**The Impact of Depression on Brain Activity During Source Memory Retrieval**

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**Abstract**

**Background:** Recollection is disrupted in Major Depressive Disorder (MDD), but this disruption can be minimized by focused attention at encoding and retrieval. The neural mechanisms responsible for these clinically important phenomena are unclear. Thus, we used event-related potentials (ERPs) to examine recollection in MDD.

**Methods:** Twenty-four unmedicated adults with MDD and 24 controls encoded words shown on the left or right (perceptual source) by making animacy or mobility judgments (conceptual source). ERPs were recorded during cued source retrieval, which depends on recollection.

**Results:** Mobility judgments prompted deeper encoding than animacy judgments, and memory performance was characterized by a *Group* x *Cue* x *Encoding Task* interaction: depressed adults were generally less accurate and less confident than controls, but they showed excellent conceptual source memory following deeper encoding. In parallel, a positive parietal ERP deflection that tracks recollection was globally reduced in depression, but sustained left parietal activation was seen during conceptual source judgments for deeply encoded words in MDD.

**Conclusions:** This study links two reliable effects of depression on recollection to electrophysiological activity over parietal cortex. First, accuracy and confidence were reduced in MDD, and the most reliable ERP correlate of recollection—a positive parietal deflection from 400-800 ms—was blunted. Second, depressed adults showed excellent memory when both the encoding and retrieval tasks demanded sustained attention, and this combination elicited sustained left parietal activity. These results link the impact of depression on recollection to parieto-hippocampal circuits, and they highlight the need for further work on this important topic.

**Introduction**

Memory retrieval plays a key role in Major Depressive Disorder (MDD) and, increasingly, in its treatment. Retrieval in depression is “overgeneral” (1): cued to recall specific episodes, depressed adults tend to offer categorical accounts, summaries that convey gist but few details. This lack of precision has consequences, as overgeneral retrieval predicts a longer course of illness (2–4). Moreover, increasing retrieval specificity can decrease hopelessness and brooding rumination while improving problem solving (5), and it can lead to sustained remission (6). In short, memory retrieval is impaired in depression and enhancing it can bring lasting relief.

Given these facts, the lack of knowledge regarding the neurobiology of memory retrieval in depression is astonishing, particularly since episodic retrieval in healthy adults has been studied extensively (7–9). This does not reflect lack of desire; a decade ago, the National Institutes of Mental Health, Aging, and Neurological Disorders and Stroke called for integrated research on depression and memory (10). Furthermore, the scope of the problem is clear. As one might expect from work on overgeneral memory, depression impairs recollection—the retrieval of contextual details specifying the spatiotemporal source of memories (11–14). However, despite dozens of event-related potential (ERP) and functional magnetic resonance imaging (fMRI) studies of recollection in healthy adults, a similar literature in MDD has not emerged.

This study addresses this gap by using ERPs to study source memory in MDD. We adapted a design that dissociates neural systems engaged by conceptual versus perceptual source retrieval (15–17), using neutral stimuli to avoid confounds associated with mood-congruent encoding (18–20). At study, participants viewed words presented on the left or right above a question specifying either an animacy judgment or a mobility judgment. At test, they were cued to retrieve the presentation side (perceptual source) and the encoding task (conceptual source).

A recent fMRI/ERP study (15) found that both conceptual and perceptual retrieval elicited the most well-studied ERP marker of recollection: a positive deflection over parietal cortex that extends from about 400-800 ms post-stimulus, often with a left hemisphere maximum, and that is thought to reflect information transfer between the hippocampus and parietal lobes (7). Furthermore, both forms of retrieval also recruited the precuneus and elicited a negative polarity ERP maximal over posterior electrodes and commonly referred to as the late posterior negativity, or LPN (21–23). Critically, the LPN extended over left frontal cortex only during conceptual retrieval, and this was mirrored by dorsolateral PFC activation in the fMRI session.

These findings suggest that retrieval attempts activate parieto-hippocampal circuits, bringing candidate memories to mind and generating the parietal ERP effect. Next, those candidate memories are reviewed until one is selected and endorsed. The review and selection of perceptual memories strongly engages posterior cortical regions, but conceptual retrieval differentially activates left PFC regions that support semantic encoding, elaboration, and selection (24). Because MDD is associated with volumetric loses in hippocampus and PFC (25), we expected reduced source accuracy in MDD. In addition, since rumination may occupy left PFC circuits, we anticipated especially sharp disruption of conceptual source memory.

However, in the course of our analysis it became clear that we had overlooked a key factor. Specifically, several studies report good memory in depression provided attention is sustained at encoding or retrieval (26–30). As detailed below, one of our tasks promoted deeper encoding than the other, and when words from that task were targeted for conceptual source retrieval, the MDD group was quite accurate. Thus, this study highlights neural mechanisms linked to disrupted source memory in MDD, as well as activity that supports memory when encoding and retrieval conditions are salubrious.

**Materials and Methods**

**Participants and self-report**

Participants (18-62 years old, right-handed, no neurological or unstable medical conditions) were recruited from the community and compensated ($25/hour), using a protocol approved by the Partners HealthCare Human Research Committee. Participants were screened by phone or online, and we assessed psychiatric history with the MINI International Neuropsychiatric Interview, version 6.0 (31), and also administered the Beck Depression Inventory II (BDI-II; 32). Controls had to report no current or past psychiatric conditions. Depressed adults had to report current depression, no history of other DSM-IV Axis I diagnosis (except generalized anxiety, social anxiety, and specific phobia secondary to MDD), no medication use in the past two weeks (six weeks for fluoxetine, six months for neuroleptics), and a BDI-II score ≥ 14. Thirty-four controls and 26 depressed adults completed the ERP session. Data from 10 controls and 2 depressed adults were excluded due to excessive artifacts (see below), leaving 24 individuals per group.

We also administered the Mood and Anxiety Symptom Questionnaire(MASQ; 33), the Ruminative Responses Scale (RRS; 34), and the Pittsburgh Sleep Quality Index (PSQI; 35). The Wechsler Test of Adult Reading (WTAR; 36) was used to assess IQ. One depressed participant did not complete the PSQI.

**Task**

The task was programmed in PsychoPy (37). RT data were not recorded for one control and one depressed participant.

**Stimuli.** We used the MRC Psycholinguistic Database (38) to select 25 words from 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*). ANOVA yielded no differences for number of letters (mean±S.D.; 5.27±1.29) or syllables (1.52±0.50), frequency of occurrence (35.58±79.02), concreteness (598.87±20.18), or imageability (596.80±25.31), *ps* > 0.06. Words are listed in the Supplement.

**Encoding.** The task included six encoding-retrieval cycles. Each encoding block included 16 trials (Figure 1, *left*) in which a word appeared on the left or right above one of two questions: “living/non-living?” or “mobile/immobile?” Participants responded by pressing a button. A jittered interval (500-2000 ms) separated the trials.

**Counting.** Immediately after encoding, a 3-digit number (e.g., 931) was shown and participants counted backwards from that number in steps of three for 30 s. Counting served to disrupt rehearsal and clear working memory (39).

PLEASE INSERT FIGURE 1 ABOUT HERE

**Retrieval.** Each block comprised 48 trials that included a cue, word, and response screen (Figure 1, *right*). On 16 trials each, the cue was “Side” or “Question” and the word came from the preceding encoding block; these cues prompted perceptual and conceptual source retrieval, respectively. On the remaining trials the cue was “Odd/Even” and the word was a numeral between “one” and “ninety-six”, and the participant judged parity. All trials involved reading a cue, interpreting it, and retrieving information, but on Odd/Even trials, retrieval was directed at semantic rather than episodic memory. Thus, comparing ERP data from Side or Question trials versus Odd/Even trials should isolate activity mediating episodic retrieval. Presentation order of words and cues was random. The response screen consisted of ‘RESPOND’ printed above the word with the numbers 1-5 printed below and corresponding to a choice and level of confidence in that choice (Figure 1, *right*). A jittered interval (500-2000 ms) separated the trials.

**EEG Recording**

The EEG was recorded during retrieval with a 128-sensor HydroCel GSN Electrical Geodesics Inc (EGI) net (sample rate: 1000 Hz, 0.02–100 Hz). Data were referenced to vertex and impedances were kept below 45 kΩ when possible (maximum: 75 kΩ).

**Behavioral Analysis**

We analyzed trial-level data using linear mixed models implemented with the R (40) library *lme4* (41), as this method easily accommodates covariates that might influence memory or depression, such as age and gender (42; 43). Specific models are described below, but in all cases we computed a first model with task elements and covariates as fixed effects but without *Group*. We added *Group* in a second model and used likelihood ratio tests to compare model fits by chi-square. If the second model was a significant improvement, we report its parameters; otherwise, we report parameters from the first model. All models used *Word* and *Subject* as random effects. When modeling encoding accuracy (coded 0 or 1), we used glmer with the logit link function. We extracted *p*-values with the R library *lmerTest*.

**Encoding**. We dropped trials (< 1%) with no response or where RT exceeded the participant’s mean±3SD. The first accuracy model included *Encoding Task*, *Side*, *Block*, *Gender*, and *Age*. The first RT model included the same factors plus *Accuracy*. The second models included the same factors plus *Group*.

**Retrieval**. We dropped trials with no response or where RT exceeded the participant’s mean±3SD (< 2%). Next we analyzed the Odd/Even trials.Accuracy 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). *Group* did not improve models that included *Block, Age*, and *Gender*, χ2s < 2.1, *p*s > 0.14. Thus, Odd/Even trials elicited similar behavior across groups and are suitable as a control condition.

For Side and Question trials, accuracy was coded: incorrect, high confidence = 1; incorrect, low confidence = 2; guess = 3; correct, low confidence = 4; correct, high confidence = 5. Confidence was coded guess = 1, low confidence = 2, high confidence = 3. We computed three models for accuracy and confidence. The first included *Block*, *Cue*, *Encoding Task*, *Encoding Side*, *Age*, and *Gender*. The second added a *Cue* x *Encoding Task* interaction, and the third added a *Group* x *Cue* x *Encoding Task* interaction, plus the main effect and two-way interactions involving *Group*. We used similar models to analyze correct RT.

**ERP Analysis**

**Pre-processing.** Pre-processing was conducted with EEGLAB (44) and ERPLAB (45) toolboxes for MATLAB (MathWorks, Natick). EEG data were merged, re-referenced to the average of all electrodes, and filtered (0.1-30 Hz). Bad channels were interpolated, independent component analysis was used to remove activity due to blinks, HEOG, and EKG, and the cleaned data were time-locked to word onsets and segmented (-200 to 2000 ms). The pre-stimulus interval was used for baseline correction, and segments where any raw value or the maximum-minimum voltage difference (200 ms intervals, 100 ms sliding window) exceeded 100 μV were rejected. We used *a priori* criteria of > 18 bad channels or more than 50% of trials rejected to exclude datasets (10 controls, 2 MDD). The mean number of clean segments in each bin defined by *Group* x *Cue* x *Task* ranged from 21-28 for source hits.Guesses were excluded from ERP analysis and there were too few clean segments for analysis of misses.

**Group-level analyses**. We first inspected the ERP waveforms associated with correct responses to the Question, Side, and Odd/Even cues, regardless of encoding task. There was a clear group difference in the parietal ERP from 400-800 ms (see Results), thus we extracted mean amplitude data over this window from electrodes in the left (P1, P3, P5, P7) and right (P2, P4, P6, P8) hemispheres for a *Group* x *Cue* x *Hemisphere* ANOVA. This focus on a few electrodes in one time window constitutes a traditional ERP analysis, which has been used in many studies of recollection (7; 46; 47)

Additional analyses used a newer approach and were intended to parallel the memory accuracy data, which were characterized by a *Group* x *Cue* x *Encoding Task* interaction. To identify activity mediating this interaction, we computed Question minus Side difference waves separately for words from the mobility and animacy tasks in each group. We then submitted the difference waves to mass univariate analysis (48), focusing on mean amplitudes from 400-800 ms, 800-1400 ms, and 1400-2000 ms. Mass univariate analysis is widely used in fMRI research (49) and here entails a one-sample *t*-test (within-group analysis) or a two-sample *t*-test (between-group analysis) at each electrode. By examining every electrode and multiple time windows, this makes better use of the spatiotemporal richness of ERP data than traditional methods. To correct for multiple comparisons, we used cluster-based permutation (50). All electrodes within 4 cm of each other were considered neighbors, and neighboring electrodes significant at *p* < 0.05 (uncorrected) were considered clusters. The sum of all *p*-values in a cluster constituted its mass. We then performed 2500 permutations, selecting the most extreme cluster mass from each permutation to generate a distribution (51) that was used to judge the probability of observing clusters of various sizes. Only clusters significant at *p* < 0.05 are reported.

**Results**

**Demographics**

There were no group differences in gender, age, education, or estimated IQ (Table 1). Relative to controls, the MDD group endorsed poorer sleep plus more depression, anxiety, and rumination, with the mean BDI-II score indicating moderate depression.

PLEASE INSERT TABLE 1 ABOUT HERE

**Behavior**

**Encoding**. The mobility task was harder than the animacy task, as assessed 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 were faster when correct (*Accuracy*: *Z* = -3.46, *p* < 0.001) and RT decreased over the session (*Block*: *Z* = -6.34, *p* < 0.001). *Group* did not improve the models, χ2s < 1.93, *p*s > 0.16, thus depressed and healthy adults performed similarly.

**Source accuracy**. Source accuracy was influenced by depression and adding *Group* improved the model, χ2 = 26.40, *p* < 0.001. There was 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 plus main effects of *Cue* and *Encoding Task* (*Z*s > 2.7, *p*s < 0.006). Figure 2A (left panel) shows that the triple interaction emerged because accuracy under the Side cue did not vary by encoding task, but accuracy under the Question cue was better following mobility versus animacy judgments, with this effect larger in MDD. In the MDD group, a Question minus Side subtraction (Figure 2A, right) was positive for the mobility task but negative for the animacy task, *t*(23) = 4.47, *p* < 0.001, *d* = 0.91. In controls the Question minus Side subtraction was negative for both tasks but less negative for the mobility task, *t*(23) = 2.04, *p* = 0.053, *d* = 0.42. A between-groups test on Question minus Side difference scores for the animacy task was not significant, *t* < 1, but difference scores for the mobility task were more positive in MDD compared to healthy adults, *t*(46) = 3.04, *p* = 0.004, *d* = 0.88.

Because the ERP analysis focused on hits, we repeated this analysis with hit rates (Table 2). A *Group* x *Cue* x *Encoding Task* ANOVA on hit rates did not yield a triple interaction, *F* < 1. However, for depressed adults the Question minus Side accuracy subtraction was again more positive for the mobility task (5.03±11.95) versus the animacy task (-8.76±9.82), *t*(23) = 3.82, *p* = 0.001, *d* = 1.26. The same was true for controls (mobility: -2.97±9.74; animacy: -12.27±14.11; *t*(23) = 2.83, *p* = 0.010, *d* = 0.76). As before, there was no group difference for the animacy task, *t*(46) = 1.00, *p* = 0.32, *d* = 0.29, but Question minus Side difference scores for the mobility task were again larger in depressed adults, *t*(46) = 2.54, *p* = 0.015, *d* = 0.73.

Finally, simple pairwise comparisons showed better accuracy for depressed versus healthy adults only in the Question/mobility cell of the design, *Z* = 1.98, *p* = 0.048; in all other cells accuracy was (non-significantly) higher in controls, *Z*s < 1.63, *p*s > 0.10. Thus, depressed adults generally performed worse than controls, except for words from the mobility task presented under the Question cue. Finally, the best-fitting model included effects of *Age*, *Z* = ‑3.31, *p* < 0.002, *Gender*, *Z* = 3.32, *p* < 0.002, and *Block, Z* = 3.23, *p* = 0.001, reflecting higher accuracy in younger adults, in men, and in later blocks.

PLEASE INSERT FIGURE 2 AND TABLE 2 ABOUT HERE

**Source confidence**. Figure 2B (top panel) shows that depressed adults were less confident than controls. Accordingly, the model was improved by *Group*, χ2 = 18.46, *p* = 0.001, and included a trending *Group* x *Cue* interaction, *Z* = -1.65, *p* = 0.098, as the difference in confidence was stronger under the Side cue, *Z* = 2.42, *p* = 0.016, than the Question cue, *Z* = 1.14, *p* = 0.255. The model also revealed effects of *Cue*, *Z* = -5.33, *p* < 0.001, *Encoding Task*, *Z* = 2.91, *p* = 0.004, and *Block*, *Z* = 3.69, *p* < 0.001, as participants were more confident when responding to the Question cue, to words from the mobility task, and in later blocks.

**Source RT**. Correct RT was similar across groups, with everyone slower in response to Question vs. Side cues (Figure 2B, bottom). Accordingly, the model was not improved by *Group*, *p =* 0.08, but it included an effect of *Cue*, *Z* = -45.51, *p* < 0.001. There were also effects of *Run*, *Z* = -18.82, *p* < 0.001, *Confidence*, *Z* = 21.61, *p* < 0.001, and *Gender*, *Z* = -3.09, *p* = 0.003, reflecting shorter correct RTs in later blocks, for high confidence responses, and in males.

**ERPs**

Figure 3 displays waveforms elicited by correct responses to Question, Side, and Odd/Even cues. There was robust activity over parietal electrodes from 400-800 ms in controls that was markedly reduced in MDD, yielding an effect of *Group*, *F*(1,46) = 4.35, *p* = 0.043. There was also an effect of *Cue*, *F*(2,92) = 10.37, *p* < 0.001, with reliable differences between all conditions (REGWQ; Question > Side > Odd/Even, *ps* < 0.043). These data suggest that recollection was strongest under the Question cue and reduced in MDD. In both groups, the LPN is apparent at Oz from 800-2000 ms on Question and Side (but not Odd/Even) trials, and it extends over left frontal cortex on Question trials.

PLEASE INSERT FIGURE 3 ABOUT HERE

To test our *a priori* hypothesis, we subtracted activity on Odd/Even trials from Question and Side trials. Figure 4 shows that the Question condition drove activity over left parietal electrodes from 400-800 ms, although this effect was only reliable in controls (a negative difference over right frontal cortex was only reliable in the MDD group). From 1400-2000 ms, this subtraction revealed a negative difference over left PFC in both groups. By contrast, the Side condition elicited an LPN over midline posterior sites from 800-1400 ms. Contrary to expectations, between-groups tests yielded no reliable findings.

PLEASE INSERT FIGURE 4 ABOUT HERE

***Group x Cue x Encoding Task***. Our planned ERP analysis did not reveal group differences but it was not designed to capture the *Group* x *Cue* x *Encoding Task* interaction that characterized source accuracy. To address this limitation, we computed Question minus Side difference waves for words from each encoding task and submitted them to within and between-groups analysis, duplicating our approach to the accuracy data. Figure 5 shows that, in depressed adults, the Question minus Side difference varied drastically by encoding task (see Table 3). Words from the mobility task elicited sustained activation over left parietal cortex, leading to significant effects in all time windows. By contrast, words from the animacy task elicited a negativity over fronto-central sites that was stronger over the left hemisphere; again, significant differences were observed in all time windows. In controls, no significant effects were seen in any time window. Between-groups comparisons revealed reliable differences for the mobility task over left centro-parietal electrodes from 400-800 and 800-1400 ms, with stronger activation in the MDD group. Thus, the Question (minus Side) cue had a strong, task-dependent effect on brain activity in MDD that was muted in controls, paralleling the source accuracy data.

PLEASE INSERT FIGURE 5 AND TABLE 3 ABOUT HERE

**Individual Differences**

We computed Pearson correlations in the MDD group to determine if variation in depressive severity, brooding rumination, or sleep disruption affected source accuracy or ERP amplitudes. We found no relationship with source accuracy, left parietal activity averaged over encoding tasks, or left frontal activity on Question/animacy trials (|*p*s| < 0.31, *p*s > 0.15). However, as shown in Figure 6, the magnitude of parietal activity isolated by the Question minus Side subtraction for words from the mobility task was negatively correlated with PSQI scores from 400-800 ms and 800-1400 ms (*r*s < -0.47, *ps* < 0.02). To confirm that these results were not simply a correlate of depressive severity, we computed hierarchical regressions using ERP amplitude as the criterion and entering BDI-II and PSQI scores as predictors in steps 1 and 2, respectively. PSQI significantly predicted ERP amplitude after accounting for BDI-II in both windows (400-800 ms; β = -0.45, *p* = 0.03; 800-1400 ms; β = -0.49, *p* = 0.03), and adding PSQI improved both models (Δ*R*2s > 0.16, Δ*F*s > 4.5, *p*s < 0.05).

PLEASE INSERT FIGURE 6 ABOUT HERE

**Discussion**

This study yielded two sets of behavioral and ERP findings. Relative to controls, depressed adults were less accurate and less confident in their memories, and they showed reduced parietal ERP amplitude from 400-800 ms. The negative effect of MDD on memory was modest, but in addition to reporting lower confidence than controls in all four cells of the design, the depressed adults were numerically less accurate in three cells. Worse performance in 7/8 cells is improbable under the null (binomial test, *p* = 0.035 one-tailed), thus recollection and brain activity indexing recollection were weaker in MDD.

However, depressed adults showed excellent memory for words from the mobility task presented under the Question cue, which we interpret as reflecting sustained attention. At encoding, the mobility task elicited longer RTs and lower accuracy than the animacy task. It is easy to see why—for example, because trees sway in the breeze, deciding whether *oak* is “mobile” is harder than deciding whether an oak is alive—and we think the additional consideration needed to render mobility judgments led to deeper encoding. At retrieval, the Question cue elicited longer RTs and more confident responses than the Side cue, suggesting more extended and successful memory searches. Thus, directing conceptual retrieval at words from the mobility task pairs a deep retrieval search with deep encoding. Behavioral studies report good performance in depression under these conditions (29; 30), and our ERP data highlight a possible neural mechanism of this effect: sustained recruitment of left parietal cortex, which was otherwise hypoactive.

We speculate that this ERP effect may track relatively effortless recovery of episodic details, because memory accuracy was lower and left parietal activity was not seen when the Question cue was paired with words from the shallower encoding task (animacy judgment). Instead, there was lasting activity over the left PFC, which may reflect additional cue elaboration or careful selection from candidate memories following relatively poor encoding. Interestingly, the only other imaging study of source memory in MDD we know of reported increased left frontal activation during recollection attempts in depressed versus healthy adults (52). That study did not manipulate encoding difficulty, however; based on our data we predict that left PFC activation during source retrieval in MDD will be strongest when encoding is shallow and recollection is weakest.

Our data may have treatment implications. As described earlier, imprecise retrieval is associated with depression and enhancing retrieval can speed recovery. Consideration of treatment mechanisms suggests an explanation. During cognitive behavioral therapy (CBT), patients recall difficult episodes from their lives and then reappraise them to reduce distress; here the importance of accurate retrieval is self-evident. But patients are also asked to imagine similar situations unfolding in the future so they can envision themselves effectively using new coping skills (53). Imagining future events depends on the same parieto-hippocampal circuitry that supports retrieval (54-55), and we have shown that activity in these circuits is blunted in MDD but can recover with adequate support. By extension, we speculate that effective CBT may be associated with improved functioning in parieto-hippocampal circuits. Given links between antidepressant effects and both functional and structural changes in the hippocampus (56), this argument may extend to psychopharmacological interventions as well. Finally, we expect that a sleep intervention would enhance memory retrieval in MDD, based on the negative relationship between sleep quality and ERP amplitudes observed in Figure 6.

In summary, this study provides novel insight into the impact of depression on brain activity during retrieval. The central role of parieto-hippocampal activity in episodic memory is widely-known. These data indicate that the same circuitry may play an important but underappreciated part in depression and its treatment.

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**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. 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”.

*Figure 2*. Source memory (A) accuracy, (B, *top*) confidence, and (B*, bottom*) correct RT. Bar heights correspond to the mean, error bars = SEM. Asterisks denote *p* < 0.05.

*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; the late posterior negativity (LPN) was maximal at a midline occipital electrode. Gray shading demarcates the parietal ERP associated with recollection, asterisks indicate the reduction in parietal activity in depressed adults.

*Figure 4*. Topographies showing activity elicited by Question and Side hits, with activity on correct Odd/Even trials subtracted out. Columns correspond to the three time windows analyzed (400-800, 800-1400, 1400-2000 ms). Electrodes in clusters associated with significant effects (within-group) are shown in white. Between-group comparisons revealed no differences.

*Figure 5*. Results of the mass univariate analysis conducted on Question minus Side difference waves, sorted by group and encoding task. Columns correspond to the three time windows analyzed (400-800, 800-1400, 1400-2000 ms). Electrodes in clusters associated with significant effects are shown in white. Paralleling the behavioral analyses, there were MDD > control differences in response to words from the mobility task but not the animacy task.

*Figure 6.* ERP amplitudes are related to sleep quality in depressed adults. There were significant negative correlations between sleep disturbance as measured by the PSQI (*x*-axis) and ERP amplitudes captured by the Question minus Side difference wave for words from the mobility task (*y­*-axis) in the 400-800 (left) and 800-1400 (right) ms time windows.