# Semantic Congruence Enhances Memory of Episodic Associations: Role of Theta Oscillations

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## Abstract

■ Growing evidence suggests that theta oscillations play a crucial role in episodic encoding. The present study evaluates whether changes in electroencephalographic theta source dynamics mediate the positive influence of semantic congruence on incidental associative learning. Here we show that memory for episodic associations (face–location) is more accurate when studied under semantically congruent contexts. However, only participants showing RT priming effect in a conceptual priming test (priming group) also gave faster responses when recollecting source information of semantically congruent faces as compared with semantically incongruent faces. This improved episodic retrieval was positively correlated with increases in theta power during the study phase mainly in the bilateral parahippocampal gyrus, left superior temporal gyrus, and left lateral posterior parietal lobe. Reconstructed signals from the estimated sources showed higher theta power for congruent than incongruent faces and also for the priming than the nonpriming group. These results are in agreement with the attention to memory model. Besides directing top–down attention to goal-relevant semantic information during encoding, the dorsal parietal lobe may also be involved in redirecting attention to bottom–up-driven memories thanks to connections between the medial-temporal and the left ventral parietal lobe. The latter function can either facilitate or interfere with encoding of face–location associations depending on whether they are preceded by semantically congruent or incongruent contexts, respectively, because only in the former condition retrieved representations related to the cue and the face are both coherent with the person identity and are both associated with the same location. ■

## INTRODUCTION

The ability of encoding, storage, and explicit retrieval of personal contextual knowledge (episodic memory) critically depends on interaction between memory systems that are functionally and anatomically distinct (Tulving, 1983) like, for example, the memory of meanings and concepts not related to personal experiences (semantic memory). Much of the research concerned with the interaction between semantic and episodic memory has been conducted using the levels-of-processing theory originally proposed by Craik and Lockhart (1972). According to this framework, episodic memory performance is enhanced when subjects actively engage in deep (semantic) processing relative to shallow (nonsemantic) encoding operations. However, neuroimaging studies have shown that effective episodic encoding is accompanied by activation of the prefrontal cortex and medial-temporal lobe (MTL) regardless of the nature of processing requirements (semantic vs. nonsemantic) (e.g., Prince, Daselaar, & Cabeza, 2005; Nyberg et al., 2003; Otten, Henson, & Rugg, 2001; Cabeza & Nyberg, 2000; Kapur et al., 1994), suggesting that neural dynamics underlying episodic encoding and depth of processing effects, evenly dissociable, may interact in specific brain regions to help acquire new episodic information.

Successful formation of episodic memories depends not only on interaction between semantic and episodic processing of single items but also on the ability to form and bind associations between items. Communication between the MTL and the neocortex seems to be of particular relevance for associative memory, although the neural coding of this interface remains to be elucidated. For instance, it has been found that semantic associations during encoding are sustained by the hippocampus and the left inferior frontal gyrus (e.g., Addis & McAndrews, 2006; Sperling et al., 2003), whereas episodic associations, for example, object–location, involve hippocampus and related MTL structures (e.g., Hannula & Ranganath, 2008; Sommer, Rose, Gläscher, Wolbers, & Büchel, 2005). Now the question arises as whether semantic processing operations improve formation of new semantic and episodic associations. In support of the former relation (semantic processing-semantic association), recent evidence has shown that incidental semantic associations between words are formed more efficiently if the words are embedded in semantically coherent sentences as compared with semantically non-coherent sentences (Prior & Bentin, 2008). In contrast, it is uncharted whether semantic congruence equally enhances memory of episodic associations. This hypothesis is tested in the present study. Based on previous evidence of improved recognition memory for images associated with semantically congruent sounds (Lehmann & Murray,

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2005), we predict better performance during retrieval of episodic associations initially accompanied by semantically congruent contexts than during retrieval of associations preceded by semantically incongruent information at encoding.

The specific areas where semantic congruence may enhance memory of episodic associations are unknown as well as the neural dynamics associated with this process. Different theories on the basis of behavioral and physiological data (Buzsáki, 2005) as well as on computational models (Hasselmo, 2005) consider that theta oscillations (4–7 Hz) play a crucial role in facilitating formation of episodic memories. Accordingly, human studies using subsequent memory paradigms have reported increased theta synchronization within and between the hippocampus and related MTL structures (e.g., Mormann et al., 2005; Fell et al., 2003) as well as within frontal and parietotemporal regions of the cortex (Rieger et al., 2008; Osipova et al., 2006; Summerfield & Mangels, 2006; Sederberg, Kahana, Howard, Donner, & Madsen, 2003; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Klimesch, Doppelmayr, Russegger, & Pachinger, 1996). In addition, preliminary results indicate that changes in theta oscillatory dynamics may mediate interaction between frontoposterior regions during successful encoding (Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005; Sauseng et al., 2004; Weiss & Rappelsberger, 2000). Nevertheless, the contribution of theta oscillatory activity to encoding of semantic information is still unclear. For example, there is recent evidence that theta-band modulations are specifically related to nonsemantic encoding processes (Hanslmayr, Spitzer, & Bäuml, 2009). In this study, increases in theta power for later remembered versus later forgotten words were found only in the group that performed an alphabetical (shallow) encoding task. In contrast, the semantic group showed subsequent memory effects in other frequency ranges (decreases in alpha and beta power and increases in gamma power). The need for further research in this direction is undeniable on the basis of contradictory results linking theta oscillations with successful encoding of episodic memory in a semantic task. Accordingly, the second focus of the present study was to evaluate the role of induced theta oscillations in memory formation of incidental episodic associations when they were accompanied by either a congruent or an incongruent semantic context.

## METHODS

### Subjects

Behavioral and electroencephalographic (EEG) data were collected from 30 right-handed native Spanish speakers (17 women; age range = 20–22 years; mean age = 20.1 years), all of them university students. All participants had normal or corrected-to-normal vision and were instructed to abstain from drugs, alcohol, and caffeine during the day before the experimental session and during the course of the experiment. None of them had a history of neurological or psychiatric disorders. Informed consent was obtained from each participant after a full explanation of the experiment.

### Stimuli

Stimuli consisted of 64 pictures of Spanish celebrities (actors, politicians, musicians, and television personalities) and 32 pictures of nonfamous individuals (found on the Internet) matched in gender, age, and emotional expression (either neutral or positive). The appearance of famous and nonfamous faces was similar and included only an oval of the face. Grayscale faces were presented against a black background framed by a white rectangle in one of four possible locations (top left, top right, bottom left, and bottom right). Rectangles were 5.9 cm wide × 7.3 cm high. At the 100-cm viewing distance from the center of a 17-in., flat-panel computer monitor and the oval face center subtended a visual angle of approximately 2.5° × 3.9° (width × height).

In a pilot study, a different group of 20 young subjects (same age and cultural level as experimental subjects) were presented with a list of 288 names of celebrities accompanied by three biographical cues each, including profession and profession-related information (the title of a film or song, a television program, or a political position, etc.). Participants were required to mark with a cross if they knew the personage who represented the name and if they did, they had to mark with additional crosses whether they knew the remaining biographical information provided about the person in question. We selected names and two additional biographical cues for each one of the 96 celebrities recognized by at least 75% of the pilot participants. Each name and the corresponding biographical information were included in the actual experiment in one of the three conditions mentioned below.

### Procedure

The actual experiment started with a biographical matching task, was followed by a conceptual priming memory test, and finished with a visual–spatial association memory test. For a schematic representation of each task, see Figure 1. The two first tasks are a modified version of the tasks used by Voss and Paller (2006), whereas the episodic task is an adapted version of the Face Place Test (Dudas, Clague, Thompson, Graham, & Hodges, 2005). The three phases were divided into six blocks of 48 trials each. The study phase lasted approximately 60 min and the memory tasks 30 min each with resting intervals of 10 min in between.

### Biographical Matching Task in the Study Phase

To evaluate the influence of congruent semantic processing on incidental associative learning, access to conceptual information was manipulated as follows. During the study

**Figure 1.** Schematic representation of the experimental design. (A) Study phase included three conditions: semantically congruent faces (SCF), semantically incongruent faces (SIF), and semantically incongruent nonfamous faces (NF). Biographical cues only matched famous faces in the semantically congruent condition. (B) Conceptual priming memory task. Faces are presented in the same location as in the study phase without any preceding biographical cue. Subjects are required to respond if they think that faces belong to famous or nonfamous individuals. (C) Visual–spatial memory task. Half of the faces are presented in the same location as in the previous two phases and the other half are presented in a different location. For each face, participants are required to identify whether faces match the previous location. All faces in the three phases are presented three times each in nonconsecutive blocks.
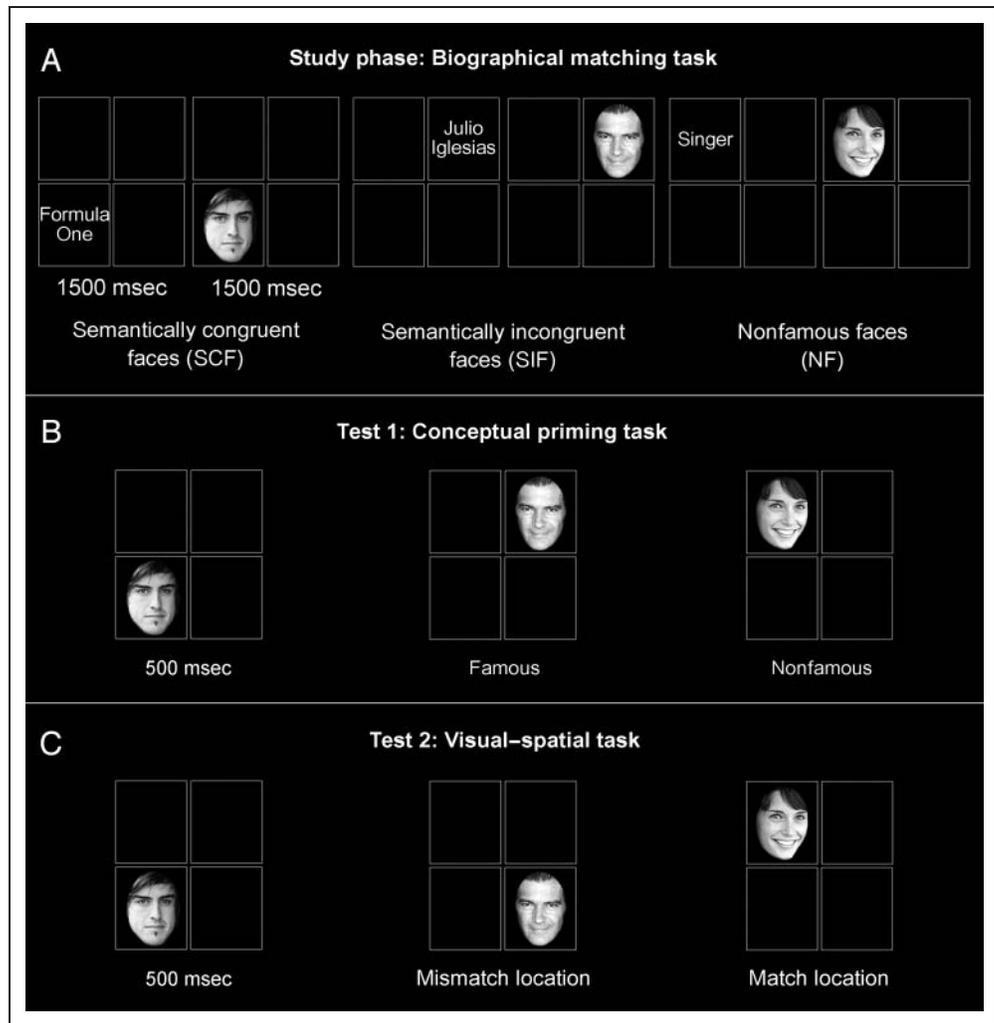


phase, half of the famous faces presented in one particular position were preceded by a congruent biographical cue at the same position (semantically congruent faces [SCF]). The remaining famous faces were preceded by biographical information from other celebrities whose faces were not presented in the current experiment (semantically incongruent faces [SIF]). Finally, nonfamous faces (NF) were preceded by biographical cues from SIF. Because subjects were not required to pay attention to the position where faces were shown, any association between the face and the location is assumed to be incidental.

Faces and their corresponding cues were pseudorandomly presented in different locations within different blocks. All face–location associations appeared three times in alternating blocks, but they were preceded by a different cue in each block. Participants were instructed to respond if the face was semantically congruent with the prior biographical cue via button press. Although processing of a famous face involves accessing conceptual information, the biographical cues are supposed to activate additional semantic nodes that represent specific information about individuals that could be used in the process of face recognition (Burton, Bruce, & Johnston, 1990). This activation

is expected to be greater for SCF than for SIF, which in turn should result in faster and more accurate responses in the subsequent conceptual priming test (Voss, Reber, Mesulam, Parrish, & Paller, 2008; Voss & Paller, 2006). In the context of the present study, conceptual priming is a nonconscious form of memory, denoting changes in face classification as a result of a previous encounter with the face in a congruent semantic context. Should the mechanism underlying this form of memory also positively affect memory for episodic associations, the prediction would be that participants showing priming effects in the conceptual priming task may also show a better performance in the visual–spatial task.

Presentation software (Neurobehavioral Systems, Inc., Albany, CA) controlled both the timing of the stimuli (onset and duration) and the registration of the responses. Trials begin with one white fixation cross at the center of one of the four rectangles for 2000 msec. The offset of the cross is followed by a biographical cue for 1500 msec, and next the face is presented in the same location for another 1500 msec. Subjects are given a maximum of 5000 msec to respond if the face matched the biographical cue by pressing either the left or the right button in the response box (Cedrus,

model RB-530; Cedrus Corporation, San Pedro, CA) with the left or the right index finger, respectively (subjects were told that NF never matched the semantic cue).

## Conceptual Priming Test

During the conceptual priming task, all faces were displayed another three times in nonconsecutive blocks (but only for 500 msec) in the same location as before and without any preceding cue. Subjects were asked to identify as accurately and quickly as possible by pressing a button in the response box whether each face was from a famous or a nonfamous individual. Responses faster than 300 msec and slower than 2000 msec were excluded from analyses. As will be reported in the Results section, only 18 out of 30 subjects showed the expected priming effect in RTs (faster responses for SCF than for SIF). Therefore, only these subjects were considered beneficiaries of the positive influence of a congruent semantic context while accessing a person's identity. As mentioned before, these results were crucial in evaluating the effect of congruent semantic processing during the study of the subsequent visual–spatial association task. To achieve this goal, subjects were split into two groups for subsequent analyses, priming and nonpriming. The reasoning is that subjects able to give faster responses to SCF than to SIF while sorting the faces as famous or nonfamous are more likely to benefit from this conceptual information while trying to retrieve associated episodic information (e.g., face–location).

## Visual–Spatial Association Test

After performing the study phase and the conceptual priming task, subjects have seen all faces in the same position six times (three times in the study task and another three times in the conceptual priming task). Next, famous and nonfamous are presented again for 500 msec without any preceding cue, either at the same location as in previous phases (match location) or at any of the three remaining locations (mismatch location). For each face, participants are required to identify as quickly and accurately as possible whether faces match the previous location. Responses faster than 600 msec and slower than 2500 msec were excluded from analyses. As mentioned above, successful episodic retrieval implies that face and spatial location were correctly associated in an integrated neural representation during previous encoding. As long as congruent semantic processing is advantageous for episodic encoding, location of SCF will be remembered better and faster than the position of either SIF or NF faces.

## Performance Measurement and Statistical Analysis

Hits and correct rejections obtained during the visual–spatial association task were collapsed. Error responses included omissions (no button press) and incorrect identifications of face–location associations. Mean RTs were calculated for correct responses only (hits and correct rejections). Measures of recognition performance ($d'$) were derived from signal detection analysis of the individual subject data. The impact of semantic congruence on recognition performance (accuracy) and RT was evaluated by one-way ANOVA of repeated measures with semantic congruence (SCF, SIF, and NF) as the within-subjects factor. To evaluate the null hypothesis that differences between SCF and SIF are equal in the priming and the nonpriming groups, we computed a two-way mixed ANOVA. This analysis included semantic congruence (SCF and SIF) as the within-subjects factor and group (priming and nonpriming) as the between-subjects factor. Pairwise comparisons were performed to evaluate the interaction effect.

## Data Acquisition and Preprocessing

EEG was recorded while participants performed the study phase from 59 scalp sites using gold electrodes, following the 10/20 standard system. Electrode locations were AFz, Fz, FCz, Cz, CPz, Pz, and POz and Fp1, AF3, AF7, F1, F3, F5, F7, FC1, FC3, FC5, FT7, C1, C3, C5, T7, CP1, CP3, CP5, TP7, P1, P3, P5, P7, PO3, PO7, and O1, together with their right-sided counterparts. Additional electrodes were used for monitoring horizontal and vertical eye movements as well as submental muscle activity. Impedance was maintained below 5 kΩ. EEG signals were filtered between 0.1 and 100 Hz using a notch filter at 50 Hz, digitized at a 250-Hz sampling rate, and referenced on-line to linked mastoids.

Independent component analysis was applied for ocular and muscle artifact reduction by using the Infomax algorithm implemented in the BrainVision Analyzer software version 1.05 (Brain Products GmbH, Munich, Germany). Additional manual artifact rejection was performed when necessary after data segmentation.

To examine the effect of congruent semantic processing on memory formation of episodic associations, only those famous faces whose positions were later remembered (hits and correct rejections) were analyzed for the congruent and incongruent condition separately. A similar number of trials were analyzed for each SCF (mean = 59.7, $SD$ = 10.7) and SIF conditions (mean = 58, $SD$ = 10).

## Data Analysis

To determine the time interval of maximal intensity of the oscillatory activity in the theta range, time frequency representations (TFRs) were calculated using the fast Fourier transform implemented in BESA version 5.2 (MEGIS Software Inc.) after transformation to average montage. The TFR covered a frequency range from 4 to 8 Hz in 1-Hz steps and a time interval from −2100 msec before to 1000 msec after the face onset in 50-msec steps. TFRs of event-related decreases/increases in the power in relation to a baseline value were computed according to the formula (100% (TFR − $P_{baseline}$) / $P_{baseline}$). Here $P_{baseline}$ is the TFR of the

signal averaged during the baseline period. The baseline epoch ranged from −2100 to −1600 msec before face onset to avoid the contribution of the activity elicited by the semantic cue (the 100 msec before the onset of the cue was not included in the baseline to prevent expectations on the arrival of the face). Because we were interested in induced oscillatory activity (nonphase locked to the stimulus), the TFR of the averaged waveform (time and phase locked to the stimulus) was subtracted from the TFR of each individual trial. The calculations were done for each channel separately. Within each subject, all the trials of different conditions were averaged.

## Multiple Source Localization with Beamforming

After identifying the time interval at which theta activity showed its maximal increase in power with respect to the baseline during the study phase (300–800 msec after face onset), the single-trial EEG surface activity was transformed into brain space by applying a multiple source beamforming method as implemented in BESA. Application of this adaptive spatial filter allows us to image nonphase-locked oscillatory brain activity at each single voxel while minimizing as much as possible brain activity from the remaining voxels (Gross et al., 2001). Then, a beamformer image is constructed from values of power $q(r)$ normalized with the power in a reference time-frequency interval (i.e., baseline). The same length was used for the poststimulus and baseline interval (500 msec each). Source localization was performed using the BESA standard head model, with a voxel grid of 6 mm and a regularization parameter singular value decomposition percentage of 0.001.

## Statistical Parametric Mapping (SPM)

Volumetric spatial images resulting from applying multiple source beamforming were analyzed using SPM5 (Wellcome Department of Cognitive Neurology, London). Images from each subject were normalized to the Montreal Neurological Institute (MNI) space using as template the T1 single-subject magnetic resonance image provided by SPM5 (Colin27) and using as source image the BESA standard magnetic resonance image. Statistical analyses of estimated sources were carried out in several steps. First, we conducted regression analyses across subjects to identify the cortical regions where the magnitude of theta power difference between conditions during the study phase (percent of beamformer's power change difference between SCF and SIF) was correlated with performance in the face–location recognition task (RT difference between SCF and SIF). Our hypothesis is that increasing difference in theta power is associated with an increase in the RT difference between congruent and incongruent conditions during the visual–spatial memory test. Adjustments for multiple comparisons were done using the false discovery rate (FDR) correction at .05 level of significance. Second, and in addition to these whole brain analyses, hypothesis-driven ROI analysis of bi-

lateral parahippocampus and temporo-parietal lobe ($p < .05$ corrected for multiple comparisons with FDR) was conducted to specifically assess whether the activity of these regions was correlated with changes in performance in the episodic memory task on the basis of a priori hypotheses regarding the role of these structures in associative learning (e.g., Uncapher & Wagner, 2009; Bar, Aminoff, & Ishai, 2008; Bar, Aminoff, & Schacter, 2008; Aminoff, Gronau, & Bar, 2007). Masks for these regions were created using the Wake Forest University (WFU) Pick Atlas (Maldjian, Laurienti, Kraft, & Burdette, 2003), which allows the generation of atlas-based ROI masks on the basis of the Talairach Daemon database (Lancaster et al., 2000).

As subjects were split into two groups according to whether they showed RT priming effect in the conceptual priming memory test, a two-sample $t$ test model was conducted over significant voxels obtained from the abovementioned regression. FDR ($p < .05$) was also applied to correct for multiple comparisons. Given that this analysis revealed no significant differences between groups after FDR correction, only results from regression are reported in the Results section. All the coordinates listed in the sections below are MNI coordinates obtained with SPM5.

## Conversion of Theta Sources to Time Domain and Statistical Analysis

After statistical parametric analyses, MNI coordinates of significant peak voxels were transformed into the original Talairach space (Talairach & Tournoux, 1988) by using the nonlinear transformation (approach 2) described by M. Brett (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach). Time series were reconstructed from each selected voxel after applying a spatial filtering to each subject by using the source montage tool implemented in BESA. By this procedure, signals from the recorded channels are transformed onto virtual source channels (only the radial component was exported) for each subject. Next, TFRs were computed over the time-domain waveforms obtained from each regional source by following the same procedure as applied at the sensor level. For each subject and experimental condition, we selected the frequency bin showing maximal theta power within the time window in the TFR where the beamformer analysis was applied (300–800 msec after face onset). Statistical analyses were computed on these frequency bin-associated signal outputs.

The influence of semantic congruence and the group effect were evaluated separately by means of randomization distributions estimated from the observed data. As the EEG estimated sources are assumed to be independent, there is no need for comparing topographies of the different conditions. Therefore, univariate (instead of multivariate) independent and paired-sample $t$ tests were applied to evaluate differences between conditions and groups, respectively. The $T$ statistic was first computed on the original data for every time window of 50 msec, beginning at 200 msec from stimulus (face) onset to avoid interferences

from early visual, evoked responses. Next, for every time window, we computed the appropriate $T$ statistic on each randomization (10,000) and selected the maximum $T$ for each randomization, denoted as max ($T$). The 95th quantile of this randomization distribution of max ($T$) was used as a critical value to retain or reject the null hypothesis of no differences either between conditions or between groups. This procedure controls the family-wise error (FWE) rate for all time windows jointly (Maris, 2004).

To evaluate the effect of semantic congruence (SCF vs. SIF), one of these conditions was randomly multiplied by $+1$ or $-1$ for each participant. However, to evaluate differences between the priming and the nonpriming group, we randomly assigned 18 of 30 participants to the priming group and the remainder to the nonpriming group. The same analysis was run in a smaller subset of subjects. In particular, the priming group was restricted to those subjects who showed significant differences in RT when comparing SCF with SIF in the conceptual priming task (9 of 18). In this case, 9 of 21 participants were randomly allocated to the priming group and the remainder to the other group.

Significant differences determined by this procedure were later confirmed by applying a typical mixed ANOVA including semantic congruence (SCF vs. SIF) and window (time windows where randomization tests yielded significant differences) as the within-subjects factors and group (priming vs. nonpriming group) as the between-subjects factor. Greenhouse–Geisser correction was used when the sphericity assumption was violated. Pairwise comparisons were performed to assess the interaction effect between semantic congruence and group, which could not be evaluated with the randomization test.

## RESULTS

### Behavioral

Episodic remembering was significantly improved by semantic information provided during the study phase, $F(2, 58) = 68.5, p < .001$. Discrimination accuracy was better for famous ($d'$ mean = 2.2, $SEM$ = .11) than for NF ($d'$ mean = 1.1, $SEM$ = .09) conditions ($p < .001$), suggesting that access to conceptual information related to a familiar face was important in establishing and/or retrieving the association between the face and the location. Similarly, post hoc T tests corroborated a beneficial effect of semantic congruence on episodic retrieval ($p < .001$). In fact, participants were more accurate (~20%) in identifying the location of SCF as compared with SIF.

Differences in RTs between SCF and SIF were only evident when subjects were sorted according to whether they showed priming effects on the famous/nonfamous category identification task ($n = 18$). These results are illustrated in Figure 2. The percentage of RT priming effect in this group ([$SIF_{RT} - SCF_{RT}$] / $SIF_{RT} \times 100$) ranged from 0.43% to 10.37%. In agreement with previous reports (Voss & Paller, 2006), the priming group showed not only faster

RTs ($T = -5.8, p < .001$) but also higher accuracy ($T = 12.7, p < .001$) to SCF than SIF in the conceptual priming task (Figure 2A and B). Indeed, accuracy for SIF (mean = 1.5, $SEM$ = .10) was around 35% smaller than that observed for SCF (mean = 2.3, $SEM$ = .12).

As mentioned above, only the priming group produced faster RTs to SCF (mean = 924.7, $SEM$ = 40.6) relative to SIF (mean = 954, $SEM$ = 43.3) in the spatial association task (Figure 2D) as revealed by the significant interaction effect yielded by the two-way mixed ANOVA, $F(1, 28) = 7.6, p < .01$. However, neither group nor Priming × Group interaction effect was found for accuracy in the face–location memory test (Figure 2C). These results were additionally confirmed for the subset of subjects (9 of 18 subjects of the priming group) in which the difference in RT between SCF and SIF during the conceptual priming task was statistically significant ($p < .05$). Accordingly, the mixed ANOVA revealed a significant Semantic Congruence × Group interaction, $F(1, 19) = 8.6, p < .009$. Post hoc analyses indicated that only the priming group, $F(1, 8) = 20.45, p < .002$, showed shorter RT in response to SCF (mean = 967.8, $SEM$ = 60.2) as compared with SIF (mean = 1009.5, $SEM$ = 64.7).

### Estimation of Brain Theta Sources

Source imaging of the EEG induced theta activity was performed in the time-frequency domain with two aims: (i) approximately identifying (with a low spatial resolution) brain regions that may be involved in the generation of induced theta activity during encoding of incidental episodic associations under congruent/incongruent semantic contexts and (ii) reducing multichannel EEG data to meaningful source estimates for further analysis of theta-band power modulations across time.

TFRs of the signal recorded at the sensor level during the study phase were averaged for trials, electrodes, conditions (SCF and SIF), and subjects ($N = 30$). Figure 3 illustrates modulations of theta oscillatory activity across three different time periods including 600 msec of baseline, 1500 msec after presentation of the semantic cue, and 1000 msec after presentation of the face. The grand average TFR confirmed the presence of a strong power increase with respect to the baseline interval in the theta range following both presentation of the semantic cue and presentation of the face. As a decision on the congruence between semantic context and face takes place after presentation of the latter, sources of enhanced theta power were estimated between 300 and 800 msec after face onset.

Correlation analysis across subjects was first performed to determine where in the brain improving performance during episodic retrieval (faster responses to SCF relative to SIF) is associated with increasing theta power (higher increase in the theta power to SCF as compared with SIF). MNI coordinates and $p$ values for the peak voxels (FDR correction) are listed in Table 1. We found a posi-

**Figure 2.** Effect of the semantic congruence on behavior over the whole population (global, $N = 30$), priming ($n = 18$), and nonpriming group ($n = 12$). (A) Average accuracy ($d'$) in the two conditions, SCF and SIF, during the conceptual priming task. (B) Average RT in the two conditions, SCF and SIF, during the conceptual priming task. (C) Average accuracy ($d'$) in the two conditions, SCF and SIF, during the visual–spatial task. (D) Average RT in the two conditions, SCF and SIF, during the visual–spatial task. Asterisks indicate significant differences between conditions after T tests. Error bars represent *SEM*. SCF = semantically congruent faces; SIF = semantically incongruent faces.
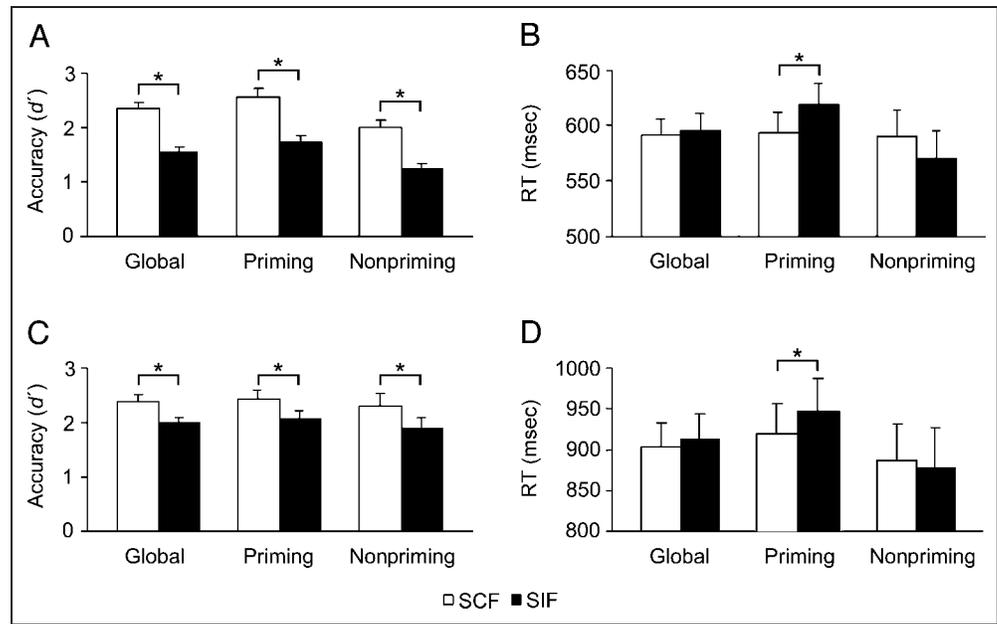
tive correlation in the left and right superior parietal lobe (lSPL and rSPL, respectively) as well as in the left superior temporal gyrus (lSTG), close to regions in the MTL. These correlations, however, did not achieve statistical significance after FDR correction ($p < .068$). On the basis of these results and a priori hypotheses regarding the role of different regions in the MTL and temporo-parietal lobes in successful encoding of associative learning (see Methods), we performed ROI analyses to examine whether activity of these regions correlated with performance. Results revealed a maximum positive correlation in regions of the left parietotemporal lobe (see Figure 4 and Table 1) such as STG (BA 22), superior (BA 7), and inferior parietal lobe (IPL; BA 40) as well as in bilateral parahippocampal gyrus (PHG). Figure 5 shows parahippocampal sources of theta activity that correlated with performance and the scatter plots showing the significant degree of relationship between the percent beamformer's power difference be-

tween SCF and SIF ($q'(r)$) and the RT benefit achieved in the visual–spatial recognition task.

Behavioral analyses suggested that performance in the priming conceptual memory task predicted subsequent performance in the face–location association task. In fact, similar results (accuracy and RTs) were found when the priming group was restricted to subjects whose RTs were shorter for SCF than for SIF (9 of 18 subjects) in the conceptual priming task. Should this subdivision have significance for recall of source information memory in the visual–spatial task, similar neural correlates would be expected from analyses limited to this subset of subjects. Accordingly, regression analyses yielded similar estimates of EEG-theta sources for participants who either showed no benefit from conceptual information in the conceptual priming test or showed significant differences in RT between SCF and SIF ($n = 21$). The MNI coordinates of peak voxels provided by the SPM maps of correlation

**Figure 3.** Time frequency representation (TFR) of power change relative to baseline, averaged over trials, electrodes, conditions, and subjects ($n = 30$). Modulations of the induced oscillatory activity at the theta frequency are illustrated for three different time periods in the study epoch (600 msec of baseline before the semantic cue, 1500 msec after presentation of the cue, and 1000 msec after presentation of the face). The



dashed line square indicates the frequency range (4–7 Hz) and the time interval (300–800 msec after face onset) where sources of theta oscillatory activity were estimated. The color scale indicates percent power changes of theta activity compared with the baseline. The cue (Julio Iglesias) and the face (Antonio Banderas) used as examples correspond to a semantically incongruent condition.
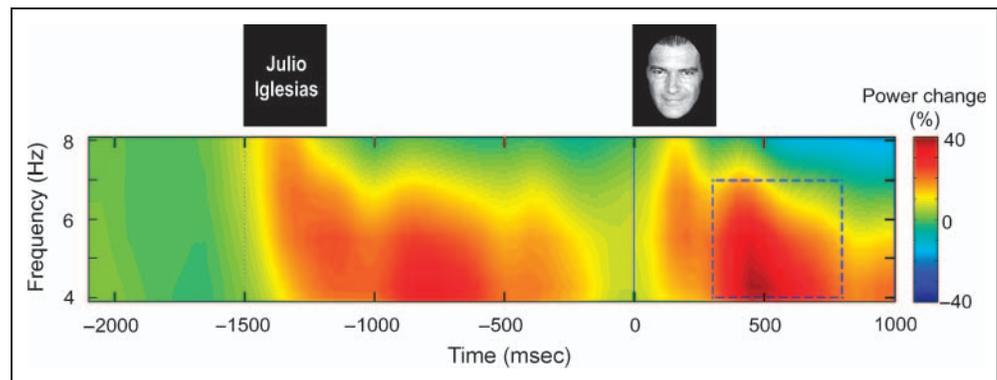
**Table 1.** MNI Coordinates of Peak Voxels in the Regression Analysis between SCF-SIF Theta Oscillations in the Study Phase and RT% in the Visual–Spatial Task ($N = 30$)

| Brain Region | x | y | z | T | Z Score | k | $P_{FDR}$ | R |
|---|---|---|---|---|---|---|---|---|
| *Whole Brain Analysis* | | | | | | | | |
| L. STG (BA 22) | −32 | −40 | 12 | 3.58 | 3.22 | 3269 | .068 | .56 |
| L. SPL (BA 7) | −28 | −68 | 40 | 3.31 | 3.02 | 3269 | .068 | .53 |
| R. SPL (BA 7) | 28 | −68 | 40 | 2.95 | 2.73 | 3269 | .068 | .49 |
| *Parietotemporal ROI Analysis* | | | | | | | | |
| L. STG (BA 22) | −36 | −40 | 12 | 3.58 | 3.22 | 3975 | .039 | .56 |
| L. SPL (BA 7) | −28 | −68 | 40 | 3.31 | 3.02 | 3975 | .039 | .53 |
| L. IPL (BA 40) | −40 | −28 | 24 | 3.28 | 2.99 | 3975 | .039 | .53 |
| *Parahippocampal ROI Analysis* | | | | | | | | |
| L. parahippocampus | −32 | −40 | 0 | 3.47 | 3.14 | 136 | .018 | .55 |
| R. parahippocampus | 16 | −32 | −4 | 2.69 | 2.51 | 103 | .022 | .45 |
| | 28 | −40 | 0 | 2.53 | 2.47 | 103 | .022 | .43 |

$k$ = number of voxels in the cluster; $P_{FDR}$ = voxel-level $p$ values corrected with FDR; L. = left; R. = right; $R$ = Pearson's correlation.

between changes in theta power and changes in RT in 21 of 30 participants are listed in Table 2. All EEG-theta sources estimated by the ROI analysis in the left hemisphere in the 30 subjects were also estimated in the sample that was almost one third decreased in size, but with lower statistical power. Consequently, none of the peak voxels were significant after FDR correction, although the left parahippocampus was close to statistical significance ($p < .059$) and the size effect ($R^2$) of all estimated sources was large and hardly varied when the population was reduced.

## Time Course of Theta Source Activity

The time courses of the reconstructed signals from the different EEG-theta sources estimated for each condition



**Figure 4.** Statistical parametric maps (SPM) of $T$ statistic showing the significant cerebral activations resulting from a whole-brain multiple regression analysis (percent beamformer's power change difference between SCF and SIF was the independent variable and RT difference between SCF and SIF the dependent variable). (A) Results extracted from the whole population ($N = 30$, 18 of 30 subjects belonged to the priming group and the remainder to the nonpriming group). (B) Results extracted from a subset of subjects ($n = 21$, 9 of 21 subjects belonged to the priming group and the remainder to the nonpriming group). Activated regions are shown on the sagittal (left), coronal (central), and axial (right) views of the MNI glass brain at $T > 2.47$, $p$(uncorrected) $< 0.01$, $N = 30$, and at $T > 1.73$, $p$(uncorrected) $< 0.05$, $n = 21$. Correlations are significant in regions of the temporal and dorsal parietal cortex (gray areas). Peak voxels of positive correlations are listed in Table 1 ($N = 30$) and Table 2 ($n = 21$). SCF = semantically congruent faces; SIF = semantically incongruent faces.
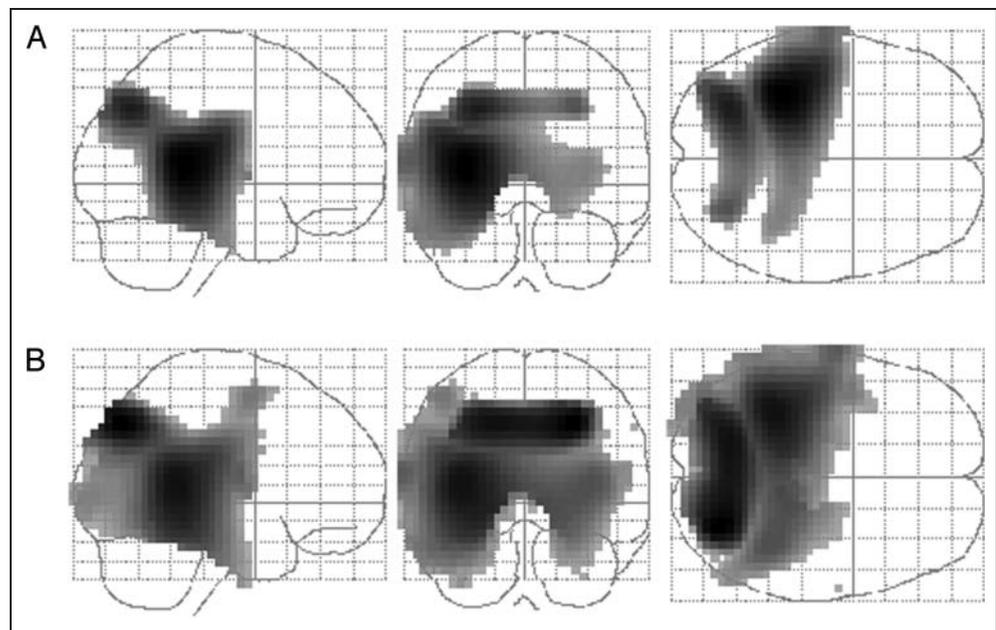
**Figure 5.** Results from a hypothesis-driven ROI regression analysis between activity in bilateral PHG (percent beamformer's power change difference between SCF and SIF) and performance in the visual–spatial task (percent RT difference between SCF and SIF). (A) Sagittal (left) and coronal (right) planes indicate activation of the left and right PHG theta source, $p$(FDR) < 0.05). Cross hairs indicate MNI coordinates for the posterior part of the left parahippocampus [peak MNI coordinates: −32 −40 0]. Increases in theta power in the right parahippocampal source [peak MNI coordinates: 16 −32 −4] also correlated with faster RT in the episodic task. The color scale indicates voxel $T$ statistic values. (B) Scatter plots showing the relation between activity of the significant peak voxel of the left and right PHG (percent beamformer's power difference between SCF and SIF) and performance in the visual–spatial task (RT difference between SCF and SIF). The lines in scatter plots indicate regression line (solid black line). SCF = semantically congruent faces; SIF = semantically incongruent faces; lPHG = left parahippocampal gyrus; rPHG = right parahippocampal gyrus.
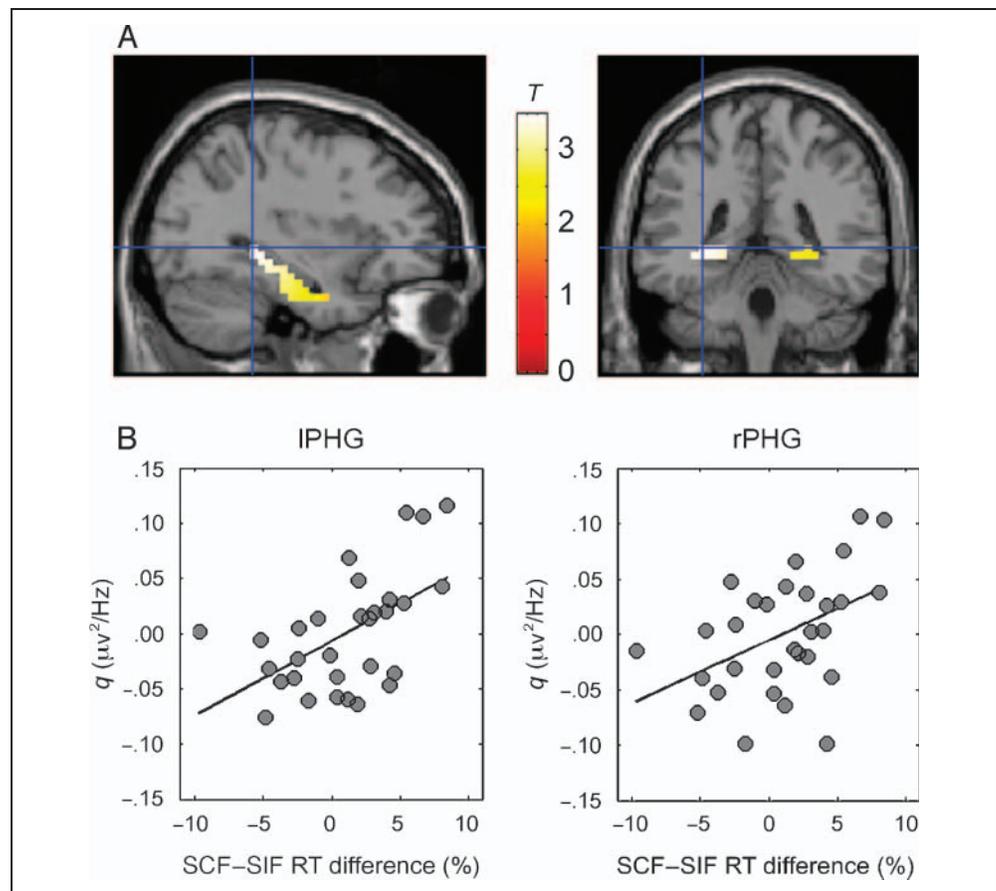


**Table 2.** MNI Coordinates of Peak Voxels in the Regression Analysis between SCF–SIF Theta Oscillations in the Study Phase and RT% in the Visual–Spatial Task ($n = 21$)

| Brain Region | x | y | z | T | Z Score | k | $P_{FDR}$ | $P_u$ | R |
|---|---|---|---|---|---|---|---|---|---|
| *Whole Brain Analysis* | | | | | | | | | |
| L. SPL (BA 7) | −16 | −68 | 40 | 2.87 | 2.58 | 6286 | .180 | .005 | .55 |
| L. STG (BA 22) | −36 | −44 | 8 | 2.86 | 2.58 | 6286 | .180 | .005 | .55 |
| *Parietal ROI Analysis* | | | | | | | | | |
| L. SPL (BA 7) | −16 | −68 | 40 | 2.87 | 2.58 | 1168 | .104 | .005 | .55 |
| L. IPL (BA 40) | −32 | −44 | 24 | 2.60 | 2.37 | 1168 | .104 | .009 | .51 |
| *Temporal ROI Analysis* | | | | | | | | | |
| L. STG (BA 22) | −36 | −44 | 8 | 2.86 | 2.58 | 1359 | .103 | .005 | .55 |
| *Parahippocampal ROI Analysis* | | | | | | | | | |
| L. parahippocampus | −32 | −40 | 0 | 2.80 | 2.53 | 101 | .059 | .006 | .54 |

$k$ = number of voxels in the cluster; $P_{FDR}$ = voxel-level $p$ values corrected with FDR; $P_u$ = voxel-level $p$ values uncorrected; L. = left; R = Pearson's correlation.

of semantic congruence and for each group (priming vs. nonpriming) are presented in Figures 6–8. Figure 6 shows results from the estimated theta sources in the PHG of the two hemispheres. The univariate max ($T$) statistic provided by the randomization tests revealed significant differences between SCF and SIF in bilateral parahippocampus (left PHG within 450–800 msec, all $T > 2.05$, all $p < .05$; right PHG within 350–950 msec, all $T > 1.95$, all $p < .05$). These results were confirmed by the mixed ANOVA including the time window as an additional within-subjects factor: left PHG, $F(1, 28) = 10.15$, $p < .004$; right PHG, $F(1, 28) = 17.82$, $p < .001$. Neither priming nor interaction effects were found.

When the same analysis was run in the group of 21 subjects for the left parahippocampus (because the source in the right side was not significant), semantic congruence was also associated with an enhanced theta power between 600 and 800 msec from face onset (all $T > 2.09$, all $p < .05$), $F(1, 19) = 5.35$, $p < .04$. However, neither the randomization test nor the mixed ANOVA showed higher theta power increase for the priming group than for the nonpriming group. The ANOVA neither yield significant interaction effects.

Figure 7 shows the reconstructed signals for each condition in the remaining estimated sources for the whole population ($N = 30$). Significant theta power increases

for SCF with respect to SIF were observed in the lSTG within 450–700 msec (all $T > 2.02$, all $p < .04$) and in the lSPL within 450–550 msec from face onset (all $T > 2.04$, all $p < .05$). As for the PHG, these results were also proved by the ANOVA in the lSTG, $F(1, 28) = 6.95$, $p < .02$, but in the lSPL, the congruence effect depended on the group, $F(1, 28) = 4.4$, $p < .05$. In particular, post hoc analyses indicated that theta power was twofold for SCF relative to SIF only in the priming group, $F(1, 17) = 7.65$, $p < .02$. The effect of congruence in the power of theta oscillations was almost significant in the left IPL between 400 and 450 msec (all $T < 1.96$, $p > .055$), $F(1, 28) = 3.95$, $p < .057$. Group differences were only evident for this region between 350 and 600 msec (all $T > 2.66$, all $p < .04$), $F(1, 28) = 16$, $p < .001$.

Analyses limited to 21 subjects yielded similar results (see Figure 8). The STG and the SPL in the left hemisphere also generated higher theta power for SCF relative to SIF between 200 and 850 msec (all $T > 1.75$, all $p < .05$), $F(1, 19) = 14.08$, $p < .001$, and between 500 and 750 msec (all $T > 2.25$, all $p < .05$), $F(1, 19) = 8.56$, $p < .001$, respectively. Group differences were again close to statistical significance in the lSTG between 300 and 500 msec as indicated by the max ($T$) statistic (all $T > 3.07$, all $p < .02$) and statistically significant according to results yielded by the ANOVA, $F(1, 19) = 14.3$, $p < .001$. In the case of the



**Figure 6.** Grand-averaged source power change of induced theta activity produced by the left and right PHG in response to famous faces during the biographical matching task. (A) Power change in response to SCF (black line) and SIF (gray line) for all subjects ($N = 30$). The shaded area indicates the time interval where differences between groups reached statistical significance at the randomization test. (B) Mean power change in response to famous faces for the priming ($n = 18$; black line) and nonpriming group ($n = 12$; gray line). The vertical dashed gray line in panels A and B indicates presentation of the semantic cue, whereas the vertical solid gray line signals presentation of the face. Power change is relative to baseline (from −600 msec to −100 msec before cue onset). SCF = semantically congruent faces; SIF = semantically incongruent faces; lPHG = left parahippocampal gyrus; rPHG = right parahippocampal gyrus.
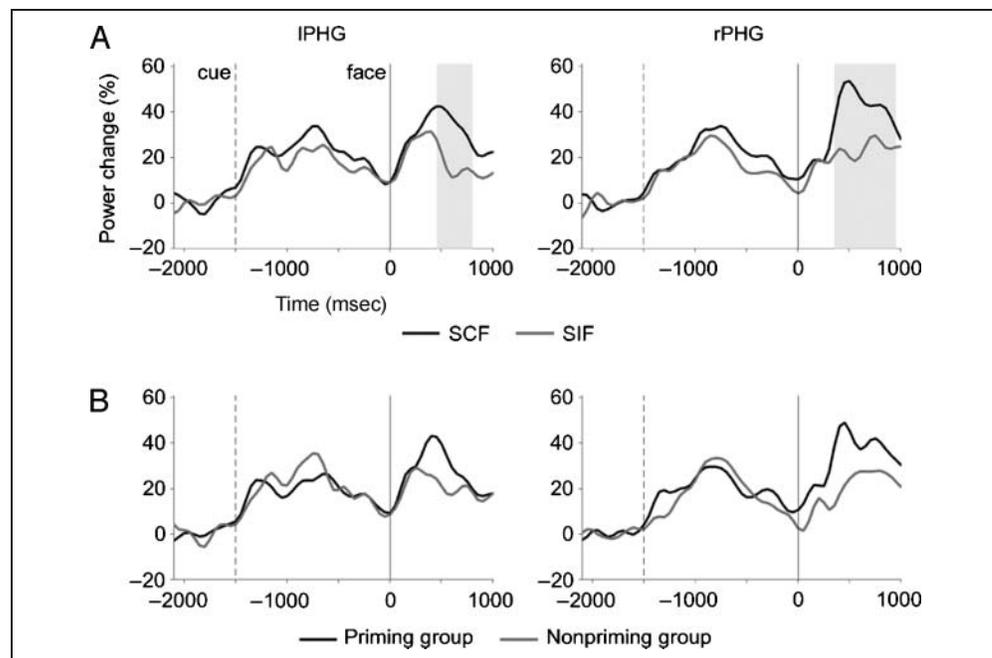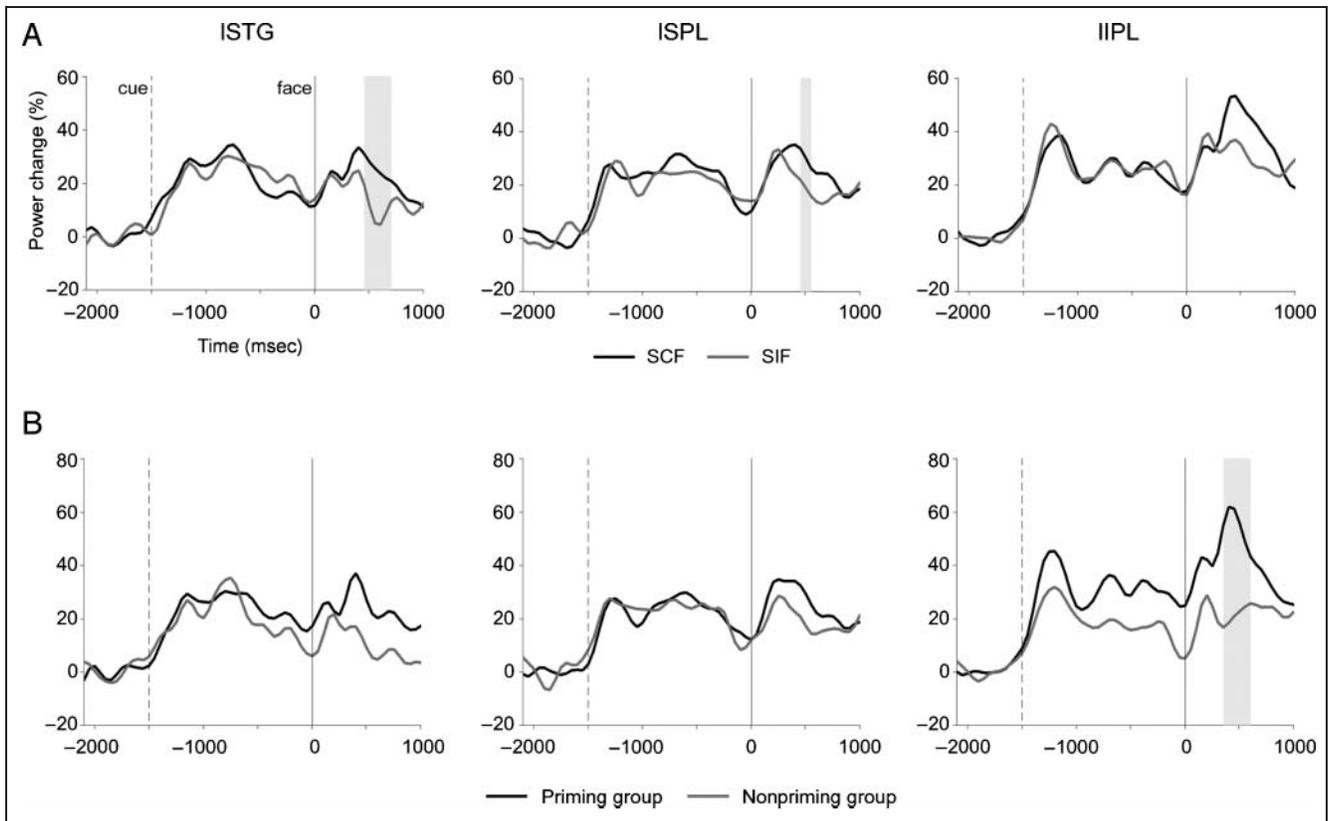
**Figure 7.** Grand-averaged source power change of induced theta activity produced by the left superior temporal gyrus (lSTG), left superior (lSPL), and left inferior parietal lobe (lIPL) in response to famous faces during the biographical matching task. (A) Power change in response to SCF (black line) and SIF (gray line) for all subjects ($N = 30$). (B) Mean power change in response to famous faces for the priming ($n = 18$; black line) and nonpriming group ($n = 12$; gray line). The shaded area in panels A and B indicates the time interval where differences between groups reached statistical significance at the randomization test. The vertical dashed gray line indicates presentation of the semantic cue whereas the vertical solid gray line signals presentation of the face. Power change is relative to baseline (from $-600$ to $-100$ msec before cue onset). Note that theta activity increases after face onset in the priming group as compared with the nonpriming group only for the lIPL. SCF = semantically congruent faces; SIF = semantically incongruent faces.

lSPL, randomization tests found significant differences between groups from 400 to 550 msec (all $T > 2.77$, all $p < .05$; $F(1, 19) = 11.24$, $p < .003$). The left IPL not only showed higher theta power in the priming than in the nonpriming group between 350 and 450 msec (all $T > 2.88$, all $p < .04$), $F(1, 19) = 9.48$, $p < .006$, but also showed a significant effect of semantic congruence between 350 and 700 msec (all $T > 2.29$, all $p < .03$), $F(1, 19) = 10.41$, $p < .004$. The ANOVAs revealed no significant interaction effects.

## DISCUSSION

### Semantic Congruence Enhances Memory of Episodic Associations

Results of the present study provide the first evidence that memory formation of new episodic associations benefits from semantic congruence. Specifically, accuracy in identifying location of the face was selectively improved for those associations preceded during study by semantically congruent biographical cues. Interestingly, only subjects showing priming effect in RT while performing the concep-

tual priming task also produced faster responses to semantically congruent relative to semantically incongruent faces in the visual–spatial task. The effect of conceptual priming was even larger when the priming group was restricted to participants showing significant differences in RT between SCF and SIF on the famous/nonfamous category identification task. Unfortunately, the present experimental design does not allow us to determine at what level of processing semantic congruence positively influenced incidental associative learning. Semantic congruence may have facilitated sensory processing of the face and/or spatial location at encoding through a more efficient use of attentional resources. In agreement with this hypothesis, it has been demonstrated that the presence of semantically congruent cues in different sensory modalities enhances behavioral performance, whereas the incongruent semantic content of multisensory stimuli results in behavioral decrements (Laurienti, Kraft, Maldjian, Burdette, & Wallace, 2004). In addition, semantic congruence may have facilitated the reactivation of perceptual/memory representations of the faces from the long-term memory either during the study phase or when the face–location item was presented without the semantic component at retrieval (Lehmann & Murray,

2005). Alternatively, semantically congruent biographical cues may have worked at the level of the face–location association through a repetition-like priming effect. Although face–location events under the three conditions were repeated three times each to avoid repetition priming effects, this hypothesis is feasible because the cue was presented at the same location as the face during the study phase. Consequently, every time a cue was congruent with a face, the same individual was associated with a particular location twice. For example, under semantically congruent conditions, the name "Fernando Alonso" at the bottom-left position would be followed by Fernando Alonso's face at the same location, whereas under semantically incongruent conditions, the name "Julio Iglesias" at the top-right position would be followed by Antonio Bandera's face at the same location. In the latter condition, two celebrities are associated to the same position only once each, whereas in the former the same celebrity is associated to a particular location twice and very close in time. Thus, one prediction from the repetition priming hypothesis is that subjects would also produce faster responses in the visual–spatial task when they are presented with semantic cues instead of faces at the studied location. The same may be applicable to contextual representations reactivated from long-term memory during encoding. The output of

this reactivation would also be associated with the same location as were the semantic cue and the face. In conclusion, although the present results indicate that semantic congruence improves memory for face–location associations, further investigation is required to assess whether the semantic cue led to effective encoding, retrieval, or both.

## Incidental Associative Learning Under Semantically Congruent Contexts Is Mediated by Local Increases in Theta Power

The second purpose of the present study was to examine whether increases in theta power in distributed regions of the brain support the positive effect of semantic congruence on memory formation of incidental episodic associations. The main result was that semantically congruent face–location associations later remembered not only generated higher theta power with respect to the baseline during the study phase than semantically incongruent associations, but these differences in theta oscillatory activity correlated with behavioral benefits (faster responses to SCF than to SIF) in the episodic task in bilateral parahippocampus, lSTG, and regions of the left lateral posterior parietal lobe.
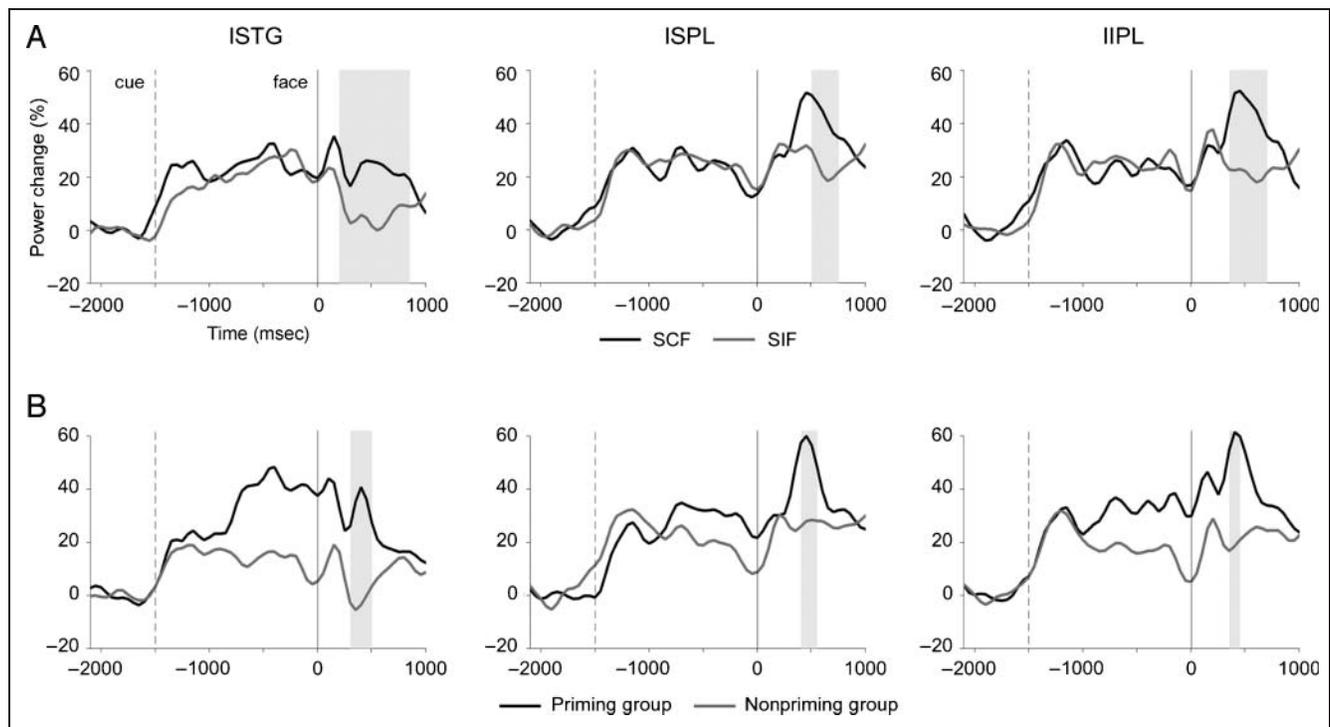


**Figure 8.** Grand-averaged source power change of induced theta activity produced by the left superior temporal gyrus (lSTG), left superior (lSPL), and left inferior parietal lobe (lIPL) in response to famous faces during the biographical matching task. (A) Power change in response to SCF (black line) and SIF (gray line) for a subset of subjects ($n = 21$). (B) Mean power change in response to famous faces for the new priming ($n = 9$, include subjects showing significant faster responses in the SCF compared with SIF; black line) and nonpriming group ($n = 12$; gray line). The shaded area in panels A and B indicates the time interval where differences between groups reached statistical significance at the randomization test. The vertical dashed gray line indicates presentation of the semantic cue whereas the vertical solid gray line signals presentation of the face. Power change is relative to baseline (from $-600$ to $-100$ msec before cue onset). Note that theta activity increases after face onset in the priming group as compared with the nonpriming group for the lSTG, the lSPL and the lIPL. SCF = semantically congruent faces; SIF = semantically incongruent faces.

To date, few studies have reported changes in theta power during successful encoding of context–item associations (Sato & Yamaguchi, 2007; Summerfield & Mangels, 2005). In the study of Summerfield and Mangels (2005), encoding of later remembered words was associated with increases in theta activity in the left frontal cortex, whereas successful encoding of word and its associated font color context led to right frontal lateralized increases of theta oscillatory activity. The same asymmetry was observed for long-range coherence between frontal and posterior regions of the cortex, suggesting that processing of semantic and sensory context at encoding is supported differently by the left and right hemisphere, respectively. In the present study, it was also the theta activity of the left temporo-parietal regions that mainly contributed to faster retrieval of face–location associations that were semantically congruent during study relative to those episodic associations that were semantically incongruent. A study using ERPs during emotional word encoding has also provided evidence favoring the left lateralized effect of semantic congruence. Indeed, it has been found that like emotional arousal, semantic cohesion of neutral words also enhances the amplitude of the late positive polarity potential. Whereas the effect of emotion is evident in frontal regions of the right hemisphere, the effect of semantic cohesion is restricted to centroparietal regions of the left hemisphere (Dillon, Cooper, Grent-'t-Jong, Woldorff, & LaBar, 2006). Taken together, these results suggest that the left hemisphere may play a critical role in processing semantically coherent stimuli and that this semantic coherence may additionally facilitate encoding and subsequent retrieval processes.

## Contribution of the Parahippocampal Cortex

The parahippocampal cortex plays a crucial role in analyzing contextual associations (Bar et al., 2008; Aminoff et al., 2007; Bar, 2004; Bar & Aminoff, 2003). The fact that it mediates both spatial and nonspatial contextual associations is especially relevant for the present study because famous faces are not particularly associated with spatial contexts and, however, activate this region of the MTL (Bar et al., 2008). Our results indicated that activity of bilateral PHG in the theta frequency range was correlated with performance in the visual–spatial task, suggesting that the two hemispheres are functionally implicated in encoding of spatial contextual associations. Evidence of bilateral temporal contribution to object–location associations gives strong support to this assumption (e.g., Sommer et al., 2005; Incisa della Rocchetta et al., 2004; Stepankova, Fenton, Pastalkova, Kalina, & Bohbot, 2004). In a recent study, patients with right and/or left mesial temporal lobe epilepsy showed similar impairments in three different measures of spatial memory (navigation, object location, and plan drawing) as well as a similar relationship between memory performance and hippocampal volume (Glikmann-Johnston et al., 2008).

Although our results suggest that integrity of this region in the two hemispheres may be required for memory formation of spatial contextual associations, the para-hippocampal activity in each hemisphere may have different functional specialization (e.g., Köhler, Danckert, Gati, & Menon, 2005). The effect of semantic congruence on theta parahippocampal activity of the left side is consistent with results from previous studies showing stronger activation in the left hemisphere during visual imagery of faces (Ishai, Haxby, & Ungerleider, 2002; Ishai, Ungerleider, & Haxby, 2000) and when contrasting famous with NF (Bar et al., 2008). Likely, both imagery and contextual associations evoked by faces refer to information that is not physically present. Accordingly, differences between SCF and SIF in the left parahippocampus may reveal the different amount of contextual associations evoked by the two categories of faces due to the experimental manipulation of access to semantic information.

The activity of the right side could be associated either with the well-known right hemisphere preference for facial identification (e.g., Kelley et al., 1998) or with the unconscious nature of the processing. The latter hypothesis is supported by results from neuroimaging studies that observed a right hemisphere preference during encoding of masked faces (Henke et al., 2003; Paller et al., 1999) and a left hemisphere preference for unmasked presentations of the same faces (Paller et al., 1999). On the basis of these results, the large amplitude of theta oscillations in the right parahippocampus might indicate that participants in the present study were unaware most of the time of locations where faces and cues were presented (as subjects used to inform us after they were provided with instructions for performing the task).

## Contribution of the Lateral Posterior Parietal Lobe

Most research related to encoding of episodic memories has focused on the role of the MTL and the prefrontal cortex. However, in the last decade, the lateral posterior parietal lobe is also becoming associated with processes engaged during episodic encoding to create an integrated memory of a new event. Uncapher and Wagner (2009) have provided an excellent meta-analysis of the functional neuroimaging studies that have used the traditional subsequent memory paradigm. The main result is that the majority of positive subsequent memory effects are limited to the dorsal parietal lobe, whereas all negative effects are confined to the ventral region of parietal lobe. According to the dual-attention model proposed by Corbetta and Shulman (2002), the dorsal and the ventral parietal lobe of the right hemisphere would be involved in the voluntary and automatic orienting of attention to specific aspects of environment, respectively. In line with this idea, it has been advanced that the posterior parietal lobe could play the same role in memory as it does in attention. Indeed, the attention to memory model posits that

the dorsal parietal lobe would mediate the allocation of top–down attention to memory retrieval, whereas the ventral region in the left but not in the right hemisphere would cause the dorsal parietal lobe to redirect attention to bottom–up-driven memories (Cabeza, Ciaramelli, Olson, & Moscovitch, 2008; see also reviews by Cabeza, 2008; Ciaramelli, Grady, & Moscovitch, 2008). From this perspective, Uncapher and Wagner (2009) have suggested that engagement of the dorsal mechanisms that mediate goal-directed attention would increase the probability that the encoded event will be later remembered, whereas the capture of reflexive attention mediated by the ventral parietal lobe may have negative consequences for successful encoding. According to this framework, we hypothesize that the theta power enhancement for SCF as compared with SIF in the SPL, specially in those participants showing a significant conceptual priming effect, would mediate allocation of top–down attention to different features of the face that would facilitate activation of the *person identity nodes* and subsequent access to person-specific semantic information (Valentine, Brennen, & Brédart, 1996), which is required to establish whether the face matched conceptual information activated by the preceding cue. These features of the face are not processed in isolation, but they are bound to spatial information (Treisman, 1988). However, the location of an object is encoded partly automatically (e.g., Köhler, Moscovitch, & Melo, 2001; Ellis, 1990), and bottom–up attention guided by the left IPL (through an increase of theta power) may extract useful information about location of the face that can be further used by the MTL mechanisms to establish the item-location association.

In addition and in line with the expanded hypothesis on the role of the lateral posterior parietal lobe in redirecting attention to internal mnemonic representations (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008), the cue and the face may not only reactivate goal-relevant semantic information from long-term memory during encoding but may also reactivate contextual information irrelevant for the task. The dorsal parietal lobe would direct top–down attention to the goal-relevant semantic information, whereas the left ventral parietal lobe (including the left IPL and the STG; see Cabeza, 2008; Ciaramelli et al., 2008) would mediate bottom–up capture of attention by the goal-irrelevant information spontaneously evoked by either the cue or the face through connections with the MTL. Finally, the signal provided by the ventral parietal lobe (and the STG) would make the dorsal parietal lobe to redirect attention to the spontaneously reactivated contextual information. Under congruent conditions, the additional contextual information is associated with the same location as the semantic information provided by the cue and the face, which in turn may increase the probability that item-location associations are successfully encoded into long-term memory. On the contrary, under semantically incongruent conditions, the cue and the face reactivate contextual information associated to the same spatial location but not always coherent with the face. In this particular case, communication between the ventral and the dorsal parietal lobe may interfere with encoding of memory (Uncapher & Wagner, 2009). This interpretation matches well the hypothesized role of the posterior parietal lobe as an episodic buffer between working memory and episodic retrieval (Baddeley, 2000; and discussed in Olson & Berryhill, 2009). According to this hypothesis, information reactivated by the cue and the face from long-term memory during the study phase would increase the probability that location of the SCF is stored in long-term memory (successful encoding) and, consequently, making possible the probability of successful recollection (conscious retrieval of contextual information) during retrieval. However, if retrieved information and person identity nodes only match partially (as for SIF), less coherent information is associated with a particular location, reducing the probability of transferring a strong episodic association to long-term memory.

## Conclusions

There is previous evidence that semantic processing operations improve formation of new semantic associations (Prior & Bentin, 2008). The present study extends these results to episodic associations. In addition, our results suggest that the positive influence of semantic congruence in associative learning is mediated by changes in theta oscillatory activity mainly in the PHG and left temporo-parietal lobe. Although the parahippocampus was likely essential in supporting associative processes to bind distributed representations of face and spatial information into a long-lasting memory trace, our results suggest that this associative process is mediated by parietal attention mechanisms acting upon internal representations retrieved from long-term memory. In particular, we conclude that theta oscillatory activity in the dorsal parietal lobe may improve successful encoding for SCF in two different ways: (i) directing top–down attention to goal-relevant information provided by the biographical cue and the face and (ii) redirecting attention to task-irrelevant features (e.g., spatial context or additional reactivated memories by either the cue or the face) by engaging automatic attention via the connections between the MTL and the ventral parietal lobe of the left hemisphere, which not only includes the IPL but also the STG.

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