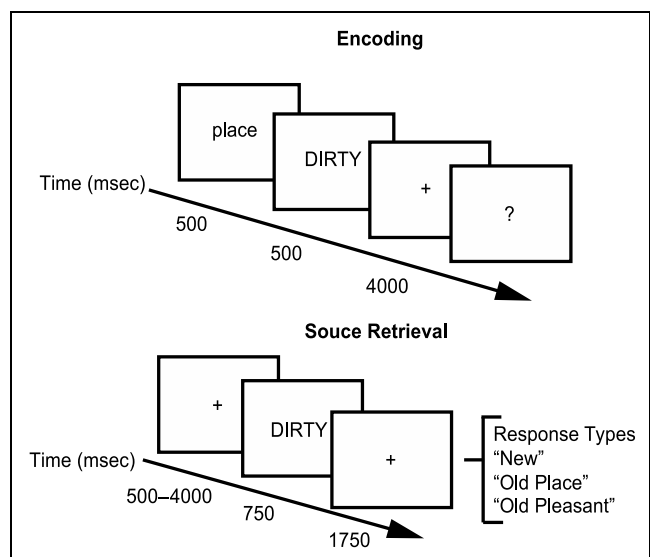

Figure 1. Experimental paradigm.

which they performed the encoding task. The fixation cross then changed to a question mark during which the participants made their response (see Figure 1).

After the study block, participants were fitted with the EEG electrode cap (see EEG Recording and Analysis section) and then performed a short practice test block. Practice test blocks consisted of 15 test words. After completing the practice test block, participants began the test blocks in the MRI scanner. The interval between the end of the study list and beginning of the test list was approximately 1 hr.

Across all test blocks, participants viewed 800 words. Test sessions contained the 400 studied words intermixed with 400 new words. Participants were tested in blocks of 100 words with a self-timed break in between the blocks. Test trials included a variable duration (1–4 sec) green fixation cross (+) followed by a test word. For each test word, participants decided if the word was new, or if they recognized the word, which task they had performed with it. Each test word was presented for 750 msec, followed by a red fixation (+) for 1750 msec. Upon appearance of the test word, participants could provide a response using an MRI safe button box. Using their index, middle, and ring fingers of their right hand, participants pressed one key for New, one key for Place, and one key for Pleasant (see Figure 1). Responses made after display offset were counted as nonresponse trials. Participants took approximately 3.5 hr to complete the study/test block.

EEG Recording and Analysis

During the testing phase of the experiment, scalp voltages were collected with a 64-channel MR-compatible BrainAmp system with a SyncBox (Brain Products, Munich, Germany). The SyncBox synchronizes the clock output of the MR scanner with the EEG acquisition, which improves removal of MR gradient artifact from the EEG signal. The electrocardiogram was recorded with an electrode on the lower left back for cardioballistic artifact removal. Amplified analog voltages (0.1–250 Hz bandpass) were digitized at 5 kHz. Individual sensors were adjusted until impedances were less than 25 kΩ.

Before further processing, MRI gradient artifact and cardioballistic artifact were removed using the average artifact subtraction method (Allen, Josephs, & Turner, 2000; Allen, Polizzi, Krakow, Fish, & Lemieux, 1998) implemented in Brain Vision Analyzer (Brain Products). MR gradient artifact was first detected using repetition time (TR) onset markers in the EEG and then removed by subtracting an MR artifact template consisting of a moving average window of 15 intervals in each channel followed by downsampling to 250 Hz. Cardioballistic artifact was first detected by filtering the electrocardiogram channel at 20 Hz, and then R-peaks were automatically detected using the correlation with a cardioballistic artifact template and amplitude threshold and then manually adjusted where necessary. Cardioballistic artifact was then removed by subtracting a cardioballistic artifact template consisting of a moving average window of 21 intervals in each channel.

Following MR gradient and cardioballistic artifact removal, EEG was further preprocessed using EEGLab (Delorme & Makeig, 2004). EEG data were selected from the onset to the offset of each scanner run. The EEG was digitally high-pass filtered at 1 Hz and low-pass filtered at 100 Hz. Individual channels were replaced on a trial-by-trial basis with a spherical spline algorithm (Srinivasan, Nunez, Tucker, Silberstein, & Cadusch, 1996). EEG was measured with respect to a vertex reference (Cz), but an average reference transformation was used to minimize the effects of reference site activity and accurately estimate the scalp topography of the measured electrical fields (Dien, 1998). EEG was segmented from 800 msec before the stimulus onset to 2000 msec after the stimulus onset in each condition. An infomax-based independent component analysis (Bell & Sejnowski, 1995) was run. The resulting component activities were manually inspected, and noise components (residual MR and cardioballistic artifact, eyeblink, and eye movement artifact) were removed. Average spectral power changes relative to baseline in posterior channels were compared across conditions.

fMRI Recording and Analysis

During the testing phase of the experiment, whole-brain images were collected with a Siemens 3T TIM Trio MRI system (Erlangen, Germany) equipped with a 12-channel head coil. A high- resolution T1-weighted 3-D multiecho magnetization-prepared rapid acquisition gradient-echo image was collected for anatomical visualization. fMRI data were acquired in eight runs of 170 volume acquisitions using a gradient-echo, echo-planar pulse sequence (TR = 2 sec, echo time = 28 msec, 33 axial slices, 3 × 3 × 3 mm, flip angle = 90°). Padding around the head was used to restrict motion. Stimuli were projected onto a rear projection screen and made visible to the participant via an angled mirror attached to the head coil.

fMRI was preprocessed using SPM8 (Wellcome Department of Cognitive Neurology, London). Data quality was first inspected for movement and artifacts. Functional data were corrected for slice acquisition timing by resampling slices to match the first slice, motion-corrected across all runs; functional and structural images were normalized to Montreal Neurological Institute stereotaxic space using a 12-parameter affine transformation along with a nonlinear transformation using a cosine basis set and spatially smoothed with an 8-mm FWHM isotropic Gaussian kernel.

EEG/fMRI Analysis

The entire time course of the EEG from the onset of the first TR to 2 sec after the last TR was used in the EEG/

fMRI analysis. EEG power was computed using the Hilbert transform on EEG data filtered in the beta frequency band from 17 to 20 Hz for posterior channels selected from the EEG analysis. Each sample in the EEG time course was z-scored, and outliers ($z > 4.5$) were replaced with the average EEG power.

Psychophysiological interaction analysis (PPI) is usually used to examine how a psychological variable affects the correlation of activity between two brain regions. We extend this analysis method to include EEG to characterize overall levels of EEG beta power and its relationship to the BOLD response and to characterize the modulation of the relationship between EEG power and BOLD depending on task condition. PPI analyses included the following regressors: a stimulus onset regressor for each condition with a duration of 2.5 sec, an EEG regressor that was orthogonalized relative to the stimulus onset regressor, and an interaction regressor (stimulus onset * EEG) that was orthogonalized relative to the stimulus onset and EEG regressors. All three regressors were convolved with the canonical hemodynamic response function and its temporal derivative, and the EEG regressors were downsampled to the TR sampling rate (0.5 Hz). Trials with no response within the response period and six additional head movement regressors were modeled as nuisance regressors.

Participant-specific effects for all conditions were estimated using a fixed-effects model, with session effects and low-frequency signal treated as confounds. Participant effects were then submitted to a second-level group analysis, treating participant as a random effect, using a one-sample t test against a contrast value of zero at each voxel. Unless otherwise noted, group effects are reported for voxels significant at a family-wise error (FWE) rate-corrected threshold of $p < .05$ at the cluster level.

RESULTS

Behavioral Results

Recognition memory analyses were performed on item and source discrimination (d') and response bias (c). Item d' and c were measured independently from source d' and c as previous studies have done for source memory (Slotnick & Dodson, 2005; Murnane & Bayen, 1996). For the place and the pleasantness task, an item

Table 1. Item Behavioral Data

Condition	Place	Pleasantness
Hit	0.71 (0.02)	0.73 (0.02)
FA	0.27 (0.03)	
Item d'	1.24 (0.08)	1.30 (0.09)
Item c	0.04 (0.05)	0.01 (0.06)

Means with standard errors in parentheses.

Table 2. Source Behavioral Data

	Condition	
Hit	Place correct source	0.64 (0.02)
FA	Pleasantness incorrect source	0.38 (0.02)
Source d'		0.68 (0.07)
Source c		−0.02 (0.05)

Means with standard errors in parentheses.

hit was defined as a "Place" or "Pleasant" response to an old item, regardless of whether they classified the source correctly. Conversely, an item false alarm (FA) was a "Place" or "Pleasant" response to a new item. A source hit was anytime a participant responded "Place" for an item studied in the place task, and a source FA was anytime a participant responded "Place" for an item studied in the pleasantness task. Item d' and c were calculated by comparing old to new words for both the place and the pleasantness task (hit place task − FA and hit pleasantness task − FA), whereas source d' was calculated for item hits only (hit place correct source − hit pleasant incorrect source). Assignment of the place versus pleasantness tasks to hits versus FAs for computing sources d' and c was completely arbitrary, and equivalent results would be obtained through the opposite assignment.

Item d' and c were compared with a Task (place, pleasantness) repeated-measures ANOVA. Item d' and c were similar following the place and pleasantness tasks, d': $F(1, 23) = 2.93$, $MSE = .02$, $p = .10$, and c: $F(1, 23) = 2.92$, $MSE = .004$, $p = .10$ (see Table 1).

Source d' was significantly above chance, $F(1, 23) = 98.72$, $MSE = .06$, $p < .01$, and source c was close to zero, $F(1, 23) = .15$, $MSE = .025$, indicating no bias to choose one source more often than the other (see Table 2).

RTs on only correct trials were analyzed first with a Memory status (correct rejection of new words, place, pleasantness) repeated-measures ANOVA. RTs were faster for new words than words following the place and pleasantness tasks, $F(1.20, 27.48) = 32.18$, $MSE = 9870.26$, $p < .01$. The difference between old and new words was significant following the place, $F(1, 23) = 42.45$, $MSE = 6976$, $p < .01$, and pleasantness tasks, $F(1, 23) = 28.87$, $MSE = 9444$, $p < .01$ (see Table 3).

Second, RTs on only item-correct old trials were analyzed with a Task × Source accuracy (correct, incorrect) ANOVA. RTs were faster for correct than incorrect source judgments, $F(1, 23) = 7.36$, $MSE = 3746$, $p = .01$. Task

Table 3. Item RT Data

Condition	New	Place	Pleasantness
RT	1207 (43)	1364 (37)	1358 (38)

Means with standard errors in parentheses.

Table 4. Source RT Data

Condition	Place	Pleasantness
RT		
Correct source	1318 (35)	1369 (39)
Incorrect source	1410 (42)	1346 (39)

Means with standard errors in parentheses.

interacted with source accuracy, such that RTs were faster for correct than incorrect source judgments for words following the place but not the pleasantness task, $F(1, 23) = 14.36$, $MSE = 5502$, $p < .01$. The difference between correct and incorrect source judgments was significant only for words following the place task, $F(1, 23) = 25.84$, $MSE = 3868$, $p < .01$ (see Table 4).

EEG Results

The spatiotemporal ROI was defined according to previous research (Nyhus & Badre, 2015; Waldhauser et al., 2012, 2015; Ketz et al., 2014; Hanslmayr et al., 2011;

Khader & Rosler, 2011). The ROI was a posterior channel group (see Figures 2B and 3B); mean beta (17–20 Hz) power from 700 to 1000 msec was computed by averaging the channels within this region for each condition/participant. Time–frequency spectrograms across times and frequencies in a central parietal channel and topographic plots of beta power across all channels from 700 to 1000 msec are shown in Figures 2 and 3. Beta power on only correct trials was analyzed first with a Memory status repeated-measures ANOVA. Beta power was greater for new words than words following the place and pleasantness tasks, $F(1.67, 38.46) = 11.12$, $MSE = .07$, $p < .01$. The difference between old and new words was significant following the place, $F(1, 23) = 24.98$, $MSE = .03$, $p < .01$, and pleasantness tasks, $F(1, 23) = 15.64$, $MSE = .07$, $p < .01$.

Second, posterior beta power from 700 to 1000 msec on only item-correct old trials was analyzed with a Task × Source accuracy repeated-measures ANOVA. Beta power was marginally greater for incorrect than correct source judgments, $F(1, 23) = 4.05$, $MSE = .13$, $p = .06$.

To consider the broader spatiotemporal effects for beta frequency of 17–20 Hz and more standard beta
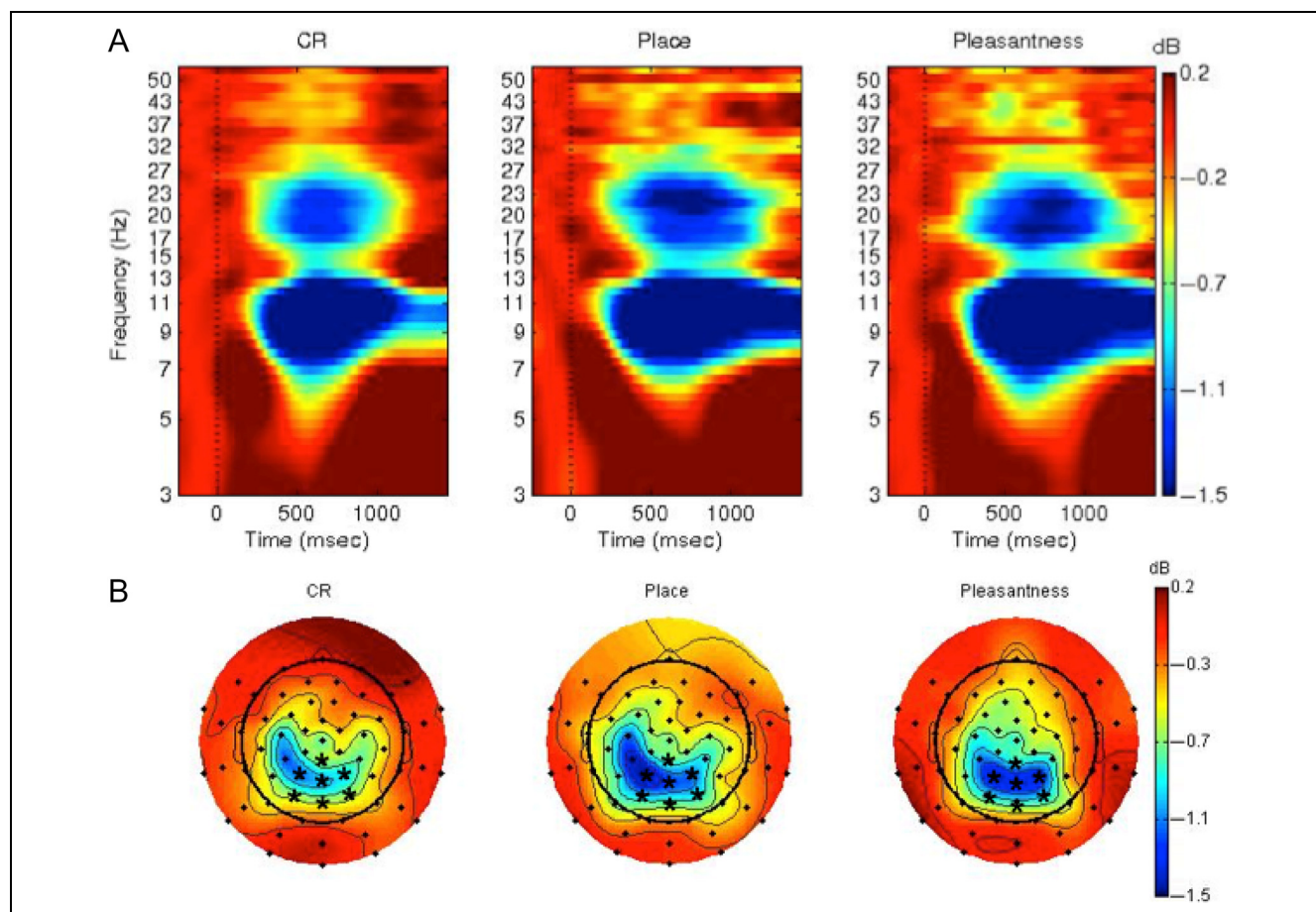

Figure 2. Beta power for hits from the place and pleasantness tasks compared with correct rejections (CR). Time–frequency spectrograms across times and frequencies in a central parietal channel (A). Beta power across all channels from 700–1000 msec. Black * marks analyzed channels in parietal regions (B). Color scale: decibel change from prestimulus baseline.

Figure 3. Beta power for hits with correct source compared with hits with incorrect source. Time–frequency spectrograms across times and frequencies in a central parietal channel (A). Beta power across all channels from 700–1000 msec. Black * marks analyzed channels in parietal regions (B). Color scale: decibel change from prestimulus baseline.
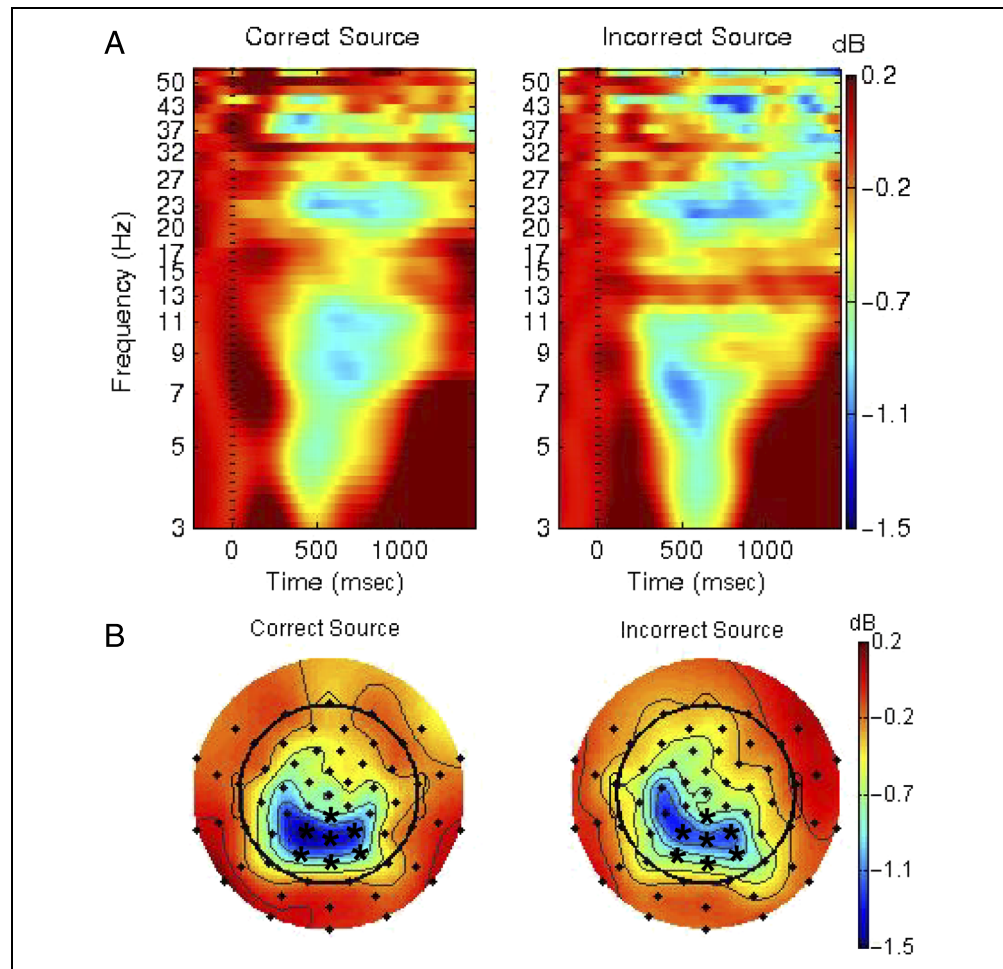
frequency of 12–20 Hz, additional analyses were performed in frontal central and right frontal channels between 700–1000 msec, 0–500 msec, 500–1000 msec, and 1000–1440 msec. Although the pattern of results was similar to the reported results for both frequency bands (17–20 Hz and 12–20 Hz) in frontal central and right frontal channels for the later time points (500–1440 msec), the old/new effects were generally weaker and there were no significant source accuracy effects.

In addition, we examined EEG effects in other frequencies that have been related to episodic memory, including theta (4–8 Hz), alpha (8–12 Hz), and gamma (25–50 Hz) frequencies. EEG recordings inside the scanner can be contaminated with both scanner artifact and cardioballistic artifact. We took several steps to ensure that the data were uncontaminated by residual artifact. First, we removed scanner artifact and cardioballistic artifact and removed residual artifact with independent component analysis. In addition, to confirm that our EEG power results were not contaminated by residual scanner or cardioballistic artifact, we compared the present results to a previous EEG study using a similar design (Nyhus & Badre, 2015). The beta old/new effects replicate our previous EEG results, both in timing and topography. Therefore, the current study showed reliable beta power

results acquired in the fMRI scanner. Although higher frequencies, including alpha, beta, and gamma, were reliably recovered and replicated our previous EEG results, lower frequencies have proved challenging to fully recover in simultaneous EEG/fMRI recording. Theta frequency old/new effects did not reliably replicate our previous EEG results. Therefore, we do not report the results here.

fMRI Results

To examine the correlation between beta power effects and BOLD activity, we first identified a memory network that was more active for old than new words. To assess task effects, functional activation on only correct trials was compared between conditions. Activity was greater for words following the place and pleasantness tasks than new words in a widespread frontal, parietal, and temporal network (FWE cluster-corrected $p < .05$; see Table 5 and Figure 4).

EEG/fMRI Results

Overall EEG power in the beta frequency negatively correlated with the BOLD response in a frontal, parietal

Table 5. fMRI Activations (FWE Cluster-Corrected $p < .05$)

Region	Stereotaxic Coordinates			Broadman's Area	Peak Z
	x	y	z		
Left dorsal medial pFC	−4	28	40	32	7.65
	−6	14	54	6	6.81
Left inferior parietal cortex	−36	−64	50	7	6.69
	−36	−56	46	7	5.95
	−4	−70	36	7	5.86
Left VLPFC	−50	18	26	48	6.64
	−30	22	−8		6.59
	−48	40	2	45	6.51
Right caudate	10	12	2	25	6.34
	−12	10	4		5.90
	−8	−12	2		5.69
Left middle temporal cortex	−60	−42	−10	20	6.02
Right insula	32	22	−6	47	5.70
Right precentral	30	−4	50	6	4.35
	38	2	50	6	4.03
	40	4	60	6	3.43
Right VLPFC	46	28	28	45	4.33
	56	24	36		3.50
	62	6	30	6	3.43

network (FWE cluster-corrected $p < .05$; see Table 6 and Figure 5).

In addition, we examined task-related modulations of the beta power/BOLD correlations using ROI analysis. EEG beta power differed for old compared with new words, but the difference between old and new words was similar for words from the place task and words from the pleasantness task. In addition, BOLD activity was greater for old than new words, but again, the pattern of activity was similar across tasks. Although there was a marginal beta power effect of source accuracy, there was no difference in the BOLD response for correct and incorrect source judgments across tasks. Therefore, we focused the EEG/fMRI analysis on regions that were part of the memory network defined by the contrast of all hits (place + pleasantness) to correct rejections in the univariate fMRI results. Functional ROIs were first defined by group-level voxel-wise contrasts of all Hits > CR (see Table 5 for regions). To examine effects in specific regions within the functional ROIs, ROIs were also defined based on overlapping group-level voxel-wise contrasts of all Hits > CR and anatomical definitions based on the Automatic Anatomical Labeling masks (Tzourio-

Mazoyer et al., 2002). Average beta values for the Hits > CR * beta frequency and Correct Task > Incorrect Task * beta frequency contrasts from the PPI analysis for each participant were extracted for each ROI and compared across ROIs.

Previous studies have shown beta oscillation effects related to activity in the right frontal cortex. Therefore, we were particularly interested in task related modulations of the beta power/BOLD correlations in right frontal regions. ROI analysis revealed a correlation between beta power and BOLD in right frontal regions, including the right DLPFC and the right VLPFC (see Figure 6A for selected regions). The correlation between beta power and BOLD was marginally greater for hits than correct rejections in right frontal regions, $F(1, 23) = 3.45$, $MSE = .000004$, $p = .08$, including significant effects in the right DLPFC, $F(1, 23) = 4.42$, $MSE = .000004$, $p = .05$, and right VLPFC, $F(1, 23) = 4.76$, $MSE = .000004$, $p = .04$ (see Figure 6B). Other regions showing significantly greater correlation between beta power and BOLD for hits than correct rejections were medial frontal regions, $F(1, 23) = 4.61$, $MSE = .000005$, $p = .04$, including a significant effect in the left dorsal medial pFC, $F(1, 23) =$
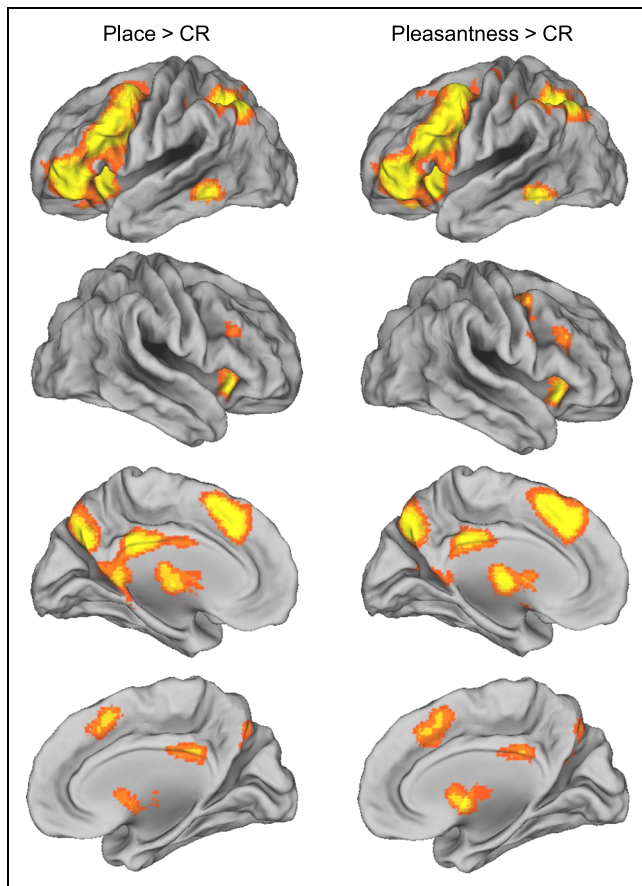
Figure 4. BOLD response for hits > correct rejections (CR) contrast at FWE rate cluster-corrected $p < .05$. BOLD activity was greater for words following the place and pleasantness tasks than new words in a widespread frontal, parietal, and temporal network.

6.43, $MSE = .000005$, $p = .02$, and a marginal effect in right precentral regions, $F(1, 23) = 3.62$, $MSE = .000001$, $p = .07$, including a significant effect in the right precentral cortex, $F(1, 23) = 5.10$, $MSE = .000001$, $p = .03$.

Because there was a marginal difference between correct and incorrect source judgments in the beta power results, we also examined the correlation between beta power and BOLD for correct and incorrect source judgments in right frontal regions. The beta power/BOLD correlation was marginally greater for incorrect than correct source judgments in right frontal regions, $F(1, 23) = 3.00$, $MSE = .00002$, $p = .10$, including a marginal effect in the right DLPFC, $F(1, 23) = 3.45$, $MSE = .00002$, $p = .08$, but not the right VLPFC, $F(1, 23) = 2.42$, $MSE = .00001$ (see Figure 6C).

To consider brain–behavior relationships, we examined the correlation between EEG/fMRI effects in right frontal regions and behavior (d' and RTs). Specifically, the difference in beta power/BOLD correlation for hits and correct rejections and correct and incorrect source judgments were correlated with item d', source d', RT differences between hits and correct rejections, and RT differences between correct and incorrect source judgments. There was a positive correlation between beta power/BOLD old/new effects in right frontal regions and source d' ($r = .42$, $p = .04$, two-tailed). In addition, there was a positive correlation between beta power/BOLD old/new effects in right frontal regions and the difference in RTs for hits and correct rejections ($r = .45$, $p = .03$, two-tailed).

To examine the relationship between EEG/fMRI effects in right frontal regions and activity in the episodic retrieval network, we correlated EEG/fMRI effects in right frontal regions and BOLD activity in other memory-related ROIs. Specifically, the difference in beta power/BOLD correlation for hits and correct rejections and correct and incorrect source judgments were correlated with the difference in BOLD for hits and correct rejections in functional ROIs. There was a positive correlation between old/new effects for beta power/BOLD in right frontal regions and BOLD activity in left frontal regions ($r = .56$, $p < .01$,

Table 6. Beta Power/BOLD Correlation (FWE Cluster-Corrected $p < .05$)

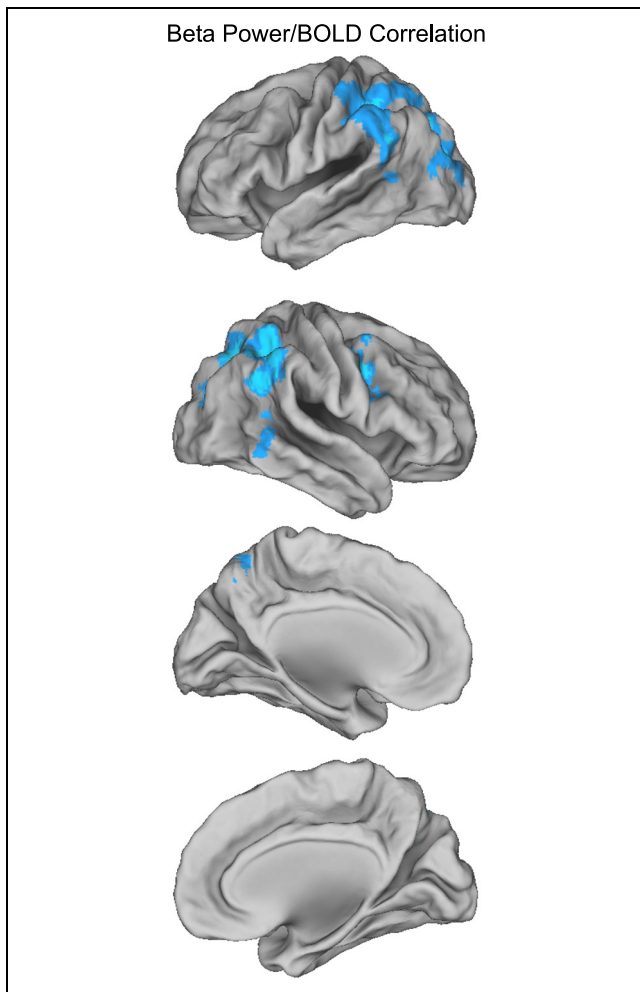| Region	Stereotaxic Coordinates			Broadman's Area	Peak Z
	x	y	z		
Left inferior parietal cortex	−58	−34	52		4.88
	−22	−74	38	19	4.85
	−32	−44	48	40	4.63
Right inferior parietal cortex	40	−44	56	40	4.60
	58	−50	32	40	4.41
	26	−66	36	7	4.40
Right precentral	42	6	38	6	4.28
	50	8	54		3.95
	48	14	28	48	3.94

Figure 5. Negative EEG beta power/BOLD correlations in a frontal, parietal, network at FWE rate cluster-corrected $p < .05$.

two-tailed) and a marginally significant correlation in left parietal regions ($r = .37$, $p = .08$, two-tailed), the striatum ($r = .37$, $p = .07$, two-tailed), and the right insula ($r = .37$, $p = .07$, two-tailed).

In addition, we examined EEG/fMRI effects for alpha and gamma frequencies, which have been related to episodic memory and that showed EEG old/new effects that replicated a previous EEG study using a similar design (Nyhus & Badre, 2015). EEG/fMRI effects for alpha and gamma frequencies were not significant. The lack of significant task-related effects for other frequencies is perhaps due to the nature of the BOLD response and EEG oscillatory effects. The BOLD response depends on changes in metabolic demands from an increase or decrease in neural firing. In contrast, EEG oscillations can occur due to increases in neural firing at a particular frequency or by synchronization of ongoing oscillations without affecting the number of neurons firing. Therefore, increased synchronization of ongoing oscillations may not change metabolic demands. In this case, we would not expect a significant change in the correlation with the BOLD response.

DISCUSSION

The purpose of the present experiment was to examine the relationship between beta oscillations and BOLD activity during episodic memory retrieval. Item discrimination was similar following the place and pleasantness tasks, and source discrimination was above chance, suggesting that participants were successful in remembering source information. RTs were faster for new words than words following the place and pleasantness tasks and for correct than incorrect source judgments for words following the place task. EEG results revealed that posterior beta power between 700 and 1000 msec was greater for new than old words and was marginally greater for incorrect than correct source judgments. fMRI results revealed activity in a frontal, parietal, temporal network that was greater for old than new words. Importantly, this study is the first to show beta power/BOLD correlations during memory retrieval. Overall, there was a negative correlation between beta power and BOLD in a frontal, parietal network. Importantly, task-related effects in right frontal regions showed differences between beta power and BOLD correlations for old and new words and marginal differences for incorrect and correct source judgments. The EEG/fMRI effects correlated with behavioral performance, such that better memory and greater differences in RTs were correlated with greater differences in beta power/BOLD correlations for old than new words. In addition, beta power/BOLD old/new effects in right frontal regions correlated with BOLD activity in left frontal regions and marginally correlated with BOLD activity in left parietal regions, the striatum, and the right insula.

The EEG results are consistent with previous research showing greater power decreases in the beta band for correctly remembered items than new items (Khader & Rosler, 2011; Spitzer et al., 2009; Düzel et al., 2003). The fMRI results replicated previous studies showing a broad frontal, parietal, and temporal network that was more active for correctly remembered items than new items. All of the regions reported, except for right precentral regions, overlap with regions shown to be more active for correctly remembered items than new items in a previous meta-analysis of retrieval success effects (Spaniol et al., 2009).

In addition to old/new effects, we examined source accuracy effects. For EEG beta power, there was a marginal effect of source accuracy across tasks. There was not a significant interaction between task and source accuracy, but follow-up analyses revealed a marginal effect for the place task but not the pleasantness task. In addition, BOLD activity did not differ for correct than incorrect source judgments across tasks, but follow-up analyses revealed that activity was greater for correct than incorrect source judgments for the place task in the left parahippocampal cortex (FWE cluster-corrected $p < .05$). Therefore, for the behavioral (RTs), EEG beta power, and
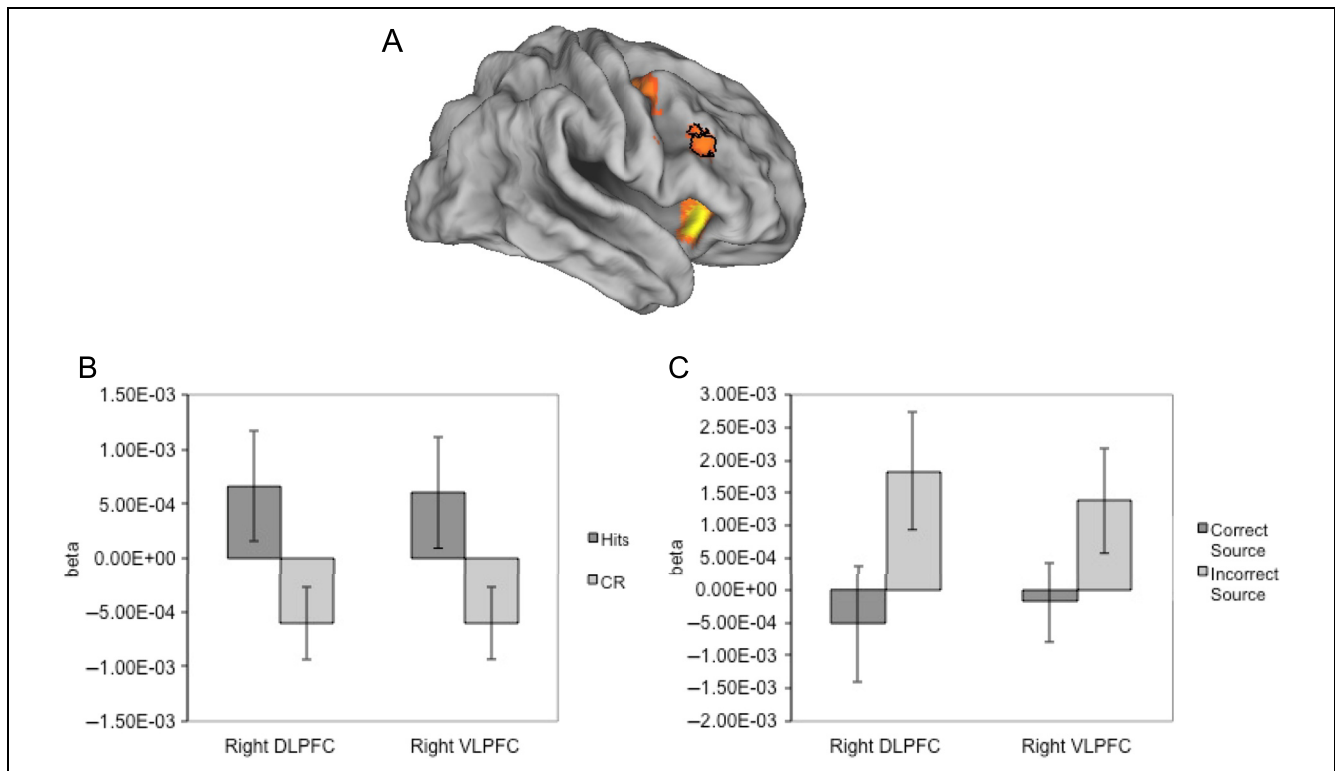
Figure 6. Task-related effects identified with ROI analysis. Selected ROIs in the right DLPFC and in the right VLPFC, indicated by black outline (A). ROI analysis revealed differences between beta power and BOLD correlations for hits and correct rejections (CR) in the right DLPFC and in the right VLPFC (B). ROI analysis revealed marginal differences between beta power and BOLD correlations for incorrect and correct source judgments in the right DLPFC, but not in the right VLPFC (C). Error bars are the standard errors of the mean.

fMRI results, source accuracy effects were greater for the place task than the pleasantness task. These results indicate that source accuracy effects are greater for the place task because this task required encoding of more self-generated visuospatial information. Although the fMRI source accuracy results replicate the results from the source memory retrieval task that this study was adapted from (Kahn et al., 2004) in showing no source accuracy effect across tasks, but a source accuracy effect for the place task in the left parahippocampal cortex, we did not find source accuracy effects in other regions reported. The results from Kahn et al. (2004) and the meta-analysis by Spaniol et al. (2009) showed weaker effects for source accuracy than retrieval success. Other regions showing source accuracy effects in Kahn et al. (2004) at an uncorrected threshold of $p < .001$ did not survive cluster correction for multiple comparisons in this study.

Importantly, the results of this study provide the first evidence linking brain oscillatory activity to fMRI retrieval effects. Combined EEG/fMRI results showing an overall negative correlation between beta power and BOLD in a frontal, parietal network suggest that overall increased beta power may lead to decreased metabolic demands in a frontal, parietal network that overlaps with the memory control network. But, above and beyond the overall correlation of beta and BOLD, there were task-related effects within right frontal areas. The present data showed a dif-

ference in the beta power/BOLD correlation for hits compared with correct rejections as well as a marginally significant difference in the beta power/BOLD correlation for incorrect compared with correct source judgments. Previous research has suggested a role for the right pFC in postretrieval control operations such as postretrieval monitoring and inhibition of memory retrieval (Anderson & Hanslmayr, 2014; Butler & James, 2010; Kuhl et al., 2008; Depue et al., 2007; Anderson et al., 2004; Rugg et al., 1996, 1999, 2003; Henson et al., 1999, 2000; Fletcher et al., 1998; Schacter et al., 1996). In addition, previous research has suggested a role for beta oscillations in controlled retrieval, specifically inhibition of task-irrelevant information (Waldhauser et al., 2012; Khader & Rosler, 2011) and directed memory suppression (Waldhauser et al., 2015; Ketz et al., 2014; Hanslmayr et al., 2012). And outside the memory domain, beta oscillations have been related to response inhibition within the right inferior frontal cortex (George et al., 2013; Swann et al., 2009, 2011, 2012). These postretrieval/decision-level functions should be greater when decisions are uncertain, which is more likely for incorrect than correct memory judgments. Consistent with this idea, previous research has shown greater activity in right prefrontal brain regions for uncertain responses (Henson et al., 2000; Schacter, Buckner, Koutstaal, Dale, & Rosen, 1997). Combined, these results suggest that beta power

correlations with right frontal activity may be related to postretrieval control operations of the right frontal cortex, and the beta power and BOLD correlations for old relative to new items and incorrect relative to correct source judgments suggest that the beta power/BOLD correlations are greater for conditions requiring more postretrieval control (hits and incorrect source).

In addition, the difference between beta power/BOLD correlations in the right frontal cortex correlated with both source discrimination and RTs showing that both better memory performance and slower RTs correlated with greater beta power/BOLD correlations. It is possible that, in conditions of uncertainty (hits and incorrect source), participants are engaging more cognitive control and searching memory longer. In addition, those who slow down and engage postretrieval control operations may do better on the memory task. The pattern of the beta power effects in right frontal brain regions is consistent with a slowing or a threshold change to look for more mnemonic evidence during the memory decision. Therefore, higher levels of beta oscillations in the right frontal cortex may act to inhibit responses until further memory evidence is retrieved leading to better memory performance.

Beta power/BOLD old/new effects in right frontal regions correlated with BOLD activity in a frontoparietal network that has been related to postretrieval control operations. Previous research has indicated functional specificity for controlled episodic retrieval within pFC with distinct networks involved in controlling retrieval versus postretrieval control operations (reviewed in Nyhus & Badre, 2015). Specifically, the more dorsal frontoparietal network including mid-VLPFC, DLPFC, inferior parietal cortex, and BG supports postretrieval control operations, such as selecting appropriate representations, setting decision criteria, and monitoring the outcome of retrieval. Therefore, the correlation between beta power/BOLD old/new effects in right frontal regions and BOLD activity in left frontal regions, left parietal regions, and the striatum indicate that beta oscillations in the right frontal cortex are more broadly involved in a dorsal frontoparietal postretrieval control network.

Conclusions

Both EEG and fMRI have been used to study episodic memory retrieval, but no previous study has reported simultaneous EEG and fMRI during episodic retrieval. EEG can tell us about the dynamic interactions between neurons and fMRI can localize activity related to memory retrieval. Taken together, EEG and fMRI provide a more elaborate picture of both the regional network supporting episodic retrieval, as well as its putative network dynamics. Using simultaneous EEG and fMRI, the present results indicate that beta oscillations in the right frontal cortex are greater under conditions requiring more cognitive control, are related to inhibitory processes that

slow responding to retrieve more information for better memory, and act as part of a broader postretrieval control network.

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