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Hemispheric differences in the recruitment of semantic processing mechanisms

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Abstract

This study examined how the two cerebral hemispheres recruit semantic processing mechanisms by combining event-related potential measures and visual half-field methods in a word priming paradigm in which semantic strength and predictability were manipulated using lexically associated word pairs. Activation patterns on the Late Positive Complex (LPC), linked to controlled aspects of processing, showed that previously documented left hemisphere (LH) processing benefits for word pairs with a weak forward but strong backward association stem from the ability to appreciate meaning relations in an order-independent fashion and/or strategically reorder them. Whereas there is a LH benefit for such strategic processing during comprehension in passive tasks, the present study further showed that the RH is also able to make use of these mechanisms when explicit semantic judgments are required. In both hemispheres, N400 responses, linked to initial semantic activation, were largely graded by association strength, with more amplitude reduction for forward associates and strong, symmetrically associated pairs compared to backward associates and matched weak, symmetrically associated pairs. However, responses to moderately associated pairs were more facilitated after initial presentation to the LH than to the RH. This pattern converges with sentence processing findings that point to LH advantages for using context information to predict features of likely upcoming words. Together, the results suggest that an important basis for hemispheric asymmetries in language comprehension arises from when and how each uses top-down semantic mechanisms to shape initial semantic activation over time.

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Research Highlights

- In both hemispheres, N400 responses, linked to initial semantic activation, were largely graded by association strength, with greater facilitation for strongly associated than weakly associated word pairs.
- However, the left hemisphere is better than the right hemisphere in predicting likely upcoming information based on existing context.
- Activation patterns on the Late Positive Complex (LPC), linked to controlled aspects of processing suggest that left hemisphere is also better able to appreciate meaning relations in an order-independent fashion.
- Whereas there is a left hemisphere benefit for such controlled processing during comprehension in passive tasks, the right hemisphere is also able to make use of these mechanisms when explicit semantic judgments are required.
- An important basis for hemispheric asymmetries in language comprehension arises from when and how each hemisphere uses top-down semantic mechanisms to shape initial semantic activation over time.

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Keywords

language; ERPs; N400; LPC; word priming; lexical association

Introduction

The fact that both the left and right cerebral hemispheres (LH and RH) contribute to the apprehension of language meaning has been shown through a combination of research conducted with patients who have unilateral brain damage (for reviews, see, Tompkins, Fassbinder, Lehman-Blake, & Baumgaertner, 2002; Johns, Tooley, & Traxler, 2008) and with healthy participants, using the visual-half field (VF) presentation method to induce lateralized processing biases (see Banich, 2002 for detailed description of this technique). Two main classes of theories have been put forward to account for hemispheric differences in semantic processing – those that postulate asymmetries in how semantic information is represented and/or initially activated, and those that instead locate differences in how the hemispheres use top-down mechanisms to shape that initial activation over time.

For example, Deacon et al. (2004) have suggested that words and concepts are differentially represented and organized in the cerebral hemispheres, with the LH storing a localist, association-based network of concepts and words and the RH instead maintaining a distributed feature-based conceptual network. This theory is based on evidence from visual-half field studies with event-related potential (ERP) measures, which found that purely associatively-related words (e.g., *dog-bone*) were selectively facilitated in the LH whereas categorically-related, unassociated word pairs (e.g., *mosquito-flea*) were facilitated only in the RH. Another theory that postulates hemispheric differences in relatively early semantic processes is the coarse coding hypothesis (Jung-Beeman, 2005). This view claims that the LH activates a narrow set of concepts strongly related to a given language input, whereas more diffuse activation in the RH leads to the facilitation of a broader range of concepts, including those that may only be weakly related. Data showing that although strongly associated word pairs (*sofa-chair*) from a category are primed in both hemispheres, unassociated pairs from the same category (*lamp-chair*) are primed only in the LVF/RH have been taken as support for coarse coding (Chiarello et al., 1990; Chiarello, 1991).

However, several recent findings have pointed to broad similarity in the hemispheres' representation and initial activation of semantic information (Richards & Chiarello, 1995; Kandhadai & Federmeier, 2007, 2008, 2010). Such results bolster views that comprehension asymmetries may be driven, instead, by differences in how top-down mechanisms are used to shape initial semantic activation over time. In particular, it has been suggested that the LH is more likely to strategically recruit attentionally-driven semantic processes to glean meaning from words (Burgess & Simpson, 1988; Chiarello, Senehi, & Nuding, 1987; Chiarello, Richards, & Pollock, 1992; Nakagawa, 1991; Collins, 1999).

For example, Burgess and Simpson (1988) investigated the activation and maintenance of the dominant and subordinate meanings of lexically ambiguous words (e.g., *bank*) and found a LH benefit for selecting dominant meanings. In the left visual field (LVF/RH), there was rapid activation of the dominant meaning and a slower ramp up of activation for the subordinate meaning. In contrast, in the right visual field (RVF/LH) both meanings were activated rapidly, but only subordinate meaning activation faded over time. In fact, in conditions that encouraged controlled processing (long stimulus onset asynchronies), response times to subordinate meanings were actually longer than response times to unrelated words, suggesting a LH mechanism that actively inhibits the non-dominant meanings of ambiguous words. Nakagawa (1991) found that such controlled inhibition of weak meaning relations in the LH was disrupted by the presence of a concurrent auditory shadowing task, suggesting that these inhibitory processes were largely initiated and shaped through the use of attentional resources.

Similarly, researchers have observed a LH benefit for other kinds of controlled semantic processing. For instance, Chiarello, Richards and Pollock (1992) presented participants with word pairs that were categorically related and lexically associated (e.g., *dog-cat*), only associated (e.g., *dog-bone*), or only categorically related (e.g., *dog-goat*). Under conditions that fostered the recruitment of controlled semantic processing, the LH showed more facilitation for categorical associates than for either pure associates or unassociated category members, whereas the RH did not exhibit this pattern. The authors argued that the LH is better able to strategically integrate multiple sources of facilitation, such as that from lexical association and feature overlap.

Based on several such findings, it has been suggested that the LH has access to more efficacious strategic selection, inhibition and integration processes (Burgess and Simpson, 1988; Nakagawa 1991; Chiarello, Richards, & Pollock, 1992; Chiarello, Senehi, & Nuding, 1987; Faust and Chiarello, 1998a; Faust and Chiarello, 1998b; Faust and Gernsbacher, 1996; Federmeier, 2007). These attentionally-driven semantic mechanisms might be especially useful for rapid sentence or discourse comprehension (e.g., Faust and Chiarello, 1998a; Coney & Evans, 2000; Federmeier, 2007), but may also be expected to affect word processing under conditions that promote recruitment of top-down mechanisms. For example, in a prior study using ERPs in conjunction with VF presentation methods, we examined hemispheric asymmetries in both automatic and controlled aspects of semantic processing in a word priming paradigm (Kandhadai & Federmeier, 2010). Semantic strength was manipulated within the same pair of words through the use of asymmetrically associated word pairs (e.g., *pillow-sleep*). When the words were presented in one order (the forward condition), there was a strong association from the prime to the lateralized target. However, presented in the opposite order (the backward condition), there was a weak association from prime to target. The appreciation of the backward pairs may be especially promoted by the ability to strategically reorder concepts and/or process semantic relations in an order-independent fashion to allow a better appreciation of the strong reverse association from target to prime.

The N400, a negative ERP component shown to be sensitive to relatively automatic aspects of semantic processing (Federmeier & Laszlo, 2009), revealed that, in both hemispheres, meaning activation was graded by associative strength. There was greater N400 facilitation (reduction in amplitude) for forward pairs than backward pairs in both VFs, and no differences in facilitation across VF for any condition, suggesting similar automatic meaning activation in the cerebral hemispheres. Hemispheric differences emerged, however, on the late positive complex (LPC), a posterior positivity seen around 500 to 900 ms post stimulus onset that has been consistently linked to more strategic and effortful aspects of cognitive processing, including semantics (e.g., Van Petten, Kutas, Kluender, Mitchiner, & McIsaac, 1991; Swaab, Brown, & Hagoort, 1998; Olichney et al., 2000). In the LVF/RH, LPC priming patterns tracked N400 effect patterns, with greater priming for forward than backward pairs. However, in the RVF/LH, there was equivalent priming for both forward and backward pairs. In particular, even though there was equivalent LPC facilitation for forward pairs across VFs, there was significantly greater LPC priming for backward pairs in the RVF/LH than in the LVF/RH indicating that the LH was better able to strategically appreciate weak but relevant meaning relations, such as the backward pairs.

These findings were thus consistent with a number of prior studies (Chiarello, 1985; Chiarello et al., 1987; Burgess & Simpson, 1988; Nakagawa, 1991; Hagoort, 1993; Faust & Gernsbacher, 1996; Collins, 1999; Meyer & Federmeier, 2008) in suggesting that the LH is better able or more likely than the RH to engage in effortful semantic processing. However, there is evidence that the RH is also able to use certain kinds of controlled semantic mechanisms, especially in situations that promote effortful semantic analyses (e.g., Gouldthorp & Coney, 2009; see review by Federmeier et al., 2008). For instance, in the Chiarello et al. (1992) study described earlier, when experimental conditions tapped into controlled inhibitory processes (e.g., longer prime duration and intermediate stimulus-onset-asynchronies), the RH was also able to inhibit irrelevant meanings under some circumstances. Strikingly, in some cases, the RH seems to be even better than the LH in apprehending meaning relations when supported by explicit task conditions. For example, several studies that have found a RH benefit for apprehending remote meaning relations have employed explicit semantic tasks such as sensicality or meaning judgments (Anaki, Faust, & Kravetz, 1998; Schmidt, DeBusea, & Segera, 2007), insight verbal problem solving (Bowden & Jung-Beeman, 2003), and higher-order discourse comprehension (Beeman, 1998).

Thus, taken together, these findings suggest each hemisphere's recruitment of attentionally driven processes, which are often goal oriented, may be modulated by the nature of the task. In Kandhadai and Federmeier (2010), ERPs were recorded as participants passively read the stimuli (for a later memory task). Although this type of paradigm is useful for trying to uncover neural processing during natural language comprehension, these may also be conditions that are particularly likely to elicit LH advantages for strategic aspects of semantic processing. Under task conditions that instead promote more active assessment of semantic relationships, it is possible that the RH may also be capable of recruiting these same strategic processes. Thus, a first goal of the present study was to examine the processing of asymmetrically associated word pairs in the context of an explicit, semantic judgment task, using ERPs with VF presentation methods. Of interest is whether, under these explicit task conditions, the RH, like the LH, will show enhanced LPC priming for the backward pairs.

A critical question, then, concerns the nature of the strategic processing benefit for backward pairs observed in Kandhadai and Federmeier (2010). This benefit might arise from a general ability to amplify weak meaning relations, for example through increased effort to retrieve additional information about concepts in order to better appreciate how they are related (e.g., Paller, Kutas, and McIsaac, 1995). Alternatively, because the backward pairs contain a strong semantic association presented in a noncanonical order, the LPC pattern may reflect processing that flexibly links words and concepts in a manner that is less constrained by the linear order of input, thus, effectively, “reordering” the pairs and thereby allowing a better appreciation of the strong reverse association from target to prime. Therefore, the second and primary goal of the present study was to adjudicate between these two possibilities. Accordingly, the present experiment examined the processing of symmetrically associated word pairs of strong, medium, and weak strength, alongside that for the asymmetrically associated word pairs used in the prior study. Critically, we matched the weak symmetrically associated pairs with the backward pairs on a one-by-one basis for associative strength (prime to target) as well as frequency, length and common parts of speech. The only difference between these pairs, therefore, lies in the strength of the reverse (target to prime) association, which is strong for the backward pairs but weak for the symmetric pairs. Thus, event-related response differences between these pairs can be attributed to an appreciation of that reverse association. For instance, if the LPC facilitation for the backward pairs observed in the prior study (Kandhadai & Federmeier, 2010) was due to a general ability to amplify weak prime-to-target associations, then, in the current study, we would expect to see equivalent LPC priming for both backward and weakly associated pairs. In contrast, if the LPC pattern reflects a strategic appreciation of the strong reverse association from target to prime, then LPC priming effects in the current experiment should be larger for backward pairs than for weakly associated symmetrical pairs.

Finally, in addition to testing hypotheses about the availability and nature of strategic semantic processing mechanisms in the two hemispheres, the present study will allow further examination of more automatic aspects of semantic processing, through measurement of N400 priming patterns. Because N400 effects are relatively more stable across changes in task requirements, we expect to replicate prior patterns of N400 priming for forward and backward pairs (Kandhadai & Federmeier, 2010), with greater facilitation for forward than backward pairs in both VFs. As with the LPC, comparisons between N400 priming for backward and weak symmetrical pairs will reveal whether automatic meaning processing in either hemisphere is sensitive to the reverse association from target to prime. Comparisons across strong, medium, and weakly associated symmetrical pairs will also provide a picture of each hemisphere's sensitivity to graded levels of stimulus predictability. Because lexical association is defined by predictability, the use of associates provides a means of capturing, in a word priming paradigm, the kind of expectancy driven processing that has been shown to be important for sentence comprehension and that has been hypothesized to be a central factor in hemispheric processing differences at the sentence level (see, e.g., Federmeier, 2007). In particular, sentence-processing studies have pointed to a specific LH benefit for predictive processing of likely upcoming information based on current context. Wlotko and Federmeier (2007) manipulated the degree to which sentence-final words were predictable using cloze probability measures[1], and found stronger facilitation for low-to-moderately predictable completions in the RVF/LH. In particular, in the RVF/LH moderately predictable completions were as facilitated as the strongly predictable (high cloze) completions, whereas, in the LVF/RH, moderately predictable completions were in fact no more facilitated than completely unexpected but plausible sentence endings. We might expect a similar pattern of LH benefit for processing moderately associated word pairs because lexical associative strength and cloze probability measures are both based on generative norms in response to context information, and thus could tap into similar processes.

Experimental Procedures

Participants

Thirty-two right-handed University of Illinois undergraduates (16 men) between the ages of 18 and 22 (mean age: 18.9 years) participated for cash or course credit. All were screened for normal vision and had no history of neuropsychological or psychiatric disorders. Participants were native English speakers who had not had early exposure (before age 5) to any other language. They were all right-handed (11 reported left-handed family members) with a mean handedness quotient of 0.76 (range: 0.31-1) as measured by the Edinburgh handedness inventory (Oldfield, 1971), where "1" is strongly right handed and "-1" is strongly left-handed.

Stimuli

Stimuli consisted of asymmetrically and symmetrically associated word pairs that shared minimal feature overlap[2]. Examples and associative strength characteristics are given in Table 1. Frequency measures were based on Kucera and Francis (1967) and measures of word association were based on association norms from Nelson et al. (1998).

One hundred and twenty-eight asymmetrically associated word pairs (e.g., *pillow-sleep*) were the same stimuli used in Kandhadai and Federmeier (2010); these were strongly associated in one direction, but weakly associated in the reverse direction. Half of these (64 items) were presented as forward pairs, which had a strong association from the prime to target. The other half were presented as backward pairs, with a weak association from the prime to target (and

[1]The cloze probability of a word in a given context (sentence fragment) is defined by the proportion of people who completed that particular sentence fragment with that particular word.

[2]All critical pairs were associated thematically; they were not synonyms, did not share categorical or whole-part relations, and did not have obvious feature overlap.

thus a strong association from the target to the prime). A set of sixty-four weakly but symmetrically associated pairs was chosen such that prime and target characteristics (frequency, length and parts of speech), and prime-to-target associative strength were matched one-to-one with those of the backward pairs[3]. In addition, forty-seven symmetrically associated word pairs that were moderately associated in both directions and forty-eight symmetrically associated pairs that were strongly associated[4] in both directions were included in the critical stimulus set. Finally, a set of two hundred and eighty-seven unrelated prime-target pairs were then matched for part of speech, length, and frequency with each subset of critical prime-target pairs using the MRC Psycholinguistic Database (Coltheart, 1987). Half of the targets in each condition appeared in each VF.

A second list was then created in which the order of the primes and targets in the original list of asymmetrical associates was reversed, such that the forward pairs became the backward pairs and vice versa. A new set of sixty-four weak symmetrical associates was chosen such that prime and target characteristics and prime-to-target associative strength were again matched on a one-to-one basis with those of the backward pairs in this second list. Matched unrelated word pairs for the new set of weakly associated pairs were created using the same procedure as for the first list. Moderately and strongly associated word pairs in the second list were the same as those used in the first list. Again, half of the targets in each condition appeared in each VF.

An additional set of two lists was created in which the VF of presentation from the two original lists was reversed. The resulting four lists were counterbalanced such that, across participants, each word pair appeared the same number of times in each VF (RVF, LVF).

Procedure

Stimuli were presented one word at a time on a 21″ SVGA monitor placed at a distance of 40″ from the participant, who was seated in a dim, quiet testing room. All words were presented in white, upper case letters against a black background; a red asterisk remained in the center of the screen throughout the experiment to help participants maintain central fixation. Participants received a short practice block before the experimental session, which was divided into six equal blocks.

At the start of each trial, four pluses appeared foveally for 500 ms with a random SOA of 800 to 1600 ms, used to minimize the influence of anticipatory potentials. The central prime was presented for 200 ms, followed, after an SOA of 950 ms, by the lateralized target, which was displayed for 200 ms. The target was lateralized so that its inside edge was two degrees from horizontal center; on average, targets subtended 2.5 degrees of horizontal visual angle (range: 1.5 to 4 degrees) and 0.5 degrees of vertical visual angle. 1300 ms after the target, a question mark appeared in the center of the screen for 2500 ms, at which point participants made a judgment as to whether the prime and the target were semantically related to each other. They were asked to press “yes” if the prime and the target “go together” in any meaningful way and were asked to press “no” otherwise. The purpose of this task was to ensure that participants were explicitly integrating the prime and target meanings. Hand used for the “yes” responses was counter-balanced across participants. Participants were instructed to blink only during the question mark. The next trial sequence then began after 500 ms.

[3]The prime-to-target strengths for backward pairs were significantly lower than the prime-to-target associative strengths for forward pairs (0.007 vs. 0.41; $F_{1,127} = 1690.73$; $p < 0.001$). However, the prime-to-target associative strengths for backward pairs were statistically indistinguishable from prime-to-target associative strengths for weakly associated symmetric pairs (0.007 vs. 0.007; $F_{1,127} < 1$).

[4]To obtain a large enough set of items that were strongly symmetrically related without significant feature overlap, it was necessary to include a number of antonym pairs, making these items different in important ways from the other pair types.

Data Collection

The EEG was recorded using 26 evenly spaced (see icon in Figure 1 for arrangement) Ag/AgCl electrodes placed in an electrode cap, referenced to the left mastoid. Electrode impedances were kept below 2 k-Ohms. Eye movements were recorded via electrodes placed on the outer canthus of each eye (referenced to one another) and blinks were monitored via an electrode placed on the left infraorbital ridge (also referenced to the left mastoid). EEG signals were amplified with a Sensorium 32 channel polygraph set to a band pass of 0.02 - 100 Hz, digitized at 250 Hz.

Data Analysis

The EEG activity was digitally filtered with a band pass of 0.2 - 20Hz and rereferenced offline to the algebraic mean of the left and right mastoids. One-second averages of artifact-free ERPs were calculated for target words in each condition after subtraction of the 100 millisecond pre-stimulus baseline. Trials contaminated by eye-movements, amplifier blocking, signal drift, or muscle activity was rejected off-line before averaging. Trials with eye blinks were corrected for those 9 participants with sufficiently stable blink filters (Dale, 1994) and rejected otherwise. Approximately 8.5% of trials were lost due to artifacts.

Results

Behavior

One participant was dropped from the behavioral analyses because of an error in recording the behavioral data. Response times were not analyzed because semantic judgment was a delayed task in this experiment. Accuracy measures (Table 2) were examined using separate repeated measures ANOVA analyses for asymmetrically and symmetrically associated word pairs.

Asymmetrically associated pairs—Response accuracy (percent correct) for asymmetrically associated targets was subjected to a three-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of relatedness (related, unrelated) and 2 levels of directionality (forward, backward) as factors. There were significant main effects of VF ($F_{1,30} = 13.97$, $p < 0.001$; RVF = 86.6% and LVF = 84.1%) and directionality ($F_{1,30} = 44.86$, $p < 0.001$; forward pairs = 86.6% and backward pairs = 84.1%) and an interaction between the two ($F_{1,30} = 10.02$, $p < 0.01$), reflecting a greater VF accuracy difference for the backward pairs. There was no main effect of relatedness ($F_{1,30} = 1.07$, $p > 0.3$), but relatedness interacted with VF ($F_{1,30} = 14.70$, $p < 0.001$), since differences across VF were driven by the related items. Relatedness also interacted directionality ($F_{1,30} = 91.61$, $p < 0.001$); within forward pairs, responses were most accurate for the related items, but, within backward pairs, were most accurate for the unrelated items.

Symmetrically associated pairs—Response accuracy (percent correct) for symmetrically associated pairs was subjected to a three-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of relatedness and 3 levels of strength (strong, moderate, weak) as factors. There was a main effect of VF, with more accurate responses to RVF than LVF targets (84.9% vs. 82.1%, $F_{1,30} = 14.41$, $p < 0.001$), and a main effect of relatedness, with more accurate responses to unrelated than related targets (86.2% vs. 80.8%, $F_{1,30} = 7.47$, $p < 0.05$). There was also a main effect of strength ($F_{2,60} = 67.57$, $p < 0.001$), revealing a graded pattern: strong: 88.3%, moderate: 85.8%, weak: 76.4%. VF interacted with both relatedness ($F_{1,30} = 25.96$, $p < 0.001$) and strength ($F_{2,60} = 10.88$, $p < 0.001$), which also interacted with each other ($F_{2,60} = 89.80$, $p < 0.001$). Mirroring patterns for asymmetrically associated pairs, differences across VF were more pronounced for moderately and weakly related pairs than for strongly related pairs, and were driven by responses to the related rather than the unrelated pairs. Within strongly associated pairs, responses were most accurate for the related items, but, within weakly associated pairs, were most accurate for the unrelated items.

Electrophysiological Recordings

Similar to prior studies using lateralized words (e.g., Kandhadai & Federmeier, 2008), target words in all conditions elicited early sensory ERP components characteristic of visual stimuli, which were larger and earlier over sites contralateral to presentation VF. Visual evoked potentials were followed by a centro-posterior negativity peaking around 400 ms (N400) and a posterior positivity (LPC) between about 500 and 900 ms. Effects on the N400 and LPC were characterized using separate repeated measures analyses of variance (ANOVAs) for asymmetrically and symmetrically associated targets. Further, the nature of semantic priming for backward pairs was explored through direct difference wave comparisons (a point by point subtraction of the related from the lexically matched unrelated ERPs for each condition) between backward and matched weakly associated targets. Electrode main effects and interactions are not reported, as these were not of theoretical significance. All *p*-values for repeated measures with greater than one degree of freedom are reported after Greenhouse–Geisser epsilon corrections.

Asymmetrically associated pairs—Grand average ERP waveforms in each VF for asymmetrically associated targets in each condition (forward, backward, unrelated) at all 26 electrode sites are shown in Figure 1.

N400: N400 mean amplitudes for asymmetrically associated targets, measured between 350 and 500 ms over the 11 centro-posterior channels (marked on Figure 2) that typically exhibit maximal N400 effects, were subjected to a four-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of relatedness (related, unrelated), 2 levels of directionality (forward, backward), and 11 levels of electrode as factors. There was no main effect of visual field ($F_{1,31} = 2.41$, $p > 0.13$), but there were main effects of relatedness ($F_{1,31} = 71.04$, $p < 0.001$) and directionality ($F_{1,31} = 47.48$, $p < 0.001$). N400 amplitudes were reduced to related targets compared with unrelated targets (1.83 μV vs. -0.99 μV) and were reduced for forward compared with backward targets (1.04 μV vs. -0.20 μV). The only significant interaction was between relatedness and directionality ($F_{1,31} = 12.47$, $p < 0.01$). Follow-up comparisons revealed that in both the forward and backward conditions related targets elicited significantly reduced N400 amplitudes relative to their unrelated counterparts (Fwd: 2.89 μV vs. -0.85 μV, $F_{1,31} = 57.15$, $p < 0.001$; Bwd: 0.73 μV vs. -1.13 μV, $F_{1,31} = 33.09$, $p < 0.001$). However, whereas responses to the unrelated targets were comparable across forward and backward conditions ($F_{1,31} = 1.33$, $p > 0.25$), responses to related targets were more facilitated (smaller N400s) in the forward than in the backward condition ($F_{1,31} = 32.23$, $p < 0.001$).

Planned comparisons were conducted on the difference waves (a point by point subtraction of the related from the lexically matched unrelated ERPs for each condition) to focus on priming effects within and across VF. As shown in Figure 2, in both VFs, related targets were more facilitated in the forward than in the backward condition (RVF: 4.03 μV vs. 1.62 μV, $F_{1,31} = 14.65$, $p < 0.001$; LVF: 3.26 μV vs. 1.87 μV, $F_{1,31} = 4.31$, $p < 0.05$). Comparisons across VF revealed no significant differences in priming for either the forward or backward conditions (Fwd: $F_{1,31} = 2.28$, $p > 0.14$; Bwd: $F_{1,31} < 1$). These priming effects replicated patterns of N400 facilitation obtained in the prior study (Kandhadai & Federmeier, 2010).

LPC: The 11 electrode sites used for the N400 analyses were also analyzed in the later time window (600-900 ms) to examine effects on the LPC. A repeated measures ANOVA on the LPC mean amplitudes for asymmetrically associated targets was conducted with 2 levels of VF (RVF, LVF), 2 levels of relatedness (related, unrelated), 2 levels of directionality (forward, backward), and 11 levels of electrode as factors. Different from the results obtained in the passive task (Kandhadai & Federmeier, 2010), there was no main effect of visual field and no main effect of directionality. There was a main effect of relatedness, with more positive LPC amplitudes to related targets than unrelated targets (4.93 μV vs. 1.52 μV, $F_{1,31} = 177.05$, $p < 0.001$). None of the interactions was significant.

Planned comparisons (see Figure 2) conducted on the difference waves (subtraction of related targets from lexically matched unrelated targets) showed that, in both VFs, there were no differences between priming for forward and backward pairs (RVF: 3.88 μV vs. 3.20 μV, $F_{1,31} = 1.55$, $p > 0.20$; LVF 2.79 μV vs. 3.00 μV, $F_{1,31} < 1$). There was significantly greater LPC priming in the RVF than in the LVF for forward pairs (3.88 μV vs. 2.80 μV, $F_{1,31} = 5.95$, $p < 0.03$). However, crucially, facilitation for backward pairs was statistically indistinguishable across VFs ($F_s < 1$). These results diverge from the LPC effect patterns obtained in the previous study (Kandhadai & Federmeier, 2010), in that, under the conditions imposed by an explicit semantic judgment task, both hemispheres strategically amplified priming for the backward pairs.

Symmetrically associated pairs—Grand average ERPs at the 26 electrode sites for all symmetrically associated targets (strong, moderate, weak, unrelated) are shown in Figure 3.

N400: As for asymmetrically associated targets, N400 mean amplitudes for symmetrically associated targets were subjected to a four-way repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of relatedness (related, unrelated), 3 levels of strength (strong, moderate, weak), and 11 levels of electrode as factors. There was no main effect of visual field ($F_{1,31} = 2.24$, $p > 0.14$), but there were main effects of relatedness ($F_{1,31} = 80.79$, $p < 0.001$) and strength ($F_{2,62} = 58.70$, $p < 0.001$, $\varepsilon = 0.99$). N400 amplitudes were reduced to related targets compared with unrelated targets (2.23 μV vs. -0.96 μV) and were graded by strength, with the most facilitated (smallest) N400s to the strongly associated targets (strong: 2.15 μV, moderate: 0.34 μV, weak: -0.59 μV). There was a significant interaction between visual field and relatedness ($F_{1,31} = 12.42$, $p < 0.01$), between relatedness and strength ($F_{2,62} = 51.60$, $p < 0.001$, $\varepsilon = 0.82$) and among visual field, relatedness and strength ($F_{2,62} = 5.24$, $p < 0.01$, $\varepsilon = 0.86$).

As before, these interactions were explored by means of planned pairwise comparisons on the difference waves (subtraction of the related ERPs from lexically matched unrelated ERPs) to investigate priming effect patterns within and across VF. In the RVF (shown in Figure 4), N400 facilitation was graded by associative strength: strongly associated targets (6.49 μV) were significantly more facilitated ($F_{1,31} = 22.79$, $p < 0.001$) than moderately associated targets (3.50 μV) which, in turn, were significantly more facilitated ($F_{1,31} = 27.09$, $p < 0.001$) than weakly associated targets (0.73 μV). However, in the LVF, N400 facilitation was significantly greater ($F_{1,31} = 19.44$, $p < 0.001$) for strong associates (4.73 μV) than moderate associates (1.89 μV), which did not differ significantly ($F_{1,31} = 1.92$, $p > 0.17$) from facilitation for weak associates (1.15 μV).

Across VF, there was significantly more priming in the RVF/LH than in the LVF/RH for both strongly associated targets (6.49 μV vs. 4.73 μV, $F_{1,31} = 11.71$, $p < 0.002$) and moderately associated targets (3.50 μV vs. 1.89 μV, $F_{1,31} = 8.21$, $p < 0.008$), but there were no priming differences across VF for weakly associated targets (0.73 μV vs. 1.15 μV, $F_s < 1$).

LPC: Using the same strategy as for the N400 time window, LPC mean amplitudes for these pairs were subjected to a repeated measures ANOVA with 2 levels of VF (RVF, LVF), 2 levels of relatedness (related, unrelated), 3 levels of strength (strong, moderate, weak), and 11 levels of electrode as factors. There was a main effect of visual field, with more positive LPC amplitudes in the RVF than in the LVF (3.45 μV vs. 2.97 μV, $F_{1,31} = 5.02$, $p < 0.05$), and a main effect of relatedness with more positive LPC amplitudes for related targets than for unrelated targets (4.82 μV vs. 1.61 μV, $F_{1,31} = 121.66$, $p < 0.001$). There was also a main effect of strength ($F_{2,62} = 37.18$, $p < 0.001$, $\varepsilon = 0.91$) such that LPC amplitudes were graded according to the strength of association, with the most positive LPC amplitudes to strongly associated targets (strong: 4.02 μV, medium: 3.48 μV, weak: 2.14 μV). There was a significant interaction between strength and visual field ($F_{2,62} = 3.86$, $p < 0.05$, $\varepsilon = 0.99$) and between strength and relatedness ($F_{2,62} = 21.29$, $p < 0.001$, $\varepsilon = 0.85$).

In both VFs, there was marginally greater LPC enhancement for strongly associated than moderately associated targets (RVF: 4.92 μV vs. 3.59 μV, $F_{1,31} = 2.90$, $p < 0.10$; LVF: 4.22 μV vs. 2.83 μV, $F_{1,31} = 3.60$, $p < 0.07$). Moderately associated targets, in turn, elicited significantly greater LPC enhancements than weakly associated targets (RVF: 3.59 μV vs. 1.15 μV, $F_{1,31} = 20.18$, $p < 0.001$; LVF: 2.83 μV vs. 1.56 μV, $F_{1,31} = 5.28$, $p < 0.05$). There were no significant differences in priming across VF in strong, moderate or weakly associated conditions ($F_s < 1.33$, $p > 0.25$ in all cases). LPC effect patterns are shown in Figure 4. Thus, different from the effect pattern on the N400, in both VFs LPC facilitation for symmetrically associated pairs was graded by associative strength.

Priming for backward vs. weakly associated pairs—Because prime-to-target associative strength was specifically controlled for between backward and weakly associated pairs, priming effects for backward (asymmetric) and weakly associated (symmetric) conditions could be compared within each VF to explore the influence of strong target-to-prime associative strength for backward pairs. Again, as with symmetrically and asymmetrically associated pairs, priming effect comparisons were conducted on the difference waves (related minus lexically matched unrelated ERPs for each condition).

N400: In the RVF (see Figure 5), there was marginally greater N400 facilitation for backward pairs than weakly associated pairs (1.62 μV vs. 0.73 μV, $F_{1,\,31} = 3.20$, $p = 0.083$) whereas in the LVF there were no priming differences between backward and weakly associated pairs (1.87 μV vs. 1.15 μV, $F_{1,\,31} = 1.71$, $p > 0.20$).

LPC: Of greatest import to the goals of the current study, priming effects for backward (asymmetric) and weakly associated (symmetric) conditions were compared to elucidate the nature of the LPC priming observed for the backward pairs. In both VFs (see Figure 5), targets in the backward pairs were more facilitated than matched targets in the weakly associated symmetrical pairs (RVF: 3.20 μV vs. 1.15 μV, $F_{1,\,31} = 20.29$, $p < 0.001$; LVF: 3.00 μV vs. 1.56 μV, $F_{1,\,31} = 4.77$, $p < 0.05$). Thus, in both VFs, the strategic processing of backward pairs seemed to, at least in part, reflect an ability to flexibly reorder and/or process associative relations in an order-independent fashion in service of apprehending the strong reverse association from target to prime.

Summary

Analyses of accuracy measures (percent correct) revealed that overall accuracy was good in both VFs (RVF = 85.6% and LVF = 82.9%), confirming that participants paid attention to the experimental stimuli and succeeded in making explicit semantic judgments. Participants generally made more accurate judgments for RVF than for LVF words, consistent with general biases favoring word recognition in the RVF/LH (e.g., Jordan, Patching, & Thomas, 2003). Participants' accuracy was graded based on associative strength, with more accurate responses to forward and strong symmetrically associated targets than to backward and weak symmetrically associated targets.

The ERP effect patterns showed that the two hemispheres elicited similar patterns of responses on the LPC, which has been linked to strategic aspects of, in this case, semantic processing. Different from the findings in the passive version of this paradigm (Kandhadai & Federmeier, 2010), in the present task where participants explicitly judged semantic relations, there was equivalent facilitation for forward and backward pairs in both hemispheres. These results show that the RH, much like the LH, is capable of recruiting strategic processes to aid meaning processing under some task conditions. Critically, in both VFs, targets in the backward pairs were more facilitated than those in weakly associated pairs, suggesting that at least part of the strategic processing of the backward pairs involved an appreciation of the strong reverse association from target to prime.

N400 amplitudes, linked to earlier, more implicit aspects of semantic activation, were largely graded by associative strength in both VFs. In both VFs, there was greater N400 priming for forward and strong symmetrically associated targets than for backward and weak symmetrically associated targets. Further, in both VFs, strong symmetrically associated targets were significantly more facilitated than the moderately associated targets. However, whereas moderately associated targets were more facilitated than weakly associated targets in RVF/LH, these pairs were similarly facilitated in the LVF/RH. Patterns of N400 priming thus suggest that there was a LH benefit for processing moderately associated word pairs.

Discussion

In a prior study (Kandhadai & Federmeier, 2010), we found a LH benefit for the strategic processing of asymmetrically associated backward pairs (e.g., *sleep-pillow*) that possessed a weak association from prime to target but a strong reverse association from target to prime. In particular, the late positive complex (LPC), an ERP component shown to be sensitive to more strategic, controlled aspects of processing, in semantics as well as other cognitive domains (Van Petten et al., 1991; Swaab et al., 1998; Olichney et al., 2000), was larger in the RVF/LH than in the LVF/RH for these backward pairs. In fact, in the RVF/LH, LPC priming for backward pairs was equivalent to that for forward pairs (e.g., *pillow-sleep*). Therefore, under the passive task conditions used in that study – participants read the words silently with the goal of remembering them for later – only the LH seemed to be able to strategically reshape weak meaning relations.

The current follow-up study, therefore, had two main goals. First, we examined whether the RH might also be capable of strategic semantic processing under task conditions that promote explicit appreciation of semantic relationships, as when making overt semantic judgments. Consistent with prior findings (Kandhadai & Federmeier, 2010), LPC enhancements were similar for forward and backward pairs in the RVF/LH. However, different from the pattern in the passive task, when participants actively judged the semantic relationship between the words, LPC priming in the LVF/RH showed the same pattern as the RVF/LH, with as much facilitation for backward as for forward pairs. These data clearly suggest that both hemispheres are able to strategically enhance the processing of backward pairs, although the LH seems more likely to naturally recruit such controlled semantic mechanisms even under passive task conditions. These results thus accord with prior work suggesting that the RH is more likely to engage in effortful semantic processing mechanisms when these are actively called upon by the task demands (e.g., (Meyer & Federmeier, 2008; Bowden & Jung-Beeman, 2003).

The second and primary goal of the present study was to more precisely delineate the nature of this controlled semantic processing. In particular, we examined whether the enhanced LPC response to the backward pairs reflects a general ability to amplify weak meaning relations or a more specific ability to flexibly appreciate the strong reverse association from target to prime. To address this issue, we compared priming patterns for backward pairs and matched symmetrically associated word pairs, which had the same weak meaning relationship in the forward direction but did not have the strong reverse relationship. In both VFs, we found greater LPC enhancements for backward pairs than for weakly associated pairs, suggesting that the benefit for backward pairs was, at least in part, due to a strategic appreciation of the strong reverse association from target-to-prime.

The ability to strategically build and appreciate semantic relations beyond the constraints imposed by the linear order of input is a skill that, on any model, would seem to be critical for the processing of sentences and other higher-order language structures, allowing, for example, the flexible establishment of agreement and coreferencing (e.g., “Fred needed the file, so Jennifer gave it to him”; “Because he needed it, Jennifer gave the file to Fred”). The “reordering” of conceptual information in the service of comprehension has been linked to working memory resources (e.g., Munte, Schiltz, & Kutas,1998), and, consistent with this, functional neuroimaging and lesion studies have suggested that at least part of the source for LPC activity may be left inferior frontal gyrus, a region that has been associated with controlled semantic retrieval and verbal working memory (see, Swick, Kutas, & Knight, 1998; Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Van Petten & Luka, 2006). Taken together, the present results, along with those from our prior study (Kandhadai & Federmeier, 2010) suggest that the LH may naturally engage such mechanisms across a wide range of task circumstances, but that the RH can also recruit these processes given sufficient task support (see also Meyer & Federmeier, 2007, 2008).

We also examined N400 activity to further investigate relatively automatic semantic processing in the cerebral hemispheres. The priming patterns replicated N400 effects observed in our prior study (Kandhadai & Federmeier, 2010), such that, in both VFs, forward pairs were more facilitated than backward pairs and there were no priming differences across VFs for either the forward or the backward pairs. Thus, contrary to the view that RH has impoverished access to associative information (Deacon et al., 2004), both the LH and the RH were similarly sensitive to associative strength. Similarly, we also failed to endorse the idea of coarse semantic coding in the RH (Jung-Beeman, 2005), as there was no RH processing advantage for either the backward or the weakly associated word pairs, suggesting broad similarity in semantic representations and activation in the two hemispheres.

However, patterns of N400 priming for the symmetrically associated pairs point to hemispheric differences that parallel asymmetries seen in sentence processing. For example, Wlotko and Federmeier (2007) found that, in the LVF/RH, moderately predictable sentence completions were no more facilitated than weakly predictable (low cloze) completions. In contrast, in the RVF/LH, these same moderately predictable completions were as facilitated as strongly predictable sentence completions. These findings were taken as support for the hypothesis that the LH is better able to make use of context information to predict likely upcoming words, even when that context information has only moderate predictive value (Federmeier, 2007). A similar pattern emerged in the current study. In the RVF/LH, N400 facilitation was graded by associative strength: strongly associated targets were more facilitated than moderately associated targets, which in turn, were more facilitated than weakly associated targets. In contrast, in the LVF/RH, even though strongly associated targets were significantly more facilitated than moderately and weakly associated targets, priming for the latter two conditions was statistically indistinguishable. Thus, whether predictability arises through sentential constraints, as indexed by cloze probability, or through lexical association, as indexed by generation norms, the LH seems to make more effective use of moderately predictive context information. These results are consistent with the “PARLO” (Production Affects Reception in Left Only)” framework (Federmeier, 2007) in suggesting that the LH is able to better recruit top-down semantic mechanisms to predict and prepare for likely upcoming information based on current context. The PARLO framework posits that comprehension mechanisms are integrated with language production mechanisms only in the LH, which is dominant for speech. Therefore, whereas processing in the RH will tend to be feed-forward in nature, the LH is able to make use of strong feedback connections that allow context-based predictions – even from moderately predictive cues – to shape processing for likely upcoming words at multiple levels during comprehension.

In conclusion, the cerebral hemispheres differ in when and how they recruit top-down semantic mechanisms to glean meaning from words. Consistent with findings that emanate from the sentence processing literature, the current work suggests that the left hemisphere predicts likely upcoming information based on current context and is also more likely to flexibly reorder and/or process language elements in an order-independent fashion to apprehend meaning relations even under passive task conditions. In turn, the right hemisphere also seems able to recruit such strategic semantic integration processes, but may require more task support to do so.

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References

Anaki D, Faust M, Kravetz S. Cerebral hemispheric asymmetries in processing lexical metaphors. Neuropsycholgia 1998;36:353–362.

Banich, MT. The divided visual field technique in laterality and interhemispheric integration.. In: Hugdahl, K., editor. Experimental methods in neuropsychology. Kluwer; Boston: 2002. p. 47-64.

Beeman, M. Coarse semantic coding and discourse comprehension.. In: Chiarello, C.; Beeman, M., editors. Right hemisphere language comprehension: Perspectives from cognitive neuroscience. Lawrence Erlbaum Associates; Mahwah, NJ: 1998. p. 255-284.

Beeman M, Friedman R, Grafman J, Perez E, Diamond S, Lindsay M. Summation priming and coarse semantic coding in the right hemisphere. Journal of Cognitive Neuroscience 1994;6:26–44.

Bowden EM, Jung-Beeman M. Aha! Insight experience correlates with solution activation in the right hemisphere. Psychonomic Bulletin and Review 2003;10:730–737. [PubMed: 14620371]

Burgess C, Simpson GB. Cerebral hemispheric mechanisms in the retrieval of ambiguous word meanings. Brain and Language 1988;33:86–103. [PubMed: 3342321]

Chiarello C. Hemisphere dynamics in lexical access: Automatic and controlled priming. Brain and Language 1985;26:146–172. [PubMed: 4052742]

Chiarello C, Richards L, Pollock A. Semantic additivity and semantic inhibition: Dissociable processes in the cerebral hemispheres? Brain and Language 1992;42:52–76. [PubMed: 1547469]

Chiarello C, Senehi J, Nuding S. Semantic Priming with abstract and concrete words: Differential asymmetry may be post-lexical. Brain and Language 1987;18:153–163.

Collins M. Differences in semantic category priming in the left and right cerebral hemispheres under automatic and controlled processing conditions. Neuropsychologia 1999;37:1071–1085. [PubMed: 10468370]

Coltheart M. MRC Psycholinguistic Database: Machine Usable Dictionary. The Quarterly Journal of Experimental Psychology 1987;33A:497–505.

Coney J, Evans KD. Hemispheric asymmetries in the resolution of lexical ambiguity. Neuropsychologia 2000;38:272–282. [PubMed: 10678693]

Dale, AM. Source localization and spatial discriminant analysis of event-related potentials: Linear approaches. University of California San Diego; LaJolla, CA: 1994.

Deacon D, Grose-Fifer J, Yang CM, Stanick V, Hewitt S, Dynowska A. Evidence for a new conceptualization of semantic representation in the left and right cerebral hemispheres. Cortex 2004;40:467–478. [PubMed: 15259327]

Faust M, Chiarello C. Constraints on Sentence Priming in the Cerebral Hemispheres: Effects of Intervening Words in Sentences and Lists. Brain and Language 1998a;63:219–236. [PubMed: 9654432]

Faust M, Chiarello C. Sentence context and lexical ambiguity resolution by the two hemispheres. Neuropsychologia 1998b;36:827–835. [PubMed: 9740356]

Faust ME, Gernsbacher MA. Cerebral mechanisms for suppression of inappropriate information during sentence comprehension. Brain and Language 1996;53:234–259. [PubMed: 8726535]

Federmeier KD. Thinking ahead: the role and roots of prediction in language comprehension. Psychophysiology 2007;44:491–505. [PubMed: 17521377]

Federmeier, KD.; Laszlo, S. Time for meaning: Electrophysiology provides insights into the dynamics of representation and processing in semantic memory.. In: Ross, BH., editor. Psychology of Learning and Motivation. Vol. 51. Academic Press; Burlington: 2009. p. 1-44.

Federmeier KD, Wlotko E, Meyer AM. What's "right" in language comprehension: ERPs reveal right hemisphere language capabilities. Language and Linguistics Compass 2008;2:1–17. [PubMed: 19777128]

Gouldthorp B, Coney J. The sensitivity of the right hemisphere to contextual information in sentences. Brain and Language 2009;110:95–100. [PubMed: 19525004]

Hagoort P. Impairments of lexical-semantic processing in aphasia: Evidence from the processing of lexical ambiguities. Brain and Language 1993;45:189–232. [PubMed: 8358597]

Johns CL, Tooley KM, Traxler MJ. Discourse Impairments Following Right Hemisphere Brain Damage: A Critical Review. Language and Linguistics Compass 2008;2:1038–1062.

Jordan TR, Patching GR, Thomas SM. Assessing the Role of Hemispheric Specialisation, Serial-Position Processing, and Retinal Eccentricity in Lateralised Word Recognition. Cognitive Neuropsychology 2003;20:49–71. [PubMed: 20957564]

Jung-Beeman M. Bilateral brain processes for comprehending natural language. Trends in Cognitive Sciences 2005;9:512–518. [PubMed: 16214387]

Kandhadai P, Federmeier KD. Multiple priming of lexically ambiguous and unambiguous targets in the cerebral hemispheres: The coarse coding hypothesis revisited. Brain Research 2007;1153:144–157. [PubMed: 17459344]

Kandhadai P, Federmeier KD. Summing it up: Semantic activation processes in the two hemispheres as revealed by event-related potentials. Brain Research 2008;1233:146–159. [PubMed: 18675257]

Kandhadai P, Federmeier KD. Automatic and controlled aspects of lexical associative processing in the two cerebral hemispheres. Psychophysiology. 2010

Kucera, H.; Francis, WN. Computational analysis of present day American English, Providence. Brown Univ. Press; Providence, RI: 1967.

Matsumoto A, Iidaka T, Haneda K, Okada T, Sadato N. Linking semantic priming effect in functional MRI and event-related potentials. Neuroimage 2005;24:624–634. [PubMed: 15652298]

Meyer AM, Federmeier KD. The effects of context, meaning frequency, and associative strength on semantic selection: Distinct contributions from each cerebral hemisphere. Brain Research 2007;1183:91–108. [PubMed: 17936727]

Meyer AM, Federmeier KD. The divided visual world paradigm: eye-tracking reveals hemispheric asymmetries in lexical ambiguity resolution. Brain Research 2008;1222:166–183. [PubMed: 18585683]

Munte TF, Schiltz K, Kutas M. When temporal terms belie conceptual order: an electrophysiological analysis. Nature 1998;395:71–73. [PubMed: 9738499]

Nakagawa A. Role of anterior and posterior attention networks in hemispheric asymmetries during lexical decision. Journal of Cognitive Neuroscience 1991;3:313–321.

Nelson, DL.; McEvoy, CL.; Schreiber, TA. The University of South Florida word association, rhyme, and word fragment norms. 1998. http://www.usf.edu/FreeAssociation/

Oldfield RC. The assessment and analysis of handedness: The Edinburgh Inventory. Neuropsychologia 1971;9:97–113. [PubMed: 5146491]

Olichney J, Van Petten C, Paller K, Salmon D, Iragui V, Kutas M. Word repetition in amnesia: Electrophysiological measures of impared and spared memory. Brain 2000;123:1948–1963. [PubMed: 10960058]

Paller KA, Kutas M, McIsaac HK. Monitoring conscious recollection via the electrical activity of the brain. Psychological Science 1995;6(2):107–111.

Richards L, Chiarello C. Depth of associated activation in the cerebral hemispheres: mediated versus direct priming. Neuropsychologia 1995;33:171–179. [PubMed: 7746362]

Schmidt GL, DeBusea CJ, Segera CA. Right hemisphere metaphor processing? Characterizing the lateralization of semantic processes. Brain and Language 2007;100:127–141. [PubMed: 17292739]

Swaab TY, Brown C, Hagoort P. Understanding ambiguous words in sentence contexts: electrophysiological evidence for delayed contextual selection in Broca's aphasia. Neuropsychologia 1998;36:737–761. [PubMed: 9751439]

Swick D, Kutas M, Knight RT. Prefrontal lesions eliminate the LPC but do not affect the N400 during sentence reading. Journal of Cognitive Neuroscience Supplement 1998;5:29.

Tompkins, CA.; Fassbinder, W.; Lehman-Blake, MT.; Baumgaertner, A. The nature and implications of right hemisphere language disorders: Issues in search of answers.. In: Hillis, A., editor. Handbook of adult language disorders: Integrating cognitive neuropsychology, neurology, and rehabilitation. Psychology Press; New York: 2002. p. 429-448.

Van Petten C, Kutas M, Kluender R, Mitchiner M, McIsaac H. Fractionating the word repetition effect with event-related potentials. Journal of Cognitive Neuroscience 1991;3:131–150.

Van Petten C, Luka BJ. Neural localization of semantic context effects in electromagnetic and hemodynamic studies. Brain and Language 2006;97:279–293. [PubMed: 16343606]

Wlotko E, Federmeier KD. Finding the right word: Hemispheric asymmetries in the use of sentence context information. Neuropsychologia 2007;45:3001–3014. [PubMed: 17659309]

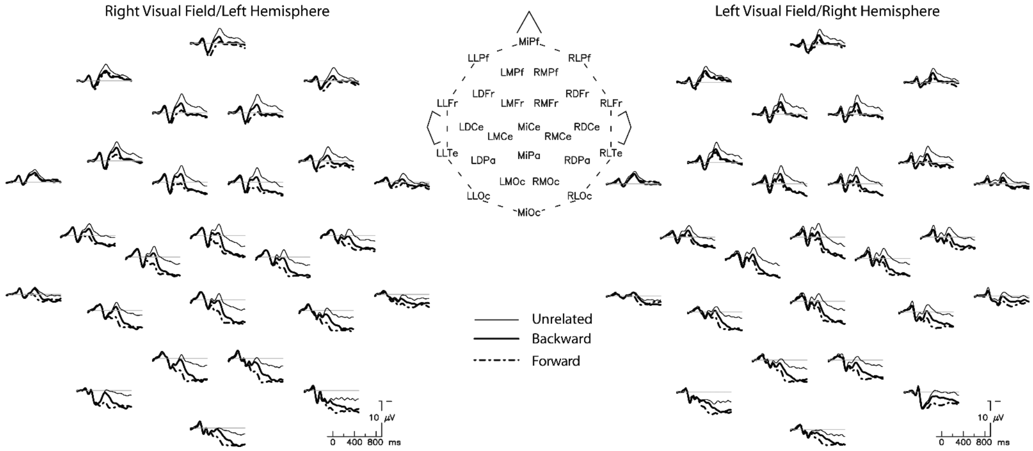

Figure 1.

Plotted are grand average (N=32) ERPs at all 26 electrode sites for target words in the forward and backward pairs and a representative unrelated (backward-matched) condition. The head diagram shows the electrode arrangement. Right visual field (RVF/LH) targets are plotted on the left side of the figure and left visual field (LVF/RH) targets are plotted on the right. Negative is plotted up here and in all subsequent figures. In both VFs, N400 amplitudes were graded by associative strength and LPC amplitudes were more positive for associated (forward and backward) compared to unrelated targets.

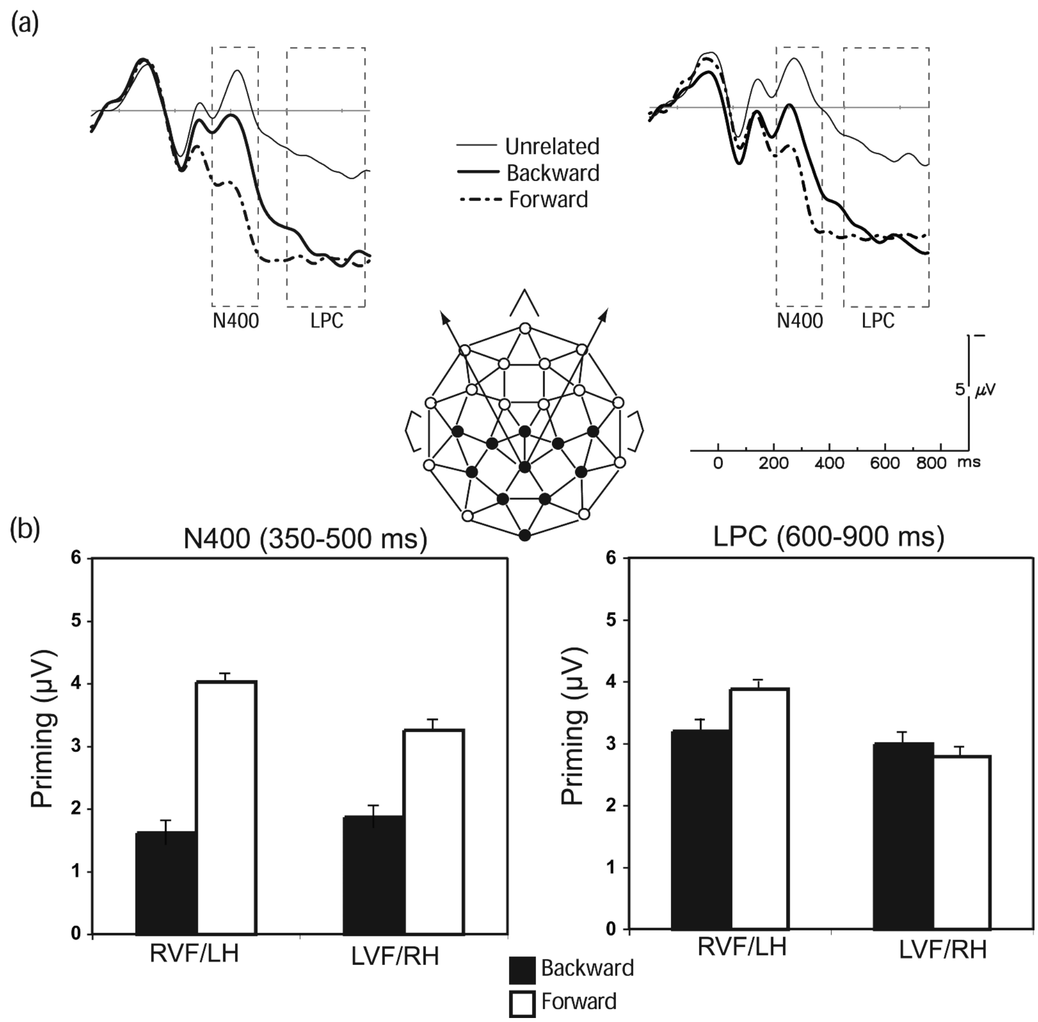

Figure 2.
(a) Plotted are grand average ERPs to targets in the forward, backward and unrelated conditions at a representative channel (middle parietal), with N400 (350-500 ms) and LPC (600-900 ms) time windows marked. Statistical analyses were always conducted using the eleven central-posterior channels marked (filled circles) on the head diagram. (b) In both VFs, N400 priming (related minus lexically matched unrelated) was sensitive to prime-to-target associative strength, with more priming for forward than backward pairs. However, LPC (600-900 ms) facilitation was statistically indistinguishable for forward and backward pairs in both VFs.

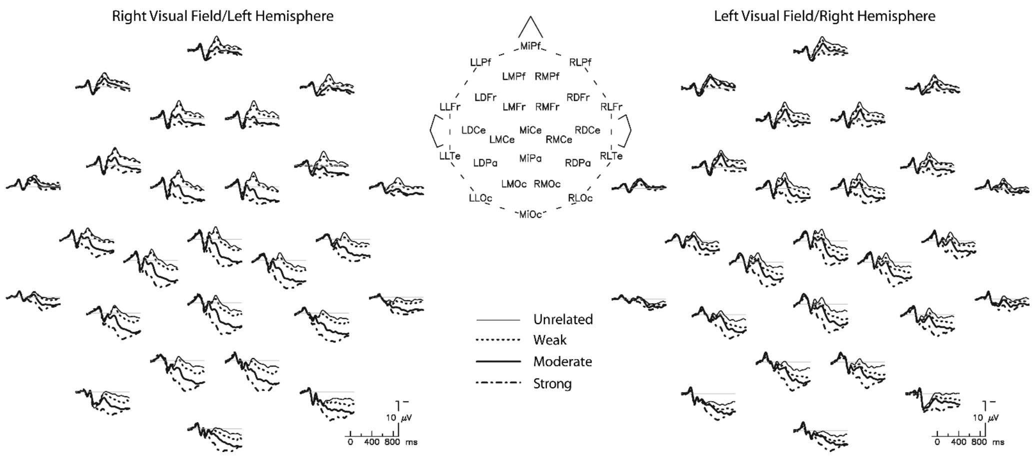

Figure 3.

Plotted are grand average ERPs to symmetrically associated (strong, moderate, weak) and unrelated targets at all 26 scalp sites. Again, in both VFs, N400 amplitudes were graded by associative strength and LPC amplitudes were more positive for associated (forward and backward) than for unrelated targets.

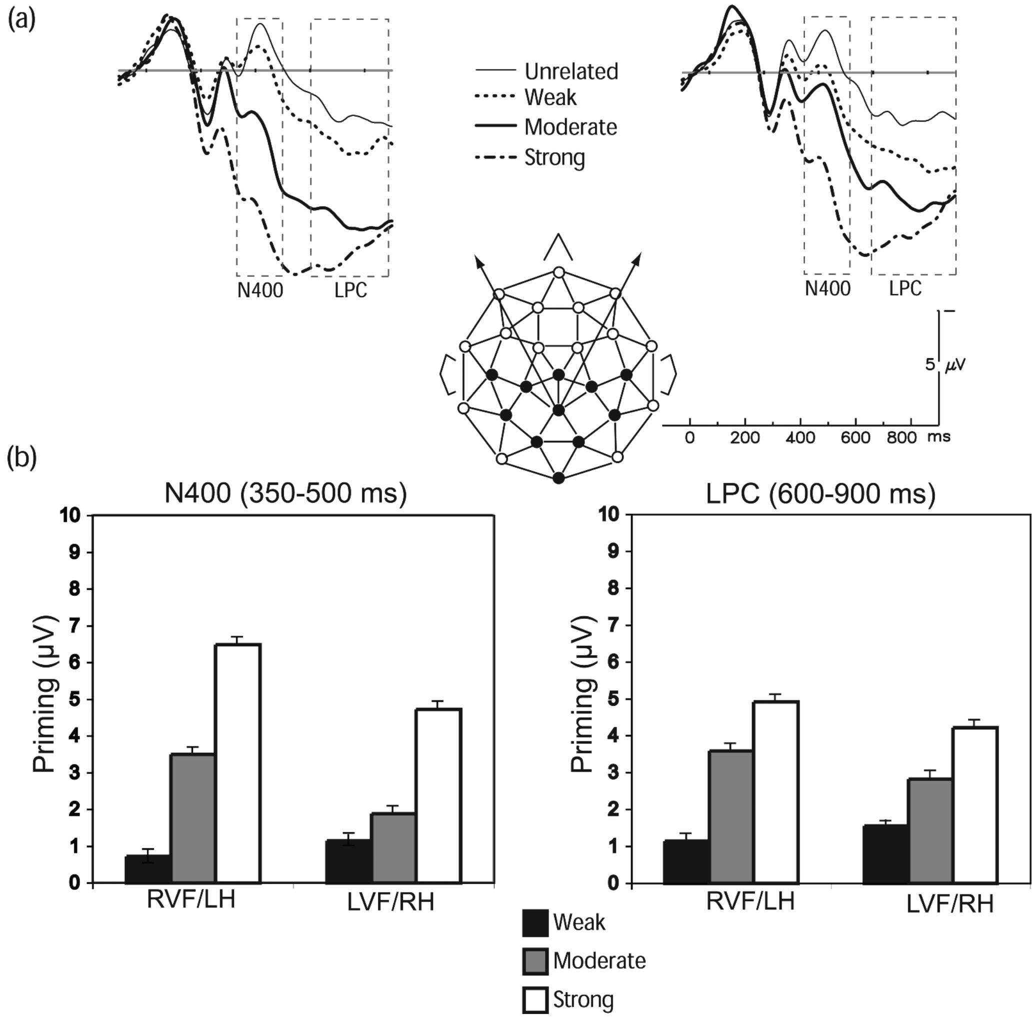

Figure 4.
(a) Plotted are grand average ERPs to targets in the symmetrical conditions (strong, moderate, weak, and unrelated) at the middle parietal scalp site. (b) In the RVF/LH, N400 facilitation was graded by associative strength, with significantly greater facilitation for strongly associated than moderately associated targets, which, in turn, elicited significantly greater priming than weakly associated targets. In the LVF/RH, there was significantly greater facilitation for strongly associated targets than moderately and weakly associated targets; priming for the latter two conditions was statistically indistinguishable.

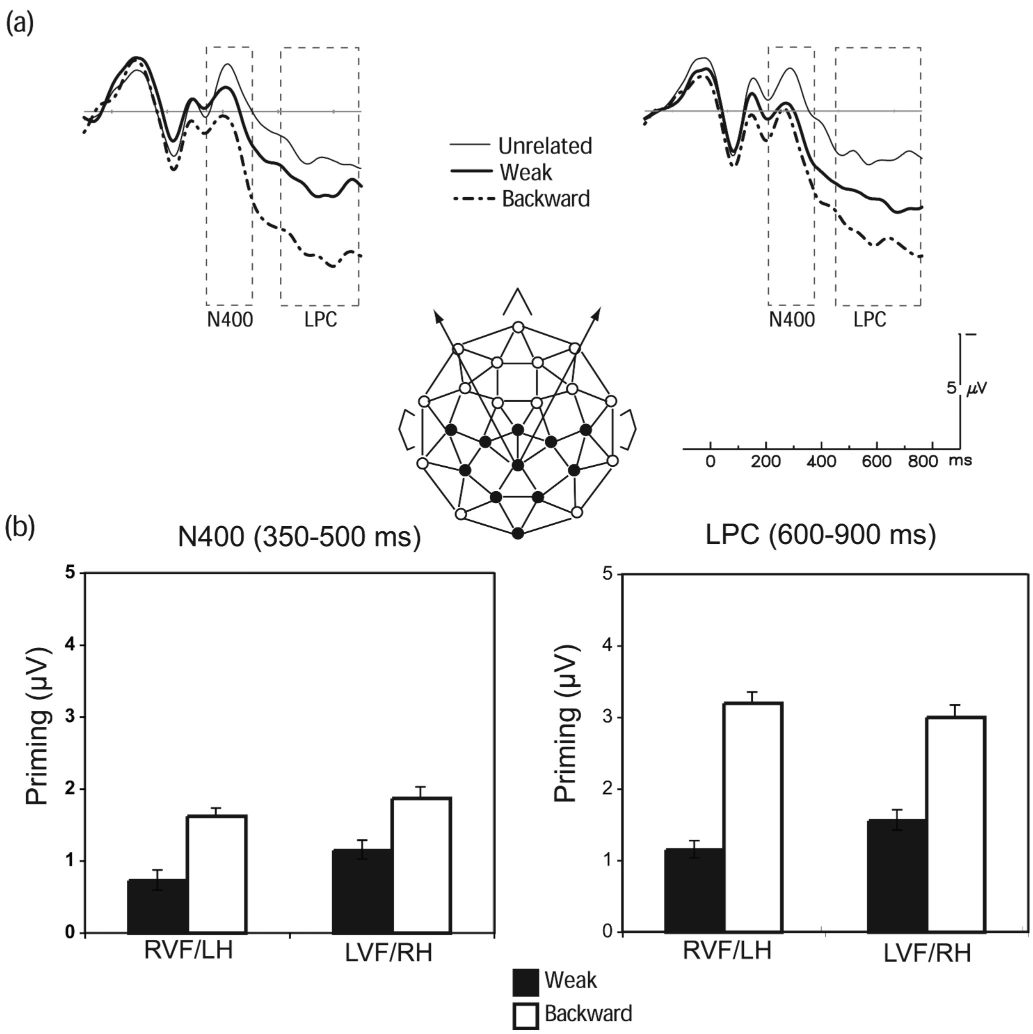

Figure 5.

(a) Plotted are grand average ERPs to targets in the backward, weak symmetrical and unrelated pairs at the middle parietal channel (b) In the RVF/LH, there was significantly greater N400 facilitation for backward than weakly associated pairs, but, in the LVF/RH, N400 priming for these conditions was statistically indistinguishable. In both VFs, there was significantly greater LPC facilitation for the backward than for the weak symmetrically associated targets.

Table 1

Associative strength characteristics with examples for each associated pair (backward, weak, forward, strong, moderate)

Related Pair Type	Related Pair	Mean Prime to Target Strength (range)	Mean target to prime strength (range)	Unrelated Pair
Weak prime-to-target strength				
Backward	House-Mortgage	0.007 (0-0.029)	0.41 (0.28-0.81)	Cheese-Intruder
Weak	Devil-Curse	0.007(0-0.029)	0.018 (0.01-0.029)	Grasp-Employ
Strong prime-to-target strength				
Forward	Pillow-Sleep	0.41 (0.28-0.81)	0.007 (0-0.029)	Monkey-Beach
Strong	Coral-Reef	0.46 (0.25-0.76)	0.47 (0.28-0.81)	Scar-Chat
Moderate prime-to-target strength				
Moderate	Cast-Ballot	0.11(0.08-0.19)	0.12 (0.08-0.18)	Fruit-Menace

Table 2

Mean percent correct (with standard error means in parentheses) for each condition in each VF

Condition	**RVF/LH**		**LVF/RH**	
	Related	**Unrelated**	**Related**	**Unrelated**
Asymmetrically associated pairs				
Forward	91.6 (3.1)	84.6(3.7)	89.1 (3.0)	87.2 (3.4)
Backward	82.4 (3.0)	87.7(3.2)	73.9 (2.6)	86.2 (3.6)
Symmetrically associated pairs				
Strong	92.0 (3.2)	83.8 (3.2)	90.1 (3.1)	87.4 (3.3)
Moderate	87.8 (3.2)	87.0 (3.5)	81.6 (2.9)	86.5 (3.6)
Weak	72.1 (2.7)	86.8 (3.3)	61.1 (2.4)	85.8 (3.4)