**An ERP Study of Source Memory in Unipolar Depression**

Elyssa M. Barrick and Daniel G. Dillon

Number of words:

Number of figures:

Number of tables:

Supplemental information: none

Keywords:

Corresponding author:

Daniel G. Dillon, Ph.D.

Center for Depression, Anxiety and Stress Research

McLean Hospital

115 Mill Street, Belmont, MA 02478

Email: ddillon@mclean.harvard.edu

Phone: 617-855-4233

Fax: 617-855-4231

**Abstract**

**Background:** Major Depressive Disorder (MDD) is characterized by memory deficits whose is unclear. We used event-related potentials (ERPs) to determine how MDD affects source memory retrieval for neutral words.

**Methods:** Twenty-four adults with MDD and 24 controls encoded neutral words shown on the left or right (perceptual source) by making animacy or mobility judgments (cognitive source). The electroencephalogram was recorded as participants were cued to retrieve the perceptual and cognitive source of each word.

**Results:** Across participants, memory was characterized by a *Cue* x *Encoding Task* interaction: cognitive source memory was better after mobility vs. animacy judgments, but perceptual source memory did not vary by encoding task. Brain activity was marked by a late posterior negativity (LPN) that was confined to posterior electrodes during perceptual retrieval but extended over left frontal cortex during cognitive retrieval from 800-2000 ms post-stimulus. Depressed adults were less confident and less accurate than controls, and a positive deflection over parietal cortex from 400-800 ms was sharply reduced in MDD. However, depressed adults showed excellent cognitive source memory for words from the mobility task and similar LPN effects.

**Conclusions:** The *Cue* x *Encoding Task* interaction and shifts in LPN distribution confirm that manipulating retrieval cues can profoundly affect memory and regional brain activity. Moreover, the consistent (if modest) reductions in accuracy and confidence seen in depression indicate that source retrieval is disrupted in MDD. Reduced left parietal activity from 400-800 ms suggests that impaired recollection—mediated by hippocampal-parietal circuitry—is to blame.

**Introduction**

**Materials and Methods**

**Participants**

Participants were recruited from the community and compensated ($25.00/hour) for their time. All participants were 18-62 years old, right-handed, with no history of neurological or unstable medical conditions. Informed consent was obtained with a protocol approved by the Partners HealthCare Human Research Committee. To determine eligibility, prospective participants were screened by phone or online with an instrument that inquired about physical and mental health, medication use, and substance abuse. Controls had to report no current or past psychiatric conditions or unstable medical illness. Individuals were invited to participate in the MDD group if they reported current depression, no history of other DSM-IV Axis I diagnosis (excepting secondary generalized anxiety, social anxiety, or specific phobia due to their high comorbidity with MDD), and no medication use in the past 2 weeks (6 weeks for fluoxetine, 6 months for neuroleptics). Based on the screen, 34 healthy and 30 depressed adults were invited to complete the ERP session.

To confirm that the screening was accurate, immediately after each ERP session we assessed psychiatric history with the MINI International Neuropsychiatric Interview, version 6.0 (Sheehan et al., 1998) and administered the Beck Depression Inventory II (BDI-II; Beck, Steer, & Brown, 1996). Data from depressed participants (*n* = 26) were retained if they met criteria for MDD but no other DSM-IV Axis I diagnosis with previously noted exceptions, and provided they had a BDI-II score ≥ 14. Data from healthy individuals (*n* = 34) were retained if they reported no current or past psychiatric illness. Finally, data from 2 depressed and10 healthy individuals were excluded due to excessive EEG artifacts (see section *EEG pre-processing*). Thus, the final sample consisted of 24 unmedicated adults with MDD and 24 healthy controls.

**Self-report Measures**

In addition to the BDI-II, we administered the Mood and Anxiety Symptom Questionnaire(MASQ; Watson et al., 1995), the Ruminative Responses Scale (RRS; Treynor, Gonzalez, & Nolen-hoeksema, 2003), and the Pittsburgh Sleep Quality Index (PSQI; Buysse et al., 1989) (PSQI). The MASQ includes scales for anhedonic depression (MASQ-AD), anxious arousal (MASQ-AA), and general distress due to depression (MASQ-GDD) and anxiety (MASQ-GDA). The RRS provides measures of maladaptive (brooding) vs. adaptive (reflection) rumination, along with a scale that captures more general symptoms of depression. The PSQI assesses several sleep domains over the prior four weeks, including subjective sleep quality, sleep latency, sleep duration, habitual sleep efficiency, sleep disturbances, use of sleeping medications, and daytime dysfunction. The PSQI also includes questions for the bed partner or roommate to complete, but these were not administered. Finally, the Wechsler Test of Adult Reading (WTAR; Holdnack, 2001) was used as a brief assessment of IQ. We included all these measures to characterize the MDD sample and to determine if any deficits associated with depression could be better understand as the consequence of a more narrowly defined process (e.g., brooding rumination, acute sleep disturbance).

**Task**

The task was programmed in PsychoPy (Peirce, 2008). Due to a hardware change, RT data were not acquired for one control and one depressed participant.

**Stimuli.** Over the course of 100 encoding trials participants made animacy and mobility judgments for individual words. Therefore, we selected 100 words from the MRC Psycholinguistic Database (Coltheart, 1981), with 25 words from each of four categories: “living/immobile” (e.g., *oak*), “non-living/immobile” (e.g., *shed*), “living/mobile” (e.g., *dog*), and “non-living/mobile” (e.g., *kite*). One-way analyses of variance (ANOVA) yielded no significant differences among the lists for number of letters per word (mean±S.D. = 5.27±1.29), number of syllables (1.52±0.50), frequency of occurrence (35.58±79.02), concreteness (598.87±20.18), or imageability (596.80±25.31), all *ps* > 0.064. Emotionally neutral words were selected to avoid effects associated with mood congruent encoding or retrieval (G H Bower, 1981; Gordon H. Bower, 1987) and thus isolate the cognitive impact of depression on retrieval. Word lists are printed in the appendix.

**Encoding.** The task included six encoding-retrieval cycles. Each encoding block consisted of 16 trials (Figure 1) in which a word appeared on the left or right side of the screen directly above one of two questions: “Living/Nonliving?” (animacy judgment) or “Mobile/Immobile?” (mobility judgment) (duration: 3.5 s). Participants responded by pressing a button corresponding to the correct answer. Thus, each word was encoded in relationship to a perceptual source defined by screen position (left vs. right) and a conceptual source defined by the encoding task (animacy vs. mobility). Each block included four words from every category (living/immobile, non-living/immobile, living/mobile, non-living/mobile), each of which was assigned to one of the four encoding conditions defined by screen position and task (left/animacy, right/animacy, left/mobility, right/mobility). A jittered inter-trial interval (500-2000 ms) separated the encoding trials.

Immediately after each encoding block, a 3-digit number (262, 931, 888, 704, 557, or 474) was centrally presented for 30 s and participants counted backwards from that number, in steps of three, out loud. This task was used to disrupt sub-vocal rehearsal, clear working memory, and thus increase the difficulty of the upcoming retrieval test (Reitman, Higman, Lifson, & Rosenblum, 1974). To minimize stress, participants were told to strive for accuracy but, in case of a mistake, to simply proceed as though no error had been committed. The experimenter observed the counting but no data were collected during this task.

PLEASE INSERT FIGURE 1 ABOUT HERE

**Retrieval.** Each retrieval block comprised 48 trials that included a cue, word, and response screen (Figure 1). On 32 trials, the cue was “Side” or “Question” (16 trials each) and the word came from the immediately preceding encoding block. These cues prompted retrieval of the perceptual (“On what side did this word appear?”) and conceptual (“What question was answered for this word?’) sources, respectively. On the remaining 16 trials, the cue was “Odd/Even” the word was a numeral between “one” and “ninety-six”, and the participant was asked to judge parity. Odd/Even trials served as a control condition: the participants had to read a cue, interpret it, and retrieve information from memory before responding, but—in contrast to Side and Question trials—retrieval was directed towards semantic rather than episodic memory. Thus, comparing ERP data from Side and Question trials relative to Odd/Even trials should isolate activity due to episodic retrieval. Cues were printed directly above words, and presentation order of words and cues was randomized.

The response screen consisted of ‘RESPOND’ printed above the word with the numbers 1-5 printed below. The numbers corresponded to response options indicating a choice and level of confidence in that choice: 1 = high confidence (*left* or *living/non-living* or *odd*), 2 = low confidence (*left* or *living/non-living* or *odd*), 3 = guess, 4 = low confidence (*right* or *mobile/immobile* or *even*), 5 = high confidence (*right* or *mobile/immobile* or *even*). Participants were told to select “guess” when they were unable to retrieve any information from encoding.

Each cue appeared for 1 s and was then joined by the word, which remained visible along with the cue for 3 s. At this point the response screen was presented and remained onscreen until the participant pressed a button or 10 s had elapsed. Cues were displayed before words because we anticipated time-locking the EEG data to the word onsets in order to study source retrieval. By presenting the cues first, we aimed to allow participants sufficient time to prepare a search strategy such that they could engage in retrieval as soon as each word appeared, increasing the likelihood that the ERP analysis would capture retrieval rather than preparation for retrieval. Similarly, we delayed the response screen in order to reduce the effect of motor preparation on the ERPs to words, and we allowed participants 10 seconds to respond in case of global slowing in MDD. Finally, a centrally presented fixation cross was continuously visible throughout retrieval, and the cues and words were presented directly above and below fixation, respectively, such that participants could see all the stimuli without needing to move their eyes. As at encoding, a jittered inter-trial interval (500-2000 ms) separated the retrieval trials.

**Procedure.** Following application of the EEG net, participants were given detailed instructions. For the mobility task, participants were instructed to respond “mobile” if the word described an object whose primary purpose was to move (e.g., car) or that could move under its own power (e.g., dog); otherwise, they were told to respond “immobile”. Next, participants completed a practice cycle with four encoding and ten retrieval trials (four Side, four Question, and two Odd/Even). Thus, participants knew their memories would be tested from the outset.

**EEG Recording**

The EEG was recorded during retrieval with a 128-sensor HydroCel GSN Electrical Geodesics Inc (EGI) net connected to a Net Amps 300 amplifier (sample rate = 1000 Hz, 0.02–100 Hz bandpass filter). Data were referenced to the vertex during acquisition. Impedances were kept below 45 kΩ when possible; none exceeded 75 kΩ.

**Behavioral Data Analysis**

To isolate effects of depression on retrieval it is critical to first consider other factors that can affect memory, including age (Cabeza et al., 2004; Mark & Rugg, 1998), depth of encoding (Craik & Tulving, 1975), and the influence of different recognition cues (Konkel, Selmeczy, & Dobbins, 2015; Marsh & Hicks, 1998). Moreover, because depression is more prevalent in women it is important to consider gender (Nolen-Hoeksema, 2001). Therefore, we analyzed the behavioral data using linear mixed models implemented with the R (R Developement Core Team, 2015) library *lme4* (Bates, Maechler, Bolker, & Walker, 2015), as these can account for covariates more easily than conventional ANOVAs. The specific models used for each dependent variable are described below, but in each case we computed an initial model with task elements (e.g., encoding task, recognition cue) and covariates (age, gender) as fixed effects but with *Group* omitted. Next, we computed another model including *Group*, either as a main effect or in interaction with other factors, and then used likelihood ratio tests implemented in the R library *anova* to compare model fits by chi-square test. If the second model was a significant improvement on the first, we report its parameters; otherwise, we report parameters from the first model. All models used *word* and *subject* as random effects, for which we modeled intercepts but did not adjust slope. When modeling encoding accuracy (coded 0 or 1), we used glmer with the logit link function. Finally, we extracted *p*-values for parameters from the best-fitting models using the R library *lmerTest*.

**Encoding**. Prior to analysis, we dropped trials with no response or where RT exceeded the participant’s mean±3SD; fewer than 1% of trials were dropped. We analyzed accuracy and RT. Our first accuracy model included *Task* (animacy, mobility), *Side* (left, right), *Block*, *Gender*, and *Age* as fixed effects. Our first RT model included the same factors plus *Accuracy*. We compared these to models that included *Group* as an additional fixed effect.

**Retrieval**. We dropped trials with no response or where RT exceeded the participant’s mean±3SD (fewer than 2% of trials). Next we analyzed the Odd/Even trials to judge their suitability as a control condition for the ERP analysis.As expected, accuracy (percent correct) on these trials was at ceiling (controls: 98.43±0.12; MDD: 99.13±0.09), and RT (in ms) was similar between groups (controls: 862.58±51; MDD: 779.00±48). Adding *Group* did not improve models that included *Block, Age*, and *Gender* as factors, χ2s < 2.1, *p*s > 0.14, indicating that MDD did not affect performance. Thus, the Odd/Even trials proved suitable as a control condition for both groups.

For the remaining trials, we conducted separate analyses for accuracy and confidence. Accuracy was coded as follows: incorrect, high confidence = 1; incorrect, low confidence = 2; guess = 3; correct, low confidence = 4; correct, high confidence = 5. Confidence was treated as orthogonal to accuracy and was coded as follows: guess = 1, low confidence = 2, high confidence = 3. We computed three models for accuracy and confidence. The first included *Block*, *Cue* (Side, Question), *Encoding Task* (animacy, mobility), *Encoding Side* (left, right), *Age*, and *Gender*. The second model added a *Cue* x *Encoding Task* interaction, and the third added a *Group* x *Cue* x *Encoding Task* interaction, which automatically added the main effect and all two-way interactions involving *Group*. We used similar models to analyze RT on correct trials.

**ERP Analysis**

**Pre-processing.** Pre-processing was conducted with the EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes for MATLAB (MathWorks, Natick). EEG data were merged across blocks and re-referenced to the average of all electrodes prior to bandpass filtering from 0.1 to 30 Hz. Bad channels were visually identified and interpolated. We set an *a priori* cut-off of up to 18 bad channels (14% of the total); datasets that exceeded this cut-off were excluded from further analysis (controls, *n* = 10; MDD, *n* = 2). Next, data marked by gross artifacts were manually removed and independent component analysis was used to extract components capturing blinks, HEOG, and EKG. The cleaned data were then time-locked to word onsets and segmented from 200 ms pre-stimulus to 2000 ms post-stimulus; the pre-stimulus interval was used for baseline correction. Segments where the maximum-minimum voltage difference (computed over 200 ms intervals with a 100 ms sliding window) exceeded 100 μV, or where any raw value exceeded +/- 100 μV, were rejected as artifacts.The cleaned, segmented data were then averaged into bins used for group-level analyses. Elyssa, please confirm: above it says we lost 10 controls and 2 MDDs based on the “number of bad channels” criterion. That implies we did not lose anyone for >50% artifactual trials based on ERPLAB, right? I had text describing that but I removed it because I now think it’s extraneous, please correct me if I’m wrong.

**Group-level analyses**. DD will update.

**Results**

**Demographics**

There were no group differences for gender, age, or education (Table 1). As expected, the MDD group endorsed more depression and anxiety than the controls, with the mean BDI-II score indicating moderate depression. The MDD group also reported more rumination and poorer sleep, but there was no difference in IQ as estimated from WTAR scores.

PLEASE INSERT TABLE 1 ABOUT HERE

**Behavior**

**Encoding**. Encoding was not affected by depression but the mobility task was harder than the animacy task, judging by percent correct (mobility: 92.42±0.26; animacy: 95.85±0.20; *Z* = -4.91, *p* < 0.001) and RT (mobility = 1,801±552 ms; animacy = 1,664±535 ms; *Z* = 10.54, *p* < 0.001). Participants responded faster when making correct (1,720±541 ms) vs. incorrect (1,923±619 ms) judgments, *Z* = -3.46, *p* < 0.001, and RT decreased over the session (linear *Block* effect, *Z* = -6.34, *p* < 0.001). Adding *Group* did not improve the accuracy or the RT model, χ2s < 1.93, *p*s > 0.16, thus depressed and healthy adults performed similarly.

**Recognition accuracy**. Figure 2A shows that depressed adults were less accurate than controls except for words encoded in the mobility task and presented under the Question cue (raw percentages of each type of response are given in Table 2).The figure also depicts a *Cue* x *Encoding Task* interaction that was present across both groups: under the Question cue accuracy was higher for words from the mobility vs. animacy task, whereas responses to the Side cue did not vary by encoding task.

These impressions were captured by the linear models, which were improved by the addition of *Group*, χ2 = 26.40, *p* < 0.001. The best-fitting model included a *Group* x *Cue* x *Encoding Task* interaction, *Z* = -2.13, *p* = 0.033, which subsumed significant *Cue* x *Encoding Task* and *Group* x *Encoding Task* interactions as well as significant main effects of *Cue* and *Encoding Task* (*Z*s > 2.7, *p*s < 0.006). Two sets of follow-up analyses unpacked the triple interaction. First, pairwise comparisons confirmed that depressed adults were more accurate than controls when responding to words from the mobility task presented under the Question cue, *Z* = 1.98, *p* = 0.048. In all other cells accuracy was higher for healthy versus depressed adults, but no pairwise test was significant (*Z*s < 1.63, *p*s > 0.10). Second, breaking down the data by cue type revealed a *Group* x *Encoding Task* interaction for responses to the Question cue, *Z* = 3.25, *p* = 0.001: both groups responded more accurately to words from the mobility vs. animacy task, but the difference was larger in depressed (*Z* = 9.21, *p* < 0.001) vs. healthy (*Z* = 4.62, *p* < 0.001) participants. By contrast, the *Group* x *Encoding Task* interaction was not significant for the Side cue, *Z* = 0.57, *p* = 0.57. Thus, all participants showed better memory for words from the mobility vs. animacy task under the Question cue, but this difference was pronounced in MDD.

Finally, the best-fitting model also revealed effects of *Age*, *Z* = -3.31, *p* < 0.002, *Gender*, *Z* = 3.32, *p* < 0.002, and *Block, Z* = 3.23, *p* = 0.001. Thesereflected higher accuracy in younger vs. older adults, in men vs. women, and in later vs. earlier blocks, respectively.

PLEASE INSERT FIGURE 2 AND TABLE 2 ABOUT HERE

**Recognition confidence**. As shown in Figure 2B, depressed adults were less confident than controls. Consistent with this impression, the model was improved by the addition of *Group*, χ2 = 18.46, *p* = 0.001, and included a trend for a *Group* x *Cue* interaction, *Z* = -1.65, *p* = 0.098. The interaction reflected the fact that the group difference in confidence was stronger under the Side cue, *Z* = 2.42, *p* = 0.016, than under the Question cue, *Z* = 1.14, *p* = 0.255. The model also revealed main effects of *Cue*, *Z* = -5.33, *p* < 0.001 and *Encoding Task*, *Z* = 2.91, *p* = 0.004, as well as a linear effect of *Block*, *Z* = 3.69, *p* < 0.001. These results reflect the fact that participants were more confident when responding to the Question cue vs. the Side cue, when responding to words encoded in the mobility vs. the animacy task, and when responding in later vs. earlier retrieval blocks. Confidence was not affected by *Age* or *Gender*.

**Recognition RT**. Figure 2C shows that correct RT was similar across the groups, with all participants noticeably slower in response to the Question vs. Side cue. This impression was confirmed by the linear modeling, which was not improved by the addition of *Group*, *p =* 0.08, but which revealed a strong effect of *Cue*, *Z* = -45.51, *p* < 0.001. There was also a negative linear effect of *Run*, *Z* = -18.82, *p* < 0.001, a strong effect of *Confidence*, *Z* = 21.61, *p* < 0.001, and an effect of *Gender*, *Z* = -3.09, *p* = 0.003. These reflected shorter correct RTs in later vs. earlier blocks, for high vs. low confidence responses, and in males vs. females.

**Summary**. Source memory in depressed adults was generally less accurate and less confident than in controls. Indeed, the MDD group generated a lower score in 7 of the 8 cells analyzed (8 cells: *Cue* x *Encoding Task* x *Dependent Variable* [accuracy, confidence]) which is improbable under the null hypothesis of no group difference, binomial *p* = 0.035 (one-tailed). However, the effect of MDD on accuracy was modest and reversed when words from the mobility task were presented under the Question cue. At encoding, the mobility task was associated with lower accuracy and longer reaction times, suggesting that it elicited deeper processing than the animacy task (Craik & Tulving, 1975). Thus, the retrieval data indicate a mild negative effect of MDD on source memory for neutral material that can be corrected by combining especially deep encoding with a retrieval cue that directs attention to the cognitive operations performed at study. This pattern is anticipated by the cognitive initiative framework, which argues that depressed adults perform poorly in unconstrained environments but can display excellent memory if their attention is focused at encoding and retrieval (Hertel, 1997).

Finally, the presence of a *Cue* x *Encoding Task* interaction that extended across all participants is reminiscent of results from cue-framing studies, which demonstrate that source memory is strongly shaped by the particular retrieval cues presented (Dobbins & McCarthy, 2008; Marsh & Hicks, 1998). One might imagine that source memory is all-or-none—that an entire episode is either remembered or forgotten—but the *Cue x Encoding Task* interaction demonstrates that this is not so. Perceptual source memory was not influenced by the encoding task, but cognitive source memory was better after mobility vs. animacy judgments; this implies that participants could sometimes recall the side on which a word was presented while misremembering the task they completed. This result also demonstrates that encoding may be “deeper” along one dimension (conceptual processing) without influencing memory for another dimension (perceptual information).

**ERPs**

Figures 3 and 4 display waveforms and topographic maps of correct responses to the Question, Side, and Odd/Even prompts, respectively. In controls, the three ERPs most frequently associated with episodic retrieval are readily apparent. From 400-800 ms there is robust activity over parietal electrode sites, and it is clear from the topographies that this effect is stronger over the left vs. right hemisphere; this potential has been consistently associated with recollection (Rugg & Curran, 2007). From 800-2000 ms, a positive potential is evident over right frontal cortex. This potential was initially thought to reflect post-retrieval monitoring but subsequent studies found that it can be elicited during semantic retrieval and decision-making more generally (Fleck, Daselaar, Dobbins, & Cabeza, 2006; Hayama, Johnson, & Rugg, 2008; Hayama & Rugg, 2009). Consistent with this conceptualization, the late right frontal potential is evident even during Odd/Even judgments. Finally, a late negative potential (LPN) is evident during the same time window (800-2000 ms) as the right frontal effect (Cycowicz, Friedman, & Snodgrass, 2001). The LPN is not evident on Odd/Even trials, it has a medial posterior focus on Side trials, and it extends into left frontal cortex on Question trials.

The topographies from depressed adults are broadly similar but one difference was immediately apparent: parietal activity from 400-800 ms is markedly weaker in the MDD group. To determine whether this visual impression was reliable, we extracted the mean ERP amplitude between 400-800 ms from four parietal electrodes in the left (P1, P3, P5, P7) and right (P2, P4, P6, P8) hemispheres and submitted them to a *Group* x *Condition* (Question, Side, Odd/Even) x *Hemisphere* ANOVA. This yielded a main effect of *Group*, *F*(1,46) = 4.35, *p* = 0.043, due to decreased activity in depressed vs. healthy adults. There was also a main effect of *Condition*, with follow-up tests using the REGWQ procedure yielding reliable differences between all three conditions (Question > Side > Odd/Even, all *ps* < 0.043).

PLEASE INSERT FIGURES 3 AND 4 ABOUT HERE

**Difference waves**. To isolate brain activity reflecting source retrieval, we created difference waves by subtracting activity on correct Odd/Even trials from activity elicited by hits in all four cells of the design (Question/animacy, Question/mobility, Side/animacy, Side/mobility), and then used the mass univariate approach to identify significant activations within and across the groups (Groppe, Urbach, & Kutas, 2011a). In contrast to traditional ERP analysis, which typically involves conducting a few tests on a handful of electrodes specified *a priori*, mass univariate analysis involves a separate test at each electrode, conducted at each time point or on mean amplitude data over a pre-specified time window. This is very similar to the approach commonly taken in fMRI research (Friston et al., 1995), and it makes much better use of the spatiotemporal richness of ERP data than the traditional method. However, appropriate correction for multiple comparisons can sharply limit power. To limit this concern, we used a cluster-based permutation procedure that can identify relatively weak effects so long as they extend over several electrodes (Groppe, Urbach, & Kutas, 2011b).

Briefly, for within-subject tests we submitted the mean amplitude of each difference wave over three time windows (400-800, 800-1400, 1400-2000 ms) to one-sample *t*-tests against zero. A separate *t*-test was computed at 123 electrodes (128 minus 5 electrodes placed on the face to monitor eye movements), andall electrodes within 4 cm of each other were considered neighbors. Neighboring electrodes with *p*-values less than 0.05 (uncorrected) were considered clusters. The sum of all *p­*-values within a cluster was considered its mass, and then 2500 within-subject permutations were performed to generate a null distribution of cluster mass values (Bullmore et al., 1999). Clusters whose mass probability was more extreme than all but 5% of the null distribution were considered reliable and are reported. Because the mass univariate toolbox does not currently support ANOVAs, after conducting within-group analyses we computed between-groups *t*-tests for each difference wave, again using the mass univariate approach with cluster-based permutation to correct for multiple comparisons.

**Figure Captions**

*Figure 1*. Encoding (left) and recognition (right) trial structures. Encoding trials began with three centrally presented arrows pointing to the side on which the word would appear. The encoding task was presented next, either “living or non-living?” (animacy judgment) or “mobile or immobile?” (mobility judgment, not shown). Finally, a word was presented directly above the encoding question; participants had 3500 ms to respond. Retrieval trials began with presentation of one of three cues (“Side”, “Question”, or “Odd/Even”). After a 1000 ms delay, a word was presented. On Side and Question trials, the word came from the immediately preceding encoding block, while on Odd/Even trials the word was a numeral (e.g., “seventy-seven”). Finally, a response screen was presented and persisted until the participant responded or 10 seconds had elapsed, whichever came first. The response options for a Side trial are displayed. On Question trials, “left” and “right” were replaced with “living/non-living” and “mobile/immobile”, respectively; on Odd/Even trials they were replaced with “odd” and “even”. EEG data were only collected during retrieval.

*Figure 2*. Source memory (A) accuracy, (B) confidence, and (C) correct RT. Bar heights correspond to the mean, error bars = SEM.

*Figure 3*. Waveforms elicited by correct responses to the Question (black), Side (red), and Odd/Even (blue) cues. Representative electrodes from the left and right hemisphere are depicted for frontal and parietal scalp; a midline occipital electrode is displayed as this is where the late posterior negativity (LPN) was maximal. Gray shading highlights the effects of interest. Note the reduction in activity over parietal sites from 400-800 ms in depressed adults.

*Figure 4*. Topographies showing correct responses to the Question, Side, and Odd/Even cues. Note that parietal activity from 400-800 ms is blunted in depressed adults. In both groups, the LPN is confined to medial posterior sites on Side trials but extends over left frontal cortex on Question trials.