Episodic temporal structure modulates associative recognition processes: An MEG study

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Abstract

The formation of mnemonic associations can occur between items processed in temporal proximity. It has been proposed that such intertemporal associations are not unitizable, and may therefore be retrieved only via recollective processes. To examine this claim, we conducted a magnetoencephalograph study of recognition memory for items encoded and retrieved sequentially. Participants studied successively presented pairs of object pictures, and subsequently made old-new item judgments under several retrieval conditions, differing in degree of reinstatement of associative information. Correct recognition was accompanied by an early event-related field (ERF) component, seemingly corresponding to the FN400 event-related potential component asserted to reflect familiarity; this retrieval success effect was not modulated by degree of associative binding. A later ERF component, corresponding to the late positive component asserted to reflect recollection, was modulated by degree of associative reinstatement. These results suggest that memory of intertemporal associations, which are not amenable to unitization, is accessed via recollection.

Descriptors: Episodic memory, Familiarity, Recollection, Intertemporal associations, MEG

Memory regarding spatiotemporal relationships between objects of our experience, (i.e., episodic association), is an essential aspect of mnemonic function. Such associations between discrete stimuli have been the subject of much research, and the attempt to understand their formation and retrieval has influenced several models of memory. Among these are dual-process models of recognition memory. Such models propose that recognition is based on two independent processes: familiarity, which relies on a sense that an event has been previously experienced, without retrieval of specific contextual details; and recollection, which involves the retrieval of specific details of a past experience. Recollection is asserted to allow the retrieval of episodic associative information in a fashion that is not enabled by familiarity (Yonelinas, 2002).

One method of evaluating such dual-process models of recognition is by examining the electrophysiological correlates of successful recognition. A common finding in such electroencephalograph (EEG) studies is that presentation of studied items elicits more positive-going event-related potentials (ERPs) than does presentation of unstudied items (e.g., Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007). On the basis of differ-

ential latencies, scalp topographies, and sensitivities to manipulation of experimental variables (e.g., Allan, Wilding, & Rugg, 1998; Mecklinger, 2000; Rugg, 1990; Smith & Halgren, 1989), it has been shown that ERP old/new effects comprise at least two dissociable components: an earlier effect often referred to as the FN400 component (due to the more negative-going deflection associated with new stimuli, and the component's frontal focus), and a late positive component (LPC). In recent years, most researchers have interpreted these ERP retrieval effects in light of dual-process models of recognition memory. According to this approach, the FN400 effect, which is maximal between 300–500 ms at midfrontal electrodes, is assumed to reflect familiarity (e.g., Allan et al., 1998; Graham & Cabeza, 2001; Guo, Duan, Li, & Paller, 2006). The LPC, maximal at 500–800 ms over posterior sites, is assumed to reflect the process of recollection (e.g., Cycowicz & Friedman, 2003; Friedman, Cycowicz, & Bersick, 2005; Senkfor & Van Petten, 1998). This assertion is supported by findings that the LPC exhibits sensitivity to contextual or associative factors. For example, in a study by Speer and Curran (2007), participants studied pairs of arbitrary fractals (some viewed more times than the others), and were subsequently asked to differentiate studied from unstudied pairs. A modulation of the LPC related to the nature of the association was found: LPC was more positive for repeated associations (both weak and strong) compared to new and rearranged pairs. Another example of the identification of the LPC with recollective processes is provided by a study that compared inter- and intradomain associations, and showed a double dissociation between modulation of FN400, which was more sensitive to intra- than for interitem associations, and LPC, which showed the

inverse pattern (Jäger, Mecklinger, & Kipp, 2006). Going beyond tests of recognition, we recently employed an associative cued recall paradigm to compare between concurrently and sequentially encoded associations. We identified a posterior ERP component, reminiscent of the LPC reported in recognition studies, which exhibited larger modulation for the successful cued recall of sequentially than concurrently encoded pairs (Tibon & Levy, 2014).

Nevertheless, associative reinstatement does not always modulate the LPC. In the study conducted by Tsivilis, Otten, and Rugg (2001), participants studied object pictures presented against various backgrounds and were asked to mentally place the object in a specific location within the background landscape, creating an internal narrative to justify the object placement. Hence, that task required interactive encoding of two temporally synchronous stimuli of the same (visual) modality. Subsequently, the stimuli were presented again in five possible retrieval conditions, and participants were asked to make an old-new judgment regarding the object probes. In that study, the LPC component (measured at left parietal electrodes at 700–900 ms) was more positive in the same (repeat), rearranged (re-pair), and old/new conditions compared to the new/old and new/new conditions. Thus, its modulation was sensitive to repetition of the target object (whether old or new), but not to the associative binding between the object and the background (whether the association was repeated or re-paired). In another study, conducted by Ecker, Zimmer, Groh-Bordin, and Mecklinger (2007), a similar design was used, and once again, activation was more positive when the target object was old, regardless of the nature of the association between the object and the background.

Thus, while some studies find that associative binding modulates LPC, other studies fail to report such a pattern. These conflicting findings do not contradict the notion that the LPC is related to recollection, but they do indicate that the mnemonic processes reflected by the LPC, and possibly by the FN400, may not simply map onto recollection and familiarity. A slightly more nuanced approach is suggested by the proposal that intraitem associations may be recognized via familiarity-based retrieval, while interitem associations can only be recognized through recollection-based retrieval (Aggleton & Brown, 2006; Norman & O'Reilly, 2003). In a recent taxonomy of episodic associations, the "domain-dichotomy" (DD) approach, it is proposed that associative memory comprises three types of associations, reflecting differing degrees of unitization: intraitem associations, i.e., items that were unitized into one entity (e.g., two interactively encoded object pictures); within-domain associations, formed between similar kinds of items that are not remembered as one entity (e.g., two unrelated words); and between-domain associations, formed between different kinds of items or modalities, such as faces and voices (Mayes, Montaldi, & Migo, 2007). Yonelinas, Kroll, Dobbins, and Soltani (1999) proposed that unitized stimuli may be recognized via processes that rely on familiarity rather than recollection. Following up on that proposal, Bastin, van der Linden, Schnakers, Montaldi, and Mayes (2010) report that within-domain (face-face) associative recognition was mainly supported by familiarity, while between-domain (face-name) associative recognition required a major contribution of recollection. Additionally, studies conducted in our lab suggest that unitization of memoranda depends not only on domain similarity between stimuli, but also on temporal features of the presentation, and that the degree of unitization at encoding affects the processes involved in retrieval. By examining the effect of contextual reinstatement on recognition success (i.e., a context effects [CE] paradigm) under conditions in which unitization of memoranda is not readily achieved (using cross-domain and intertemporal associations), we found that the standard CE—better recognition of probes under contextual reinstatement—was only found when participants explicitly recognized the contextual stimuli, but not if they were unable to endorse the contextual stimuli as having been previously presented (Tibon, Vakil, Goldstein, & Levy, 2012). These results contrasted with findings that, for concurrent encoding of same-domain stimuli, CEs are obtained even in the absence of explicit memory for contexts (Levy, Rabinyan, & Vakil, 2008). This contrast supported the assertion that, in the absence of unitization, associative memory is dependent on recollection, while retrieval of unitized associations may be supported by familiarity strength.

In two recent studies (Bader, Mecklinger, Hoppstädter, & Meyer, 2010; Kriukova, Bridger, & Mecklinger, 2013), a parietal-maximal old/new ERP effect was found only for nonunitized associations, suggesting a clear contribution of recollection to associative recognition for that kind of pairs. The authors concluded that the presence of an early midfrontal old/new effect in the absence of the parietal ERP effect for unitized associations indicates that familiarity alone may be sufficiently diagnostic for associative recognition in unitized pairs. In contrast, when associatively encoding arbitrary shapes, as in the paradigm of Speer and Curran (2007), unitization cannot occur, and the LPC, which indexes recollection, would be modulated by that nonunitized association.

The current work was inspired by this suggestion that differences in the degree of unitization during encoding result in modulation of the processes associated with retrieval. We expected that recollection (indexed by LPC), but not familiarity (indexed by FN400), would be sensitive to the maintenance or disruption at test of such associations formed at encoding. We explored this idea by measuring event-related fields (ERFs, the magnetic correlate of event-related electrical potentials) in an intertemporal target-context paradigm, in which two stimuli are presented sequentially rather than concurrently, thus rendering unitization unlikely. We hypothesized that, in this case, the later LPC elicited by correctly recognized stimuli would be modulated by the maintenance versus disruption of study-phase associations at test, and would thus differ between the repeat and re-pair conditions. In other words, we predicted that the behavioral phenomenon of improved recognition of stimuli presented at test in the same context as at study would be accompanied by a stronger LPC in response to such probes than in response to probes that were correctly individually recognized in the absence of contextual reinstatement.

Method

Participants

Forty-two students (13 males, mean age 22.77 years, $SD = 2.67$, range 19–29), with normal or corrected-to-normal vision and without history of neurologic or psychiatric disorders participated in the experiment. One participant was excluded from the analysis, due to subsequent discovery of a posttraumatic stress disorder diagnosis and the usage of medical marijuana. Two other participants were excluded due to increased noise during the experiment and due to repeated electrical blackouts. All participants participated in the study in return for academic requirement credits, and gave written informed consent.

Stimuli

We employed 480 drawings of common objects used in our lab in previous studies (e.g., Levy et al., 2008). Of these, 240 pictures were paired to form 120 study-pairs. An additional 240 pictures supplemented them to form various test-pairs combinations. Each object was approximately 8×6 cm in size on screen, and was presented on a screen located 50 cm from the participant, at an angle of ~9.15°.

To rule out possible influences of semantic relatedness within object pairs at encoding on subsequent retrieval, for each participant, we marked each stimulus that was analyzed at the retrieval phase according to the judgment made on the pair at encoding. Next, for each participant, we calculated the Phi coefficient to correlate between judged relatedness (related/unrelated) and accuracy at retrieval (success/failure). The coefficient was significant at $p < .05$ for 7 of the 39 participants, and at $p < .01$ for 2 participants. Thus, for the majority of participants, semantic relatedness within object pairs did not influence retrieval accuracy rates. In the current sample, 37.6% of the pairs were judged as being related. We further correlated the proportion of pairs judged as semantically related at encoding and the general hit and CR rates, to check whether participants who more frequently tended to judge object pictures as related perform differently in a subsequent memory test. The results were not significant, indicating that accuracy rates were not related to the semantic relatedness judgment. Hence, for the current participants, semantic relations between encoded pairs did not seem to have a behavioral effect on subsequent retrieval.

Procedure

Participants were told that in each trial two object pictures would be presented sequentially. They were asked to judge whether the pair of portrayed objects were likely to be found in the same location under normal circumstances. Participants were further instructed to remember the target object, which was thus marked by a 2-cm blue border. Presentation order was counterbalanced across subjects such that, for half of the participants, the first picture presented was marked as the to-be-remembered target, and for the other half of the participants, the second picture presented was marked as the target. Each object picture appeared for 2 s, with a 0.5-s blank interstimulus interval. Yes/no responses were given by pressing corresponding keys after the disappearance of the objects, immediately initiating presentation of the next set of stimuli. Four training trials preceded the 120 study trials. During each study, one self-paced break was provided.

During a 20-min delay period, participants performed a Trail Making Task (Lezak, Howieson, & Loring, 2004), and the Digit Span subtest from the WAIS III (Wechsler, 1997). Next, participants were told that they would then see studied and unstudied target pictures, accompanied by the same or different studied and unstudied context pictures. They were instructed to indicate if each of those probe pictures had appeared at study (old) or not (new), irrespective of the other picture now accompanying it. They then viewed 240 picture pairs presented in random order. Each object picture appeared for 1 s, with a 0.2-s blank interstimulus interval. The order of presentation of pictures at test was the same as at study (i.e., a picture that was presented as the first probe at study was presented first at test and vice versa). The second probe picture (to which ERFs were locked, see below) was marked by a 2-cm blue border. Five types of picture pairs were presented: (1) 40 originally studied pairs (repeat); (2) 40 pairs of pictures that both had been studied, but not together (re-pair); (3) 40 pairs in which the first-position picture was new and the second-position picture was studied (first-new, second-old; N-O); (4) 40 pairs in which the first-position picture was studied and the second-position picture was new (first-old, second-new, O-N); (5) 80 pairs of new object pictures in both positions (N-N).

After the presentation of both pictures of each test pair, to query recognition of the first stimulus, the legends "first object appeared" (in green) and "first object did not appear" (in red) were shown, and participants responded using the corresponding keys. That response triggered the appearance of the next set of legends, to query the second stimulus, which stated "second object appeared" (in green) and "second object did not appear" (in red), to which participants gave a second response, triggering the next set. Eight training trials and three self-paced breaks were provided during the test. The experiment was presented using e-Prime software (Psychology Software Tools, Inc.).

Data Acquisition

Magnetoencephalography (MEG) recordings were conducted with a whole-head, 248-channel magnetometer array with real-time noise reduction (4-D Neuroimaging, Magnes 3600 WH). In this array, each sensor senses the magnetic field with a single coil loop, thus measuring one component of the magnetic field in one location (Toga & Mazziotta, 2002). Recordings were performed in a dimly lit, magnetically shielded room. Data was acquired using the Magnetic Source Imaging (MSI) software (UUMSI at the University of Utah). Participants wore nonmagnetic clothing and were asked by the experimenter about possible metal accessories, to exclude metal artifacts. Reference coils, located approximately 30 cm above the head oriented by the *x*, *y*, and *z* axis, were used to remove environmental noise. An additional channel recorded the 50 Hz signal from the power outlet. The data was digitized with a sample rate of 1017 Hz, and an online 1–400 Hz band-pass filter was applied. Data analyses included 246 sensors, since two non-adjacent sensors (of the 248) were removed from analysis due to excessive sensor noise.

MEG Procedure

Participates with possible metal body artifacts were screened over the phone. The day before the experiment, the experimenter called the participants and instructed them to wear nonmagnetic clothing. Upon arrival at the lab, participants filled out a consent form and a personal details form. Next, they were positioned as closely as possible to the MEG sensors. The experimenter made sure that the position of the participant's head was left–right symmetric and not tilted around the anterior–posterior axis. In order to verify the suitability of the participant, in terms of possible electromagnetic artifacts, participants were tested prior to the initiation of the experimental task. This was done by asking the participants to perform a series of deep breaths and to blink 5–10 times. Included participants had no large signals associated with these tasks (see Gross et al., 2012, and Keil et al., 2013, for good practice in MEG research).

Five coils were attached to the participant's scalp for recording the head position relative to the sensor. The head shape was digitized (Polhemus Fastrack digitizer), and the experiment was run with the subjects in supine position. A photosensitive diode on the screen recorded the exact onset time of visual stimuli. After registration of the head position, instructions were presented on the screen. Participants were asked to refrain, as much as possible,

from moving their head and from blinking during the experiment. MEG ERFs were recorded in two separate sessions (study and test sessions). Head position was recorded prior and following each session. The exclusion criterion for head movements was set for 1 cm. None of the participants were excluded due to this criterion. Task responses were collected using a Photon Control LUMItouch nonmetallic response box.

MEG Preprocessing

Power-line noise was removed using an extra channel, which recorded the 50 Hz signal from the power outlet. Calculating the average 50 Hz cycle on every MEG sensor allowed cleaning the power-line noise without a notch filter. Heartbeat artifacts were removed using an event-synchronous cancellation algorithm. The algorithm is a two-pass procedure, which allows the estimation of the true interference in one signal cycle prior to adaptive cancellation (Strobach, Abraham-Fuchs, & Härer, 1994, implemented by Tal & Abeles, 2013, using MATLAB, Mathworks, Natick, MA). Using FieldTrip toolbox for MATLAB (Oostenveld, Fries, Maris, & Schoffelen, 2011), data were segmented into epochs starting 100 ms before presentation of the second stimulus in each pair and up to 800 ms after. The data was then low-pass filtered with an offline cutoff of 50 Hz, using a Butterworth filter, and the baseline was adjusted by subtracting the mean amplitude of the prestimulus period (50 ms) of each trial from all the data points in the segment. Spatial independent component analysis (ICA) was applied in order to clean eye movements and blink artifacts (e.g., Makeig et al., 1999). ICA decomposition was performed using the logistic infomax ICA algorithm (as implemented by Oostenveld et al., 2011) and was based on all segmented trials. The correction procedure was applied manually. Other trials containing jump and muscle artifacts were visually rejected.

Statistical Analyses

Behavioral analyses. Accuracy rates and ERFs calculated separately for hits and correct rejections (CRs) were collected for all participants, for responses to the second stimulus of each pair. Responses were also collected for the first pair member, for additional behavioral analyses reported elsewhere (Tibon et al., 2012).

As CEs affect both hit rates and false alarm/CR rates (e.g., Vakil, Raz, & Levy, 2007), we performed separate analyses for hits and CRs. For hits, we performed repeated measures analysis of variance (ANOVA) with reinstatement condition (repeat vs. re-pair vs. N-O) as a repeated factor and stimulus role at study (target vs. context) as a between-subjects factor. Significant effects related to reinstatement condition were further analyzed using Bonferroni-corrected pairwise comparisons. For CR, we performed repeated measures ANOVA with context reinstatement condition (O-N vs. N-N) as a repeated factor and stimulus role (foils in the target vs. context positions) as a between-subjects factor.

MEG data segmentation. Since no interactions were found in the behavioral data between reinstatement conditions and object position, either for hits or for CRs (see behavioral results below), for the MEG analyses we collapsed over the stimulus role factor.

For each participant, correct response trials were averaged to compute seven ERFs. As described above, recording began 100 ms before the second stimuli of each pair was presented, and lasted for 800 ms after presentation; trials comprising this 900-ms epoch were binned into sets of ERF waveforms. First, we binned trials to form the "recognition memory" contrast: (1) "old" condition (presentation of an "old" second probe, preceded by either old or new first probe); and (2) "new" condition (presentation of a "new" second probe, preceded by either old or new first probe). We additionally binned all trials into five ERF waveforms to form the "context-effect" contrasts, comprising the different reinstatement conditions: (3) "repeat" condition (presentation of an old object, preceded by the same old encoded pair member); (4) "re-pair" condition (presentation of an old object, preceded by a different old encoded pair member); (5) "N-O" condition (presentation of an old object, preceded by a new object; (6) "O-N" condition (presentation of a new object, preceded by an old object; and (7) "N-N" condition (presentation of a new object, preceded by a new object). Since there were not enough error trials to yield reliable ERFs in every condition, incorrect responses were omitted from the analysis.

ERF old/new effect. There are few prior studies of ERF correlates of recognition memory, and even fewer studies of associative recognition memory that would dictate the time windows and sensors of interest for analysis. Therefore, we first conducted a whole-helmet analysis in order to identify ERF differences related to recognition memory (i.e., the old/new contrast). The mean amplitudes of "old" and "new" ERFs were computed in 50-ms bins from 100 before to 800 ms after the presentation of the second stimulus, and the difference between the ERFs representing the old/new effect was calculated at each of the 246 sensors. As detailed in the Results section, this comparison identified the time window in which recognition memory success effects were extant.

ERF context effect. After identifying the two time windows of interest, we computed three additional differences between ERFs at each of the 246 sensors, representing contextual effects: two for hits, representing the difference between the repeat and re-pair conditions and the difference between the re-pair and N-O conditions; and one for CRs, representing the difference between the O-N and the N-N conditions.

As our phenomenon of interest is associative binding, for hits, we located the sensors in which the difference between repeat and re-pair in the time window of interest was maximal. In order to avoid inflated Type I error due to multiple comparisons, the selection of sensors was constrained by a Monte Carlo simulation, performed by randomly swapping the conditions across participants 1,000 times and calculating the F statistics for each permutation at each sensor. The distribution of the permutation statistic was compared with the observed statistics. Only comparisons with $p < .05$ after 1,000 iterations were considered to be significant. The selection of clusters was further constrained by a criterion of a minimal cluster size of six adjacent sensors. This procedure yielded no loci of interest for the early epoch (350–500 ms, see below), and three loci of differences for the late epoch (650–800 ms), each composed of multiple sensors.

These loci were further utilized for the other comparisons (repeat vs. N-O and re-pair vs. N-O; see Figure 1 for a topographic map of the differences and for a detailed spatial map of the loci, and Figure 2 for grand-averaged ERF waveforms). We performed two-way repeated measures ANOVA with the amplitude of the magnetic field as the dependent measure, and with location (left anterior, right anterior, and left posterior), and context reinstatement condition (repeat vs. re-pair vs. N-O) as repeated factors (see Figure 3 for the results of this analysis).

A. 350 – 500 ms

Repeat vs. Re-pair   Re-pair vs. N-O
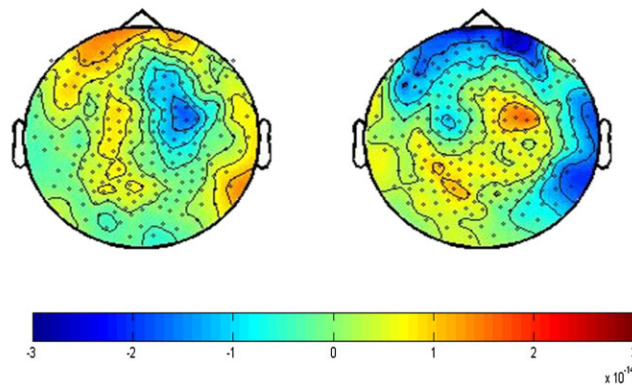
B. 650 – 800 ms
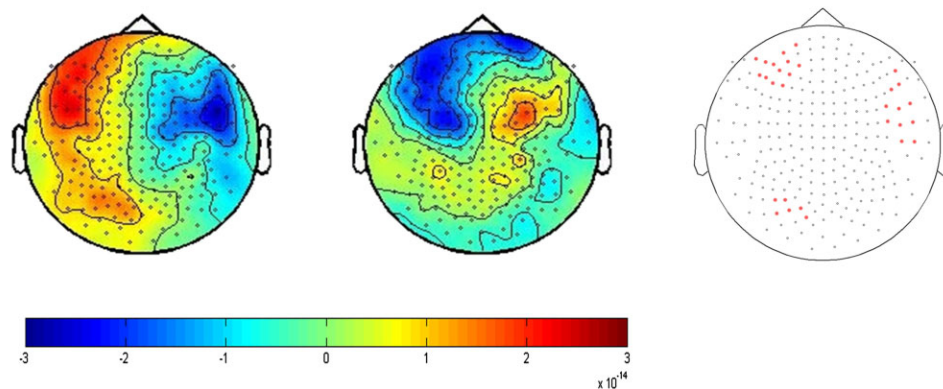
Repeat vs. Re-pair   Re-pair vs. N-O

Figure 1. Topography of the grand-averaged ERF differences between context reinstatement conditions for hits in time windows of interest. Sensors selected for analyses are shown on the right. A: Differences between repeat and re-pair (left) and between re-pair and N-O (center), in the early time window (350–500 ms). B: Differences in the late time window (650–800 ms).

For CRs, we located the sensors in which the absolute value of the difference between O-N and N-N was maximal, after controlling for inflated Type I error, using the same Monte Carlo approach described above. This procedure yielded two loci of maximal differences at the early time window and four loci at the late time window (see Figure 4 for a topographic map of the differences and for a detailed spatial map of the loci, and Figure 5 for grand-averaged ERF waveforms). We then compared mean ERF amplitude for each locus in each time window of interest, and compared the effects using repeated measures ANOVA. As above, we conducted separate analyses for hits and CRs. For the early epoch, we performed two-way repeated measures ANOVA, with location (left anterior, right anterior) and reinstatement condition (O-N vs. N-N) as repeated factors. For the late epoch, we used repeated measures ANOVA with location (left anterior, right anterior, central, left posterior) and reinstatement condition (O-N vs. N-N) as repeated factors (see Figure 6 for the results of these analyses).

Greenhouse-Geisser corrected degrees of freedom are reported as required. We further employed pairwise comparisons in order to identify the sources of significant effects. As in the previous analyses, in order to avoid inflated Type I error due to multiple pairwise comparisons, the analysis was based on a Monte Carlo simulation of 1,000 iterations, and calculation of the t statistics for each permutation. Only comparisons with $p < .05$ after 1,000 iterations were considered to be significant.

Results

Behavioral Results

Descriptive statistics of the behavioral analyses are shown in Table 1. For hits, the analysis only revealed a significant effect of context reinstatement condition, $F(2,74) = 23.66$, $p < .001$, $\eta_p^2 = .39$, with hit rates in the repeat condition higher compared to those in the re-pair condition, $t(38) = 5.59$, $p < .001$, and compared to the N-O condition, $t(38) = 5.07$, $p < .001$; there was no difference between hit rates in the re-pair and the N-O conditions. For CRs, the analysis also revealed a significant effect of condition, $F(1,37) = 15.11$, $p < .001$, $\eta_p^2 = .29$, as CR rates in the O-N condition were lower than those in the N-N condition, $t(38) = 3.97$, $p < .001$. There was also an effect of stimulus role, $F(1,47) = 4.09$, $p = .05$, $\eta_p^2 = .1$, with

CR rate for contexts exceeding those of targets, $t(37) = 2.1$, $p < .05$; this last comparison did not survive Bonferroni correction.

ERF Results

Old-new effects. Visual inspection of the distribution of sensors showing significant old-new differences indicated two distinct epochs in which retrieval-success effects were apparent: 350–500 ms and 650–800 ms. These time windows were used as epochs of interest to examine CE contrasts.

Context effects. The results of the ERF analyses for hits are shown in Figure 3. In the early epoch, no clusters were found in which CEs were significant. For the late epoch, the analysis revealed a main effect of cluster, $F(1.68,63.82) = 3.47$, $p = .045$, $\eta_p^2 = .084$, and a significant interaction between location and reinstatement condition, $F(2.84,107.93) = 4.71$, $p = .005$, $\eta_p^2 = .11$. To further explore this interaction, we performed repeated measures ANOVA separately for each location. For left anterior sensors, this analysis revealed a significant effect of reinstatement condition, $F(2,76) = 5.1$, $p = .008$, $\eta_p^2 = .12$. Monte Carlo pairwise comparisons revealed a significant difference between repeat and re-pair, $p = .004$, and between re-pair and N-O, $p = .002$, but not
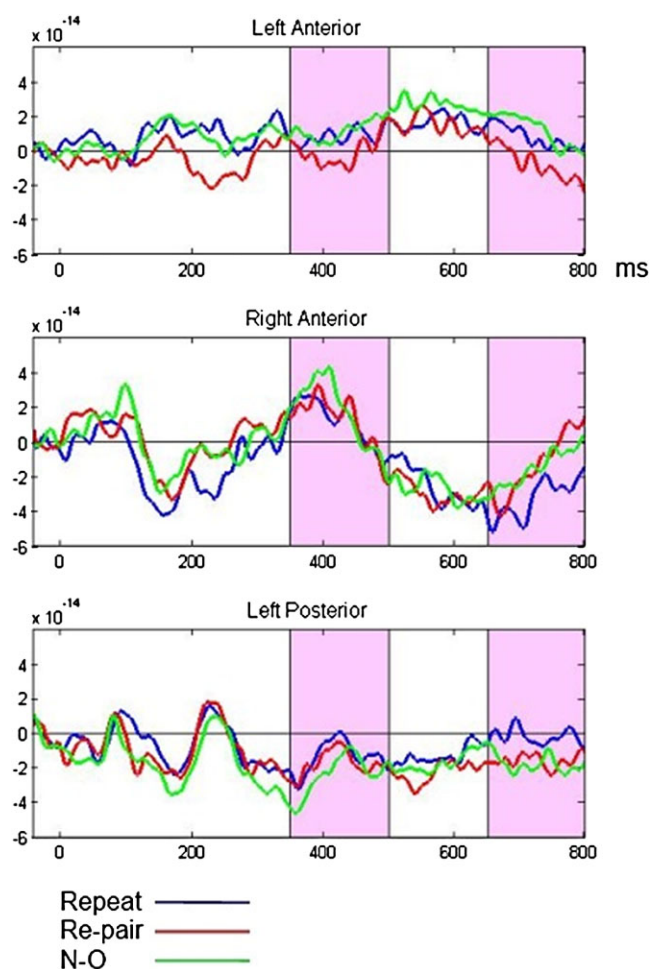

Figure 3. Magnetic field amplitudes for hits in loci of interest, for the three reinstatement conditions in the late time window (350–500 ms). Error bars represent standard errors. Significant differences are marked with asterisks. *$p < .05$; **$p < .01$; ***$p < .005$.

between repeat and N-O. For the right anterior sensors, repeated measures ANOVA revealed a significant effect of reinstatement condition, $F(2,76) = 3.45$, $p = .037$, $\eta_p^2 = .08$. Pairwise comparisons revealed a significant difference between repeat and re-pair conditions, $p = .003$, and between repeat and N-O, $p = .012$. For left posterior sensors, repeated measures ANOVA revealed a significant effect of reinstatement condition, $F(2,76) = 3.4$, $p = .039$, $\eta_p^2 = .08$. Pairwise comparisons revealed significant differences between repeat and re-pair, $p = .027$, and between repeat and N-O, $p = .004$, but not between re-pair and N-O.

Topographic differences related to CRs are shown in Figure 4. The results of the analyses relating to CRs are shown in Figure 6. The analysis of the early epoch revealed a significant interaction between location and reinstatement condition, $F(1,38) = 12.85$, $p = .001$, $\eta_p^2 = .25$, suggesting that the context-reinstatement effect was more pronounced in right anterior sensors ($p < .001$) than in left anterior sensors ($p = .004$). The analysis of the late epoch revealed a significant effect of location, $F(1.7,74.9) = 20.62$, $p < .001$, $\eta_p^2 = .35$, and a significant interaction, $F(2.36,89.66) = 9.3$, $p < .001$, $\eta_p^2 = .21$. Further analysis revealed a significant effect of reinstatement condition in all locations (all $ps < .005$), but this effect was more pronounced in anterior and central compared to the left posterior location.

To sum up the main ERF findings, for hits, CE-related differences emerged in the late epoch (650–800 ms). These ERFs differed between the contextual reinstatement conditions in both anterior and posterior locations. For CRs, early (350–500 ms) CE-related differences emerged in central locations, while late differences emerged in all locations.

Figure 2. Grand-averaged ERF waveforms elicited by hit-trials in the repeat, re-pair, and N-O conditions. Data are shown for the three sensor clusters selected as loci of interest. Shadings indicate the two time windows used for statistical analyses: 350–500 ms and 650–800 ms.
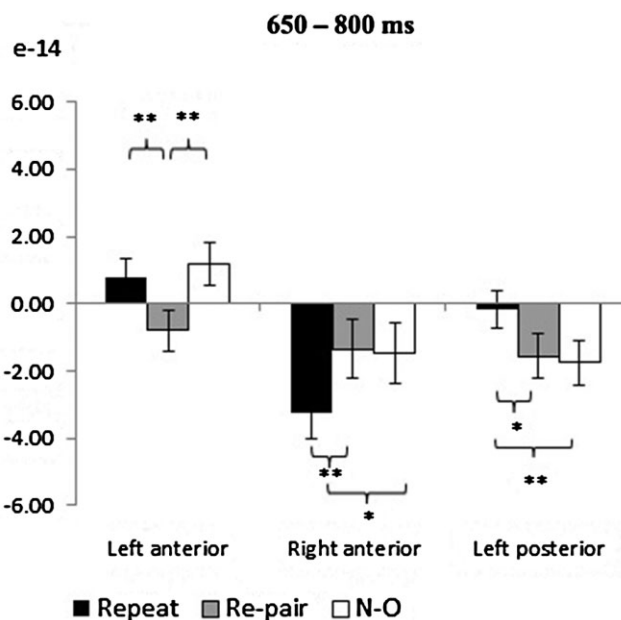
Discussion

Our main goal was to explore how the presence or absence of unitization of stimuli at encoding modulates ERF correlates of

A. 350 – 500 ms

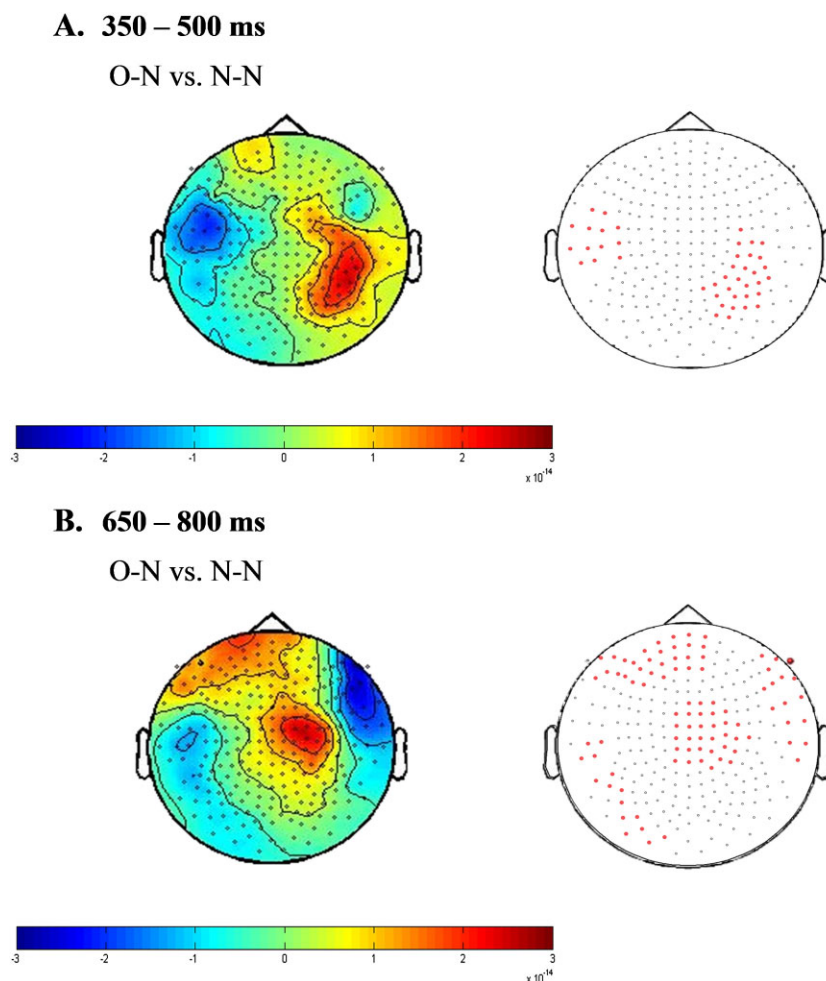O-N vs. N-N

B. 650 – 800 ms

O-N vs. N-N

Figure 4. Topography of the differences for CRs in time windows of interest. Sensors selected for analyses are shown on the right. A: Differences between O-N and N-N in the early time window (350–500 ms). B: Differences in the late time window (650–800 ms).

associative recognition processes. We evaluated the hypothesis that, when associated stimuli are not unitized, due to temporal separation of their presentation, access to the associative information requires recollective processes, and cannot be accessed by familiarity-related retrieval processes. We examined this proposal in a CE paradigm, in which contextual reinstatement improves recognition success, an effect dependent on access to associative information. Behavioral findings associated with the current data are detailed in Tibon et al. (2012). These findings provide support for the notion that contextual reinstatement facilitates recognition memory, but that in the absence of unitization, such an associative retrieval depends on recollection. The current examination focused on the magnetophysiological correlates of this phenomenon. Our finding was that while the FN400 component, generally associated with familiarity processes, was not modulated by access to the associative contextual information, the LPC component, generally identified with recollective processes, was sensitive to the CE, i.e., to the reinstatement of associative contextual information.

The lack of modulation of the earlier ERF old/new effect is compatible with the identification of the analogous FN400 ERP component with retrieval processes based on familiarity. It is asserted that familiarity does not contribute to associative recognition unless the to-be-associated items are unitized into a single

representation (e.g., Jäger et al., 2006; Quamme, Yonelinas, & Norman, 2007; Rhodes & Donaldson, 2007; Yonelinas et al., 1999). In the current study, unitization at encoding was not likely due to the sequential presentation of the picture pairs. Therefore, associative familiarity strength seemingly did not contribute to the recognition of the item embedded with its original contextual information. Accordingly, the reinstatement conditions did not differ in the ERF seemingly analogous to the FN400 old/new effect.

These results converge with the DD framework, pointing to dissociation between different types of associations, based on the ability to unitize the associated stimuli (Mayes et al., 2007), and further extend this theory to account for differences along the temporal course of the episodic experience. According to DD theory, associations can be created at encoding between unitized intraitem associations, interitem associations between similar kinds of items (within-domain associations), or different kinds of items coming from distinct sensory modalities (between-domain associations). We proposed that associations can also be fractionated along the axis of temporal overlap, that is, to what extent the encoded stimuli share the same temporal frame (Tibon & Levy, 2014; Tibon et al., 2012). We proposed that, like between-domain associations, retrieval of intertemporal associations, even between items of the same domain, must rely on recollection. In accordance with this
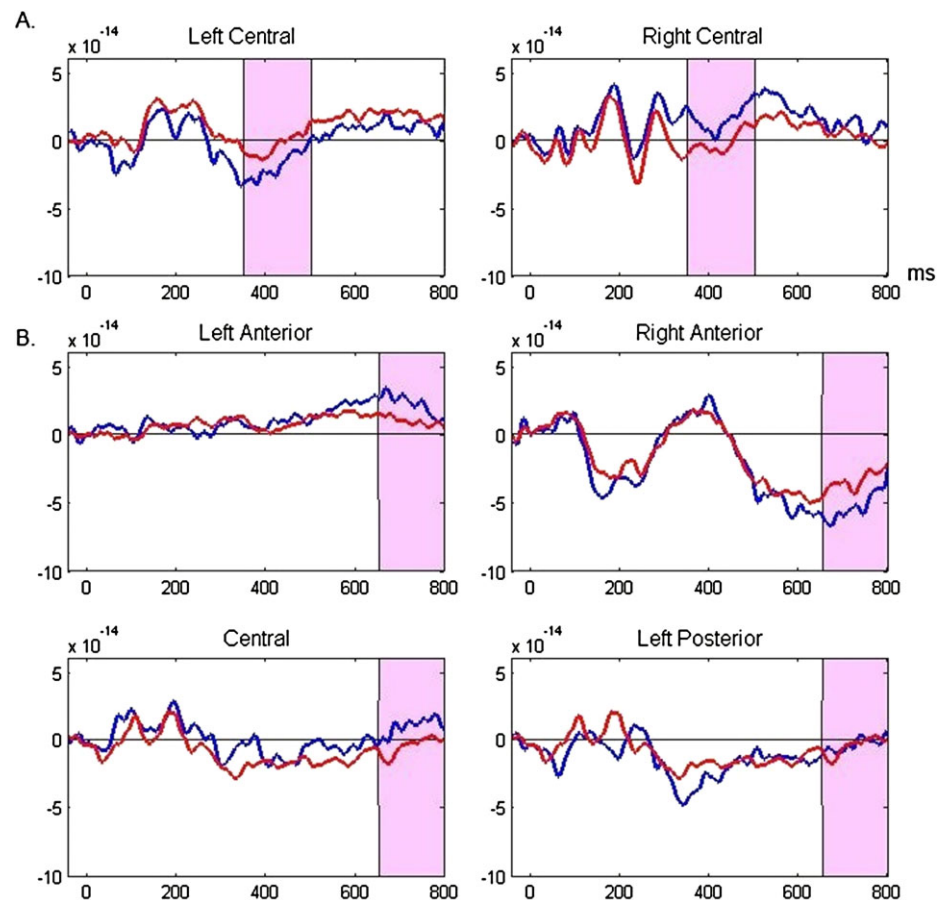
Figure 5. Grand-averaged ERF waveforms elicited by trials in the O-N and N-N conditions. A: Data for the two sensor clusters used in the statistical analyses in the early time window (350–500 ms). B: Data for the four sensor clusters used in the statistical analyses in the late time window (650–800 ms).
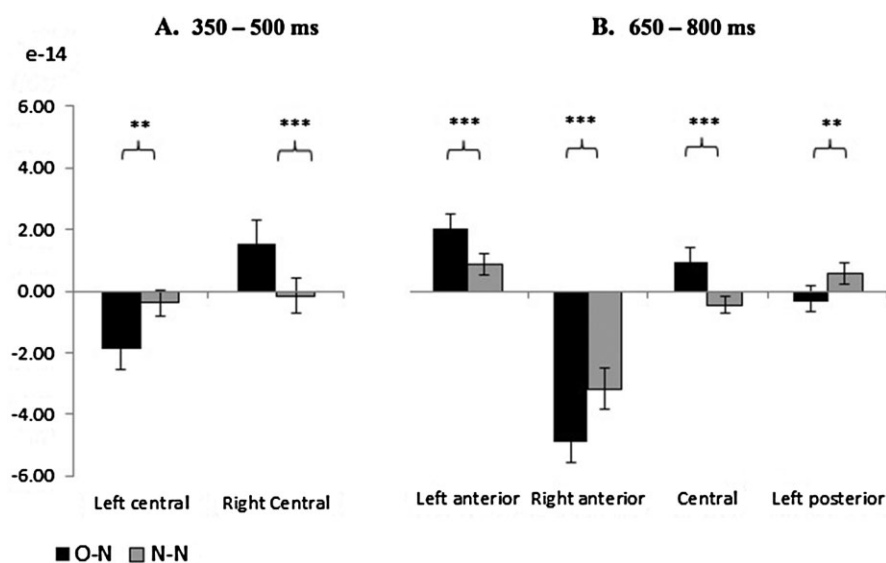

Figure 6. Magnetic field amplitudes for CRs in different loci of interest, in two context reinstatement conditions. Left: activation in two locations in the 350–500 ms time window. Right: activation in four locations in the 650–800 ms time window. Error bars represent standard errors. Significant differences are marked with asterisks. *$p < .05$; **$p < .01$; ***$p < .005$.

Table 1. *Rates of Hits (for Repeat, Re-pair, and N-O Conditions) and Correct Rejections (for O-N and N-N Conditions) for Object Pictures in Various Stimulus Roles and Reinstatement Conditions*

Role at encoding	Condition	Mean	SD	SE	Minimum	Maximum
Target	Repeat	.853	.086	.019	.65	1.00
(*N* = 21)	Re-pair	.798	.100	.022	.55	.97
	N-O	.782	.129	.028	.55	1.00
	O-N	.847	.099	.022	.60	.97
	N-N	.899	.067	.015	.76	.99
Context	Repeat	.816	.135	.032	.58	.95
(*N* = 18)	Re-pair	.696	.148	.035	.40	.90
	N-O	.722	.131	.031	.45	.88
	O-N	.901	.042	.009	.83	.98
	N-N	.927	.054	.013	.75	.99

suggestion, this type of associative information does not modulate retrieval-related ERP/ERF components associated with familiarity.

We did, however, find a modulation of this component for CRs: activation was considerably higher in the O-N condition compared to the N-N condition in both left and right anterior sites. This modulation, reflecting item rather than associative familiarity, was expected according to the multifactorial model of CE (Vakil, Raz, & Levy, 2007), which claims that the additive recognition effect of the items differs between these conditions, since in the O-N condition one item is familiar, whereas in the N-N condition both items are new. Thus, a modulation of the component that indexes familiarity is expected in this case.

In the later time range, context-reinstatement-based ERF modulation in posterior sites was apparent for both hits (repeat vs. re-pair and N-O contrast) and CRs (O-N vs. N-N contrast). As the ERP component analogous to this ERF (the LPC) is implicated in recollection, it may be suggested that these context-reinstatement-based ERF differences presumably reflect sensitivity to associative binding between the judged object and its associated information, which only remains intact in the repeat condition. This modulation occurred even in the present paradigm, in which the task does not require explicit associative retrieval (i.e., the items, and not associations, were judged to be old or new), such that associative memory was expressed implicitly.

Why would intertemporal associations require recollection for their retrieval? Seemingly, this effect results from the complexity of the encoding episode (Tibon & Levy, 2014). Encoding and retrieval of temporally structured memories, and specifically of sequences of discontiguous events, appear to be the province of the hippocampus. It has been suggested that hippocampal "time-cells" play the role of an associator of discontiguous events (MacDonald, Lepage, Eden, & Eichenbaum, 2011). Episodic retrieval in which the hippocampus is implicated is generally considered to be related to recollective processes (Aggleton & Brown, 1999; Eichenbaum, Yonelinas, & Ranganath 2007). Importantly, the late posterior retrieval success ERP component (LPC) is also considered to be modulated by the degree of recollection (Friedman & Johnson, 2000; Mecklinger, 2000; Rugg & Curran, 2007; Wilding & Ranganath, 2011). The pattern of modulation in the posterior sensors in the current study is reminiscent of the LPC as reported in ERP studies. In the present case, the addition of the temporal

dimension seemingly results in engagement of hippocampal recollective processes, which leads to modulation of the LPC component.

In anterior sites, during the later time window, the repeat and N-O conditions were characterized by stronger ERFs than the re-pair condition. The nonlinear relationship between the degree of similarity of the test probe to the study material and the strength of the ERF, along with the temporal and spatial dynamics of this effect, suggest that this relatively late component reflects neither familiarity nor recollection. This pattern of modulation might reflect the strength of recollective processes accompanying the evaluation of the target probe. Associative judgments may be relatively fluent when both test probe items were studied together, or when one of the items is new (allowing easy rejection). However, when both items are old, but were not studied together, the congruency between associative information (i.e., the paired probe) and associative information (i.e., the association between the two probes) is violated, and extraction of associative information is made more challenging. This interpretation is supported by reports of similar activations for rearranged and weakly associated pairs, but not for strongly associated ones (Speer & Curran 2007), and by the results of Mitchell, Andrews, and Ward (1993) who found that, during retrieval of re-paired studied sentences, a frontally distributed component differs from that elicited by repeated and new sentences. We surmise that this associative emergence can take place both when associations are judged explicitly (as, for example, in the case of Speer & Curran, 2007), or when associative strength implicitly affects recognition of a target item (as in the current case). However we interpret this finding, the current data clearly indicate that the later old/new effect cannot be considered as one unified effect, but may be decomposed into at least two functionally and spatially distinct components.

One goal of the current study was to further characterize ERF components related to associative recognition memory. Although EEG and MEG measure mostly the same signal sources, MEG is sensitive only to part of the signal (nonradial sources) but yields sharper and less distorted images; thus, ERP and ERF components are not completely alike (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). Several studies have addressed the issues of recognition memory using MEG (Bridson, Muthukumaraswamy, Singh, & Wilding, 2009; Düzel et al., 2003; Staresina, Bauer, Deecke, & Walla, 2005; Tendolkar et al., 2000), but there are few reports regarding associative recognition. Our finding that earlier and later retrieval-success ERFs are differentially modulated by recollective access to associative information indicates convergence with findings of EEG recognition memory studies. Additionally, the suggested functional and spatial decomposition of the late recognition success effect into two separate components adds to the EEG literature, which is not always able to map such dissociations.

In conclusion, the current study reveals that differences between ERFs elicited by correct recognition of object picture probes in two time windows are differentially modulated by the amount of associated information reinstated at retrieval, even when such contextual information is expressed only implicitly. When the association between stimuli is formed over time, as is the case in sequential presentation at encoding, the retrieval of such associative information seemingly requires recollective processes, and elicits their neural substrates.

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