

Spatiotemporal pattern of brain electrical activity related to immediate and delayed episodic memory retrieval

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ABSTRACT

In the present study we used the event-related brain potentials (ERP) technique and eLORETA (exact low-resolution electromagnetic tomography) method in order to characterize and compare the performance and the spatiotemporal pattern of the brain electrical activity related to the immediate episodic retrieval of information (words) that is being learned relative to delayed episodic retrieval twenty-minutes later. For this purpose, 16 young participants carried out an old/new word recognition task with source memory (word colour). The task included an *immediate memory phase* (with three study-test blocks) followed (20 min later) by a *delayed memory phase* with one test block. The behavioural data showed progressive learning and consolidation of the information (old words) during the immediate memory phase. The ERP data to correctly identified old words for which the colour was subsequently recollected (H/H) compared to the correctly rejected new words (CR) showed: (1) a significant more positive-going potential in the 500–675 ms post-stimulus interval (parietal old/new effect, related to recollection), and (2) a more negative-going potential in the 950–1850 ms interval (LPN effect, related to retrieval and post-retrieval processes). The eLORETA data also revealed that the successful recognition of old words (and probably retrieval of their colour) was accompanied by activation of (1) left medial temporal (parahippocampal gyrus) and parietal regions involved in the recollection in both memory phases, and (2) prefrontal regions and the superior temporal gyrus (in the *immediate* and *delayed memory phases* respectively) involved in monitoring, evaluating and maintaining the retrieval products. These findings indicate that episodic memory retrieval depends on a network involving medial temporal lobe and frontal, parietal and temporal neocortical structures. That network was involved in immediate and delayed memory retrieval and during the course of memory consolidation, with greater activation of some nodes (mobilization of more processing resources) for the delayed respect to the immediate retrieval condition.

1. Introduction

Episodic memory (EM), defined as a neurocognitive system that enables us to consciously recall past experiences (Tulving, 2002), has received increasing attention in cognitive, neuropsychological, psychophysiological and neuroimaging studies in the past decade (Rugg & Vilberg, 2013; Rugg & Yonelinas, 2003; Yonelinas, 2002). EM studies have provided insights into how information is acquired, organized and retrieved in long-term memory, by evaluating (1) encoding processes (or storage of new information involving changes in the strength and/or number of synaptic connections within the nervous system, known as memory traces), (2) consolidation (stabilization of memory traces

following the initial encoding), and (3) retrieval (i.e. recall of previously stored information) (Squire, Wixted, & Clark, 2007).

The *Standard Consolidation Theory* (SCT) (Squire & Alvarez, 1995) proposed that the encoding, consolidation and retrieval of memories are always dependent on direct connections between the hippocampal formation and neocortical regions; however, once consolidation stabilizes the memory traces, the retrieval of episodic memories is supported by activation of neocortical regions that are more independent of hippocampal formation, i.e. connections between hippocampal formation and neocortical regions become less critical for retrieving the stored information. However, this view was later questioned, and it is becoming more widely accepted that most memories never become

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independent of hippocampal formation (see Skelin, Kilianski, & McNaughton, 2019). The *Multiple Trace Theory* (MTT) (Nadel & Moscovitch, 1997) and the later *Trace Transformation Theory* (TTT) (Sekeres, Winocur, & Moscovitch, 2018) postulate that the repeated activation of memories creates new memory traces and that the retrieval of episodic memories (recent or remote) will always depend on activation of hippocampal formation.

The three aforementioned theories were proposed in relation to the *systems consolidation*. Two essential components of the consolidation process were proposed (Dudai, 2004; Dudai, Karni, & Born, 2015; Sekeres et al., 2018; Winocur & Moscovitch, 2011): (1) a cellular/synaptic component (*synaptic consolidation*, which is achieved within minutes to hours), related to early and rapid changes at local synaptic connections and cellular nodes in local neuronal assemblies. It is mediated by intracellular molecular mechanisms, and refers to the post-encoding transformation of information into a long-term form; and (2) a systems component (*systems consolidation*, with variation in its duration, from minutes to decades), which is associated with the post-encoding time-dependent reorganization of long-term memory representations over distributed (medial temporal-neocortical) networks. Both were considered as a part of a continuous and dynamic process, so that *synaptic consolidation* could be deemed as subroutines into *systems consolidation* process (Dudai et al., 2015).

Neuroimaging and behavioural studies in humans have demonstrated the importance of the medial temporal lobe (MTL) in episodic memory (Eichenbaum, Yonelinas, & Ranganath, 2007; Nadel & Moscovitch, 1997; Squire et al., 2007; Tulving, 2002). EM processes imply the continuous exchange of information in a network of brain areas centered on the medial temporal lobe (MTL) and neocortical regions (Battaglia, Benchenane, Sirota, Pennartz, & Wiener, 2011; Ison, Quiñero, & Fried, 2015). However, as far as we are aware, no previous studies have used a brain activity recording technique with high temporal resolution to disentangle the role of the MTL and neocortical regions in the successful episodic retrieval at different times across memory consolidation.

With the aim of addressing this lack of information, in the present study we applied exact low resolution tomography (eLORETA) software to event-related brain potential (ERP) data, obtained during two different conditions of successful EM retrieval: immediate and delayed (twenty minutes later).

The ERP technique, which has a high temporal resolution, has been widely used in psychophysiological studies to evaluate the time course of brain electrical activity during different EM processes. Recognition memory is commonly evaluated using old/new recognition tasks, in which participants must classify items as previously presented (old stimuli) or not presented (new stimuli, correct rejection). The difference between the ERPs elicited by correctly rejected new items (CR) and the ERPs elicited by correctly recognized old items (Hit) reflects EM retrieval phenomena (Friedman, 2013). Specifically, between 300 and 500 ms post-stimulus, a negative ERP component is observed at frontal and central scalp sites, with a smaller negative voltage in response to old stimuli than in response to new stimuli: this difference is commonly known as the *mid-frontal old/new effect* or *frontal N400 effect* -FN400- (Curran, 2000). Most evidence suggests that this effect is a correlate of familiarity, as variations in amplitude are observed depending on the familiarity confidence (Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010). Familiarity-based recognition is considered a fast-acting, relatively automatic process that does not provide qualitative information about the study episode (Rugg & Curran, 2007).

A parietal positive component is identified between 500 and 800 ms post-stimulus and with larger voltage in response to old stimuli than in response to new stimuli: this difference, which is commonly known as the *parietal old/new effect* (Wilding, Fraser, & Herron, 2005), is frequently larger at left scalp sites when the stimuli are words. This component has been associated with recollection, which is considered a slower and more effortful process than familiarity-based recognition

and which provides information about qualitative aspects of a prior event, including its context (Rugg & Vilberg, 2013). The *parietal old/new effect* shows amplitude modulations in recognition memory tasks that demand conscious recall of previously studied contextual details (source or context memory task). In particular, this effect has been found to have a larger amplitude in episodic relative to semantic (knowing facts) judgments (Macleod & Donaldson, 2017), in correct relative to incorrect source memory judgments (Macleod & Donaldson, 2017; Wilding & Rugg, 1996), and also when retrieval of a large amount of information is required (Vilberg, Moosavi, & Rugg, 2006). However, some evidence suggests that variations in the magnitude of the *parietal old/new effect* might not always predict variations in episodic recollection between participants (Macleod & Donaldson, 2017).

Another two late onset old/new ERP effects have been identified from 600 ms onwards: (1) *the right frontal old/new effect* (RFE), whereby old stimuli elicit a larger positive voltage than new stimulus over right frontal scalp sites. Evidence suggests that the RFE indicates monitoring and evaluation processes that act on the retrieval products (Cruse & Wilding, 2009); and (2) *the late posterior negativity* (LPN) effect, which shows the opposite pattern over parieto-occipital scalp sites, i.e. old stimuli elicit a more negative-going voltage than new stimuli. Evidence suggests that LPN may reflect mnemonic processes involved in the reconstruction of a previous study episode when some item attribute is not readily retrieved or when the information retrieved needs additional evaluation, and/or non-mnemonic processes of monitoring that act in highly demanding tasks (Sommer, Vita, & De Pascalis, 2018; for a review see Mecklinger, Rosburg, & Johansson, 2016).

In the present ERP study, we evaluated the old/new ERP effects in an old/new word recognition task with source memory (i.e. the colour of the old word) to characterize the spatiotemporal pattern of the brain electrical activity during the immediate and the delayed EM retrieval. Some previous studies have evaluated the old/new ERP effects in young adults, also using an old/new recognition task with words, with different temporal intervals from the study task to the recognition test: immediately (Wang, de Chastelaine, Minton, & Rugg, 2012), one minute (see experiment one of Macleod & Donaldson, 2017), 39 min (Wolk et al., 2006), one week (see experiment two of Macleod & Donaldson, 2017) and one day (Wolk et al., 2006). However, as far as we are aware, only one study (Wolk et al., 2006) have evaluated within the same experiment the old/new ERP effects using different study-test delay intervals: 39 min *versus* one day. In the aforementioned study, the researchers did not observe any differences in the ERP parameters (obtained in response to correctly recognized old or new words) between both delay conditions; moreover, although they identified the *mid-frontal* and *parietal old/new effects* in each delay condition, they did not evaluate the brain areas involved in these effects.

Although the spatial resolution of ERPs is lower than in the functional magnetic resonance imaging (fMRI) technique, two studies have previously evaluated the spatiotemporal pattern of the brain activity related to the old/new effects (Alhaj, Massey, & McAllister-Williams, 2006; Kim et al., 2009), by applying the LORETA brain source estimation algorithm (Pascual-Marqui, Michel, & Lehmann, 1994, 2011) to ERP data. In both studies, participants performed an old/new recognition task with source memory, in which words were used as stimuli and the gender of the voice that spoke the words as the source to remember. These studies demonstrated the involvement of multiple brain areas in the successful immediate retrieval, at around 600–700 ms post-stimulus, specifically in the hippocampus, the right inferior parietal lobe, and also some regions of the superior temporal and frontal cortex. EM studies using fMRI, a technique with a much lower temporal resolution than ERP, showed high consistency in the same activated brain areas identified in the aforementioned studies in which LORETA was applied to ERP data (Bergström et al., 2013; Eichenbaum et al., 2007; Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Rugg et al., 2002; Scalici, Caltagirone, & Carlesimo, 2017; Vilberg & Rugg, 2008).

In summary, evaluation of old/new ERP effects allows us to assess

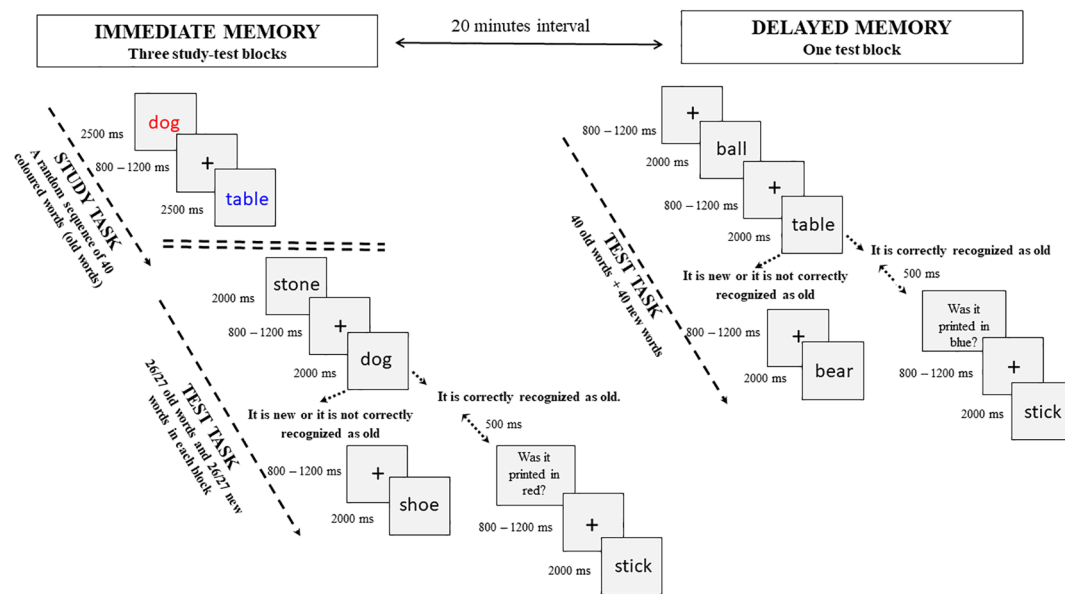


Fig. 1. Task scheme.

changes in the brain electrical activity related to immediate and delayed EM retrieval, as well as to delimit, with a good temporal resolution, the temporal ranges (considering the latency of these effects) within which we can estimate the network of different brain areas involved. Moreover, we considered that the neural data obtained (with good temporal resolution) might shed some light on the role of MTL and neocortical regions in different times of memory consolidation and retrieval processes.

In the present study, we used an old/new word recognition task with source memory (word colour) to compare the performance and the spatiotemporal patterns of brain electrical activity during successful EM retrieval in an *immediate memory phase* (with three study-test blocks) and in a *delayed memory phase* (with a test presented twenty minutes later). Previous studies showed that the presentation of multiple study-test blocks (as in the *immediate memory phase* of the present study) improved the old/new discrimination ability of young adults when they had to recognize symbols (De Chastelaine, Friedman, Cycowicz, & Horton, 2009) and words (Jacoby, Jones, & Dolan, 1998). This improvement was reflected not only by an increase of the old/new discrimination accuracy across test repetitions (De Chastelaine et al., 2009; Jacoby et al., 1998) but also by a reduction in the reaction times during the recognition of old and new items (De Chastelaine et al., 2009).

The specific aims of the study were as follows:

- (1) To compare performance between the *immediate memory phase* and the *delayed memory phase*.
- (2) To identify and evaluate the old/new ERP effects in each memory phase (*immediate and delayed*) and to compare these between both phases.
- (3) To apply eLORETA to the intervals of the old/new ERP effect identified in order to determine:
 - a. Which brain areas are more activated during the successful EM retrieval of old words relative to the correct identification of new words, in each memory phase (*immediate and delayed*).
 - b. Which brain areas are activated differently between both memory phases, during the successful retrieval of old words and during the correct identification of new words.
 - c. The involvement of MTL and neocortical regions (e.g. prefrontal cortex and posterior parietal cortex) during the successful retrieval of old words, in each memory phase.

In line with previous studies that revealed an increase in the old/new discrimination ability in young adults during the presentation of multiple study-test blocks (De Chastelaine et al., 2009; Jacoby et al., 1998), we expected to observe a learning process of the old words across the three study/test blocks of the *immediate memory phase*, demonstrated behaviourally by (1) a gradual improvement in the performance across the blocks, and (2) no differences between the third block of the *immediate memory phase* and the test of the *delayed memory phase*, which would indicate that early consolidation is maintained during the 20-minute delay interval (during which participants had to perform a visuospatial working memory task: see Task in Method section). On the other hand, we expected to find the following in both memory phases: (1) *old/new ERP effects*, especially in the temporal ranges of the *mid-frontal old/new effect* related to the familiarity and the *parietal old/new effect* related to the recollection; and (2) greater activation of the MTL and neocortical regions during the retrieval of old words relative to the correct identification of new words.

2. Materials and method

2.1. Participants

Sixteen university students (8 women, 8 men) between 18 and 25 years old (mean age: 21 years old, SD: 2.1) participated voluntarily in the study. All participants had normal audition and normal or corrected to normal vision, and none had any history of neurological or psychiatric disorders. All participants were right-handed, as evaluated by the Edinburgh Handedness Inventory (Oldfield, 1971), and all of them gave their written informed consent prior to participation in the study. The research project was approved by the Galician Clinical Research Ethics Committee (Xunta de Galicia, Spain) and was performed in accordance with the ethical standards established in the 1964 Declaration of Helsinki (Lynöe, Sandlund, Dahlqvist, & Jacobsson, 1991).

2.2. Task and stimuli

2.2.1. Task

During the electroencephalographic (EEG) recording, participants performed an old/new word recognition task with source memory (word colour) and formed by an *immediate memory phase* and a *delayed memory phase* (see Fig. 1). A practice block with five words was presented before the task, to ensure that participants had understood and

performed the task correctly.

The *immediate memory phase* consisted of three study-test blocks, with an inter-block rest interval of 2–3 min. In the study task, the same list of 40 words (names of living beings and common objects), printed in red or blue, were randomly presented across blocks. Participants were instructed to memorize the word and the colour in which it was printed and to simultaneously make a judgment about whether the words represented living/non-living things and to respond by pressing as quickly and accurately as possible one of two different buttons on a CEDRUS Model RB-834 device (left button: index finger; right button: middle finger). The test began immediately after the study task. During each test, 26 or 27 words that had been presented in the study task (old words) were randomly interspersed with 26 or 27 new words, both printed in black (Block 1: 26 old/26 new; Block 2: 26 old/26 new; Block 3: 27 old/27 new). Thus, a total of 79 new words and 79 old words (the 40 old words presented in the study task were repeated twice, except for one word) were presented in all three tests. Participants were instructed to decide whether the word was old or new and to respond by pressing (as quickly and accurately as possible) one of two buttons (left button: index finger; right button: middle finger), depending on the category of the word: “old” if it had been presented in the study task or “new” if it had not. If the word was correctly recognized as old, participants were required to respond 500 ms later to the question “was it printed in blue?” or “was it printed in red?”, by pressing the same buttons as before (yes/no).

After finishing the third block of the *immediate memory phase*, participants performed a different task (visuospatial working memory task, lasting 20 min, with non-verbal visual stimuli). After a short rest interval, an unexpected delayed memory test (*delayed memory phase*) was presented. In this phase, the 40 old words (memorized during the study task of the three blocks of the *immediate memory phase*) were randomly interspersed with 40 new words. All words were printed in black and participants were again instructed to press one of two different response buttons corresponding to old/new and, for correctly recognized old words, to answer the question about the colour in which words were printed in the study tasks (red or blue). Response buttons (yes/no) during the *immediate* and *delayed memory phases* were counterbalanced among participants.

2.2.2. Stimuli

A total of 159 words were selected from two Spanish word databases: APO –“Animal-Persona-Objeto”– (Ferré, Guasch, Moldovan, & Sánchez-Casas, 2012) and EsPal (Duchon, Perea, Sebastián-Gallés, Martí, & Carreiras, 2013). The words were presented in lower case and Chicago font (size 80: red or blue for the study task and black for the test) on a light grey background and were displayed in the centre of a 17-inch flat monitor located at a distance of one metre from the participant. In the study task, the duration of each stimuli was 2500 ms, and a random inter-stimulus interval of between 800 and 1200 ms was used. In the test, each stimulus lasted up to 2000 ms (the word disappeared from the monitor screen when the participant pushed the response button), and the duration of the inter-stimulus interval was between 800 and 1200 ms. In the study task and the test, a black cross was presented in the centre of the monitor on a light grey background during the inter-stimulus interval, and the participants were instructed to keep their gaze fixed on the cross.

The 159 words (of which 80 referred to living beings and 79 to non-living items) were selected according to the following criteria: valence, arousal and familiarity of the word in the context of Spanish speech, degree of concreteness, frequency of use and length.

2.3. EEG recording

Participants were seated on a comfortable chair in an electrically shielded room, with attenuated levels of light and noise, and were instructed to move as little as possible during the recording. EEG activity

was recorded with a Brain Vision Recorder device, via 60 active electrodes placed in an elastic cap (EasyCap, GmbH), according to the International 10–10 system. All electrodes were referenced to an electrode attached to the tip of the nose and an electrode positioned at Fpz served as a ground. The horizontal electro-oculogram (HEOG) was recorded via two electrodes placed at the outer canthi of both eyes, whereas the vertical EOG (VEOG) was recorded via two electrodes placed supra and infraorbitally to the right eye. The EEG was continuously digitized at a rate of 500 Hz (bandpass filter 0.01–100 Hz) and electrode impedances were maintained below 10 k Ω .

Once the signal was stored, the EEG data were exported to Matlab (R2017a version) and processed using EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014). The signal was passed through a digital 0.1–30 Hz (12 dB/octave slope) bandpass filter, and ocular artefacts were corrected off-line by Independent Component Analysis (ICA). In order to study the brain activity related to test blocks of the *immediate* and *delayed memory phases*, the EEG was then segmented by extraction of epochs from –200 to 2000 ms post stimuli, only for correctly recognized old words and with correct colour recollection (Hit/Hit, H/H), and for correctly rejected new words (CR). All epochs were corrected to the mean voltage of 200 ms pre-stimulus recording period, and EEG segments exceeding $\pm 100 \mu\text{V}$ were automatically rejected. EEG corresponding to old words that were correctly recognized without posterior colour recollection (Hit/Miss, H/M) were not analyzed in the present study because the number of epochs for the averages in each phase (*immediate* and *delayed*) was insufficient (< 20 epochs). The mean number of averaged epochs (SD: standard deviation) for each phase was as follows: *Immediate memory phase*: 46.9 (± 9.4) for H/H and 65.6 (± 11.2) for CR; *Delayed memory phase*: 27.8 (± 5.2) for H/H and 34.6 (± 4.2) for CR. EEG related to each study block were not analyzed.

2.4. Procedure

2.4.1. Data analysis

2.4.1.1. Behavioural data. Reaction times (RT, between the onset of the word and pressing the key) and the percentage of responses were recorded in the following experimental conditions: H/H, H/M, CR, errors in the recognition of old words (as they were considered new words), false alarms (new words were considered old words) and misses (response omissions). In the present study we only evaluated the responses: H/H, H/M and CR.

2.4.1.2. ERPs data. The same ERP components were identified in the grand-average ERP waveforms of the *immediate* and *delayed memory phases*. All ERP waveforms included a positive followed by a negative peak at about 100 and 200 ms (P100 and N170 components) respectively, but only the ERP components identified from 200 ms onwards were analyzed. The associated parameters (amplitude and latency) were evaluated in different temporal ranges determined from the grand-average ERP waveforms.

The following ERP components were evaluated: a negative component, with maximal amplitude at frontal scalp sites, in the 200–500 ms post-stimulus interval (coinciding with the temporal range described in the literature for the *mid-frontal old/new effect* or *FN400 effect*), and a positive component with maximal amplitude at parietal scalp sites, in the 400–900 ms post-stimulus interval (coinciding with the temporal range described in the literature for the *parietal old/new effect*). Mean amplitudes were measured for both components considering an interval around the peak, which was estimated at the electrode sites where the amplitude of each component was largest: at Fz for the frontal negative component, and at Pz for the parietal positive component. In the *immediate memory phase*, the mean amplitude of the frontal negative component was measured in the 250–350 ms interval (considering ± 50 ms around the peak), and the mean amplitude of the parietal positive component in the 500–650 ms interval (considering ± 75 ms

around the peak in the ERP waveforms to the old words). Similar measurements were made in the *delayed memory phase*, although with slightly different temporal intervals compared to the *immediate memory phase* due to slight differences in the latency of the peak amplitude: 270–370 ms (± 50 ms around the peak) for the frontal negative component and 525–675 ms (± 75 ms around the peak) for the parietal positive component. Mean amplitudes of both components were evaluated at the following electrode clusters (scalp regions of interest -ROI- for statistical analyses), previously employed in the literature (Voss & Federmeier, 2011): Mid frontal (F1, Fz, F2, FC1, FCz, FC2, C1, Cz, C2), mid posterior (CP1, CPz, CP2, P1, Pz, P2, POz), left posterior (TP7, CP5, CP3, P7, P5, P3, PO7, PO3) and right posterior (TP8, CP6, CP4, P8, P6, P4, PO8, PO4).

In addition, the 50% fractional area latency was also estimated for both components. This involved computing the area under the ERP waveform over a given latency range and then finding the time point that divides the area into a 50% fraction (Luck, 2014). The latency range for calculation of the area of each component was established observing the grand-average ERP waveforms comprising the complete duration of the component (onset to end). Fractional area latency was evaluated for the frontal negative component and the parietal positive component at those electrodes where these components showed maximal amplitude, that is, Fz for the frontal negative component and Pz for the positive parietal component. In both memory phases of the task (*immediate* and *delayed memory phases*), the latency of the frontal negative component for both conditions (H/H and CR) was estimated in the 200–500 ms interval. In addition, the latency of the parietal positive component was estimated: (1) in the *immediate memory phase*, using different temporal intervals for the H/H (400–850 ms) and CR (400–900 ms) conditions, and (2) in the *delayed memory phase*, using the 350–900 ms interval for both conditions (H/H and CR).

The LPN was identified at parieto-occipital locations, i.e. from 800 ms onwards in the *immediate memory phase*, and from 950 ms onwards in the *delayed memory phase*. In order to evaluate this component in both conditions (H/H and CR), mean amplitudes were also measured at the four ROIs aforementioned (mid frontal, mid posterior, left posterior and right posterior), in seven temporal windows (each of 150 ms) between 950 and 2000 ms post-stimuli, in the *immediate* and *delayed memory phases*.

Voltage maps were also obtained for topographic analysis of the frontal negative component, the parietal positive component and the LPN, in each phase (*immediate* and *delayed*) and condition (H/H and CR). The voltage maps were calculated in the temporal ranges where the mean amplitudes of these components were identified.

2.4.1.3. Brain source localization analysis. Exact low-resolution electromagnetic tomography (eLORETA) software (publicly available, free academic software, at <http://www.uzh.ch/keyinst/loreta.htm>) was used to estimate cortical sources of EEG activity (recorded at 60 scalp electrodes) in the intervals where the frontal negative component, the parietal positive component, and the LPN were identified for the H/H and CR conditions during both phases of the task.

This software is a three-dimensional, discrete, linear, weighted minimum norm inverse solution method that estimates the sources of EEG recorded on the scalp. A 3 shell-spherical head model is used as a reference (using the Talairach human brain atlas) and is divided in 6239 voxels at a spatial resolution of 5 mm. eLORETA represents the electrical activity at each voxel in neuroanatomical Montreal Neurological Institute (MNI) space, although Talairach coordinates, anatomical structures and Brodmann areas are also provided. For a more detailed description of the method and the exact zero-error localization property, see Pascual-Marqui et al. (2011).

2.5. Statistical analysis

2.5.1. Behavioural data

Regarding the *immediate memory phase*, repeated measures analysis of variance (ANOVA) with two within-subject factors, *Condition* (three levels: H/H, H/M, CR) and *Test Block* (three levels: first, second and third), was conducted to compare the percentage of responses and the RTs among H/H, H/M, CR conditions and across the three test blocks. Regarding the *delayed memory phase*, a repeated measures ANOVA with one within-subject factor, *Condition* (three levels: H/H, H/M, CR), was used to compare the percentage of responses and the RTs among the three conditions. In addition, paired-sample *t*-tests were used to compare the RTs and the percentage of H/H responses, between the third test block of the *immediate memory phase* and the test of the *delayed memory phase*.

2.5.2. ERPs data

Repeated measures ANOVAs with three within-subject factors, *Phase* (two levels: Immediate, Delayed), *Condition* (two levels: H/H, CR) and *ROI* (four levels: mid frontal, mid posterior, left posterior, right posterior), were conducted in order to compare, between phases and conditions and among ROIs, the mean amplitudes of the frontal negative component and the parietal positive component.

In the case of the LPN, a repeated measures ANOVA with four within-subject factors *Phase* (two levels: Immediate, Delayed), *Condition* (two levels: H/H, CR), *ROI* (four levels: mid frontal, mid posterior, left posterior, right posterior) and *Interval* (seven levels: 950–1100 ms, 1100–1250 ms, 1250–1400 ms, 1400–1550 ms, 1550–1700 ms, 1700–1850 ms and 1850–2000 ms) was performed in order to compare the mean amplitude between phases and conditions, and among ROIs and temporal intervals.

In addition, fractional area latency was evaluated via a repeated measures ANOVA with two within-subject factors, *Phase* (two levels: Immediate, Delayed) and *Condition* (two levels: H/H, CR) in order to compare, between phases and conditions, the latencies of the frontal negative component (at Fz) and the parietal positive component (at Pz).

Greenhouse-Geisser corrections to the degrees of freedom were applied in all cases in which the condition of sphericity was not met. In these cases, the original degrees of freedom are presented together with the corrected *p* and ϵ values. When the ANOVAs showed significant effects of the factors and/or their interactions for the behavioural or ERP data, post-hoc testing of the mean values was carried out by paired multiple comparisons (with Bonferroni corrections). In addition, partial eta squared (η^2_p) was calculated for each significant comparison, with the aim of determining the size of the effects. Statistical significance was considered to be $p \leq 0.05$. The statistical analyses were performed with IBM SPSS Statistics package v.21 for Windows.

2.5.3. Brain source localization analysis

The eLORETA software package was used to perform (voxel-by-voxel) within-subject comparisons. This non-parametric method is based on estimation, via randomization, of the empirical probability distribution for the max-statistic under the null hypothesis, and it corrects for multiple testing (Nichols & Holmes, 2002). The following statistical comparisons were made: (1) H/H relative to CR conditions, in each memory phase (*immediate* and *delayed*), in order to compare the activation of neural sources between both conditions, and (2) *immediate* relative to *delayed* memory phases for each condition (H/H and CR), in order to compare activation of neural sources between both memory phases, for the correctly recognized old words (which were posteriorly accompanied by correct colour recollection, H/H) and for the correctly rejected new words (CR). These comparisons were performed (1) in both temporal ranges in which the frontal negative and the parietal positive components were identified: the 200–500 ms interval and 400–900 ms interval, respectively, and (2) in the 1200–1600 ms interval, around which the maximum amplitude differences between

Table 1

Mean values and standard deviations (between parentheses) for the percentage of responses (%) and the reaction times (RTs, ms), in each condition: Hit/Hit (H/H), Hit/Miss (H/M) and Correct Rejection (CR), errors to old words, false alarms and misses.

	Immediate Phase						Delayed Phase			
	Test-Block 1		Test-Block 2		Test-Block 3		Mean Test Blocks		Delayed test	
	%	RT	%	RT	%	RT	%	RT	%	RT
H/H	54.8 (11.5)	872 (129)	68.7 (9.5)	792 (140)	75.0 (13.7)	722 (136)	66.2 (8.4)	796 (124)	75.8 (11.0)	698 (110)
H/M	31.7 (14.6)	896 (215)	23.3 (11.3)	795 (156)	19.4 (12.3)	716 (167)	24.8 (10)	802 (145)	18.7 (9.8)	718 (142)
CR	86.5 (9.6)	921 (141)	92.8 (8.3)	789 (121)	98.2 (3.8)	705 (98)	92.5 (6.2)	805 (102)	97.0 (3.1)	686 (101)
ERRORS TO OLD WORDS	6.7 (8.4)	857 (219)	3.9 (5.3)	1084 (412)	2.8 (4.6)	769 (200)	4.5 (5.6)	873 (256.4)	2.8 (4.7)	783 (164)
FALSE ALARMS	7.2 (7.1)	1067 (287)	2.9 (3.6)	766 (202)	0.2 (0.9)	- ^a	3.4 (3.2)	- ^b	1.9 (2.5)	775 (210)
MISSES TO OLD WORDS	6.7 (9.1)		4.1 (4.3)		2.8 (4.2)		4.5 (4.6)		2.7 (4.5)	
MISSES TO NEW WORDS	6.3 (10)		4.3 (8.5)		1.6 (3.8)		4.1 (7.0)		1.1 (2.7)	

^a Mean and standard deviation of the mean reaction time to false alarms in the third test block were not calculated because there was only one participant with one false alarm in that block of the task.

^b Mean and standard deviation of the mean reaction times to false alarms was not calculated because most of participants did not have false alarms in one or more test blocks.

conditions (H/H and CR) were observed for LPN, in based on the grand-average ERP waveforms of the immediate memory phase (in which a significant LPN was obtained, see Results section). Statistical comparisons between conditions or phases, for the current density distribution, were estimated using paired sample *t*-test. Statistical significance was considered to be $p \leq 0.05$.

3. Results

3.1. Performance

The mean values of RTs and the percentage of responses in each condition (H/H, H/M, CR, errors to old words, false alarms and misses) are shown in Table 1. Mean values of RTs and the percentage of responses in H/H, H/M and CR are represented in Fig. 2.

3.1.1. Reaction times

Regarding the *immediate memory phase*, the repeated-measures ANOVA (Test Block \times Condition) showed a significant effect of the *Test Block* factor ($F(2,30) = 26.4, p < 0.001, \epsilon = 0.71; \eta^2p = 0.63$). *Post hoc* comparisons showed that the mean RT in the three conditions was significantly longer in the first than in the second ($p = 0.002$) and the third ($p < 0.001$) test blocks, and significantly longer in the second than in the third ($p = 0.001$) test block. No significant differences were

observed for the RTs between the H/H, H/M and CR conditions in each phase, nor between the third test block of the *immediate memory phase* and the test of the *delayed memory phase* in the H/H condition.

3.1.2. Percentage of responses

Regarding the *immediate memory phase*, the repeated measures ANOVA (Test Block \times Condition) showed a significant effect of the *Test Block* factor ($F(2,30) = 37.7, p < 0.001, \epsilon = 0.72, \eta^2p = 0.71$), *Condition* factor ($F(2,30) = 189.7, p < 0.001, \epsilon = 0.61, \eta^2p = 0.93$) and of the *Test Block* \times *Condition* interaction ($F(4,60) = 11.3, p < 0.001, \epsilon = 0.51, \eta^2p = 0.43$). *Post hoc* comparisons revealed that the percentage of CR and H/H responses was significantly lower in the first than in the second and third test blocks [CR first vs second: $p = 0.03$, first vs third: $p < 0.001$] [H/H first vs second: $p = 0.003$, first vs third: $p = 0.001$], and the percentage of CR responses was also significantly lower in the second than in the third test block ($p = 0.008$). In addition, the percentage of H/M responses was significantly higher in the first than in the third test block ($p = 0.03$).

In the three blocks, the percentage of CR responses was significantly higher than the percentage of H/H and H/M responses [CR versus H/H in first block: $p < 0.001$, second block: $p < 0.001$, third block: $p < 0.001$] [CR versus H/M in the first block: $p < 0.001$, second block: $p < 0.001$, third block: $p < 0.001$], and the percentage of H/H responses was significantly higher than the percentage of H/M

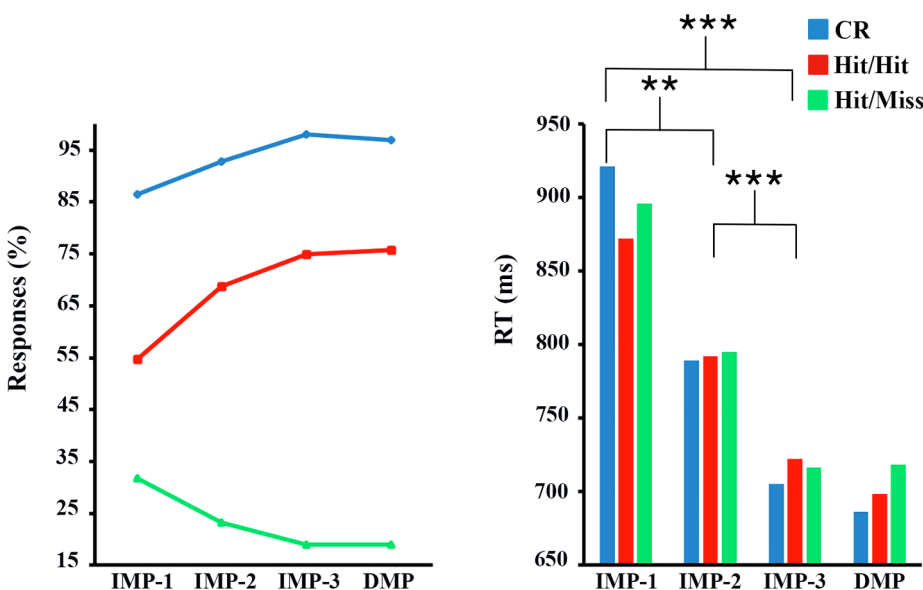
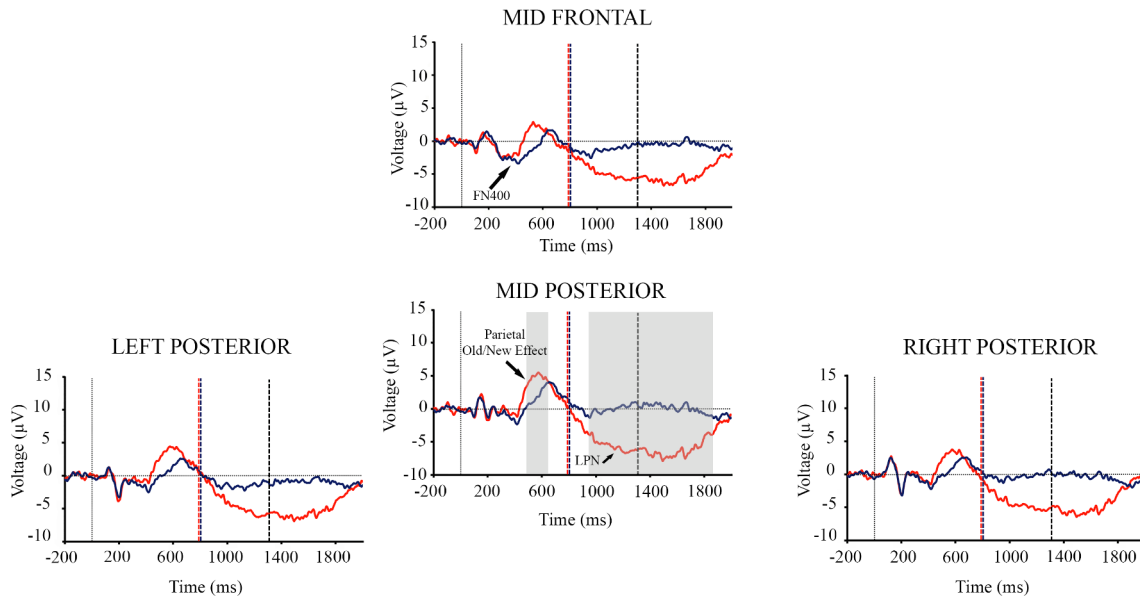


Fig. 2. Mean values of the percentage of responses (left) and reaction times (RTs, right) in each condition: correct recognition of old words with retrieval of their colour (Hit/Hit), correct rejection of new words (CR) and correct recognition of old words without retrieval of their colour (Hit/Miss). IMP-1: Immediate memory phase-Test 1; IMP-2: Immediate memory phase-Test 2; IMP-3: Immediate memory phase-Test 3; DMP: Delayed memory phase test. ** $p < 0.01$, *** $p < 0.001$.

IMMEDIATE MEMORY PHASE



DELAYED MEMORY PHASE

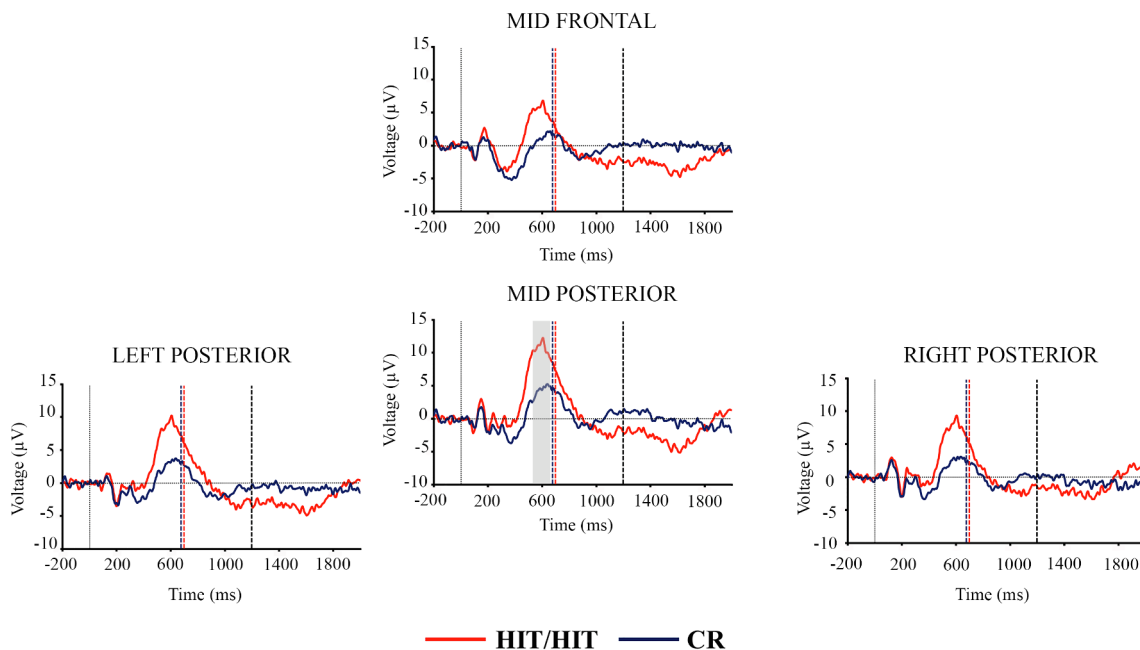


Fig. 3. Grand-average ERP waveforms at the mid frontal, mid posterior, left posterior and right posterior electrode clusters in the H/H and CR conditions, during the *immediate memory phase* and *delayed memory phase*. The red and blue dotted lines represent the mean RT of the H/H and CR conditions, respectively. The black dashed line represents the mean time of the presentation of the colour question. The grey shaded area represents intervals with significant results.

responses (first block: $p = 0.006$, second block: $p < 0.001$, third block: $p < 0.001$).

Regarding the *delayed memory phase*, the repeated measures ANOVA (Condition) revealed a significant effect of the factor ($F(2,30) = 248.7$, $p < 0.001$, $\eta^2p = 0.9$), as the percentage of CR responses was significantly higher than the percentage of H/H ($p < 0.001$) and H/M ($p < 0.001$) responses, and the percentage of H/H was significantly higher than the percentage of H/M responses ($p < 0.001$).

The percentage of H/H responses was not significantly different between the third test block of the *immediate memory phase* and the test of the *delayed memory phase*.

3.2. Event-related potentials (ERPs)

Grand-average ERP waveforms for the H/H and CR conditions at mid frontal, mid posterior, left posterior and right posterior ROIs in the *immediate* and *delayed memory phases*, are shown in Fig. 3, and the voltage maps are shown in Fig. 4. Mean amplitude and fractional latency results for the frontal negative component and the positive parietal component are summarized in Table 2. Mean amplitude results for the LPN are summarized in Table 3.

For the amplitude of the frontal negative component, the repeated measures ANOVA (Phase \times Condition \times ROI) showed a significant

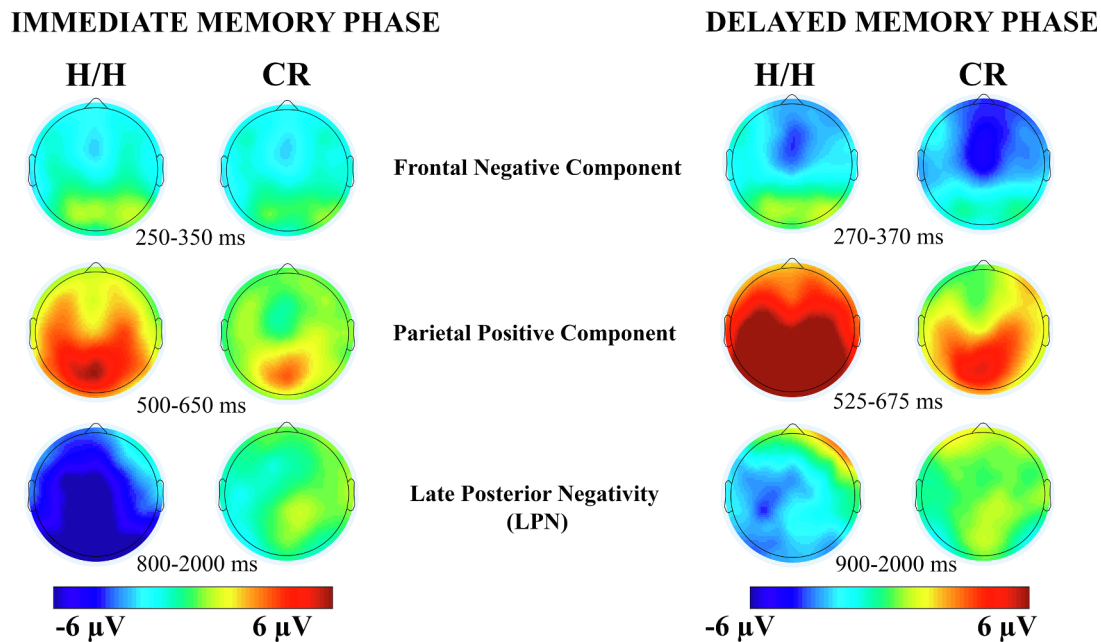


Fig. 4. Voltage maps for the mean amplitude of the frontal negativity component (top), the parietal positive component (middle) and the late posterior negativity (LPN, bottom), in the H/H and CR conditions, during the *immediate and delayed memory phases*.

Table 2

F values in repeated measures ANOVA (Phase × Condition × ROI) for the mean amplitudes and 50% fractional area latencies of the frontal negative component and the parietal positive component.

	Frontal negative component	Parietal positive component
Mean Amplitude		
ANOVA (P × C × R)		
P	1.4, $\eta^2_p = 0.09$	4.6*, $\eta^2_p = 0.24$
C	4.4, $\eta^2_p = 0.23$	24.2***, $\eta^2_p = 0.62$
R	7.3***, $\eta^2_p = 0.33$	11.2***, $\eta^2_p = 0.43$
P × C	1.4, $\eta^2_p = 0.08$	6.5*, $\eta^2_p = 0.30$
P × R	5.1*, $\epsilon = 0.56$; $\eta^2_p = 0.25$	10.8***, $\eta^2_p = 0.42$
C × R	0.8, $\epsilon = 0.52$; $\eta^2_p = 0.05$	2.8, $\epsilon = 0.71$; $\eta^2_p = 0.16$
P × C × R	0.1, $\epsilon = 0.51$; $\eta^2_p = 0.006$	2.4, $\epsilon = 0.56$; $\eta^2_p = 0.14$
Fractional Area Latency		
ANOVA (P × C)		
P	2.2, $\eta^2_p = 0.13$	0.003, $\eta^2_p < 0.001$
C	0.7, $\eta^2_p = 0.04$	11.2**, $\eta^2_p = 0.43$
P × C	3.6, $\eta^2_p = 0.2$	0.95, $\eta^2_p = 0.06$

P: Phase factor; C: Condition factor; R: ROI factor; ϵ = epsilon, η^2_p = partial eta squared value. Degrees of freedom for: P: 1,15; C: 1,15; R: 3,45 and the interactions P × C: 1,15; P × R: 3,45; C × R: 3,45; P × C × R: 3,45. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$

effect of the ROI factor and the Phase × ROI interaction. Post hoc comparisons revealed that, during the *immediate memory phase*, the amplitude was significantly more negative at the mid frontal than at the mid posterior ($p = 0.007$) and the right posterior ($p = 0.047$) ROIs. In addition, during the *delayed memory phase*, it was significantly more negative at the mid frontal than at the mid posterior ($p = 0.003$), the left posterior ($p = 0.044$) and the right posterior ($p = 0.008$) ROIs.

The repeated measures ANOVA (Phase × Condition) did not show any significant effect of the factors or their interaction for the latency of the frontal negative (FN400) component.

For the amplitude of the parietal positive component, the repeated measures ANOVA (Phase × Condition × ROI) showed a significant effect of the Phase, Condition and ROI factors as well as the Phase × Condition and the Phase × ROI interactions. Post hoc

Table 3

F values in repeated measures ANOVA (Phase × Condition × ROI × Interval) for the mean amplitudes of the LPN in seven temporal windows of 150 ms.

	Late Posterior Negativity (LPN)
Mean Amplitude	
ANOVA (P × C × R × I)	
P	9.4**, $\eta^2_p = 0.39$
C	12.1**, $\eta^2_p = 0.45$
R	2.6, $\eta^2_p = 0.15$
I	2.4, $\eta^2_p = 0.14$
P × C	10.6**, $\eta^2_p = 0.41$
P × R	1.7, $\eta^2_p = 0.10$
P × I	0.8, $\eta^2_p = 0.47$
C × R	3.7*, $\epsilon = 0.55$; $\eta^2_p = 0.20$
C × I	8.8***, $\epsilon = 0.42$; $\eta^2_p = 0.37$
R × I	2.1**, $\eta^2_p = 0.12$
P × C × R	2.9, $\eta^2_p = 0.16$
P × C × I	0.5, $\eta^2_p = 0.03$
P × R × I	1.5, $\eta^2_p = 0.09$
C × R × I	6.5***, $\eta^2_p = 0.30$
P × C × R × I	1.1, $\eta^2_p = 0.07$

P: Phase factor; C: Condition factor; R: ROI factor; I: Interval; ϵ = epsilon, η^2_p = partial eta squared value. Degrees of freedom for: P: 1,15; C: 1,15; R: 3,45; I: 6,90 and the interactions P × C: 1,15; P × R: 3,45; C × R: 3,45; P × C × R: 3,45; P × I: 6,90; C × I: 6,90; P × C × I: 6,90; R × I: 18,270; P × R × I: 18,270; C × R × I: 18,270; P × C × R × I: 18,270. * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

comparisons revealed that the mean amplitude was significantly larger: (1) in the H/H than in the CR condition in both memory phases (*immediate*: $p = 0.005$, *delayed*: $p < 0.001$), indicating a significant *parietal old/new effect*; (2) at the mid posterior than at the mid frontal ROI ($p = 0.005$) during the *immediate memory phase*, (3), at the mid posterior than at the mid frontal ($p < 0.001$) and the right posterior ($p = 0.01$) ROI, and at the left posterior than at the mid frontal ROI ($p = 0.02$), during the *delayed memory phase*; (4) in the *delayed* than in the *immediate memory phase* ($p = 0.02$), in the H/H condition; and (5) in the *delayed* than in the *immediate memory phase* in the mid posterior ($p = 0.03$) and left posterior ($p = 0.03$) ROIs.

For the parietal positive component latency, the repeated measures ANOVA (Phase × Condition) showed a significant effect of the

Condition factor. Post hoc comparisons revealed that the latency was significantly shorter in the H/H than in the CR condition ($p = 0.004$).

For the LPN mean amplitude, the repeated measures ANOVA (Phase \times Condition \times ROI \times Interval) showed a significant effect of the *Phase* and *Condition* factors, as well as the following interactions: *Phase* \times *Condition*, *Condition* \times *ROI*, *Condition* \times *Interval*, *ROI* \times *Interval*, and *Condition* \times *ROI* \times *Interval*.

Post hoc comparisons revealed that the mean amplitude of LPN was significantly more negative in the H/H condition than in the CR condition ($p = 0.001$) in the *immediate memory phase*; and no significant differences were obtained between both conditions ($p = 0.07$) in the *delayed memory phase*, although the differences were in the same direction (H/H more negative than CR). In addition, the mean amplitude of the H/H condition was significantly more negative in the *immediate* than in *delayed memory phase* ($p = 0.002$).

On the other hand, post hoc comparisons also revealed that the mean amplitude in the H/H condition was significantly more negative than the CR condition, at the following ROIs and intervals: (1) Mid frontal locations, in the 950–1100 ms ($p = 0.004$), 1100–1250 ms ($p = 0.001$), 1250–1400 ms ($p = 0.001$), 1400–1550 ms ($p < 0.001$), 1550–1700 ms ($p = 0.002$), 1700–1850 ($p = 0.017$) intervals; (2) Mid posterior locations, in the 950–1100 ms ($p = 0.001$), 1100–1250 ms ($p < 0.001$), 1250–1400 ms ($p < 0.001$), 1400–1550 ms ($p = 0.001$), 1550–1700 ms ($p = 0.002$), 1700–1850 ($p = 0.049$) intervals; (3) Left posterior locations, in the 950–1100 ms ($p = 0.017$), 1100–1250 ms ($p = 0.002$), 1250–1400 ms ($p = 0.002$), 1400–1550 ms ($p = 0.003$), 1550–1700 ms ($p = 0.007$) intervals and (4) Right posterior locations, in the 950–1100 ms ($p = 0.001$), 1100–1250 ms ($p = 0.001$), 1250–1400 ms ($p = 0.001$), 1400–1550 ms ($p = 0.005$) and 1550–1700 ms ($p = 0.018$) intervals.

In addition, post hoc comparisons revealed that the mean amplitude of LPN in the H/H condition was significantly more negative: (1) at the left posterior than at the right posterior locations in the 1250–1400 ms interval ($p = 0.031$) and the 1850–2000 ms interval ($p = 0.041$), and (2) at the mid posterior and the left posterior than the right posterior locations in the 1550–1700 ms interval ($p = 0.002$ and $p = 0.016$, respectively) and in the 1700–1850 ms interval ($p = 0.037$ and $p = 0.012$, respectively).

The mean amplitude of LPN in the CR condition was significantly more negative: (1) at the left posterior than at the mid posterior locations during the 950–1100 ms ($p = 0.018$) and the 1100–1250 ms ($p = 0.005$) intervals, (2) at the mid frontal ($p = 0.049$) and at the left posterior ($p = 0.003$) than at the mid posterior locations, as well as at the left posterior than at the right posterior locations ($p = 0.05$), during the 1250–1400 ms, and (3) at the left posterior than at the mid posterior locations in the 1400–1550 ms ($p = 0.006$) and the 1550–1700 ms intervals ($p = 0.039$).

Finally, post hoc comparisons also revealed that the mean amplitude of LPN in the H/H condition was significantly more negative: (1) in the 1550–1700 ms ($p = 0.018$) and 1700–1850 ms ($p = 0.016$) intervals than in the 1850–2000 ms interval, at the mid posterior locations, (2) in the 1100–1250 ms ($p = 0.02$), 1550–1700 ms ($p = 0.014$) and 1700–1850 ms ($p = 0.013$) intervals than in the 1850–2000 ms interval, at the left posterior locations, and (3) in the 950–1100 ms ($p = 0.002$), 1100–1250 ms ($p = 0.008$), 1400–1550 ms ($p = 0.037$), 1550–1700 ms ($p = 0.004$) and the 1700–1850 ms ($p = 0.007$) intervals than in the 1850–2000 ms interval, as well as in the 1550–1700 ms than in the 1700–1850 ms interval ($p = 0.034$), at the right posterior locations.

3.3. Brain source localization analysis

Table 4 shows the MNI coordinates and Brodmann areas of those brain regions in which significant difference in activation was observed in the following: (1) the H/H $>$ CR contrast, during the *immediate* and *delayed memory phases*; and (2) the *delayed memory phase* $>$ *immediate*

memory phase contrast, in the H/H and CR conditions.

During the *immediate memory phase*, the paired sample *t*-test did not reveal any significant differences in brain activation between the H/H and CR conditions in the temporal interval of the frontal negative component (200–500 ms); however, they showed significantly greater neural activity in the H/H than the CR condition in the *parietal positive component* interval (400–900 ms) [$t(15) = 4.1$, $p < 0.05$], specifically in the inferior parietal lobule (BA: 40), parahippocampal gyrus (BA: 28, 34), uncus (BA: 28, 34), precuneus (BA: 7) and lingual gyrus (BA: 18) of the left hemisphere, and in the right posterior cingulate (BA: 30). In the temporal interval of LPN (1200–1600 ms), the paired sample *t*-test showed significantly greater neural activity in the H/H than the CR condition [$t(15) = 3.8$, $p < 0.05$] in the parahippocampal gyrus (BA: 28), anterior cingulate gyrus (BA: 32), insula (BA: 13), superior, medial and middle frontal gyri (BA: 10, 32, 46), uncus (BA: 28) and transverse temporal gyrus (BA: 41) of the left hemisphere, as well as in the rectal gyrus (BA: 11), inferior frontal gyrus (BA: 46), subcallosal gyrus (BA: 25) and posterior cingulate gyrus (BA: 30) of the right hemisphere (see Table 4 and Fig. 5).

Regarding the *delayed memory phase*, the paired sample *t*-test did not reveal any significant differences in brain activation between the H/H and CR conditions in the frontal negative component interval (200–500 ms). In the parietal positive component interval (400–900 ms), the paired sample *t*-test showed significantly greater neural activity for the H/H than the CR condition [$t(15) = 4.0$, $p < 0.05$] in the insula (BA: 13), posterior cingulate gyrus (BA: 31), uncus (BA: 28), precuneus (BA: 7) and parahippocampal gyrus (BA: 34) of the left hemisphere, the bilateral superior temporal gyrus (BA: 22, 42) and also the posterior cingulate gyrus (BA: 23) of the right hemisphere. In the LPN temporal interval (1200–1600 ms), the paired sample *t*-test showed significantly greater neural activity for the H/H than the CR condition ($t(15) = 3.9$, $p < 0.05$) in the superior temporal gyrus (BA: 41) and insula (BA: 13) of the left hemisphere, and also in the right parahippocampal gyrus (BA: 28) (see Table 4 and Fig. 5).

Finally, within the H/H condition, the paired sample *t*-tests revealed significantly greater activation [$t(15) = -3.9$, $p < 0.05$] of the left insula (BA: 13) and the right medial frontal gyrus (BA: 10) in the *delayed* compared to the *immediate memory phase* during the LPN temporal interval (1200–1600 ms) (see Table 4 and Fig. 6). In addition, for the CR condition, significantly greater activation [$t(15) = -4.4$, $p < 0.01$] of the right parahippocampal gyrus (BA: 19) was observed in the *delayed memory phase* than in the *immediate memory phase*, during the temporal interval of LPN (1200–1600 ms) (see Table 4 and Fig. 6); however, no differences between both memory phases were observed in the 400–900 ms interval.

4. Discussion

In the present ERP study using the exact low electromagnetic resolution tomography (eLORETA), we characterized and compared the performance and the spatiotemporal pattern of the brain electrical activity related to the successful immediate episodic retrieval of information which is being learned relative to delayed episodic retrieval (twenty minutes later) of the same information.

For this purpose, young participants carried out an old/new word recognition task with source memory, which included an *immediate memory phase* (with three study-test blocks) followed (after 20 min) by a *delayed memory phase* with one test block. Behavioural data showed gradual learning and consolidation of the information (old words) during the *immediate memory phase*. The ERP data showed that, relative to correctly identified new words (CR responses), correctly judged old words (H/H responses) elicited the following in both memory phases: (1) a more positive-going potential, demonstrating a *parietal old/new effect* (around 500–675 ms post-stimulus interval) related to recollection, and (2) a more negative-going potential, demonstrating an LPN effect (in the 950–1850 ms post-stimulus interval at the mid frontal and

Table 4

Brain areas showing significant activation differences for the intervals 400–900 ms and 1200–1600 ms, in: (1) the H/H > CR contrast during the immediate and delayed memory phases, (2) the H/H delayed memory phase > H/H immediate memory phase contrast, and (3) the CR delayed memory phase > CR immediate memory phase contrast.

Interval	Anatomical region	BA	H	MNI Coordinates			p	
				X	Y	Z		
400–900 ms	H/H > CR Immediate memory phase							
	Inferior Parietal Lobule	40	L	–40	–45	40	*	
	Posterior Cingulate	30	R	20	–60	10	*	
	Parahippocampal Gyrus	34, 28	L	–15	0	–15	*	
	Uncus	34,28	L	–15	0	–25	*	
	Precuneus	7	L	–30	–50	50	*	
	Lingual Gyrus	18	L	–10	–80	0	*	
	H/H > CR Delayed memory phase							
	Posterior Cingulate	23	R	10	–55	15	**	
	Insula	13	L	–35	–35	20	**	
	Superior Temporal Gyrus	22	R	65	–35	10	**	
		42	L	–65	–30	5	*	
	Cingulate Gyrus	31	L	–5	–35	40	*	
	Uncus	28	L	–15	0	–30	*	
	Precuneus	7	L	–5	–35	45	*	
	Parahippocampal Gyrus	34	L	–15	0	–20	*	
	H/H Delayed versus H/H Immediate							
	No significant differences							
	CR Delayed versus CR Immediate							
	No significant differences.							
	1200–1600 ms	H/H > CR Immediate memory phase						
		Parahippocampal Gyrus	28	L	–20	–15	–15	**
		Anterior Cingulate	32	L	–20	45	10	**
		Insula	13	L	–40	–30	15	**
		Superior Frontal Gyrus	10	L	–30	50	25	**
		Medial Frontal Gyrus	32	L	–20	40	15	**
		Middle Frontal Gyrus	10,46	L	–25	50	25	**
		Uncus	28	L	–15	–5	–30	*
		Rectal Gyrus	11	R	5	20	–30	*
		Inferior Frontal Gyrus	46	R	45	40	10	*
		Subcallosal Gyrus	25	R	5	20	–15	*
		Posterior Cingulate	30	R	15	–60	10	*
		Transverse Temporal Gyrus	41	L	–40	–30	10	*
		H/H > CR Delayed memory phase						
Parahippocampal Gyrus		28	R	25	–20	–10	**	
Superior Temporal Gyrus		41	L	–45	–35	15	*	
Insula		13	L	–45	15	5	*	
H/H Delayed > H/H Immediate								
Medial Frontal Gyrus		10	R	5	55	5	*	
Insula		13	L	–40	–40	20	*	
CR Delayed > CR Immediate								
Parahippocampal Gyrus		19	R	35	–45	–5	**	

BA: Brodmann area, H: Hemisphere: Left (L) and Right (R), MNI: Montreal Neurological Institute.

* $p < 0.05$; ** $p < 0.01$.

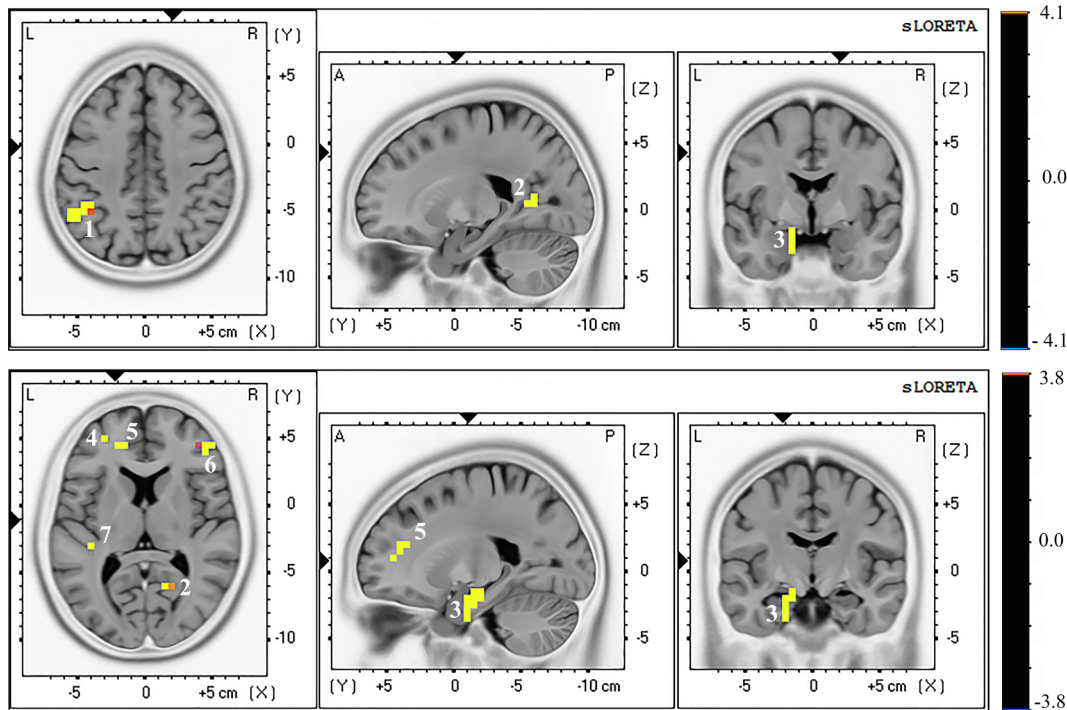
the mid posterior locations and in the 950–1700 ms post-stimulus interval at the left and right posterior locations) associated with retrieval and post-retrieval process. Furthermore, in the H/H condition, the mean amplitude of the parietal positive component (identified in the temporal range of the *parietal old/new effect*) was significantly larger in the *delayed* than in the *immediate memory phase*; while the mean amplitude in the temporal range of the LPN effect was significantly more negative in the *immediate* than in the *delayed memory phase*.

As mentioned above, the eLORETA was used to evaluate the brain regions involved in both memory phases of the task. The results obtained with this analytic tool must be taken with caution due to its low spatial resolution, even though the results obtained in the present study are in line with other found in previous studies that used higher spatial resolution techniques. The eLORETA results showed that while information is being learned and consolidated, the successful immediate recognition memory (accompanied by contextual details) of old words compared to the correct recognition of the new words, required greater involvement of left inferior parietal lobe and medial temporal regions

(principally in the left hemisphere), in the 400–900 ms interval, related to the recollection; while in the 1200–1600 ms interval, related to post-retrieval processes, the left prefrontal regions were more activated. Furthermore, compared to the immediate memory phase, the successful delayed (20 min) retrieval of old words also required greater activation of the left insula and the right medial frontal gyrus in the 1200–1600 ms interval. The left lateralized brain activity observed in the present study, in both memory phases, is consistent with the important functional role of the left hemisphere in word processing (Riès, Dronkers, & Knight, 2016).

Finally, the involvement of the medial temporal areas (particularly the parahippocampal gyrus) in the successful recognition memory (accompanied by contextual details), as much when the consolidation process was in course (immediate retrieval) as when the consolidation was more strengthened (delayed retrieval), is consistent with the MTT and TTT theoretical models, which propose that retrieval of episodic memories (recent or remote) will be always dependent on the MTL.

IMMEDIATE MEMORY PHASE



DELAYED MEMORY PHASE

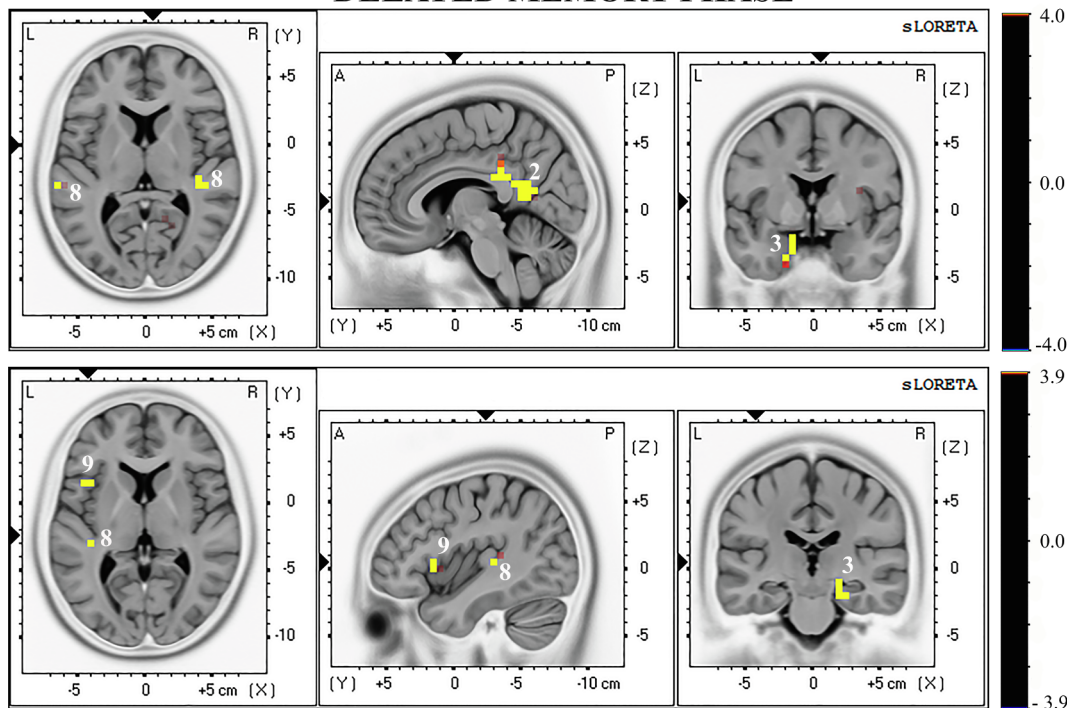


Fig. 5. eLORETA maps with the brain regions that showed significant differences of activation in the H/H > CR contrast, during the *immediate memory phase* and the *delayed memory phase*. Cluster of voxels showing significant differences in the parietal positive component interval (400–900 ms) (top) and in the LPN interval (1200–1600 ms) (bottom), in each memory phase. Yellow voxels represent significant differences in the H/H > CR contrast and blue voxels the inverse direction (CR > H/H). Location of the loci of activation: 1: Inferior Parietal Lobule; 2: Posterior Cingulate; 3: Parahippocampal Gyrus; 4: Superior Frontal Gyrus; 5: Middle Frontal Gyrus; 6: Inferior Frontal Gyrus; 7: Transverse Temporal Gyrus; 8: Superior Temporal Gyrus; 9: Insula.

4.1. Performance

Behavioural results across the three study-test blocks of the *immediate memory phase* showed (1) a significant increase in the percentage of CR (i.e. correct rejections in response to new words), as well as

in the percentage of H/H (hit/hit, correct recognition and correct source memory of old words) responses, and (2) a significant decrease in H/M responses (hit/miss, correct recognition of old words, without source memory). On the other hand, a significant reduction in the RTs was also observed across the three blocks, in the three conditions (H/H,

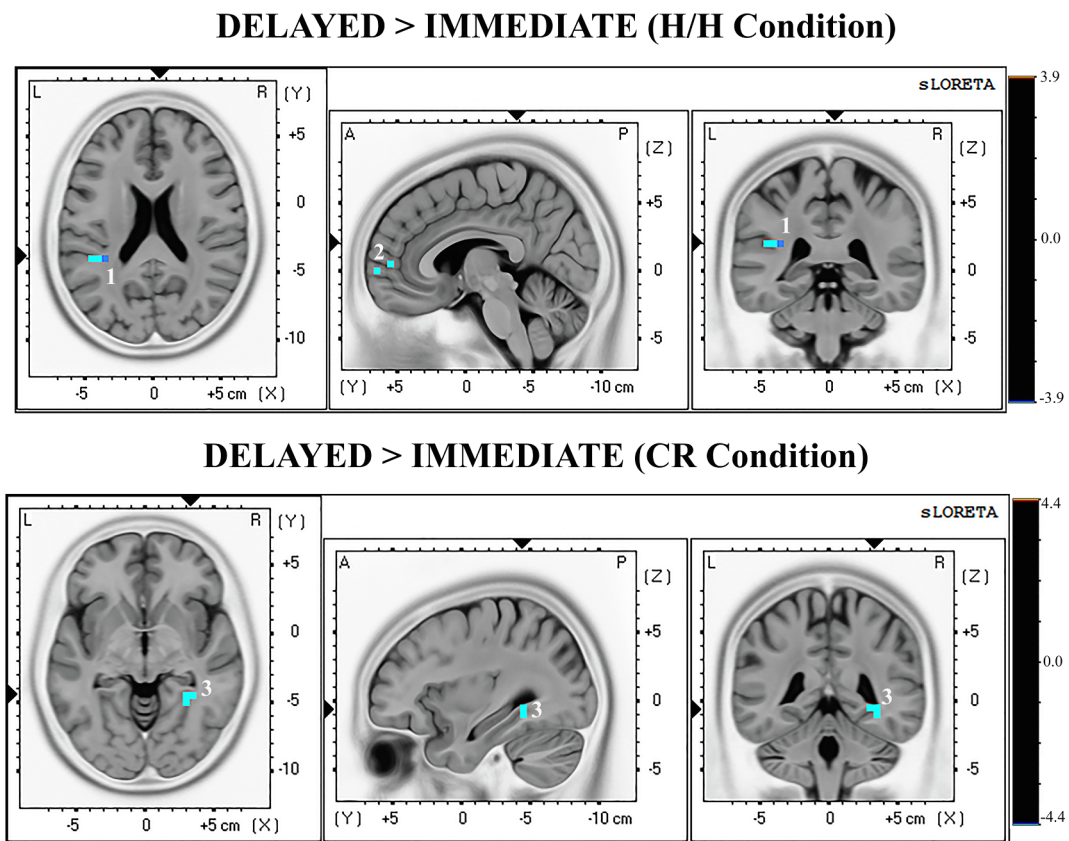


Fig. 6. eLORETA maps with the brain regions that showed significant differences in activation in the Delayed > Immediate contrast in the H/H condition (top) and in the CR condition (bottom). Cluster of voxels showing significant differences in the LPN interval (1200–1600 ms). Blue voxels represent significant differences in the Delayed > Immediate contrast and yellow voxels the inverse direction (Immediate > Delayed). Location of the loci of activation: 1: Insula; 2: Medial Frontal Gyrus; 3: Parahippocampal Gyrus.

CR and H/M). The gradual increase in correct responses (H/H and CR) and decrease in the corresponding RTs may indicate that during the *immediate memory phase*, the old words were gradually learned (and consequently, the old words were gradually consolidated in episodic memory), thus improving the performance of participants, as well as their ability to discriminate between old and new words and to recall the colour in which old words were presented.

Moreover, the lack of differences between the third test block of the *immediate memory phase* and the test of the *delayed memory phase* (20 min later), for the percentage of H/H responses and the RTs, demonstrate that the previously learned information (old words) remained stored in memory without being affected by the 20-minute interval between the immediate and the delayed tests, nor for the performance of a visuospatial working memory task during that interval. These results thus indicate early consolidation of the information already in the third test block of the *immediate memory phase*, which persisted in the *delayed memory phase* twenty minutes later.

4.2. Brain activity in the immediate and the delayed memory phases

4.2.1. Differences between HH and CR conditions in each memory phase

In both memory phases, a *mid-frontal old/new ERP effect* (or FN400 effect) was not observed, as the amplitude of the frontal negative component (identified in the 200–500 ms post-stimulus interval) did not differ significantly between the H/H and CR conditions. Moreover, the eLORETA analysis in the temporal range of this component did not show any significant differences in brain activation between conditions (H/H versus CR). Our findings are consistent with those of several studies that also used words as stimuli during an old/new recognition task with source memory and that did not observe this effect in young adults

(Alhaj et al., 2006; Kim et al., 2009); however, they are not consistent with those of other studies that observed this ERP effect in a similar task (Ross, Smolen, Curran, & Nyhus, 2018, see Source Memory Experiment) or in an old/new recognition task with items endorsed either as recollected or highly familiar (Wang et al., 2012; Wolk et al., 2006) or a simple old/new recognition task (Wolk et al., 2009). The *mid-frontal old/new effect* has been proposed as a neural correlate of familiarity (Curran, 2000), and the results of the present study therefore suggest that the correct recognition of the old words did not (mainly) rely on familiarity.

As expected, a *parietal old/new effect* was observed in both memory phases (*immediate and delayed*), with significantly larger mean amplitude of ERP waveforms in the H/H than in the CR condition (in the 500–650 ms post-stimulus interval of the *immediate memory phase*, and in the 525–675 ms post-stimulus interval of the *delayed memory phase*). This finding is consistent with those of previous studies using source memory tasks with words and reporting significantly larger amplitude in correct source judgments of old words compared to correctly rejected new words when the recognition test began immediately (Alhaj et al., 2006; Kim et al., 2009; see experiment one of Macleod & Donaldson, 2017) or one week (see experiment two of Macleod & Donaldson, 2017) after the study of the words. Therefore, our results appear to support the functional relationship between the *parietal old/new effect* and recollection, i.e. the conscious retrieval of the item and the contextual details (Rugg, Schloerscheidt, & Mark, 1998; Wilding & Rugg, 1996).

The present findings also appear to suggest that the correct recognition of the old words (for which contextual details were also retrieved) mainly relied on recollection. This interpretation is supported by the brain source localization analysis results, using eLORETA for the H/H > CR contrast in the 400–900 ms post-stimulus interval

(temporal range of the positive parietal component). These findings showed that the left precuneus, uncus, and parahippocampal gyrus were more activated in the H/H than in the CR condition, as well as the right posterior cingulate gyrus, in both memory phases (*immediate and delayed*). Greater activation in H/H than in CR condition was also located (1) in the inferior parietal lobe and lingual gyrus, of the left hemisphere, in the *immediate memory phase* and (2) in the left insula and the bilateral superior temporal gyrus in the *delayed memory phase*.

These findings are consistent with those of some studies that have consistently related the activation of MTL regions, together with parietal regions, to recollection. Specifically, some MEG and ERP/LORETA studies observed recollection-related brain activity in the parahippocampal gyrus (Breier, Simos, Zouridakis, & Papanicolaou, 1998; Dhond, Witzel, Dale, & Halgren, 2005; Tendolkar et al., 2000), in the right inferior parietal lobe (Kim et al., 2009) and in the precuneus (Dhond et al., 2005; Tendolkar et al., 2000). In addition, our results are in line with previous studies that used higher spatial resolution techniques such as fMRI, which have also emphasized the role of the parahippocampal gyrus (Cansino, 2002; Kahn, Davachi, & Wagner, 2004), the inferior parietal lobe (Herron, Henson, & Rugg, 2004; Vilberg & Rugg, 2007; Yonelinas, Otten, Shaw, & Rugg, 2005), as well as other nearby regions such as the precuneus, the posterior cingulate gyrus and the retrosplenial cortex (Donaldson, Wheeler, & Petersen, 2010; Kahn et al., 2004), in the recollection (for a review see, Eichenbaum et al., 2007; Ranganath & Ritchey, 2012; Vilberg & Rugg, 2008).

Furthermore, the activation combined of medial temporal areas and neocortical areas in both memory phases during the successful recollection, together with the absence of behavioural differences between the third test block (of the *immediate memory phase*) and the 20-minutes delayed test, may evidence that medial temporal-neocortical crosstalk occurs during the blocks of learning and persists onwards, while *synaptic* and *systems consolidation* of information are in course. In addition, these results are in consonance with the assumption that memory information becomes distributed across medial temporal-neocortical circuits already since early stages of the post-encoding reorganization of long-term memory representations (Dudai et al., 2015).

The access to the episodic information of the old words seemed to facilitate faster classification of these words than of the new words, as demonstrated by a significantly shorter latency of the parietal positivity (in the temporal range of the *parietal old/new ERP effect*) in the H/H than in the CR condition, in both memory phases.

From 950 ms onwards, an LPN effect was observed in the *immediate memory phase*, as the ERP waveforms associated with the H/H condition were more negative than those in the CR condition. In the *delayed memory phase*, no significant differences were obtained between H/H and CR conditions, although the ERP waveforms were also more negative in H/H than in CR condition.

According to Herron (2007), the LPN effect comprises an early effect (600–1200 ms post-stimulus) related to information searching processes in episodic memory, which is followed by a late effect (1200–1900 ms post-stimulus) involved in maintaining the retrieved information. In the present study, the onset of the LPN is included in the temporal interval of the early effect proposed by Herron (2007) and takes place after the button is pressed in the correct old/new recognition task (see RTs in Table 1 and Fig. 3). Based on the grand-average ERP waveforms of the *immediate memory phase* (in which a significant LPN effect was observed), the difference in the mean amplitude of the LPN between H/H and CR conditions was maximal around the 1200–1600 ms post-stimulus interval, a temporal range (1) coinciding with the late effect proposed by Herron (2007), and (2) posterior to the appearance of the colour question on the screen, when the participants should access the colour shown during the study. Thus, according to previous studies that addressed the functional significance of the LPN (Herron, 2007; Sommer et al., 2018; Wolk et al., 2007), our findings support previous evidence relating the LPN to cognitive control

processes that take place during the late stage of memory retrieval, particularly when memory attributes require the involvement of searching, evaluation and maintenance processes (for a review see Mecklinger et al., 2016).

We also evaluated the neural sources that would support these later retrieval and post-retrieval processes in the 1200–1600 ms temporal range. To the best of our knowledge, only one previous study has directly evaluated the neural sources of the LPN (Bergström et al., 2013). Bergström and colleagues used a combination of high temporal (EEG/MEG) and spatial (fMRI) resolution techniques, showing that LPN could be generated in the precuneus, a posterior parietal region related to retrieval processes (Wagner, Shannon, Kahn, & Buckner, 2005) and also to post-retrieval processes such as evaluation of the quality of memories (Bergström et al., 2013; Chua, Schacter, Rand-Giovannetti, & Sperling, 2006) and elaborative processing of the retrieval products (Bergström et al., 2013; Daselaar et al., 2008).

The eLORETA findings revealed greater activation of the parahippocampal gyrus and the insula in the H/H condition than in the CR condition, through the 1200–1600 ms interval, in both memory phases (*immediate and delayed*). In the *immediate memory phase*, the differences H/H > CR were also located in (1) different prefrontal regions such as the anterior cingulate gyrus, and the superior, middle and medial frontal gyri, of the left hemisphere, and in the right rectal and inferior frontal gyri; (2) in temporal areas, specifically the left uncus and the transverse temporal gyrus, and (3) the right posterior cingulate gyrus. In the *delayed memory phase*, the differences H/H > CR were also located in the left superior temporal gyrus.

These findings are consistent with those of previous fMRI studies showing greater activation of regions of the prefrontal cortex (PFC) in a source memory task relative to an item recognition task, suggesting that PFC is specially involved in monitoring and evaluating episodic recollection (Dobbins, Foley, Schacter, & Wagner, 2002; for a review see Mitchell & Johnson, 2009). The greater PFC activation observed in the *immediate* but not in the *delayed memory phase* for the H/H > CR contrast may reflect the mobilization of neural resources directed towards these processes, in the *immediate memory phase*, during the course of the learning and consolidation of words. Our findings are also consistent with the description of a *posterior medial system* related to episodic memory comprising regions such as the posterior cingulate, precuneus and angular gyrus, connected with the medial PFC and the parahippocampal cortex (Ranganath & Ritchey, 2012).

4.2.2. Differences between immediate and delayed memory phases in each condition (HH and CR)

In the H/H condition, the mean amplitude of the parietal positive component was significantly larger in the *delayed* than in the *immediate memory phase* (while in the CR condition no differences between phases were observed), possibly reflecting that, after a delay interval of twenty minutes (in which a working memory task was presented to the participants), the amount of cognitive resources mobilized for the recollection and the classification as “old word” was higher than in *immediate memory phase*.

In the H/H condition, the mean amplitude of LPN was significantly more negative in the *immediate* than in the *delayed memory phase*. In a recent review of LPN (Mecklinger et al., 2016) it has been proposed that the amplitude modulations of this component depend on factors such as the amount of contextual attributes needed to reconstruct the previous study episode, the similarity between attributes, the number of contextual details required to remember or even the strength of memory traces. Specifically, it has been suggested that continuous evaluation is necessary when the memory traces are weaker and therefore the amplitude of LPN will be larger; by contrast, for stronger memory traces, continuous evaluation will not be necessary and the LPN amplitude will be smaller (Mecklinger et al., 2016). Similarly, our findings seem to suggest that the involvement of monitoring, evaluation and maintenance processes, that act upon the retrieval products during

strengthening of the memory traces and their consolidation, were more necessary in the *immediate memory phase* than in the *delayed memory phase*.

We cannot rule out that mean amplitude differences between both memory phases in the parietal positive component and the LPN intervals during the H/H condition could be explained because different retrieval processes are involved in both memory phases. The word-colour recognition judgment is rather simple and can be based on a familiarity judgment by imaging the presented word in one colour or the other. This strategy might have been employed during the *immediate memory phase* but not during the *delayed memory phase*, resulting in more recollection-related activity during the *delayed memory phase*. Such differences might be reflected by the larger mean amplitude in the *delayed* than in the *immediate memory phase* in the parietal component interval but the opposite pattern in the LPN interval (larger mean amplitude in the *immediate* than in the *delayed memory phase*). Thus, mean amplitude differences between both memory phases could not only be explained by the difficulty of retrieving a stimulus immediately or with a 20-minute delay, but also because different retrieval processes could be involved in each memory phase.

When brain activity was compared between both memory phases in the 1200–1600 ms post-stimulus interval, greater activation was observed in the *delayed* than in the *immediate memory phase* for the left insula and the right medial frontal gyrus in the H/H condition, as well as for the right parahippocampal gyrus in the CR condition. Medial PFC activation has been related to consolidation and retrieval of gist and schematic features of previously studied events (for a review see Gilboa & Marlatte, 2017), and insula activations with recall of previously learned information (Kurth, Zilles, Fox, Laird, & Eickhoff, 2010). On the other hand, previous studies that reported parahippocampal activation during the correct rejections of new pictures have suggested that this region would support the detection of novelty (Bowman & Dennis, 2015). Thus, taking the previous evidence into account, the present findings seem to indicate that in the *delayed memory phase* (when the information was largely consolidated in memory), the evaluation and retrieval of the old words relied as much on gist or general schemes as on specific details. However, in the case of the new words, greater activation of the parahippocampal gyrus was necessary in order to evaluate and verify presentation of a new word.

Finally, it should be noted that the results of the present study support the MTT (Nadel & Moscovitch, 1997) and TTT (Sekeres et al., 2018) theoretical models, according to which the retrieval of recent and remote episodic memories will always depend on MTL structures. In both memory phases, greater activation of medial temporal regions (particularly the parahippocampal gyrus) in the H/H than in the CR condition was observed for all temporal intervals evaluated (400–900 ms and 1200–1600 ms). The findings also showed the important involvement of other temporal regions in the H/H > CR contrast, specifically the uncus (in both memory phases) and the superior temporal gyrus in the *delayed memory phase*.

Study of the changes in the spatiotemporal pattern of the brain activity during the consolidation of information in memory throughout the three study-test blocks was not possible, because of an insufficient number of artefact free trials in each test block of the *immediate memory phase*. In future studies, it would be interesting to address this point by including a larger number of stimuli in each block. Moreover, we did not obtain a sufficient number of epochs for the H/M condition which could allowed us to evaluate more accurately the brain regions functionally related to familiarity-based judgments.

5. Conclusions

In summary, the behavioural and psychophysiological findings of the present ERP/eLORETA study, in which a sample of young adults performed an old/new word recognition task (with source memory) while their EEG activity was recorded, showed the following:

1. Gradual learning and consolidation of the information (old words) in episodic memory after the information was repeated across three study-test blocks during an *immediate memory phase*. The consolidation remained stable after an interval of twenty minutes in which the participants executed another task.
2. During the memory consolidation, correct recognition of the old words (for which contextual details, i.e. colour, were also retrieved) did not mainly rely on familiarity, as the *mid-frontal old/new ERP* effect (or FN400 effect) was not observed, but (1) on recollection, as indicated by the identification of a *parietal old/new effect* in the post-stimulus 500–675 ms interval and (2) on the monitoring, evaluation and maintenance processes that act on the retrieval products, as indicated by the LPN effect between 950 ms and 1850 ms.
3. The recollection was associated with activation of the left precuneus, uncus, and parahippocampal gyrus, regardless of whether the successful EM retrieval was immediate or delayed for 20 min.
4. Monitoring, evaluation and maintenance processes that acted upon the retrieval products were associated with (1) activation of the parahippocampal gyrus and insula, regardless of whether the successful EM retrieval was immediate or delayed for 20 min, (2) greater activation of the left insula and the right medial frontal gyrus in the delayed than in the immediate EM retrieval of old words, and (3) greater activation of the right parahippocampal gyrus, in the delayed than in the immediate recognition of new words.
5. In line with the MTT and TTT models, the successful recognition and episodic retrieval was supported by medial temporal areas (specifically the parahippocampal gyrus and uncus) in immediate and delayed retrieval during the course of memory consolidation.

CRedit authorship contribution statement

Miguel Ángel Rivas-Fernández: Methodology, Formal analysis, Writing - original draft, Visualization. **Santiago Galdo-Álvarez:** Conceptualization, Methodology, Investigation, Visualization, Supervision, Project administration. **Montserrat Zurrón:** Conceptualization, Investigation, Resources, Supervision, Project administration, Funding acquisition. **Fernando Díaz:** Conceptualization, Investigation, Resources, Supervision, Project administration, Funding acquisition. **Mónica Lindín:** Conceptualization, Methodology, Investigation, Visualization, Supervision, Project administration.

Declaration of competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationship that could be construed as a potential conflict of interest.

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