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Separating the FN400 and N400 potentials across recognition memory experiments

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Abstract

There is a growing debate as to whether frontally distributed FN400 potentials reflect familiarity-based recognition or are functionally identical to centro-parietal N400 reflecting semantic processing. We conducted two experiments in which event-related potentials (ERPs) associated with semantic priming and recognition were recorded, either when priming was embedded within a recognition test (Experiment 1), or when these two phases were separated (Experiment 2). In Experiment 1, we observed 300–500 ms differences between primed and unprimed old words as well as differences between old and new primed words, but these two effects did not differ topographically and both showed midline central maxima. In Experiment 2, the N400 for priming was recorded exclusively during encoding and again showed a midline central distribution. The ERP component of recognition was only found for unrelated words (not primed previously during encoding), and also showed a midline central maximum, but, in addition, was present in the left frontal area of the scalp. Conversely, the priming effect was absent in the left frontal cluster. This pattern of results indicate that FN400 and N400 potentials share similar neural generators; but when priming and recognition are not confounded, these potentials do not entirely overlap in terms of topographical distribution and presumably reflect functionally distinct processes.

Keywords

Event-related potentials; FN400; N400; Familiarity; Semantic priming; Recognition memory

1. Introduction

In the dual-process model of recognition memory two distinct memory processes, familiarity and recollection, are separated (Aggleton & Brown, 1999; Atkinson & Juola, 1974; Jacoby & Dallas, 1981; Mandler, 1980; Yonelinas, 1999, 2002). Recognition judgments made on the basis of familiarity are fast, automatic, and reflect a general feeling of knowing that a

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given item in the recognition test was presented previously. On the other hand, recollection requires more details about studied items and results in slow, more effortful judgments.

ERP studies on recognition memory revealed that two distinct ERP components can be attributed to familiarity and recollection. The FN400 potential (also known as the early midfrontal old/new effect), recorded in 300–500 ms time window, mostly at midfrontal sites, is regarded as an electrophysiological index of familiarity. The left parietal old/new effect (or late positive component, LPC), found in 500–800 ms, mostly at left parietal sites, reflects the process of recollection. Many experimental studies provided evidence that these two potentials can be dissociated by variables related to familiarity and recollection (Rugg et al., 1998; Curran, 2000, Rugg & Curran, 2007).

Even though the functional interpretation of the LPC causes no controversy, there is an ongoing debate over whether the FN400 potential reflects familiarity (Paller, Voss, & Boehm, 2007). The FN400 is very similar to the standard N400 potential, which reflects semantic processing of meaningful stimuli and is not typically considered to be related to episodic memory processes (Kutas & Federmeier, 2011). In some studies that used stimuli without semantic meaning the FN400 component was not found, although strong familiarity-based responses (as measured by other techniques, e.g. “remember/know” procedure) were observed (MacKenzie & Donaldson, 2007; Voss & Paller, 2009; Yovel & Paller, 2004). A primary difference between the FN400 and the N400 is the topography, which is more frontal for the first, and more centro-parietal for the latter. Voss and Federmeier (2011) argue that “FN400” is in fact the N400 potential and its frontal distribution, found in previous studies, results from item-type differences. In recognition memory paradigms, concrete words or pictures are used particularly often, and the N400 component for concrete stimuli is recorded mostly at frontal sites. This is in contrast to abstract stimuli, which yield central and posterior distribution (Kounios & Holcomb, 1994). Voss and Federmeier (2011) directly compared two experimental conditions that were designed to capture ERP correlates of semantic priming without recognition and ERP correlates of recognition without semantic priming. In both conditions concrete words were used and the N400 component was observed at central and parietal sites, but the FN400 component was not identified.

Recently, however, Voss and Federmeier’s study (2011) has been criticized. Bridger et al. (2012) argue that the process of semantic priming was not separated from the process of recognition because semantic priming manipulations were embedded in a recognition test. Therefore, the conclusions drawn by Voss and Federmeier are not reliable. Bridger et al. conducted their own experiment in which concrete nouns were employed and a semantic priming task was separated from a subsequent recognition test. The N400 component was observed at central and parietal sites in the semantic priming task, whereas the FN400 component was found at frontal sites in the recognition test. Bridger et al. claim that the FN400 and N400 potentials are functionally different and reflect qualitatively distinct processes.

The aim of the present paper is to directly compare whether conducting experiments confounding semantic priming with a recognition task might produce topographically identical or distinct N400/FN400 potentials. So far, we can only compare results from two different laboratories that differed in terms of stimuli, recording, and data analysis procedures used. We conducted two experiments, both based on standard recognition memory procedures. In Experiment 1 there was no priming during the encoding phase, but during recognition each word was preceded by related or unrelated primes (primes were not presented in the study phase). We hypothesized that old/new effects for primed words will be topographically indistinguishable from priming effects, because the ERP waveform for the old/new effect will be strongly affected by ERP indices of priming. These predictions are in line with Voss and Federmeier's results (2011) and with their explanation by Bridger et al. (2012), who argue that when recognition process is strongly confounded with priming "[…] one consequence may be that the electrophysiological indices of recently priming these items remain observable on their second presentation" (Bridger et al., p. 1335).

In Experiment 2, priming was present only during the encoding phase, and the recognition memory was tested for new words and for unrelated and related old words (i.e., for words that were unprimed or primed during encoding). We hypothesized that the old/new effect will be topographically distinct from the priming effect, because procedures applied in this experiment will clearly separate familiarity from priming, allowing to establish clear ERP signals associated with those functionally distinct processes. Moreover, constructing separate new/unrelated and new/related contrasts allows us to determine whether priming effects from the previous encoding stage may still be present at the later recognition stage and influence the topography of N400/FN400 potentials. This is a substantial difference when compared to Bridger et al. (2012) paper, where only old unrelated words were analyzed. Taken together, our present study might help to clarify the nonuniformity of the N400/FN400 potentials and their distinct functional roles under specific experimental procedures.

2. Results

2.1. Experiment 1

2.1.1. Behavioral Results—During the test phase of Experiment 1 participants were given four recognition judgments options: "remember old", "know old", "guess old", and "new". We entered the mean proportions of responses assigned to three "old" options into two-way repeated measures analysis of variance (ANOVA) with Priming Condition (primed/unprimed) X Confidence (remember/know/guess). The main effect of Priming Condition was not significant. The main effect of Confidence was found [$F(1.65;37.86) = 33.32$, $p < 0.001$, $\eta^2 = .59$]. Bonferroni corrected post-hoc comparisons showed that the mean proportion of "remember old" responses (M=0.69; SEM=0.08) was larger than the mean proportions of "know old" (M=0.2; SEM=0.06; $p < .001$) and "guess old" responses (M=0.11; SEM=0.05; $p < .001$), whereas mean proportions of know and guess responses did not differ [$p = 0.63$]. A Priming Condition X Confidence interaction was not found. In the subsequent analysis old recognition judgments are collapsed across remember/know/guess responses, as all of them were correct for the presentation of a target word that had previously appeared in the study phase.

Then, we conducted a two-way repeated measures analysis of variance (ANOVA) with Priming Condition (primed/unprimed) X Recognition Condition (old/new). The dependent variable was mean proportion of correct responses. In this analysis old recognition judgments were collapsed across remember/know/guess responses. The main effect of Priming Condition was found [$F(1,23) = 40.29$, $p < .001$, $\eta^2 = .64$], indicating that accuracy was higher to unprimed words (M=0.79; SEM=0.03) than to primed words (M=0.74; SEM=0.03). The main effect of Recognition Condition was also observed [$F(1,23) = 60.86$, $p < .001$, $\eta^2 = .73$], showing that the mean proportion of correct recognition of old words (M=0.93; SEM=0.01) was higher than the mean proportion of correct rejection of new words (M=0.61; SEM=0.06). A Priming Condition X Recognition Condition interaction was found [$F(1,23) = 26.15$, $p < .001$, $\eta^2 = .53$]. Bonferroni corrected post-hoc comparisons revealed that the higher accuracy of responses to unprimed words than to primed words was present only for correct rejection of new words [$p < 0.001$], and not for correct recognition of old words [$p = 1.0$]. Mean proportions and standard errors of the means for recognition judgments in Experiment 1 are summarized in Table 1.

We also conducted behavioral analyses on mean reaction times recorded during the test phase of Experiment 1. The procedure of this experiment required that subjects first rated the emotional valence of each word and then gave the memory judgments. Thus, we conducted analyses both on mean reaction times for positive/negative judgments and for old/new responses. Only reaction times for targets that were correctly recognized or rejected were analyzed (reaction times to primes were not analyzed). First, we conducted a two-way repeated measures analysis of variance (ANOVA) with Priming Condition (primed/unprimed) X Recognition Condition (old/new) on mean reaction times for valence judgments of the targets. The main effect of Priming Condition was marginally significant [$F(1,23) = 3.28$, $p = 0.083$, $\eta^2 = .13$], showing that valence judgments reaction times were faster for primed (M=1246.88; SEM=37.63) than for unprimed words (M=1271.93; SEM=36.99). The main effect of Recognition Condition was found [$F(1,23) = 20.61$, $p < .001$, $\eta^2 = .47$], indicating that valence judgments reaction times were faster for words that were subsequently correctly recognized (M=1205.99; SEM=38.99) than for words that were subsequently correctly rejected (M=1312.83; SEM=38.02). A Priming Condition X Recognition Condition interaction was also found [$F(1,23) = 18.79$, $p < 0.001$, $\eta^2 = .45$]. Bonferroni corrected post-hoc comparisons indicated that faster valence judgments reaction times for primed than for unprimed words were observed only for subsequent correct recognition [$p < 0.001$], but not for subsequent correct rejection [$p = 0.21$].

The last behavioral analysis was performed on mean reaction times for correct memory judgments to targets during the test phase of Experiment 1. The design was the same as above: Priming Condition (primed/unprimed) X Recognition Condition (old/new). The main effect of Priming Condition was nonsignificant [$F(1,23) = 1.49$, $p = 0.24$]. The main effect of Recognition Condition was found [$F(1,23) = 15.49$, $p = .001$, $\eta^2 = .40$], indicating that reaction times for correct recognition were faster (M=3009.35; SEM=18.29) than reaction times for correct rejection (M=3071.67; SEM=25.76). A Priming Condition X Recognition Condition interaction was nonsignificant [$F(1,23) = 1.37$, $p = 0.25$]. Mean reaction times and standard errors of the means, both for valence and memory judgments, are summarized in Table 2.

Summary: Subjects gave more "remember old" than "know old" and "guess old" responses. Correct recognition of old words (collapsed across remember/know/guess options) was higher than correct rejection of new words. Priming decreased accuracy for new words, but did not significantly influence accuracy to old words. Valence judgment reaction times were faster for correct recognition than for correct rejection. They were also faster for primed than for unprimed words, but only for correct recognition of old words. Memory judgment reaction times were faster for correct recognition than for correct rejection.

2.1.2. ERP Analysis Strategy—In order to cover the scalp sites densely we analyzed ERP data from twelve electrode clusters: LF (left frontal), MF (midline frontal), RF (right frontal), LC (left central), MC (midline central), RC (right central), LP (left parietal), MP (midline parietal), RP (right parietal), LO (left occipital), MO (midline occipital), and RO (right occipital). Each cluster consisted of six electrodes, one main electrode (F3, Fz, F4, C3, Cz, C4, P3, Pz, P4, O1, Oz, and O2, respectively), and five adjacent electrodes (see Figure 1). Mean amplitude values were computed across all six electrodes within each cluster in the 300–500 ms and 500–800 ms time windows. The analyses of the late positive component (LPC) in the 500–800 ms time window are not necessary to investigate the main hypothesis. Nevertheless, streamlined LPC analyses are presented for completeness, but not discussed further. A four-way repeated-measures analysis of variance (ANOVA) with Priming Condition (primed/unprimed) X Recognition Condition (old/new) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed, separately for each time window. ERPs for old recognition judgments were collapsed across ERPs for "remember old", "know old" and "guess old" responses. In Experiment 1, as well as in Experiment 2, Hyunh-Feldt adjustment was incorporated when appropriate. Bonferroni correction was applied to multiple post-hoc comparisons, separately for each analysis in each experiment. The region and laterality effects are noted only if they significantly interact with priming or recognition conditions. In both experiments the topographic analyses were conducted on rescaled data taken from the priming and recognition difference waveforms, and the range normalization procedure was used for rescaling (McCarthy & Wood, 1985; Wilding, 2006). Any interaction of priming/recognition with region and/or laterality would indicate qualitative differences between the priming and recognition topographies that are not attributable to overall differences in amplitude.

2.1.3. ERP Results

2.1.3.1. 300–500 ms: Grand-averaged ERPs elicited by primed new, primed old, unprimed new, and unprimed old words are depicted in Figure 2. In order to allow for comparisons with results from other studies in which a linked mastoid reference was used (e.g., Voss and Federmeier, 2011; Bridger et al., 2012), we present grand-averaged ERPs re-referenced to the average of the two mastoid electrodes in the Appendix (Figure A1). A main effect of Priming Condition was observed [$F(1,23) = 28.85$, $p < .001$, $\eta^2 = .56$], indicating that ERPs for unprimed words were more negative than ERPs for primed words. Also, the main effect of Recognition Condition was observed [$F(1,23) = 21.97$, $p < .001$, $\eta^2 = .49$], indicating that

ERPs for new words were more negative than ERPs for old words. The Priming Condition X Recognition Condition interaction was found [$F(1,23) = 11.67$, $p < .01$, $\eta^2 = .34$]. Post-hoc comparisons showed that ERPs for unprimed words were more negative than ERPs for primed words, but only for old words [$p < .001$]. For new words, these priming differences were nonsignificant [$p = 1.0$]. Also, ERPs for new words were more negative than ERPs for old words, but only for primed words [$p < .001$], and not for unprimed words [$p = 1.0$].

The Priming Condition interacted significantly with Region [$F(1.75,40.27) = 17.65$, $p < .001$, $\eta^2 = .43$], and with Region and Laterality [$F(5.04,115.89) = 6.03$, $p < .001$, $\eta^2 = .21$]. The three-way interaction was deconstructed by conducting separate ANOVAs with Priming Condition (primed/unprimed) X Laterality (left/midline/right) for each level of Region (frontal/central/parietal/occipital). Main effects of Priming Condition were found in frontal [$F(1,23) = 32.09$, $p < .001$, $\eta^2 = .58$], central [$F(1,23) = 55.33$, $p < .001$, $\eta^2 = .71$], and parietal [$F(1,23) = 23.01$, $p < .001$, $\eta^2 = .50$] regions. Eta-squared measures of these effects indicated that the largest effect size was found in the central region. Also in the central region, a significant Priming Condition X Laterality interaction was found [$F(2,46) = 13.24$, $p < .001$, $\eta^2 = .36$]. Paired t-tests in each cluster in the central region indicated that the difference between primed and unprimed words was largest in the midline central (MC) cluster [$t(23) = 8.68$, $p < .001$, Cohen's $d = 1.77$], and was relatively smaller in the left central (LC) cluster [$t(23) = 5.26$, $p < .001$, Cohen's $d = 1.07$], and in the right central (RC) cluster [$t(23) = 5.92$, $p < .001$, Cohen's $d = 1.21$].

The Recognition Condition interacted significantly with Region [$F(2.17,49.8) = 5.3$, $p < .01$, $\eta^2 = .19$], Laterality [$F(1.5,34.4) = 4.83$, $p < .05$, $\eta^2 = .17$], and with Region and Laterality [$F(6,138) = 4.55$, $p < .001$, $\eta^2 = .16$]. Follow-up ANOVAs revealed main effects of Recognition Condition in frontal [$F(1,23) = 9.97$, $p < .01$, $\eta^2 = .30$], central [$F(1,23) = 28.77$, $p < .001$, $\eta^2 = .56$], and parietal [$F(1,23) = 18.87$, $p < .001$, $\eta^2 = .45$] regions. The largest effect size was observed in the central region. Significant Recognition Condition X Laterality interactions were also found in central [$F(2,46) = 9.53$, $p < .001$, $\eta^2 = .29$] and parietal [$F(2,46) = 4.71$, $p < .05$, $\eta^2 = .17$] regions. Paired t-tests in each cluster in the central region indicated that the difference between old and new words was largest in the midline central (MC) cluster [$t(23) = 5.59$, $p < .001$, Cohen's $d = 1.14$] and in the left central (LC) cluster [$t(23) = 4.44$, $p < .001$, Cohen's $d = .91$], and was relatively smaller in the right central (RC) cluster [$t(23) = 2.98$, $p < .01$, Cohen's $d = .61$]. Paired t-tests in each cluster in the parietal region indicated that the difference between old and new words was largest in the left parietal (LP) cluster [$t(23) = 5.00$, $p < .001$, Cohen's $d = 1.02$], and was relatively smaller in the midline parietal (MP) cluster [$t(23) = 3.64$, $p < .01$, Cohen's $d = .74$], and in the right parietal (RP) cluster [$t(23) = 3.01$, $p < .01$, Cohen's $d = .61$].

2.1.3.2. ERP Topographic Comparison: The priming effect and the old/new effect showed broad topographical distributions, both with the maximum effect size in the midline central area of the scalp. We conducted topographic comparison in the 300–500 ms time window to verify whether these effects differ in terms of their distribution over the scalp. For the priming contrast, ERPs to unprimed old words were subtracted from ERPs to primed old words. For the recognition contrast, ERPs to new primed words were subtracted from ERPs to old primed words. The difference waves were rescaled using range normalization. A three-way repeated-measures analysis of variance (ANOVA) with Contrast (priming contrast/recognition contrast) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed on rescaled data. This revealed a nonsignificant interaction between Contrast and Region [$F(1.9,43.61) = 0.46$, $p = .62$], and a nonsignificant interaction between Contrast, Region, and Laterality [$F(5.14,118.29) = 0.88$, $p = .50$]. The only significant interaction was found between Contrast and Laterality [$F(1.51,34.85) = 4.93$, $p < .05$, $\eta^2 = .18$]. Bonferroni corrected post-hoc comparisons revealed that in the right hemisphere the distribution of the priming contrast was broader than the distribution of the recognition contrast [$p = 0.056$]. Thus, more right hemisphere regions showed significant priming contrasts than recognition contrasts. The topographic maps for both the priming and recognition contrasts are depicted in Figure 3.

2.1.3.3. 500–800 ms: In this time window, the main effect of Priming Condition was not observed [$F(1,23) = 0.86$, $p = .36$]. The main effect of Recognition Condition was significant [$F(1,23) = 8.67$, $p < .01$, $\eta^2 = .27$], indicating that ERPs for old words were more positive than ERPs for new words. The Recognition Condition interacted significantly with Region [$F(1.84,42.26) = 3.54$, $p < .05$, $\eta^2 = .13$], Laterality [$F(2,46) = 9.02$, $p < .001$, $\eta^2 = .28$], and with Region and Laterality [$F(6,138) = 5.35$, $p < .001$, $\eta^2 = .19$], such that old/new differences were greatest in the left parietal and midline central clusters.

Summary: In the 300–500 ms time window, ERPs for unprimed words were more negative than ERPs for primed words, but only for old words. ERPs for new words were more negative than ERPs for old words, but only for primed words. The largest effect sizes for both of these comparisons were found in the midline central (MC) cluster. The priming contrast in the right hemisphere was more broadly distributed than the recognition contrast. No other topographical differences between these two effects were found. In the 500–800 ms time window we found the standard LPC effect.

2.1.4. Discussion of Experiment 1—Behavioral results of Experiment 1 revealed that subjects were more accurate in recognizing old words than in rejecting new words. Among correct recognition of old words there was an apparent advantage of remember responses as compared to know or guess responses, both for unprimed and primed words. This might indicate that correct recognition judgments were based predominantly on recollection rather than familiarity, irrespectively of whether those words were primed or not primed. However, it could merely reflect a bias to respond “remember” more than “know” or “guess”, not being influenced by the actual mnemonic characteristics. Also, for correct rejection of new words, the accuracy was larger for unprimed new words than for primed new words. The latter result indicates that primes increased false “old” judgments to new items. This is in line with previous behavioral work on the influence of semantic priming on the recognition judgments. Ngo, Sargent, and Dopkins (2007) conducted a series of experiments in which they demonstrated that semantic priming hindered correct recognition judgments to new words but had no effect on recognition judgments to old words. This is exactly the same pattern of results as obtained in our study. Ngo et al. (2007) attributed these results to the potentiated familiarity. According to their hypothesis, processing related primes increased the likelihood that new words will be treated as familiar and falsely classified as old. One might expect that the potentiated familiarity should also facilitate correct recognition judgments to old words, but that was not the case. The possible reason why the influence of semantic priming is not evident for old items is that those words might have been recognized mainly on the basis of recollection, and the related primes had no effect on recollective experiences. The high proportion of “remember old” responses assigned to correct recognition is consistent with this claim.

The analysis of reaction times to targets during the test phase of Experiment 1 revealed that subjects were faster while making valence judgments for primed than unprimed target words, but only for words that were subsequently correctly recognized as old (and not for subsequent correct rejection). This indicates that behavioral priming effect during making positive/negative judgments was present only if words were remembered from the study phase. This is particularly interesting in relation to electrophysiological priming effect that was also observed only for old words (see next paragraphs). With regard to reaction times while making memory judgments, we have not observed any influence of priming. Primed and unprimed words were given recognition judgments with comparable speed. Thus, it seems that priming was no longer evident when subjects were giving old/new responses. This is probably because memory judgments were delayed in time with regard to the primes. Therefore, the influence of primes was observed only for preceding valence judgments reaction times.

ERP results in the 300–500 ms time window showed that the old/new effect was present only for primed words. This was most likely due to increased familiarity triggered by the preceding primes, which had not taken place in the case of unprimed words. This explanation is strengthen by the fact that the old recognition judgments were given mostly on the basis of recollection (as indexed by the high proportion of “remember old” responses in comparison to “know old” and “guess old” responses, both for primed and unprimed items). Assuming that the level of recollection was comparable for primed and unprimed words, the advantage of primed words in terms of increased familiarity might have been crucial for the old/new effect to emerge. Thus, the ERP old/new effect was observed when targets were primed, but diminished when there was no priming. However, this explanation is not entirely satisfactory as there were no advantage in the proportion of “know old” responses for primed than for unprimed words. Still, it might have been the case that the increased familiarity was manifested in the ERP old/new effect, but not in the behavioral responses.

Interestingly, the electrophysiological priming effect (more negative N400 amplitude for unprimed than for primed items) was present only for old words, and was absent for new words. This is in line with the results of valence judgments reaction times, which indicated that the behavioral priming effect was observed only for subsequent correct recognition of old words, but not for subsequent correct rejection of new words. It seems plausible that new words may not have been successfully primed at all, which explains the lack of ERP priming effect for these words. Another possible explanation of this is that rejecting new primed words was more difficult than rejecting new unprimed words. This is because preceding primes might have elicited feeling of familiarity towards target words and made it harder to reject them. This probably produced interference between larger N400 amplitude for new primed words (because it was harder to reject them) and for new unprimed words (because unprimed words usually produce more negative N400 amplitude than primed words which reflects enhanced semantic processing). This is a good illustration of how confounding priming with recognition leads to some discrepant results. Moreover, there was another factor in the procedure of Experiment 1 that might have enhanced this confound, namely, subjects had to judge the emotional valence of words both during study and test phases (following Voss & Federmeier, 2011). This might have established some sort of resemblance between encoding and recognition causing recognition judgments to be influenced by priming. In order to separate familiarity from semantic priming more thoroughly, in Experiment 2 we employed emotional valence ratings only during the study phase, similarly to Bridger et al. (2012).

With regard to the consequences of confounding priming with recognition, the most important result of Experiment 1 was that the topographic comparison between the old/new effect for primed words and the priming effect for old words yielded no significant Condition X Region interaction. This interaction is of most relevance to the issue of separating FN400 and N400 potentials. This is because the hypothesized uniformity of these two ERP components is based on the assumption that the frontal distribution of FN400 results merely from item-type differences, i.e. the fact that concrete stimuli, which are generally used in recognition memory experiments, yield frontal distribution of the standard N400 (Voss & Federmeier, 2011). Thus, any anterior/posterior differences between old/new and priming effects (given the same stimuli for both effects) might indicate that FN400 and N400 potentials are not identical, but exhibit functional diversity. Other topographical differences between these effects, i.e. laterality differences discussed below, are of less concern and might reflect minor discrepancies within single cognitive process across different conditions. For this reason, the lack of significant Condition X Region interaction indicated that the old/new effect for primed words and the priming effect for old words were mainly distributed in the same regions of the scalp. This was in line with our hypothesis and indicated that we have not found the FN400 potential with frontal distribution for recognition contrast. Instead, we have found the typical N400 component with more posterior distribution which was indistinguishable from N400 recorded for the priming contrast. This pattern of result replicates the findings of Voss & Federmeier (2011) and confirms the prediction that when priming is embedded within a recognition test there is no evidence that FN400 and N400 are separate potentials. However, the topographic comparison yielded significant Condition X Laterality interaction, which indicated that the priming effect for old words was more right-lateralized in comparison to the old/new effect for primed words. Although in most studies the priming effect shows bilateral activation, there are some reports in which it is mainly observed in the right hemisphere. For example, Kiefer, Weisbrod, Kern, Maier, and Spitzer (1998) found the centro-parietal N400 potential for indirectly related words only over the right hemisphere, whereas the same potential for nonrelated and directly related word pairs was elicited bilaterally. This pattern of results might suggest that the right hemisphere is involved in the processing of remote semantic information. This is also consistent with a broader theoretical framework in which right hemisphere is regarded as the one that codes semantic information more coarsely than the left hemisphere, which can result in the activation of the wider context of a word (Beeman et al., 1994). In our study, the procedure of Experiment 1 required that subjects should rate the emotional valence of each word in the test phase before answering whether it was old or new. The priming was embedded in recognition test so each prime-target pair was separated by valence judgment and memory response for the primes. Thus, before primes exerted any influence on targets, subjects had been engaged in different kind of cognitive operations regarding primes. This delay in priming might have activated a broader range of word meanings, which, in turn, might have influenced the topography of the N400 potential towards right hemisphere. However, it is worth noting that this shift was very subtle and the overall effect was bilateral.

In general, the results of the topographic comparison in Experiment 1 show that the old/new effect for primed words and the priming effect for old words are observed in the same region of the scalp, but differ in laterality, probably because of the delay in priming. Thus, as predicted, we have not found separate FN400 potential for old/new effect and separate N400 potential for priming effect. Still, it does not necessarily have to mean that these potentials are identical, but only that under certain procedures that confound priming with recognition the differences between these potentials are impossible to observe.

2.2. Experiment 2

We conducted the second experiment in order to ascertain whether separating priming from recognition will produce topographically distinct FN400 and N400 potentials. In Experiment 2 priming was employed only during the study phase, and the recognition test consisted of words that were unprimed or primed during encoding. We hypothesized that the differences between ERP indices of familiarity and priming will be larger than in Experiment 1 because of separating these two processes.

2.2.1. Behavioral Results—First, we analyzed mean reaction times for emotional judgments of primes and words that were primed or not primed during the study phase of Experiment 2. We conducted two-way repeated measures analysis of variance on mean reaction times to each word from the prime-target word pairs, controlling for whether the primes and targets were actually related or unrelated. The design included Word Category (primes/targets) and Priming Condition (related/unrelated). The main effect of Word Category was observed [$F(1,28) = 13.45$, $p < .001$, $\eta^2 = .33$], showing that mean reaction times for target words were significantly faster (M=737.69; SEM=49.45) than mean reaction times for primes (M=783.48; SEM=54.24). The main effect of Priming Condition was also found [$F(1,28) = 6.91$, $p < .05$, $\eta^2 = .2$], indicating that mean reaction times collapsed across primes and targets from related word pairs were significantly faster (M=744.79; SEM=51.86) than mean reaction times collapsed across primes and targets from unrelated word pairs (M=776.37; SEM=51.88). The Word Category X Priming Condition interaction was marginally significant [$F(1,28) = 3.35$, $p = .078$, $\eta^2 = .11$]. Bonferroni corrected post-hoc comparisons revealed that faster reaction times for target words than for primes were observed only for related word pairs ($p < 0.001$), but not for unrelated word pairs ($p = 0.318$). Also, faster reaction times from related word pairs than from unrelated word pairs were observed only for targets ($p < 0.01$), but not for the primes ($p = 0.799$). Thus, the behavioral priming effect was observed during the study phase of Experiment 2, especially when mean reaction times for related and unrelated targets were compared.

During recognition test of Experiment 2 participants were given six recognition judgments options: “sure old”, “probably old”, “guess old”, “sure new”, “probably new”, and “guess new”. We conducted two-way repeated measures analysis of variance on mean proportions of correct responses assigned to these options with the Recognition Condition (unrelated/related/new) and Confidence (sure/probably/guess) factors. The main effect of Recognition Condition was not found [$F(2,56) = .43$, $p = .653$]. The main effect of Confidence was observed [$F(1.12,31.4) = 195.14$, $p < .001$, $\eta^2 = .88$], showing that there was a high proportion of “sure” responses (M=0.71; SEM=0.03), and relatively small proportions of “probably” (M=0.2; SEM=0.02) and “guess” responses (M=0.09; SEM=0.01). Bonferroni corrected post-hoc comparisons revealed that the mean proportion of “sure” responses was significantly larger than the mean proportions of “probably” and “guess” responses, and the mean proportion of “probably” responses was significantly larger than the mean proportion of “guess” responses [all ps < 0.001]. There was also a significant Recognition Condition X Confidence interaction [$F(1.71,47.79) = 168.63$, $p < .001$, $\eta^2 = .86$], indicating that aforementioned confidence differences were observed at each level of recognition condition (correct recognition of unrelated old words, correct recognition of related old words, correct rejection of new words), except that for correct rejection there was no difference in mean proportions between sure and probably responses [$p = 1.0$].

Then, we conducted one-way repeated measures analysis of variance with the Recognition Condition (unrelated/related/new) on mean proportion of correct responses. In this analysis old and new correct recognition judgments were collapsed across sure/probably/guess responses. The main effect of the Recognition Condition was observed [$F(1.13,31.59) = 33.14$, $p < .001$, $\eta^2 = .54$]. Bonferroni corrected post-hoc comparisons indicated that the mean proportion of correct rejection of new words (M=0.83; SEM=0.02) was lower than the mean proportion of correct recognition of unrelated words (M=0.95; SEM=0.01; $p < 0.001$), and lower than the mean proportion of correct recognition of related words (M=0.96; SEM=0.01; $p < 0.001$). There was no significant difference between accuracy for unrelated and related words [$p = 0.96$]. Mean proportions and standard errors of the means for recognition judgments in Experiment 2 are summarized in Table 3.

We also conducted one-way repeated measures analysis of variance on mean reaction times recorded during the recognition test of Experiment 2. The design included the Recognition Condition (unrelated/related/new) as a factor. Only reaction times to correctly classified old or new items were analyzed. The main effect was found [$F(2,56) = 34.83$, $p < .001$, $\eta^2 = .55$]. Bonferroni corrected post-hoc comparisons showed that mean reaction times for correct rejection of new words (M=779.83; SEM=49.64) were significantly slower than mean reaction times for correct recognition of both unrelated (M=571.07; SEM=33.93) and related old words (M=570.92; SEM=36.08; ps < .001), and did not differ between the latter two [$p = 1.0$]. Mean reaction times and standard errors of the means for recognition judgments in Experiment 2 are summarized in Table 4.

Summary: Mean reaction times for emotional judgments during the study phase were faster for targets than for primes, but only for related word pairs. These reaction times were also faster from related word pairs than from unrelated word pairs, but only for targets. Correct recognition of unrelated and related old words (collapsed across sure/probably/guess options) was higher than correct rejection of new words, but related and unrelated words did not differ. Mean reaction times for memory judgments during the recognition test were faster for correct recognition of unrelated and related old words than for correct rejection of new words, but related and unrelated words did not differ.

2.2.2. ERP Analysis Strategy—The same scalp clusters and time windows were used as in Experiment 1. At the study phase in the 300–500 ms time window, three-way repeated-measures ANOVA with Priming Condition (primed/unprimed) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed to quantify the priming effect. At the test phase, three-way repeated-measures ANOVA with Recognition Condition (unrelated/related/new) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed to quantify the early old/new effect. The last analysis was also performed in the 500–800 ms time window to capture the late old/new effect. In these analyses ERPs for old and new correct recognition judgments were collapsed across “sure”, “probably” and “guess” responses.

2.2.3. ERP Results

2.2.3.1. 300–500 ms: Grand-averaged ERPs elicited by primed and unprimed words in the study phase are depicted in Figure 4, and those elicited by old related, old unrelated and new words in the test phase are depicted in Figure 5. Mastoid-referenced grand-averaged ERPs are presented in the Appendix (Figures A2 and A3). At the study phase, the main effect of Priming Condition was observed [$F(1,28) = 24.82$, $p < .001$, $\eta^2 = .47$], indicating that ERPs for unprimed words were more negative than ERPs for primed words. Priming Condition X Region [$F(2.03,56.84) = 7.48$, $p < .01$, $\eta^2 = .21$], and Priming Condition X Region X Laterality interactions [$F(4.63,129.6) = 3.85$, $p < .01$, $\eta^2 = .12$] were also observed.

The three-way interaction was deconstructed by conducting separate ANOVAs with Priming Condition (primed/unprimed) X Laterality (left/midline/right) for each level of Region (frontal/central/parietal/occipital). Main effects of Priming Condition were found in frontal [$F(1,28) = 4.25$, $p < .05$, $\eta^2 = .13$], central [$F(1,28) = 28.77$, $p < .001$, $\eta^2 = .51$], and parietal [$F(1,28) = 26.78$, $p < .001$, $\eta^2 = .49$] regions. Eta-squared measures of these effects indicated that the largest effect size was found in central and parietal regions. In the central region a significant Priming Condition X Laterality interaction was also found [$F(1.73,48.58) = 5.62$, $p < .01$, $\eta^2 = .17$]. Paired t-tests in each cluster in the central region indicated that the difference between primed and unprimed words was largest in the midline central (MC) cluster [$t(28) = 5.94$, $p < .001$, Cohen’s $d = 1.1$], and was relatively smaller in the left central (LC) cluster [$t(28) = 3.86$, $p < .001$, Cohen’s $d = .72$], and in the right central (RC) cluster [$t(28) = 3.52$, $p < .01$, Cohen’s $d = .65$].

At the test phase, the main effect of Recognition Condition was observed [$F(1.71,48) = 5.91$, $p < .01$, $\eta^2 = .17$]. Post hoc comparisons indicated that ERPs for new words were more negative than ERPs for unrelated words [$p < 0.01$]. There was no difference in ERP amplitude between new and related words [$p = .36$]. There was also marginally significant interaction between Recognition Condition and Region [$F(3.33,93.15) = 2.37$, $p = .07$, $\eta^2 = .08$], significant Recognition Condition X Laterality interaction [$F(2.69,75.28) = 4.3$, $p < .01$, $\eta^2 = .13$], and significant Recognition Condition X Region X Laterality interaction [$F(8.66,242.27) = 2.1$, $p < .05$, $\eta^2 = .07$]. Follow-up ANOVAs revealed a marginally significant main effect of Recognition Condition in the frontal region [$F(2,56) = 2.8$, $p = .07$, $\eta^2 = .09$], and significant main effects in the central region [$F(2,56) = 10.21$, $p < .001$, $\eta^2 = .27$] and in the parietal region [$F(2,56) = 5.00$, $p < .05$, $\eta^2 = .15$]. The largest effect size was observed in the central region. Significant Recognition Condition X Laterality interactions were found in the frontal region [$F(4,112) = 3.36$, $p < .05$, $\eta^2 = .11$] and in the central region [$F(4,112) = 5.41$, $p < .001$, $\eta^2 = .16$]. A marginally significant Recognition Condition X Laterality interaction was also observed in the parietal region [$F(4,112) = 2.32$, $p = .06$, $\eta^2 = .08$]. One-way repeated measures ANOVAs in each frontal cluster indicated that the main effect of condition was found only in the left frontal (LF) cluster [$F(2,56) = 7.16$, $p < .01$, $\eta^2 = .20$], and was nonsignificant in the midline frontal (MF) cluster [$F(2,56) = 2.04$, $p = .14$] and in the right frontal (RF) cluster [$F(2,56) = .29$, $p = .75$]. Post-hoc tests in the left frontal cluster indicated that the only significant difference was found between new and unrelated words ($p < .01$). One-way repeated measures ANOVAs in each central cluster indicated that the main effect of condition was found in the left central (LC) cluster [$F(2,56) = 12.41$, $p < .001$, $\eta^2 = .31$] and in the midline central (MC) cluster [$F(1.61,45.09) = 10.92$, $p < .001$, $\eta^2 = .28$], and was nonsignificant in the right central (RC) cluster [$F(2,56) = 1.26$, $p = .29$]. Post-hoc tests in the left central cluster indicated that significant differences were found between new and related words ($p < .05$), and between new and unrelated words ($p < .001$). Post-hoc tests in the midline central cluster indicated that significant differences were found between new and unrelated words ($p < .001$), and between related and unrelated words ($p < .01$). One-way repeated measures ANOVA in each parietal cluster indicated that the main effect of condition was found in the left parietal (LP) cluster [$F(2,56) = 8.3$, $p < .001$, $\eta^2 = .23$] and in the midline parietal (MP) cluster [$F(2,56) = 3.22$, $p < .05$, $\eta^2 = .10$], and was nonsignificant in the right parietal (RP) cluster [$F(2,56) = 2.35$, $p = .10$]. Post-hoc tests in left and midline parietal clusters indicated that significant differences were found between new and unrelated words ($p < .001$ in the LP cluster; $p < .05$ in the MP cluster).

2.2.3.2. ERP Topographic Comparison: The priming effect at the study phase and the recognition effect at the test phase showed broad topographical distribution, both with the maximum effect sizes in the midline central cluster. However, the recognition effect for unrelated words was also substantially present in the left frontal cluster, and was completely absent in the right hemisphere. Conversely, the priming effect was absent in the left frontal cluster, but was broadly distributed in the right hemisphere. This pattern of results indicate that these two effects do not entirely overlap in terms of topographic distribution and may have, at least in part, distinct neural generators. We conducted topographic comparison in the 300–500 ms time window to test whether the topographic distribution of these effects differ. For the priming contrast, ERPs to unprimed words were subtracted from ERPs to primed words. For the recognition contrast for unrelated words, ERPs of correct rejection of new words were subtracted from ERPs of true recognition of unrelated words. The difference waves were rescaled using range normalization. Three-way repeated-measures analysis of variance (ANOVA) with Contrast (priming/recognition for unrelated words) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed on rescaled data. This revealed a significant Contrast X Laterality interaction [$F(1.51,42.28) = 3.59$, $p < .05$, $\eta^2 = .11$], and a marginally significant Contrast X Region X Laterality interaction [$F(5.15,144.15) = 2.19$, $p = .057$, $\eta^2 = .07$].

The three-way interaction was deconstructed by making separate ANOVAs with Contrast (priming/recognition for unrelated words) X Laterality (left/midline/right) for each level of Region (frontal/central/parietal/occipital). This revealed significant Contrast X Laterality interaction [$F(1.69,47.37) = 8.42$, $p < .01$, $\eta^2 = .23$], only in the frontal region. Bonferroni-corrected post-hoc comparisons indicated that the difference in the distribution of priming and recognition contrasts was found only in the left frontal cluster [$p < 0.001$], such that this cluster showed significant recognition contrast (the old/new difference for unrelated words), but no significant priming contrast (the primed/unprimed difference). The topographic maps for both priming contrast and recognition for unrelated words contrast are depicted on Figure 6.

We also conducted topographic comparisons in the 300–500 ms time window in which a random sample of 24 participants was selected. This is because all the above results from Experiment 2 are reported for 29 subjects, whereas data from Experiment 1 were reported for 24 subjects. One might argue that because more participants contributed to Experiment 2 than Experiment 1, the differences observed in Experiment 2 could have been due to additional statistical power rather than to experimental manipulations. Again, three-way repeated-measures analysis of variance (ANOVA) with Contrast (priming/recognition for unrelated words) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed. For rescaled data, significant interaction between Contrast, Region, and Laterality was found [$F(6,138) = 2.82$, $p < .05$, $\eta^2 = .11$]. Separate ANOVAs with Contrast (priming/recognition for unrelated words) X Laterality (left/midline/right) for each level of Region (frontal/central/parietal/occipital) revealed significant Contrast X Laterality interaction, only in the frontal region [$F(1.67,38.45) = 7.91$, $p < .01$, $\eta^2 = .26$]. Bonferroni-corrected post-hoc comparisons revealed that the difference in the distribution of priming and recognition contrasts was found only in the left frontal cluster [$p < 0.001$], such that this cluster showed significant recognition contrast, but no significant priming contrast. Thus, because the results of the subsidiary analyses were consistent with the results of initial analyses of the full sample of 29 participants, the differences found in Experiment 2 were not merely due to additional statistical power but were triggered by the experimental manipulations.

2.2.3.3. 500–800 ms: At the test phase in the 500–800 ms time window, the main effect of Recognition Condition was observed [$F(1.78,49.85) = 22.21$, $p < .001$, $\eta^2 = .44$], indicating that ERPs for old words were more positive than ERPs for new words, both when new words were compared to unrelated words [$p < 0.001$], and to related words [$p < 0.001$]. Significant Recognition Condition X Region [$F(3.5,97.95) = 7.07$, $p < .001$, $\eta^2 = .20$], Recognition Condition X Laterality [$F(3.02,84.46) = 2.82$, $p < .05$ $\eta^2 = .09$], and marginally significant Recognition Condition X Region X Laterality interactions [$F(8.13,227.6) = 1.94$,

$p = .053$, $\eta^2 = .06$] were also found, such that old/new differences were greatest in the left parietal, left central and midline central clusters.

Summary: In the 300–500 ms time window, during the study phase, ERPs for unprimed words were more negative than ERPs for primed words. The largest effect size for this comparison was found in the midline central (MC) cluster. During the test phase, ERPs for new words were more negative than ERPs for unrelated old words, but new words did not differ from related old words. The largest effect size for new-unrelated comparison was observed in left central (LC) and midline central (MC) clusters, but this comparison was also found in the left frontal (LF) cluster. The difference in the distribution of priming and recognition contrasts was found only in the left frontal cluster, such that this cluster showed significant old/new difference for unrelated words, but no significant primed/unprimed difference. In the 500–800 ms time window we found the standard LPC effect.

2.2.4. Comparison between Experiment 1 and Experiment 2—To directly compare topographic distributions of priming and recognition effects in Experiment 1 and Experiment 2, we submitted range normalized difference waves from both experiments to single repeated-measures ANOVA with Experiment (experiment 1/experiment 2) X Contrast (priming/recognition) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right). This revealed a significant Experiment X Contrast X Region X Laterality interaction [$F(6,306) = 2.18$, $p < .05$, $\eta^2 = .04$].

To deconstruct this four-way interaction, separate Experiment X Contrast X Laterality ANOVAs were conducted at each level of Region. Significant Experiment X Contrast [$F(1,51) = 4.56$, $p < .05$, $\eta^2 = .08$] and Experiment X Contrast X Laterality [$F(2,102) = 5.11$, $p < .01$, $\eta^2 = .09$] interactions were found, but only in the frontal region. Bonferroni corrected post-hoc comparisons showed that in Experiment 2, the difference in the distribution of priming and recognition contrasts was found only in the left frontal cluster [$p < .001$], such that this cluster showed significant recognition contrast (the old/new difference for unrelated words), but no significant priming contrast (the primed/unprimed difference).

Lastly, we conducted topographic comparisons of priming and recognition effects in Experiment 1 and Experiment 2 in which a random sample of 24 participants from Experiment 2 was selected. Again, repeated measures analysis of variance (ANOVA) with Experiment (experiment 1/experiment 2) X Contrast (priming/recognition) X Region (frontal/central/parietal/occipital) X Laterality (left/midline/right) was computed. Significant interaction between Experiment, Contrast, Region, and Laterality was found [$F(6,276) = 2.84$, $p < .05$, $\eta^2 = .06$]. Separate Experiment X Contrast X Laterality ANOVAs were computed at each level of Region. This revealed significant Experiment X Contrast [$F(1,46) = 5.03$, $p < .05$, $\eta^2 = .09$] and Experiment X Contrast X Laterality [$F(2,92) = 5.82$, $p < .01$, $\eta^2 = .11$] interactions, but only in the frontal region. Bonferroni corrected post-hoc comparisons showed that in Experiment 2, the difference in the distribution of priming and recognition contrasts was found only in the left frontal cluster [$p < .001$], such that this cluster showed significant recognition contrast, but no significant priming contrast.

2.2.5. Discussion of Experiment 2—The behavioral results of Experiment 2 indicated that the priming was evident during the study phase as mean reaction times to primed words were faster than mean reaction times to unprimed words. During the test phase, the mean proportion of correct recognition (hits) was larger than the mean proportion of correct rejection, both for unrelated and related words. There was no difference between mean proportion of hits for unrelated and related words. Also, mean reaction times to correctly recognized unrelated and related old words were faster than mean reaction times to correctly rejected new words.

The false alarms rate in Experiment 2 was smaller than in Experiment 1, most probably because we changed the demands for the memory judgments. In Experiment 1 subjects were given four response categories to choose from (“remember old”, “know old”, “guess old”, “new” judgments). Three categories were associated with “old” responses, which might have promoted choosing them more often than single “new” category. In Experiment 2 we applied the same number of response categories for old and new responses (“sure”, “probably”, “guess”). This was a successful attempt to reduce the liberal response bias observed in Experiment 1. Moreover, there were a relatively large proportion of “sure” responses, indicating that subjects based their recognition judgments mainly on recollection. This resembles the outcome of Experiment 1 in which old responses were also given mostly on the basis of recollection. However, as recollection and familiarity are not exclusive, we can not rule out the possibility that familiarity was also exerting some influence on recognition judgments.

ERP results in the 300–500 ms time window at the study phase showed a typical priming effect, i.e. more negative amplitude for unprimed words than for primed words. This effect was mainly found in the midline central cluster and in the parietal region of the scalp, which is consistent with its typical distribution found in previous studies and in Experiment 1 reported here.

In the 300–500 ms time window at the test phase the old/new effect was found, but only for unrelated words. Unrelated old words that were submitted to the recognition contrast were not primed during study. Thus, the ERPs for the old/new effect for unrelated words were not affected by the ERPs associated with priming effects from the study phase. The old/new effect was not observed for related words. A possible explanation of this outcome assumes that semantic priming at study might have hindered the encoding of related words leading to weaker memory signals for those words at test. This is in line with existing evidence that priming from past experiences might impair new episodic encoding (Wagner, Maril, & Schacter, 2000)[1].

The old/new effect for unrelated words showed topographical maximum in the midline central cluster, the same as the priming effect, but was also present in the left frontal cluster, where the priming effect was not found. Moreover, the recognition effect was not observed in the right hemisphere, where the priming effect was broadly distributed. Direct topographical comparison between these two effects showed that the distribution of the

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[1] We thank an anonymous reviewer for this insightful suggestion.

old/new effect for unrelated words was significantly different than the distribution of the primed/unprimed effect, but only in the left frontal cluster. Thus, similarly as in the Bridger et al. (2012) paper, the old/new effect was more frontally distributed than the priming effect, which is an indicator of the FN400 component. The priming effect showed centro-parietal distribution, which is typical for the standard N400 potential reflecting semantic processing. This pattern of results suggests that FN400/N400 potentials are not identical and, under procedures that clearly separate recognition from priming, the topography of them differ, indicating that they reflect distinct cognitive processes.

One might ask whether the left lateralized frontal old/new effect for unrelated words found in the present study reflects the FN400 potential, given the fact that in most recognition studies the FN400 is typically largest over midfrontal scalp sites. However, Ecker & Zimmer (2009) found a slightly left lateralized old/new effect in 350–500 ms time window when there was conceptual overlap between study and test. This conceptual overlap was caused by general category-based retrieval orientation, which was implemented by instructing subjects to accept as old both objects identical to study items and objects that were different exemplars of studied items. Also, Curran & Doyle (2011) observed the FN400 in the left hemisphere when subjects studied pictures but were tested with words. This particular study/test incongruity might have established conceptual overlap between study and test because of naming pictures at study and transferring the resulting verbal memory trace to test. Similarly, MacKenzie & Donaldson (2009) presented subjects with compound face-name stimuli and found a left lateralized old/new effect in 300–500 ms time window when names were presented at test, but not when faces were presented at test. Again, it seems plausible that participants have been naming test stimuli which caused a conceptual overlap with study items. This was not the case when perceptually identical faces were presented at study and test. Thus, although distinct contrasts were used in these three studies, their results uniformly suggest that the left-frontal effect could reflect the greater ease of naming repeated test items. This might have also been the case in our experiment, probably because of the presence of related items at test, which might have established a sort of conceptual overlap between study and test. It is worth noting that Bridger et al. (2012) found a standard mid-frontal FN400 effect (which was topographically distinct from the N400), but they tested only unrelated test items, which were not primed during encoding and therefore any possible influences of priming on the recognition were impossible or much less probable.

To directly ensure that Experiment 1 and Experiment 2 yielded topographically distinct FN400/N400 potentials because of different procedures applied, we conducted one additional analysis on range normalized difference waves taken from 300–500 ms time window from both experiments. The results showed that the only significant difference between topographical distribution of priming and old/new effects was found in the left frontal cluster in Experiment 2, where the old/new effect was significant, but the priming effect was absent. Although comparisons between experiments can yield some general objections, particularly because of lack of random assignment of participants to different conditions, age [M=21.46, SD=2.90 in Experiment 1; M=20.86, SD=2.18 in Experiment 2; $t(51)=0.85$, p=0.40] and gender statistics [12 females, 12 males in Experiment 1; 12 females, 17 males in Experiment 2; $\chi^2(1)=0.39$, p=.53] for both experiment were similar. Therefore, our results support the notion that confounding priming with recognition in Experiment 1 yielded indistinguishable N400 potentials both for priming and old/new effects (indistinguishable in terms of the lack of anterior/posterior topographic differences), and separating priming from recognition in Experiment 2 resulted in topographically and functionally distinct FN400 and N400 potentials. However, we acknowledge the limitations from comparing results across experiments with distinct samples measured at different time points.

3. General Discussion

In summary, our results have confirmed the prediction that embedding primes within a recognition test makes it difficult to clearly separate the process of familiarity from the process of semantic priming. Therefore, the old/new and priming effects in Experiment 1 were indistinguishable from each other in terms of topographic distribution, except from the fact that the priming effect was right-lateralized. In Experiment 2, when priming and recognition processes were separated, we found a 300–500 ms old/new effect, but only for unrelated words. This effect indicates that the recognition contrast is susceptible to any confounds with previous priming, even if those two phases are separated. Moreover, the old/new effect for unrelated words was topographically distinct from the priming effect. Although both contrasts showed midline central maximum, the recognition effect showed distribution in the left frontal cluster, where the priming effect was absent.

This pattern of results indicates that the FN400 and N400 might not be clearly dissociated components, but only under experimental procedures that confound familiarity with semantic priming. When experimental procedures clearly separate these two processes, the FN400 show expected frontal distribution and is, at least in part, topographically distinct from N400. Still, those components share most of the topographical distribution (mostly in the midline central cluster, but also in parietal regions), which indicates that they have similar neural generators.

Also, it is important to acknowledge the extent to which topographic contrasts employed in Experiment 1 and Experiment 2 are comparable. Because of the pattern of results obtained in both experiments, the old/new contrast in Experiment 1 was limited to primed items, whereas the same contrast in Experiment 2 was limited to unrelated (unprimed) items. Other comparisons were not possible because the old/new effect to unprimed words was absent from Experiment 1, and the old/new effect for related (primed) words was not observed in Experiment 2. This calls into question the reliability of comparing the topographic distributions of these effects across experiments. However, this inconsistency is justifiable given the fact that the procedures of Experiment 1 intermixed priming with recognition (thus allowing observation of the recognition effect only for primed items) and the procedures of Experiment 2 separated these two processes (thus restricting the recognition effect only for unrelated words). Actually, the fact that these two contrasts were not identically matched only strengthens our main finding that under particular experimental procedures FN400 and N400 potentials can be treated as functionally distinct ERP components. This is because the first contrast (the old/new effect for primed items in Experiment 1) turned out to be topographically indistinguishable from the priming effect (in terms of anterior/posterior distribution), whereas the second contrast (the old/new effect for unrelated words in Experiment 2) was proved to be topographically distinct from the priming effect. It is clear that the reason for this discrepant pattern of results is the fact that for the first contrast the old/new effect was confounded with priming, whereas for the second contrast it was separated from priming. Thus, we believe that the direct comparison of topographic distributions of the old/new effects between these two experiments is of substantial relevance to the theoretical issue of whether the N400 and FN400 are identical or distinct. Nonetheless, future research should address the issue of whether the old/new effect for unprimed items observed under procedures similar to those applied in Experiment 1 (or the old/new effect for primed items observed under procedures we used in Experiment 2) is distinguishable from the priming effect.

Another methodological difference between our experiments was that subjects tested in Experiment 1 were required to make valence judgments before making memory responses at test, whereas in Experiment 2 valence judgments were not required at test. This discrepancy resulted from the fact that we intended to design the Experiment 1 in a way that would be very similar to the study of Voss & Federmeier (2011), in which valence judgments preceded memory responses. On the other hand, the design of Experiment 2 was meant to reflect the study of Bridger et al. (2012), in which valence judgments at test were not applied. Nevertheless, this inconsistency makes it difficult to compare the topographic contrasts across our experiments. However, it seems that the delay in requiring memory responses in Experiment 1 have for the most part influenced the neural activity related to priming rather than to memory judgments. In that study, the priming and recognition test were crossed. Each prime was followed by the valence judgment and the memory response, and only then the target word was presented. The results demonstrated that the priming effect was right-lateralized, which might indicate the activation of broader word meanings that resulted from the delayed priming. This interpretation fits well into theoretical framework of the differences between the hemispheres in language processing (Beeman et al., 1994), and is consistent with the existing results of the N400 that is right lateralized when indirectly related word pairs were used in priming (Kiefer et al., 1998). It is more difficult to assess in which way the valence judgments have influenced memory related neural activity. In fact, valence ratings are used to support semantic processing, so it is possible that judging the emotional valence might have promoted semantic priming and diminished familiarity-based frontal old/new effect. Voss & Federmeier (2011) also used valence judgments before each memory judgment in a continuous recognition task and they have not found frontally distributed old/new effect. On the other hand, Bridger et al. (2012) did not use valence judgments during test and they have found the familiarity related FN400 potential. Thus, applying valence judgments before memory judgments seems to be an important procedural factor that might influence the processing of the stimuli and the resulting topography of the old/new effects. This was exactly the reason why we resigned from emotional valence ratings in Experiment 2. Nonetheless, future studies might directly test whether valence judgments influence the memory old/new effects under identical experimental procedures.

Aforementioned between-experiment differences raise the question of whether confounding priming with recognition (or separating them) was a main factor that has influenced the dissociation of the FN400 and N400 potentials. Rather, it could be the degree to which familiarity was elicited[2]. Some other differences in the design of these experiments also speak for this claim. In Experiment 1 each word list during test consisted of 160 words, whereas in Experiment 2 we utilized word lists consisted of 80 items. Different list lengths resulted from two causes. Firstly, priming in Experiment 1 was embedded within a recognition test so each target word in this test (old or new) required the presence of preceding prime. Secondly, we used shorter word lists in Experiment 2 in order to resemble the procedure of Bridger et al. (2012), where only 110 words were presented in the recognition phase. Moreover, each experiment required different memory responses. In Experiment 1 subjects selected one from four possible responses (“remember old”, “know old”, “guess old”, “new”). In Experiment 2 subjects were given six possible options (“sure old”, “probably old”, “guess old”, “sure new”, “probably new”, “guess new”). The change of pattern of responses was applied in order to include the same number of old and new responses. Three possible “old” responses and only one “new” response in Experiment 1 resulted in liberal response bias, i. e. relatively large proportion of new words incorrectly endorsed as “old”. It is also possible that longer word lists and unequal proportion of possible old and new responses during test (as well as the delay in memory judgments mentioned in the paragraph above) contributed to a greater reliance on recollection than familiarity in Experiment 1. The relatively small degree to which familiarity was elicited in this experiment may have resulted in no dissociable FN400 potential. However, this does not have to exactly be the case as recollection and familiarity are not exclusive and evidence for strong recollection does not mean that familiarity is lacking.

The pattern of memory responses in both experiments was similar and showed high proportions of recollection-based judgments (“remember old” in Experiment 1 and “sure old” in Experiment 2) as compared to familiarity-based or guess responses. It might indicate that the absence of familiarity was evident in both experiments, at least when self-reported data are taken into consideration. Thus, we argue that the dissociation of the topographic distribution of the FN400 and N400 potentials between experiments is due to the modifications we applied in the design of Experiment 2 that were intended to separate familiarity from semantic priming more thoroughly. Nevertheless, we acknowledge the limitations imposed by other procedural inconsistencies between these experiments and we believe that they might be clarified in future studies.

Turning back to the results of Experiment 2, they do not show that the largest ERP difference between new and unrelated old words was found in the left frontal cluster. Rather, this difference was mostly distributed in the midline central cluster, but also was found in the left frontal cluster. This is a somewhat different pattern of results than those obtained by Bridger et al. (2012), who found the old/new effect mostly pronounced at fronto-central sites. Moreover, we have observed the old/new effect in the left hemisphere and in midline areas, whereas Bridger et al. found it primarily over midline areas and the right hemisphere. Some detailed differences in procedures used in our experiments and in the study of Bridger et al. might help to better understand this discrepancy. First of all, Bridger et al. used only

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[2] Again, we thank an anonymous reviewer for suggesting this alternative explanation.

unprimed old words at the recognition test, while we used words that were primed and unprimed during encoding. Moreover, Bridger et al. used two distractor tasks after study/priming phase that required 20–25 minutes to complete, while we only used very short, 2–3 minutes breaks between study/priming and recognition phases and did not use any distractor tasks. Generally, procedures used by Bridger et al. were even more effective in separating the processes of familiarity and semantic priming. In our experiment, the presence of old related words in the recognition test and lack of a break between study and test might have still caused some of the ERP indices of priming present during recognition testing, therefore making it difficult to obtain a midfrontal maximum for old/new contrast.

There is also a question of whether the left-lateralized FN400 found in Experiment 2 is simply an effect of conceptual priming or whether it has some familiarity-based mnemonic characteristics. However, these two possibilities are not mutually exclusive. The standard mid-frontal old/new effect found in 300–500 ms time window is considered to reflect the outcome of a series of different subprocesses, like assessing stimulus novelty, recency, and familiarity (Ecker & Zimmer, 2009). Familiarity itself is sensitive to both conceptual and perceptual features of objects (Ecker, Zimmer, & Groh-Bordin, 2007; Groh-Bordin, Zimmer, & Ecker, 2006; Schloerscheidt & Rugg, 2004). The left-lateralized FN400 might indicate an activation of a specific subcomponent of familiarity that is triggered by particular experimental procedures or task demands. In fact, Ecker & Zimmer (2009) found a slightly left lateralized 350–500 ms old/new effect in the condition in which subjects were instructed to rely on conceptual relations and had to accept perceptually different exemplars of categories as old. According to Ecker & Zimmer (2009), this outcome could point to a link between conceptual familiarity subprocess and left lateralization. Moreover, neuroimaging studies suggest that conceptual priming is linked to left-frontal brain regions (Buckner, Koutstaal, Schacter, & Rosen, 2000; Meister, Buelte, Sparing, & Boroojerdi, 2007). Thus, the left-lateralized FN400 that we have found in Experiment 2 might have also been the result of conceptual processing, triggered probably by the presence of related test items during recognition. However, this conceptual subprocess can still be the part of familiarity-related memory signal.

In conclusion, we believe that our study is the first direct comparison between an experiment in which priming and recognition are confounded (like Voss & Federmeier, 2011) and an experiment where the two processes are separated (like Bridger et al., 2012). The outcome of our study provides evidence that only the latter condition reveal topographic differences between the N400 and FN400 potentials. This indicates that the electrophysiological indices of familiarity and priming can be topographically distinct when experimental procedures clearly separate these two processes. Further research is needed to determine the exact level of uniformity of these two ERP components.

4. Experimental Procedures

4.1. Experiment 1

4.1.1. Participants—Behavioral and electrophysiological data are reported for 24 right-handed, native speakers of English (12 females, 12 males). The mean age of participants was *M*=21.46 years (*SD*=2.90; Range=18–29 years). All subjects had normal or corrected-to-normal vision and had no known neurological problems. Data from six additional subjects was discarded from analyses because of failure to control eye blinking. All procedures were approved by University of Colorado Institutional Review Board. Subjects were paid $15 per hour or received course credit for their participation.

4.1.2. Stimuli—Verbal stimuli in the experiment included 960 common English words (3–13 letters in length). These words were divided into 320 triplets. Each of the triplets was comprised of a semantically related target-cue pair (e.g., *doctor-nurse*), with forwards (*M*=0.27, *SD*=0.17, Range=.08–.89) and backwards (*M*=0.25, *SD*=0.20, Range=.08–.89) association ratings (Nelson, McEvoy, & Schreiber, 1998). Frequency ratings were ranging from 1 to 808 (*M*=59.57, *SD*=104.55), and concreteness ratings from 4 to 7 (*M*=5.45, *SD*=0.79; on a scale in which 1 is most abstract and 7 is most concrete). The third word in the triplet was a completely unrelated word from the first two, having the same number of letters as the cue word, as well as frequency (*M*=48.44, *SD*=111.48, Range=1–1207) and concreteness ratings (*M*=5.50, *SD*=0.79, Range=4–7) that were similar to the cue. An additional 16 words served as buffers, two preceding and two following each of the four study portions of the experiment. Stimuli were counterbalanced across subjects such that target words appeared equally often as studied or non-studied words, as well as being equally often preceded by related or unrelated primes.

4.1.3. Behavioral Procedures—The experiment was split into four blocks, each consisting of a study and test phase. During each study phase 40 words were presented on the screen one at a time for 2000 ms. Subjects were instructed to make a judgment for each word regarding its emotional valence, pressing one of four buttons to indicate that the word was “very pleasant”, “pleasant”, “unpleasant” or “very unpleasant”, as a means to help the subject encode the word more efficiently. Each word was followed by a fixation cross that lasted 500–1000 ms, during which time the subject gave their response to the prior word. Voss and Federmeier (2011) and Bridger et al. (2012) also instructed their subjects to make judgments about emotional valence of encoded words in order to support semantic processing.

Each study phase was followed by a test phase during which the subject’s memory was tested using words that were studied in the study portion (old words) versus words that were not (new words). During each test phase 160 words (80 word pairs) were presented. The test phase included target words, which were either repeated from the study phase or seen for the first time in the test phase. The target words were preceded by either semantically related or unrelated primes, all of which were not presented in the study phase. The subjects were instructed to make two judgments for each word, both targets and primes. First they rated the emotional valence of the word, this time by choosing between a “+” or “−” judgment, similar to their task in the study phase, yet with only two options in this portion. This was done so that all words would be processed similarly to the study phase (note that Voss and Federmeier also used valence ratings at each trial but they employed a continuous recognition task rather than separate study and test blocks; on the other hand, Bridger et al. used separate study and test phases but they did not use emotional valence ratings during test). Each word was presented on the screen one at a time for 500 ms, followed by a fixation cross that lasted 2000 ms, during which subjects made their emotional valence ratings. After that, the letter “R”, a recognition prompt, would then be flashed in the middle of the screen for 2500 ms, indicating that the subject should make a memory judgment for the given word. The next trial followed with a 500–1000 ms fixation cross. The interstimulus interval (ISI) between primes and targets was 5000–5500 ms. Subjects pressed one of four buttons indicating “remember old”, “know old”, “guess old”, or “new” judgments. Each subject was told to indicate “remember old” if they could consciously remember specific details of the appearance of a word or of their experience learning the word during the study list. Alternatively, they were told to indicate “know old” if they knew that the word was studied but lacked the recollection of specific details about studying the word. If they wanted to indicate that a word was old, but were not sure of this decision they were to respond with “guess old”, and if they did not recognize the word from the study list, they indicated that it had not been repeated and was therefore “new”. “Remember old”, “know old” and “guess old” were correct for the presentation of a target word that had appeared in the study list, and the “new” response was correct for all other stimuli.

Each of the study-test portions were comprised of their own set of stimulus words, and there were no words from previous study lists on later test phases. To familiarize the subject with the procedures of the experiment, each individual completed a practice portion before the start of the actual experiment. The practice portion comprised of 20 words that were not utilized later. The key assignments during the test phase were counterbalanced across all subjects. Electrode impedances were checked before the start of each test phase, lasting at least 5 minutes each time.

4.1.4. ERP Procedures—During the recognition memory task, scalp voltages were collected with a 128-channel HydroCel Geodesic Sensor Net (Tucker, 1993) connected to an AC-coupled, 128-channel, high-input impedance amplifier (200 MΩ, Net Amps, Electrical Geodesics, Eugene, OR). Amplified analog voltages (0.1- to 100.0-Hz band-pass) were digitized at 250 Hz. Individual sensors were adjusted until impedances were less than 50 kΩ. The EEG was digitally low-pass filtered at 40 Hz. Trials were discarded from analyses if they contained incorrect responses, eye movements (eye channel amplitudes over 70 μV), or more than 20% of the channels were bad (average amplitude over 100 μV or transit amplitude over 50 μV). Individual bad channels were replaced on a trial-by-trial basis with a spherical spline algorithm (Srinivasan et al., 1996). EEG was measured with respect to a vertex reference (Cz), but an average-reference transformation was used to minimize the effects of reference-site activity and accurately estimate the scalp topography of the measured electrical fields (Dien, 1998; Picton, Lins, & Scherg, 1995). The average reference was corrected for the polar average reference effect (Junghofer, Elbert, Tucker, & Braun, 1999). ERPs were obtained by stimulus-locked averaging of the EEG recorded in each condition. ERPs were baseline-corrected with respect to a 200-ms pre-stimulus recording interval. Only trials associated with correct recognition judgments were included in the initial ERP analyses. The number of trials per subject per condition used to calculate ERPs are as follows: primed new (*M*=37.53, *SD*=17.34, Range=19–73), primed old (*M*=68.53, *SD*=6.64, Range=55–76), unprimed new (*M*=48.0, *SD*=14.49, Range=27–75), and unprimed old (*M*=68.0, *SD*=7.84, Range=51–77).

4.2. Experiment 2

4.2.1. Participants—Behavioral and electrophysiological data are reported for 29 right-handed, native speakers of English (12 females, 17 males). The mean age of participants was *M*=20.86 years (*SD*=2.18; Range = 18–25 years). All subjects had normal or corrected-to-normal vision and had no known neurological problems. Data from two additional subjects were discarded from analyses because of failure to control eye blinking. All procedures were approved by University of Colorado Institutional Review Board. Subjects were paid $15 per hour or received course credit for their participation. None of the participants in Experiment 2 participated in Experiment 1.

4.2.2. Stimuli—The same set of stimuli as in Experiment 1 was used.

4.2.3. Behavioral Procedures—The Experiment 2 was split into four blocks, each consisting of a study and test phase. At the study phase 80 words (40 word pairs) were presented. Each word was preceded by either a related or an unrelated semantic prime. Subjects were instructed to make an emotional judgment for each word with one of four options (“very pleasant”, “pleasant”, “unpleasant”, “very unpleasant”), the same as in Experiment 1. All words were presented for 2000 ms and followed by a fixation cross that lasted 500–1000 ms.

A recognition test was administered after each study phase. During each test phase 80 words were presented one at a time for 2000 ms. Half of these words were new (not presented during study), and the other half was old. Half of the old words was primed during study (related old words), and the other half was not primed during study (unrelated old words). After each word a recognition prompt was presented and subjects were asked to make memory judgments by pressing one of six buttons indicating “sure old”, “probably old”, “guess old”, “sure new”, “probably new”, “guess new”. The next trial followed with a 500–1000 ms fixation cross. The different pattern of responses than in Experiment 1 was applied in order to include the same number of new and old responses as an attempt to reduce the liberal response bias observed in Experiment 1. Also, positive/negative judgments were removed from the test phase and subjects were asked only for memory responses. This was done in order to avoid any resemblance between encoding and recognition and separate familiarity from semantic priming more thoroughly.

Similar to Experiment 1, each of the study-test phases were comprised of their own set of stimulus words. Each subject completed a practice session prior to the main experiment. The key assignments during the test phase were counterbalanced across all subjects. Electrode impedances were checked at the start of each test phase, lasting at least 5 minutes each time.

4.2.4. ERP Procedures—The same recording and data processing procedures as in Experiment 1 were used. The numbers of trials per subject per condition used to calculate ERPs were as follows: primed (*M*=72.34, *SD*=6.17, Range=58–80), unprimed (*M*=72.21, *SD*=6.29, Range=51–80), old related (*M*=68.34, *SD*=8.76, Range=49–78), old unrelated (*M*=68.90, *SD*=7.73, Range=54–79), and new (*M*=119.97, *SD*=24.73, Range=77–155).

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Appendix

Figures A1, A2, and A3 show mastoid-referenced grand-averaged ERPs elicited by primed new, primed old, unprimed new, and unprimed old words in Experiment 1 (Figure A1); by primed and unprimed words in the study phase of Experiment 2 (Figure A2); and by old related, old unrelated, and new words in the test phase of Experiment 2 (Figure A3).

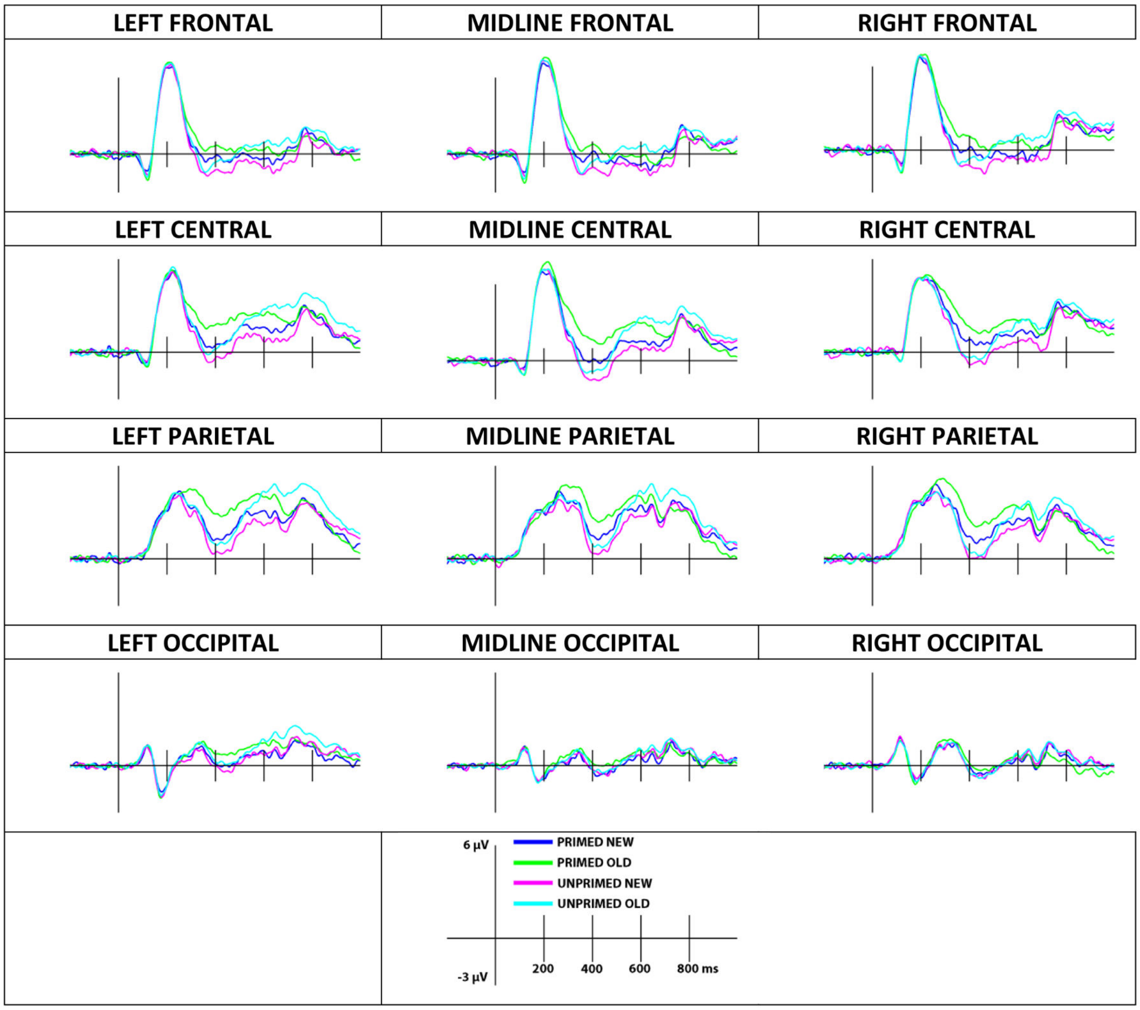

Figure A1.

Mastoid-referenced grand-averaged ERPs elicited by primed new, primed old, unprimed new, and unprimed old words in Experiment 1.

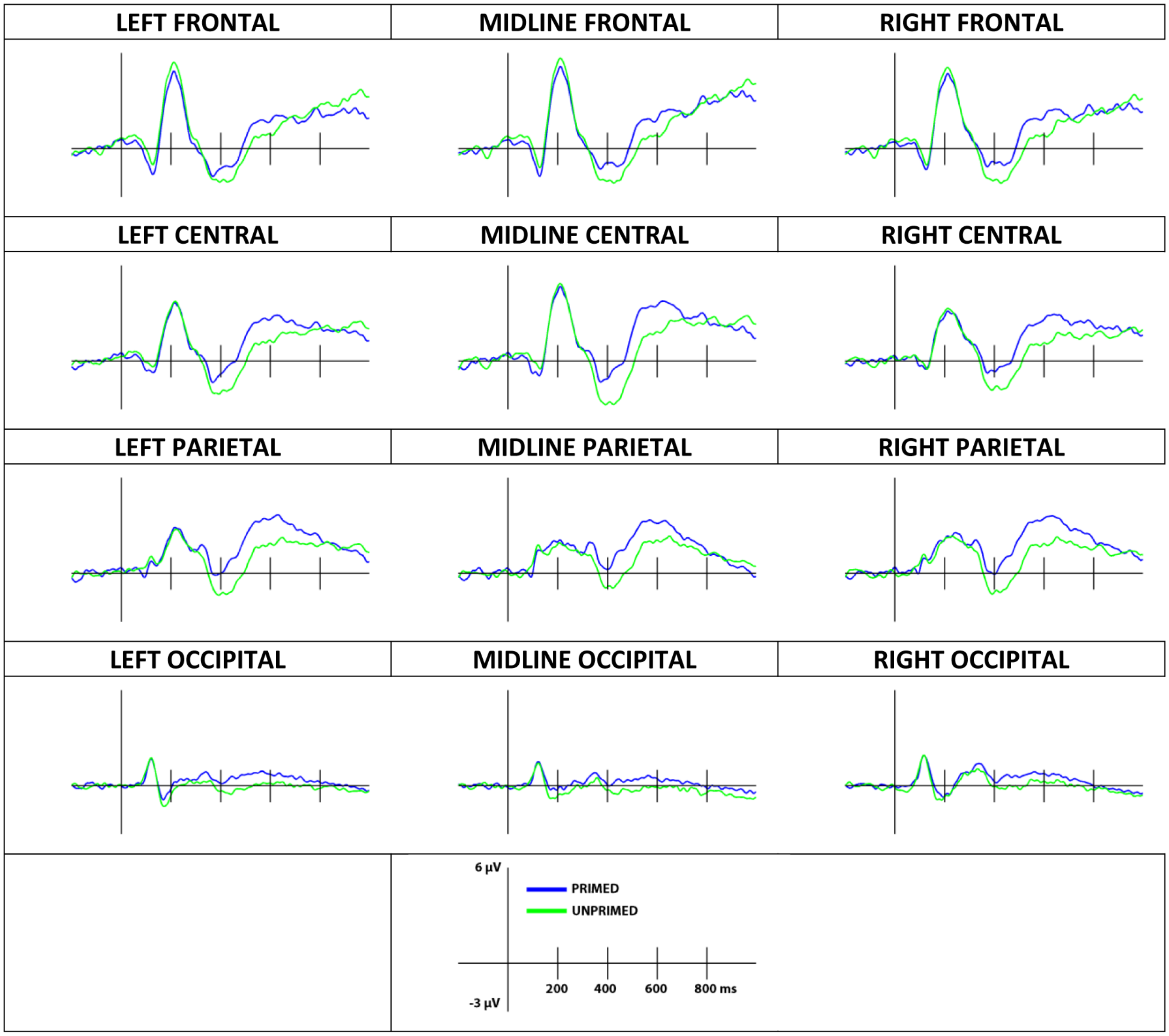

Figure A2.
Mastoid-referenced grand-averaged ERPs elicited by primed and unprimed words in the study phase of Experiment 2.

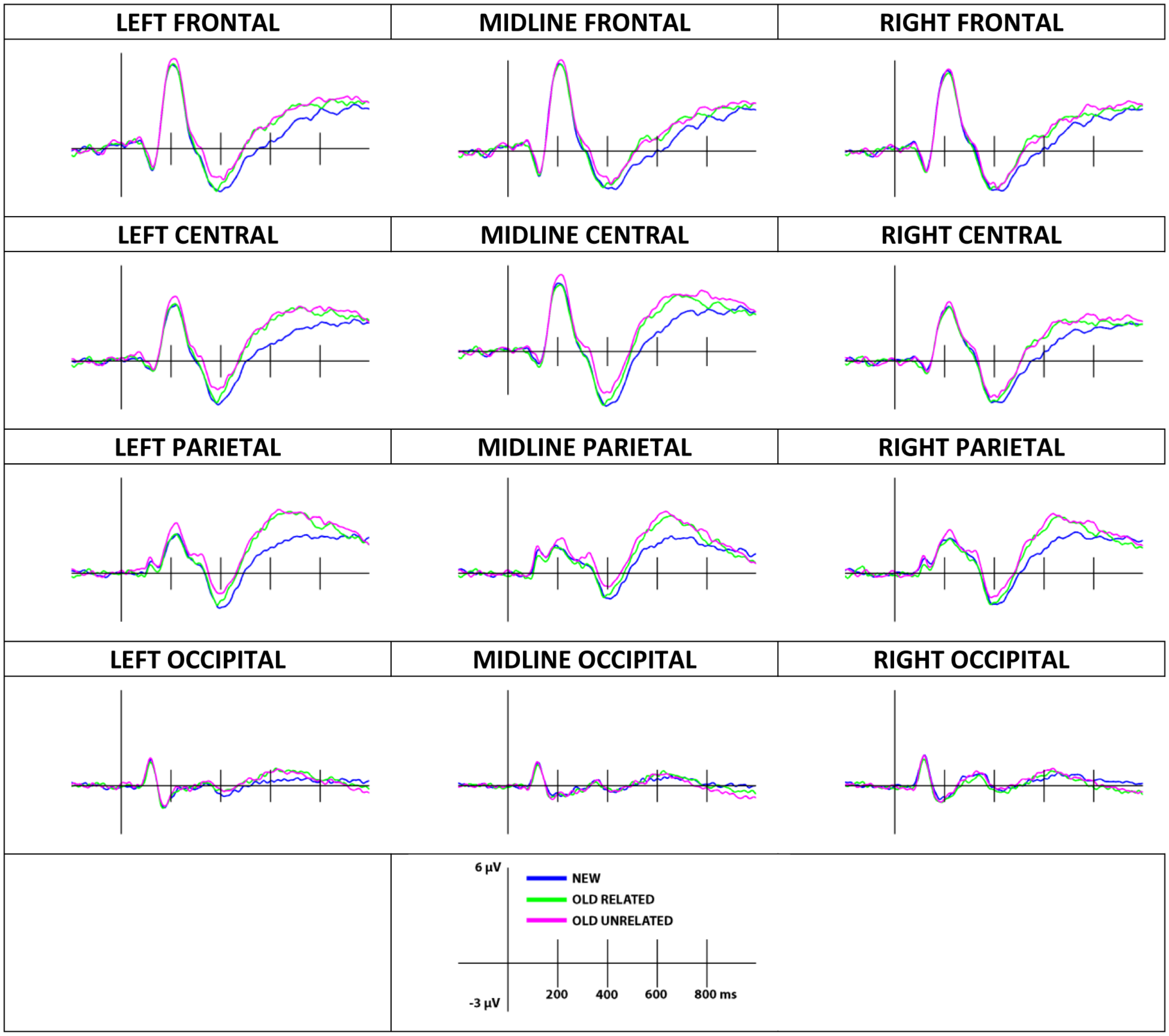

Figure A3.

Mastoid-referenced grand-averaged ERPs elicited by old related, old unrelated, and new words in the test phase of Experiment 2.

Highlights

- We evaluated whether the FN400 and N400 event-related potentials are identical
- In Experiment 1 priming was embedded within a recognition test
- In Experiment 2 priming and recognition test were separated
- The FN400 and N400 potentials showed distinct topographical distribution only in Experiment 2
- Our results suggest that the FN400 and N400 potentials might reflect functionally distinct processes when priming and recognition are not confounded

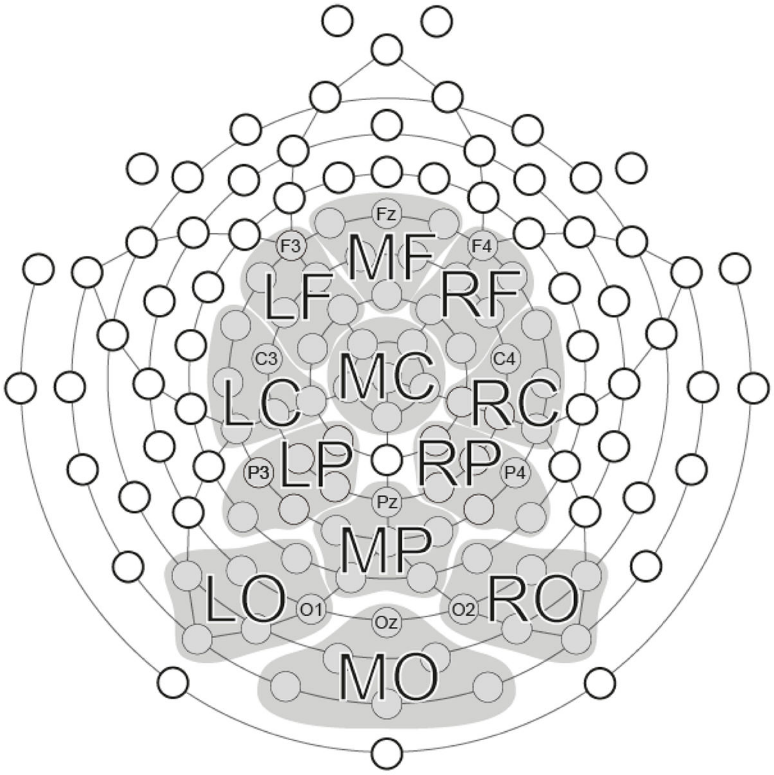

Figure 1.

Sensor locations on the 128-channel HydroCel Geodesic Sensor Net. Twelve electrode clusters included in ANOVAs are denoted: LF (left frontal), MF (midline frontal), RF (right frontal), LC (left central), MC (midline central), RC (right central), LP (left parietal), MP (midline parietal), RP (right parietal), LO (left occipital), MO (midline occipital), and RO (right occipital).

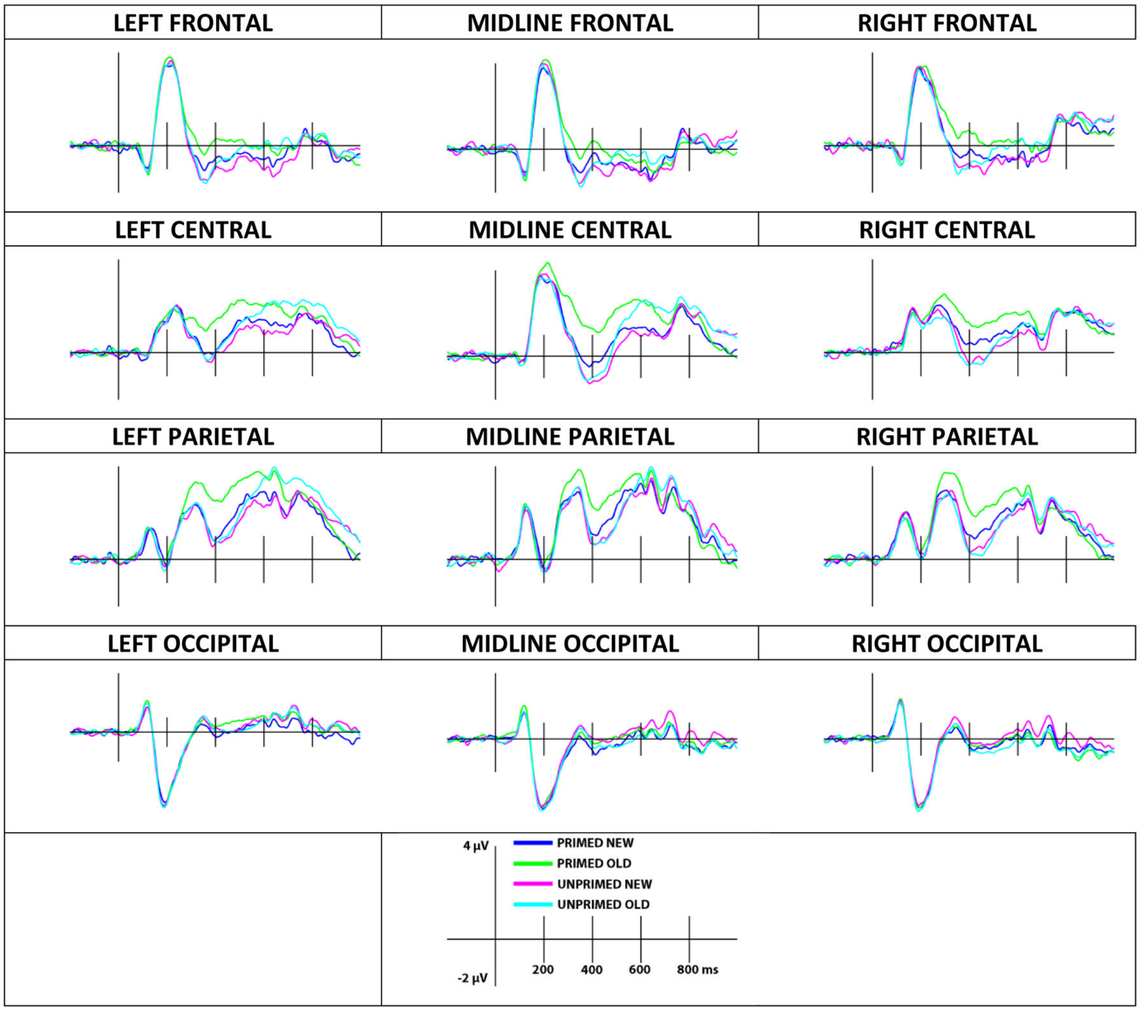

Figure 2.

Grand-averaged ERPs elicited by primed new, primed old, unprimed new, and unprimed old words in Experiment 1.

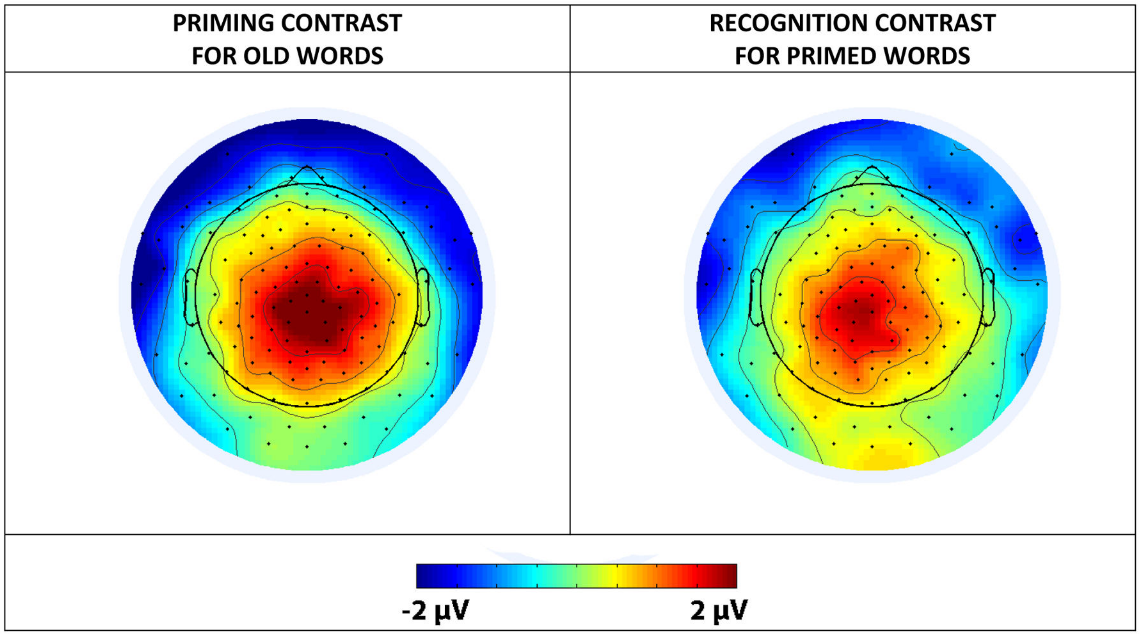

Figure 3.

Topographic maps for the priming contrast for old words (ERPs to unprimed old words subtracted from ERPs to primed old words), and the recognition contrast for primed words (ERPs to correct rejection of new primed words subtracted from ERPs to true recognition of old primed words) in the 300–500 ms time window in Experiment 1. Area outside the cartoon head represents the signal from channel locations below head center.

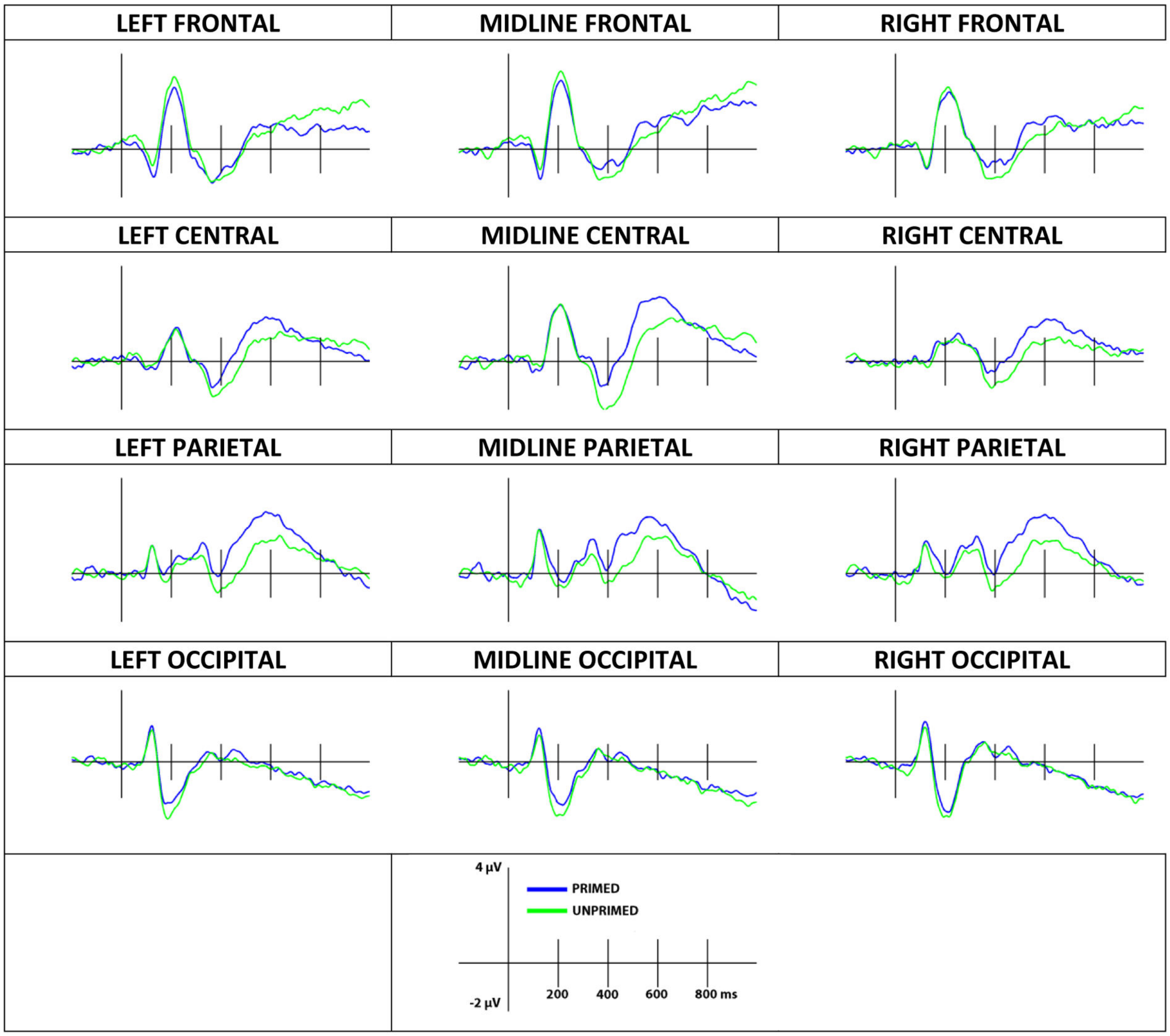

Figure 4.

Grand-averaged ERPs elicited by primed and unprimed words in the study phase of Experiment 2.

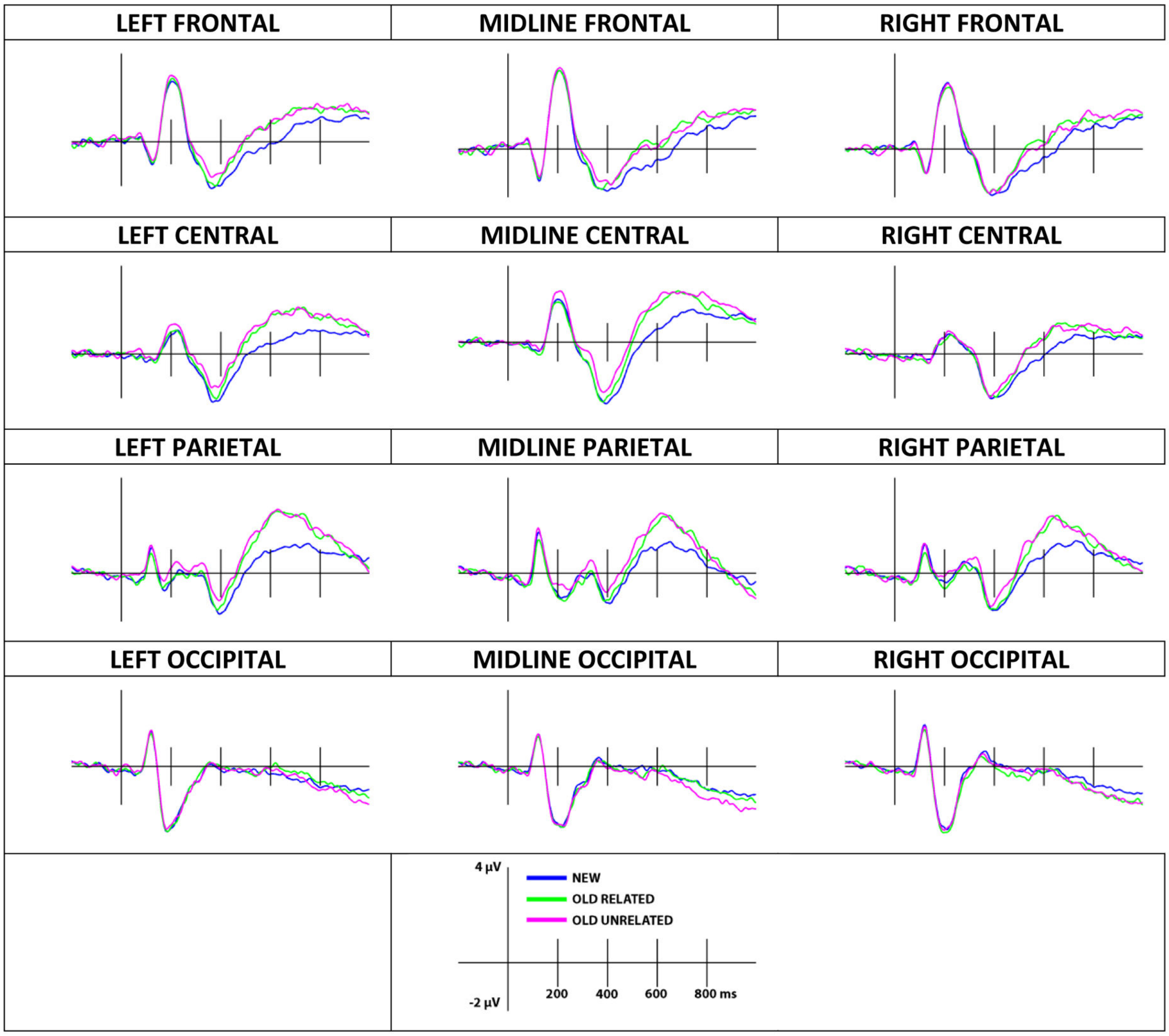

Figure 5.

Grand-averaged ERPs elicited by old related, old unrelated, and new words in the test phase of Experiment 2.

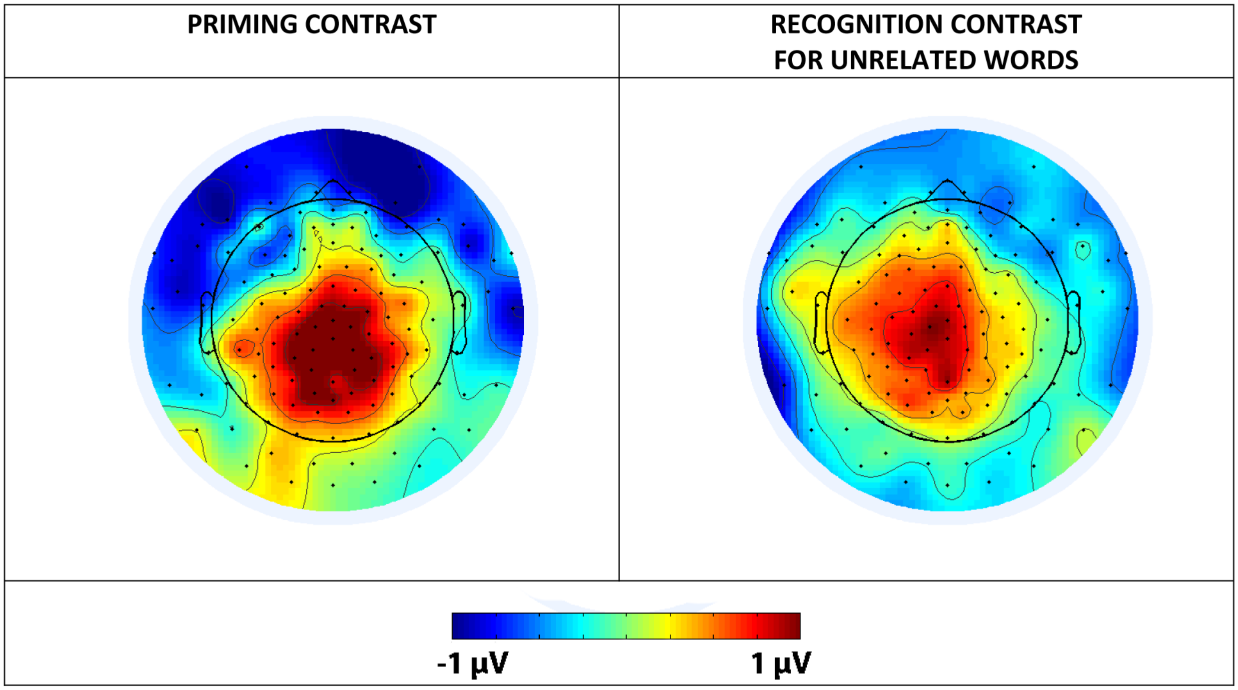

Figure 6.

Topographic maps for the priming contrast (ERPs to unprimed words subtracted from ERPs to primed words), and the recognition contrast for unrelated words (ERPs to correct rejection of new words subtracted from ERPs to true recognition of unrelated old words) in the 300–500 ms time window in Experiment 2. Area outside the cartoon head represents the signal from channel locations below head center.

Table 1

Mean proportions and standard errors of the means for recognition judgments in Experiment 1 for primed and unprimed words (overall and for different confidence levels for correct recognition of old words)

	Correct recognition of old words			
	Primed		**Unprimed**	
	M	***SEM***	***M***	***SEM***
Overall	.93	.01	.93	.01
Remember	.69	.06	.69	.05
Know	.21	.04	.20	.04
Guess	.10	.04	.11	.04
	Correct rejection of new words			
Overall	.55	.04	.66	.04

Table 2

Mean reaction times and standard errors of the means for valence and memory judgments to targets in Experiment 1

	Valence judgments			
	Correct recognition of old words		**Correct rejection of new words**	
	M	***SEM***	***M***	***SEM***
Primed	1167.29	42.22	1326.47	38.9
Unprimed	1244.68	37.08	1299.19	39.96
	Memory judgments			
Primed	3010.55	19.03	3082.58	26.58
Unprimed	3008.14	18.67	3060.76	27.32

Table 3

Mean proportions and standard errors of the means for recognition judgments in Experiment 2 (overall and for different confidence levels)

	Correct recognition of old unrelated words		**Correct recognition of old related words**		**Correct rejection of new words**	
	M	***SEM***	***M***	***SEM***	***M***	***SEM***
Overall	.95	.01	.96	.01	.83	.02
Sure	.85	.14	.86	.13	.40	.20
Probably	.11	.11	.11	.12	.39	.13
Guess	.04	.04	.03	.03	.21	.10

Table 4

Mean reaction times and standard errors of the means for recognition judgments in Experiment 2

Correct recognition of old unrelated words		**Correct recognition of old related words**		**Correct rejection of new words**	
M	***SEM***	***M***	***SEM***	***M***	***SEM***
571.07	33.93	570.92	36.08	779.83	49.64