



Cognitive association formation in episodic memory: Evidence from event-related potentials

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ABSTRACT

The present study focused on the processes underlying cognitive association formation by investigating subsequent memory effects. Event-related potentials were recorded as participants studied pairs of words, presented one word at a time, for later recall. The findings showed that a frontal-positive late wave (LW), which occurred 1–1.6 s after the presentation of the second word of a pair during study, was associated with later paired associate recall. The observed LW likely reflected cognitive association formation processing. Paired associate recall was also associated with a larger P555 to each word of a pair, likely reflecting the encoding of each individual word of a pair, which necessarily precedes association formation between the two words. Moreover a larger N425 was elicited by pairs that were encoded in a low context-similarity condition compared to that of a high context-similarity condition, likely reflecting semantic integration. Minimum norm source analyses showed that the likely sources of these ERP effects changed dynamically in time: a widespread fronto-temporo-parietal activation during the N425 was followed by a fronto-temporal activation during the P555, and finally by a left prefrontal activation during the LW.

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1. Introduction

We often remember through associations. For example, when we hear a specific song we may vividly remember an episode from the last vacation we spent in the Caribbean, or perhaps our first kiss. Understanding how cognitive associations between different memoranda are formed during encoding, particularly when and where in the brain, remains a classic problem in memory research. The present study examined cognitive association formation by replicating and extending the previous work on subsequent memory effects using event-related potentials (ERPs). The subsequent memory paradigm is commonly used to study how information is encoded into memory. In this paradigm brain responses are measured while participants are presented with to-be-remembered items. Afterwards participants are asked to retrieve these items. The brain responses are then sorted and averaged according to whether the corresponding item was subsequently retrieved or not. The brain responses to subsequently retrieved and non-retrieved

items can then be compared to reveal the location and timing of the brain activity that occurs during effective encoding.

The use of paired associates provides an opportunity to study not only the encoding of individual words but also the associative processes that occur at study. In order to separate the encoding of the individual words from the association formation, the words can be presented sequentially. If they are presented together, as in the typical procedure in the experimental psychology laboratory (Lockhart, 2000; Weyerts, Tendolkar, Smid, & Heinze, 1997), the brain responses recorded for the encoding of the first word, the encoding of the second word, and the association between them, are inextricably bound together. However, if the words of a pair are presented sequentially, it is possible to record the encoding of the first word separately from the other components, and then use the evidence thus obtained to sort out the encoding of the second word from the cognitive association formation process(es).

In a previous study of cognitive association formation by Kounios, Smith, Yang, Bachman, and D'Esposito (2001), participants classified pairs of words at encoding according to whether the association was formed through (1) conceptual integration or (2) simple juxtaposition. Each word of a pair was presented sequentially. Participants were later asked to retrieve the order of the words of a pair. The results showed that for pairs of words that were associated through conceptual integration, sustained ERP positivity after

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the second word was greater for those pairs whose order was later retrieved more quickly. The opposite pattern was observed for pairs that were associated by juxtaposition, suggesting that different neural mechanisms underlie these two strategies of association formation. However, Kounios and colleagues only analyzed successfully retrieved pairs according to order retrieval speed, which is an indirect measure of the effectiveness of association formation.

In the first ERP study that investigated subsequent memory effects using paired associates (Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980), participants judged whether two words of a pair were the same or different based on orthographic, phonemic, or semantic attributes. Each word of a pair was presented sequentially. Participants were then tested on recognition for the second word of a pair. Semantic processing led to the highest percentage of recognized words, followed by the phonemic and then the orthographic comparisons. In three subjects, judgment-task waveforms were averaged on the basis of subsequent recognition. Subsequently recognized words elicited a larger late positive component (LPC) and slow wave compared to subsequently unrecognized words. Unfortunately, these data were not statistically analyzed.

Other studies have found similar ERP effects for the recognition and recall of single words (for reviews see Donchin & Fabiani, 1991; Johnson, 1995; Rugg, 1995). In one such study (Karis, Fabiani, & Donchin, 1984), subsequently recalled words elicited greater positivity compared to subsequently non-recalled words, with a peak latency of 520 ms. The topography and time-course of this effect varied as a function of the encoding strategy that was used. For participants who used rote rehearsal strategies, the amplitude of the parieto-central P300 elicited by subsequently recalled words was larger than that of subsequently non-recalled words (Karis et al., 1984; also see Fabiani, Karis, & Donchin, 1986). For participants who used elaborative rehearsal strategies, a frontal-positive slow wave, which began around 500 ms and slowly increased over the next several hundred milliseconds, was larger for subsequently recalled, compared to non-recalled, words (also see Fabiani, Karis, & Donchin, 1990).

Paller, Kutas, and Mayes (1987) examined ERPs during an incidental memory paradigm. They found greater parietal positive activity in the 400–800 ms latency range for subsequently recalled and recognized words, compared to subsequently non-retrieved words. Paller et al. referred to the difference between ERPs to subsequently retrieved and forgotten words as ‘Dm’ and defined it operationally as “any ERP Difference based on later memory performance”. They found that Dm could not be accounted for solely in terms of changes in the typical P300 amplitude, since the Dm was largest for the semantic tasks over the anterior scalp area. Further, Dm scalp distribution for words (Friedman, 1990) and faces (Sommer, Heinz, Leuthold, Matt, & Schweinberger, 1995) are significantly different from that characteristic of the P300. Thus, although Dm and the P300 may overlap temporally, the topographic distributions suggest that the two have different brain origins.

In addition to the parietal P300 and frontal-positive slow wave Dm effects, other studies have revealed a left fronto-temporal negative Dm around the same time as the P300. For example, Mangels, Picton, and Craik (2001) found a fronto-temporal N340 that was larger for subsequently recognized, compared to unrecognized, words. However, the N340 did not differentiate between items based on Remember (R)/Know (K) judgments (Tulving, 1985; also see Friedman & Trott, 2000; data reanalyzed in Friedman & Johnson, 2000).

The results of the aforementioned studies and the extant literature indicate distinct encoding processes: whereas the posterior positivity and fronto-temporal negativity may reflect encoding pro-

cesses that enable subsequent item retrieval without additional contextual details, long lasting frontal positivity may index elaborative encoding processes that enable subsequent retrieval with rich contextual details.

In the present study we investigated subsequent memory ERP effects with paired associates, extending the previous literature by examining the Dm effect for paired associates. We did so by focusing on the brain responses recorded after the presentation of the second word of a to-be-learned pair during the encoding phase of the experiment, when cognitive association formation is likely to occur. Furthermore we did so under two experimental conditions in which the subjects’ behavioral performance, for identical studied items, was expected to vary greatly because of differences in the to-be-learned pairs’ intra-list context. In the present study, the ERP response that followed the second word of a pair was examined to see whether there are any ERP correlates for the successful cognitive association formation between the two words. Extrapolating from the literature on Dm effects reviewed above, we hypothesized that subsequently recalled pairs, compared to non-recalled pairs, would be associated with a larger frontal-positive component.

Paired associate learning is enhanced when each pair in a list belongs to a different conceptual category compared to when all pairs in the list belong to the same conceptual category. This effect of context was demonstrated by Bower, Thompson-Schill, and Tulving (1994) in a study where participants were presented with pairs composed of items from the same conceptual category. Consequently, the participants in this study were able to predict the category of the target when they were given the cue during test. The effect of context on recall may likely be related to the distinctiveness of each pair in a given list in relation to all other pairs in the list: an increase in distinctiveness would lead to a decrease in response uncertainty to a given cue and less interference.

In the present study, we sought to examine further whether cognitive association formation varies as a function of intra-list encoding context. Based on the extant literature, we hypothesized that paired associates in the Different condition would be better recalled than those in the Same condition. Moreover, we sought to examine differences between the evoked potentials recorded for the two context conditions (Same and Different) during encoding. The N400 is a negative ERP component that is typically observed over the centro-parietal regions of the scalp, and has been observed to be larger to words that deviate from the semantic context compared to those that do not (Federmeier & Kutas, 1999; Kutas & Hillyard, 1980; Kutas & Hillyard, 1982). Based on the existing literature, we predicted that items in the Different condition, where intra-list semantic similarity was low, would elicit a larger N400 compared to items in the Same condition, where intra-list semantic similarity is relatively higher. The present study was set up to answer the question of whether subsequent memory ERP effects for cognitive association formation vary as a function of intra-list context manipulation. However, since we did not find any past studies that we could soundly ground a relevant hypothesis upon, this portion of the study was exploratory, without a specific *a priori* hypothesis.

2. Methods

2.1. Participants

Fourteen healthy, young adults (7 female; mean age: 24, range: 19–32; first language: English) participated in this experiment. All subjects had normal or corrected-to-normal vision and no history of neurological or psychiatric disorder. The study was approved by the Baycrest Research Ethics Board and all subjects provided written informed consent prior to the experiment. The data from two subjects were discarded: one of these subjects had too few trials in one of the conditions to allow ERP analysis, and the other subject had large movement artifacts throughout the recordings. As a result, ERP averages were obtained from 12 participants.

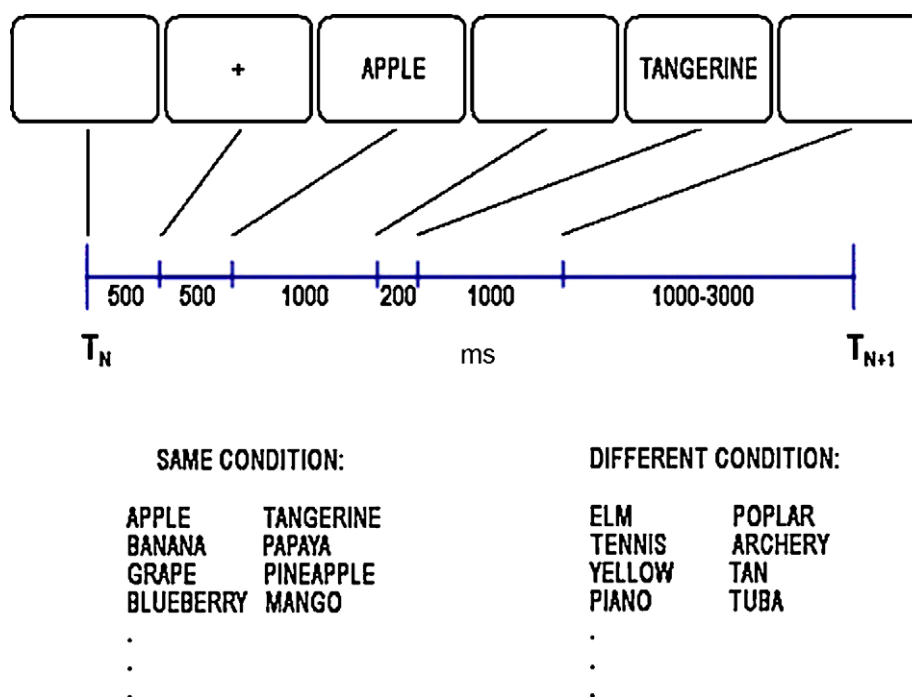


Fig. 1. The time-course for the evoked potential trial to the paired associates (above) and example of paired associates used in the Same and Different conditions (below). T_N is the beginning of the N th trial and T_{N+1} the beginning of the subsequent trial.

2.2. Materials

Two hundred paired associates were generated for this experiment by selecting 20 names of instances of each of 20 conceptual categories. The 200 pairs of nouns were used to compose 20 lists of 10 pairs each. Each pair used in the experiment, in all lists, consisted of nouns representing the same conceptual category (e.g., BLACKBIRD–PENGUIN; TENNIS–ARCHERY; ITALY–NORWAY; THUNDER–SMOG; CHEMISTRY–ARCHEOLOGY; TRUMPET–CELLO). The 20 conceptual categories used in the present experiment were: four-legged animals, articles of clothing, birds, boats, chemical elements, cities, colours, countries, fields of study, fish, flowers, fruits, insects, musical instruments, human body parts, professions, sports, trees, vegetables, weather phenomena.

The 200 pairs were used to make up two types of lists: 10 “Same” lists, consisting of pairs that all belonged to the same conceptual category; 10 “Different” lists, consisting of pairs that each belonged to a different conceptual category. An example of a Same list is as follows: BATTLESHIP–LINER; SPEEDBOAT–TANKER; SUBMARINE–CARGOSHIP; DESTROYER–SCHOONER; SAILBOAT–STEAMSHIP; TUGBOAT–FERRY; WARSHIP–CLIPPERSHIP; ROWBOAT–DINGHY; FREIGHTER–CANOE; CRUISER–MOTORBOAT. An example of a Different list is as follows: CRIMSON–BEIGE; STOCKHOLM–RENO; POTASSIUM–BARIUM; MOUSE–RABBIT; TENNIS–ARCHERY; BLACKBIRD–PENGUIN; LOUSE–TICK; ITALY–NORWAY; NOSE–KNEE; BALSAM–SYCAMORE. The use of the two types of lists allows us to generalize (some of) our findings over conditions of learning in which behavioral retention performance varies considerably although the individual to-be-learned associations are held constant. Knowledge of such generalizations may provide useful guidance in future studies of cognitive association formation.

None of the pairs appeared in more than one list for a given subject, and the pairs as such were never changed. The pairs of words were counterbalanced across subjects in the experiment so that each pair appeared equally frequently in both the Same and Different lists.

2.3. Experimental procedure

Each subject participated in one experimental session. The experimental task consisted of three phases: encoding, an intermediate delay and cued recall. Each session began with a short practice block to familiarize the subjects with the experimental task. Each subject then studied and recalled 20 lists, with short breaks after every fifth list. The type of list alternated between Same and Different. Subjects were asked to memorize the pairs, knowing that they would be later tested for paired associate recall. They were not instructed to use any specific encoding strategy.

At the start of the evoked trial (Fig. 1) a 500 ms delay was followed by central ‘+’ which served as a warning and lasted for 500 ms. The first word of a pair (W_1) was then presented for 1000 ms, followed by a 200 ms blank screen. The second word of a pair (W_2) was then presented for 1000 ms. The interval between trials lasted 1000–3000 ms.

During the delay, subjects solved eight arithmetic equations of the form: $A + B + C = ?$, where A , B and C were randomly selected digits from 0 to 9. Each equation was presented on the screen for 3750 ms, followed by a 250 ms blank screen. Within this 4000 ms period, participants were asked to respond vocally, as quickly and accurately as possible, with the correct answer. After giving their response, participants moved on to the next equation without delay.

During recall, participants were presented with a central ‘+’ for 200 ms, followed by a cue word for 7000 ms. Within this 7000 ms interval, subjects responded vocally with the word that they believed was paired with the presented cue. The next cue word occurred once they had given a response or when a time limit of 7000 ms was reached. The cue word had an equiprobability of being either W_1 or W_2 of the pair. A question mark was presented with each cue word: if W_1 was used to cue the pair, a question mark was presented to the right of the cue word, and if W_2 was used to cue the pair the question mark was presented to the left of the cue word. Subjects responded verbally and the experimenter coded whether the response was correctly recalled (R) or not (NR). Both an incorrect word and the absence of any recalled word were classified as non-recalled.

2.4. Behavioral data analyses

Paired associate recall performance, measured as the percentage of correctly recalled pairs, was calculated separately for the Same and Different conditions. For both conditions the mean percentage of pairs correctly recalled at each serial position in the list was calculated.

2.5. Electrophysiological recording

EEG activity was recorded during all three phases of the experimental task but only the recordings from the encoding phase will be reported in the present study. EEG activity was recorded from a 64-channel EEG cap (Electro-Cap international, 10–10 system) using a Neuroscan Synamps (El Paso, TX, USA), amplified (500 times), filtered (0.05–50 Hz), sampled at 250 Hz, and referenced to Cz. Electrodes were located over all scalp regions with four electrodes near the eyes and nine electrodes below the Fpz–T7–Oz–T8 “equator.” All impedances were kept under 5 kOhms. Eye blinks, horizontal and vertical eye movements were recorded immediately before and after the experiment to allow ocular artifacts to be compensated using source components (Picton et al., 2000).

2.6. Electrophysiological data analyses

For each subject, continuous EEG files were evaluated using the Brain Electromagnetic Source Analysis software of BESA 5.1.8. The EEG data was epoched into 4200 ms segments beginning 500 ms before the ‘+’ stimulus and lasting 1000 ms after the offset of the second word in the pair.

The ERPs recorded during study were sorted based on whether the corresponding pair of words was later recalled or not-recalled during test. This sorting of study phase ERPs based on memory performance was done separately for the Same and Different conditions, yielding the following four categories of ERPs: (a) subsequently recalled pairs from the Same condition (SameR); (b) subsequently non-recalled pairs from the Same condition (SameNR); (c) subsequently recalled pairs from the Different condition (DiffR); (d) subsequently non-recalled pairs from the Different condition (DiffNR). Individual subject waveforms were created by averaging the ERPs in these four categories. These average files were corrected for eye artifacts and filtered with a low cut-off of 0.05 Hz. Eye artifact correction was done in BESA 5.1.8 using source components derived from the recordings made immediately before and after the experimental session. The mean trial counts going into the grand-mean waveforms were 42.4 (range: 28–60) for SameR, 57.6 (range: 40–72) for SameNR, 70.9 (53–89) for DiffR and 29.1 (11–47) for DiffNR.

2.7. Partial least squares

Partial least squares (PLS, <http://www.rotman-baycrest.on.ca/pls>) is a multivariate technique that describes the relation between a set of independent experimental variables and a large set of dependent measures. This technique has previously been used to analyze ERP data (Lobaugh, West, & McIntosh, 2001; Vallesi, Stuss, McIntosh, & Picton, 2009). In the present study, spatio-temporal mean-centered and non-rotated PLS analyses were used to detect where on the scalp the strongest experimental effects were expressed and when during the epoch these effects occurred.

Mean-centered PLS computes the optimal least squares fit to part of a cross-block covariance matrix (Wold, 1982). In this matrix, the sequence of time-points for each electrode is ordered as columns, whereas the subjects within each experimental condition are ordered as rows. A singular value decomposition of this matrix yields latent variables (LVs), that describe how strongly a specific pattern of experimental conditions (design scores) is expressed at each time point in terms of ERP amplitude. The number of LVs extracted is equal to the number of experimental conditions, with the first LV accounting for the most variance. A salience is then calculated for the LV at each electrode at each time-point. The polarity and magnitude of the electrode salience denote the direction and strength, respectively, of the identified differences among the experimental conditions shown in the design scores. Scalp scores for each LV are obtained by multiplying the electrode saliences by the raw waveforms of each subject. These scalp scores measure how strongly each individual subject contributes to the patterns depicted by the LV.

Statistical significance of the whole spatio-temporal pattern expressed by each LV was assessed by a permutation test using 500 permutations across the different experimental conditions (Edgington, 1980; McIntosh, Bookstein, Haxby, & Grady, 1996). Permutations consist of sampling without replacement to reassign the order of conditions for each subject. Mean-centered PLS is recalculated for each new permuted sample, and the number of times the permuted singular values exceeded the observed singular values in each LV is calculated and expressed as a probability. A LV was considered significant at $p < 0.05$.

A bootstrap test of over 100 bootstrap samples was used to assess the stability of the saliences identified for each LV, on each electrode and time-point. This was done to detect those portions of the ERP waveforms that express robust experimental effects across subjects and to circumvent the effects of possible outliers (Efron & Tibshirani, 1986). Bootstrap samples are produced by sampling with replacement and keeping the assignment of experimental conditions to each subject fixed. Mean-centered PLS is recomputed for each bootstrap sample. The ratio of the salience to its standard error, estimated through the bootstrap procedure, approximately corresponds to a z-score. Bootstrap ratios equal to or greater than 2.81 (roughly corresponding to a p level ≤ 0.005) were chosen as the cut-off for stable non-zero saliences.

A mean-centered PLS analysis was first conducted on the entire 4200 ms epoch, considering 4 conditions: 2 intra-list context conditions (Same and Different) \times 2 response types for paired associate recall performance (R and N). Since the full sweep results were complex to interpret, we conducted analyses on shorter periods of the recorded waveforms to hone in on particular experimental effects. For separate mean-centered PLS analyses, the following segments were extracted from the epoch and baseline corrected to the preceding 100 ms interval: duration in which W1 was displayed (1000 ms), duration in which W2 was displayed (1000 ms), 1000 ms interval starting at the offset of W2. As described for the full 4200 ms epoch, each of these segments was then analyzed using the mean-centered PLS technique and then again using the non-rotated PLS technique.

The non-rotated PLS analyses were conducted to assess the main effects and their interactions more directly, as done in previous studies (e.g. Itier et al., 2007; Michel et al., 2004). The logic underlying the non-rotated PLS technique is similar to that of the mean-centered PLS technique. However, in the non-rotated technique, the design contrast is defined a priori by the experimenter and the analysis is constrained so that the specified contrast represents 100% of the cross-block covariance. The significance of the specified contrast and the corresponding electrode saliences are assessed through the permutation tests. The bootstrap ratios are used to assess the time-points at which there is a reliable difference between the contrasted conditions. In the present study, a separate non-rotated analysis was conducted for each contrast. The following contrasts were examined for each of the W1, W2 and LW

time windows: all recalled pairs vs. all non-recalled pairs (i.e., DiffR: 1; DiffNR: -1; SameR: 1; SameNR: -1); all pairs in the Same condition vs. all pairs in the Different condition (i.e., DiffR: 1; DiffNR: 1; SameR: -1; SameNR: -1). Non-rotated PLS analyses were also conducted to examine further the interaction between context conditions (Same and Diff) and memory performance (R vs. NR). Based on the results of the mean-centered PLS analysis, a non-rotated analysis was conducted on the LW segment to examine further the interaction between context conditions (Same and Diff) and memory performance (R vs. NR) using the following contrast: DiffR vs. DiffNR (i.e., DiffR: 1; DiffNR: -1; SameR: 0; SameNR: 0).

2.8. Classical mean amplitude analysis

To focus further on the ERP components of interest, we also adopted a classical mean amplitude approach. Since the mean-centered PLS analysis did not show any interaction for W1 and W2 between the two experimental variables (i.e., intra-list semantic similarity condition at encoding and subsequent memory performance), the individual subject waveforms were then averaged at the group level for the following four categories: all recalled pairs, collapsed across the Same and Different conditions (AllR); all non-recalled pairs, collapsed across the Same and Different condition (AllNR); all pairs in the Same condition, collapsed across memory performance (AllSame); all pairs in the Different condition, collapsed across memory performance (AllDiff). Difference waves were obtained from the following subtractions: AllR–AllNR and AllDiff–AllSame.

Two peaks were identified in the grand-mean difference waveforms. A negative wave peaking around 425 ms (N425) near the vertex and a positive wave in the parietal region peaking around 555 ms (P555) were evaluated using mean amplitude measurements from the 400–450 ms and 530–580 ms latency windows after the onset of each word in a pair, respectively. A fronto-central late wave (LW) occurring near the vertex one second after the onset of the second word and lasting for several hundred ms was measured as the mean amplitude from 1000 to 1600 ms after W2 onset. Each of these measurements were analyzed at the electrode location where the derived differences were maximally recorded, using a multivariate repeated-measures ANOVA with intra-list context condition (Same and Different), cued recall performance (R and NR) and word order (W1 and W2) as factors.

2.9. Source analysis

Source estimation techniques allow temporal information provided by ERPs to be complemented with valuable spatial information resulting in a dynamic representation of the spatio-temporal pattern of brain activity. In order to prevent overlap with sensory evoked potentials, the source analysis was performed on the difference waveforms: AllDiff–AllSame for the N425 and AllR–AllNR for the P555 and LW. Source analysis was carried out using BESA programs for minimum norm analysis (Hämäläinen & Ilmoniemi, 1994; Michel et al., 2004). The minimum norm analysis places current sources on an extensive grid of locations in the brain. This analysis fits the scalp recorded activity to minimize the total power of all current sources on the grid. Such an analysis is particularly appropriate for late ERP components, when the source activity is more likely to be widespread than focal.

3. Results

3.1. Behavioral results

Subsequent memory performance was calculated as a function of intra-list context condition (Same and Different). The percentage of paired associate recall was higher for Different (70.9 ± 3.1) than Same (42.4 ± 3.4 ; $t(11) = 9.70$, $p < 0.001$). Evaluating recall performance as a function of serial position showed a borderline main effect of serial position [$F(9, 111) = 1.99$, $p = 0.046$], but post hoc comparisons indicated no significant differences between positions other than between serial positions 3 and 9 ($p = 0.04$).

3.2. Electrophysiological results

The warning stimulus (+) elicited a visual evoked potential followed by a contingent negative variation that was maximal over the center of the scalp. Both W1 and W2 elicited visual evoked potentials which contained a positive wave (115 ms), followed by a negative wave (185 ms) that were maximally recorded over the occipital regions and that were of opposite polarity over fronto-central areas. These visual evoked potentials were followed by a large negative wave around 425 ms (N425) and a positive wave around 555 ms (P555) over the centro-parietal region. The scalp topography differed for the N425 and P555, as the latter was max-

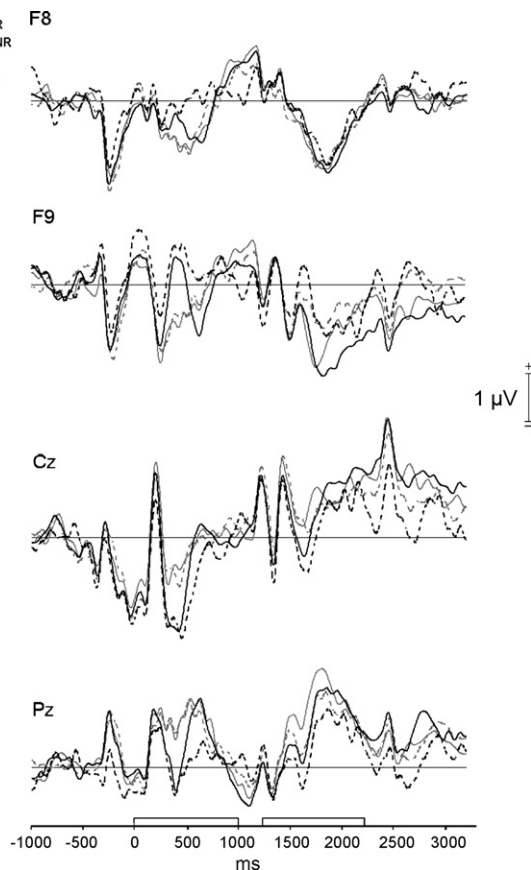


Fig. 2. Grand-mean ERP waveforms at encoding at electrode sites F8, F9, Cz and Pz: SameR=subsequently recalled pairs from the Same condition; SameNR=subsequently non-recalled pairs from the Same condition; DiffR=subsequently recalled pairs from the Different condition; DiffNR=subsequently non-recalled pairs from the Different condition. The presentation duration of the first word (W1) and the second word (W2) of a pair is marked on the time scale.

imally recorded over the parietal region whereas the former was maximal over the center of the scalp. The evoked potential to W2 was followed by a large broad positive wave, which began around one second after the onset of W2 and lasted for several hundred milliseconds: this wave will hereon be referred to as the late wave (LW). The scalp topography of this wave was complex with a broad positive distribution over the frontal region and a negative focus over the left fronto-temporal area. Fig. 2 displays an overview ERP graph with all four conditions (DiffR, DiffNR, SameR and SameNR) at four electrode sites (F8, F9, Cz and Pz). These data are quite complex. The PLS analyses served to simplify these results.

3.3. Mean-centered PLS results

Mean-centered PLS allowed us to determine the main findings in all of the available data (65 electrodes, 4200 ms, 2 conditions and 2 recall states). For each of the mean-centered PLS analyses reported below, the permutation test ($p < 0.005$) revealed that only the first LV was significantly affected by the experimental variables. The mean-centered PLS results are graphed in the following manner. The upper left represents the LV as seen at the electrode locations where it was most salient. The circles at the top of each electrode plot indicate when during the epoch the saliences for the first LV were stable across subjects (i.e., bootstrap ratio ≥ 2.81). The upper right represents the scalp topography of the saliences. The average amplitude waveforms for the four conditions included in the PLS analysis are shown in the bottom left. The lower right indicates

the design scores, which show how the LV changed with the different experimental conditions. Interpreting the saliences requires that they be seen through the polarity of the design scores. Positive saliences indicate when waveforms were more positive for more positive design scores. Thus, if the salience at particular electrode (upper left) shows a positive deflection and the design score (lower right) is negative, the corresponding average waveform will be negative.

3.3.1. Full 4200 ms epoch

Only the first LV was significant. It accounted for cross-block variance of 56% ($p < 0.028$). This LV was intricate and showed a salience pattern that could represent either a prolonged activation or multiple sequential brief activations. We attempted to dissect out different patterns in the ERP by considering briefer portions of the total waveform, covering the responses to the onset of W1 and W2 and the offset of W2. Each 1000 ms period of the ERP was then referred to a baseline calculated over the preceding 100 ms. This baseline procedure would remove the sustained effect noted over the whole ERP waveform and allow us to focus on transient effects.

3.3.2. W1 segment

Only the first latent variable (LV1; Fig. 3) was significant, and it accounted for cross-block variance of 56% ($p < 0.006$). A negative salience peak occurred within the 300–500 ms latency window, peaking at around 425 ms and maximally recorded at CPz. The polarity of this effect reversed in the fronto-temporal regions (more on the left than the right), peaking at FT9.

3.3.3. W2 segment

Only LV1 (Fig. 4) was significant, and it accounted for cross-block variance of 77% ($p < 0.000$). Within the 250–700 ms latency window, a negative salience peak occurred covering the latencies over which both the N425 and P555 occurred. This salience was most negative at P2 (right parietal electrode, close to Pz). The polarity of this effect was reversed in the fronto-temporal regions, with maximal positivity at FT9.

3.3.4. Final 1000 ms segment

Only LV1 (Fig. 5) was significant, and it accounted for cross-block variance of 64% ($p < 0.01$). The saliences for LV1 were stable throughout the 120–600 ms latency window. This effect was negative in the fronto-central regions most evidently at C4 (right central). The polarity of this effect reversed in the inferior frontal region and was strongest at F9.

3.4. Non-rotated PLS analysis

The non-rotated PLS analyses complemented the mean-centered analyses by allowing for a direct test of the main effects and their interactions. Each non-rotated analysis examined one contrast, so that the specified contrast represented 100% of the cross-block covariance. The results of the non-rotated analysis were consistent with the results of the mean-centered analyses. A summary of the significant contrasts is shown in Fig. 6. For the W1 segment, the contrast between the Same and Different conditions was significant ($p < 0.02$), but there was no significant effect of subsequent memory performance. For the W2 segment, there was a significant effect of subsequent memory performance ($p < 0.002$), and also a main effect of intra-list encoding context ($p < 0.02$). For the LW segment, there was a significant effect of subsequent memory performance ($p < 0.01$), but no main effect of intra-list encoding context. For the LW segment, the interaction contrast, DiffR vs. DiffNR, was significant at $p < 0.02$.

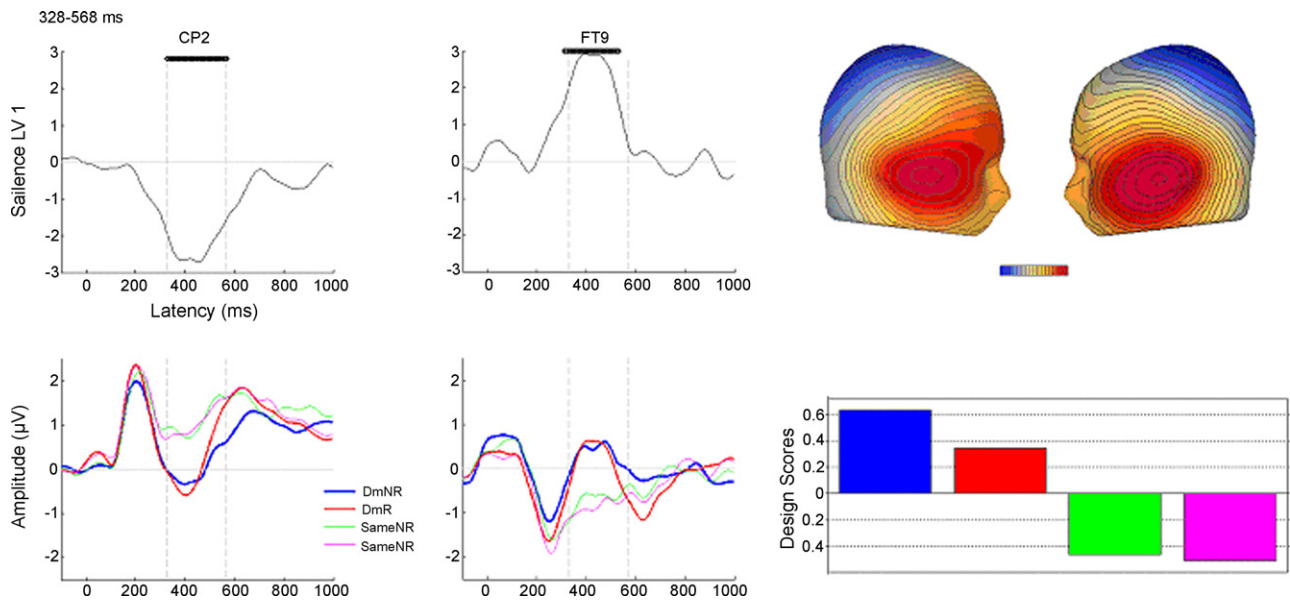


Fig. 3. Mean-centered PLS results for the analysis of the W1 segment. Peak electrode saliences for the first latent variable (LV1) is shown at electrode sites CPz and FT9 (upper, left panel). The circles at the top of each electrode plot indicate when during the epoch the saliences for LV1 were stable across subjects (bootstrap ratio > 2.81). The average amplitude waveforms for the four conditions included in the PLS analysis are shown in the bottom, left panel: DiffNR = not-recalled pairs in the Different condition; DiffR = recalled pairs in the Different condition; SameNR = not-recalled pairs in the Same condition; SameR = recalled pairs in the Same condition. The normalized topographical distribution of the saliences for all electrodes is shown on the top right and the LV1 design scores are shown on the bottom right.

3.5. Difference waveforms

The simple difference waveforms allowed for the identification and measurement of peaks. The grand-mean ERP waves recorded over the center and mid-parietal regions of the scalp are shown in relation to intra-list context in Fig. 7 and in relation to subsequent memory performance in Fig. 8. Whereas the N425 was related to intra-list context, the P555 and LW were related to subsequent memory performance. This is most clearly shown in the difference waveforms in the figures.

The N425 wave was larger for Different than for Same [$F(1, 11) = 13.74$, $p = 0.003$] at CPz, where the difference between the two conditions was maximally recorded, and was slightly smaller for W2 than for W1 (borderline $p = 0.057$), with no significant interactions. Fig. 9 shows the scalp topography of the mean N425 amplitude that was measured over the 400–450 ms latency window after the onsets of W1 and W2 for the Different-Same waveform.

The P555 was larger for R trials than for NR trials at Pz, where it was maximal, but only approached significance when both W1 and

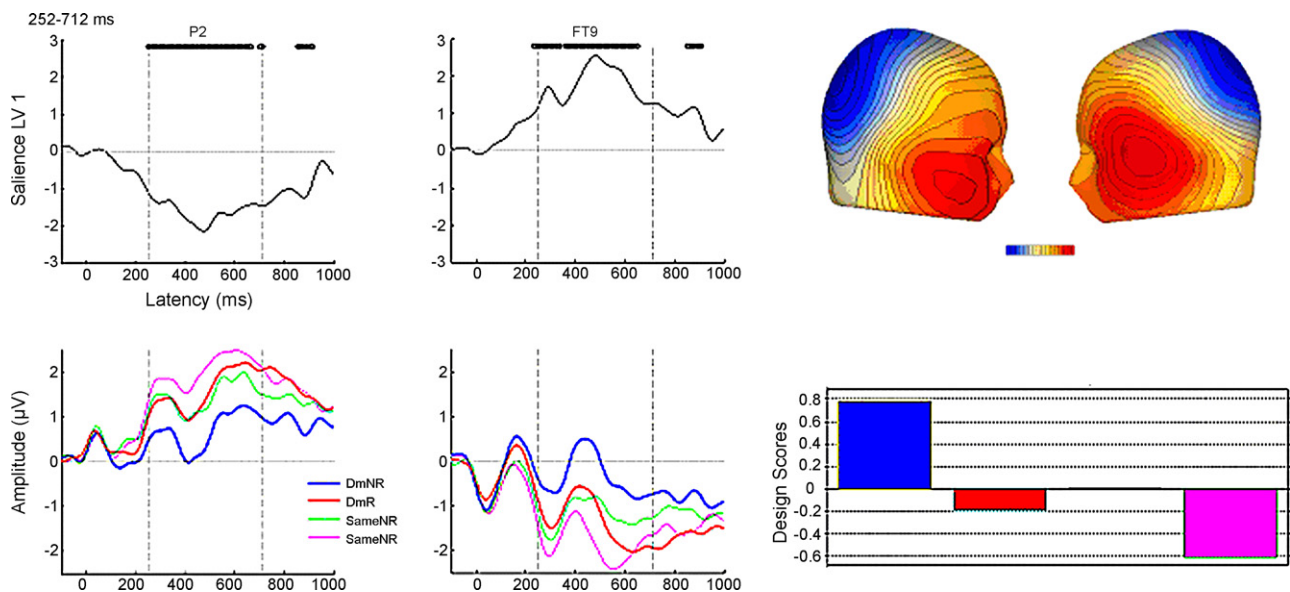


Fig. 4. Mean-centered PLS results for the analysis of the W2 segment. Peak electrode saliences for the first latent variable (LV1) is shown at electrode sites P2 and FT9 (upper, left panel). The circles at the top of each electrode plot indicate when during the epoch the saliences for LV1 were stable across subjects (bootstrap ratio > 2.81). The average amplitude waveforms for the four conditions included in the PLS analysis are shown in the bottom, left panel: DiffNR = non-recalled pairs in the Different condition; DiffR = recalled pairs in the Different condition; SameNR = non-recalled pairs in the Same condition; SameR = recalled pairs in the Same condition. The normalized topographical distribution of the saliences for all electrodes is shown on the top right and the LV1 design scores are shown on the bottom right.

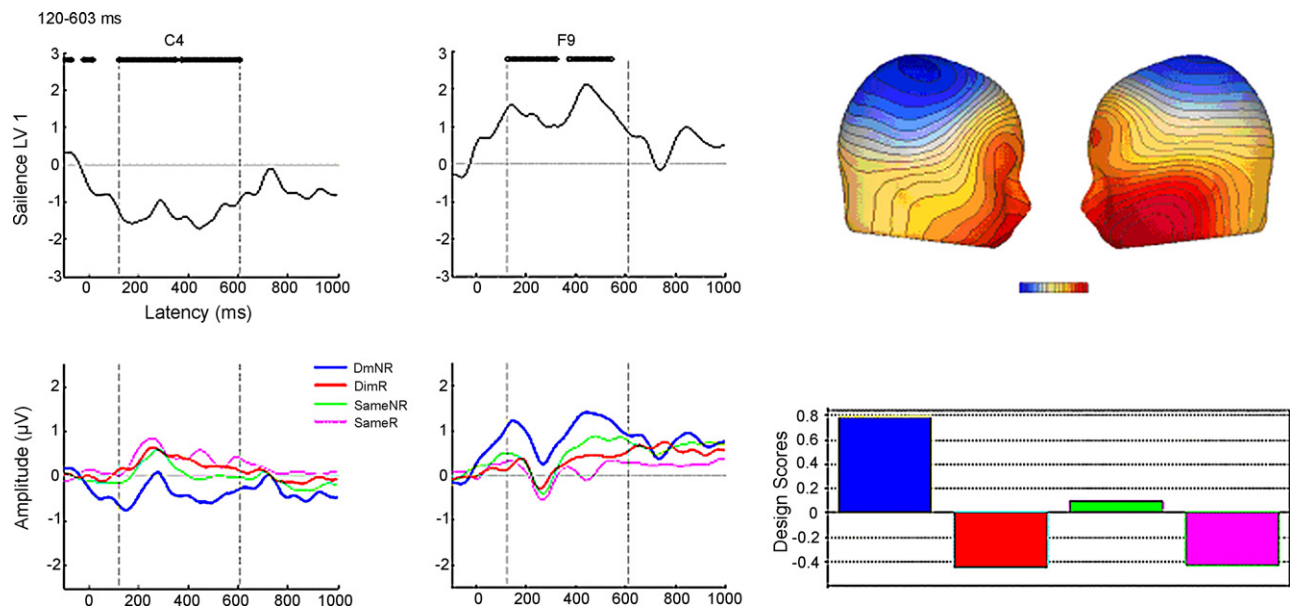


Fig. 5. Mean-centered PLS results for the analysis of the final 1000 ms interval. Peak electrode saliences for the first latent variable (LV1) is shown at electrode sites C4 and F9 (upper, left panel). The circles at the top of each electrode plot indicate when during the epoch the saliences for LV1 were stable across subjects (bootstrap ratio > 2.81). The average amplitude waveforms for the four conditions included in the PLS analysis are shown in the bottom, left panel: DiffNR = non-recalled pairs in the Different condition; DiffR = recalled pairs in the Different condition; SameNR = non-recalled pairs in the Same condition; SameR = recalled pairs in the Same condition. The normalized topographical distribution of the saliences for all electrodes is shown on the top right and the LV1 design scores are shown on the bottom right.

W2 were analyzed together [$F(1, 11) = 4.49, p = 0.058$]. However, when W1 was analyzed by itself (2 recall states \times 2 context conditions), it showed a significant R vs. NR difference [$F(1, 11) = 8.86, p = 0.01$]. Fig. 9 shows the scalp topography of the mean P555 amplitude that was measured over the 530–580 ms latency window after the onsets of W1 and W2 for the R–NR waveform. The topography of the P555 was oriented along an anterior–posterior axis (between F7, F8 and Pz) and differed from the more vertically oriented topography of the N425.

The LW was larger for R items than NR items [$F(1, 11) = 6.35, p = 0.028$] at C2, where the difference between the two conditions was maximally recorded, with the component having a larger R–NR difference for the ERPs during the Different lists than during the Same lists. There was an interaction between subsequent memory performance and intra-list context [$F(1, 11) = 11.41, p = 0.006$]. Fig. 9 shows the scalp topography of the mean LW amplitude that was measured over the 1000–1600 ms latency window after the onset of W2 for the R–NR waveform.

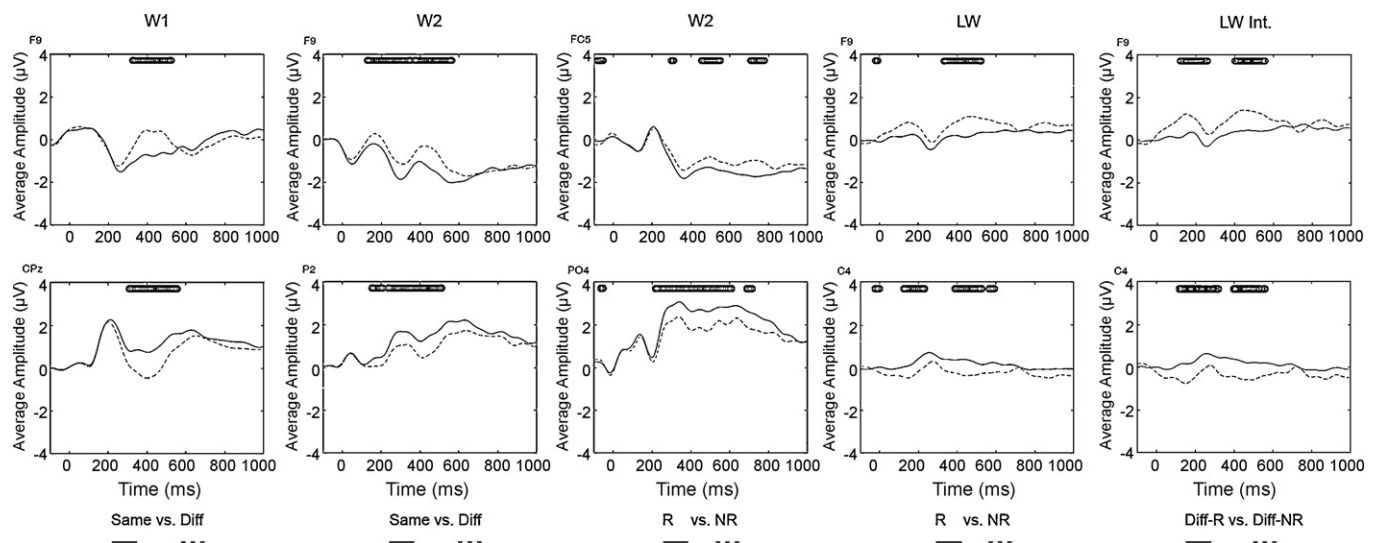


Fig. 6. Non-rotated PLS results for the time windows corresponding to the presentation duration of the first word of a pair (W1), second word of a pair (W2), the interval corresponding to the late wave (LW; 1000 ms interval starting at the offset of the second word of a pair), and the interaction between context conditions and memory performance for the late wave interval (LW Int.): Diff = Different condition; Same = Same condition; R = subsequently recalled pairs; NR = subsequently non-recalled pairs; DiffNR = non-recalled pairs in the Different condition; DiffR = recalled pairs in the Different condition. For each of the time windows, the collapsed waveforms corresponding to each significant contrast are displayed at two electrodes: for the W1 time window, Same vs. Diff waveforms at electrodes F9 and CPz; for W2, Same vs. Diff waveforms at electrodes P2 and F9; also for W2, R vs. NR waveforms at electrodes FC5 and PO4; for the LW, R vs. NR waveforms at electrodes F9 and C4. The circles at the top of each electrode plot indicate when during the epoch there is a reliable difference between the contrasted conditions (bootstrap ratio > 2.81).

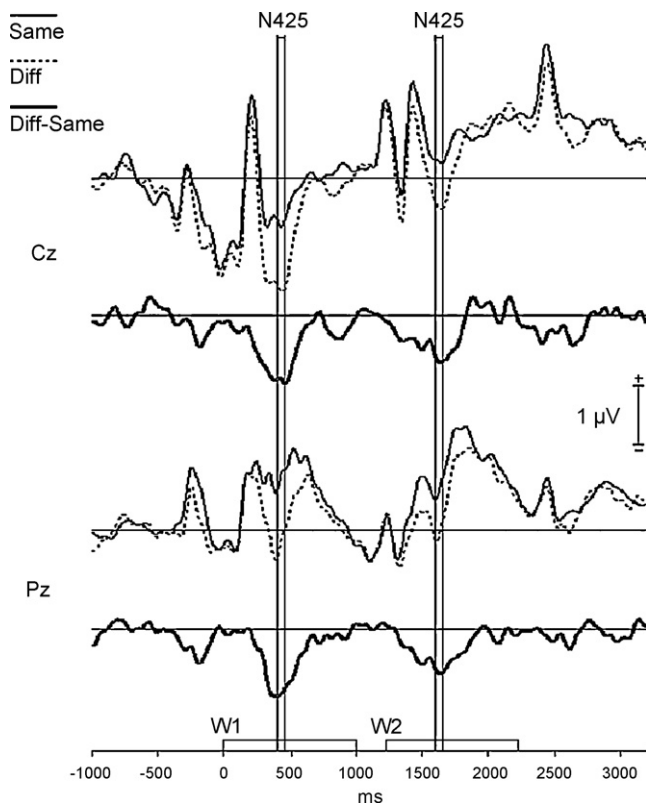


Fig. 7. Grand-mean ERP waveforms at encoding associated with intra-list context conditions. Waveforms are collapsed across subsequent memory performance at Cz and Pz: Diff=Different condition; Same=Same condition. For each electrode, the Diff-Same waveform is shown below the corresponding superimposed Diff and Same waveforms. The presentation duration of the first word (W1) and the second word (W2) of a pair is marked on the time scale. The two sets of parallel lines, labelled N425, depict the latency windows (400–450 ms after the onsets of W1 and W2) over which mean amplitudes were measured to evaluate the N425.

3.6. Source analysis

Source analysis was carried out on the topographies of the difference waveforms shown in Fig. 9. The analysis, performed using the default settings of the BESA program, provided the source activations shown in Fig. 10. The N425 showed widespread activation in temporal, frontal and parietal regions. The P555 showed activation in the inferior frontal and anterior temporal regions. The LW showed left frontal activation. All source patterns were much larger on the left than on the right. Although the superior scalp showed large potentials, the source activity was much more concentrated in the deeper regions of the brain, suggesting that these surface potentials were recorded at a distance from the deeper sources.

4. Discussion

4.1. Behavioral findings

Greater similarity within the intra-list encoding context (Same condition) was associated with a lower level of subsequent paired associate recall, compared to lower intra-list semantic similarity (Different condition). These findings are consistent with past behavioral studies (Bower et al., 1994).

Neither primacy nor recency effects were found when recall performance was analyzed as a function of serial position, demonstrating that there was no processing difference among word pairs according to the intra-list order of presentation. The lack of a recency effect was likely due to the use of a distractor task

(Murdock, 1967). The lack of a primacy effect finding is consistent with other studies of paired associates (Davis, Geller, Rizzuto, & Kahana, 2008; Palmer & Ornstein, 1971). Unlike with single items, participants likely did not have time to rehearse previously presented pairs, because they were preoccupied learning the association of the pair that was being presented at the time.

4.2. ERP findings

The ERP data were complex, involving multiple time-points, multiple electrodes and several experimental conditions. The data were analyzed using three different approaches: (1) PLS (mean-centered and non-rotated techniques), (2) difference waveforms and (3) source analysis. The PLS multivariate analysis was used to initially assess the main components of the waveforms in an unbiased manner, and it demonstrated significant effects within the temporal window of the N425 and P555 waves. Although these peaks were not clearly distinguished from each other, the response to W1 was more like the N425 and the component identified on the W2 analysis was more like P555. PLS did identify a clear LW effect of recall. The difference waveforms showed most clearly the effects of the two experimental manipulations. Source analysis for late ERP waves is difficult, because many different interacting processes occur simultaneously and the effects are relatively small (compared, for example, to cortical sensory responses). A minimum norm analysis, which estimates the distribution of intracerebral currents to explain the surface recorded electrical fields, was there-

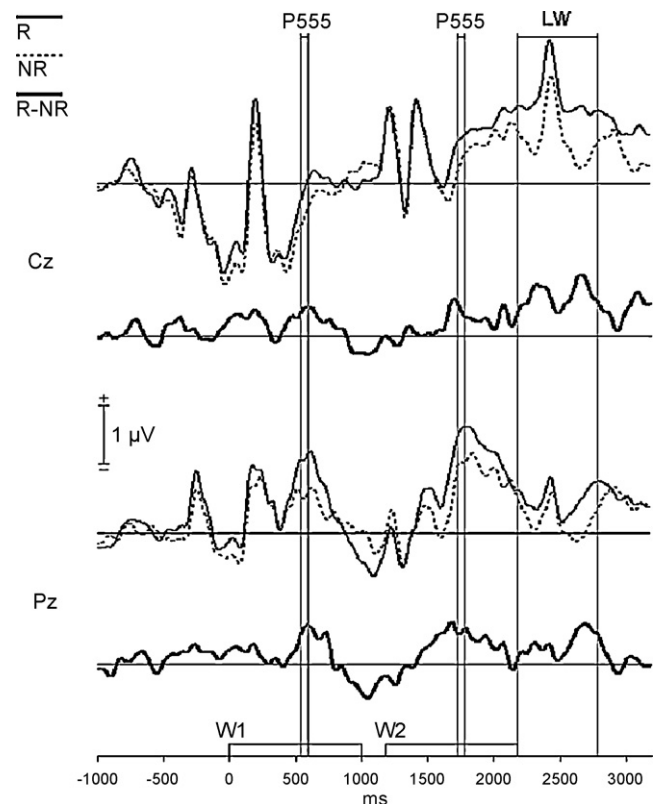


Fig. 8. Grand-mean ERP waveforms at encoding associated with subsequently recalled (R) and non-recalled (NR) items. Waveforms were collapsed across intra-list context condition at electrodes Cz and Pz. For each electrode, the R-NR waveform is shown below the corresponding superimposed R and NR waveforms. The duration in which the first word (W1) and the second word (W2) of a pair were presented is marked on the time scale. The two sets of parallel lines, labelled P555, depict the latency windows (530–580 ms after the onsets of W1 and W2) over which mean amplitudes were measured to evaluate the P555. The parallel lines, labelled LW (for late wave), depicts the latency window (1000–1600 ms after the W2 onset) over which the mean amplitude was measured to evaluate the LW.

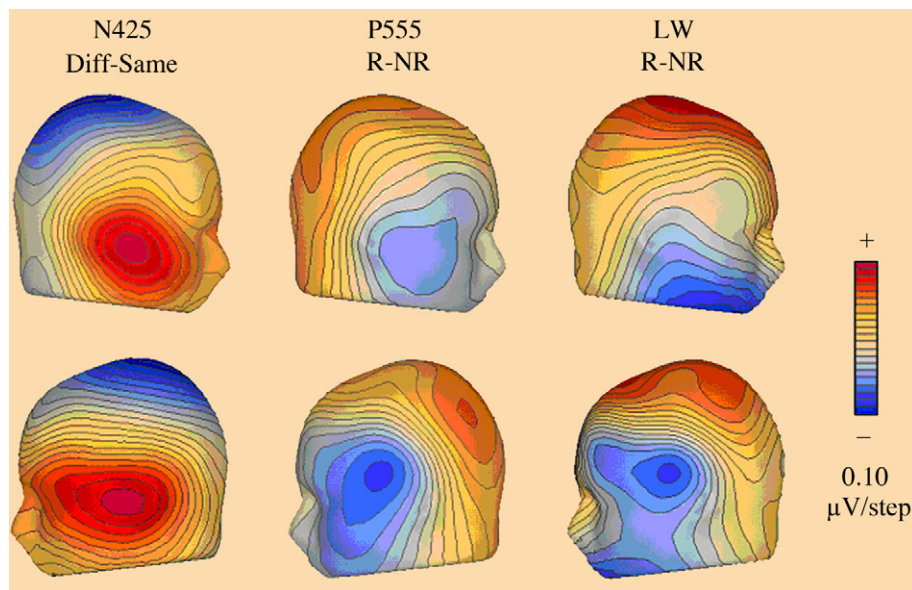


Fig. 9. Scalp topographies for the N425, P555 and LW; Diff= Different condition; Same = Same condition; R= recalled; NR= not-recalled. The N425 scalp topography reflects the mean amplitude that was measured over the 400–450 ms latency windows after the onsets of W1 and W2 for the Diff-Same waveform. The P555 scalp topography reflects the mean amplitude that was measured over the 530–580 ms latency window after the onsets of W1 and W2 for the R-NR waveform. The LW scalp topography reflects the mean amplitude measured over the 1000–1600 ms latency window after the onset of W2 for the R-NR waveform.

fore probably more appropriate than the use of focal regional sources.

Three distinct processes were identified in our ERP data. The N425 varied as a function of intra-list encoding context but was not related to subsequent memory. The P555 varied as a function of subsequent memory, but not intra-list encoding context. Finally, the LW showed an interaction between subsequent memory and intra-list encoding context.

4.2.1. N425

The N425 was significantly affected by intra-list semantic similarity, but did not appear to vary with subsequent memory performance. Paired associates presented in the Different condition elicited a larger N425 relative to paired associates presented in the Same condition. The observed N425 effect was maximal over the centro-parietal region and distributed bilaterally, with a ten-

dency to be larger over the right than left hemisphere, which is consistent with past studies that have examined the N400 related to sentence incongruity (Kutas, Van Petten, & Besson, 1988). In our data, there was an inversion of the parietal wave in the temporal regions more so on the left than on the right.

The N425 in our study likely reflects processes associated with semantic processing. In the classical N400 paradigm this semantic processing is associated with outright incongruity, but in other paradigms the N400 can be associated with processing the meaning of stimuli that are not expected on the basis of the preceding semantic context. For example, Brown and Hagoort (1993) examined whether changes in the N400 amplitude reflect the automatic process of lexical access or the controlled process of lexical integration; whereas the former leads to the activation of items within the lexicon along with their associated syntactic and semantic properties, the latter matches the activated syntactic and semantic properties

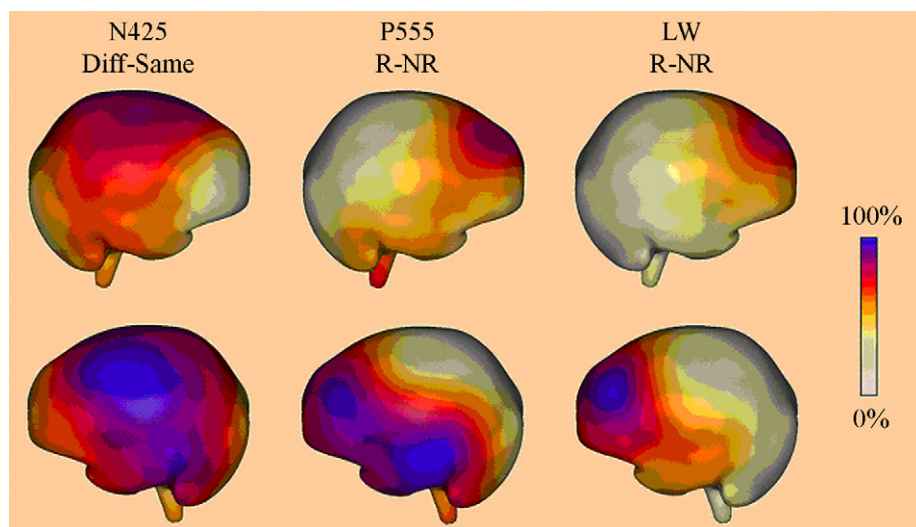


Fig. 10. Minimum norm source distributions for the N425, P555 and LW; Diff= Different condition; Same = Same condition; R= recalled; NR= not-recalled. The current distributions displayed in this figure were derived from the scalp topographies shown in Fig. 9. The distributions were normalized so that each distribution spanned the complete color scale.

of items to a representation of the current context. To that purpose, Brown and Hagoort compared the effects of masked and unmasked presentations of a prime on the N400 to a following target and found a significant N400 effect for the unmasked presentation of the prime only, suggesting that the N400 reflects aspects of controlled semantic integration processes and not automatic processes of lexical access.

In the present study, in the Same condition all of the words presented in a list belonged to the same semantic category, whereas in the Different condition each word of a pair belonged to the same semantic category but each pair belonged to a different semantic category. Thus, according to the semantic integration account one would expect the N425 effect to be larger for the Different than Same condition, and this was indeed observed.

The minimum norm analysis of the N425 sources suggests widespread temporo-parietal activation, more in the left hemisphere than in the right. Many different sources are probably simultaneously active during the N425, but deep seated sources in the left temporal lobe are likely predominant. The centro-parietal N400 scalp potential has been related to activity in the ventromedial temporal lobe by intracranial ERP recordings (Nobre & McCarthy, 1995). The brain structures that comprise the ventromedial temporal lobe (parahippocampal cortex, perirhinal cortex, fusiform gyrus) have been demonstrated to be of importance for semantic processing using PET (Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996) and fMRI (Tyler et al., 2004).

4.2.2. P555

The P555 was significantly affected by subsequent memory performance, but did not vary with the intra-list encoding context. Subsequently recalled items elicited a larger P555 compared to items that were subsequently non-recalled. The P555 scalp topography that was derived using the R-NR waveform demonstrated maximal positivity over the parietal region. The combination of the observed peak latency and scalp distribution suggested that this component of the Dm effect was similar to the late positive component (P500) recorded in many previous studies of subsequent memory (for review see Donchin & Fabiani, 1991).

Interestingly, the P555 scalp topography also demonstrated maximal negativity over the left fronto-temporal region. As mentioned above, other studies have also demonstrated a left fronto-temporal negative Dm effect around the same time as the P500 (Friedman & Trott, 2000; Mangels et al., 2001). Moreover, as outlined in the introduction, past studies indicate that posterior positivity and fronto-temporal negativity may reflect encoding processes that enable subsequent item retrieval independently of contextual details, whereas long lasting frontal positivity may index elaborative encoding processes that enable subsequent retrieval with rich contextual details. Thus, the P555 observed in the present study may reflect processes underlying the encoding of each word of a pair, which is a necessary precursor to cognitive association formation between two words of a pair (Underwood & Schultz, 1960). Encoding would activate the “meaning” of the word, likely bringing up many associations of the word in addition to its specific definition. These associations could then be used for linking together the words of a pair. The processes involved in encoding each word of a pair may be associated with attention, as effects of attention on subsequent tests of explicit retrieval have been shown (Craig, Govoni, Naveh-Benjamin, & Anderson, 1996; Gardiner & Parkin, 1990).

In the present study, the generators of the P555 scalp topography were estimated in the left prefrontal and left temporal regions, as shown in the minimum norm map in Fig. 10. Like for the N400 wave, the generators may be deep in the brain though maximally recorded over the parietal region. These estimated locations are consistent with the findings of past fMRI studies. In one of the

initial fMRI studies that examined subsequent memory effects, subsequent recognition for incidentally encoded words was predicted by the magnitude of activity primarily in the left inferior prefrontal cortex, left fusiform cortex and left medial temporal regions (Wagner et al., 1998). Consistent findings have been reported by other fMRI studies that have examined subsequent memory effects (Henson, Rugg, Shallice, Josephs, & Dolan, 1999; Otten, Henson, & Rugg, 2001). Consequently, verbal encoding has been associated with left inferior prefrontal and medial temporal brain responses, which is consistent with the left prefrontal and left temporal activity displayed in the minimum norm image for the P555 in the present study (Fig. 10).

In another study that focused on episodic encoding (Otten, Henson, & Rugg, 2002), participants were scanned over a series of task blocks that consisted of animacy and syllable judgment word tasks. Later during recognition, participants judged whether the presented words were shown during study, and whether they were ‘sure’ or ‘unsure’ about their decision. Studied words were categorized as ‘remembered’ if they received a “confident old” judgment during the recognition test and ‘forgotten’ if they were misclassified as new. Neural activity correlated with successful item-related encoding was identified by determining where event-related activity varied according to whether items were subsequently remembered or forgotten. Consistent with the results of the present study, item-related subsequent memory effects were found in the left inferior frontal gyrus, left inferior temporal cortex and bilateral fusiform gyrus for the semantic task, and in left inferior frontal gyrus, bilateral fusiform gyrus and left lateral parietal cortex for the phonological task.

4.2.3. Late wave

The LW occurring after the offset of W2 demonstrated a subsequent memory effect. Although it did not vary directly as a function of intra-list encoding context, there was a significant interaction between context and subsequent memory. Subsequently recalled pairs elicited greater LW positivity compared to subsequently non-recalled pairs: this difference was significantly greater for the Different lists than for the Same lists. The component showed a broad positive maximum over the frontal region, slightly more over the right than left hemisphere with a corresponding negativity in the left inferior frontal regions (Fig. 9). The corresponding minimum norm estimate revealed left prefrontal activity, which has been associated with episodic memory encoding (Habib, Nyberg, & Tulving, 2003; Tulving, Kapur, Craik, Moscovitch, & Houle, 1994). Exactly what this component represents in terms of cerebral processes is not clear. We speculate that it might reflect the abstraction and binding of the material available in working memory from the processing of each word. If this process is more effective, the recall process will be more accurate.

The interaction between context and subsequent memory for the LW was likely due to a difference in the degree of response uncertainty to a given cue between the Same and Different lists. For both types of lists, once participants were given the cue, they were able to predict the category of the target. However, the number of primed response terms in that predicted category was much larger for the Same lists than the Different lists. Consequently, the material available for binding in the Different lists was more distinctive than the material in the same lists. Thus, the potency of the retrieval cue to specify the target was likely better in the Different, than Same, lists. Whereas the processes underlying the N425 made the semantic material available for encoding, the LW processes showed how much of this information was actually used in encoding the associations between the words: response uncertainty to a given cue was relatively high in the Same lists compared to the Different

lists, consequently semantic information about the to-be-encoded material was more helpful for recall of pairs in the Different lists than those pairs in the Same lists.

Past studies have reported frontal-positive Dm effects for the presentation of single items (Fabiani et al., 1990; Friedman, Nessler, & Johnson, 2007; Mangels et al., 2001) and items of a pair presented at the same time (Weyerts et al., 1997). The advantage of the paired associate paradigm with sequential presentation of the two words is that the process of cognitive association formation between the two words of the pair cannot begin until both words have been presented. Thus we can separate ERP effects that are related to item encoding (similar for the two words) from those that are related to association formation (only after the second word onset).

Similarly to the present study, Mangels et al. (2001) observed greater frontal positivity elicited by words that were subsequently recalled and given remember judgments compared to words that were subsequently missed or given know judgments. Consistent with the present study, the corresponding scalp distribution demonstrated maximal positivity over the prefrontal cortex, slightly more over the right than left hemisphere. Moreover, Weyerts et al. (1997) examined Dm effects for pairs of words, with both words of a pair presented at the same time. Interestingly, Weyerts et al. also observed a frontal-positive Dm effect that was maximal over the frontal region and larger over the right than over the left hemisphere, but only for paired associates that were encoded using an associative, compared to non-associative, task. Importantly, these findings coincide with the early Dm studies that reported frontal-positive Dm effects when elaborative encoding strategies were used, whereas posterior-positive Dm effects were observed when rote encoding strategies were used (for review see Donchin & Fabiani, 1991).

The minimum norm sources for the LW were definitely located in the left hemisphere. It is possible that the deep seated sources in one hemisphere (e.g. in the left inferior frontal region) may show as positive waves over the superior scalp and these surface fields may be contralateral to the sources. It is also possible that both left and right frontal regions are simultaneously active.

In a previous study (Kounios et al., 2001), integrative association formation showed ERP effects whose sources were mainly located on the right frontal regions. However, these sources were obtained for the difference waveforms between word pairs whose order was later retrieved quickly vs. slowly. It is possible that both these waveforms had left prefrontal sources at encoding, since both were successfully retrieved (regardless of the speed of retrieval), and that this left prefrontal source was cancelled out in the difference waveform. In our case, we focused on the difference between pairs whose association was later retrieved successfully and those whose association was missed.

Left prefrontal activity has been associated widely with episodic memory encoding (Habib et al., 2003; Tulving et al., 1994). Moreover, a left prefrontal source for successful associative encoding is in line with the cerebral activation literature concerning the 'depth of processing' effect (Craik & Lockhart, 1972) that demonstrates greater activation in the left prefrontal cortex for deep (e.g. semantic) vs. shallow (e.g. perceptual, orthographic, etc) encoding tasks (Kapur et al., 1994; Shallice et al., 1994). These effects likely depend mainly on semantic processing, but other processes such as attentional control may also be involved.

Thus, past studies in combination with the reported characteristics of the present LW suggest that the LW reflects episodic, associative encoding. Although future studies must be conducted to disentangle the relation between the LW with item encoding and associative encoding, this suggestion is grounded on the observation that the LW only occurred after the presentation of W2, an event that necessarily precedes associative encoding.

4.2.4. Summary

Analysis of the ERPs associated with the intra-list encoding context, which varied in the degree of semantic similarity, and subsequent memory revealed a sequence of components that represent cognitive processes underlying the encoding of semantically related paired associates into episodic memory. The N425 was sensitive to intra-list encoding context and may have reflected item-specific semantic processing, specifically the lexical integration of a given item into the current lexical context. The P555 may have reflected processes involved in item-related encoding, which is a necessary precursor to cognitive association formation between the two items. The LW occurring over frontal regions, but likely generated deep within the left inferior frontal lobe, may have reflected subsequent paired associate recall. The results of the present study extend those reported by other ERP studies of memory encoding. The use of paired associates with sequential presentation of the paired stimuli provided more direct evidence regarding the different underlying processes of item-related encoding (P555) and cognitive association formation (LW).

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