Functional neural networks underlying semantic encoding of associative memories

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Abstract

Evidence suggests that theta oscillations recruit distributed cortical representations to improve associative encoding under semantically congruent conditions. Here we show that positive effects of semantic context on encoding and retrieval of associations are mediated by changes in the coupling pattern between EEG theta sources. During successful encoding of semantically congruent face-location associations, the right superior parietal lobe showed enhanced theta phase synchronization with other regions within the lateral posterior parietal lobe (PPL) and left medial temporal lobe (MTL). However, functional coordination involving the inferior parietal lobe was higher in the incongruent condition. These results suggest a differential engagement of top-down and bottom-up mechanisms during encoding of semantically congruent and incongruent episodic associations, respectively. Although retrieval processes operated on a similar neural network, the main difference with the study phase was the larger amount of functional links shown by the lateral prefrontal cortex with regions of the MTL and PPL. All together, these results suggest that theta oscillations mediate, at least partially, the positive effect of semantic congruence on associative memory by (i) optimizing top-down attentional mechanisms through enhanced theta phase synchronization between dorsal regions of the PPL and MTL and (ii) by adjusting the control of automatic attention to sensory and contextual information reactivated in the MTL through functional connections with the inferior parietal lobe during both encoding and retrieval processes.

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Introduction

There are multiple factors that determine the fate of a particular event in our memory. Evidence has shown that past events are better remembered when they are emotionally salient (e.g., Ochsner, 2000) or immersed in an emotional context (Erk et al., 2005), succeeded by an intervening period of sleep (e.g., Maquet, 2001; Stickgold et al., 2001), or when they are subjected to deep semantic analysis (Craik and Lockhart, 1972). Since Craik and Lockhart proposed their theory on the levels of processing, a large number of studies have demonstrated that both single items and associations are better remembered when subjects are actively engaged in semantic processing relative to non-semantic encoding operations. Semantic congruence between a particular item and its context can also impact the strength of the memory trace for that specific item. For instance, objects presented alone or within contexts semantically incongruent are remembered less than those immersed in congruent semantic contexts, e.g., objects paired with semantically incongruent sounds (Lehmann and Murray, 2005; Laurienti et al., 2004) or target words presented with contextual and task-irrelevant related words (Bowler et al., 2008; Mayes et al., 1992). Therefore, one might expect that memory for new episodic associations should also benefit from semantic congruence with the material under study. We previously tested this hypothesis by asking participants to remember whether famous faces that were either preceded by congruent or incongruent semantic information during the study phase appeared in the same or in a different studied location (Atienza et al., 2009; also see Greve et al., 2007, for associations using verbal material). As predicted, face-location associations were better remembered when preceded by congruent rather than incongruent semantic information during the study phase. This enhanced episodic retrieval for semantically congruent relative to semantically incongruent faces was positively correlated during successful encoding with increases in non-phase-locked theta (4–7 Hz) power in bilateral parahippocampal gyrus as well as in ventral and dorsal regions of the left PPL.

A vast number of studies in the last few years have supported the role of the MTL in associative episodic memory along with structures of the prefrontal and posterior parietal cortices or even with perceptual regions involved in the processing of the study material (e.g., Sommer et al., 2005a,b; Cansino et al., 2002). However, few studies to date have focused on how the MTL and other structures of this global network may interact during encoding and retrieval of associative learning.

Functional integration in the human brain has been mainly explored by studying connectivity patterns derived from the analysis of hemodynamic responses related to neural activity. This approach
has demonstrated that areas containing content-specific representations exhibit decreased activation with learning during associative encoding paralleled by an increase in effective connectivity (von Kriegstein and Giraud, 2006; Büchel et al., 1999). The strong functional relationship found between domain-specific regions and structures of the prefrontal cortex suggests that top-down signals originating in the dorsolateral prefrontal cortex may control aspects of the perceptual representations are either bound into the new episodic memory trace (Summerfield et al., 2006) or reactivated during retrieval (Nyberg et al., 2000). As binding of new associations are mainly supported by the hippocampal formation (e.g., Piekema et al., 2009; Eichenbaum et al., 2007; Mayes et al., 2007; Davachi, 2006), the hippocampus and other regions of the MTL are also expected to communicate with other neocortical regions during successful encoding. Accordingly, it was found that the degree of functional connectivity between the right hippocampus and regions, such as the right fusiform gyrus and the left inferior frontal gyrus, during encoding, predicted success in learning the name associated with an unknown face (Sperling et al., 2003; see also Tsukiura and Cabeza, 2008). Similarly, Addis and McAndrews (2006) reported reciprocal effective connections between the left inferior frontal gyrus and the left hippocampus (but stronger input from the former to the latter) during successful encoding of word triads regardless of the number of semantic associations among them. Altogether, these findings suggest that regions of the lateral prefrontal cortex direct associative encoding through their positive influence upon hippocampus and other neocortical regions.

Results from animal and human studies indicate that encoding into long-term memory may be supported by increased theta synchronization within hippocampus and other structures of the MTL (Fell et al., 2003) or between hippocampus and other neocortical regions as suggested by increases in long-range coherent EEG activity between frontal and temporoparietal regions during successful encoding of words (Sausseng et al., 2004; Weiss and Rappelsberger, 2000). Different properties of theta oscillatory behavior have also been related to distinct retrieval processes (Gruber et al., 2008; Jacobs et al., 2006; Osipova et al., 2006). To our knowledge, only two studies to date have evaluated how functional integration emerges at the neuronal level during associative episodic encoding in humans (Sato and Yamaguchi, 2007; Summerfield and Mangels, 2005). These studies evidenced that item-context binding during encoding is accompanied by enhanced intra- and inter-hemispheric EEG theta coherence between anterior and posterior cortical regions. Whether a similar connectivity pattern is reactivated during retrieval processes remains to be elucidated.

We have previously reported that theta oscillations in the parahippocampal gyrus and regions of the lateral PPL mediate the positive effect of semantic congruence on memory of episodic associations during successful memory encoding (Atienza et al., 2009). If the hypothesized role for theta oscillations in recruiting and binding distributed cortical representations during recollection (Guderian and Düzel, 2005) extends to encoding of long-term memory, the above-mentioned EEG theta sources are expected to become more strongly coupled under congruent than under incongruent semantic contexts. This prediction is tested in the present study by evaluating the time course of theta phase synchrony between regions of the MTL and other neocortical structures (regions of the lateral prefrontal cortex and PPL) known to play a crucial role in encoding and retrieval processes of associative memory.

Materials and methods

Subjects

Thirty-two right-handed university students (17 females; age range, 20–22), native-Spanish speakers, with normal or corrected-to-normal vision and with no history of neurological or psychiatric disorders participated in the present study. All subjects gave informed consent to a protocol approved by the Human Subjects Committee of the University Pablo de Olavide. Data from two participants were eventually excluded from the analysis, one due to a low response rate in the study phase (50% correct responses) and the other due to a persistent headache during the experiment.

Stimuli

Visual stimuli consisted of gray-scale oval faces obtained from 64 pictures of Spanish celebrities (actors, politicians, musicians, and television personalities) and 32 pictures of nonfamous individuals selected from the internet. Gender, age and emotional expression (either neutral or positive) were proportionally matched between experimental conditions. A 17-in., flat-panel computer screen was placed about 100 cm in front of the subjects’ eyes so that the centre of the screen appeared just in their horizontal sightline. Faces were presented on a black background in one of the four possible locations (top left, top right, bottom left, bottom right) framed by white rectangles (5.9 cm wide × 7.3 cm high). The faces subtended a visual angle of approximately 2.5” × 3.9” (width × height).

In a previous pilot study, 20 different young subjects were presented with a list of 288 names of celebrities accompanied by three biographical cues including profession and profession-related information (the title of a film or song, a television program or political position, etc.). Subjects were required to report if they knew the personage who represented the name and if they did, they had to state if they knew the remaining biographical information provided about the personage. We selected names and two additional biographical cues from 96 celebrities recognized by at least 75% of the participants. Each name and its corresponding biographical information were included in one of the three experimental conditions mentioned below.

Experimental design and protocol

Participants performed three different tasks: a matching biographical task (study phase), a conceptual priming task and a visual–spatial association memory test. Each task consisted of six blocks of 48 trials, each including a face, with a short break after each block. The study phase lasted approximately 60 min and the memory tests 30 min each with resting intervals of 10–15 min in between. 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 et al., 2005). We will present here results from the matching biographical task and the visual–spatial association memory test. Therefore, only these two tasks are described in detail and illustrated in Fig. 1.

Biographical matching task at the study phase

To evaluate the influence of congruent semantic processing on incidental associative learning, access to conceptual information was manipulated as follows. The faces were presented in a particular position, preceded by a biographical cue in the same position. Half of the famous faces were preceded by a congruent cue (semantically congruent faces, SCF), whereas the other half 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. Since subjects were not required to pay attention to the location of faces, any association between the face and location is assumed to be incidental.

Faces and their corresponding cues were pseudo-randomly 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
participants are required to identify whether the face matches the previous location. Although processing of a famous face involves accessing conceptual information, the biographical cues are supposed to activate additional semantic nodes containing specific information about individuals which could be used in the process of face recognition (Burton et al., 1990). Presentation® software (Neurobehavioral Systems, Inc., Albany, CA, USA) controlled stimulus presentation and behavioral response acquisition. Trials began with one white fixation cross at the centre of one of the four rectangles for 2000 ms. The offset of the cross was followed by a biographical cue for 1500 ms, and next the face appeared in the same location for another 1500 ms. Subjects were given a maximum of 5000 ms to respond if the face matched the biographical cue by pressing either the left or right button in the response box (Cedrus®, model RB-530, Cedrus Corporation, San Pedro, CA, USA) with the left or right index finger, respectively.

**Visual–spatial association test**

After performing the study phase and the conceptual priming task, subjects saw all the faces in the same position six times. Next, faces were presented again for 500 ms without any preceding cue for another three times, 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 were required to identify as quickly and accurately as possible whether the faces matched the previous location or not. Responses faster than 300 ms and slower than 2500 ms were excluded from analyses. 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 semantically congruent faces will be remembered better and faster than position of incongruent 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 reaction times (RTs) were calculated for correct responses only (hits and correct rejections). Measurements 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 two-way analyses of variance (ANOVA) of repeated measurements with semantic context (congruent, incongruent) and face localization (same, different) as the within-subject factors. As a subset of participants ($n = 20$) showed faster responses in identifying the location of semantically congruent than incongruent faces whereas the remaining participants ($n = 10$) showed the opposite pattern, we further evaluated whether the dynamic properties of the network underlying these two patterns of results were also different.

**EEG acquisition**

The EEG was recorded with gold disk electrodes (Grass, Astro-Med, Inc.) from 59 standard positions of the extended 10–20 system (AFz, Fz, FCz, Cz, CPz, Pz, 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) and from the left and right mastoids (M1, M2) that were used as linked-mastoids online reference. Additional electrodes were used for monitoring horizontal and vertical eye movements as well as electromyogram from submental muscles. Impedance was maintained below 5 KΩ in all electrodes. All electrophysiological variables were amplified (BrainAmp MR, Brain Vision®), filtered (0.1–100 Hz bandpass), digitized (250 Hz, 16-bit resolution), and stored in digital format for off-line analysis. Ocular and muscle artifact were partly removed with the Infomax algorithm for Independent Component Analysis implemented in the BrainVision Analyzer software v. 1.05 (Brain Products GmbH). After data segmentation, epochs still showing artifacts were manually rejected.

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

Time-frequency analysis

Time-frequency representations (TFRs) were computed to determine the time interval at which non-phase-locked theta oscillations achieve their maximum power in relation to the baseline period. First, EEG of each participant was transformed into the time-frequency domain applying complex demodulation as implemented in the Brain Electrical Source Analysis software (BESA 5.2; Megis Software, Inc.; see Method in Hoechstetter et al., 2004). The complex demodulation used here computes the instantaneous envelope amplitude and instantaneous phase of EEG-oscillatory activity within a specific frequency band using the Gabor transformation, allowing the study of non-stationary signals. Frequency of interest ranged from 2 to 12 Hz, in steps of 1 Hz, including latencies from −2100 ms from face onset to 1000 ms post-stimulus for the study phase, and from −600 ms to 1000 ms for the episodic memory task. The time-frequency resolution was defined by the full width at half maximum (FWHM) of the low-pass filter applied to compute the envelope amplitude and phase. We applied a time frequency setting of 1 Hz and 50 ms, which corresponded to a FWHM in the frequency domain of 2.84 Hz and a FWHM in the time domain of 157.6 ms when computing power values. TFRs of event-related decreases/increases in the power in relation to a baseline value were computed according to the formula (100% (TFR − Pbaseline)/Pbaseline). Here Pbaseline represents the TFR of the signal averaged over baseline period. The baseline period ranged from −2100 ms to −1600 ms before face onset for the study phase, to avoid the contribution of the activity elicited by the semantic cue, and from −600 ms to −100 ms — before face onset for the episodic retrieval phase (the 100 ms prior to the onset of the stimulus was not included in the baseline to prevent expectation effects). Since we were interested in non-phase-locked theta oscillations (because they have been associated with recall, see, e.g., Düzel et al., 2005; Guderian and Düzel, 2005; Klimesch et al., 2000), the TFR of the averaged waveform (time- and phase-locked to the stimulus) was subtracted from the TFR of each individual trial. We show that even if some residual phase-locked activity appeared overlapped with non-phase-locked theta oscillations after subtraction, the effect of semantic congruence on the latter could not be accounted for by differences in evoked theta activity (see Supplementary material).

Multiple source localization with beamforming

Beamforming analysis was performed on each subject using the multiple source beamformer (MSBF) method implemented in BESA 5.2 (Megis Software Inc.). Beamformer analysis involves a direct transformation of EEG signal space into source space (the brain) by using spatial filters. This method estimates the amount of activity that a neuroelectric source at each defined voxel contributes to scalp EEG recordings in each trial, minimizing the contribution of sources at other voxels (Gross et al., 2001). Applying this procedure for each point in the three-dimensional source space yields volumetric beamformer images, constructed from values of power q(r) normalized with the power in a reference time-frequency interval (i.e., baseline) of the same length. Source localization was performed using the BESA standard MRI, which stems from a Talairach average of 24 subjects, with a voxel grid of 6 mm and a regularization parameter 5VD (singular value decomposition) of 0.001. The forward solution was calculated using a four shell ellipsoidal head model. It is important to note that beamforming analyses performed in BESA are computed for the average-referenced montage; therefore results reported here are not dependent on the reference originally employed.

There is evidence that even when theta generators in the hippocampus and cortical regions may be independent (Cantero et al., 2003), they can interact in the theta frequency for solving task demands and stimulus-specific encoding or retrieval operations (e.g., Guderian and Düzel, 2005; Fell et al., 2003). This finding suggests that theta long-synchronization does not require high correlation between sources. However, highly correlated bilateral activity in the two hemispheres often occurs during processing of external stimuli, and single-source beamformers are known to fail at localizing EEG sources when they are highly correlated. This drawback is overcome by using a bilateral beamformer where contributions from the homologue source in the opposite hemisphere are taken into account. On the other hand, although high correlation is unlikely between spatially disparate non-symmetrical sources, the beamformer method is able to provide resultant activity in between the real active areas, as any other localization algorithm associated with underestimation of the number of sources would do (van Veen et al., 1997). It should be noted that the beamformer method allowed us to identify the EEG sources that correlated with performance in the memory test which were later added to a discrete multiple source model to analyze phase synchrony (see below).

Statistical parametric mapping

Regression analyses were performed to determine regions in which neural oscillatory activity during successful encoding of famous faces predicted behavioral performance at episodic retrieval. Images from each subject were first normalized to the Montreal Neurological Institute (MNI) space using the T1 single subject MRI image (Colin27) provided by SPM5 (Wellcome Department of Cognitive Neurology, London) as template, and using the BESA standard MRI as source image. Volumetric beamformer difference images (semantically congruent minus semantically incongruent faces) during the study phase and RT or accuracy indexes during the memory test were used to construct corresponding statistical parametric maps (SPMs) of their relationships by using SPM5. To determine whether the same correlating regions were recruited during encoding and retrieval, a similar procedure was applied to the data obtained while participants performed the memory test. Adjustments for multiple comparisons were done using the false discovery rate (FDR) correction (p < 0.05). Based on obtained SPMs and on a priori hypotheses concerning the role of the MTL and some domain-specific regions in encoding and retrieval of associative memories, regions of interest (ROIs) masks were created using the WFU_PickAtlas (Maldjian et al., 2003) to perform regression analyses. We applied a temporoparietal ROI (including bilateral temporal and parietal lobes), a frontal ROI (including the right frontal lobe) and a parahippocampal ROI (including bilateral parahippocampal gyri). Coordinates of each significant peak voxel obtained from the SPMs (p < 0.05, corrected for multiple comparisons) were transformed into the Talairach space (Talairach and Tournoux, 1988) by using the nonlinear transformation (approach 2) described by M. Brett (http://imaging.mrc-cbu.cam.ac.uk/ Imaging/ MniTalairach).

Reconstruction of the source waveforms from scalp space into brain source space

Before reconstruction of the source signals, EEG data sets were transformed from the linked-mastoids to the common average reference to attenuate the spurious contributions of the active reference electrode to phase synchronization measurements (Nunez et al., 1997; Guevara et al., 2005) as suggested by Schiff (2005) to deal with the reference problem inevitably associated to phase analyses. Intracranial EEG activities were estimated by applying a fixed spatial filtering that is an adapted version of the discrete multiple source model implemented in BESA named “BR_Brain Regions.” This spatial
filter transforms the recorded EEG channels onto virtual source channels (only the radial component was used) and reconstructs their temporal waveforms in units of current dipole moment (nAm) (Hoehstetter et al., 2004). The original version of the BR/Brain Regions separates the activity of 15 different brain regions, covering lateral and midline frontal, central and parietal cortex, midline fronto-polar and occipito-polar cortex as well as anterior and posterior temporal lobes bilaterally. Since we were interested in specific brain areas involved in successful episodic memory encoding and retrieval, we seeded additional sources on the geometrical centres of regions showing correlated activity with performance according to the regression analysis mentioned above. These regions included the inferior frontal gyrus, parahippocampal gyrus, inferior parietal lobe, and superior parietal lobe in both hemispheres. Geometrical centres were computed using the WFU_PickAtlas-masks coordinates for each mentioned region. Each source waveform represents the activity recorded by a virtual electrode with an approximate 3- to 4-cm diameter placed over the cortical area that is modeled (Scherg et al., 2002). To keep a minimum distance of 3 cm between sources, we removed four original sources placed on the bilateral central cortex and temporal anterior lobes. The 19 sources montage coordinates used for reconstruction of the source waveforms are listed in Table 1.

### Measuring neural synchrony in source space

To study oscillatory coupling between EEG sources, time series were reconstructed from coordinates listed in Table 1. Source signals were filtered in the theta frequency range (4–7 Hz) using a finite impulse response filter with a Kaiser window. The filter order was 1326, which ensured frequency attenuation within 0.5 Hz. Next, instantaneous phases were calculated with the Hilbert transform. And finally, synchrony between source signals was computed using the phase lag index (PLI) defined by Stam et al., (2007):

$$\text{PLI} = |\langle \sin(\Delta \phi(t)) \rangle|$$

where $\Delta \phi(t_i)$ is the phase difference between the two sources in the time sample $t_i$. To our knowledge, the PLI has only been applied to spontaneous EEG/MEG activity and averaged over epochs of several seconds. In order to adapt this measure to event-related brain activity, each trial, including the baseline and post-stimulus periods detailed above, was divided into 140 ms time windows (35 samples) overlapping by 60 ms. Homologous time windows from different trials were concatenated to build up epochs of 140×N ms (35 samples × N, where N refers to the number of trials). The time window of 140 ms is the minimum duration required for a theta cycle of 7 Hz, thus providing meaningful values of phase synchronization. Each PLI value was then computed averaging all time points within each new built-up epoch which further included information from all trials. This approach allows us to maintain temporal information and stationarity of the signal.

PLI was introduced as a novel measure to quantify neural phase synchronization that is less affected by the field spread and active reference electrodes (Stam et al., 2007). A strict definition of phase synchronization between two sources requires a phase locking between them (a constant phase difference). In practice, however, the difference of their phases only has to remain below some constant (2π). In particular, PLI measures the asymmetry of the phase difference distribution between two sources, which means that their phase difference not only remains bounded but also has a preferred orientation to one of the two halves of the unit circle. In other words, PLI reflects the consistency with which one signal is phase leading or lagging with respect to another signal (Stam et al., 2007). PLI values vary between 0 (no coupling, due to a symmetric distribution or the coupling with a phase difference centred on 0 mod π, caused by a common source) and 1 (perfect phase locking between sources at a value of Δφ different from 0 mod π).

### Testing significant phase synchrony

To determine whether phase synchronization between two specific EEG sources was meaningful, we tested the significance of PLI values for each time window with respect to random background values using a bootstrap method (Lachaux et al., 1999). This method compares original PLI values with the non-normal distribution of PLI values obtained from surrogate data. For each pair of sources, 5000 surrogate data were created by randomly shuffling the trials from one of the two source signals (Pereda et al., 2005), so that signals from the same trial were never paired together. Surrogate data were then used to compute 5000 PLI time series between all source pairs for each subject. For each experimental condition and for each time window, we determined that the grand-average original PLI values were significant if they surpassed 95% of the distribution of grand-average PLIs obtained from the surrogate data (see Lachaux et al., 1999).

To examine time evolution of synchronized activity between EEG sources we only considered those grand-averaged PLI values that exhibited significant phase synchrony (above surrogate threshold) for each defined 140-ms time window at least in one of the two semantic contexts. To evaluate the effect of semantic congruence, one of the two conditions was randomly multiplied by +1 or −1 for each participant. Univariate squared T statistic (paired samples t tests) was first computed on the original data for each defined time window of 140 ms every 60 ms, within both baseline and post-stimulus time intervals (after face onset). Next, the maximum $T^2$ was selected for each randomization (10,000), denoted as max (1). The 95th quantile of this randomization distribution of max ($T^2$) was used as a critical value to retain or reject the null hypothesis of no differences between conditions. This procedure has been reported to control the family-wise error rate for all time points jointly (Maris, 2004).

Comparison to surrogate values and between conditions by means of randomization tests were first applied to PLI values without baseline correction since the baseline period might contain useful information. However, to remove phase synchronies unrelated to the task before comparison between conditions during post-stimulus period, we repeated the procedure using standardized PLIs (PLIs) of original and surrogate data. PLIs were obtained by subtracting the mean PLI of the baseline interval from the mean PLI obtained in each 140-ms time window and dividing the difference by the standard deviation of PLI values in the baseline. The positive values refer to increased synchronization related to baseline whereas the negative ones indicate decreased synchronization related to baseline.

### Table 1

<table>
<thead>
<tr>
<th>Brain region</th>
<th>X</th>
<th>Y</th>
<th>Z</th>
</tr>
</thead>
<tbody>
<tr>
<td>11 Original sources from BESA brain regions standard montage</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R/L frontal cortices (FR/FL)*, BA 9/46</td>
<td>±34</td>
<td>+33</td>
<td>+26</td>
</tr>
<tr>
<td>R/L parietal cortices (PR/PL), BA 39</td>
<td>±34</td>
<td>−69</td>
<td>+16</td>
</tr>
<tr>
<td>R/L temporal posterior lobes (TPR/TPL), BA 21</td>
<td>±47</td>
<td>−37</td>
<td>−4</td>
</tr>
<tr>
<td>M fronto-polar cortex (Fpm), BA 10</td>
<td>0</td>
<td>+55</td>
<td>+5</td>
</tr>
<tr>
<td>M frontal cortex (FM), BA 8</td>
<td>0</td>
<td>+30</td>
<td>+47</td>
</tr>
<tr>
<td>M central cortex (CM), BA 6</td>
<td>0</td>
<td>−23</td>
<td>+61</td>
</tr>
<tr>
<td>M parietal cortex (PM), BA 7</td>
<td>0</td>
<td>−72</td>
<td>+37</td>
</tr>
<tr>
<td>M occipito-polar cortex (OpM), BA 18</td>
<td>0</td>
<td>−87</td>
<td>−9</td>
</tr>
<tr>
<td>8 Additional sources placed at geometrical centres of ROIs</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>R/L inferior frontal gyrus*, BA 47</td>
<td>±44</td>
<td>+24</td>
<td>−1</td>
</tr>
<tr>
<td>R/L inferior parietal lobe*, BA 40</td>
<td>±47</td>
<td>−41</td>
<td>+38</td>
</tr>
<tr>
<td>R/parahippocampal gyrus*</td>
<td>±21</td>
<td>−18</td>
<td>−18</td>
</tr>
<tr>
<td>R/L superior parietal lobe*, BA 7</td>
<td>±25</td>
<td>−59</td>
<td>+53</td>
</tr>
</tbody>
</table>

Note. L = left; R = right, M = midline; (*) Selected sources for synchronization analyses. FR and FL original BESA sources were very near the geometrical centre of the right and left middle frontal gyrus and were included on synchronization analyses. Coordinates were rounded to the nearest integer.
Results

Behavioral

Participants were more accurate in remembering spatial source information ($F_{1,29} = 7.45; P < 0.02$) when faces had been preceded in the study phase by cues semantically congruent (mean $d' = 2.57; \text{SEM} = 0.13$) than cues that had been semantically incongruent (mean $d' = 2.20; \text{SEM} = 0.13$). This finding was independent of whether or not faces were presented at the same location as during the study phase (i.e., no interaction effect between semantic context and face location was found). Participants were also around 15 ms faster in responding to semantically congruent trials for faces appearing either in the same or in different location, but this behavioral gain did not reach statistical significance. In particular, the average gain in RT was around 38 ms in 20 out of 30 subjects, whereas the 10 remaining participants gave faster responses on semantically incongruent trials (~32 ms faster in mean RT). When subjects were split based on whether their speed responses were better for congruent or incongruent trials (group), the mixed ANOVA indicated that both groups kept showing accuracy benefit of semantic congruence during retrieval as derived from a significant effect of semantic context ($F_{1,28} = 12.47; P < 0.001$) and the lack of semantic context × group interaction. No group differences were found for either RT or $d'$ measurements.

Localization of theta activity that correlated with performance in the memory task

TFRs of the non-phase-locked activity recorded at the sensor level were averaged over trials, electrodes, semantic contexts, and subjects ($N = 30$) during the study phase and during retrieval of episodic associations. Fig. 2A illustrates modulations (power change percent relative to baseline) of slow oscillatory activity in each condition across three different time periods including 600 ms of baseline, 1500 ms after presentation of the semantic cue, and 1000 ms after presentation of the face. The grand-average TFR confirmed the presence of a strong power increase in the non-phase-locked activity with respect to the baseline interval for slow frequencies (see Fig. 2). The maximum power increase was found for 3–5 Hz following both presentation of the semantic cue and presentation of the face. These frequency bins are on the border between delta and theta bands but we restricted our analyses to the human theta band (4–7 Hz). As the congruence decision between semantic context and face takes place after presentation of the latter, beamformer analysis was performed between 300–800 ms after face onset during the study phase. Likewise, the same time interval was considered to estimate the generators of non-phase-locked theta oscillations during retrieval where maximum differences between semantically congruent and incongruent faces were found (Fig. 2B; see Supplementary material to discard differences in theta-evoked activity within this time interval).

Source imaging of the EEG-theta activity was performed in the time-frequency domain to identify those brain regions involved in the theta generation during encoding and retrieval of incidental episodic associations under congruent/incongruent semantic contexts. By using this approach, multi-channel-EEG recordings were reduced to their meaningful source estimates for further across time connectivity analysis.

Linear regression analyses were performed across subjects to identify where increasing theta power in the brain (higher amplitude of the theta power to congruent as compared to incongruent semantic context) is associated with improving performance during episodic retrieval (either more accurate or faster responses to congruent relative to incongruent semantic context). As shown in Fig. 3, these analyses revealed that activity of different theta sources were correlated with RT (Fig. 3A) and accuracy ($d'$) (Fig. 3B) during the study phase and visual–spatial memory task respectively. Faster RT in identifying the location of semantically congruent faces relative to semantically incongruent faces were correlated with enhanced activation for congruent faces in the right and left parahippocampal gyrus and domain-specific regions as the left superior temporal gyrus, left inferior parietal lobe and bilateral superior parietal lobe. In contrast, only regions in the right ventral (inferior frontal gyrus) and right dorsolateral prefrontal cortex (middle frontal gyrus) showed significant correlations with accuracy ($d'$) during the memory task. Table 2 shows the MNI coordinates of the different peak voxels that
were correlated with performance parameters during the study phase and during the visual–spatial memory task.

**Spatiotemporal connectivity patterns during successful encoding**

The time course of functional connectivity between different EEG theta sources during the study phase is illustrated in Fig. 4. Fig. 5 shows a schematic representation of phase synchrony between different estimated theta sources. PLI values higher for congruent than for incongruent conditions are indicated by thick solid lines, whereas the opposite pattern of results is represented by dotted lines (Fig. 5, left panel). Sources showing similar levels of synchrony in both conditions are indicated by thin solid lines (Fig. 5, right panel). These functional connections are interpreted as a measure of modulation in long-range synchronization.

**Synchronization patterns involving the dorsolateral prefrontal cortex (DLPFC)**

According to the hypothesized role of the DLPFC (middle frontal gyrus in the present study, BA 45) in implementing control processes that promote encoding of associations among items active in working memory (Murray and Ranganath, 2007), this region is expected to maintain high levels of functional coordination with other brain nodes involved in binding of new associations like those in the MTL. This hypothesis is supported by results obtained with synchronization analysis in the present study. Indeed, theta phase synchronization between bilateral DLPFC and bilateral parahippocampus (PH) was evident regardless of which semantic context was used to encode the episodic association (see Fig. 5, right panel). These regions maintained longer periods of phase synchrony with the left PH during encoding of semantically congruent associations and with the same area in the

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**Table 2**

MNI coordinates of significant peak voxels in the regression analysis between SCF/SIF theta oscillations and behaviour in the study phase and the visual–spatial task.

<table>
<thead>
<tr>
<th>Brain region</th>
<th>x</th>
<th>y</th>
<th>z</th>
<th>T</th>
<th>Z-score</th>
<th>k</th>
<th>pFDR</th>
<th>R</th>
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<tr>
<td>L. superior temporal gyrus, BA 22</td>
<td>−32</td>
<td>−40</td>
<td>12</td>
<td>3.58</td>
<td>3.22</td>
<td>3269</td>
<td>.068</td>
<td>.56</td>
</tr>
<tr>
<td>L. superior parietal lobe, BA 7</td>
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<td>−68</td>
<td>40</td>
<td>3.31</td>
<td>3.02</td>
<td>3269</td>
<td>.068</td>
<td>.53</td>
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<td><strong>Parietotemporal ROI analysis</strong></td>
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<tr>
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<td>12</td>
<td>3.58</td>
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<td>L. superior parietal lobe, BA 7</td>
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<td>−68</td>
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<tr>
<td><strong>SCF-SIF correlation with d’ Retrieval phase</strong></td>
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<tr>
<td>Right Frontal ROI analysis</td>
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<td>36</td>
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<td>3.07</td>
<td>1859</td>
<td>.038</td>
<td>.54</td>
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Note. Contrasts were performed over the whole brain and using ROI masks. Voxel-level p-values are uncorrected. L = left; R = right.

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**Fig. 3.** Statistical parametric maps showing the significant cerebral activations resulting from a ROI based regression analysis with performance. (A) Results of correlating percent beamformer’s power change difference between semantically congruent and incongruent faces with RT difference between semantic contexts during the biographical matching task. (B) Results of correlating percent beamformer’s power change difference between semantically congruent and incongruent faces with d’ difference between semantic contexts during the visual–spatial task. Activated regions are shown on the left and right lateral views of a volume-rendered MRI at p<0.05 (corrected with FDR). Peak voxels of positive correlations are listed in Table 2.
regions in the PPL, firstly because they represent the items that are to be associated (Summerfield et al., 2006) and secondly because these regions are suggested to play a key role in directing attention not only to sensory information (Corbetta and Shulman, 2002) but also to neural representations reactivated from long-term memory in the MTL (Cabeza, 2008; Cabeza et al., 2008). Accordingly, the IMFG was functionally coupled to the inferior parietal lobe (IPL) bilaterally (Fig. 5, right panel). Interestingly, connections with the right IPL, which has been hypothesized to direct bottom-up attention to different aspects of environment, were common to both semantic conditions; whereas phase synchrony with the left IPL, hypothesized to direct bottom-up attention to memory, was specific for incongruent associations and significantly higher as compared to the semantically congruent condition between 420 and 560 ms ($T^2 > 4.8, p < 0.05$).

Synchronization patterns involving the ventrolateral prefrontal cortex (VLPFC)

Functional neuroimaging studies evaluating the subsequent memory effect has shown that the VLPFC (inferior frontal gyrus in the present study, BA 47) plays a crucial role in long-term memory encoding by selecting the relevant aspects of the item that are to be remembered (Blumenfeld and Ranganath, 2007). In support of this assumption, successful encoding of semantically congruent and incongruent associations was accompanied by significant phase synchronization of the left and right inferior frontal gyrus (IFG) with bilateral PH and right superior parietal lobe (SPL) respectively, whose role in long-term memory encoding processes is gaining support in the last few years (e.g., Uncapher and Wagner, 2009).

In addition, the left IFG participated in fronto-frontal connections, showing significant increased synchrony with the right MFG during encoding of faces congruent with the biographical cue between 600 and 740 ms after stimulus onset (Fig. 5, left panel). In the same direction, an intrahemispheric connection with the left MFG between 480 and 620 ms was almost significant ($T^2 = 6.47, p = 0.052$).

Synchronization patterns involving regions of the posterior parietal lobe (PPL)

Ventral region of the PPL is extensively connected with visual areas of the SPL and with the parahippocampal cortex among other regions in monkeys (e.g., Cavada and Goldman-Rakic, 1989; Andersen et al., 1990; Rozzi et al., 2005). The latter connection receives further support from human studies (Rushworth et al., 2006). There is even evidence that information mainly flows from the MTL to the IPL (Clower et al., 2001). As expected from these anatomical findings, phase synchrony between PH and IPL in the right hemisphere was evident during encoding of episodic associations between 400 and 600 ms from face onset under the two semantic contexts (Fig. 4, bottom panel), likely indicating engaging of automatic attention towards representations of space continuously updated in the MTL. Note that these representations are irrelevant for the biographical matching task but are crucial for successful encoding of place-location associations under the two contexts. Contrary to this context-independent functional connection, later theta phase synchronization with the left IPL was exclusive of the incongruent condition and significantly higher in this condition as compared with semantically congruent faces within the 660–800-ms interval ($T^2 > 5.0, p < 0.05$). Functional connectivity with the left ventral region of the PPL may index automatic shift of attention towards memory representations (rather than towards external aspects of the stimuli) in the MTL, as will be debated in the discussion section.

The left PH only showed significant phase synchrony with the dorsal regions of the PPL in the right hemisphere. This pattern of functional coupling took place at different time windows depending on the semantic context, early (50–200 ms) for incongruent conditions and late (720–860 ms) for congruent contexts. In the latter time window, differences between conditions achieved
neural coordination between the left DLPFC and the right IPL that were restricted to the 600–1266 ms time frame following face onset. This early connectivity pattern matches well the role of these regions in the constructions of representations of surrounding space. In fact, these neurons in the IPL are not only modulated by position of the head but also by the orbital position of the eye (e.g., Andersen et al., 1997). However, from 600 ms forward synchrony between these regions was only evident during encoding of semantically congruent faces. Significant differences between conditions were restricted to the 600–740-ms time interval ($T^2 > 5.7, p < 0.05$). The latter functional coupling might be more related to the role of the IPL in triggering reorientation of top-down attention by the SPL towards representations reactivated in the MTL as will be discussed in the following section.

Finally, major white matter tracts connect the IPL with the ventral and dorsolateral regions of the prefrontal cortex which may be relevant for visual attention and working memory (Cavada and Goldman-Rakic, 1989). Phase synchrony analyses revealed significant neural coordination between the left DLPFC and the right IPL that endured longer in the incongruent condition. The left DLPFC also connected to the left IPL but only under incongruent conditions, and synchrony was significantly higher than in semantically congruent contexts between 420 and 560 ms ($T^2 > 4.8, p < 0.05$). Thus, the left DLPFC might mediate, through theta phase synchrony, engagement of attention by the left IPL.

**Functional connectivity during successful retrieval**

The DLPFC is considered to play an important role in post-retrieval monitoring processes during associative recognition tests (Achim and Lepage, 2005). As shown in Figs. 6 and 7, theta oscillatory activity in this region was synchronized with that in the left PH and IPL in the two contexts during early and late time intervals. Note that the longest synchronization pattern was seen between the right MFG and the left PH (Fig. 6, bottom panel). However, none of these functional connections allowed us to distinguish between semantically congruent and incongruent faces. Only connections with the VLPFC showed a different pattern of theta synchrony. In particular, faces encoded under semantically congruent contexts produced higher theta synchrony than in the right MFG and the left IFG from 660 to 800 ms ($T^2 > 9.5, p < 0.02$).

Connections between bilateral ventral PPL and PH were even more relevant during retrieval of episodic associations. Again, functional coordination between these regions was higher when successfully retrieving location of faces that were encoded in semantically incongruent contexts. Significant differences in neural phase synchronization between the right PH and the right IPL started from 180 to 320 ms ($T^2 > 14.3, p < 0.01$) and continued between 360 and 500 ms ($T^2 > 7.6, p < 0.05$). The right PH also showed differential synchrony with the IPL of the left hemisphere between 480 and 620 ms ($T^2 > 6.2, p < 0.05$). During the same time window, the ventral and dorsal theta sources of the PPL within the right hemisphere showed higher synchrony during the congruent compared to the incongruent condition ($T^2 > 6.8, p < 0.05$).

**Discussion**

The best memory for spatial source information, when faces were preceded by congruent than by incongruent semantic cues during the study phase, was correlated with increased non-phase-locked theta activity in regions of the MTL along with structures of the lateral prefrontal and posterior parietal cortices. All these regions have been reported as constituting important nodes of the global network that governs the different processes supporting associative episodic
memory (for reviews in humans, see Wagner et al., 2005; Simons and Spiers, 2003; for a review of equivalent structures in monkeys see Osada et al., 2008). Successful encoding and subsequent retrieval is, in fact, predicted by the degree to which the nodes of the brain network are functionally interconnected (Summerfield and Mangels, 2005; Weiss and Rappelsberger, 2000). In particular, our results suggest that, although regions of the MTL are pivotal for the formation of episodic associations (see also Sommer et al., 2005a,b), regions of the lateral prefrontal cortex and PPL likely provide the control signals that regulate the positive influence of semantic congruence on incidental formation of new associative memories during both encoding and retrieval processes.

**Global network dynamics during encoding**

The connectivity pattern revealed by the parahippocampal gyrus during semantic encoding of memories was likely critical to bind distributed representations of face and spatial information into a long-lasting memory trace. This hypothesis is mainly supported by human neuroimaging studies showing either functional or effective connectivity between regions of the MTL and frontal and parietal regions (Addis and McAndrews, 2006; Summerfield et al., 2006; Sperling et al., 2003; Nyberg et al., 2000; Büchel et al., 1999), as well as by neural computational studies (Sato and Yamaguchi, 2005). However, the main result of the present study was that integration of sensory and contextual information was better encoded under semantically congruent contexts as a result of the differential but complementary top-down and bottom-up influences exerted by different regions in the lateral prefrontal and posterior parietal cortices.

**Influence of top-down control-signal dynamics in the lateral prefrontal cortex**

In an elegant review of neuropsychological and neuroimaging studies, Blumenfeld and Ranganath (2007) concluded that dorsal and ventral regions of the prefrontal cortex provide complementary control signals that regulate encoding and retrieval processes. The core idea is that the ventrolateral prefrontal cortex (VLPFC) would orient attention toward high level or semantic features of single items that have to be remembered (Thompson-Schill et al., 1997), whereas the dorsolateral prefrontal cortex (DLPFC) would direct attention toward processing of relationships among items.

Based on this framework, and independently of semantic congruence manipulation, the inferior frontal gyrus (corresponding to the anterior part of the VLPFC) is expected to support associative memory through its connections with the MTL (as suggested by theta phase synchronization between the left inferior frontal gyrus and bilateral PH; for complementary fMRI results see Addis and McAndrews, 2006) and through connections with regions containing person-specific and/or spatial representations (as the one found between the right inferior frontal gyrus and the right SPL). Given that associations were learned incidentally, the right lateralization of the frontal–parietal phase synchrony likely reflects bottom-up capture of attention driven by spatial information (Corbetta and Shulman, 2002). Consistent with this interpretation, Summerfield and Mangels (2005) found that semantic processing was accompanied by increased theta-band coherence between anterior–posterior cortical regions within the left hemisphere, whereas processing of sensory context was mainly mediated by theta coherence in the right hemisphere.

The parahippocampal cortex is part of a brain network that mediates the processing of contextual associations (Bar et al., 2008a, 2008b). Given that famous faces and the preceding semantic cues evoke many contextual associations, it seems feasible that theta synchronization between the middle frontal gyrus (corresponding to the anterior part of the DLPFC) and PH reflects the top-down control of attention towards contextual associations spontaneously evoked by these stimuli. Under congruent conditions, all reactivated information is associated with the same location, which may, in turn, increase the probability of successful encoding and subsequent retrieval. On the contrary, under incongruent conditions, the system is expected to reduce the number of non-coherent semantic meanings that enter the focus of attention. According to this interpretation, synchrony between the DLPFC and the left PH was shorter under incongruent conditions, likely to prevent interferences with encoding processes.

**Influence of top-down and bottom-up control-signal dynamics in the PPL**

The dorsal and ventral regions of the PPL along with regions of the prefrontal cortex are associated with top-down and bottom-up control of attention toward task-relevant information respectively (Corbetta and Shulman, 2002). But in the last few years, this system has gained popularity as part of the network that mediates both encoding (Uncapher and Wagner, 2009) and retrieval of episodic memory (Cabeza, 2008; Cabeza et al., 2008; Ciaramelli et al., 2008). Neuroimaging studies have consistently reported positive subsequent memory effects in the SPL (Uncapher and Wagner, 2009) and negative effects in the IPL (Uncapher and Wagner, 2009; Cabeza, 2008). A model of attention to memory has been recently proposed to account for most fMRI results during retrieval (Cabeza et al., 2008; Ciaramelli et al., 2008). According to this model, the SPL is not only expected to direct top-down attention toward the goals of the memory task like the DLPFC would do, but it can also redirect attention to bottom-up driven memories thanks to anatomical connections between the MTL and the ventral PPL.

This model of attention to memory can also account for the neural pattern of synchronization shown by the theta sources in the parietal cortex, mainly because the biographical matching task requires retrieving semantic information from long-term memory. From this perspective, the pattern of synchrony shown by the right SPL is consistent with top-down allocation of attention to goal-relevant semantic information, which might also be responsible for successful encoding of semantically congruent associations. However, the pattern of synchrony associated to the IPL more likely contributed to the automatic shift of attention toward task-irrelevant information, e.g., spatial context, or additional reactivated memories provided that these memories correspond to the person identity whose location has to be latter retrieved.

All together, these results suggest, on the one hand, that successful encoding under semantically congruent contexts is facilitated by (i) top-down mechanisms in the left VLPFC to select task-relevant semantic information in the MTL, (ii) top-down mechanisms in bilateral DLPFC and right SPL to integrate sensory and contextual information in the MTL, and (iii) bottom-up mechanisms in the right IPL to trigger reorientation of attention toward automatically detected irrelevant-task spatial information. On the other hand, changes in theta phase synchronization within this neural network suggest that encoding of semantically incongruent associations mainly depend on bottom-up driven memories reactivated in the MTL. This mechanism would be mediated by the left rather than the right IPL.

**Global network dynamics during retrieval**

As a general rule, the functional connectivity patterns shown by the theta sources in the lateral prefrontal cortex during encoding was reactivated to a large extent during retrieval, suggesting similar functions for this region during encoding and retrieval processes underlying incidental memory formation of episodic associations (Blumenfeld and Ranganath, 2007). This finding gives further support to neuronal models of episodic memory which predict that successful retrieval is partially determined by the degree to which encoding-related activity is reactivated (McClelland et al., 1995; Alvarez and Squire, 1994). Although previous neuroimaging studies have provided evidence of overlapping activity in regions of the auditory cortex
During encoding and retrieval of auditory event information (Nyberg et al., 2000), this is the first time, to our knowledge, that long-range synchronization patterns in the theta band are also reported to be reactivated during retrieval in humans.

Encoding of semantically congruent associations was accompanied by enhanced theta phase synchronization between ventral and dorsal regions within the lateral prefrontal and posterior parietal cortices. On the contrary, successful encoding of semantically incongruent associations was followed by increased synchrony between right PH and ventral regions of the PPL in the two hemispheres. These results suggest that top-down and bottom-up attention towards both sensory and contextual representations reactivated in the MTL have different weights depending on whether associations were incidentally learned under congruent or incongruent contexts. Reactivated face and spatial task-relevant information is predicted to capture automatic attention independently of the encoding context. However, this mechanism is expected to have a worse performance in incongruent conditions, mainly because fewer contextual memories coherent with the face are predicted to be reactivated for incongruent conditions. Since demands of the controlled retrieval function depend on how effective the bottom-up mechanism is in reactivating relevant information from long-term memory in the MTL, it is not surprising that more retrieval attempts of relevant semantic information are engaged by the VL PPC under incongruent conditions (for a review, see Badre and Wagner, 2007). Accordingly, phase synchrony between the left inferior frontal gyrus and left PH persisted longer under incongruent conditions. In addition, synchrony between the right middle frontal and left inferior frontal gyrus was significantly higher for semantically congruent faces, likely indicating a more effective outcome of post-retrieval monitoring processes under congruent conditions (e.g., Achim and Lepage, 2005; see however Hayama and Rugg, 2009).

Methodological observations
Computing phase synchronization in EEG recordings demands particular caution in interpreting results because of two underlying problems not solved up to now that limit the reliability of functional connectivity measures: one is related to the common reference EEG and the other refers to the field spread.

It is well known that the amplitude of the reference can introduce artifacts in the calculated measures (Fein et al., 1988; Guevara et al., 2005), therefore reformatting of EEG is always recommended. We used the common average reference not only because is typical in EEG studies of neural synchrony but also because it diminishes correlation between signals when more than 15 EEG channels are used. However, some common noise still remains (Guevara et al., 2005), and magnitude of correlation between signals tends to rise at large inter-electrode distances (Nunez et al., 1997). In the present study, the increased correlation at large distances seems not to be an important confound because the synchrony between prefrontal and posterior theta sources was not affected by manipulation of semantic context.

Besides the common reference, the electrical conduction through the head volume inevitably confounds interpretation of the synchronization results obtained between scalp EEG signals. In an attempt to attenuate this problem we have followed the two strategies suggested by Schoffelen and Gross (2009): (i) to analyze experimental contrasts rather than the strength of the connectivity, because the effects of volume conduction are assumed to be identical across the experimental conditions and therefore subtract out; and (ii) to perform the connectivity analysis at the source level. In addition to this, we have used an index of synchrony that is less sensitive than others to both the reference montage and the problem of field spread (Stam et al., 2007).

As mentioned above, the volume conduction effect is mitigated when working on the source level, but most inverse methods are unable to distinguish which interactions are due to field spread. Some recent methods confront the volume conduction effect before performing the inversion step (Gomez-Herrero et al., 2008; Marzetti et al., 2008). We believe that future research should adapt these promising techniques to event-related activity in order to further diminish misinterpretations of synchrony results.

Conclusions
The present results suggest that successful associative encoding and retrieval processes operate on similar neural networks, but that the dynamic of the synchronization patterns at the theta frequency can be affected by manipulation of semantic context. Thus, although EEG-theta sources in the MTL, lateral prefrontal cortex and PPL showed similar patterns of functional coupling during encoding and retrieval, semantic congruence modulated the output of this communication by enhancing the top-down control signals provided by regions of the prefrontal and parietal cortices on structures of the MTL, and by adjusting the role of bottom-up driven memories mechanisms mediated by the IPL.

Conflict of interest
None declared.

Acknowledgments
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Appendix A. Supplementary data
Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuroimage.2010.01.018.

References


