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Examining ERP correlates of recognition memory: Evidence of accurate source recognition without recollection

Richard, J. Addante[1,2,3], **Charan Ranganath**[1,2,4], and **Andrew, P. Yonelinas**[1,2,4,5]

[1]University of California, Davis

[2]Center for Neuroscience, University of Texas – Dallas

[3]Center for Vital Longevity, UC Davis Center for Neuroscience 1544 Newton Ct Davis, CA, 95616

[4]Department of Psychology, UC Davis Center for Neuroscience 1544 Newton Ct Davis, CA, 95616

[5]Center for Mind and Brain UC Davis Center for Neuroscience 1544 Newton Ct Davis, CA, 95616

Abstract

Recollection is typically associated with high recognition confidence and accurate source memory. However, subjects sometimes make accurate source memory judgments even for items that are not confidently recognized, and it is not known whether these responses are based on recollection or some other memory process. In the current study, we measured event related potentials (ERPs) while subjects made item and source memory confidence judgments in order to determine whether recollection supported accurate source recognition responses for items that were not confidently recognized. In line with previous studies, we found that recognition memory was associated with two ERP effects: an early on-setting FN400 effect, and a later parietal old-new effect [Late Positive Component (LPC)], which have been associated with familiarity and recollection, respectively. The FN400 increased gradually with item recognition confidence, whereas the LPC was only observed for highly confident recognition responses. The LPC was also related to source accuracy, but only for items that had received a high confidence item recognition response; accurate source judgments to items that were less confidently recognized did not exhibit the typical ERP correlate of recollection or familiarity, but rather showed a late, broadly distributed negative ERP difference. The results indicate that accurate source judgments of episodic context can occur even when recollection fails.

Keywords

Recollection; Familiarity; Event-related Potentials; Source Memory; Episodic Memory

Corresponding Author: Richard J. Addante UT-Dallas Center for Vital Longevity 1600 Viceroy Drive, Suite 800 Dallas, TX 75235 Phone: (972) 883-3200 Fax: (972) 883-3250 richard.addante@utdallas.edu.

1.1 Introduction

Recognition memory judgments can be based on *recollection* of qualitative information about a previous event or on assessments of stimulus *familiarity*. The familiarity process is generally assumed to reflect the rapid assessment of global familiarity or memory strength of an item, whereas recollection reflects a search of memory similar to that used in free recall, whereby associative information about the study event is retrieved. Recollection and familiarity have been shown to be functionally dissociable and to rely on partially separable brain regions (Diana, Yonelinas, & Ranganath, 2007; Eichenbaum, Yonelinas, & Ranganath, 2007; Yonelinas, 2001a, 2001b; Yonelinas & Parks, 2007),(Yonelinas et al., 2002). In addition, recollection and familiarity have been associated with distinct event related potential (ERP) modulations (Cansino & Trejo-Morales, 2008; Curran, 2000; Leynes, Landau, Walker, & Addante, 2005; Rugg & Curran, 2007; Wilding & Rugg, 1996; Yu & Rugg, 2010). That is, at time of retrieval, familiarity is associated with modulations of the FN400, an enhanced positivity for old items relative to new items observed from approximately 400–600ms post stimulus onset. The FN400 tends to have a mid-frontal scalp distribution which can extend to left and right frontal areas, plus central midline regions depending on which experimental materials are used (Friedman, 2000; Friedman & Johnson, 2000; Gruber & Otten, 2010; Rugg & Curran, 2007; Rugg, Mark, et al., 1998; Voss & Paller, 2007). In contrast, recollection has been linked with modulations of a positive going waveform that emerges approximately 600ms post stimulus and that is typically maximal over left parietal sites (Curran, 2000; Rugg, Mark, et al., 1998), and referred to as the Late Positive Component (LPC). Dissociations between these ERP modulations have been reported based on subjective reports of recollection and familiarity (Duzel, Yonelinas, Mangun, Heinze, & Tulving, 1997), as well as correct and incorrect source memory discriminations (Wilding & Rugg, 1996), for review see (Rugg & Curran, 2007). In addition, the FN400 is found to increase gradually as a function of item recognition confidence whereas the LPC is limited to high confidence recognition responses (Woodruff, Hayama, & Rugg, 2006; Yu & Rugg, 2010), consistent with cognitive models of familiarity and recollection (Yonelinas, 1999; Yonelinas, Aly, Wang, & Koen, 2010).

Although the distinction between recollection and familiarity is relatively well established, important debates remain about the functional nature of these processes and about how to best separate these processes, for a review see (Yonelinas, 1999, 2001a; Yonelinas, et al., 2010; Yonelinas & Levy, 2002). One approach is to use tests of source memory as measures of recollection (i.e., tasks that require subjects to retrieve where or how an item was studied), and compare this to performance on tests of item recognition (i.e., tasks that require subjects to discriminate between old and new items). The idea is that, if accurate source discriminations rely exclusively on recollection then performance on these tests can be used as an index of recollection. In contrast, if an item is recognized as old but leads to an incorrect source memory judgment then this can be used as a measure of familiarity. An alternative approach is to estimate recollection on the basis of recognition confidence judgments. The idea is that the recollection of qualitative information about a study event should lead to confident recognition memory responses, whereas familiarity in the absence of recollection should support lower confidence recognition responses. Thus in standard item recognition tests recollection should be restricted primarily to high confidence recognition responses whereas familiarity should increase gradually across levels of confidence, see (Parks & Yonelinas, 2007, 2009; Yonelinas & Parks, 2007).

Usually, correct source judgments are associated with the highest level of recognition confidence, so these two approaches often lead to the same conclusions. However, subjects can often recognize items with less than the highest level of item confidence, and yet go on to accurately determine the source of those items (Hicks, Marsh, & Ritschel, 2002; Levine, Freedman, Dawson, Black, & Stuss, 1999; Quamme, Frederick, Kroll, Yonelinas, & Dobbins, 2002; Wais, Squire, & Wixted, 2010; Yonelinas, 2001a; Yonelinas, Hopfinger, Buonocore, Kroll, & Baynes, 2001). What memory process might support these source discriminations is not yet clear. If they are based on recollection, one might expect that items associated with lower recognition confidence but correct source should be associated with an LPC modulation, perhaps in a graded fashion (Leynes & Phillips, 2008). In contrast, if they are based on familiarity (Diana, Van den Boom, Yonelinas, & Ranganath, 2011) or conceptual implicit memory (Paller, Voss, & Boehm, 2007), one might expect these trials to be associated with an ERP modulation resembling the FN400.

We sought to test these alternatives by examining the ERPs related to item recognition confidence and source memory judgments. In Experiment 1, we recorded ERPs during a recognition memory test in which subjects made old/new recognition judgments and source memory judgments (see Figure 1). Based on prior work, we expected to see an early fronto-central effect related to familiarity from 400–600ms (FN400) and a later left hemisphere effect related to recollection from 600–800ms (LPC). The FN400 effect was expected to increase gradually across item recognition confidence with increases in familiarity strength, whereas the LPC was expected to be restricted to the high confidence recognition responses. Moreover, we hypothesized that items leading to correct source memory judgments should produce a recollection effect compared to incorrect source judgments. Most importantly, we then examined the ERPs associated with correct source memory responses that were not recognized with the highest levels of recognition confidence. No prior study that we are aware of has examined this critical condition. If these items reflect the operation of recollection then they should exhibit the late left hemisphere ERP signature consistent with recollection. In contrast, if these source memory responses are reflecting the operation of familiarity, they should exhibit the FN400 ERP effect consistent with familiarity. Experiment 1 produced a pattern of results that was not consistent with either the recollection or the familiarity account, but rather suggested that source correct responses for low confidence item recognition might reflect the contribution of some other memory process. To assess the extent to which this novel finding could be replicated, we examined the results from a similar ERP experiment (Addante, Watrous, Yonelinas, Ekstrom, & Ranganath, 2011) and found similar results, which are reported as Experiment 2.

2.1 Methods

2.2 Subjects & Stimuli

Twenty-five right-handed undergraduate students (eight males) were recruited from the University of California–Davis Psychology Department subject pool, and received credit for participation. Subjects were free from neurological, visual, motor, or other medical disorders, and the experiment was conducted as approved by the University of California – Davis IRB protocol for research on human subjects.

Word stimuli were selected from the Medical Research Council Psycholinguistics Database (http://www.psych.rl.ac.uk/MRC Psych Db.html). Word stimuli had an average rating of concreteness of 589.50 (min=400, max=670), image-ability of 580.11 (min=424, max=667), Kucera-Francis Frequency of 30.38 (min=3, max =198), and an average number of 4.89 letters in each word (min=3, max=8). Stimuli were presented in uppercase letters in a white font, centered on a black background screen (Figure 1). Subjects were seated approximately 44 inches away from the screen.

2.3 Procedure

During study, subjects encoded 200 words (presented in 4 lists of 50 words each) during an incidental encoding task. Two separate encoding tasks (i.e., `Animacy' and `Manmade' judgments), were used, which served as the basis for source memory decisions during retrieval (i.e., subjects made a yes/no responses to indicate if the item was alive, or to indicate if the item was manmade). These encoding tasks were selected to lead to comparable levels of source memory performance while allowing for reasonable levels of source discriminability, i.e., (Ranganath et al., 2004). The two encoding tasks were presented in a blocked ABBA design, counterbalanced between subjects for the order of the two tasks. Prior to each stimulus presentation, a fixation cross appeared in the middle of the screen for 750ms. The encoding probe then appeared on the screen for 1500ms, during which time the subject viewed the stimuli, but were not yet cued to respond. After the 1500ms trial, subjects were then asked to decide either “yes” or “no” to either the animacy or manmade task by responding with a button press (i.e.: a subject-paced response). Prior to each study block, subjects heard the instructions and there was a practice session of 10 stimuli that the experimenter and subject performed together in order to be sure that the subject understood the task. None of the practice stimuli appeared in the test phase. After the 4 study blocks were presented there was a break, during which the ERP cap was affixed to the subjects, before the retrieval phase of the experiment commenced.

During retrieval, the 200 stimuli presented during the encoding phase were randomly intermixed with 100 new words (lures), for a total of 300 test stimuli (Figure 1). The test stimuli were presented in 6 test blocks of 50 stimuli each. Prior to each stimulus presentation, a fixation cross appeared in the middle of the screen for 650ms, during which subjects were instructed not to blink, so as to minimize ocular artifacts in the EEG. The retrieval probe then appeared on the screen for 1500ms, during which time the subject viewed the stimuli, but were not yet cued to respond (Figure 1). Subjects were also instructed not to blink while each stimulus was on the screen. After the 1500ms probe, subjects were asked first to make an item recognition judgment followed by a source recognition judgment; each of these responses was subject paced and therefore provided a variable temporal jittering of each subsequent stimuli's presentation. Prior to commencement of the testing phase, subjects practiced on 10 sample trials with the experimenter present to make sure they understood instructions and used the scale correctly.

For the item recognition judgment, subjects responded on a 5-point confidence scale, with 5 indicating that they were sure it was old, 4 indicating that it was probably old, 3 indicating they were guessing, 2 indicating it was probably new, and 1 indicating they were sure it was new. For the source recognition judgment, subjects also responded on a 5-point scale with 5 indicating that they were sure it was from the animacy encoding task, 4 indicating that they thought it was from the animacy task but were not sure, 3 indicating they were guessing (or that the item was rated “new”), 2 indicating that they thought it was from the manmade task but were not sure, and 1 indicating they were sure it was from the manmade task.

During later analysis, source memory responses were analyzed only for previously studied items (e.g. “old” items), and not for source responses of new items (i.e.: source ratings of “3”), so as to avoid inclusion of random response trials or item false alarms. For ease of interpretation during data analysis, source memory responses were collapsed into a modified scale of source accuracy (1–5) that corresponded to the same direction of the item confidence ratings: source memory responses reported as “5” reflect correct source judgments reported as highly confident/sure, “4” representing correct source judgments reported as not being completely sure, “3” being source “unknown/forgotten”, “2” responses being incorrect source judgments (misattributions) though not completely sure, and “1”

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being incorrect source judgments (misattributions) that subjects reported as being highly confident/sure of.

2.4 EEG Acquisition and Analysis—EEG was recorded using a BioSemi ActiveTwo Recording System with a 32 channel electrode cap conforming to the standard International 10–20 System of electrode locations (Klem, Luders, Jasper, & Elger, 1999). Each subject was tested individually inside a sound-attenuating chamber. Stimulus presentation and behavioral response monitoring were controlled using Presentation software on a Windows PC. EEG was sampled at a rate of 1024hz. Subjects were instructed to minimize jaw and muscle tension, eye movements, and blinking. EOG was monitored in the horizontal direction and vertical direction, and this data was used to eliminate trials contaminated by blink, eye-movement, or other artifacts.

All EEG analyses were performed using custom Matlab code and functions from the EEGLab Toolbox for Matlab (Delorme & Makeig, 2004). Raw EEG data was re-referenced to averaged mastoids, downsampled to 256 Hz, and high-pass filtered at .1 Hz in order to optimize independent component analysis (ICA) decomposition for artifact correction. These data were epoched from 200 milliseconds before the onset of the retrieval item to 1.5 seconds following the retrieval item, and was baseline subtracted from −200 to 0 ms. Epochs containing single channel data which exceeded 4 standard deviations of the channel's mean across epochs were removed to optimize ICA decomposition, as were epochs containing data 6 standard deviations from the pooled channel mean. This procedure was designed to remove primarily non-biological noise, while allowing stereotypical artifacts (such as eye-blinks) to remain. Data were then decomposed into temporally independent components using Infomax ICA (Bell & Sejnowski, 1995). Artifactual components (eye-blinks, muscle tension, etc.) were manually identified and subtracted from the data and the artifact-corrected data were manually screened a second time to reject any remaining epochs with artifacts.

ERPs were averaged from the EEG data using ERPLAB software (http://erpinfo.org/erplab), a plug-in toolbox of Matlab functions for EEGLAB software (Delorme & Makeig, 2004). ERPs were grand averaged to a baseline of the 200ms preceding stimulus onset, using the un-weighted average of individual subjects' trials. Mean amplitudes of latencies of interest for each condition were obtained, and analyzed in separate statistical software.

We used *a priori* defined latencies of interest, based upon the established ERP literature of familiarity and recollection-related effects. Therefore, we focused our analysis on the time periods of 400–600 and 600–800ms, and our Old-New analysis (Figure 2) confirmed the detection of FN400 and LPC effects during these epochs in the current study. For our initial analysis (Old/New effects, i.e.: Figure 2A, 2B, 2C), we used a priori-selected mid-frontal and left parietal electrode sites of Fz and P3 to explore old/new ERP differences from 400–600ms and 600–800ms for the FN400 and LPC, respectively. These old/new effects were highly significant (each $p<.001$), but closer inspection of the topographies of these effects (Figure 2A) revealed that these sites (Fz and P3) were not the sites where effects were actually focused upon, but that they were instead most apparent at the adjacent mid-frontal and left parietal electrode sites of Cz and Cp5, respectively. The same old/new effects were also highly significant at these adjacent sites, Cz and Cp5 (each $p<.001$) (Figure 2B, 2C), consistent with findings of other labs (Wolk et al., 2004). Therefore, in order to more fully characterize these old/new effects with the additional contrasts of item and source memory responses that were of particular interest for this experiment, we focused the remaining analyses upon these representative mid-frontal (Cz) and left parietal (Cp5) sites for all ensuing analyses. When conducting ANOVA tests, results are reported after Greenhouse-Geisser corrections were performed.

For most of our contrasts, all subjects were included (N=25), and the average number of trials per condition was quite high (e.g., in the item confidence analysis an average number of trials per confidence level was of 37, 48, 26, 54, and 100 trials per subject). However, in some conditions, trial counts were quite low for a few subjects, which is to be expected given that each memory response is divided up between five different levels of confidence (as long as performance is above chance subjects cannot produce equally distributed old and new responses across levels of confidence). However, in cases in which it was necessary to exclude subjects, we report the sample size in the relevant result sections. For each ERP contrast, we followed similar criteria used by prior studies (Gruber & Otten, 2010; Kim, Vallesi, Picton, & Tulving, 2009; Otten, Quayle, Akram, Ditewig, & Rugg, 2006), and included subjects only if they had at least 13 artifact-free trials per condition. Importantly, for these particular comparisons (i.e.: Figure 5), the same overall pattern of results were still evident (and statistically significant) when every subject was included in the analysis.

3.1 Results

3.2 Behavioral Results

Memory performance for each encoding task is shown in Table 1. As expected, item recognition performance was similar for the two encoding conditions, so for all ensuing analyses we collapsed across encoding condition. On average, recognition confidence ratings were higher for old items than for new items, $t(24) = 21.58$, $p<.001$, indicating that subjects were able to discriminate between old and new items. Table 2 shows the proportions of confidence responses for the source memory judgments. An examination of source memory responses indicated that .35 of the studied items were recognized with the highest level of confidence and received a correct source response (.15 and .20 led to low and high levels of source confidence, respectively), whereas .10 of the studied items were recognized with the second highest level of confidence and received a correct source response (.09 and .01 led to low and high levels of source confidence, respectively). Table 3 shows that subjects performed at comparable levels of source accuracy for the two encoding tasks (no significant difference in source accuracy amongst the two encoding tasks, $t(24) = 1.29$, $p=.207$), so our source memory analysis proceeded by collapsing across tasks. Source memory accuracy (collapsing across low- and high-confidence recognition) was above chance (i.e., > 50 %) for both the low confidence item recognition trials ($M=.58$, $SD=.15$, $t(24)=2.50$, $p = .02$); (reflecting the proportion of source correct divided by the sum of items receiving a source correct and source incorrect response) and the high confidence item recognition trials ($M=.74$, $SD=.08$, $t(24) =14.35$, $p< .001$). Thus subjects made accurate source memory responses for items that were recognized with both high and low levels of item recognition confidence.

3.3 Electrophysiological Results

3.3.1 Recognition Memory—Item recognition was first examined by contrasting the ERPs associated with hits (old items receiving a 4 or 5 response) and correct-rejections (new items receiving a 1 or 2 response). Topographic maps of item recognition difference waves (Hits – Correct Rejections) for each 200ms time window of the recording epoch are shown in Figure 2A. ERPs for hits were more positive going that those for correct rejections (i.e., warmer colors on the topographical maps). This effect was apparent by approximately 400 ms after stimulus onset and was centrally distributed with a maximum over central midline electrode Cz (i.e.: FN400 effect), $t(24) = 5.35$, $p < .001$, though broadly evident at many adjacent electrode sites. However, between 600 and 800ms the FN400 effect diminished, and an LPC effect was observed that was maximal over left parietal electrode Cp5, $t(24) = 3.73$, $p < .001$, though this too was also quite widespread in its spatial distribution across adjacent electrode sites. The ERPs observed at the Cz and Cp5 electrodes for the hits and correct rejections are plotted in Figure 2B and 2C, respectively. The early and late ERP differences correspond temporally and topographically to those identified in previous studies with the FN400 and the LPC, respectively, for reviews see (Curran, 2000; Friedman & Johnson, 2000; Rugg & Curran, 2007). In addition, to control for potential differences in the confidence levels of the hits and correct rejections we examined performance for only the highest confidence responses (i.e., 1s and 5s), and this also led to the same pattern of FN400 and LPC effects. Thus, in our subsequent analyses, we used mean voltage amplitudes at electrode Cz from 400–600ms as a measure of the FN400, and at Cp5 from 600–800ms as a measure of the LPC.

3.3.2 Item Memory Confidence—To examine the relationship between the FN400 and LPC effects with the processes of familiarity and recollection, we plotted the average amplitude of the ERPs at each level of recognition confidence (collapsed across study status). Figs. 2D and 2E present results from an analysis which included the 14 subjects who had more than 13 trials in each of the 5 response confidence bins (the same pattern was observed, however, when we included all subjects regardless of number of trials in each cell). As shown in Figure 2D (see also Figure 3 for ERPs and topographic maps of each condition), the FN400 increased in a linear manner across confidence levels (R^2= .927, p<.001), and introducing a quadratic component did not lead to a significant increase in variance accounted for (F<1). In contrast, LPC amplitudes showed a non-linear U-shaped function across confidence levels (Figure 2E, ERPs shown in Figure 3) and introducing a quadratic component led to a significant increase in fit compared to a linear model (R^2= .994, F(1,2) = 272.56, p<.005). Subsequent analysis indicated that an LPC effect was evident for confidently recognized items (i.e., `5') compared to confidently rejected items (i.e., `1') (t(13) = 4.83, p< .001) ,whereas the low confidence recognition responses (i.e.: `4') were not different from the confidently rejected items ("1's"), t(13) = −.293, p = .77. In contrast, FN400 amplitudes were more positive for both the high and low confidence recognition responses (see Figure 2D, Figure 3) than for confidently rejected items ("1's"), (i.e. t(13) = 6.25, p <.001, and t(13) = 4.02, p =.001 for high a low confidence responses, respectively).[1]

Overall, the item recognition results are consistent with previous studies showing that recollection and familiarity are associated with topographically and temporally distinct ERP correlates (Rugg & Curran, 2007; Woodruff, et al., 2006; Yu & Rugg, 2010), and with other studies indicating that familiarity increases gradually across item recognition confidence, whereas recollection contributes primarily to high confidence recognition responses (Yonelinas, 2001b).

3.3.3 Source Recognition—ERPs were then examined to identify the correlates of recollection and familiarity on the basis of source discrimination. Thus, ERPs were examined for `source correct' trials irrespective of the preceding item judgments (i.e., old items receiving a low or high confidence correct source judgment), `source incorrect' trials (i.e., old items receiving an incorrect source judgment or a `source unknown' response) and `correct rejection' trials (i.e., new items receiving a low or high confident new response). Compared to correct rejections, source correct trials should exhibit an LPC effect indicative of recollection, whereas the source incorrect trials should exhibit a reduced or non-evident LPC because recollection has presumably failed. In contrast, both source correct and source

[1]Note that a further examination of Figure 2E indicated that the confident new responses (i.e., `1' responses) were associated with a more positive going memory effect at CP5 during the 600–800 time window than the low confidence rejected items (i.e., `2' responses). Although this difference was not statistically significant (p<0.05), we examined it further and found that it had a more posterior and later scalp distribution than the recollection-related response. This pattern of results has been reported before as dissociable from recollection, and been attributed to novelty-related processing and confidence (Woodruff et. al., 2006; Curran, 2004).

incorrect trials should be familiar and thus should exhibit the FN400 effect indicative of familiarity.

As expected, FN400 amplitudes were more positive for source incorrect trials than for correct rejections, t(24) = 3.05, p= .005, and also more positive going for correct source trials than for correct rejections, t(24) = 5.72, p<.001. FN400 amplitudes were higher for source correct trials than for the source incorrect trials as well, t(24) = 5.14, p<.001. The latter effect might reflect some degree of familiarity-based source recognition (Diana et al., 2011). An examination of the scalp topography of these effects indicated that they were maximal over central midline electrode Cz (Figure 4B).

The amplitude of the LPC was significantly higher for source correct trials compared to incorrect source trials, t(24) = 5.603, p<.001 and compared to correct rejections, t(24) = 5.07, p<.001, whereas LPC amplitudes did not differ between the source incorrect trials and the correct rejections t(24) = .673, p=.50. Topographic maps contrasting the source correct and source incorrect trials to correct rejections showed that this effect exhibited a left lateralized effect (Figure 4D) for correct source memories, but no differences across the scalp for incorrect source judgments from 600–800ms.

3.3.4 Source memory for low and high-confidence item recognition hits—The preceding analyses suggested that the LPC was enhanced for items that received the highest confidence rating (i.e.: “Item5”) and/or items that were associated with accurate source decisions, which is consistent with a large body of evidence linking the LPC to recollection (Allan & Rugg, 1998; Allan, Wilding, & Rugg, 1998; Cansino & Trejo-Morales, 2008; Curran, 2000, 2004; Curran, DeBuse, & Leynes, 2007; Curran, DeBuse, Woroch, & Hirshman, 2006; Curran & Doyle, 2011; Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Duzel, et al., 1997; Friedman, 2000; Friedman & Johnson, 2000; Leynes, et al., 2005; Leynes & Phillips, 2008; Rugg & Curran, 2007; Rugg, Mark, et al., 1998; Rugg, Walla, et al., 1998; Rugg & Wilding, 2000a; Wilding, 2000; Wilding & Rugg, 1996; Woodruff, et al., 2006; Yu & Rugg, 2010). No significant LPC was seen for low confidence item hits (i.e.: “Item4”), which might indicate that these items were not recollected. Our behavioral analyses, however, indicated that source memory accuracy was above chance for item hits that were recognized with low confidence (`Item4' responses). If recollection supported accurate source decisions for low confidence item recognition hits, then it is possible that an LPC enhancement might be observed specifically for `Item4' responses that were also associated with correct source decisions (i.e.: `Item4 + Source Correct'). Alternatively, if familiarity solely supported these types of responses (i.e.: `Item4 + Source Correct'), we would expect these trials to exhibit an FN400 modulation as well. Thus, for this particular analysis, we assessed correct source memory ERPs for items that were recognized with high confidence (`Item5 + Source Correct'), as well as items recognized with low confidence (`Item4 + Source Correct'), as compared to correct rejections (new items rated “1” and “2”). In order to avoid confounding this comparison with differences in source confidence between item recognition conditions, we limited this analysis to including only source judgments with low confidence (i.e.: “Item5 + Source 4”, and “Item4 +Source 4”), so that confidence for accurate source was held constant between conditions of high and low item recognition confidence.

Figure 5 shows a series of topographic maps illustrating the time course for the amplitude difference between trials of “Item4 +Source 4” responses of accurate source memory for low confidence recognition and correct rejections, as well as ERPs at a representative left parietal electrode site (for ERPs at each electrode see Supplementary Figure 1). For comparison purposes, the time course of the difference between high confidence hits with correct source (“Item5 + Source 4”) and correct rejections is also shown. Unlike the high confidence hits with correct source, which were associated with a significant increase of the FN400 and LPC (t(12)=.4.23, p= .001; t(12)=2.297, p=.04, respectively) (Figure 5A), "Item4 + Source 4" judgments were not significantly more positive than the correct rejections, during either of the FN400 or LPC time windows (both t(12)'s<.10). Instead, these trials of "Item4 +Source 4" memories were associated with a broadly distributed negative going ERP that peaked during the 800–1000ms time window (Fig 5B).

An exploratory 2×2×2 (hemisphere [left/right] × region [anterior/posterior] × memory condition [`Item4 + Source 4" /correct rejection]) ANOVA was performed on representative electrode sites from the four scalp quadrants during the 600–800ms and the 800–1000ms window (i.e., left frontal (F3), right frontal (F4), left parietal (P3), and right parietal (P4); c.f. Curran, et al., 2006; Woodruff, et al., 2006; Yu & Rugg, 2010). From 600–800ms there was a significant effect of memory condition, F(1,12) = 6.443, p=.026) and a main effect of region (F,12)=4.788, p=049, indicating that during the LPC time window of 600–800ms these "Item4 +Source 4" ERPs for accurate source judgments were significantly more negative than ERPs for correct rejections and that this emerged as a frontally-based effect. In addition, from 800–1000ms this effect became more pronounced, with a significant effect of condition (F(1,12)=14.309, p=.003) and hemisphere (F(1,12)=6.16, p=.029), as well as a marginally significant hemisphere by condition interaction, F(1,12)=3.772,p=.076, suggesting that during this period the memory effect became robust across the scalp, and was slightly larger over the right than left hemisphere. Thus, contrary to our initial predictions, low confidence item hits that were associated with correct source decisions exhibited neither the FN400 nor the LPC modulations that have been previously associated with familiarity and recollection, respectively. Instead, these trials were associated with a late, broadly distributed, negative-going ERP.

One possible concern raised by a reviewer was that the more negative going ERP for "Item4 +Source4" trials relative to correct rejections may have been due to the fact that the correct rejections were associated with higher confidence than the "Item4 +Source 4" responses. That is, the correct rejections included both high confidence (i.e., `1' responses) and low confidence trials (i.e., `2' responses), and our initial item confidence analysis had suggested that the high confidence correct rejections were associated with a large positivity (see Figure 2E). To control for potential confidence effects we contrasted the ERPS for `Item4 +Source 4' memories to ERPs of the low confident correct rejections ("2" responses). There were fifteen subjects with a sufficient number of ERP trials for inclusion in this analysis. This contrast revealed that the 800–1000ms negative ERP for correct source memory related to low confidence recognition was still observed (see Figure 7). As in the original analysis, `Item4 + Source4' trials were more negative going than the low confidence correct rejections (F=(1,14)=5.052, p=.041), and there was a marginal memory condition by hemisphere interaction (F=(1,14)=3.945, p=.067) suggesting the effect was slightly larger over the right hemisphere.

Another possible concern was the extent to which this effect was specific to source memory accuracy, so we also contrasted the source memory ERPs of "correct source" vs. "incorrect source" for `Item4' responses, utilizing the same approach used to assess general source memory effects (i.e.: section 3.3.3, see Figure 4), and this too resulted in a similar late negative going ERP (see Figure 8). There was a marginally significant effect of condition (F=(1,14)=4.407, p=.054), a significant effect of hemisphere (F(1,14)=6.324, p=.025) and a significant condition by hemisphere interaction (F(1,14)=5.04, p=.041), indicating that the memory effect was larger over the right hemisphere. Taken together the results indicate that the late negative going source memory ERP for Item4 memories was not due to differences in overall response confidence, and that it was specific for accurate source memory.

4.1 Experiment 2

The results of Experiment 1 were unexpected in the sense that the low confidence recognition items that were associated with correct source memory (`Item 4 + Source Correct') did not exhibit ERP signatures indicative of either recollection or familiarity. Before discussing the implications of this finding, we briefly describe a reanalysis of an additional study from the lab that used a similar experimental design to that used in Experiment 1, in order to verify that this new ERP effect was also observed in an additional sample of subjects (we thank an anonymous reviewer for this suggestion). The data was from (Addante, et al., 2011), in which we examined oscillatory EEG activity related to item and source recognition confidence. The results were reanalyzed by examining ERP data in the same way that we analyzed the results of Experiment 1, reported above. Our aim was to determine if the late posterior negativity related to low confidence recognition with accurate source memory would be observed in a separate sample of subjects.

4.2 Methods and Procedure

The methods used for Experiment 2 were the same as was described for Experiment 1, with the following differences: seventeen subjects, different from Experiment 1 were tested (from Addante et. al., 2011), the encoding tasks were a "pleasantness rating task" and an "animacy judgment task", and there was a 15 minute delay between encoding and test. In our data analysis we focused on the conditions yielding the unexpected results in Experiment 1: correct source memory responses for high and low confidence recognition judgments (`Item4 +Source Correct'). Of the seventeen subjects studied, one did not have any trials in the condition of accurate source memory for low confidence recognition (the specific bin of interest for this experiment), so this subject was excluded from the analysis. Unlike Experiment 1 and the oscillatory analysis used in Addante et.al., (2011), artifact rejection for this ERP analysis was performed by individual inspection of the data unbiased to trial type, without reliance upon ICA decomposition for artifact correction (i.e.: eye blinks), - a minor change which we did not expect to significantly alter the outcome of the analysis. In addition, because there were fewer "Item4 + Source4" responses than in Experiment 1, source confidence ratings were collapsed into "Item4 +Source 4&5" in order to obtain sufficient ERP trials for analysis. This difference is not critical because if recollection was supporting accurate source memory for low confidence recognition, including the high confident source judgments (i.e.: "Source5") in the ERP analysis, then this would increase the likelihood of detecting an LPC, and thus would decrease the likelihood of observing the same negative ERP difference seen for this condition in Experiment 1.

4.3 Results

4.31 Behavior—Overall performance was similar to that observed in Experiment 1. Most importantly, source accuracy for the low confidence recognition ("Item4") was significantly greater than chance (M=.65), $t(15)=3.53$, $p=.003$, and was numerically but not significantly higher than the .58 accuracy observed in Experiment 1 ($t(39) = 1.37$, $p=.177$). Overall item recognition and source recognition accuracy (i.e., high and low confidence hits minus high and low confidence false alarms) was .78 and .18 for experiment 1, and .80 and .18 for experiment 2, respectively.

4.32 Electrophysiology—ERPs were specifically analyzed for conditions of correct source memory for low confidence recognition, "Item4 + Source 4&5", and for high confidence recognition "Item5 + Source 4&5), as compared to correct rejections. The analysis was motivated theoretically to focus on the potential roles of item familiarity and recollection in source memory via the 400–600ms and 600–800ms latencies of the FN400 and LPC, respectively, as well as the role of a negative-going ERP difference seen in

Experiment 1 that extended beyond this latency and into the 800–1000ms epochs. As such, and towards the goal of assessing the replicability of the observed patterns in Experiment 1, initial analyses were constrained to the same Cz electrode reported for FN400 effects, and left parietal electrode Cp5 where effects were evident in Experiment 1. Figure 6 shows the results of this analysis in topographic maps as well as ERPs at Cp5.

A comparison of Figure 6 (Experiment 2) and Figure 5 (Experiment 1) shows that the main ERP results of Experiment 1 replicated quite well. As in Experiment 1, an FN400 was evident at the Cz site from 400–600ms for "Item5 + Source 4&5" trials, $t(15)=2.67$, $p= .017$, but not for "Item 4 + Source 4&5" trials of accurate source memory associated with low recognition confidence ($t(15)= -.210$, $p=.836$). Similarly, in comparison to the correct rejections, an LPC was observed during 600–800ms at electrode Cp5 for the high confidence recognition responses with accurate source memory ("Item 5 + Source 4&5") $t(15)=2.19$, $p=.044$ (Figure 6), whereas, for source correct trials associated with low item confidence (Item 4 + Source 4&5), once again there was no evidence of an LPC ($t(15)=-.580$, $p=.570$). Moreover, as in Experiment 1, the ERP was significantly more negative when measured at left parietal electrode P3 ($t(15)=-3.15$, $p=.006$) (Figure 6). In addition, as in Experiment 1, from 800–1000ms this negative ERP was broadly distributed across the scalp, with a significant effect of condition ($F(1,15)=30.777$, $p<.001$) that was evident throughout the rest of the epochs.

We also performed the same follow-up analysis as was done in Experiment 1 in order to rule out the possibility that these effects could be due to confidence differences from the correct rejections. For this analysis we contrasted low confident accurate source judgments for items recognized with low confidence (i.e.: "Item4 + Source 4") to low confidence correct rejections (`new' items rated `2') on the twelve subjects who contained a sufficient number of trials in these conditions. As with Experiment 1 (see Supplementary Figure 2), `Item4 + Source 4' responses were associated with a late effect of negative ERP differences. The effect of condition was not quite significant ($F(1,11)=1.856$, $p=.20$), likely due to the substantially reduced sample size in this data set, however, there was a significant condition by region interaction, ($F(1,11)=4.69$, $p=.05$), indicating that the effects were again larger over the frontal regions than they were over posterior regions, the same pattern that was initially observed in Experiment 1. Because there were only 8 subjects with sufficient numbers of low confidence incorrect source judgments, we were unable to contrast the source correct and source incorrect trials for low confidence as was done in Experiment 1 (i.e.: Figure 8).

5.1 General Discussion

The current study examined ERPs associated with item and source memory retrieval. In line with previous studies we found evidence to suggest that two well-known ERP modulations, the FN400 and the LPC, were differentially related to recollection and familiarity, as measured by recognition confidence and source memory accuracy. Finally, we found that accurate source memory for items that were recognized with low confidence was associated with a topographically widespread, late on-setting negative ERP modulation. Below, we consider the implications of each finding in more detail.

The amplitude of the FN400 increased linearly with item recognition confidence, whereas LPC amplitudes were enhanced specifically for items that were recognized at the highest confidence level. Moreover, the LPC was enhanced specifically for old items that were associated with correct source memory judgments, whereas the FN400 was observed even for recognized items that were associated with incorrect source judgments. The FN400 and LPC results are consistent with previous ERP studies, neuroimaging studies (Kirwan et al., 2008; Montaldi, Spencer, Roberts, & Mayes, 2006; Ranganath, et al., 2004), as well as neuropsychological and behavioral studies (Bowles et al., 2007; Yonelinas, et al., 2002) that have shown that recollection supports high confidence item recognition responses, whereas familiarity strength increases gradually across levels of item confidence (Woodruff, et al., 2006; Yu & Rugg, 2010). The results are also consistent with previous studies showing that recollection supports the retrieval of qualitative source information (Duarte, et al., 2004; Guo, Duan, Li, & Paller, 2006; M. K. Johnson, Verfaellie, & Dunlosky, 2008; Leynes & Phillips, 2008; Mitchell & Johnson, 2009; Rugg & Wilding, 2000b; Vilberg, Moosavi, & Rugg, 2006; Wilding, 2000; Wilding & Rugg, 1996) and that familiarity can be observed when the retrieval of source information fails (Curran, et al., 2006; M. K. Johnson, Kounios, & Nolde, 1997; R. Johnson, Jr., Kreiter, Zhu, & Russo, 1998; Mecklinger, Brunnemann, & Kipp, 2011; Rugg, Mark, et al., 1998; Senkfor & Van Petten, 1998; Wilding, Doyle, & Rugg, 1995; Yovel & Paller, 2004).

The novel finding of the current study was related to the examination of the ERPs for low confidence item hits that were associated with correct source judgments. Unlike items that were recognized with high confidence, these trials did not exhibit modulations of the LPC. To the extent that the LPC effect indexes the recollection process (Allan & Rugg, 1998; Allan, et al., 1998; Leynes, et al., 2005; Rugg & Wilding, 2000a; Wilding, 2000); for reviews see (Curran, 2000; Eichenbaum, et al., 2007; Friedman & Johnson, 2000; Mecklinger, 2006; Rugg & Curran, 2007) the results indicate that accurate source recognition can occur even in the absence of recollection. One might argue that the lower confidence source correct items did not show an LPC simply because those responses included random guesses. However, subjects were given the opportunity to indicate that they did not know the study source (i.e., a source confidence of `3'), and these trials were not included in the analysis. Moreover, source accuracy for low confident item hits was above chance, indicating that some memory process must have supported these accurate source decisions. The lack of an LPC modulation for low confidence hits that were associated with correct source decisions also cannot be attributed to insufficient statistical power, because these trials were associated with a statistically significant *negative* going ERP effect, which is the *opposite* of the LPC that was evident in the recollection contrasts. More specifically, these trials were associated with a topographically widespread negative ERP difference that peaked between 800 and 1000ms post-stimulus. This suggests that source recognition for low confidence item hits was supported by a neurocognitive process distinct from recollection.

What processes support accurate source memory in the absence of recognition confidence? The current experiment cannot conclusively answer this question, but there are several possibilities. One possibility is that accurate source memory for lower confidence recognition trials relied on familiarity. Several studies have shown that familiarity can support accurate source memory discriminations when recollection fails (Diana, Yonelinas, & Ranganath, 2010; Quamme, et al., 2002), and that familiarity can be sensitive to contextual or source information (Tsivilis, Otten, & Rugg, 2001). For example, unitizing item and source information can lead to an increase in behavioral and ERP measures of familiarity (Bader, Mecklinger, Hoppstadter, & Meyer, 2010; Diana, et al., 2010; Wiegand, Bader, & Mecklinger, 2010). Although it is possible that familiarity supported accurate source decisions for low confidence hits, no significant FN400 modulation was observed for these items, so there is little evidence to support this hypothesis.

A second, more speculative account of the late negativity that was related to source memory for low confidence recognition is that it reflects a form of `contextual familiarity'. The background for this idea is that episodic memories may reflect the binding of neural representations of item and context information (Diana, et al., 2007; Eichenbaum, et al., 2007). According to this view, item familiarity may reflect the strength of the item representation (e.g., a word) that supports recognition memory. Context information might include information about the place and time it was encountered, and how it was processed (see Ranganath, 2010 for review). Recollection can be thought of as the recall of context information associated with an item, but it is possible that processing of a studied item could elicit weak activation of the associated context representation even when recollection fails. This type of contextual familiarity signal, in turn, could support source discrimination. This hypothesis is admittedly post hoc - though some ERP evidence exists which distinguishes between effects of context and familiarity (Ecker, Zimmer, & Groh-Bordin, 2007a; Tsivilis, et al., 2001) - so further studies that test this possibility will be necessary.

Another possible account of the negative ERP effect of accurate source for low confidence hits is that it might reflect a controlled search process, possibly via a top-down executive control mechanism. Consistent with this idea, some source memory studies have reported a similar late negative going ERP (the Late Posterior Negativity, `LPN'), which is considered a functionally heterogeneous effect with interpretations ranging from a controlled search process to response fluency (Friedman, Cycowicz, & Bersick, 2005; Herron, 2007; Johansson & Mecklinger, 2003). There are several key distinctions though, which suggest that the ERPs found in the current study are not likely to be reflecting the same type of processing as the LPN. For example, while the negative ERP observed in the current study emerged at anterior sites from 600–800ms, its topography was generally much more widespread, becoming insensitive to anterior/posterior factors from 800–1000ms. Additionally, the LPN is not generally observed in studies such as ours that utilize item judgments followed by source discriminations (Duarte, Ranganath, Winward, Hayward, & Knight, 2004; Trott, Friedman, Ritter, Fabiani, & Snodgrass, 1999; Wilding, 2000). Finally, when the LPN has been observed in source memory tasks, it has been found to be either insensitive to source accuracy (Herron, 2007) or to be even larger for inaccurate source judgments (Wilding, 1999; Johannson & Mecklinger, 2003). Together, these factors make it difficult to attribute the observed effects as an LPN.

The current results join a growing number of ERP studies that provide support for dual process models (Curran, 2000; Curran, Tanaka, & Weiskopf, 2002; Diana, Reder, Arndt, & Park, 2006; Duzel et al., 1999; Duzel, Vargha-Khadem, Heinze, & Mishkin, 2001; Leynes, et al., 2005; Rugg & Curran, 2007; Woodruff, et al., 2006; Yu & Rugg, 2010) which propose that recognition is supported by separable signals for recollection and familiarity, and provides initial evidence to suggest that there may be different forms of familiarity processing (item and context), consistent with recent theories (Diana, et al., 2007; Eichenbaum, et al., 2007; Ranganath, 2010). The finding of temporally and topographically distinct recognition memory ERP effects is consistent with the idea that recognition cannot be accounted for by a single underlying neural process. Moreover, these ERP effects were functionally dissociable with respect to how they varied across confidence, even when source accuracy was held constant. We know of no single process model of recognition that can account for these types of dissociations without additional post-hoc assumptions.

The current results have implications for how one goes about assessing the neural correlates of recollection and familiarity, and for current theories of recognition. For example, ERP and fMRI studies of recollection and familiarity are often conducted either by assessing recognition confidence or by contrasting source and item recognition judgments. The extent to which they have been successful at dissociating these processes suggests that they can provide a rough index of these processes, and these methods have largely led to converging results (Spaniol et al., 2009). However, a few studies that have used these methods have failed to find evidence for significant dissociations (Gold et al., 2006; Wais, Wixted, Hopkins, & Squire, 2006). One potential account of these latter results then is that by assessing only item confidence or source recognition they did not successfully isolate recollection from familiarity. Given the relative simplicity of collecting item confidence and source confidence responses as we did in the current study, it would seem important to do so in future studies examining these processes (Wais, et al., 2010).

The extent to which the current results generalize to other test procedures is currently unknown. However, the procedures that were used in the current experiment were chosen to reflect standard item confidence paradigms and standard source memory paradigms, so we expect the results to be quite general. It is possible that source identification tasks involving the identification of physical properties such as color and location, modalities (auditory, visual), or the time of presentation at encoding, may have yielded different findings, and source tasks with greater than two sources could also confer different processing demands. There is also evidence that distinctions between intrinsic and extrinsic source features can differentially influence source memory (Aly, Knight, & Yonelinas, 2010; Ecker, et al., 2007a; Ecker, Zimmer, & Groh-Bordin, 2007b; Nyhus & Curran, 2009), and the extent to which the current results are sensitive to these factors remains to be tested.

Moreover, although recollection was found to support only the highest confidence recognition responses, other conditions would likely lead recollection to support a wider range of responses. For example, conditions in which subjects are forced to respond using a confidence scale with many more levels of confidence should lead subjects to use a wider range of confidence responses for recollected items. Indeed, some evidence exists for graded ERP correlates of recollection (Leynes & Phillips, 2008; Vilberg, et al., 2006), consistent with the Source Monitoring Framework (SMF) and various dual process models of recognition, which contend that source monitoring can be supported by varying degrees of recollection (Hicks, et al., 2002; M. K. Johnson, Hashtroudi, & Lindsay, 1993).

6.1 Conclusions

Recollection appears to support relatively high confidence item recognition responses, whereas familiarity based responses vary directly with item confidence. In addition, recollection supports accurate source recognition, whereas familiarity can be observed even when recollection of source information fails. However, results also show that accurate source recognition can occur even when recognition confidence is not high, and reveal that episodic context can be retrieved independent of recollection. Under these conditions, it appears that accurate source recognition occurs in the absence of recollection.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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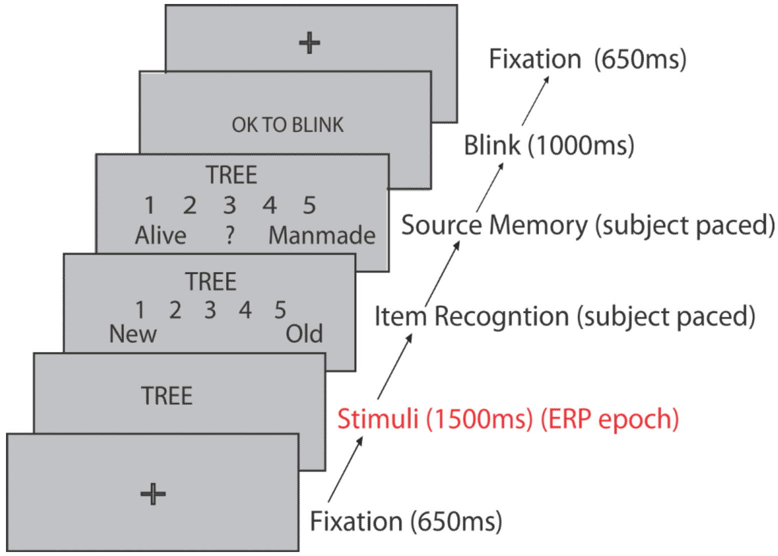

Figure 1. Schematic depiction of events during test trials

For each test item, subjects first made an item memory confidence judgment, followed by a source memory confidence judgment. ERPs were recorded during the presentation of the test word, and classified according to the ensuing item and source memory responses.

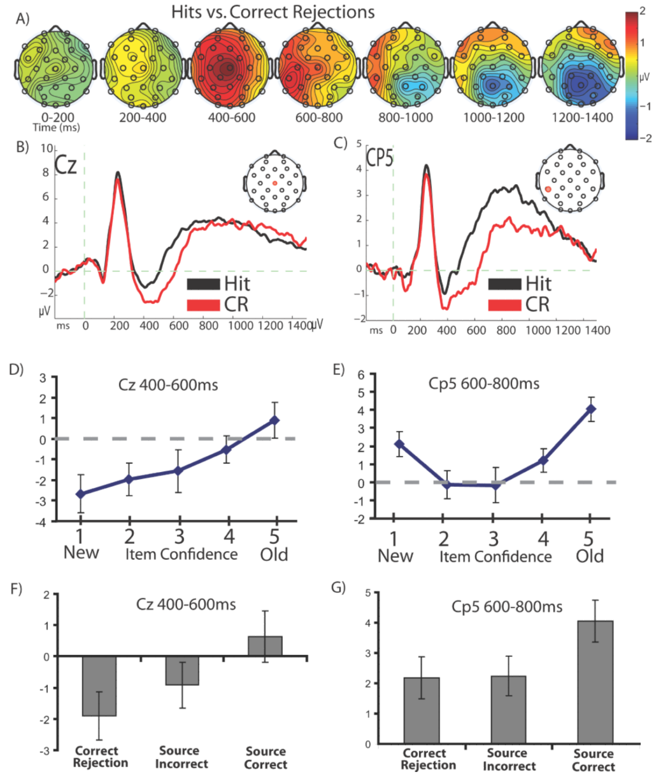

Figure 2. Recognition memory ERP effects

(A) Topographic maps of mean amplitude differences between Hits and Correct Rejections for each 200ms latency window. (B and C) Mean ERPs for hits and correct rejections plotted for electrodes Cz (B) and Cp5 (C). (D and E) Mean ERP amplitude plotted as a function of item recognition confidence (collapsed across old and new items) for Cz (D) and Cp5 (E) effects. (F & G) Mean ERP amplitudes for correct rejections, source incorrect and source correct trials for Cz (F) and Cp5 (G).

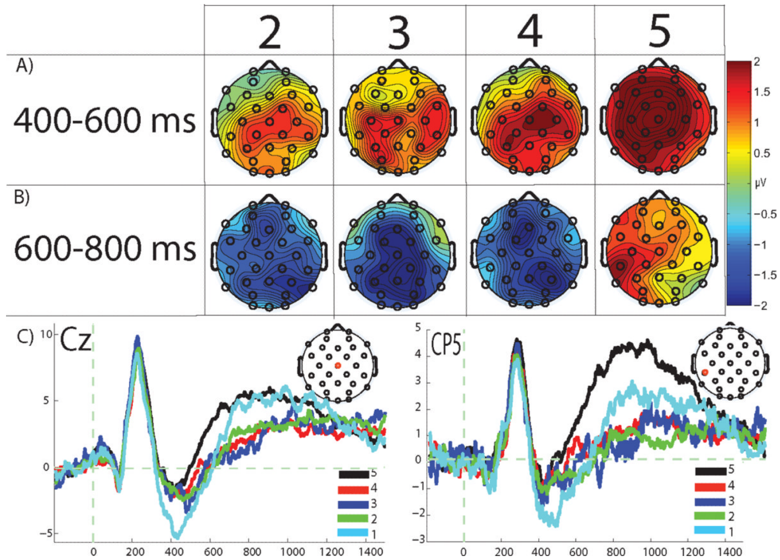

Figure 3. Electrophysiological Correlates of Item Memory Confidence

Topographic maps of the item recognition confidence (N=25). Difference waves of ERPs at each confidence level (`2', `3', `4', & `5') compared to the ERP for the items rated `new' (i.e.: `1' responses) during the early (A) and late (B) latency windows of the putative correlates of familiarity and recollection, respectively. C) ERPs for each level of item recognition confidence at electrodes Cz and Cp5.

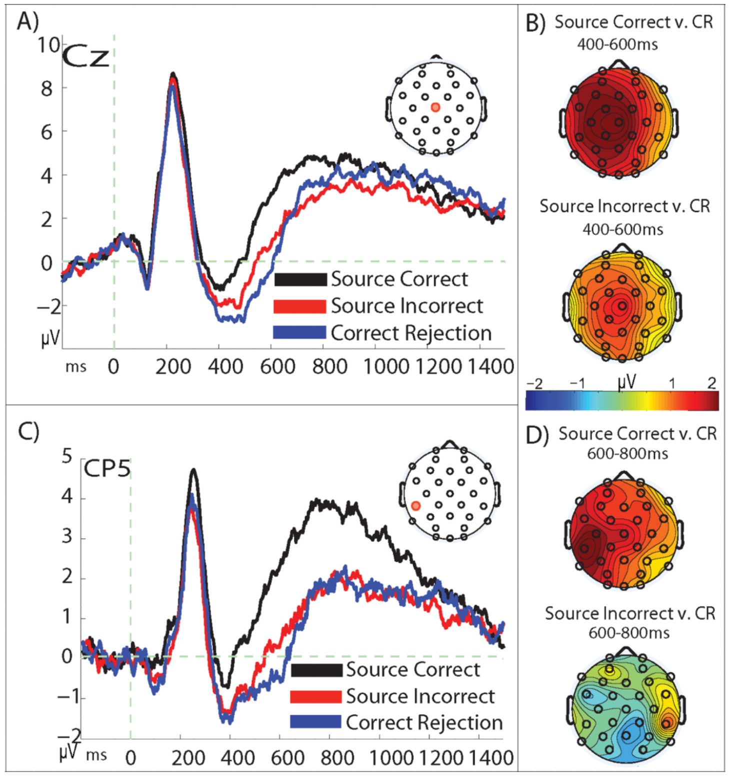

Figure 4. Source Memory Effects

(A) ERPs at electrode Cz for source correct, source incorrect and correct rejections. (B) Scalp topographies of the difference wave comparisons of `source correct' vs. `correct rejection' trials, and the `source incorrect' vs. `correct rejections' during the early period (400–600ms). (C) ERPs at electrode Cp5 for `source correct', `source incorrect' and `correct rejections'. (D) Scalp topographies of difference wave comparisons of `source correct' vs. `correct rejections', and `source incorrect' vs. `correct rejections' at Cp5 during the later period (600–800ms).

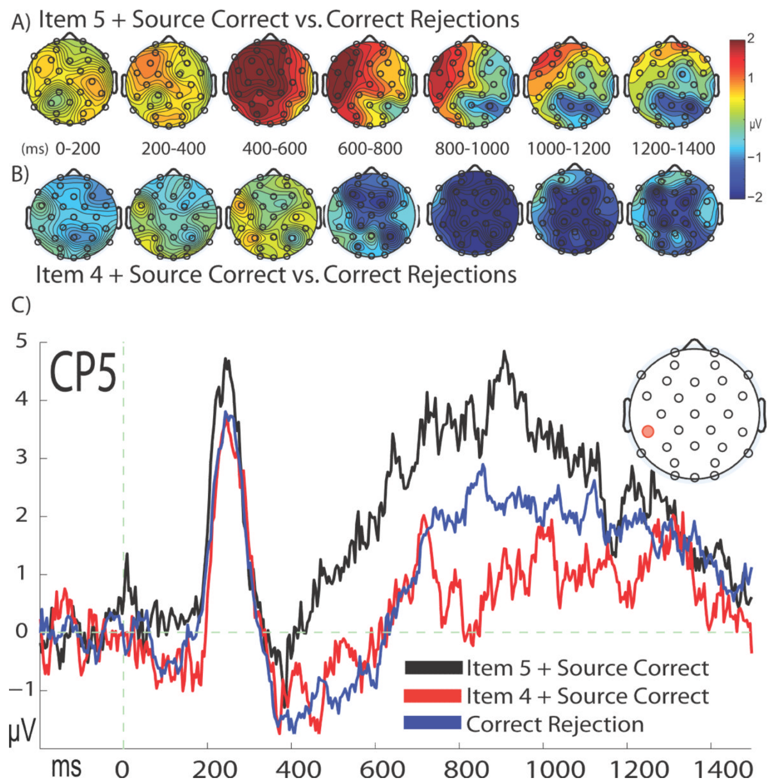

Figure 5. Correct source memory ERPs for items receiving high and low item recognition confidence

Time course of topographic maps of (A) mean ERP differences between high confidence item hits for which the source was correctly recognized (`Item5 +Source 4') and correctly rejected new items, and (B) mean ERP differences between low confidence item hits for which the source was correctly recognized (`Item 4 +Source 4') and correctly rejected new items. (C) ERPs at left parietal electrode Cp5.

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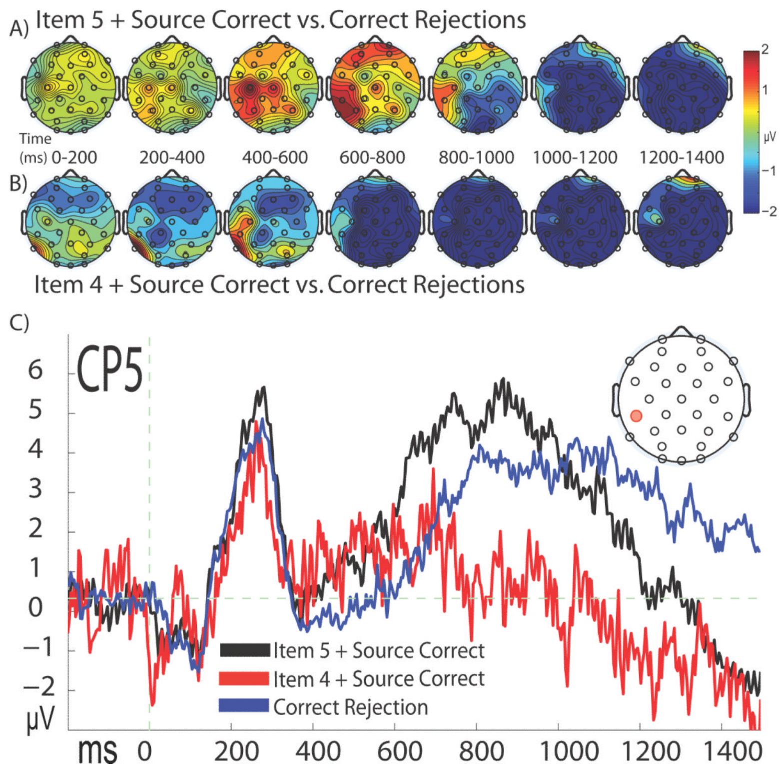

Figure 6. ERP results of Correct Source Memory in Experiment 2

(A) Topographic maps of mean ERP differences between high confidence item hits for which the source was correctly recognized (`Item 5 + Source 4&5') and correctly rejected new items, and (B) between low confidence item hits for which the source was correctly recognized (Item 4 + Source 4&5') and correctly rejected new items. (C) ERPs at representative left parietal site Cp5. Compare to similar results found in Experiment 1 (shown in Figure 5).

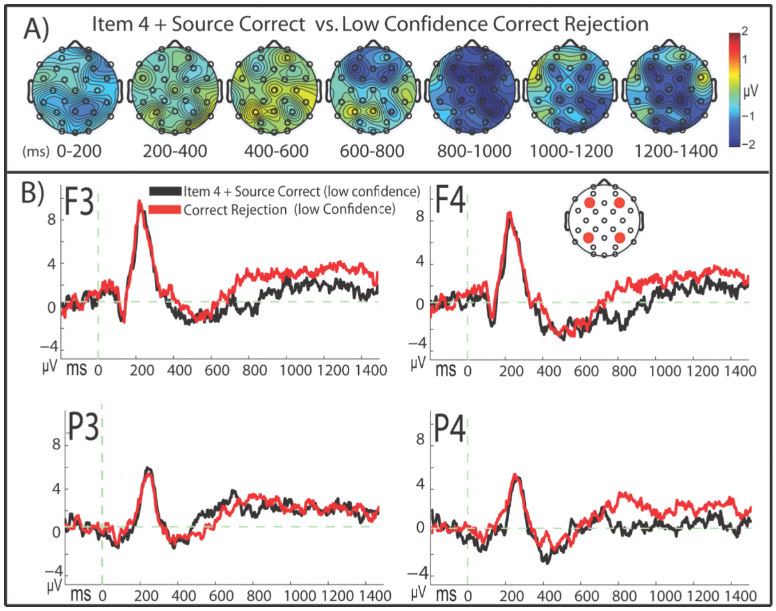

Figure 7. Source ERPs when controlling for item confidence

In this analysis, confidence of new and old responses are held constant, comparing old items recognized with low confidence of “4” and low confidence source correct (i.e.: `Item 4+ Source 4', the same ERP condition plotted in Figure 5 and Supplementary Figure 1) vs. low confidence correct rejections (new items rated “2”). A) Topographic maps throughout the 1500 ms epoch. B) ERPs from representative electrodes from left frontal (F3), right frontal (F4), left parietal (P3), and right parietal (P4) are shown. The topographic locations of each site on the scalp are shown in red dots on the electrode map inset on site F4.

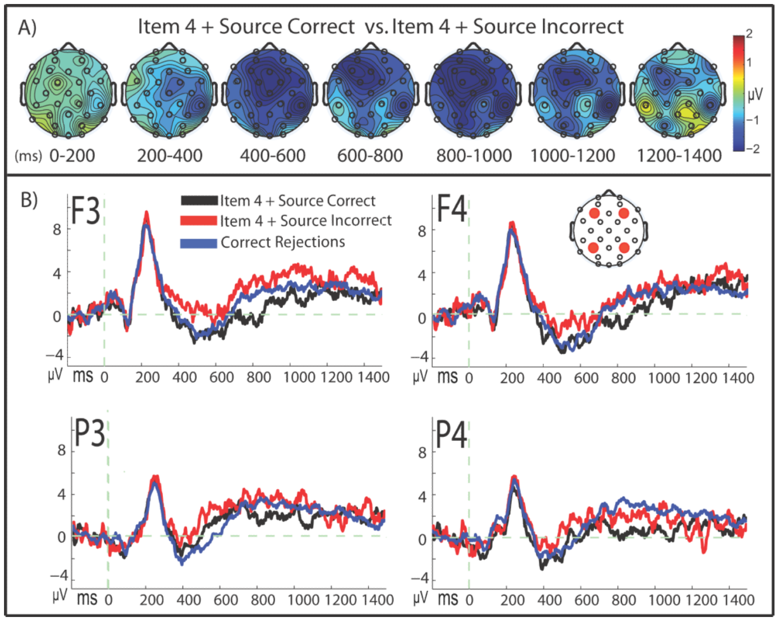

Figure 8. Source Correct vs. Source Incorrect ERPs

A) Topographic maps contrasting trials of `Item4 + Source4' vs. `Item4 + Source2' trials throughout the recording epoch. B) ERPs from representative electrodes from left frontal (F3), right frontal (F4), left parietal (P3), and right parietal (P4) are shown for trials in which subjects indicated accurate and inaccurate source memory for items recognized with low confidence. The topographic locations of each site on the scalp are shown in red dots on the electrode map inset on site F4.

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Table 1

Distribution of responses for each level of item recognition confidence, as a proportion of all responses (see response schematic Figure 1).

Item Recognition Confidence	1	2	3	4	5
All Old Items	.045	.099	.011	.245	.534
New Items	.327	.349	.146	.139	.039
Animacy Task	.054	.116	.092	.256	.483
Manmade Task	.036	.082	.062	.234	.586

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Table 2

Proportion of responses for each level of source memory confidence.

Source Memory Confidence	Incorrect High Confidence	Incorrect Low Confidence	Unknown	Correct Low Confidence	Correct High Confidence
All Old Items	.046	.154	.344	.248	.207
All New Items	.010	.073	.851	.060	.006
Animacy Task	.035	.140	.393	.244	.188
Manmade Task	.057	.168	.296	.252	.226

Table 3

Source memory accuracy. Proportions of source correct and source incorrect are given for all old items, as well as for each encoding task. Accuracy values collapse across low- and high-confidence responses, and reflect the proportion of source correct divided by the sum of items receiving a source correct and source incorrect response.

Memory Accuracy	Source Correct	Source Incorrect
All Old Items	.694	.305
Animacy Task	.711	.288
Manmade Task	.679	.320