

EEG activity underlying successful study of associative and order information

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Abstract

Two of the most well studied and ecologically relevant memory paradigms are memory for pairs (“associations”) and ordered sequences (“serial lists”). Behavioral theories comprise two classes: those that use common mechanisms and those that use distinct mechanisms for study and retrieval of associations versus serial lists. We tested the common-mechanisms hypothesis by recording electroencephalographic activity related to successful study (“subsequent memory effect;” SME) of pairs and short lists (triples) of nouns. Multivariate analysis identified four distributed patterns of brain activity: 1) right parietal activity throughout most of the study period that differentiated study of pairs from triples within subjects as well as exhibiting a SME that was significant for pairs but not for triples; 2) a left parietal and frontopolar activity that was reliable around 500 ms and later in the study trial, exhibiting a subsequent memory effect for pairs and a weaker, non-significant SME for triples; 3) a left-frontal/right-parietal topography in the middle of the study interval which covaried with speed and accuracy across subjects and 4) a pattern resembling the late positive component preceded by an early potential which together covaried with accuracy in triples but slow response times for both pairs and triples. These patterns point to the relevance of three classic SME components (early, late positive and slow components) from single-item memory to memory for structured information, but suggest that they reflect subsets of more complex spatiotemporal patterns. Our findings support common underlying mechanisms for study and recall of pairs and lists. However, existing models must be modified to account for differences in both the presence of certain study-relevant processes and in the relevance of these processes to performance measures for pairs versus serial lists.

Introduction

Psychologists have long drawn distinctions among episodic memory for three aspects of study experience (Murdock, 1974): (1) Memory for items— i.e., which words were presented in the study episode. Item memory is usually tested with free recall— “Which items were in the study set, in any order”— or recognition— “Was the word HOLLOW in the study set?” (2) Memory for associations— i.e., which pairs of words were presented together. Associative memory is usually tested with cued recall— “Which word was presented with HOLLOW?” (3) Memory for order, or serial lists— i.e., remember all the items in their correct positions. Serial list memory has been tested in many ways, but the most common is with serial recall— having studied the list ABSENCE–HOLLOW–PUPIL, “What was the entire set of words in order?” While there are reports of behavioral dissociations among these three classes of memory (e.g., Hockley and Cristi, 1996; Kahana and Caplan, 2002),

certain memory models treat two or more of them together, assuming that they rely on the same basic processes.

The original unified model of pairs and serial lists was the chaining model of Ebbinghaus (1885/1913). In this class of model, formally implemented by subsequent researchers (e.g., Metcalfe, 1985; Lewandowsky and Murdock, 1989; Caplan, 2004, 2005), memory for an ordered list is derived from memory for the nearest-neighbor pairs of items within the list (and in some model implementations, from remote associations between non-adjacent list items). The order of list items is reconstructed by “chaining” through the list, starting with the first item, using it to retrieve the second, using the second item to retrieve the third, and so forth. In a competing class of models of serial list learning, known as “positional coding” or “order coding” models (e.g. Conrad, 1965; Brown, Preece, and Hulme, 2000; Brown, Neath, and Chater, 2007), it is assumed that no direct item-to-item associations are learned; instead, each list item is associated with a separate representation of list position (or order). Thus, recall of a serial list proceeds by cueing with the first position, attempting to retrieve the item associated with that position, then cueing with the next position, and so forth. It was recently demonstrated that these positional/order coding models could also be used to explain memory for pairs (Caplan, 2005; Caplan, Glaholt, and McIntosh, 2006). There has been no conclusive evidence ruling out chaining or positional/order models of serial list learning (apart from extremely simplistic forms of each model) and it is likely that real serial list learning relies on both types of representations, depending on specific task demands as well as, potentially, individual differences in chosen study strategy. For this reason, our concern is not to select between chaining and positional/order models of serial list and association learning but rather, to ask the orthogonal question whether associations and serial lists could be explained by the same underlying processes regardless of a chaining versus positional/order framework.

Theoretical work demonstrated that memory for associations and serial lists could be modeled using the same cognitive processes (Caplan, 2004, 2005; Caplan et al., 2006). For example, pairs of words (denoted A–B, where A and B denote words within a pair) appear to be learned as holistic units rather than as two directional associations (A→B learned independently of B→A) as has been reported in numerous studies (Caplan et al., 2006; Kahana, 2002; Rizzuto and Kahana, 2000, 2001). In contrast, memory for adjacent items derived from a learned serial list do not exhibit this holistic property; namely, given a list A–B–C–D–E, probing with item C and asking for the subsequent item (D) is not highly predictive of probing with item D and asking for item C. To explain this apparent dissociation, Caplan introduced an “Isolation Principle,” which can be implemented within both associative chaining and positional/order coding models, whereby cued recall of serial lists is more susceptible to interference (which can differ depending on probe direction) than cued recall of pairs, which are

relatively more isolated from other studied items. This principle can account for differences in behavioral measures between memory for pairs and both memory for long serial lists of 19 words (Caplan, 2005) and for short lists of 3 words (Caplan et al., 2006).

These unified behavioral models are simpler than theoretical frameworks that demand separate explanations memory for pairs and serial lists, but the unified models can nonetheless explain apparent behavioral dissociations and can thus give more parsimonious accounts of behavior. However, it is still quite plausible that distinct underlying mechanisms could produce behavioral patterns consistent with the unified framework. By examining brain activity related to successful study we provide a stronger test of the common-mechanisms hypothesis. We asked whether the same or different study-activity components covary with three types of memory. Because of the wealth of published studies on single-item memory compared to the scant amount of EEG data on associative and list memory, we decided to focus on memory for associations and lists, which allowed for a dyad of tasks that were extremely well matched in terms of their study and test conditions—namely, cued recall of word pairs and triples, an adaptation of a paradigm previously used in a purely behavioral study (Caplan et al., 2006).

To find out how the brain’s activity produces effective memory, neurophysiology researchers have moved beyond simply identifying what activity is present during different task conditions. In the Subsequent Memory Effect (SME) paradigm, originally introduced as the Difference due to Memory (Dm) by Sanquist, Rohrbaugh, Syndulko, and Lindsley (1980), one identifies the subset of neural processes that are present at study that also predict accuracy on a later memory test. Processes present during study could merely be spectator processes or could even represent poor study strategies. In contrast, SME activity that covaries with memory tests is more likely to reflect the study processes most relevant to the type of memory being tested. Furthermore, the tight link to memory-test behavior in the SME approach is likely to inform cognitive modelers as to what brain activity could be used to test cognitive-process models. We therefore focus on the SME for word pairs and triples.

Our chief question was whether successful study of pairs and triples would be best described by the same or different patterns of brain activity and without biasing the analysis by pre-specifying times or electrodes of interest. This type of question calls for a multivariate method (e.g., partial least squares, PLS) which decomposes the brain–behavior relationship into several latent variables. If the unified model were true, the same latent variables should relate similarly to memory for pairs and triples. If the distinct mechanisms view were the case, then different latent variables should account for memory for pairs versus triples. Additionally, the PLS analysis was set up to identify correlates of successful study both within subjects (“Task PLS,” contrasting pairs

and triples that were subsequently recalled versus not recalled) as well as activity patterns that distinguished participants with high versus low performance on pairs versus triples (termed “Behavior PLS”).¹

In addition to multivariate analyses we were interested in whether the well established ERP components previously linked to successful study of single items would also extend to memory for structured information (associations and lists). Three chief event-related potential (ERP) components of the SME have been identified with electroencephalography (EEG; Sanquist et al., 1980; Karis, Fabiani, and Donchin, 1984). First, a late positive component (LPC) has shown a SME in numerous memory paradigms including recognition, free recall and final free recall of verbal materials (Karis et al., 1984; Friedman and Trott, 2000; Mangels, Picton, and Craik, 2001; Lian, Goldstein, Donchin, and He, 2002), incidental as well as intentional study (Fabiani, Karis, and Donchin, 1986; Paller, Kutas, and Mayes, 1987). Second, a slow potential starting around 500 ms post-stimulus onset has shown a SME in similar paradigms (Karis et al., 1984; Friedman and Trott, 2000; Mangels et al., 2001; Lian et al., 2002) and may be more linked to elaborative than rote study strategies (Karis et al., 1984). Finally, earlier components have been identified, although these components may be less robust. Friedman and Trott (2000) found a potential around 200–400 ms that showed a SME in remember/know recognition and Lian et al. (2002) found a SME in a very early, 200 ms widespread positive component.

The most closely relevant prior study is by Guo, Voss, and Paller who reported a SME for name–face pairs, encompassing the early, LPC and slow potential components relevant to a cued recall test. Their paired items, however, were of different material types and thus do not speak directly to the classic paradigm of cued recall of pairs of items of the same type (e.g., nouns). Weyerts, Tendolkar, Smid, and Heinze (1997) reported a right frontal SME beginning around 200 ms related to associative encoding instructions. They presented paired words for later paired recognition. However, their memory test was recognition for pairs of items where both items were either old and presented together or both items were new. As pointed out by Kounios, Smith, Yang, Bachman, and D’Esposito (2001), participants could perform this task by retrieving only single-item information. Thus, even though Weyerts et al. (1997) manipulated study instructions, their SME may still be missing associative encoding processes. Kounios et al. (2001) sought to test memory for item pairings by probing participants with two types of pairs: intact pairs and reversed pairs, in which the “A” and “B” items were swapped. They reported a left-lateralized SME with late timing. However, Kounios and colleagues do not report standard SMEs predicting later response accuracy. Instead, they analyzed SMEs that predicted later response speed on correct responses, so the relationship of their findings to standard SME methods is unclear. But more critically, these memory tests assessed memory for the ordering of items within the pairs. Because no test probes ever comprised

items taken from different studied pairs, the participants were never tested directly on the associations (i.e., the pairings, without regard to order).

While these three components recur in many studies, one may ask whether the components reflect separate constructs. For instance, it could be that the slow potential components comprise subcomponents that coincide in their time courses. Alternatively, it could be that multiple “components” are causally linked and thus are always present together. For instance, it is possible that the early potential and LPC are a pair of processes that always co-occur, but that their properties (amplitude and temporal duration) make the early potential more difficult to detect within noise, explaining why they are not always both reported in a single study. The multivariate approach allows us to ask the question of construct validity in a principled, multivariate way. Namely, components that explain behavior and task design similarly will tend to be assembled into a single latent variable; components that do not relate to the task design and behavior similarly will tend to appear in separate latent variables. All this occurs without biasing the method by a priori hypotheses about which timings/topographies will be relevant and the method is applied to the entire data set (electrodes and time) rather than a subset of the data that could be biased by expectations based on previous findings.

Our chief objective was to examine the EEG-SME in a standard paired associates paradigm, with cued recall which necessarily tests participants on the pairings of items. Adding word triples to the paradigm allows us to ask whether additional study of order information further alters the SME. Our specific interest was in whether SME activity for item, associative and serial list memory were similar, reflecting common processes, or different, reflecting distinct processes.

Methods

Participants

26 healthy adult volunteers whose primary language was English participated for monetary compensation (10 male, 16 female, 1 left-handed, age= 29.7 ± 9.4 years). Six participants were excluded due to ceiling (percent correct > 90%) or floor (percent correct < 10%) performance in at least one condition (pairs/AB-Triples/BC-Triples; see Materials), leaving 20 included participants (9 male, 11 female, 1 left-handed, age= 27.6 ± 7.7 years).

Behavioral methodology

The task is similar to that used by Caplan et al. (2006) except that in that study, pairs and triples were tested twice whereas here, each pair and triple was tested only once, and emphasis was given to EEG considerations (e.g., minimizing head and eye movements). The specific methods are as follows.

Materials The fixation (apart from those preceding a pair or a triple) consisted of seven asterisks presented in the centre of the screen, displayed for 3750 ms and then erased for 250 ms.

The study sets consisted of nouns from the Toronto Word Pool (Friendly, Franklin, Hoffman, and Rubin, 1982), randomly sampled without replacement. Each noun was presented visually in the centre of the screen. The study sets were grouped either into 9 pairs or into 6 triples, which kept the total number of words per study set at a constant 18 words. The order of pair study sets and triple study sets was chosen randomly, with the constraint that each set of three study sets had to include one pair set and two triple sets. Pairs and triples were presented sequentially, one item at a time. Each noun was displayed for 1750 ms, followed by 250 ms blank inter-stimulus interval (ISI). An additional interval of 4000 ms was inserted between pairs and triples. During this inter-pair/triple-interval, the participant viewed either *****2***** (sets of pairs) or *****3***** (sets of triples). This inter-pair/triple cue served to remind the participant of whether they were studying a set of pairs or triples.

The distractor consisted of 4 equations of the form $A + B + C = ?$, where A, B and C were randomly selected digits from 0 to 6, with the restriction that the identical distractor could not be used twice in succession. The equation remained on the screen for 3750 ms and then was erased for 250 ms. The participant was asked to respond vocally with the correct answer to the equation within the entire 4000 ms interval given.

Cued recall consisted of a word with six question marks, **??????** either to the left or to the right of the probe word. The participant was instructed to recall the word that followed or preceded the probe item depending on whether the question marks were placed to the right or left of the probe word, respectively. Each probe was preceded by a fixation. The probe remained on the screen for 7000 ms and then was erased for 1000 ms. The participant was asked to respond vocally within the entire 8000 ms interval given. Each pair and triple was probed exactly once, and probe order was selected at random. Triples could be probed for the first portion of the triple (A? or ?B) or for the last portion of the triple (B? or ?C). Triples probed in each way will be referred to as “AB-Triples” and “BC-Triples,” respectively.

Procedure Figure 1 illustrates the study and test phases of a single trial (example is for a study set of triples). Participants first viewed a fixation. Then, they studied the set in a single study trial. Next, they performed the

distractor task and finally, they answered cued recall questions based on the study set. A session consisted of 26 study sets.

For the first study set, self-paced instructions preceded each of the study, distractor and cued recall phases of the task. During the instruction periods, the experimenter ensured that the participants understood the instructions. The first two sets included one pure set of pairs and one pure set of triples; the order of these was randomized across participants. These first two sets were considered practice and are excluded from all analyses.

Insert Figure 1 about here

EEG methodology

EEG signal was recorded from a 64-electrode cap (Electro-Cap International), including the sites Fp1, Fp2, F4, F3, C3, C4, P4, P3, O2, O1, F8, F7, T4, T3, P8, P7, Pz, Fz, CB1, CB2, TP7, TP8, Oz, Iz, PO4, PO3, CP5, CP6, CP1, CP2, FT9, FT10, FC2, FC1, AF3, AF4, FC6, FC5, CPz, P1, POz, P2, P6, C6, P5, C1, C2, C5, F2, F6, F1, AF8, F5, AF7, Fpz, and FCz (American Electroencephalographic Society, 1991). Electrodes were also placed on the left and right mastoids (TP9, TP10), on the left and right zygomatic arch (F9, F10), at the outer canthus of the each eye (LO1, LO2), and on the infraorbital ridges directly below each eye (IO1, IO2). An electrode at AFz was used as ground and an electrode at Cz was used as reference. Inter-electrode impedances measured at 10 Hz were below 5 k Ω . EEG and EOG signals were amplified with Neuroscan SynAmps at a gain of 2500 with an online analogue filter bandpass of 0.05–100 Hz (–3 dB points; 12 dB/octave). Data were recorded at 500 Hz and converted to an average-reference montage (following EOG compensation; see next paragraph) with 65 channels. Traces were notch-filtered at 60 Hz to remove line noise and low-pass filtered at 20 Hz prior to subsequent analysis. Trials with voltage deviating more than 300 μV from baseline were excluded from all analyses.

EOG compensation was applied using ocular source components (Berg and Scherg, 1991; Picton et al., 2000). A separate ocular calibration recording was obtained during which participants blinked and made saccades in the up, down, right, and left directions. Five saccades in each of the four directions and ten blinks were averaged. An ocular data set was assembled by concatenating average recordings of each of the saccades and the blinks for each participant individually. A principal component analysis of these data for each participant provided a set of components that represented the variance related to the eye movements. Three components, each explaining more than 1% of the variance and each specifically related to the EOG waveforms

were used as source components to subtract EOG contamination from the recorded EEG. Spline maps were rendered using EEGLAB (Delorme and Makeig, 2004).

Subsequent memory analysis

To compute event-related potentials (ERPs), EEG signal was averaged over a window from 0–2000 ms following the onset of each word. The baseline was the average over a 200-ms window prior to the onset of the word. These traces were averaged across trials within participants and then analyses were performed across participants. Sites and windows of analysis were determined from a priori hypotheses based on previous research, and by visual inspection of the grand averages. These analyses appear to have captured the bulk of the effects in this data set.

Multivariate analyses

Overview The motivation of this analysis was to identify distributed patterns of EEG activity and characterize their relationship to task conditions (pair versus triple and recalled versus not recalled) and to individual differences in behavior (overall accuracy and response time were used as behavioral covariates). Multivariate methods can concisely summarize these effects and allow us to ask questions regarding similarity and difference of brain activity patterns without biasing the analysis based on preconceptions about which components will be most relevant. PLS is a multivariate technique that describes the relationship between the input, e.g., task design, and output measures, e.g., brain activity or brain-activity–behavior correlations as a function of condition that has been applied to neuroimaging data (McIntosh, Bookstein, Haxby, and Grady, 1996) and more recently to electrophysiology (including ERP) data (Itier, Taylor, and Lobaugh, 2004; Lobaugh, West, and McIntosh, 2001; McIntosh, Chau, and Protzner, 2004; McIntosh and Lobaugh, 2004; West and Krompinger, 2005; West and Wymbs, 2004). A Task PLS analyzes changes in mean brain activity as a function of conditions to assess overall presence or absence of distributed patterns of brain activity in each condition (the within-subjects approach). In a complementary approach, Behavior PLS analyzes the correlation between brain activity and behavioral covariates (e.g., accuracy or response time) to identify distributed patterns of brain activity that have relevance to individual differences in behavior (the between-subjects approach). The combination of the Task and Behavior PLS enables us to identify distributed patterns of brain activity that account for both within-subjects variability across conditions and between-subjects variability as a function of condition, respectively.

PLS input Task PLS (within-subjects approach). To compare pairs versus triples and to look for effects of SME, we had four conditions: PAIR/TRIPLE[2] \times MEMORY[2]. For each condition, activity consisted of the

ERPs (i.e., averages across trials for each participant) within the window 50–1750 ms. This window was chosen to steer clear of very early sensory evoked potentials as well as the response to the offsets of the word stimuli. In the data matrix, each row represents a different condition and columns represent electrode \times time, the values consisting of the corresponding ERP voltages. Thus, the Task PLS input matrix has size 4 rows (conditions) and 51789 columns (61 electrodes \times 849 time samples). The columns of the Task PLS matrix are mean-centered.

Behavior PLS. Two submatrices were created, one for Accuracy and one for RT. The ERPs at each electrode and each 2-ms time sample were correlated with accuracy or response time, respectively, across participants and within task condition. Note that accuracy for pairs referred to overall accuracy for pairs for each participant, thus the same accuracy values were correlated with activity during subsequently recalled pairs and subsequently not recalled pairs. The same applies to triples, as well as to response times for pairs and triples, respectively. Each row represents a different condition and columns represent electrode \times time, the value consisting of the correlation between ERP voltage and either accuracy or response time across participants. Thus, each of the two Behavior PLS submatrices (one for accuracy and one for response time) has the same dimensions as the Task PLS input matrix. The input to the Behavior PLS is the columnwise concatenation of the Accuracy and RT submatrices.

PLS procedure A singular value decomposition (SVD) is applied to the input matrix which computes an optimal least-squares fit. This produces a set of mutually orthogonal latent variables (LVs; there are the same number of LVs as there are rows in the input matrix), each consisting of two parts: a singular image (“brain LV”, or the brain portion of the latent variable) and a singular profile (“design LV” or “behavior LV”, or the design/behavior portion of the latent variable), connected by a singular value (the square root of the eigenvalue). The singular value indicates how much of the covariance of the input matrix is accounted for by its respective latent variable. We designate the singular value divided by the sum over all singular values as the percentage of cross-block covariance, where one block is either the design or behavioral measure and the other the ERP data. Brain LVs consist of a weighted linear combination of electrode/times that as a whole covary with the pattern represented in on the design/behavior LV. The numerical weights within the brain LV are called “salience” and can be positive or negative, indicating the degree to which each electrode/time is related to the design/behavior LV. For Task PLS, the saliences are essentially weighted difference waveforms, where the weighting comes from the design LV. In the Behavior PLS, the saliences are also weighted differences, but in this case, patterns depict where and when the correlation of amplitude and behavior are similar or different across tasks - the similarity or difference being represented in the behavior LV.

Note that an important difference between PLS and other multivariate methods such as principal components analysis and independent components analysis is that in those methods, brain-activity patterns would need to be projected back onto the original data to determine their relationship to the task conditions; in contrast, PLS seeks to find an optimal relationship between brain activity and task conditions (or brain-activity-behavior correlations and task conditions) in one step.

Assessing reliability The significance of each LV is assessed with a permutation test (1500 iterations) in which task condition labels are shuffled. This results in a distribution of singular values from shuffled data sets, from which the cumulative 95th percentile is taken as the significance threshold. The reliability of the contribution of each electrode/time bin to the LV is assessed by a bootstrap estimation of standard errors for the salience (300 iterations) by resampling participants. Saliences whose 95% confidence intervals (based on the standard error) do not include zero are considered reliable across participants; reliable electrode/times are denoted in brain LV figures with asterisks. We also use the results of the bootstrap to similarly compute 95% confidence intervals on correlations between the brain LV and the behavioral measures. The brain LV can be projected onto each participant’s ERP as a function of condition to obtain scalp scores (analogous to factor scores in a factor analysis), to assess how consistent each participant’s activity is to the brain LV. Confidence intervals for mean scalp scores are computed over scalp scores for each participant, corrected for between-subjects variance following Loftus and Masson (1994).

Post-hoc analyses To further understand the design LVs, for Task PLS we follow up with repeated-measures ANOVA on scalp score with the design: PAIR/TRIPLE[2]×MEMORY[2]. Note that PLS is designed to differentiate conditions; thus, the post-hocs contrasting conditions are somewhat positively biased. Only significant main effects and interactions ($\alpha = 0.05$) are reported. Post-hoc pairwise comparisons were two-tailed, paired-samples *t*-tests.

Univariate planned comparisons

Univariate planned comparisons consisted of ANOVAs including activity recorded at electrode locations FP1, FP2, F3, F4, C3, C4, P3, P4, PO3, PO4, O1 and O2 for all three components. To test whether the early component showed a SME and whether it differed between pairs and triples, we analyzed the peak amplitude (maximum amplitude within the window 100–300 ms following stimulus onset) at each included electrode, in a repeated-measures ANOVA with the design HEMISPHERE[2]×ANT-POST[6]×PAIR/TRIPLE[2]×MEMORY[2]. The factor PAIR/TRIPLE included two levels: pairs, collapsed across “A” and “B” items of pairs, and triples,

collapsed across “A” and “B” items of AB-Triples and “B” and “C” items of BC-Triples. To test whether the LPC and slow potential showed a SME and differed between pairs and triples or across the scalp, we analyzed average voltage in 50-ms time bins over the window=350–700 ms (LPC) or 200-ms time bins in the window 900–1700 ms (slow potential) following word onset. The repeated-measures ANOVA had design HEMISPHERE[2]×ANT–POST[6]×PAIR/TRIPLE[2]×MEMORY[2]×TIME BIN[7] for the LPC and HEMISPHERE[2]×ANT–POST[6]×PAIR/TRIPLE[2]×MEMORY[2]×TIME BIN[4] for the slow potential. All ANOVAs were corrected for non-sphericity using the Greenhouse-Geisser correction. Post-hoc pairwise comparisons were Bonferroni-corrected for multiple comparisons.

Results

Overview We first present analyses of behavioral measures (accuracy and response time). Then we present the results of the partial least squares analyses, testing whether the overall patterns of brain activity differentiated or linked successful study of pairs and triples. Then we analyze the chief ERP components of the subsequent memory effect for pairs versus triples.

Behavior

For the 20 participants included in the ERP analyses, accuracy and response times are listed in Table 1. A repeated-measures ANOVA on accuracy with the design TYPE[3] × DIRECTION[2] (TYPE=PAIR/AB-Triple/BC-Triple, DIRECTION=Forward/Backward probe direction) revealed only a significant main effect of TYPE [$F(2, 38) = 63.7$, $MSe = 0.013$, $p < 0.001$]. Post-hoc, Bonferroni-corrected pairwise t tests found probes of pairs to be more accurate than probes of both types of triples ($p < 0.001$) and probes of AB-Triples showed a trend toward being more accurate than probes of BC-Triples ($p = .09$). A repeated-measures ANOVA on response time with the same design revealed only a significant main effect of TYPE. Post-hoc pairwise comparisons found that probes of pairs were recalled more quickly than probes of triples ($p < 0.005$) while probes of AB-Triples and BC-Triples did not differ significantly ($p > 0.1$). The equality of forward and backward probes (lack of significant main effects or interactions involving DIRECTION) suggests that, as in prior studies, forward and backward cued recall of pairs and triples tap nearly the same memorized information (e.g., Rizzuto and Kahana, 2000, 2001; Kahana, 2002; Caplan et al., 2006). For this reason, we collapse subsequent analyses across forward and backward cued recall questions to increase power without loss of specificity.

Insert Table 1 about here

We were also interested in the types of errors that participants made. Many incorrect responses were omissions (either no response made within the allotted 8 s response time or else vocalizing the word “PASS”). However, participants also made a total of 642 intrusions, or $29 \pm 20\%$ (mean \pm standard deviation) of all probes. Of these intrusion responses, 177 were items from other pairs or triples presented within the same study set and 94 were items from prior study sets. More common than these types of intrusions, 246 intrusions were to the unprobed item of a triple (the item that was neither the probe nor the target). Thus, as in our behavioral study (Caplan et al., 2006), a major challenge to participants was to disambiguate the order of the two non-probe items in a triple.

Multivariate partial least squares analysis

Task PLS (Within-Subjects Approach).

The Task PLS explains differences in mean activity levels across conditions within participants. This analysis identified two significant latent variables (LVs), together accounting for a total of 92% of the cross-block covariance. The first LV mainly differentiated pairs from triples independent of subsequent memory whereas the second LV reflected a substantial subsequent memory effect primarily for pairs. We report each in turn.

Latent Variable #1: Pairs versus Triples The first LV (Figure 2) accounted for 55% of the cross-block covariance ($p < 0.005$). The design LV (panel **a**) tells us whether the identified activity pattern differed across conditions in overall activity; this corresponds to a within-subjects contrast. This LV contrasted study activity for pairs versus triples and may interact with subsequent memory. To complement the design LV, the scalp scores (projection of the brain LV onto each subject’s ERP) tell us the absolute levels of the brain LV. Panel **b** plots the mean scalp scores as a function of condition and 95% confidence intervals across subjects. A post-hoc repeated-measures ANOVA on the scalp scores revealed a significant main effect of PAIR/TRIPLE [$F(1,19)=17.5$, $p < 0.005$] and a significant PAIR/TRIPLE \times MEMORY interaction [$F(1,19)=8.6$, $p < 0.01$], explained in post-hoc tests by a significant SME for pairs [$T(19) = -2.4$, $p < 0.05$] but a non-significant SME for triples [$T(19) = 1.6$, ns].

The brain LV (panels **c–d**) gives the distributed pattern of brain activity, and indicates at which electrodes and times this LV was reliable. The topography is suggestive of a medial frontal source, The reversal of polarity

of design saliences between pairs and triples suggests that this is activity that is either present during pairs and suppressed during triples or vice-versa. The timing of the brain LV encompasses the slow potential as well as having some contribution from earlier lags consistent with the LPC and early potential. Thus, LV #1 identified an activity pattern, likely including medial frontal cortex, that differentiates overall activity during study of pairs versus triples and differentiates subsequent memory for pairs but not significantly for triples.

Insert Figure 2 about here

Latent Variable #2: Subsequent Memory Effect The second LV (Figure 3) accounted for 36% of the cross-block covariance ($p < 0.05$). The design LV (panel **a**) reflects a subsequent memory effect for both pairs and triples. While both pairs and triples show the subsequent memory contrast, the scalp score plot (panel **b**) shows us that the SME is reliable for pairs but smaller in magnitude and less reliable for triples. A post-hoc repeated-measures ANOVA on the scalp scores revealed a significant main effect of MEMORY [$F(1,19)=20.0$, $p < 0.001$] and a significant PAIR/TRIPLE \times MEMORY interaction [$F(1,19)=11.3$, $p < 0.01$], explained in post-hoc tests by a significant SME for pairs [$T(19) = 5.7$, $p < 0.0001$] but a non-significant trend toward a SME for triples [$T(19) = 1.9$, $p < 0.1$]. The brain LV (panels **c–d**) is more robust over left posterior electrodes, especially over left parietal sites. Its timing encompasses primarily portions of the slow potential period but also has relevant times overlapping with the LPC and early potentials. In sum, LV #2 distinguishes subsequently recalled from subsequently not recalled pairs and triples, although this is non-significant for triples. It may represent a voluntary strategy that participants engage more during study of pairs than triples.

Insert Figure 3 about here

Behavior PLS (Between-Subjects Approach).

Whereas the Task PLS explained differences across conditions within subjects, the Behavior PLS explains individual differences in participants’ behavior, namely, accuracy and response times as a function of condition. This analysis identified two LVs, together accounting for a total of 60% of the cross-block covariance.

Latent Variable #1: Individual Differences in Accuracy and Response Time The first latent variable (Figure 4) accounted for 41% of the cross-block covariance ($p < 0.01$). The behavior LVs tell us how this

pattern of activity covaried with performance across participants as a function of condition. Panels **a** and **b** plot the correlations between the brain LV and the respective behavioral covariate with 95% confidence intervals. For all conditions, RT-LV saliences were significantly negative. Accuracy-LV saliences were positive for all conditions but only reliably so for triples. This suggests that participants who invoke this pattern of activity influence their overall response times for both pairs and triples but only accuracy on triples. The brain LV (panels **c–d**) identified the most robust contribution over left frontal sites during the slow potential period, with the reverse polarity over right posterior sites. The topography suggests several foci of activity, including frontal and parietal areas. Both the topography and covariance with behavior suggest that this pattern of activity relates to the effective storage of order information (see Discussion). Study strategy could fluctuate within subjects, producing differences between subsequently recalled and subsequently not recalled materials; study strategy could also differ across subjects, which would not necessarily result in differences between recalled and not recalled trials but would appear in the correlation between activity present during study and behavioural measures across subjects. Because correlations were comparable regardless of subsequent memory, this activity likely reflects an overall strategy (i.e., between-subjects effect) that a participant invokes rather than accounting for trial-to-trial differences in the effectiveness of study processes (i.e., within-subjects effect).

Insert Figure 4 about here

Latent Variable #2: Early/LPC Complex with a Speed-Accuracy Tradeoff The second latent variable (Figure 5) accounted for 19% of the cross-block covariance ($p < 0.05$). Turning to the behavior LVs and scalp scores we find that invoking this activity pattern during study of triples was associated with better accuracy for triples but not pairs. However, response times were lengthened during all conditions (although the correlation is not reliable for study of not-recalled triples). Because correlations with accuracy and response time are both positive, this suggests that this LV reflects a strategy with a speed-accuracy tradeoff. Because only triples benefit in terms of accuracy, this study activity may involve additional storage of order information. The brain LV (panels **c–d**) indicates that the most reliable contribution to the LV is over central electrodes. The topography suggests sources in parietal areas at times coinciding with the LPC. The critical times, as well as the peak over the Cz/Pz area, coincide with previous reports of both the early component and LPC component of the SME for tests of item information. Thus, this LV identified a LPC that may serve to integrate words into ordered conceptual units. That fact that the early potential and LPC appeared in a single LV suggests that

these components represent linked functions and not independent processes, at least within the current tasks.

Insert Figure 5 about here

Planned comparisons: the Subsequent Memory Effect for pairs versus triples

The multivariate approach described the overall pattern of brain activity related to successful study of pairs and triples. Four patterns of brain activity were identified, and these included time periods overlapping with the three classic components described in the introduction: early component, LPC and slow potential. The multivariate approach answered the basic questions (whether study-relevant processes are the same or different for pairs and triples) from the perspective of global patterns of activity. However, a univariate, planned-comparisons approach could yield greater statistical power if it turned out that those classic components exhibited the strongest SME. For this reason we followed up with planned comparisons, focusing on the three specific ERP components that have been robustly linked to successful study assessed by tests of single-item memory. We examine the subsequent memory effect (SME) for pairs and triples, collapsing over words within pairs and triples, respectively. Note that as in the PLS analyses we exclude the distractor words (“C” items of AB-Triples and “A” items of BC-Triples) as these may have a different influence on subsequent memory (see next section). Results of the ANOVAs are listed in Table 2 and ERPs at sample electrodes are plotted in Figure 6. We confine discussion of the ANOVA results to effects directly relevant to our hypotheses, namely, those involving MEMORY or PAIR/TRIPLE.

Insert Table 2 about here

Early Component The early component was present in our data, as expected (Figure 6a,b). There was a 2-way interaction between PAIR/TRIPLE and ANT-POST and a 3-way interaction involving both PAIR/TRIPLE and MEMORY, namely, ANT-POST \times PAIR/TRIPLE \times MEMORY (Table 2). Simple effects at each electrode explained these interactions with main effects of PAIR/TRIPLE with more positive voltage for triples than pairs at PO3, O1 and O2 and the reverse pattern at FP2 and F4. In addition, an interaction between PAIR/TRIPLE and MEMORY was found at FP1 reflecting a positive-going SME for pairs and a negative-going SME for triples. An interaction between PAIR/TRIPLE and MEMORY was also found at PO4 with the opposite pattern. Thus,

the early component showed a SME, as predicted, but it differed at some electrode locations between pairs and triples.

Insert Figure 6 about here

Late Positive Component The LPC was also present in our recordings, as expected (Figure 6a,b), but exhibited a more complex topography. A main effect of PAIR/TRIPLE was found due to pairs exhibiting more positive voltage than triples. One 2-way interaction with PAIR/TRIPLE and one 3-way with MEMORY were significant. Explaining these interactions, simple effects at each electrode revealed effects of PAIR/TRIPLE at FP1, FP2, PO3, O1, C4 and O2 with voltage being more positive for triples than for pairs at PO3, O1 and O2 and the reverse at C4, FP1 and FP2. Simple effects also found a significant MEMORY×TIME BIN interaction at F4, explaining the 3-way HEMISPHERE×MEMORY×TIME BIN interaction. This effect is due to a crossover with voltage being more positive for triples at early time bins but more negative at later time bins. Thus, the LPC exhibited a SME and differentiated between pairs and triples but did not show differential SME for pairs compared to triples.

Slow Potential The slow potential was present in our data, as expected (Figure 6c,d). A main effect of PAIR/TRIPLE was found, due to more positive voltage for pairs than for triples. A 3-way interaction with PAIR/TRIPLE was found. Simple effects at each electrode explained this via main effects of both PAIR/TRIPLE and TIME BIN at FP1 and FP2 and a main effect of TIME BIN only at C4, O1 and O2. There was one significant interaction with MEMORY: HEMISPHERE×MEMORY. Simple effects found that MEMORY was significant only at two left-sided sites, C3 and P3, with voltage being more positive for subsequently recalled than not recalled pairs and triples (C3: $\Delta V = 0.46 \mu V$, P3: $\Delta V = 0.41 \mu V$). Thus, like the LPC, the slow potential exhibited a SME and differentiated between pairs and triples but did not show differential SME for pairs compared to triples.

Summary The three components targeted in the planned comparisons based on prior SME results were also observed in the PLS analyses. The planned comparisons confirm that these components show SMEs in our data set on when analyzed individually. The SME for the LPC and the slow potential fail to interact with the PAIR/TRIPLE factor, supporting the unified association/list theory. However, the unified theory in its strong form is challenged by the early component, which exhibits an interaction involving MEMORY and PAIR/TRIPLE.

Discussion

The multivariate, partial least squares (PLS) analyses allowed us to detect distributed patterns of brain activity that relate to the task conditions and behavioral measures in particular ways. The Task PLS analyses produced two patterns of brain activity differentiating conditions within subjects, one identifying activity specific to pairs but which also showed a SME for pairs and the other identifying a subsequent memory effect (SME) that was statistically reliable for pairs and a non-significant trend for triples. Both activity patterns had contributions from activity during the slow potential time period as well as activity during the LPC and early potential timings. The Behavior PLS identified two patterns of brain activity that explained individual variability, the first being a slow potential that benefited response times for pairs and triples but accuracy only for triples, and the second coinciding with the LPC and early potential, suggestive of a strategy involving a speed-accuracy tradeoff, resulting in particularly high accuracy on triples. Planned comparisons focused on specific ERP components based on the prior literature and confirmed that three classic ERP components that have been found to show a SME for tests of single-item memory also show a SME for tests of associations and short lists but two of the three components (LPC and slow potential) fail to differentiate successful-study activity for pairs from that for lists.

We first discuss how these findings bear upon the main theoretical question of the paper: whether effective memory for pairs and serial lists rely on the same or different cognitive processes. This is followed by more detailed discussion of the specific latent variables and ERP components analyzed.

Unified models of associative and list memory

One tradition of modeling list memory treats memory for associations and memory for lists as relying on common cognitive processes at both study and retrieval (Ebbinghaus, 1885/1913; Lewandowsky and Murdock, 1989; Caplan, 2004, 2005; Caplan et al., 2006). The other tradition of list modeling has treated memory for lists as a distinct phenomenon from memory for associations, suggesting that distinct cognitive processes underly these two paradigms (Baddeley, 1968; Brown et al., 2000, 2007; Burgess and Hitch, 1999; Conrad, 1965; Lee and Estes, 1977; Henson, Norris, Page, and Baddeley, 1996; Henson, 1998; Wickelgren, 1966). The unified approach predicts that those evoked potentials that underly successful study of associations should also underly successful study of lists, whereas the distinct-processes approach predicts that different evoked potentials will predict memory for lists versus memory for associations.

The present analyses inform this question in several ways. First, the first latent variable of the Task PLS differentiated activity during study of pairs from that during study of triples. Further, it interacted with subsequent recall, differentiating well vs. poorly studied trials within subjects for pairs but not reliably for

triples. The main effect of PAIR/TRIPLE dominates this latent variable, but the small interaction with MEMORY presents a challenge to the unified-process theory.

Second, many findings of processes related to successful study were common to both types of memory, consistent with the unified framework at a first pass, and complementing common oscillatory activity found in a companion paper that reported frequency-domain analysis of the present data set (Caplan and Glaholt, 2007). This was supported by the slow components in the planned comparisons (ANOVAs). The Within-Subjects SME (cf. Task PLS, second latent variable) showed a similar qualitative pattern for pairs as for triples but with a less reliable (non-significant) effect for triples. This is consistent with the notion that this activity pattern reflects a process that is involved in successful study of both pairs and triples but to a greater degree for pairs. A good behavioral model should be able to account for the reduced reliability, either in terms of participants invoking it to a lesser degree during study of triples, or due to an additional process dominating accuracy on triples, for instance, the relative strengths of competing list items.

Third, both latent variables in the Behavior PLS identified activity patterns that covary with response time similarly for pairs and triples but covary reliably with accuracy only for triples. However, while individual differences in response time are consistent across pairs and triples for both latent variables, both brain LVs were more sensitive to individual differences in accuracy for triples than for pairs. We have argued that such dissociations may reflect differences in the type of information necessary at retrieval, with precise order information being more helpful for probes of triples than for probes of pairs. This argument has the same flavor as the argument that has been made in the context of modeling of behavioral data (Caplan, 2004, 2005; Caplan et al., 2006).

In this study we have identified both similarities and differences between the SME for pairs and triples. The possibility remains that there are further cognitive processes that distinguish successful study of associations versus lists, but that these are more difficult to detect as ERPs, due to lower amplitudes or greater variability in timing or position or orientation of sources. Furthermore, the common-process portion of our results may hold for pairs and triples but not for longer lists, a possibility that must be addressed in follow-up studies. As a final caveat, note that it is conceivable that a single generator could carry out more than one different cognitive operations, but without producing large differences in the EEG pattern observed at the scalp. For example, analysis of rhythmic memory-related activity found a pattern of oscillations associated with effective study of pairs (within-subjects effect) but not triples (Caplan and Glaholt, 2007). This finding was accompanied by findings that suggested a large amount of common memory-relevant study activity for pairs and triples.

The combined time- and frequency-domain findings support the notion that many of the processes underlying effective study of pairs and lists may be common, but some substantial differences need to be addressed by existing unified models. These may be differences in which processes are engaged during study of pairs versus triples or in the degree to which participants invoke a given process or in the ways in which the same process at study influences subsequent performance measures (e.g., accuracy versus response time). An important follow-up direction bearing on how to modify unified models will be to investigate the effects of various commonly used study strategies on the characteristics of memory for pairs versus lists— particularly with regard to the quality of learned order information— such as the Method of Loci, imagery intensive strategies, non-imagery-based verbal strategies and explicit associative-chaining-like study strategies (e.g., Roediger, 1980).

The role of PLS in addressing brain–behavior questions

The PLS method explained the brain–task relationship most optimally (in a least-squares sense) by grouping together similar encoding-related activity (SME) for both pairs and triples within the same latent variable. Thus, in a non-confirmatory, multivariate sense, PLS is telling us that a good way to understand the memory-related brain activity is to observe several common distributed patterns of such activity that apply to both pairs and triples, along with some patterns of activity that differentiate effective study of pairs from triples. Second, the common-process hypothesis does not require identical magnitudes of SMEs for pairs and triples. In fact, it is quite implausible that pairs and triples would exhibit the same magnitude SME given that they differ in overall accuracy and response time and thus probably differ in difficulty. The key point here is that many of the same spatiotemporal patterns of brain activity covary with effective memory performance for both pairs and triples. The precise interpretation of common brain activity is subject to some important caveats, as follows.

Caveats for interpreting same/difference results and SME findings

As with all studies that rely on passive measurements of brain activity, causation cannot be definitively established. What must be done (and is routinely done in cognitive neuroscience) is to seek convergent evidence and bear in mind caveats and the limitations of their technique.

While all EEG studies have the problem that one does not know whether the observed activity relates directly to behavior or not, studies that do not attempt to relate brain activity to behavior suffer from this more. Nonetheless, the SME warrants additional caveats. In particular, the SME can be thought of as a selection effect. Simply finding brain activity during study that differentiates subsequent memory does not in itself tell us what the role of that brain activity might be, nor whether it is necessary or sufficient for subsequent memory

behavior. Memory undoubtedly relies on idiosyncratic cognitive processes, for example, certain stimuli or configurations of stimuli may be more personally meaningful to one participant than to another. The same can be said about within-subject, trial-to-trial variability. Thus, one would expect a large amount of variability in cognitive processes and thus in brain activity which would appear as random noise in group analyses and even in analyses that average across trials within participants. This makes the SME biased against potential findings both of similar and different activity between pairs and triples.

When one observes similar SME activity between pairs and triples, this activity could reflect uninteresting or non-memory-related cognitive processes such as fluctuations in attention. Likewise, when one observes different SME activity between pairs and triples, the observational approach in brain-activity studies means that we cannot determine whether this differential activity is necessary or sufficient for memory for pairs or triples. Differential SME activity could, for instance, reflect spectator processes that co-occur with effective study processes but which do not contribute directly to learning, such as self-monitoring.

Within-Subjects pair-specific activity

The first latent variable of the Task PLS (Figure 2) identified an activity pattern that contrasted study of pairs with study of triples, likely originating from a medial frontal source. Its timing encompassed the periods of the slow potential as well as the early potential and LPC. This latent variable differentiated subsequently recalled pairs from subsequently not recalled pairs but did not relate reliably to subsequent memory for triples. This latent variable may reflect processes that are related to forming associations versus triples but are only minimally relevant for subsequent retrieval of associative information.

Within-Subjects SME

The second latent variable of the Task PLS (Figure 3) identified a SME that was reliable for pairs and showed a similar pattern, though less reliable, for triples. It is most prominent over posterior sites and somewhat left-lateralized, consistent with the verbal nature of the task. The topography suggested that multiple brain areas generated the scalp topography. Posterior negative slow potentials may underlie visual perceptual processing of the stimulus words but have also been reported during word recognition (Smith and Halgren, 1988). Thus, the posterior portion of this brain LV could underlie retrieval of semantic information about the word stimuli. More likely, however, the slow potential relates to elaborative processing; the positive–negative anterior–posterior polarity is consistent with reports of SME-ERP components that underlie subsequent recollection judgements (Mangels et al., 2001) and effective learning of general-knowledge material with feedback

during study (Mangels, Butterfield, Lamb, Good, and Dweck, 2006). Participants can study verbal materials using a variety of strategies. Those that involve deeper, or more elaborative processing result in greater accuracy, but at the expense of longer response times. Elaborative strategies include forming images out of the component words or inventing sentences that involve the items (Yuille and Paivio, 1967; Paivio, 1969, 1971; Craik and Lockhart, 1972; Yuille, 1973). In addition to similar SME findings (Mangels et al., 2001, 2006), a posterior slow wave was associated with updating working memory, especially for more complex updates García-Larrea and Cézanne-Bert (1998), which could be an aspect of the type of elaborative processing employed in study of word pairs and triples. The anterior positive slow potential may relate to executive function, including elaborative processing (Fabiani et al., 1986; Weyerts et al., 1997). There are numerous types of elaborative processing strategies. Some such strategies may involve precise learning of order information while others may not. A process that relates to behavior on pairs but less reliably to behavior on triples is suggestive of the latter type of strategy. Examples may include identifying similarities or differences between pairs of items (e.g., Epstein and Phillips, 1976; Medin, Goldstone, and Gentner, 1993) or forming images involving both items in which the configuration of items does not reflect their presentation order.

Between-subjects variability: learning of order information

The first latent variable of the Behavior PLS (Figure 4) identified activity that differentiated fast and accurate participants from slower and less accurate participants. Accuracy reliably covaried with this activity pattern only for triples. The topography involved a very early negativity at middle-posterior sites, perhaps reflecting early visual processing, followed by a slower, right-sided negative deflection centered around P6 and a longer-lasting positive slow potential at left frontal sites.

The dissociation in correlation with accuracy may be explained as follows. A cued recall question for a pair A-B, consists of being presented with A and asked for B or presented with B and asked for A. In both cases, if the participant can retrieve the pair, the correct response is unambiguous. For a triple A-B-C, the participant is given only one of three items. Thus, to retrieve the correct response, it is not sufficient to retrieve the triple; the participant must still disambiguate the remaining two items to determine which one is required. The activity pattern identified in this latent variable may thus relate to study processes that involve precise storage of order information, consistent with the large saliences at frontal sites, possibly indicating top-down executive control. Participants that invoke this order-study strategy can respond faster to cued recall probes, but only with a reliable benefit for accuracy on triples. The left frontal topography is consistent with a verbal strategy for learning the order of items. An example of an order-rich verbal learning strategy would be to form grammatical

sentences that link two or more items in which the order of occurrence in the sentence reflects their original presentation order. It is also possible that this activity reflects executive processes that are used to add spatial order to a visual representation of the paired items. Corroborating this interpretation, Cansino, Maquet, Dolan, and Rugg (2002) reported a similar topography (left inferior frontal gyrus combined with right occipital) for visual stimuli whose spatial locations were successfully retrieved; this is consistent with the topography of the Behavior PLS LV 1, suggesting that this pattern of brain activity could relate to building explicit spatial representations of order.

Between-subjects variability: Late Positive Component and early potential

The second latent variable of the Behavior PLS (Figure 5) identified a spatiotemporal complex including an early potential and a late positive component (LPC), both centered over central midline sites. It identified a pattern of brain activity that embodied a speed-accuracy tradeoff that was reliable for triples; pairs showed only reliable correlations with response times. Mangels et al. (2001) found a component with similar timing which exhibited a SME but only for items that could be recognized and not recalled. These authors suggested that this component coincides with the P3b, which was found by Grune, Metz, Hagendorf, and Fischer (1996) to change over serial position in a short-term serial recall task. This is especially noteworthy given the specific relevance of this component to accuracy on triples compared to pairs. While in that study the LPC did not show a SME, it is possible that the LPC-like activity in this LV represents the same process, and that our methods are more sensitive with respect to memory assessment, either due to the probed recall technique or the use of between-subjects variability in performance. A similar potential was found to be enhanced in an oddball paradigm when stimulus onset was under voluntary control (Nittono, 2005), consistent with the notion that participants study pairs and triples by intentional analysis of to-be-associated items for similarities and differences (e.g. Epstein and Phillips, 1976; Medin et al., 1993). Consistent with this account, the topography is consistent with pre-stimulus “task-set” activity related to successful semantic processing that resulted in enhanced subsequent memory (Otten, Quayle, Akram, Ditewig, and Rugg, 2006). The finding of both the early potential and the LPC in a single latent variable suggests that these components represent processes that work in concert rather than independently within the context of the present tasks.

Planned Comparisons

The PLS analyses found solutions that identify critical times that are quite consistent with prior findings, namely, an early period around 200 ms, a late positive component centered around 550 ms and a slow potential

that appears to persist indefinitely. These components were especially prominent in the second LV of the Task PLS (Figure 3) which showed a large SME in the design LV. These analyses provided a much richer picture, showing that the specific timing interacts with location on the scalp. To more directly compare with prior research we conducted planned analyses on the three classic components.

ANOVAs demonstrated that these three ERP-SME components apply not only to memory for single items (based on prior findings since single-item memory was not directly tested here), but to memory for associations (cued recall of word pairs) and short lists (cued recall of word triples). These components are an early potential, a late positive component and a slow potential. No differences were found in the later components (LPC and slow potential) of the SME between cued recall of pairs and triples, suggesting that at least at a coarse level, many study processes relevant to memory for lists are the same as those relevant to memory for associations, supporting more parsimonious models that treat associative and list memory as fundamentally similar. However, the early potential did show a SME that differed in sign for pairs versus triples.

These three classic ERP components provide complementary information to the PLS findings, they appear to represent a more narrow view of the data than the multivariate analysis. The multivariate analysis extended our understanding of these components by a) suggesting that the early potential and the LPC occur within the same latent variable (at least within the context of our tasks), thus explaining common cross-block covariance, and b) all three components may be tapping portions of several distributed activity patterns (i.e., the brain latent variable activity patterns identified by the PLS).

Rote versus elaborative processes

The two latent variables in the Behavior PLS, as well as the second latent variable in the Task PLS, appear to have identified electrophysiological correlates of elaborative processing. Similarly, the ANOVAs found that the single-item episodic memory SME (found in previous studies) generalized to episodic memory for associations and lists. There are two possible interpretations of these findings: 1) these SMEs represent item-learning processes and 2) these SMEs represent association-learning processes. We evaluate the support for each interpretation in turn.

The item-memory account In a single-item episodic memory paradigm, the participant has pre-existing knowledge of the items in the stimulus set (semantic item memory). The episodic memory test probes the participant’s knowledge of which particular items were presented at a specific time (e.g., on the most recent trial). Clearly, to be able to respond accurately to our cued recall probes, the participant needs access to

this type of single-item episodic memory— which items were just presented. Thus, one interpretation of the present findings is that we are only observing SME components involved in effective study of episodic item knowledge (binding items to a representation of the most recent list), and that this process is a bottleneck to successful performance in our memory tests.

But consider, for example, the pairs. A forward probe requires the participant to produce the “B” item whereas a backward probe requires the participant to produce the “A” item. Participants responded nearly identically (in accuracy and response time) to cued recall probes in the forward and backward directions. Furthermore, in prior studies, forward and backward cued recall of both pairs and triples were found to be nearly perfectly correlated for pairs and both types of triples (Rizzuto and Kahana, 2001; Kahana, 2002; Caplan et al., 2006). This means that if a participant answered a cued recall question correctly in the forward direction, they would almost certainly be able to answer a probe of the same pair or triple in the backward direction. If accuracy in this task were driven primarily by the participant’s ability to recall the target item itself (i.e., item-memory effects), then forward and backward probes should not be highly correlated. The same argument can be made for recognition memory for the probe item. Thus, accuracy in this task appears to reflect primarily the quality of the learned association and order information rather than item information per se. This is consistent with Hockley and Cristi (1996) who found that when participants study for a single-item memory test (under instructions to study items without attention to possible relationships between items), they have difficulty recalling associations, whereas when studying for an associative memory test (under instructions to form relational representations of item pairs), they can perform just as well on tests of item memory. If, as the behavioral evidence suggests, our performance measures distinguish well learned associations or list structures and are relatively insensitive to the quality of learned item information alone, then our SMEs are unlikely to reflect processes specifically related to study of episodic item information.

The relational processing account The alternative account is that present and previous SME findings reflect associative or relational study processes. This would imply that the single-item SMEs reported previously also reflect relational study processes despite the fact that participants in those studies were only tested for their memory of single items without regard to the organization of the items at time of study. We cannot draw definite conclusions on this matter given that we did not include a pure test of item information. However, several findings provide support for the notion that the current (and perhaps prior) SME results reflect associative learning. Some prior SME studies have explicitly included associative or relational study instructions in their item-memory paradigms (e.g., Sanquist et al., 1980; Weyerts et al., 1997). For example, Weyerts et al.

(1997) found a reliable SME only for associatively encoded word pairs even though the memory test did not require retrieval of the association. Friedman and Trott (2000) used a “remember/know” paradigm (Tulving, 1985) designed to separate recognition judgements based on recollection of the study episode (along with contextual information) versus correct recognition based on mere familiarity. The recollection responses (“remember”) showed larger SMEs in both LPC and slow potential components. This suggests that these SME components reflect successful study of the relational information about the study episode and not merely knowledge of which items were presented. Mangels et al. (2001) found a similar recollection-specific enhancement of the slow potential. Thus, we suggest that our SME findings more likely reflect relational learning processes than learning of the individual items.

In sum, we identified patterns of brain activity that account for within-subjects variability in effectiveness of study as well as individual differences in performance, both in accuracy and response time. These patterns encompassed three classic ERP components: an early potential, a late positive component and a slow potential which, in planned comparisons, all exhibit a subsequent memory effect for memory for associations and (short) lists. This extends prior single-item memory findings to memory for structured information, consistent with Guo et al. (2005). Note, however, that Guo et al. (2005) used simultaneous, rather than sequential presentation and did not directly link their SME to association learning. We suggest that prior SMEs may have largely reflected relational, elaborative processing even though those paradigms did not test directly for detailed knowledge of the pairings or ordering of items with a study set. Much of the evidence supported the notion that common processes underly association and list memory, supporting more parsimonious models and arguing against the notion of distinct cognitive mechanisms for list memory compared to associative memory. However, some study processes differed in their relationship to behavior on pairs versus triples. We suggest that they involve learning of order information and may dissociate subsequent behavior due to the additional diagnostic value of order information for memory tests of triples compared to pairs. Thus, existing models that rely on common study and retrieval processes must be amended to take into account this insight. These findings serve both to extend our knowledge of the SME and to constrain behavioral models of associative and list memory. This set of analyses thus supports the notion that these three classic SME components represent subsets of the more complex distributed patterns of study-related brain activity evident in the multivariate analyses.

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Footnotes

¹Note that Task PLS also takes behavior into account, but as separate conditions, not as covariates. We use this nomenclature for consistency with prior work but the reader be aware that the chief difference between Task PLS and Behavior PLS in the present application is that Task PLS examines behavior as a within-subjects variable whereas Behavior PLS examines behavior as a between-subjects variable, seeking to identify EEG covariates of individual differences in accuracy and response time.

<u>Type</u>	Accuracy		Response Time [ms]	
	Forward	Backward	Forward	Backward
Pairs (AB)	0.62 (0.05)	0.63 (0.04)	2613 (111)	2705 (114)
AB-Triples (AB)	0.43 (0.05)	0.39 (0.05)	3114 (122)	3330 (206)
BC-Triples (?BC)	0.36 (0.05)	0.35 (0.05)	3547 (146)	3358 (135)

Table 1

Accuracy and response times (correct responses only) for the 20 participants included in the ERP analyses. Values in parentheses denote S.E.M. across participants.

Effect	<i>F</i> ratio	Significance
<u>Early Component</u>		
HEMISPHERE	$F(1, 19) = 9.2$	$p < 0.01$
ANT-POST	$F(2, 31) = 13.3$	$p < 0.001$
ANT-POST×PAIR/TRIPLE	$F(2, 52) = 7.1$	$p < 0.005$
ANT-POST×PAIR/TRIPLE×MEMORY	$F(2, 45) = 3.0$	$p < 0.05$
<u>LPC</u>		
PAIR/TRIPLE	$F(1, 19) = 4.9$	$p < 0.05$
ANT-POST×PAIR/TRIPLE	$F(2, 33) = 7.2$	$p < 0.005$
ANT-POST×TIME BIN	$F(2, 31) = 43.3$	$p < 0.05$
HEMISPHERE×MEMORY×TIME BIN	$F(3, 61) = 2.9$	$p < 0.05$
<u>Slow Potential</u>		
PAIR/TRIPLE	$F(1, 19) = 7.5$	$p < 0.05$
ANT-POST×PAIR/TRIPLE	$F(2, 40) = 4.6$	$p < 0.05$
HEMISPHERE×MEMORY	$F(1, 19) = 4.6$	$p < 0.05$
HEMISPHERE×TIME BIN	$F(2, 30) = 7.9$	$p < 0.005$
HEMISPHERE×PAIR/TRIPLE×TIME BIN	$F(2, 42) = 3.5$	$p < 0.05$

Table 2

Significant effects from the pair versus triple SME ANOVAs.

Figure Captions

Figure 1. Behavioral procedure. Study and test phase for a study set of triples.

Figure 2. Task PLS (within-subjects approach), Latent Variable #1. **a**, Design LV, salience is plotted as a function of condition, characterizing how the brain LV pattern varies on average as a function of condition. **b**, Scalp scores, the projection of the brain LV onto each condition. Error bars plot 95% confidence intervals across participants. **c**, Brain Latent Variable #1 at sample electrodes as a function of time. Red asterisks denote times at which the salience was reliable (bootstrap ratio magnitude > 2.58 , equivalent to z scores with a p value of 0.01). **d**, Topographic spline maps plotting salience across the scalp at sample times, wherever the bootstrap ratio magnitude exceeded a threshold of 1.96 (unreliable saliences are plotted in black). Color scale denotes salience. View angle = $(0^\circ, 67^\circ)$.

Figure 3. Task PLS (within-subjects approach), Latent Variable #2. **a**, Design LV, salience is plotted as a function of condition, characterizing how the brain LV pattern varies on average as a function of condition. **b**, Scalp scores, the projection of the brain LV onto each condition. Error bars plot 95% confidence intervals across participants. **c**, Brain Latent Variable #2 at sample electrodes as a function of time. Red asterisks denote times at which the salience was reliable (bootstrap ratio > 2.58 , equivalent to z scores with a p value of 0.01). **d**, Topographic spline maps plotting salience across the scalp at sample times, wherever the bootstrap ratio magnitude exceeded a threshold of 1.96 (unreliable saliences are plotted in black). Color scale denotes salience. View angle = $(0^\circ, 67^\circ)$.

Figure 4. Behavior PLS (between-subjects approach), Latent Variable #1. **a**, Correlation between the brain LV and accuracy as a function of condition, characterizing how the brain LV covaries with accuracy across condition. **b**, Correlation between the brain LV and RT as a function of condition, characterizing how the brain LV covaries with RT across condition. Error bars plot 95% confidence intervals. **c**, Brain Latent Variable #1 at sample electrodes as a function of time. Red asterisks denote times at which the salience was reliable (bootstrap ratio > 2.58 , equivalent to z scores with a p value of 0.01). **d**, Topographic spline maps plotting salience across the scalp at sample times, wherever the bootstrap ratio magnitude exceeded a threshold of 1.96 (unreliable saliences are plotted in black). Color scale denotes salience. View angle = $(0^\circ, 67^\circ)$.

Figure 5. Behavior PLS (between-subjects approach), Latent Variable #2. **a** Accuracy LV, Salience is plotted as a function of condition, characterizing how the brain LV covaries with accuracy across condition. **b**, Correlation between the brain LV and accuracy as a function of condition. **c** RT LV, characterizing how the brain LV covaries with RT across condition. **d**, Correlation between the brain LV and RT as a function of condition. Error bars plot 95% confidence intervals. **e**, Brain Latent Variable #2 at sample electrodes as a function of time. Red asterisks denote times at which the salience was reliable (bootstrap ratio > 2.58 , equivalent to z scores with a p value of 0.01). **f**, Topographic spline maps plotting salience across the scalp at sample times, wherever the bootstrap ratio magnitude exceeded a threshold of 1.96 (unreliable saliences are plotted in black). Color scale denotes salience. View angle = $(0^\circ, 67^\circ)$.

Figure 6. The subsequent memory effect for pairs versus triples, early and late positive components at a sample of electrodes for pairs (**a**, collapsed across “A” and “B” words) and triples (**b**, collapsed across “A” and “B” words of AB-Triples and “B” and “C” words of BC-Triples). as well as slow potential (**c**, pairs and **d**, triples).

FIGURE 1

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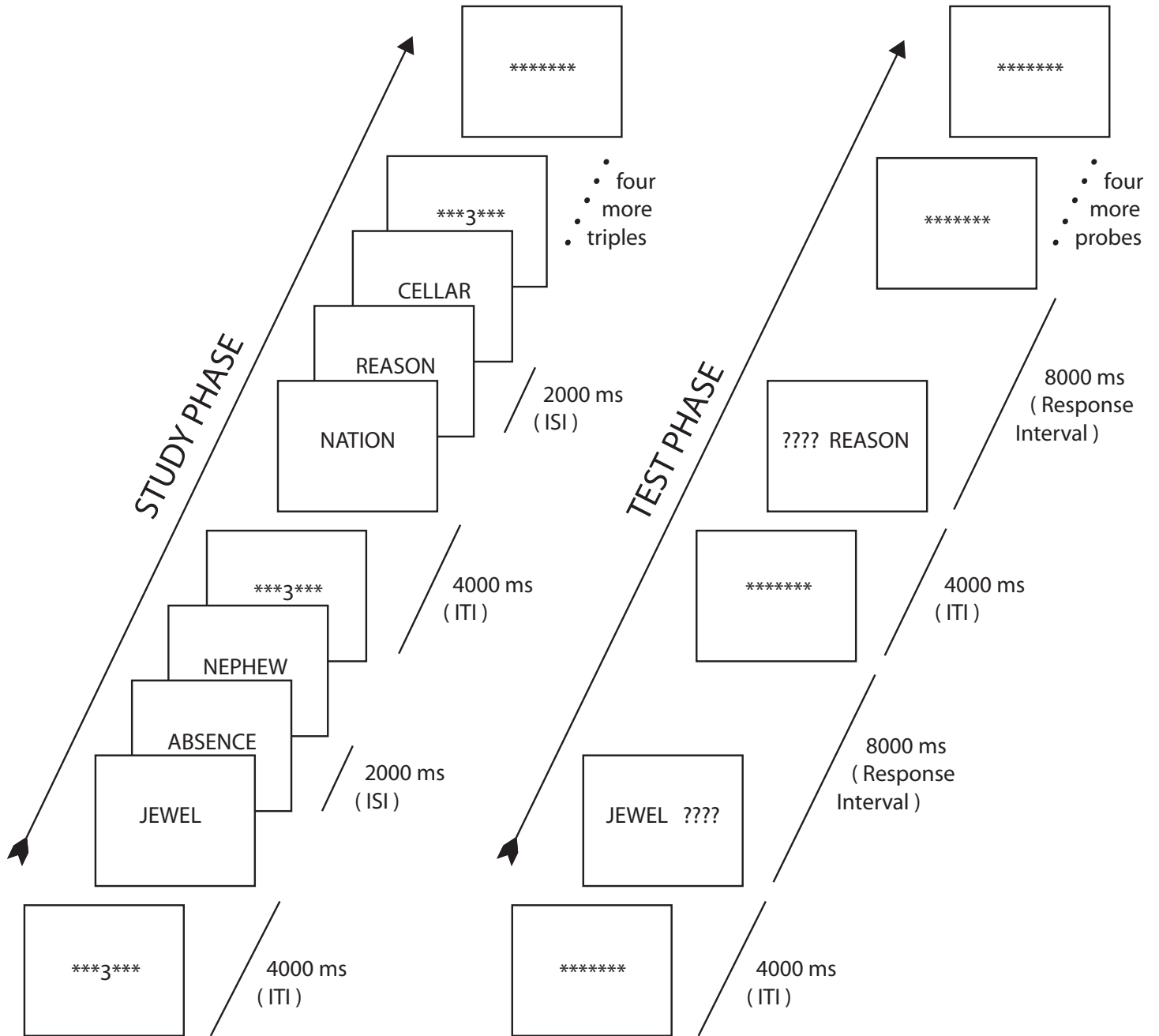


FIGURE 2

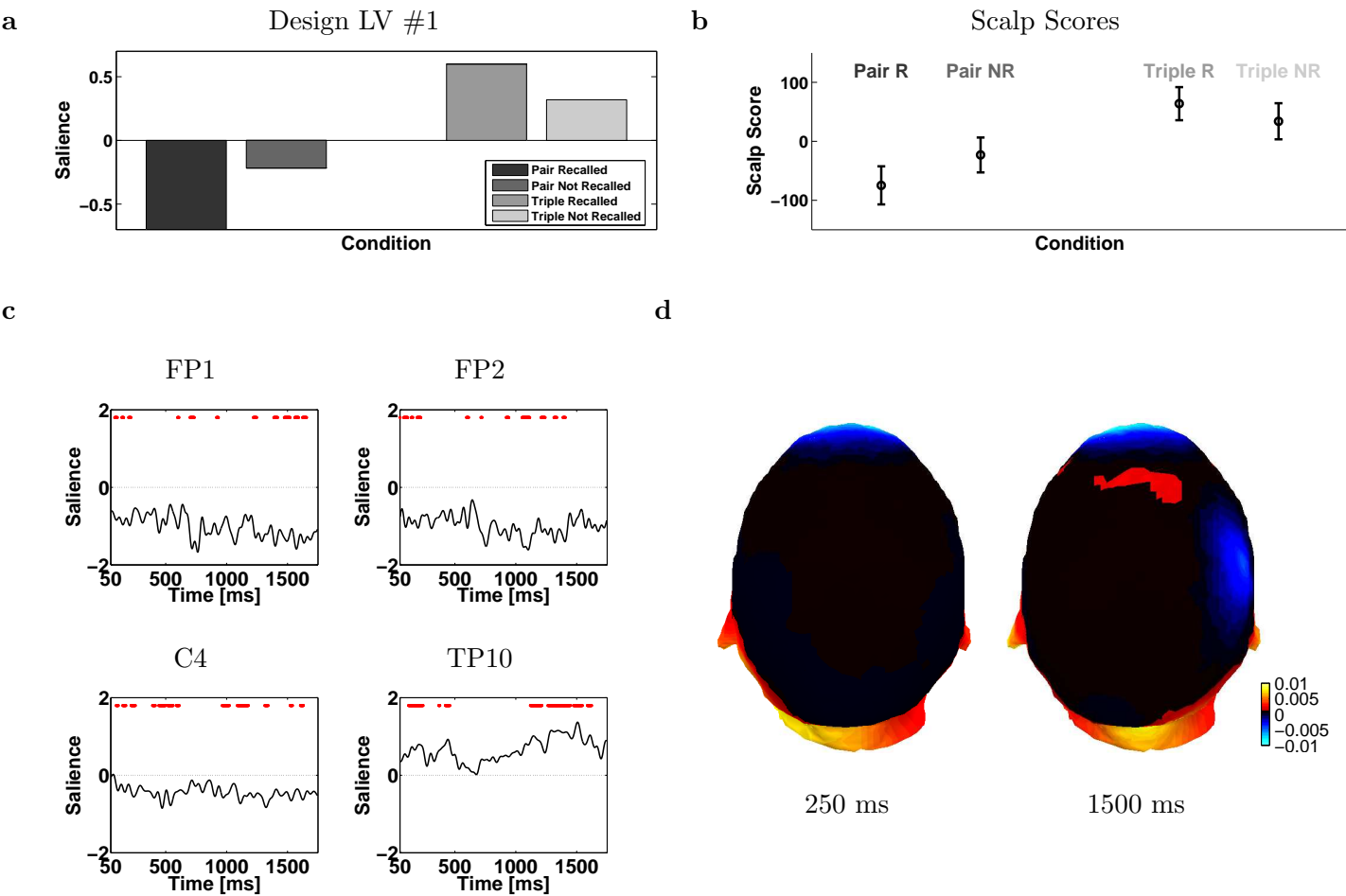


FIGURE 3

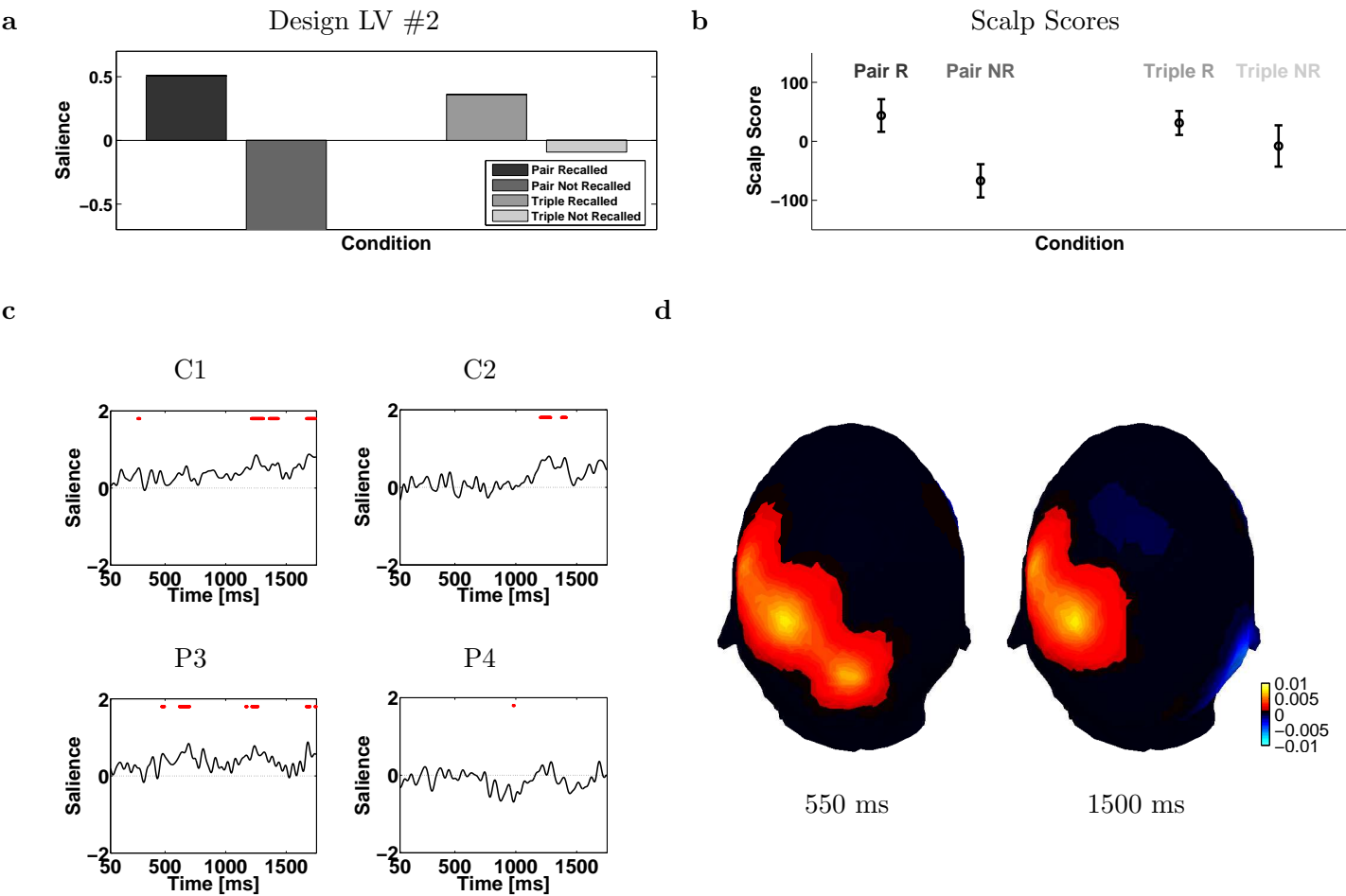


FIGURE 4

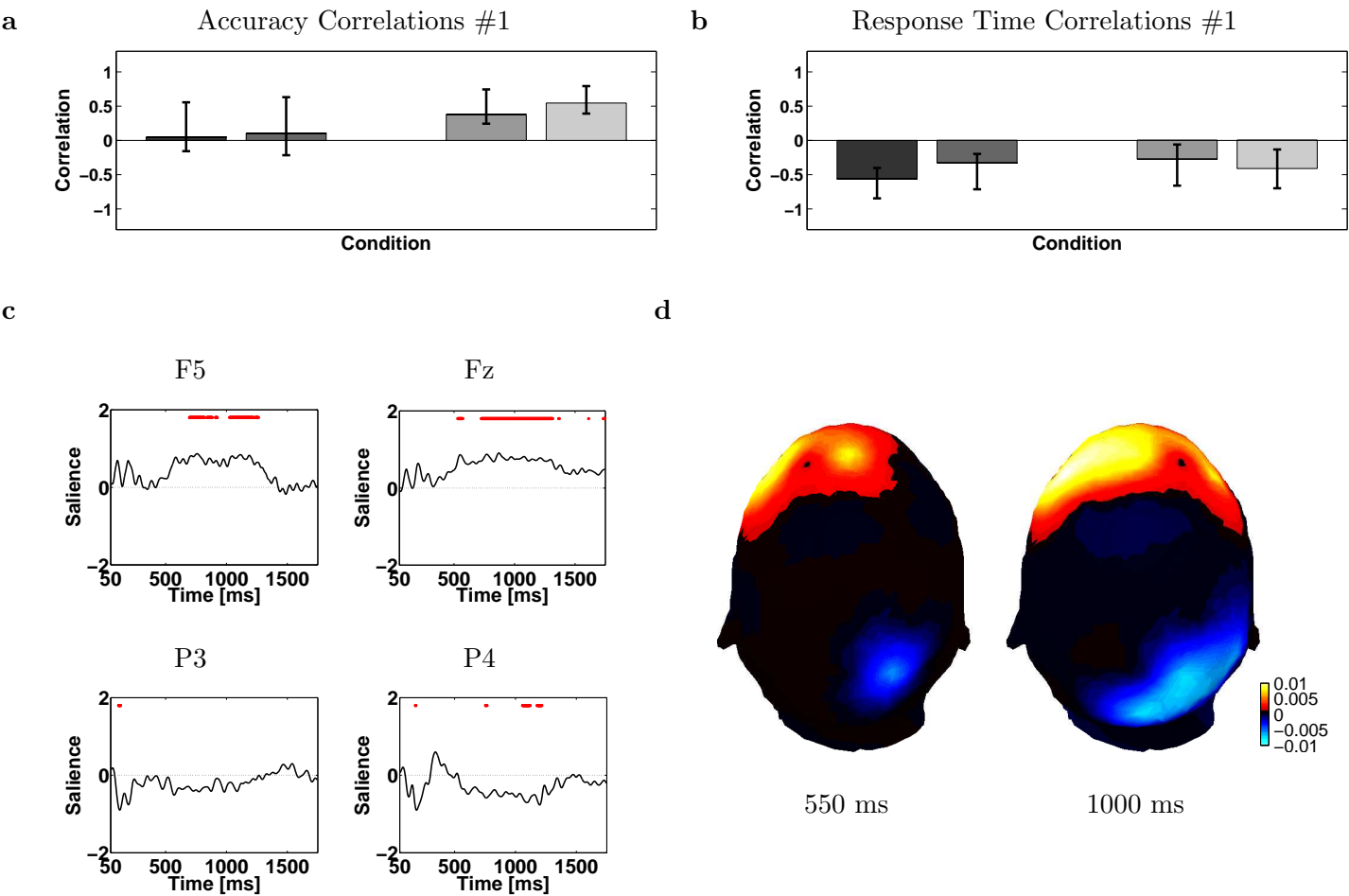


FIGURE 5

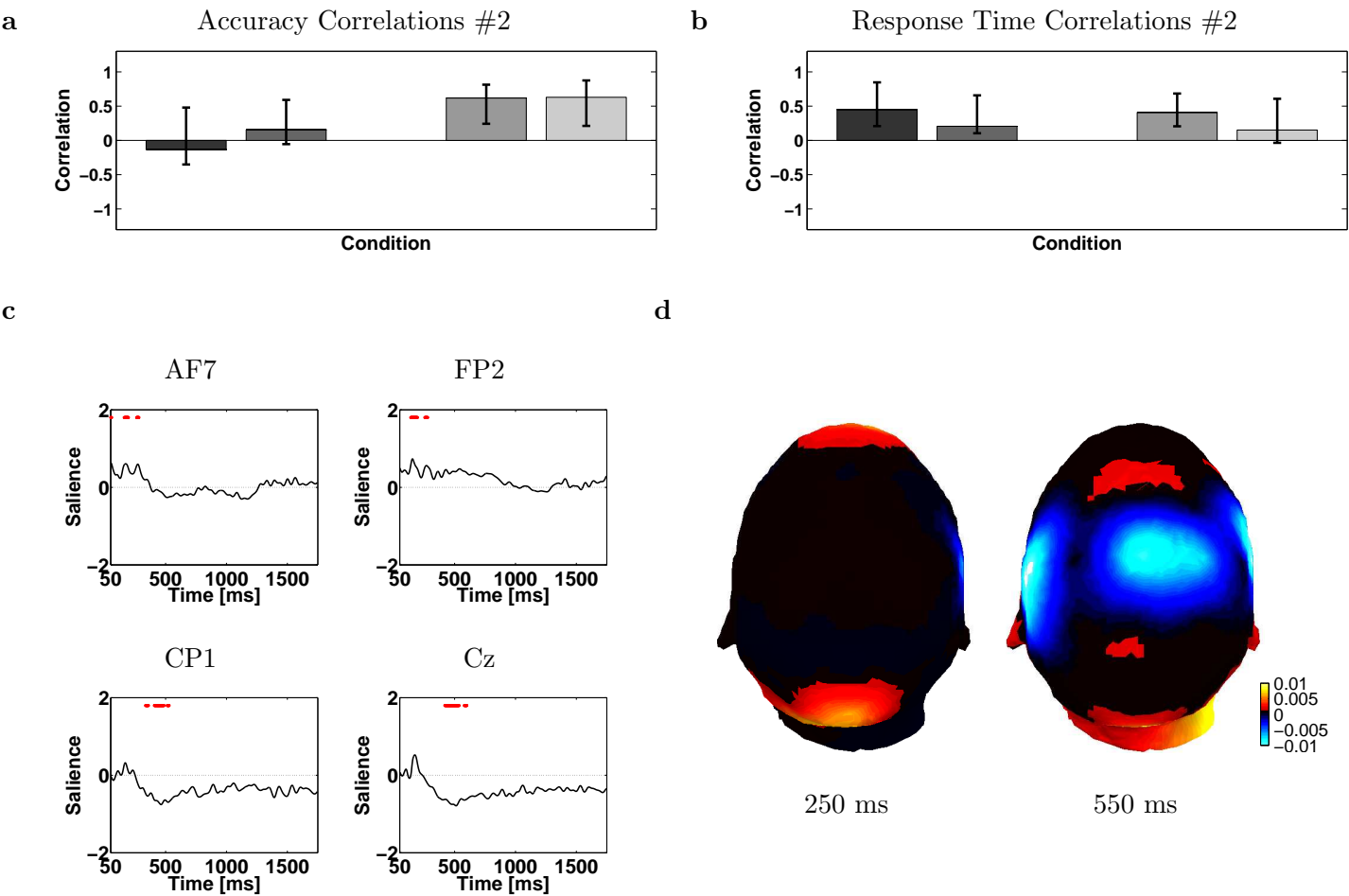


FIGURE 6

