Published in final edited form as:
Brain Res. 2008 October 3; 1233: 146–159. doi:10.1016/j.brainres.2008.07.043.

Summing it up: Semantic activation processes in the two hemispheres as revealed by event-related potentials

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Abstract

The coarse coding hypothesis suggests that semantic activation is broader in the right hemisphere, affording it an advantage over the left hemisphere for the activation of distantly related concepts or multiple meanings of lexically ambiguous words. Behavioral studies investigating coarse coding have yielded mixed results, perhaps in part because such measures sum across multiple processing stages. To more directly tap into the semantic activation processes that are the focus of the coarse coding hypothesis, the current study combined a visual half-field summation-priming paradigm with the measurement of event-related potentials (ERPs). Two primes converged onto a lateralized, unambiguous target (e.g., *lion–stripes–tiger*) or diverged onto different meanings of a lateralized, ambiguous target (e.g., *kidney–piano–organ*); in both cases, the primes were related to one another only through the target. In two experiments, participants either made lexical decisions to the targets or made a semantic-relatedness judgment between primes and target. Priming was measured as reductions in the amplitude of the N400, an ERP component that has been specifically linked to meaning activation and that showed semantic-level priming patterns in both of the tasks used in the present study. Counter to the predictions of the coarse coding hypothesis, equivalent N400 summation priming was observed for targets in the two visual fields, in both types of triplets and in both experiments. Thus, the current results fail to support the hypothesis that semantic activation patterns differ in the two hemispheres and point, instead, to other sources for observed asymmetries in verbal processing.

Keywords

Cerebral hemispheres; Event-related potentials (ERPs); N400; Lexical ambiguity; Semantic priming; Summation priming

1. Introduction

Given increasing evidence that not only the left cerebral hemisphere (LH) but also the right (RH) contributes to language comprehension (e.g., Beeman and Chiarello, 1998), a number of frameworks have been put forward to explain the nature of the differences between each hemisphere's processing of language input. Perhaps the most prominent of these is the *coarse*

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coding hypothesis (Jung-Beeman, 2005), which posits that hemispheric asymmetries in language processing might arise from differences in the breadth of semantic activation. According to this view, when a word is encountered in context, the LH strongly activates a restricted set of contextually delineated concepts, whereas the RH weakly activates a broad set of concepts, including those that may be more loosely linked to the context. It has been suggested that although coarse coding in the RH renders it less effective than the LH for the kind of rapid meaning selection and interpretation that characterizes many aspects of everyday language, the activation of more distantly linked information can confer an advantage for dealing with the multiple, sometimes incompatible interpretations that may arise during the processing of jokes and other types of figurative language (e.g., Coulson and Williams, 2005). Coarse coding has also been linked to a critical role for the RH in inference processing (Beeman, Bowden and Gernsbacher, 2000) and creative problem solving (Bowden and Jung-Beeman, 2003; Jung-Beeman, 2005).

Evidence supporting this framework has come from studies of semantic priming (facilitation for a target word when preceded by an associated and/or semantically related prime word; e.g., Neely, 1991) that have used the visual half-field (VF) technique. In this technique, stimuli are presented in the visual periphery, such that they are apprehended and initially processed by the contralateral cerebral hemisphere (i.e., stimuli presented in the right visual field (RVF) are initially apprehended by the LH and stimuli presented in the left visual field (LVF) are initially apprehended by the RH). Despite the potential for information transfer between the two hemispheres via the corpus callosum, the hemisphere that receives the stimulus directly has a processing advantage in terms of information quality and time. This technique has been extensively employed in brain-intact individuals to uncover hemispheric asymmetries in semantic priming. For instance, several studies have suggested thatwhereas strongly related primes (e.g., those that both share semantic features with and are lexically associated to the targets; *sofa–chair*) facilitate processing in both hemispheres, weakly related primes (e.g., those that are unassociated with the targets but do share some feature overlap; *lamp–chair*) facilitate processing only in the RH (Chiarello, Burgess, Richards and Pollock, 1990; Chiarello andRichards, 1992). Results like these point to a role for the RH in appreciating more distant semantic relationships between words. Additional evidence in support of coarse coding has come from a study of summation priming (Beeman et al., 1994), inwhich participants were presented with a series of three primes that were either weakly related (*white–ceremony–tuxedo*) or unrelated (*soap–tunnel–mouse*) to a lateralized target (*wedding*). Naming accuracy for the targets preceded by weak associates was facilitated only with LVF/RH presentations, again suggesting a RH benefit for integrating across multiple, weakly related concepts.

Support for coarse coding has also been seen in studies looking at the processing of lexically ambiguous words. For example, Burgess and Simpson (1988) investigated when and how the two hemispheres activate the dominant (more frequent) and subordinate (less frequent) meaning of an ambiguous prime. The LH activated all meanings of the ambiguous prime at a shorter SOA (35 ms), but by a longer SOA (750 ms) only the dominant meaning remained active. However, activation of both meanings was seen in the RH even at the longer SOA, suggesting that the RH maintains a broader range of meanings, including those that may have been eliminated by the more selective LH. Another study used the summation-priming paradigm to further investigate if there are RH benefits for activating multiple, incompatible meanings of an ambiguous word (Faust and Lavidor, 2003). In two experiments (using lexical decision and semantic judgment tasks), a lateralized target followed two primes, which either converged onto the dominant (e.g., *maybe–perhaps–might*) or the subordinate meaning (*strength–power–might*) of an ambiguous target or diverged onto two different meanings of the ambiguous target (*maybe–strength–might*). The results showed that whereas the LH benefited most in the convergent condition, the RH benefited most in the divergent condition, again alluding to a RH benefit for integrating across multiple, distinct meanings.

However, other studies manipulating semantic distance in terms of the number of intervening items in semantic memory between a prime and target have not always yielded results consistent with the idea that facilitation spreads further in the RH than in the LH. For instance, Richards and Chiarello (1995) examined naming latencies for word pairs that were associated either directly (e.g., *water–drink*) or indirectly (e.g., *soap–drink*, which are related through the mediating concept *water*). The coarse coding hypothesis should predict a RH advantage for processing the more semantically distant mediated pairs. Instead, although overall priming was greater for direct than for mediated associates, this pattern was equivalent in the two visual fields across a range of stimulus onset asynchronies (50, 250, and 750 ms). In particular, there was no indication that processing of the mediated pairs was facilitated with presentation to the LVF/RH. Livesay and Burgess (2003) obtained a similar pattern of results for mediated prime–target pairs that were likely to be experienced in the same context (e.g., *bat* and *bounce*, mediated by a common context, *ball*) and for those that were not (e.g., *summer* and *snow*, mediated by *winter*). Equivalent amounts of mediated priming (relative to an unrelated baseline) were seen in the two VFs for both types of pairs, leading the authors to suggest that lexical representations in the two hemispheres might be similar.

In a prior study (Kandhadai and Federmeier, 2007),we set out to examine the basis for the discrepancy between studies that have found results consistent (Beeman et al., 1994; Faust and Lavidor, 2003) and inconsistent (Richards and Chiarello, 1995; Livesay and Burgess, 2003) with the hypothesis of coarse coding in the RH. We employed a summation-priming paradigm using both lexically ambiguous and unambiguous targets. Participants viewed triplets of words, including two sequentially presented central primes that were each either related or unrelated to the following lateralized target. When both primes were related to the target (the “double prime” condition), they either diverged onto multiple, different meanings of an ambiguous target (e.g., *kidney–piano–organ*; similar to the divergent condition in Faust and Lavidor, 2003) or converged onto the single meaning of an unambiguous target (e.g., *lion–stripes–tiger*). In both triplet types, the two primes were never directly related to each other, such that the relationship between the primes was similar to the mediated priming conditions used in prior studies (e.g., Richards and Chiarello, 1995). The coarse coding hypothesis would predict a RH benefit (relative to the LH) for integrating across multiple, distantly related primes, perhaps especially in the divergent (ambiguous) condition.

We used two different tasks in our study to allow us to further examine the locus of any priming effects we might observe. Our stimuli were based on those previously used by Balota and Paul (1996) to examine whether priming arises at lexical (word form) or semantic (word meaning) levels of processing. At the level of word form, both unambiguous (*tiger*) and ambiguous (*organ*) targets are assumed to have a single representation. However, at the level of meaning, there is just one representation for an unambiguous target, but there are multiple representations for ambiguous targets, associated with the different meaning senses of these words (e.g., corresponding to the *body part* and *musical instrument* senses of *organ*). Based on this model, Balota and Paul (1996) hypothesized that lexical-level facilitation would manifest similarly for unambiguous and ambiguous triplets, whereas semantic-level facilitation would manifest differently—and, in particular, likely be reduced for ambiguous as compared with unambiguous triplets in the double prime condition. In a series of experiments recording response times to centrally presented targets, Balota and Paul (1996) found that patterns of activation were highly task dependent: whereas naming and lexical decision tasks seemed to index lexical-level priming, a semantic-relatedness judgment task indexed priming at the semantic level. Building on these results, our prior study (Kandhadai and Federmeier, 2007) employed both a speeded lexical decision on the lateralized target (Experiment 1) and a speeded semantic-relatedness judgment between the primes and the lateralized target (Experiment 2) in order to examine priming arising at different levels of processing.

In both tasks and in both visual fields, priming effects were graded by the number of related words, with the fastest responses to the double prime condition, responses of intermediate speed to the “single prime” conditions (only one prime related to the target), and the slowest responses to the condition in which both primes were unrelated to the target. Replicating the pattern seen with central presentation (Balota and Paul, 1996), priming patterns were also modulated by the nature of the task. Both the LH and the RH exhibited lexical patterns of activation in the lexical decision task and semantic patterns of activation in the semantic judgment task. Critically, however, there were no significant hemispheric differences in the patterns of summation priming for either ambiguous or unambiguous targets in either task. Thus, the results failed to support the prediction, derived from the coarse coding hypothesis, that the RH would have an easier time than the LH integrating multiple, distantly related words, and this was true whether the task tapped more heavily into lexical or into semantic levels of processing.

The task-related variance in priming patterns, however, raises an important point about the behavioral evidence that has been taken as support for (e.g., Beeman et al., 1994; Faust and Lavidor, 2003) or against (e.g., Richards and Chiarello, 1995; Livesay and Burgess, 2003; Kandhadai and Federmeier, 2007) coarse coding. Behavioral responses necessarily sum across multiple processing stages, including decision-related processes that, as Balota and Paul’s work (1996) and our prior study (Kandhadai and Federmeier, 2007) show, vary in their sensitivity to these processing stages as a function of task (for both hemispheres). The coarse coding hypothesis places the locus of hemispheric differences specifically at the stage of semantic activation. However, many studies investigating coarse coding have used a lexical decision task, which Balota and Paul’s (1996) work suggests may reveal more about form-based than meaning-based processing. Indeed, our results (Kandhadai and Federmeier, 2007) implicated a lexical source of activation for the priming effects in the lexical decision task in both hemispheres. On the other hand, the overt semantic judgment tasks that have been used in other studies are likely to tap into explicit, controlled aspects of semantic processing (Neely, 1991), which could mask the more implicit semantic activation processes that are the real focus of the coarse coding hypothesis. A much stronger test of the coarse coding hypothesis, therefore, requires a measure that can tap directly into semantic activation in a more task-independent fashion. Luckily, such a measure is available in the event-related potential (ERP) signal, in the form of the N400 component.

The N400 is a negative-going potential that typically peaks approximately 400 ms after the onset of a meaningful or potentially meaningful stimulus and is distributed maximally over centro-posterior scalp sites (Kutas and Hillyard, 1980b). N400 amplitude is modulated by factors known to affect ease of semantic access and integration, including repetition, word frequency, and the presence of supportive context information (see, e.g., Kutas and Federmeier, 2000, for a review), including manipulations of semantic priming (Bentin et al., 1985). However, it is insensitive to most syntactic (Kutas and Hillyard, 1983) or perceptual (Kutas and Hillyard, 1980a) manipulations, making it a functionally specific index of semantic processing. In particular, because N400 effects can be observed under masked stimulus presentation conditions (Deacon et al., 2000; Misra and Holcomb, 2003; for an alternate view, see Brown and Hagoort, 1993), during the attentional blink (Rolke et al., 2001), during implicit recognition in amnesia (Olichney et al., 2000), and even during some stages of sleep (Bastuji et al., 2002), it has been argued to be sensitive to fairly automatic, implicit aspects of semantic access. The N400 is often followed by an extended, posterior positivity – the late positive complex or LPC – that has been linked to more explicit aspects of semantic retrieval, integration, and revision (e.g., Van Petten et al., 1991; Swaab et al., 1998).

The N400 thus provides a fairly direct window into semantic activation processes, which makes it very well-suited for addressing questions about coarse coding in the two cerebral hemispheres. However, this measure has not yet been used extensively to examine hemispheric differences in word-level priming, and the extant evidence is mixed. Priming for lexically associated word pairs has been consistently found in the LH (Atchley and Kwasny, 2003; Bouaffre and Faïta-Ainseba, 2007; Coulson, Federmeier, Van Petten and Kutas 2005; Deacon, Grose-Fifer, Yang, Stanick, Hewitt and Dynowska, 2004) and sometimes in the RH as well (Coulson et al., 2005). Priming for categorically related items has been found to be limited to the RH in some studies (Grose-Fifer and Deacon, 2004; Deacon et al., 2004), but present in the LH (and delayed in the RH) in others (Bouaffre and Faïta-Ainseba, 2007). Although some of these studies have been taken as support of coarse coding (Atchley and Kwasny, 2003; Bouaffre and Faïta-Ainseba, 2007), others have argued against it (Grose-Fifer and Deacon, 2004; Deacon et al., 2004), and the collective picture that emerges from these studies is at best inconclusive in terms of support for coarse coding in the RH.

Thus, to investigate the coarse coding hypothesis, the current set of experiments employed the summation-priming visual half-field paradigm used in our previous study (Kandhadai and Federmeier, 2007), in conjunction with event-related brain potentials. Participants viewed a series of two centrally presented primes each related or unrelated to a lateralized target word (but always unrelated to one another). When both primes were related to the target, they either diverged onto two different meanings of an ambiguous homograph or converged onto the single meaning of an unambiguous word (see Table 1 for examples). Because the coarse coding hypothesis suggests that the RH is better able to activate and maintain distantly related semantic information, it should predict a RH benefit – here, in the form of greater N400 amplitude reductions – for summating across the primes in the double prime conditions, and this benefit might be particularly notable for the ambiguous condition, which requires the simultaneous activation of two different meanings of the ambiguous target.

As in our behavioral study (Kandhadai and Federmeier, 2007), we used two different tasks, in this case with a delayed response to avoid contamination of the ERPs with motor-related brain activity: participants were required to make a lexical decision on the target (Experiment 1) or a semantic-relatedness judgment between the primes and the target (Experiment 2). This will allow us to further examine the nature of the task-related differences observed in the behavioral data. If the N400 is primarily sensitive to semantic levels of processing, then N400 facilitation would be expected to show the semantic pattern, with reduced facilitation for the double prime condition in the ambiguous as compared with the unambiguous triplets, irrespective of task. This would suggest that the behavioral patterns reflect a different mix of influence from form-level and meaning-level processing on decision-making in the two tasks. Alternatively, it is possible that N400 facilitation patterns are also modulated by task (see, e.g., Chwilla and Kolk, 2003), perhaps reflecting differing levels of influence from relatively more implicit and explicit aspects of semantic processing (as the N400 has been argued to be sensitive to both; see, e.g., Deacon et al., 2000; Holcomb, 1988). Finally, it is possible that there are hemispheric biases in the tendency to process words at a lexical or semantic level. For example, studies with commissurotomized patients (Baynes and Eliassen, 1998) have suggested that the lexical-level representations that mediate word form and meaning in the LH maybe impoverished in the RH. Although the behavioral patterns in our previous experiment (Kandhadai and Federmeier, 2007) showed a similar task-dependency for both hemispheres, it is possible that we could see significant visual field differences in the pattern of N400 priming across ambiguity, which may or may not be modulated by the nature of the task.

2. Results

2.1. Experiment 1: lexical decision task

2.1.1. Behavior—Response time measures[1] were not analyzed because the lexical decision was a delayed task in this experiment. However, accuracy data (percent correct) were analyzed to make sure that participants understood and succeeded at the task. On average participants were 80.7% (SE: 0.8) correct; they were 82.6% (SE: 1.0) correct on word trials and 78.9% (SE: 1.1) accurate on non-word trials. Accuracy was higher for RVF (83.6%; SE: 1.0) than LVF (77.9%; SE: 1.1) items, consistent with biases favoring the LH for word apprehension (e.g., Jordan et al., 2003) and replicating the pattern seen in the speeded version of this task in Kandhadai and Federmeier (2007). Overall, the results indicate that participants attended to the stimuli and succeeded at making lexical decisions on the lateralized targets.

2.1.2. Electrophysiological recordings—Target items (both words and non-words) in all conditions elicited the pattern characteristic of ERPs to visual stimuli. These components include, over occipital sites, an initial positivity (P1) peaking around 50 ms, a negativity (N1) at around 125 ms, and a positivity (P2) around 225 ms, and, over frontal sites, a negativity (N1) peaking around 150 ms and a positivity (P2) peaking around 250 ms. These responses were followed by a centro-posterior negativity peaking around 400 ms (N400) and a posterior positivity (LPC) between about 600 and 900 ms; as can be seen in Fig. 1, both responses were larger (more negative N400s and more positive LPCs) to non-words than to words, in both visual fields. The VF manipulation elicited the expected modulations of the waveforms (Fig. 2): sensory components (especially the N1) were larger over sites contralateral to the VF of presentation, and these effects were followed by a posterior, lateralized negative-going effect (selection negativity) from about 300 ms to the end of the epoch, which is ubiquitously seen with lateralized presentation of visual stimuli (e.g., Federmeier and Kutas, 1999).

The main component of interest in the ERP was the N400, so mean amplitudes were measured between 350–550 ms post-stimulus-onset. The 11 electrodes chosen for all the analyses were based on the typical centro-posterior N400 distribution, including left and right dorsal central (LDCe and RDCe), left and right medial central (LMCe and RMCe), middle central (MiCe), left and right dorsal parietal (LDPa and RDPa), middle parietal (MiPa), left and right medial occipital (LMOc and RMOc) and middle occipital (MiOc) sites. These channels were also analyzed in the later time window (550–900 ms) to track patterns on the late positive complex (LPC). For each analysis of variance (ANOVA), the Huynh–Feldt adjustment to the degrees of freedom was applied to correct for violations of sphericity associated with repeated measures. Accordingly, for all F tests with more than 1° of freedom in the numerator, the corrected *p* value is reported.

Grand average ERP waveforms in each VF for each condition in each type of triplet are shown in Fig. 3 at a representative channel. To investigate N400 patterns of activation across prime conditions, mean amplitudes between 350–550 ms were subjected to a four-way repeated measures ANOVA with 2 levels of visual field (RVF, LVF), 2 levels of triplet type (ambiguous, unambiguous), 3 levels of prime condition (single, double, and unrelated), and 11 levels of electrode as factors. There was no main effect of visual field ($F_{1,39}$=1.33; p>0.25). However, there was a significant main effect of triplet type ($F_{1,39}$=6.10; p=0.018), with reduced N400 amplitudes to unambiguous targets (1.90 μV) compared to ambiguous targets (1.53 μV). There was also a main effect of prime condition ($F_{2,78}$=33.83; p<0.001) with the smallest N400 amplitudes to the double prime condition (2.77 μV), followed by the single prime (1.49 μV) and unrelated (0.90 μV) conditions. The only significant interaction was between triplet type and prime condition ($F_{2,78}$=9.85; p< 0.001).

To examine the nature of the triplet type by prime condition interaction, N400 priming effects were investigated as a difference measure between the unrelated condition and each of the related conditions (single prime and double prime). In order to ascertain that differences in N400 priming were not attributable to baseline differences, the unrelated conditions were

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[1] The average response times for the lexical decision task in the behavioral study (Kandhadai and Federmeier, 2007) for targets in RVF and LVF were 680 and 708ms respectively.

subjected to a three-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of triplet type (ambiguous, unambiguous) and 11 levels of electrodes as factors. There was no main effect of either VF or triplet type ($F_{1,39}<1$) and no interaction between VF and triplet type ($F_{1,39}=1.51$, $p>0.2$). Since there were no baseline differences, pairwise comparisons of N400 priming effects across triplet type for each related condition were then conducted; these were done in each visual field separately, given the apriori goal of determining whether N400 effect patterns in each hemisphere were lexical or semantic in nature. For both VFs, there was no significant N400 priming difference between ambiguous and unambiguous targets in the single prime condition. However, in both VFs, double primes were significantly more facilitated in unambiguous as compared with ambiguous triplets (RVF: 2.58 vs. 1.28 μV [$F_{1,39}=4.66$; $p<0.05$]; LVF: 2.71 vs. 0.92 μV [$F_{1,39}=8.34$; $p<0.01$]). Thus both hemispheres manifested a semantic activation pattern on the N400 in the lexical decision task; this pattern can be seen in Fig. 4.

To examine the predictions of the coarse coding hypothesis, the size of each priming effect was compared across VFs with planned comparisons. As can be seen in Fig. 5, these revealed no significant differences for either single or double primes in unambiguous triplets and for double primes in the ambiguous triplets ($F_{1,39}<1$ in all cases). The only difference was a trend for larger RVF (0.88 μV) than LVF (0.08 μV) N400 priming in the single prime ambiguous condition ($F_{1,39}=3.11$, $p<0.09$).

The effect patterns observed on the N400 continued into the LPC window (550–900 ms). In particular, there was a continued effect of prime condition ($F_{2,78}=27.25$; $p<0.001$), with increasingly positive LPC responses for the unrelated (1.76 μV), single prime (2.50 μV) and double prime (3.31 μV) conditions, and there was a triplet type by prime condition interaction ($F_{2,78}=11.31$; $p<0.001$), with comparable effects of single primes but reduced effects of double primes in ambiguous as compared with unambiguous triplets. There was no main effect of VF ($F_{1,39}=1.37$; $p>0.24$) and VF did not interact with any other factor.

2.2. Experiment 2: semantic-relatedness judgment task

2.2.1. Behavior—As in Experiment 1, response time measures[2] were not analyzed due to the delayed nature of the task. However, an analysis of the accuracy data (percent correct) revealed that, on average, participants were 83.8% (SE: 0.6) correct (RVF: 85.6% (SE: 0.8); LVF: 82.0% (SE: 0.9)) at judging whether or not there was a semantic relationship between at least one of the primes and the target, indicating that they were attending to the experimental stimuli and could appreciate the meaning relationships between them.

2.2.2. Electrophysiological recordings—Sensory components identical to those described in Experiment 1 were also elicited in this experiment, and these were again followed by a centro-posterior negativity peaking around 400 ms (N400) and a posterior positivity (LPC) between 600 and 900 ms. As expected, the VF manipulation again modulated sensory components (N1 amplitudes) and the selection negativity (Fig. 6).

Grand average ERP waveforms in each VF for each condition in each type of triplet are shown in Fig. 7 at a representative channel. The same analysis strategy was used in this experiment as in Experiment 1, so mean amplitudes between 350 and 550 ms post-stimulus onset were subjected to four-way repeated measures ANOVA with 2 levels of visual field (RVF, LVF), 2 levels of triplet type (ambiguous, unambiguous), 3 levels of prime condition (single, double and unrelated), and 11 levels of electrode as factors. There was no main effect of visual field

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[2] The average response times for the semantic-relatedness judgment task in the behavioral study (Kandhadai and Federmeier, 2007) for targets in RVF and LVF were 1062 and 1108ms respectively.

($F_{1,39}$=2.26; p> 0.14) but there was a main effect of triplet type ($F_{1,39}$=26.74; p< 0.001), with reduced N400 amplitudes to unambiguous targets (0.83 μV) compared to ambiguous targets (0.01 μV). There was also a main effect of prime condition ($F_{2,78}$=81.02; p< 0.001), with the smallest N400s to the double prime condition (1.80 μV), followed by the single prime (0.22 μV) and unrelated (−0.75 μV) conditions. As in Experiment 1, the only significant interaction was between triplet type and prime condition ($F_{2,78}$=8.56; p< 0.001).

Following up on this interaction, N400 priming effects (differences between each related condition and the corresponding unrelated condition for that triplet type) were investigated across triplet type in each visual field. To ascertain that the unrelated (baseline) conditions were comparable across conditions, these were subjected to a three-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of triplet type (ambiguous, unambiguous) and 11 levels of electrodes as factors. There was no main effect of either VF or triplet type ($F_{1,39}$<1) and no interaction between VF and triplet type ($F_{1,39}$=1.31, p> 0.2) thus suggesting that the baseline activations did not significantly differ from each other across conditions. Consequently, pairwise comparisons of N400 priming effects were conducted; the results revealed the same pattern as that seen in Experiment 1. In particular, whereas single prime facilitation did not differ as a function of ambiguity in either VF, double prime facilitation was greater in unambiguous than in ambiguous triplets in both VFs (RVF: 3.75 μV vs. 1.82 μV [$F_{1,39}$=10.57”;; p<0.01]; LVF: 2.97 μV vs. 1.66 μV [$F_{1,39}$=5.74; p< 0.05]). Thus, N400 amplitude patterns again showed the pattern expected for priming at the level of meaning; see Fig. 8.

The coarse coding hypothesis was examined via planned comparisons of priming effects across the two VFs (Fig. 9). As in Experiment 1, these comparisons revealed no hemispheric differences in the amount of facilitation for any condition (double prime unambiguous condition: [$F_{1,39}$=2.47; p> 0.12], with numerical trend favoring the RVF/LH; all other cases: $F_{1,39}$<1.11).

Priming effects continued into the LPC time window (550–900 ms). There was a main effect of triplet type ($F_{1,39}$=10.53; p< 0.01), with increased positivity to unambiguous (2.54 μV) compared to ambiguous (2.10 μV) targets, and a main effect of prime condition ($F_{2,78}$=64.00; p< 0.001),with increasingly positive LPC responses for the unrelated (1.14 μV), single prime (2.53 μV), and double prime (3.29 μV) conditions. There was no main effect of VF ($F_{1,39}$<1) and VF did not interact with any other factor.

3. Discussion

The goal of this set of experiments was to use the functional specificity afforded by ERP measures to test the prediction of the coarse coding hypothesis that broader and less contextually focused activation in the RH provides it an advantage for integrating across multiple, disparate word meanings. A previous behavioral study (Kandhadai and Federmeier, 2007) using a multiple priming paradigm with both lexical decision and semantic-relatedness judgment tasks failed to find evidence to suggest that there were RH advantages for summating across multiple, unrelated primes. This was true for primes linked via a mediated relationship summating onto an unambiguous target (*lion–stripes–tiger*) and for primes that pointed to different meanings associated with a lexically ambiguous target (*piano–kidney–organ*). However, because behavioral responses aggregate across multiple processing stages, it is possible that the semantic activation processes critical to the coarse coding hypothesis were overshadowed by effects at other stages. To circumvent this difficulty, the present experiment used the same paradigm with ERP measures; to our knowledge, this is the first study to investigate asymmetries in summation priming with ERPs, although this design has been used with behavioral measures in several prior studies (Beeman et al., 1994; Faust and Lavidor, 2003; Kandhadai and Federmeier, 2007). We focused in particular on the N400 component, which has been taken to be a functionally specific index of meaning activation processes (Kutas and Federmeier, 2000), including more implicit aspects of meaning activation (e.g., Olichney et al., 2000).

Indeed, supporting the claim that the N400 primarily indexes processing at the level of meaning, priming effects in both the lexical decision task and the semantic judgment task showed the pattern expected for semantic-level activations. In particular, whereas the amount of priming from a single related prime was equivalent as a function of ambiguity, facilitation from two related primes was reduced if those primes diverged onto disparate meanings associated with a lexically ambiguous target than if they converged onto the single meaning of an unambiguous target. This task-independence of the N400 priming pattern contrasts with the task-dependence that has been seen with behavioral measures for both central (Balota and Paul, 1996) and lateralized (Kandhadai and Federmeier, 2007) presentation of targets. For response time measures, there was no prime condition by ambiguity interaction in the lexical decision task, suggesting that behavioral facilitation during such tasks arises at the lexical (word form) level, where the representation of ambiguous and unambiguous items is assumed to be equivalent. An interaction (of the type seen for the N400 in both tasks in the current set of experiments) was seen in response time measures for the semantic-relatedness judgment task, suggesting facilitation at the level of meaning. In contrast, N400 priming patterns did not vary with task, such that even when participants made lexical decisions on targets, N400 amplitudes seemed to reflect facilitation at the level of meaning—and this was true for both hemispheres. Thus, the N400 would seem to be a particularly useful measure for examining possible hemispheric asymmetries in meaning activation.

Given the sensitivity of the N400 measure to the semantic activation processes of import for the coarse coding hypothesis, it is thus especially striking that there were no differences in the amount of priming across visual field for any prime condition in either task. In both hemispheres, in both tasks, facilitation (in the form of N400 amplitude reductions) was graded by the number of related primes, such that more facilitation was seen for conditions in which both primes were related to the target than when only one prime was related. However, the amount of priming was equivalent in all conditions for targets initially presented to the LH and RH (and, when numerically different, favored the LH). Thus, there was no indication that the RH was more able or more likely to summate activation over multiple, distinct meanings associated with a lexically ambiguous target. The ERP measures in the present study converge with behavioral indices of facilitation in this same multiple priming paradigm (Kandhadai and Federmeier, 2007) as well as with prior behavioral work on mediated priming (Richards and Chiarello, 1995; Livesay and Burgess, 2003) in finding no evidence for increased breadth of priming in the RH. The findings in this study are also consistent with prior ERP work using sentences as stimuli that failed to find evidence consistent with the predictions of coarse coding. For example, Federmeier and Kutas (1999) found more LH than RH facilitation for unexpected sentence endings that were semantically related to the predicted completion. Similarly, Coulson and Severens (2007) found no evidence for a RH advantage in activating the multiple meanings associated with words used in puns (e.g., “*During branding, cowboys have sore calves*.”). Instead, at a short SOA, the LH showed facilitation for probes related to both of the pun word’s meanings, whereas the RH showed activation only for the dominant meaning. By a long SOA, both hemispheres showed facilitation for both meanings (but this facilitation was not greater in the RH).

Thus, studies using a variety of stimulus types (word pairs, word triplets, sentences), tasks (lexical decision, semantic-relatedness judgments, reading for comprehension), and measures (response time, response accuracy, ERPs) have failed to find evidence consistent with the central tenet of the coarse coding hypothesis that the RH activates and maintains a broader set of meanings in response to a given lexical item. However, as described in the introduction, several studies have pointed to a RH advantage for processing weakly related information under some circumstances (e.g., Faust and Lavidor, 2003; Chiarello, 1991; Beeman et al., 1994; Coulson and Williams, 2005). A number of alternative accounts of hemispheric asymmetries in semantic processing have been put forward that might help to reconcile these sets of results.

For example, one suggestion is that asymmetries arise from differences in the timing, rather than the breadth, of semantic activation (e.g., Koivisto, 1997). According to this view, the RH undergoes the same semantic activation processes as the LH, but does so more slowly—with the result that apparent asymmetries in the pattern of activation may arise when studies tap into different points of the activation process by sampling the two hemispheres at a single point in time. There is some support for this account in the results of the present study. In the lexical decision task, facilitation for ambiguous targets preceded by a single related prime was already significant in the N400 time window with RVF/LH presentation ($F_{1,39}$=6.73; $p< 0.05$). In contrast, with LVF/RH presentation, this effect was not significant on the N400 ($F_{1,39}$<1); instead, it became significant only later in the LPC time window ($F_{1,39}$=5.46; $p< 0.05$), partially consistent with the idea of a slower ramp-up of semantic activation in the RH as compared with the LH for these items. Evidence that, in particular, activation for the subordinate meaning of an ambiguous word is slower in the RH has been seen in other ERP studies (Meyer and Federmeier, 2007) and in eyetracking measures (Meyer and Federmeier, 2008). However, in all of these studies using measures with high temporal precision, such delays were limited to ambiguous words; there was no evidence for delayed activation of meaning information associated with unambiguous words, even when associative strength was matched across the unambiguous and ambiguous conditions (e.g., Meyer and Federmeier, 2007). Thus, slowed activation in the RH seems to be linked with meaning dominance, and, as such, probably cannot explain data pointing to RH priming benefits in studies that have used unambiguous words, such as word pairs that are unassociated but categorically related (Chiarello and Richards, 1992; Grose-Fifer and Deacon, 2004; Deacon et al., 2004). Moreover, it is important to note that even though LPC follows the N400 in time in the continuous ERP measure, these components seem to reflect different underlying sets of functions occurring at different stages in the information processing stream, with the N400 related to more implicit and the LPC to more explicit/evaluative aspects of semantic processing. The functional dissociability of the N400 and LPC raise important considerations for theories that have argued for purely timing-based hemispheric asymmetries, since priming shifted in time may often reflect contributions from different mechanisms of semantic processing.

Another explanation for the RH’s particular facility with unassociated, categorically related information has been put forward by Deacon and her colleagues, who argue that there are qualitative differences in the nature of semantic representations in the two hemispheres (Deacon et al., 2004). In particular, they propose that word meanings are represented locally in a spreading activation system in the LH, but are represented in terms of semantic features in a distributed network in the RH. Supporting this view are the ERP studies of word pair priming that found lexical associative priming (which should be due to spreading activation) only with RVF/LH presentation but category-based priming (which should be due to feature overlap) only with LVF/RH presentation (Deacon et al., 2004), and then only if the categorical relationship was sufficiently strong (Grose-Fifer and Deacon, 2004). The theory of Deacon et al. (2004) postulates that the LH’s spreading activation system should allow for mediated priming (e.g., facilitation for *stripes* following *lion*), since both words will tend to spread their activation to the mediating concept (here, *tiger*). However, because these words share few, if any, semantic features in common, the theory predicts no mediated priming in the distributed feature network of the RH. When extended to the summation-priming paradigm in the current study (*lion–stripes–tiger*), this theory thus predicts the opposite pattern from coarse coding: compared to the RH, the LH should be better able to summate across multiple, mediated primes onto the target. This should be particularly true for ambiguous targets (e.g., *organ*) preceded by two divergent primes (*kidney–piano*) that contain no feature overlap. However, our current results failed to show significantly greater N400 summation priming for the double prime targets (ambiguous or unambiguous) in the LH compared to the RH. The same pattern of results was also obtained with response time measures (Kandhadai and Federmeier, 2007), suggesting that the RH, much like the LH, can summate across multiple, semantically unrelated primes. Taken together, these results are at least partially inconsistent with the idea that semantic processing in the RH arises solely from a feature-based distributed network, instead suggesting that both hemispheres may have access to spreading activation-based localist associative representations.

Finally, some accounts have focused on differences in the hemispheres' use of context information, rather than in basic semantic activation processes, as the source of asymmetries observed in semantic priming paradigms as well as in other language tasks, such as sentence processing. It has been suggested, for example, that the LH is more likely to use context information to engage in active meaning selection (e.g., Faust and Gernsbacher, 1996; for alternate view, see also Coney and Evans, 2000), such that remotely related information is discarded or actively suppressed in the LH but remains available in the less-selective RH. A similar type of proposal, the "PARLO" framework (Federmeier, 2007), suggests that asymmetries in language processing arise because the LH actively predicts upcoming information, whereas the RH integrates incoming information in a more post-hoc fashion. On this view, priming asymmetries are not due to semantic distance as such, but rather to the predictive validity of different types of cues in different processing environments. For example, because lexical association is generally defined on the basis of predictability (i.e., targets are defined as lexically associated with their primes if the prime words lead people to generate the targets), this type of relationship might be especially well-suited to LH processing strategies. On the other hand, shared category membership for unassociated words may be easier to appreciate post-hoc, leading to a RH advantage for that type of word pair. Thus, differences between the hemispheres would be expected primarily when a predictive versus an integrative strategy could confer a particular processing advantage or disadvantage. This would not seem to be the case for the type of stimuli used in the present experiment, but might have been true in other multiple priming paradigms, such as that of Faust and Lavidor (2003), in which the convergent condition provided information useful for prediction of the targets.

In the end, then, although there remain multiple possible explanations for the pattern of priming asymmetries observed across the literature, data from the present set of ERP experiments, taken together with converging evidence from behavioral measures (Kandhadai and Federmeier, 2007), strongly suggest that the two hemispheres do not differ in their ability to summate across distantly related or (in the case of ambiguous triplets) even conflicting sources of information. The present ERP data are particularly important in providing a more functionally specific measure of the semantic activation processes that are taken to be the primary source of priming asymmetries under the coarse coding hypothesis. Thus, it would seem that the RH's enhanced ability to process remotely related information under some circumstances (e.g., Coulson and Williams, 2005; Bowden and Jung-Beeman, 2003; Faust and Lavidor, 2003) must arise from processing asymmetries other than the breadth of semantic activation per se (Jung-Beeman, 2005).

4. Experimental procedures

4.1. Experiment 1: lexical decision task

4.1.1. Participants—Forty native English speakers (20 men and 20 women) between the ages of 18 and 30 (mean age 21) from the University of Illinois participated in this experiment and received either cash or course credit for their time. None had exposure to any other language before age five. All participants were right-handed; mean handedness quotient was 0.80 (range: 0.38–1.0) as measured by the Edinburgh handedness inventory (Oldfield, 1971), where “1” is strongly right-handed and “−1” is strongly left-handed. Participants were also screened for normal vision and had no history of neuropsychological or psychiatric disorders.

4.1.2. Stimuli—The stimuli were the same as those used in Kandhadai and Federmeier (2007), and were taken from the set used by Balota and Paul (1996), augmented with items from Bennett and McEvoy (1999) and additional items constructed using the MRC Psycholinguistic Database (Coltheart, 1987). They consisted of 416 triplets of words: two primes and a target. The ambiguity of the target and the relatedness between the primes and the target was manipulated. Half of the triplets contained a lexically ambiguous target (e.g., *organ*) whereas half contained an unambiguous target word (e.g., *lion*); ambiguous and unambiguous targets were matched for word frequency (Kucera and Francis, 1967) and length. Each of the primes could be related (i.e., lexically associated with) or unrelated to the target, creating three global priming conditions: double prime (both primes associated with the target, though not with one another), single prime (only one of the primes associated with the target, equally split between first and second position in the triplet) and unrelated (neither prime associated with target). In the double prime condition, the two primes were both either related to the single meaning of the unambiguous target (*lion–stripes–tiger*) or were related to different meanings of the ambiguous target (*kidney–piano–organ*). Average association values between primes and targets were 0.26 for the unambiguous items and 0.11 for the ambiguous items (Nelson, McEvoy and Schreiber, 1998). A sample set of stimuli is presented in Table 1.

To generate non-word trials, an additional set of 104 ambiguous and 104 unambiguous triplets was constructed in the same manner, with targets that matched the word target set in frequency (Kucera and Francis, 1967)and length. Non-words were constructed from these 208 targets by replacing one letter at random to form pronounceable letter strings that were not legal English words.

Eight stimulus lists were created from the full stimulus set; each contained an equal number of items from each triplet type and prime condition within each VF. Across the experiment, every target item appeared in all prime conditions in each VF. For ambiguous triplets, each participant saw an equal number of primes related to the dominant and subordinate meaning of the targets, and the order of the two primes was counterbalanced across lists for both triplet types. Within a list, targets were controlled for length and frequency across triplet type, prime condition, and VF. Stimuli within each list were presented in random order, with the constraint that no more than three targets in a row appeared within the same VF.

4.1.3. Procedure—Each participant was tested in a single session conducted in a dim, quiet testing room. Stimuli were presented one word at a time on a 21″ SVGA monitor placed at a distance of 40″ from the participant. All stimuli were in white, upper case letters presented on a black background. Each trial began with a series of pluses to indicate the beginning of a trial; these were presented centrally for 1000 ms with a random SOA of 1000 to 2000 ms used to temporally jitter anticipatory potentials. Following this, prime1 was presented for 200 ms, followed immediately by prime2, which was also displayed for 200 ms. After 800 ms, the target item was then presented for 200 ms, at the vertical center and lateralized so that its medial edge was two degrees from horizontal center. Targets subtended 2.8° of horizontal visual angle (range: 1.3 to 4.3°) and 0.68° of vertical visual angle. 800 ms following the target, a ‘?’ appeared in the center of the screen for 750 ms. At this point the participants were asked to respond to the target with a lexical decision: i.e., they were to press “yes” with one response button if the target was a legal English word and “no” with the other button if the target was a non-word. Hand used to respond “yes” was counterbalanced across participants and lists. The next trial sequence then began after a delay of 750 ms. A practice block preceded the experimental session and the session was divided into five equal blocks lasting approximately 60 min in total.

4.1.4. Data collection—

Participants' EEG was recorded using an electrode cap containing 26 geodesically arranged Ag/AgCl electrodes (see icon in Fig. 1 for arrangement). The left mastoid was used as a reference during the on-line recording. Eye movements were monitored via electrodes placed on the outer canthus of each eye and blinks were monitored via an electrode placed on the left infraorbital ridge. Electrode impedances were kept below 3 kΩ. Brain potentials were amplified with a Sensorium 32 channel polygraph set to a band pass of 0.02–100 Hz, and digitized at 250 Hz and stored on a hard disk for later analyses.

4.1.5. Data analysis—

Prior to measurement, ERPs were digitally filtered with a band pass filter of 0.2–30 Hz. ERPs were computed from 100 ms before the onset of critical words to 920 ms post-stimulus onset. Epochs containing artifacts from amplifier blocking, signal drift, excessive eye movements, or muscle activity were rejected off-line before averaging, and those contaminated by eye blinks were corrected for those 7 participants with sufficient numbers of blinks to obtain a stable filter (Dale, 1994); trials containing eye blinks were rejected for other participants. On average, 10% of trials were lost due to such artifacts. Data from each participant was then rereferenced offline to the algebraic mean of the left and right mastoids, and averages of artifact-free ERPs were calculated for target words in each prime condition for each triplet type in each VF after subtraction of the 100 ms pre-stimulus baseline.

4.2. Experiment 2

4.2.1. Participants—

Forty native English speakers (20 men and 20 women) between the ages 18–22 (mean age 19) from the University of Illinois participated in this experiment and received either cash or course credit for their time. None had exposure to any other language before age five. All participants were right-handed; mean handedness quotient was 0.75 (range: 0.36–1.0) as measured by the Edinburgh handedness inventory (Oldfield, 1971), where "1" is strongly right-handed and "−1" is strongly left-handed. Participants were also screened for normal vision and had no history of neuropsychological or psychiatric disorders.

4.2.2. Stimuli—

The stimuli consisted of all word trials from Experiment 1.

4.2.3. Procedure—

The procedure was the same as in Experiment 1 except that the response prompt ("?") appeared 1300 ms after the target for 3000 ms. At this point participants were asked to make a semantic-relatedness judgment between primes and target: i.e., they were asked to press 'yes' with one response button if one or both of the primes was related to the target or 'no' with the other button if *neither* of the primes was related to the target. Hand used to respond 'yes' was counterbalanced across participants and lists. The next trial sequence then began after a delay of 1000 ms. Each session lasted about 55min, beginning with a practice block followed by four experimental blocks.

4.2.4. Data collection and analysis—

The data collection and analysis procedures were the same as in Experiment 1. On average, 12% of trials were lost due to artifacts. Blink correction procedures on contaminated trials were applied to 11 of the participants who had sufficient blink trials to establish a stable filter (Dale, 1994). As in Experiment 1, averages of artifact-free ERPs were calculated for target words in each prime condition for each triplet type in each VF after subtraction of the 100 ms pre-stimulus baseline.

Acknowledgments

Thanks to the undergraduate members of the Cognition and Brain Lab at the University of Illinois for data collection. Support from NIA grant AG026308 to Kara D. Federmeier is gratefully acknowledged.

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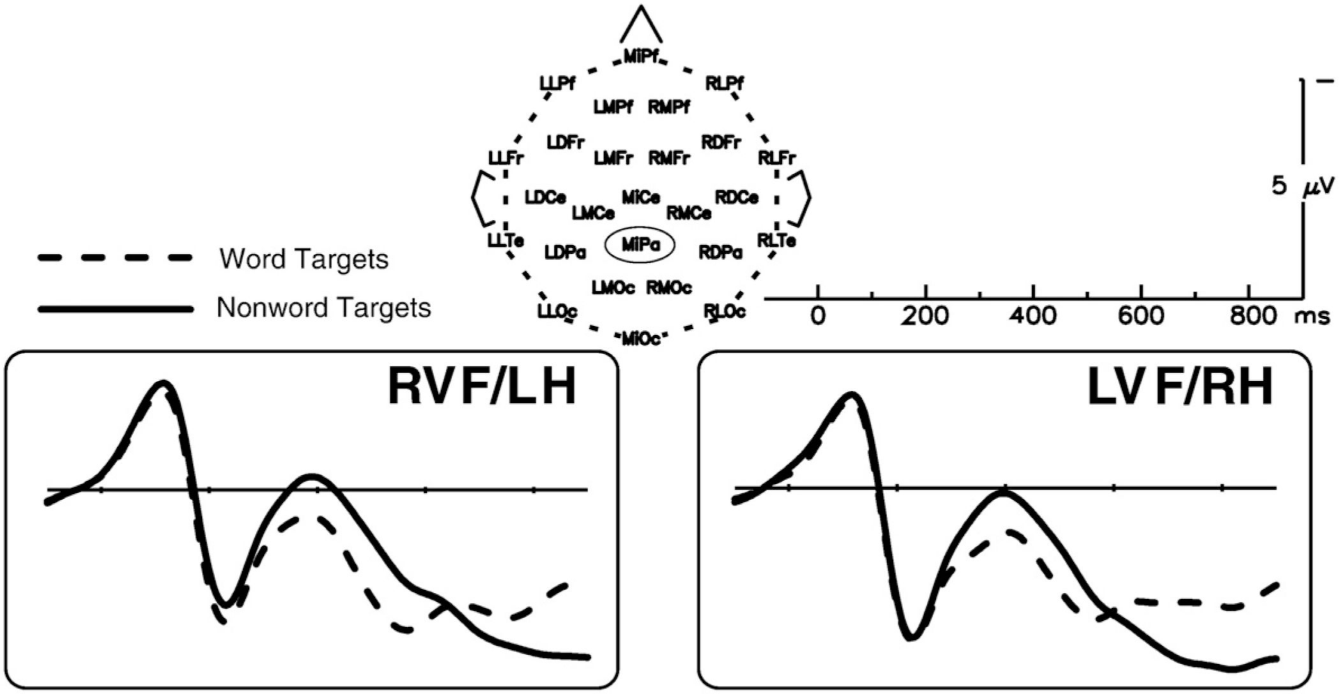

Fig. 1.

Grand average ERPs (Experiment 1, lexical decision task) to non-word and unrelated word targets in each VF, shown at a representative medial parietal channel (MiPa). In both VFs, non-words elicited larger N400 (350–550 ms) and LPC (550–900 ms) responses than did words.

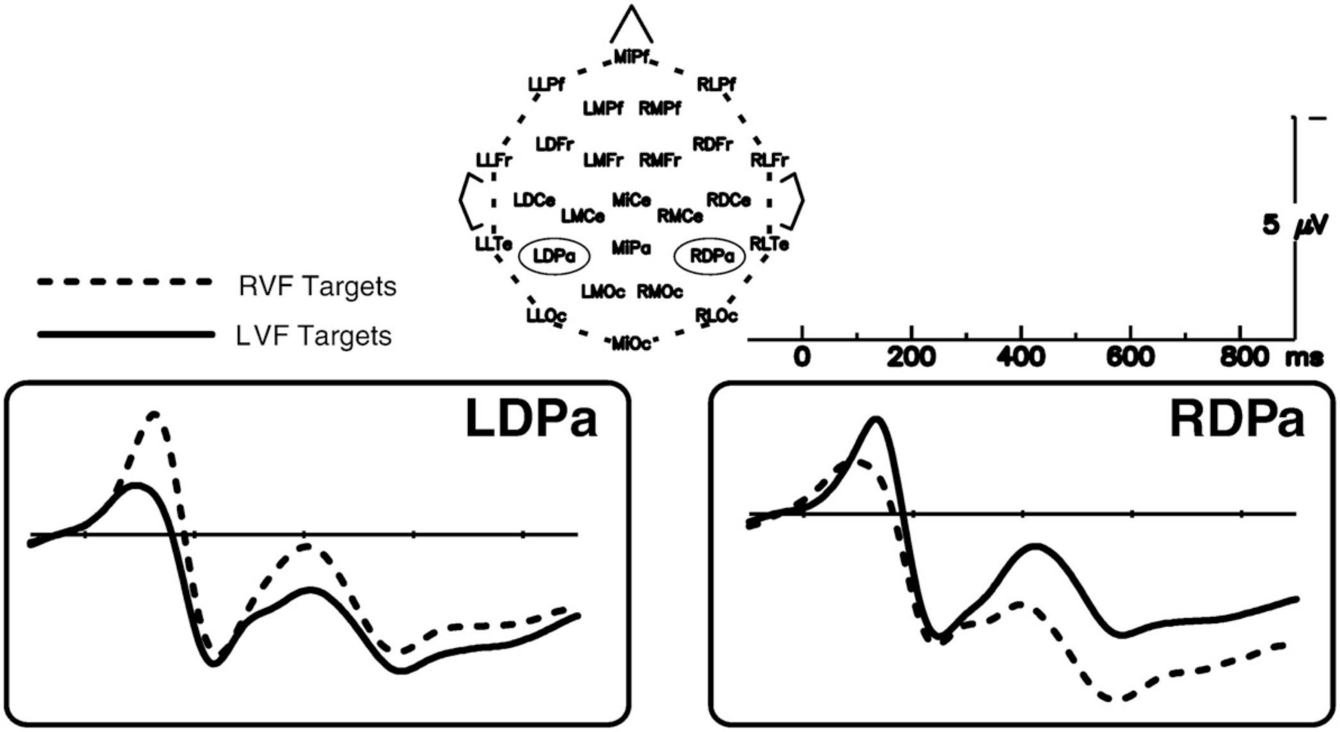

Fig. 2.

Grand average ERPs (Experiment 1, lexical decision task) to word targets presented in the RVF and LVF, shown at left and right parietal (RDPa and LDPa) electrode sites. N1 responses show the expected contralateral skew (i.e., larger over the LH to RVF items and larger over the RH to LVF items).

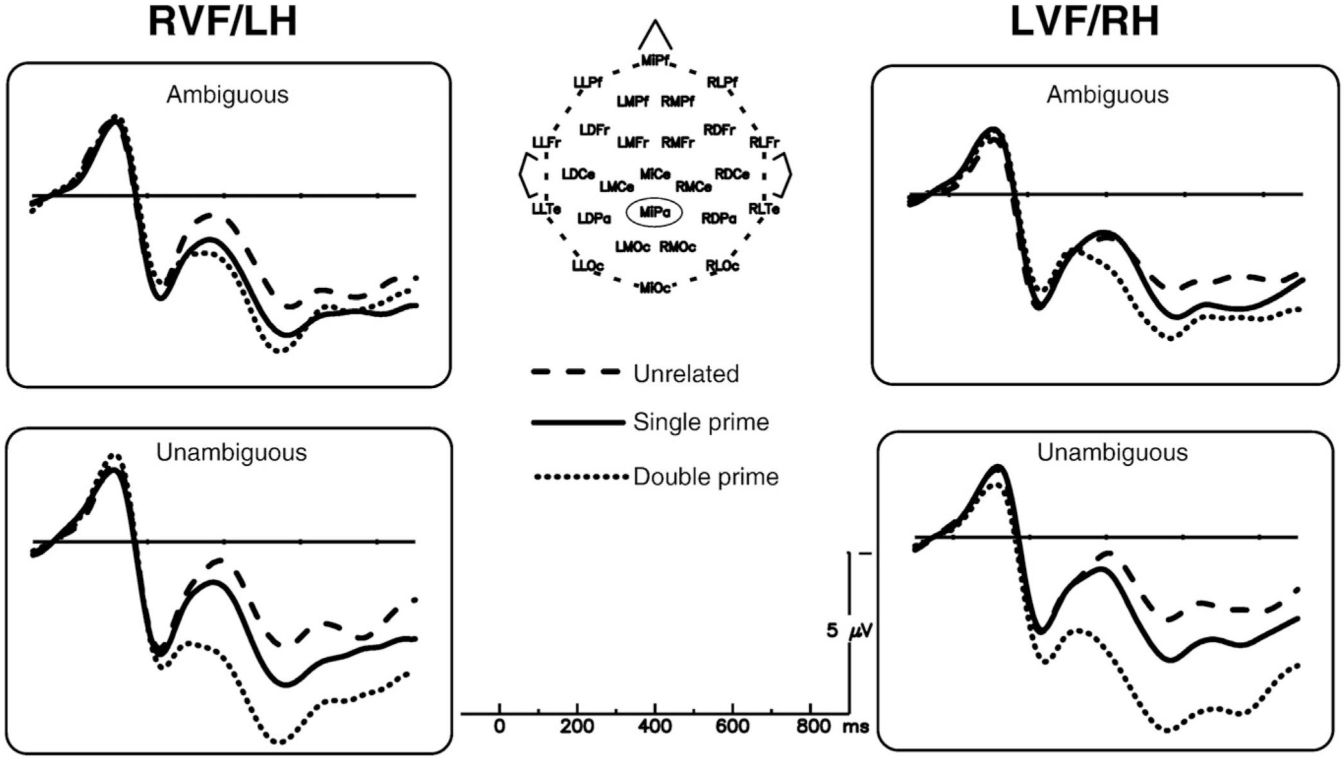

Fig. 3.

Grand average ERPs (Experiment 1, lexical decision task) to targets in the three prime conditions (double prime, single prime, unrelated) in each VF (RVF, LVF) for each triplet type (ambiguous, unambiguous) at the medial parietal (MiPa) channel. N400 amplitudes were graded by the number of related primes, with the smallest amplitude to the double prime condition, followed by the single prime and unrelated conditions.

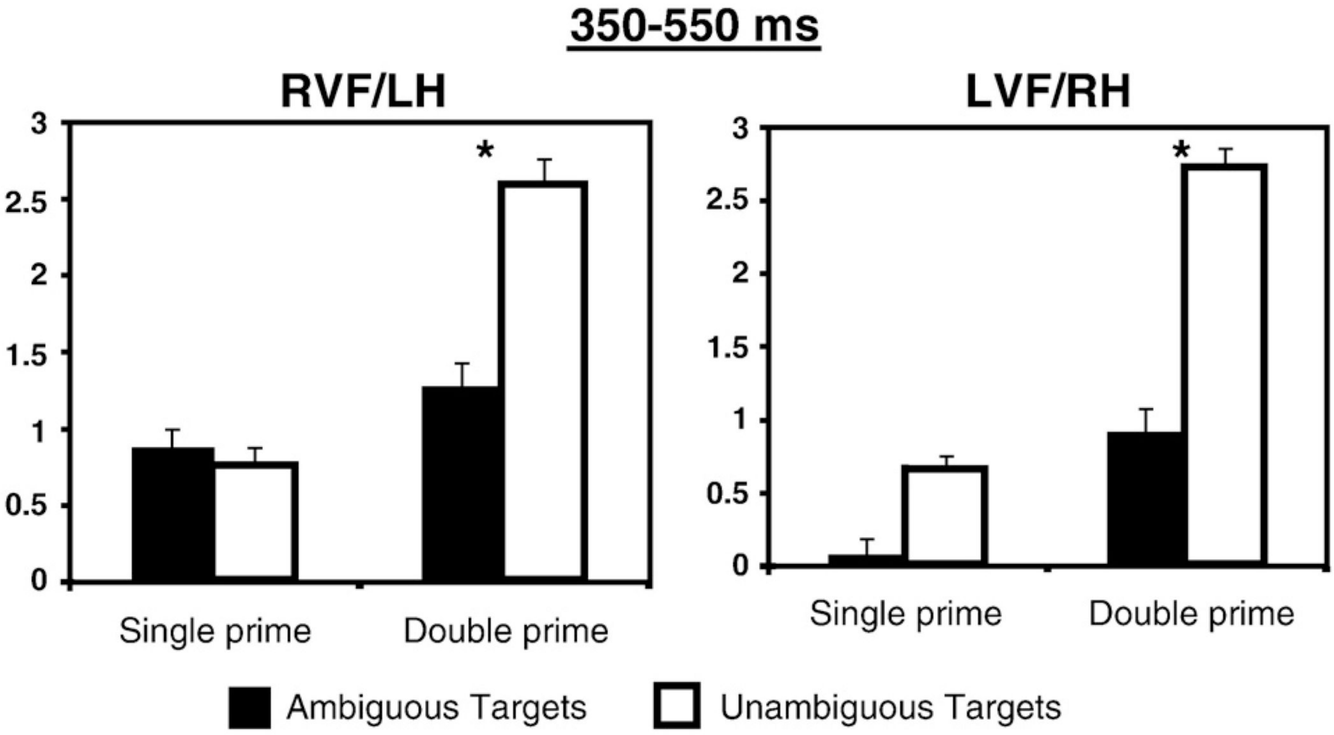

Fig. 4.
N400 priming across ambiguity in each VF (RVF/LH, LVF/RH) for each related prime condition (single prime, double prime) in Experiment 1 (lexical decision task). N400 priming was comparable across ambiguity in the single prime condition, but the amount of double prime priming for ambiguous targets was significantly smaller than that for unambiguous targets.

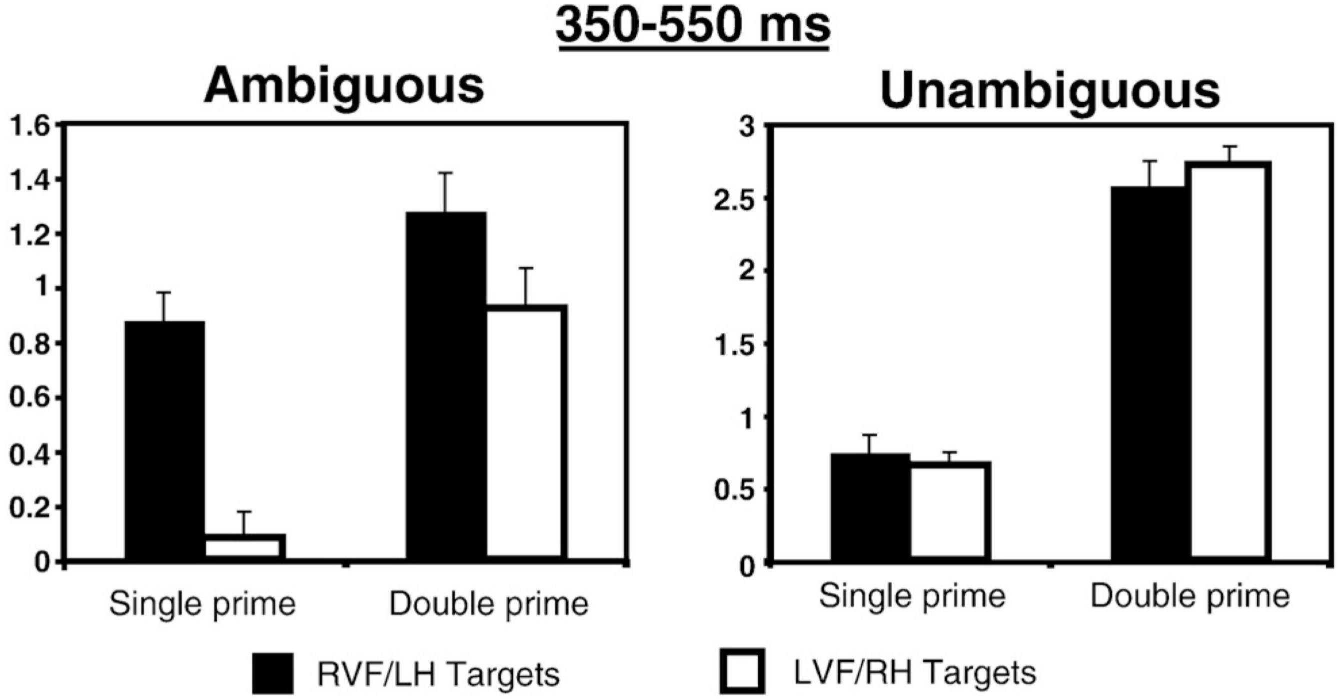

Fig. 5.

N400 priming across VF for each triplet type (ambiguous, unambiguous) for each related prime condition (single prime, double prime) in Experiment 1 (lexical decision task). There was marginally ($p < 0.09$) more priming for RVF targets than LVF targets in the single prime ambiguous condition. None of the other hemispheric differences reached significance.

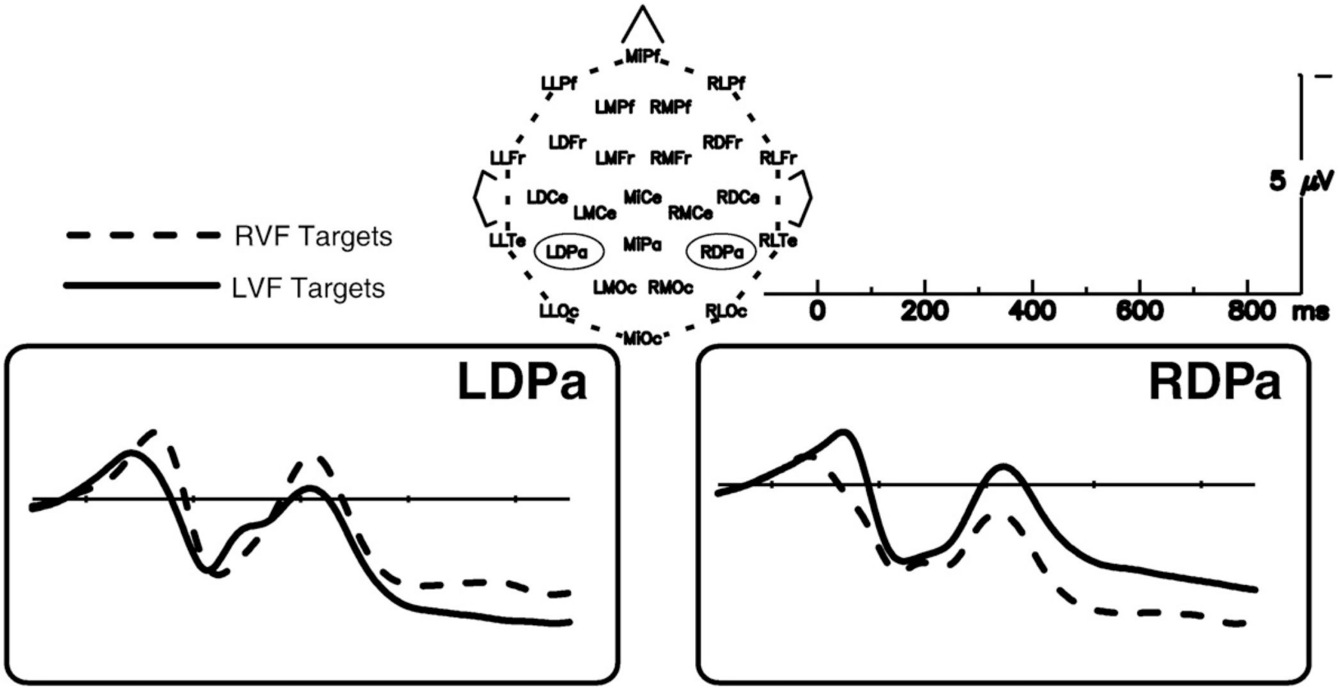

Fig. 6.
Grand average ERPs (Experiment 2, semantic judgment task) to word targets (RVF, LVF), shown at left and right parietal (RDPa and LDPa) electrode sites. Again, N1 responses show the expected contralateral skew.

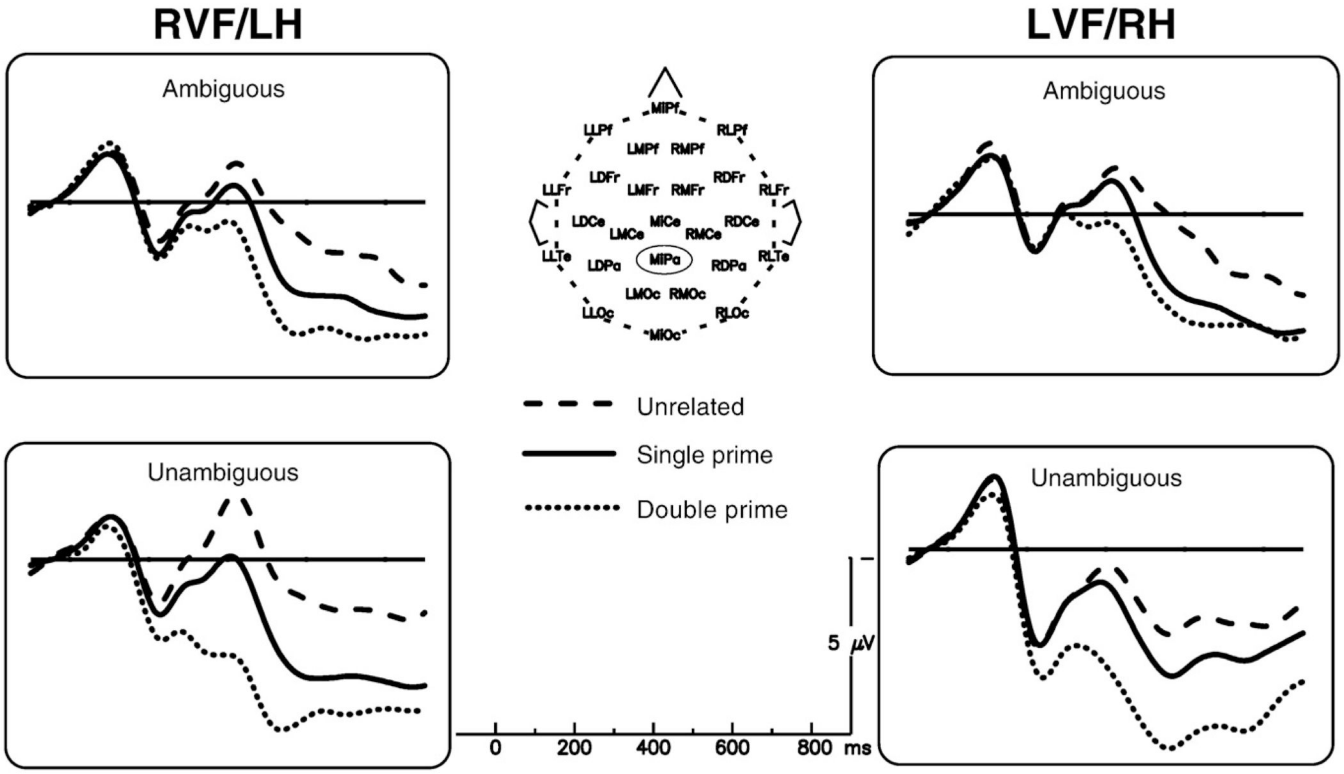

Fig. 7.

Grand average ERPs (Experiment 2, semantic judgment task) to targets in the three prime conditions (double prime, single prime, unrelated) in each VF (RVF, LVF) for each triplet type (ambiguous, unambiguous) at the medial parietal (MiPa) channel. N400 amplitudes were graded by the number of related primes, with the smallest amplitude to the double prime condition, followed by the single prime and unrelated conditions.

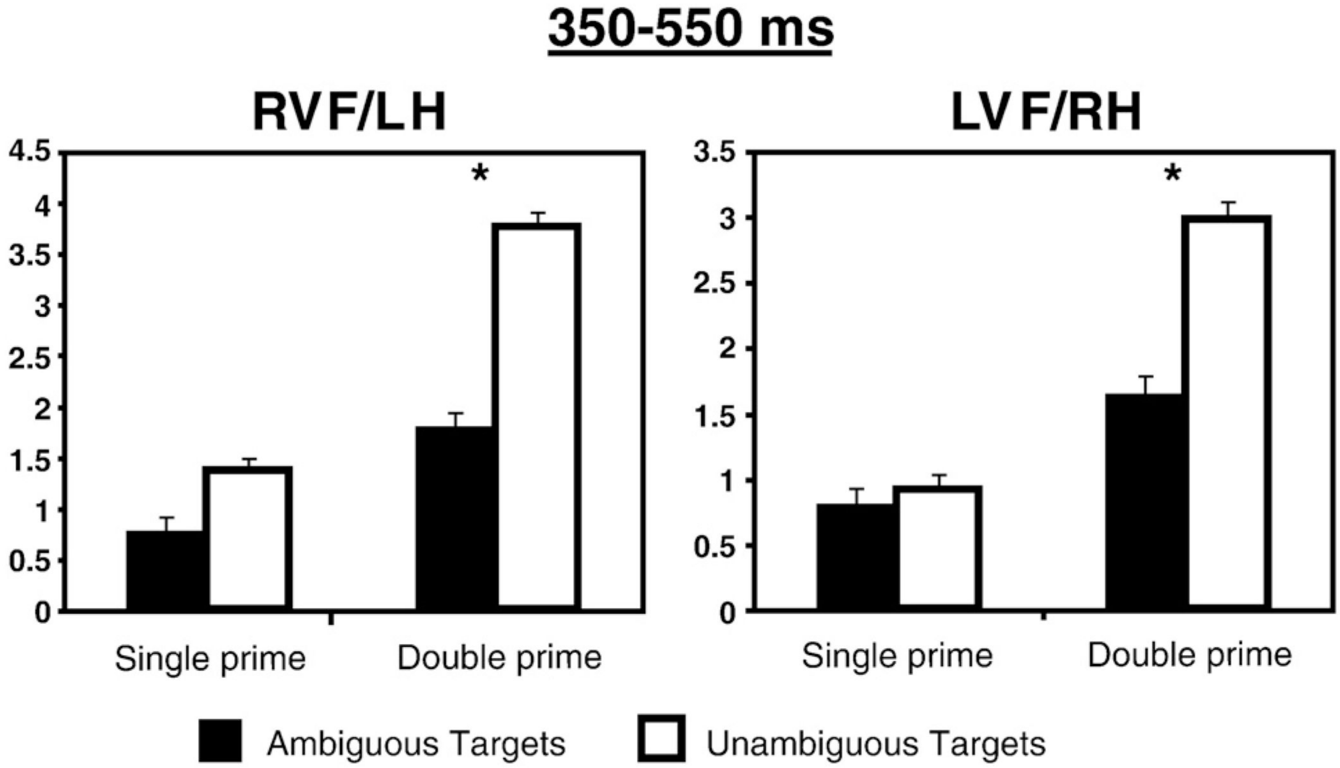

Fig. 8.

N400 priming across ambiguity in each VF (RVF/LH, LVF/RH) for each related prime condition (single prime, double prime) in Experiment 2 (semantic judgment task). N400 priming was comparable across ambiguity in the single prime condition, but the amount of double prime priming for ambiguous targets was significantly smaller than that for unambiguous targets.

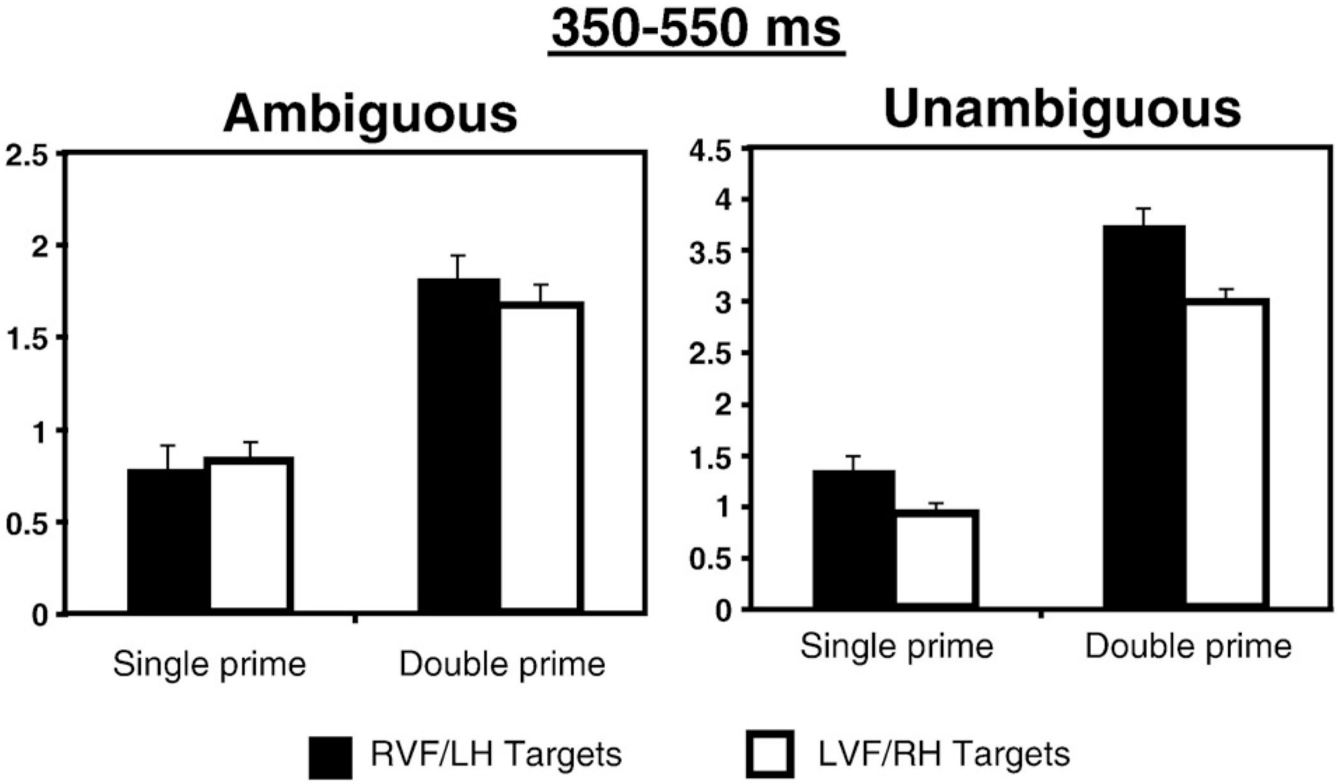

Fig. 9.

N400 priming across VF for each triplet type (ambiguous, unambiguous) for each related prime condition (single prime, double prime) in Experiment 2 (semantic judgment task). There were no significant hemispheric differences in any condition.

Table 1

Sample stimuli

Prime conditions	**Ambiguous**	**Unambiguous**
Double prime	Hospital–tolerant–patient	Tea–beans–coffee
Single prime	Champion–bother–bug Roach–hall–bug	Grime–empty–full Capacity–abandon–full
Unrelated	Gangster–melon–patient	Tax–duel–coffee

A sample set of stimuli (two primes and a target) seen by a single participant in each prime condition (double prime, single prime and unrelated) for each triplet type (ambiguous and unambiguous).