Evidence for Automatic Sentence Priming in the Fusiform Semantic Area: Convergent ERP and fMRI findings

Joseph Dien[1] and Aminda J. O'Hare[2]

[1]Birth Defects Center, University of Louisville, Louisville, KY

[2]Department of Psychology, University of Kansas, Lawrence, KS

Dien, J. and O'Hare, A.J. (2008). Evidence for Automatic Sentence Priming in the Fusiform Semantic Area: Convergent ERP and fMRI findings. Brain Research, 1243:134-145. (https://doi.org/10.1016/j.brainres.2008.09.045)

Abstract

Event-related potential (ERP) studies of semantic processing have generally focused on the N400, a component that peaks at about 400 ms in response to words and which is larger when words are incongruent with the preceding sentence context. An earlier left-lateralized posterior $N2_{p3}$ has also been found to be correlated with an "unexpectedness" rating for incongruent sentence endings (Dien, Frishkoff, Cerbone, & Tucker, 2003, Parametric analysis of event-related potentials in semantic comprehension: Evidence for parallel brain mechanisms, Cognitive Brain Research, 15: 137-153). Because the incongruent endings were too odd to be explicitly predicted, we here hypothesize that this rating, and hence the $N2_{p3}$, reflects the degree of automatic spreading activation (ASA) in the visual lexical network rather than semantic expectancy, an interpretation also consistent with the early latency of this ERP (208 ms).

In order to identify the brain systems involved in these linguistic processes, functional magnetic resonance imaging (fMRI) was utilized in a replication of the ERP study (Dien et al., 2003). We found that activation in the fusiform semantic area (FSA), an area that converges with the source solution for the $N2_{p3}$, responded to the "unexpectedness" parameter in the same manner as the $N2_{p3}$ component. These findings suggest that the FSA helps mediate ASA processes and that the $N2_{p3}$ can serve as an index of ASA. Furthermore, cloze effects were found in the superior frontal gyrus and the inferior frontal gyrus that could reflect subvocalization and semantic selection processes respectively.

Scope: 7. Cognitive and Behavioral Neuroscience

Keywords: Event-Related Potential, Language, Functional Magnetic Resonance Imaging, N200, Fusiform Gyrus, Automatic Spreading Activation

1. Introduction

Neurocognitive models of language are generally agreed to have started with the 19th Century reports of Broca's area (Broca, 1865) and Wernicke's area (Wernicke, 1874), now usually associated with syntactic and semantic processing respectively (for a review see Price, 2000). The dramatic nature of these impairments by relatively circumscribed lesions has strongly influenced thinking about language and provided strong support for the distinction between semantics and syntax.

With the development of the event-related potential (ERP) methodology, which provides millisecond resolution windows into neural processes, it was inevitable that initial efforts would focus on finding correlates of the apparently semantic Wernicke's area and the apparently syntactic Broca's area. The ERP component most consistently linked to semantic processing is the N400 (Kutas & Hillyard, 1980; Kutas & Schmitt, 2003) and is thought by some to emanate from the vicinity of Wernicke's area (Van Petten & Luka, 2006). Conversely, the left anterior negativity or LAN has been identified as a correlate of syntactic processing (Friederici, Pfeifer, & Hahne, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991) and is thought by some to emanate from the vicinity of Broca's area (Friederici, 2002; Friederici & Kotz, 2003).

The simple 19th Century language duality of Broca's area and Wernicke's area has been increasingly modified by continued elaborations of neurocognitive language models (Dien, in press; Fiez & Petersen, 1998; Jobard, Crivello, & Tzourio-Mazoyer, 2003; Joseph, Noble, & Eden, 2001; Price, 2000; Price & Mechelli, 2005; Vigneau et al., 2006). Indeed, a prominent report (Dick et al., 2001) has made the argument that both aphasia types suffer from both semantic and syntactic anomalies. Furthermore, a systematic lesion mapping study (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger,

2004) suggested that it is regions adjoining Broca's area and Wernicke's area that are most relevant to the aphasic symptoms, not the areas themselves, a conclusion that has been strengthened by reexamination of the brains of Broca's original patients (Dronkers, Plaisant, Iba-Zizen, & Cabanis, 2007).

These developments have helped shift attention to other potential language regions, especially the inferior temporal lobe, also known as the basal language area (Lüders et al., 1986; Lüders et al., 1991). Two parts of this region have been of special interest. The first is the visual word form area (VWFA), an area that has been implicated in orthographic analysis at the bigram level (Binder, Medler, Westbury, Liebenthal, & Buchanan, 2006; Dehaene, Cohen, Sigman, & Vinckier, 2005; Dien, in press; McCandliss, Cohen, & Dehaene, 2003). Another area has been termed the fusiform semantic area or FSA (Dien et al., 2008). According to a review (Moore & Price, 1999), this area, centered at [-32 -40 -20], is responsive to semantic manipulations. Recent studies (Gold et al., 2006; Wheatley, Weisberg, Beauchamp, & Martin, 2005) have reported that it reflects automatic spreading activation (ASA) effects in semantic priming paradigms.

While it is not entirely clear what the FSA does (the name was proposed to reflect its sensitivity to semantic manipulations rather than to claim that it mediates semantics), its anatomical location provides a clue. Studies strongly suggest a lexical pathway that runs along the basal language area from back to front, mediating a hierarchy of processing of increasingly higher-order representations (Dehaene et al., 2005; Dien, in press; Vinckier et al., 2007). Since the FSA lies just anterior to the VWFA, which seems to mediate associations at the bigram level, it should mediate a higher level of representation, perhaps even associations at the whole word level (Dien, in press). Such a hypothesis would be consistent with the finding (Gold et al., 2006;

Wheatley et al., 2005) that it responds to ASA. By this interpretation, this area would mediate ASA at the lexical level but not at the semantic level (if, as hypothesized, ASA can operate at either level: Collins & Loftus, 1975).

A primary obstacle in clarifying these issues is the matter of time course. Proper interpretation requires knowing whether activation is occurring during the initial stimulus analysis or at a later point. For example, in debates over the VWFA, a core question is why does a putative visual word area respond to other stimuli as well (Price & Friston, 1997; Price, Winterburn, Giraud, Moore, & Noppeney, 2003). In response (Cohen et al., 2002), it was suggested that these observations might reflect top-down activation, such as imaging the word "duck" in association with a picture of a duck. While blood flow measures lack the time resolution to distinguish between these two possibilities, it might be possible to do so with the millisecond time resolution of ERPs (Mangun, Hopfinger, & Jha, 2000; Mangun & Heinze, 1995).

The sample waveforms provided by an intra-cranial ERP report (Nobre, Allison, & McCarthy, 1994) seem to suggest that one would expect VWFA activations to peak in the range of about 150 ms and FSA to peak in the range of about 200 ms. Consistent with this observation are the reports of an $N170_{po7}$, a negativity peaking at 120-170 ms with maximum amplitude at electrode PO7 (Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Compton, Grossenbacher, Posner, & Tucker, 1991; McCandliss, Posner, & Givon, 1997; Spironelli & Angrilli, 2007) that is thought to reflect VWFA activity (for a review, see Dien, in press). As for the FSA, a possible ERP correlate peaking at 208 ms was observed in an ERP experiment (Dien, Frishkoff, Cerbone, & Tucker, 2003) that localized it to the basal language area. While tentatively identified as a Recognition Potential (Martín-Loeches, 2007; Rudell, 1991), it is now clear that it is rather a new ERP component and has been renamed an $N2_{p3}$, an N2 with

maximum amplitude at electrode P3 (Dien, in press).

This report (Dien et al., 2003) was inspired by a theory (Suls, 1972) that jokes are processed in a two-step process, first to register unexpectedness of the punch line and second to recognize that the punch line nonetheless makes sense. Lesion studies suggest that the first step is left-lateralized and the second step is right-lateralized (Bihrle, Brownell, Powelson, & Gardner, 1986; Brownell, Michel, Powelson, & Gardner, 1983). It seemed plausible that these two lateralized processes might play a role in the comprehension of normal sentences as well. In the study (Dien et al., 2003) sentences were presented to participants at the rate of one word per second. The task was to read for comprehension, with a recognition test during breaks to confirm compliance. Half the sentences ended congruently and half ended with incongruent word choices. A separate norming group rated the sentences according to how unexpected the final word was and according to how meaningful the sentences were in retrospect. Consistent with the lesion studies, a left-lateralized $N2_{p3}$ correlated with the expectancy ratings and a right-lateralized $N2_{t6}$ correlated with the meaningfulness ratings (Figure 1). Source analyses suggested that they emanated from the inferior temporal region, or even the cerebellum, of each hemisphere.

The nature of the "expectancy" effect further strengthens the hypothesized linkage to the FSA. Regarding the unexpectedness parameter, it seems unlikely that sentence endings such as "The hero who caught the thief deserves our domestic" (3.91) were any more part of the conscious expectancy set than "Fred relaxed in his chair on the back throat" (4.59). It seems more likely that this rating reflects subtle distinctions in the ASA of these words by the sentence context. Thus, when the raters of the norming group were presented with the ending word after reading the sentence stem, their ratings were influenced by the extent to which the word had already been partially

activated by indirect links. During the actual sentence reading, the expected word could be held explicitly in working memory, with automatic activation spreading from there. Since the FSA is influenced by ASA (Gold et al., 2006; Wheatley et al., 2005) one would therefore predict that the FSA should also respond to the "expectancy" parameter.

While the "expectancy" effect is likely ASA, there was another effect in the study (Dien et al., 2003) that more closely relates to what is conventionally termed expectancy. Cloze is the percentage of raters who spontaneously generate a specific sentence ending given just the sentence stem (Taylor, 1953). The ending with the highest cloze rating can be said to be consciously expected. Cloze is, by definition, only non-zero for congruent endings and can be said to be a parametric (meaning a continuous measure as opposed to a dichotomous measure) rating of congruency for congruent endings. Although neither the $N2_{p3}$ nor the $N2_{t6}$ correlated with cloze in the ERP study (Dien et al., 2003), both the conventional N400 as well as a left frontal N400 component strongly correlated with cloze (Figure 1). Source analysis of the frontal effect suggested a generator in the left dorsal premotor region, which was unexpected and therefore in need of confirmation. The cloze expectancy effect will therefore be contrasted with the "expectancy" ASA effect.

While the goal of the study is to co-register the ERP activity with fMRI activity, there is no certainty that each fMRI effect need necessarily be paired with an ERP effect (see Huettel et al., 2004; Martinez et al., 1999; Puce, Allison, Spencer, Spencer, & McCarthy, 1997). Nonetheless, both ERP and fMRI data reflect the modulation of dendritic inputs (Logothetis, Pauls, Augath, Trinath, & Oeltermann, 2001) and linearity between these measures is a good approximation (Sheth et al., 2004). Overall, it appears to be reasonable to seek correspondences between the two data modalities, with the understanding that such findings provide strong convergent validity whereas

lack of correspondence can occur for a variety of reasons and is subject to the usual caveats of a null effect. As for what constitutes a convergent result, electroencephalographic (EEG) source analysis even under ideal conditions (a single intense artificial source) has an average spatial resolution on the order of 1-2 centimeters (Cohen et al., 1990; Cuffin, Schomer, Ives, & Blume, 2001; Krings et al., 1999; Leahy, Mosher, Spencer, Huang, & Lewine, 1998). It will therefore be considered to be successful convergence if: 1) the solution falls within about 3 cm, 2) the fMRI activation shows the same pattern of responses to the manipulations as the ERP effect, and 3) the number of fMRI activations is so small (preferably just one) that it is unlikely that the proximity of the solution is due to coincidence.

A final aspect of the experimental design is that half the semantically incongruent endings were also syntactically anomalous in the sense of being the incorrect part of speech (see appendix). Although not relevant to the present purpose of this study, the stimulus list was kept unchanged in order to maximize comparability with the ERP results (Dien et al., 2003). In any case, long experience grading undergraduate papers suggests that having a mix of semantic and syntactic anomalies is more ecologically valid than having only semantic anomalies.

To summarize, this fMRI experiment replicates a prior ERP study (Dien et al., 2003) using a parametric event-related approach. A primary goal of this study is to determine if the FSA is a plausible source for the $N2_{p3}$ ASA effect, which would strengthen the case for the FSA playing a role in the initial stages of lexical processing. Of secondary interest is finding a plausible source for the $N2_{t6}$ meaningfulness effect and the frontal cloze effect. These three parametric analyses are of primary interest, although the main effects of congruency and of incongruency type will be examined as well for completeness sake.

2. Results

Behavioral Data

The average accuracy on the recognition tests was 83% with a range of 68% to 94%.

fMRI Data

For the fMRI results (Figure 2), cluster-level analysis (corrected for multiple comparisons) revealed bilateral prefrontal and left anterior cingulate areas that were more active for incongruent endings than congruent endings (Table 1). A direct comparison of the semantic and semantic+syntactic anomalies revealed two significant areas in the right occipital and the right lateral temporal regions, both more significant for semantic anomalies. No areas were significantly more active for the semantic+syntactic anomalies.

Turning to the parametric effects (Table 2), there were two significant clusters for less "expected" endings, a left ventral temporal area encompassing the FSA and a right cerebellar area. The "expectancy" effect had a most significant voxel of [-22 -40 -8] which was at the criterion distance (3 cm) from the source analysis result [-45 -60 -4] for the $N2_{p3}$ effect (Dien et al., 2003). Increased activations were also observed for high meaningfulness in the left inferior frontal gyrus and short word length in the left orbital sulcus. High cloze ratings resulted in lesser activations in the bilateral inferior and frontal gyri. No effects were observed for frequency and sentence length. Patterns of activations for the potential confounds of familiarity, imageability, and humor differed from the parameters of interest and it can therefore be concluded that these findings were not due to these potential confounds.

3. Discussion

The chief finding is that there was only a single significant cortical cluster that was parametrically sensitive to the "expectancy" (or ASA) of the incongruent sentence endings and its location was just at the criterion distance to the source analysis of the $N2_{p3}$ effect. The fMRI cluster included the FSA. It is therefore suggested that the $N2_{p3}$ effect arises from the FSA. Unfortunately, a significant posterior meaningfulness effect was not found. Finally, there were potentially interesting cloze effects in the inferior frontal gyrus and the superior frontal gyrus.

A possible limitation of the present study is that the stimuli were derived from a legacy study (in order to maximize comparability) and so they were not as well-controlled as is currently the norm. For example, a number of the parameters were correlated (for example, meanginfulness and unexpectedness). On the other hand, it is quite difficult to keep so many psycholinguistic variables orthogonal (see Morrison & Ellis, 1995). It has even been argued that doing so can result in artifactual effects (Lewis, 2006). We suggest that in the present report such correlated parameters are not a concern because they were associated with different, non-overlapping neural patterns. For example, although meaningfulness was correlated wtih unexpectedness (r=-.29), it is unlikely that the FSA activity is actually the result of a meaningfulness confound because, if so, one would not only expect it to also be significant for the meaningfulness parameter, one would expect it to be even more strongly significant to the direct measure of meaningfulness compared to an indirect measure of meaningfulness. Potential confounds are more of an issue for the main effects analyses (see Table 3) but the conclusions of this report do not rely upon them.

The effect of greatest interest was the "expectancy" effect in the vicinity of the

FSA, which as noted earlier seems to reflect ASA. This effect [-22 -40 -8] corresponded roughly (Figure 2a), given the limited spatial resolution of ERP source analyses, to the source analysis result [-45 -60 -4] for the $N2_{p3}$ effect (Dien et al., 2003). As with the ERP data, no main effect of semantic congruity was observed for the "expectancy" effect. Parametric analysis of the unexpectedness ratings given to the incongruent endings, on the other hand, revealed the same strongly significant positive correlation seen in the ERPs. Thus both the $N2_{p3}$ and the FSA displayed the same pattern of effects, reinforcing the link between them. Although the meaningfulness rating and the sentence order were both significantly correlated with this parameter, neither produced significant effects in this region when directly analyzed. One can therefore conclude that this FSA effect of "expectancy" was not due to a confound with these parameters. It therefore seems reasonable to conclude that the FSA is the source of the $N2_{p3}$ effect. Based on the reasoning provided in the introduction (the FSA responds to ASA and the expectancy rating cannot be reflecting controlled expectancies given the oddity of the incongruent endings), this finding further strengthens the inference that the FSA, and by extension the $N2_{p3}$, involves ASA. This finding reinforces the existing fMRI reports (Gold et al., 2006; Wheatley et al., 2005) in that it helps confirm that this activity does indeed take place at a latency consistent with ASA (at about 200 ms) rather than reflecting some later post-lexical process.

One issue is that one might have expected the congruent endings to be most like the more "expected" incongruent endings, except more so. Instead, the congruent endings were comparable to the mean of the incongruent endings, resulting in no main effect for congruency for either the $N2_{p3}$ or the FSA. Perhaps the presentation of a stimulus ending that is part of the expectancy set (that is, the list of expected words, Becker, 1980) qualitatively changes the process reflected by these neural measures.

This is a matter that would require further investigation.

Next, left-lateralized cloze effects were observed in the medial superior prefrontal cortex and inferior frontal gyrus. It is a well-known issue in source analysis that it can be difficult to ascertain the true number of sources responsible for an ERP effect (see Achim, Richer, & Saint-Hilaire, 1991). If a single dipole were used to model the combined electrophysiological signal from two sources, then the dipole would represent the mean of these two source locations. These two activations together, [-14 6 70] and [-54 14 28], form an average location [-34 10 49], assuming equal weighting, that could easily correspond (2 cm) with the source solution [-18 7 37] for an unusual left-lateralized frontal N400 effect that was observed in the prior ERP study (Dien et al., 2003) and which also correlated with cloze ratings (Figure 1b). It is therefore hypothesized that the ERP effect actually reflects two generator sites and that the fMRI data have helped identify this situation.

While it is unclear what this ERP effect was, it is intriguing that the scalp topography was quite similar to that of the LAN (Friederici et al., 1993; Neville et al., 1991), with a peak electrode of F3; however, the LAN has not previously been reported as being sensitive to semantics or cloze probability so we do not endorse this interpretation at this point, although we do not rule it out either. Furthermore, an inspection of the main effects for syntactic anomaly in the ERP data did not yield a clear LAN or early LAN. On the other hand, a study (Friederici, Gunter, Hahne, & Mauth, 2004) examining a mixture of semantic and syntactic anomalies reported that sentences with both displayed a LAN-P600 pattern rather than an N400 pattern. It is possible that something about the present experimental design (such as the use of visual stimuli rather than auditory) resulted in a LAN-P600 pattern to all stimuli, not just the semantically+syntactically incongruent endings. The present dataset does not provide

grounds for resolving this issue, although it is notable that the three separate samples providing the 78 total ERP participants had nearly identical averaged waveforms demonstrating that the results were stable across separate samples.

In any case, it is possible that the superior frontal activation reflects the preparedness of subvocalization activity for more expected words. The inferior frontal cloze activation could be understood in terms of the hypothesis that it is involved in controlled selection between competing semantic alternatives (Thompson-Schill, Bedny, & Goldberg, 2005; Thompson-Schill & Botvinick, 2006; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Thompson-Schill, D'Esposito, & Kan, 1999) in that the more predictable (high cloze) endings evoked less activation. For example, the peak voxel in this study [-54 14 28] was quite similar to that [-45 4 30] of the first such study (Thompson-Schill et al., 1997).

The finding of right cerebellar correlations with unexpectedness ratings is consistent with repeated findings of right-lateralized cerebellar involvement in language (e.g., Mechelli, Gorno-Tempini, & Price, 2003; Noppeney & Price, 2002; Paulesu, Frith, & Frackowiak, 1993; Petersen & Fiez, 1993; Seger, Desmond, Glover, & Gabrieli, 2000; Tan et al., 2000). The cerebellar lobes are associated with the contralateral cortical hemispheres so right cerebellar activity is indicative of left hemisphere activity (as in the FSA activity that was also found). There is a growing appreciation for the potential contributions of the cerebellum to cognitive functions, as evidenced in neuroimaging and lesion studies, but thus far consensus on their nature remains elusive (see Leiner, Leiner, & Dow, 1995; Marien, Engelborghs, Fabbro, & De Deyn, 2001; Schmahmann, 1996).

The N400 source remained elusive in this study, with none of the activations

correlating with cloze being plausible sources for it, as in our previous study (Dien et al., 2008). While some researchers continue to associate Wernicke's area with the N400 (e.g., Van Petten & Luka, 2006), we favor the position of other researchers (e.g., Friederici, 2002) who point towards the anterior medial temporal lobe (AMTL) as the likely source. For example, intracranial ERP studies (which provide more accurate spatial localization than scalp-recorded ERP methods) have reported N400-like activity in this region (McCarthy, Nobre, Bentin, & Spencer, 1995; Nobre et al., 1994; Nobre & McCarthy, 1995). One study (Devlin et al., 2000) showed that it is difficult to obtain fMRI signals from the AMTL because of susceptibility artifact from the nearby sinuses but that positron emission tomography (PET) methods do indeed show semantic incongruity effects in the AMTL. Likewise, although the source of the P600 is unclear, source localization of the apparent P600 in the ERP study (Dien et al., 2003) also pointed towards the AMTL, which would similarly render its source invisible to fMRI.

Conclusion

In summary, the results of an fMRI replication of an earlier ERP study (Dien et al., 2003) provided evidence that a left-lateralized $N2_{p3}$ that correlated with unexpectedness ratings of incongruent sentence endings emanated from the FSA. This ERP component may provide a window into the temporal dynamics of ASA (Gold et al., 2006; Wheatley et al., 2005) and helps strengthen the case that the FSA may help mediate ASA. Furthermore, cloze effects were found in the superior frontal gyrus and the inferior frontal gyrus that could reflect subvocalization and semantic selection processes respectively.

4. Experimental Procedure

Participants

Thirteen participants (F= 3, M= 10) aged 20-32 years were recruited for monetary compensation after approval of the study protocol by the University of Kansas Medical Center institutional review board. All participants were right handed, native-English speaking, had no history of neurological damage or disorders, and were not taking psychotropic medications.

Statistical Analysis

For the inferential tests of the stimuli and the behavioral data, SAS/IML code (Keselman, Wilcox, & Lix, 2003) for conducting robust statistical tests (made available at http://www.umanitoba.ca/faculties/arts/psychology/) was ported to Matlab (available for download at http://wwwpeople.ku.edu/~jdien/downloads. html). A 5% symmetric trim rule was used (1 observation dropped at either extreme within each cell). The seed for the number generation was set at 1000. The number of simulations used for the bootstrapping routine was set at 50,000 to ensure stable *p*-values. The robust statistic (T_{WJt}/c) is meant to improve on (more closely comply with the nominal alpha rate than) the conventional ANOVA by: 1) not assuming a normal distribution, 2) being more resistant to outliers, and 3) not assuming a homogenous variance-covariance structure. Further description of the inferential issues, as they apply to ERP data, is available elsewhere (Dien, Franklin, & May, 2006). P-values are rounded to the second significant digit.

Stimuli

The stimuli consisted of 120 sentences (Appendix A) used in two prior studies

(Curran, Tucker, Kutas, & Posner, 1993; Dien et al., 2003). 60 sentences ended in congruent endings, 30 ended in semantically incongruent (i.e., selection restriction anomaly) endings, and 30 ended in semantically+syntactically incongruent endings; the latter were word class syntactic anomalies as well as being semantic anomalies (e.g., "Walter wanted to buy a beer but he was too department."). The most highly associated sentence ending was used for the congruent sentence endings (Bloom & Fischler, 1980), resulting in a mean congruent cloze rating of .57.

The stimulus list was matched in some respects but not others (Table 3). The main effect comparisons of interest were for congruent versus incongruent sentences and for semantically incongruent versus semantically+syntactically incongruent endings. Word frequency (Francis & Kucera, 1982) was matched, both for raw values and for log-transformed. Word length was equivalent between incongruity types but shorter for congruent endings: $T_{WJt}/c(1,74.52) = 26.79$, $p < .0001$. Sentence length was matched. Finally, for sentence order (order of presentation over the session) the congruent and incongruent endings were matched but the semantically+syntactically incongruent endings were overall later than the semantically incongruent: $T_{WJt}/c(1,45.96) = 4.29$, $p = .047$.

The stimuli were also rated on two parameters on seven-point scales by a norming group of 44 students (Dien et al., 2003) as also seen in Table 3. In brief, "expectancy" ratings were obtained by presenting the sentence stem, asking the raters to predict the ending, presenting the ending, and then having them rate how unexpected it was. The "meaningfulness" ratings were obtained by presenting the full sentence and asking the raters to indicate how meaningful the sentence was. Unexpectedness of the sentence endings was greater for the incongruent endings ($T_{WJt}/c[1,90.24] = 834.72$, $p < .0001$) and it was greater for the semantically+syntactically incongruent endings

(T_{WJt}/c[1,44.97] = 5.19, p = .027). Meaningfulness of the overall sentences was greater for the congruent endings (T_{WJt}/c[1,53.7] =5126.7, p < .0001) and it was greater for the semantically incongruent versus the semantically+syntactically incongruent endings (T_{WJt}/c[1,38.63] = 9.53, p = .0035). Additionally, ratings were obtained for the potential confounds of familiarity, imageability, and humor. No parameters were significantly correlated with cloze. For incongruent endings, only meaningfulness was correlated wtih unexpectedness (r=-.29). Frequency (r=.34), familiarity (r=.29), imagery (r=-.26), and humor (r=.30) were also correlated with meaningfulness.

Data Acquisition

Data were acquired using a gradient echoplanar imaging sequence (EPI) on a 3T Siemens Allegra scanner at the Hoglund Brain Imaging Center at the University of Kansas Medical Center. Functional data were scanned using single-shot gradient EPI imaging fMRI scans consisting of 29 contiguous axial slices (TR/TE = 2100/30, flip angle equal to 90 degrees, field of view equal to 192 mm, matrix equal to 64x64, slice thickness equal to 4 mm with a .5 mm interslice gap, in plane resolution equal to 3x3 mm). Four 5.78 min runs were recorded from each participant. The scans were begun two TRs (4.2 s) before the trials began. These two scans plus three more (10.5 seconds total) were dropped to allow for scanner stabilization, leaving 160 scans for analysis. The anatomical scan consisted of T1-weighted images using a 3D MP-RAGE sequence (TR/TE = 2300/4.4, flip angle of 8 degrees, field of view equal to 256 mm, matrix equal to 256x256, and 208 slices with slice thickness equal to 1 mm, in plane resolution equal to 1x1 mm). A vitamin E capsule was used to confirm L/R orientation of the image.

Procedure

Each experiment session began with an anatomical scan. Next there was a 10-

trial practice run followed by an 8-trial memory test. Then there were 120 trials, divided into four runs of 30 each. The task was to read sentences for comprehension in preparation for a recognition memory test at the end of each run. Stimuli were presented to participants via goggles that binocularly relayed the display from the E-Prime program. The sentences were presented in the same randomized order in all sessions.

Each trial consisted of the presentation of a sentence, one word at a time, beginning with a 1300 ms fixation, followed by the consecutive presentation of each word in the sentence for 105 ms each, separated by a 900 ms interstimulus interval. The first word of each sentence was capitalized and the last word was followed by a period. There was a 1000 ms intertrial interval between each trial. The stimuli were presented in black on a white background in Arial 26 point font. An asterisk (18-point CourierNew font) was present at all times other than during stimulus presentation in order to help participants maintain fixation. The fixation point size was chosen to be sufficiently large to be clearly visible while still being small enough to avoid masking the words. It is not possible to provide visual angle information as the nature of the stimulus presentation equipment precluded measurement of both the screen size of the stimuli and the distance from the viewer.

Each experimental run was succeeded by a memory test of 26 sentences with the final word omitted and replaced with "+++++". The sentences were presented on the screen in their entirety, one at a time. Half of the sentence stems were new and half were presented during the experiment run. The task was to indicate which had been presented during the experiment with a button press. The button press was not counterbalanced since no scanning was being conducted.

The stimulus presentation rate was chosen to maintain comparability with the prior ERP study (Dien et al., 2003) and to provide optimal separation of hemodynamic responses to the sentence ending words (the average separation between ending words was 10.22 seconds). The 1 word/sec rate is also the same as that used in two previous fMRI sentence studies (Dien et al., 2008; Kiehl, Laurens, & Liddle, 2002). Also, an ERP study (Kutas, 1987) has reported no apparent differences in the semantic effects for slow (700 ms SOA) and fast (100 ms SOA) presentation rates.

In order to optimize the characterization of the hemodynamic response, a staggered timing design (Josephs, Turner, & Friston, 1997) was utilized in which the TR (2100 ms) is not an even multiple of the trial length (10.22 sec); such a design results in the scans corresponding to different points of the hemodynamic response on each trial, in a manner transparent to the participant.

Neuroimaging Analysis

Imaging analysis was conducted using SPM5 version 826 (Wellcome Department of Imaging Neuroscience, http://www.fil.ion.ucl.ac.uk) under Matlab 7.3 and 7.4 on OS X. The data were imported directly from DICOM using DICOMviewer. Slice timing correction was conducted before realignment due to the use of interleaved slice order acquisition, with the middle slice as the reference slice. This step was followed by realignment and unwarping. Spatial normalization (affine registration followed by nonlinear deformations) was performed by matching mean functional images to the SPM EPI (echoplanar imaging) template and the data were resliced into 2 mm isotropic voxels. The images were spatially smoothed with a 12 mm full-width half-maximum kernel based on the SPM convention of using 2-3x the original voxel size (of which the largest dimension was 4 mm); an empirical study (Hopfinger, Buchel, Holmes, & Friston,

2000) recommended 10 mm using 3 mm voxels.

In addition to the two TRs dropped from the beginning of each run, 3 more TRs of experiment recording were removed (for a total of 10.5 s of data removed) to minimize stabilization artifact. Data were analyzed using event-related random effects analysis with a temporal derivative. AR(1) correction was made for temporal autocorrelation (see Smith, Singh, & Balsters, 2007). The default 128 sec high-pass filter was employed and no proportional scaling was performed to avoid artifacts (see Desjardins, Kiehl, & Liddle, 2001). The voxelwise height threshold was set at .005.

The SPM analysis was conducted in an event-related manner with congruent endings and incongruent endings as the events of interest. Both types of incongruities were entered as a single type of event since the ERP data (Dien et al., 2003) suggested that responses to them were quite similar for the effects of interest. The other words of the sentences were not entered into the analysis because it was found that doing so only reduced statistical power. A further analysis was conducted to directly contrast the two types of incongruent endings, entering in the three types of events as separate predictors and then entering only the two incongruent types into the contrast. Parametric analyses (where the parameters are entered as continuous variables in the multiple regression computations) were conducted using the congruent and incongruent event types. Only the parameter was entered into the contrasts. The parameter was applied to all the endings except for cloze (parameter only defined for congruent endings), meaningfulness and unexpectedness (ERP data indicates these parameters were at ceiling for congruent endings so only incongruent endings analyzed). The frequency parameter was transformed into the log of the frequency plus one in order to better linearize it.

Tables

Cluster p	k_E	Voxel p	Voxel T	Coords	BA	Anatomical Landmark
Incongruent vs. Congruent						
0.000	1254	0.973	5.58	-18 2 48	6	L Superior Frontal Sulcus
		0.997	5.12	16 2 54	6	R Cingulate Sulcus
		1.000	4.76	-22 -14 70	6	L Precentral Sulcus
0.000	1025	0.978	5.53	-10 2 20	-	L Caudate Nucleus
		0.998	5.06	-10 10 32	24	L Anterior Cingulate
		1.000	4.77	-4 -24 26	23	L Anterior Cingulate
0.014	407	1.000	4.89	26 44 36	9	R Superior Frontal Sulcus
		1.000	4.26	26 36 40	8	R Superior Frontal Sulcus
		1.000	3.73	38 36 34	9	R Middle Frontal Gyrus
Semantic vs. Semantic+Syntactic errors						
0.001	629	0.477	7.21	42 -86 -12	18	R Inferior Occipital Gyrus
		0.995	5.18	34 -84 -10	19	R Inferior Occipital Gyrus
		1.000	4.29	22 -90 -2	18	R Middle Occipital Gyrus
0.046	336	0.986	5.38	42 -40 6	22	R Superior Temporal Sulcus
		1.000	4.55	56 -52 -22	37	R Inferior Temporal Gyrus
		1.000	4.38	48 -36	22	R Superior Temporal Sulcus

				0		

Table 1. Results of Main Effects Analyses. Cluster p-values are corrected. BA is Brodmann Area. Voxel p-values are FWE-corrected. Coordinates are MNI coordinates.

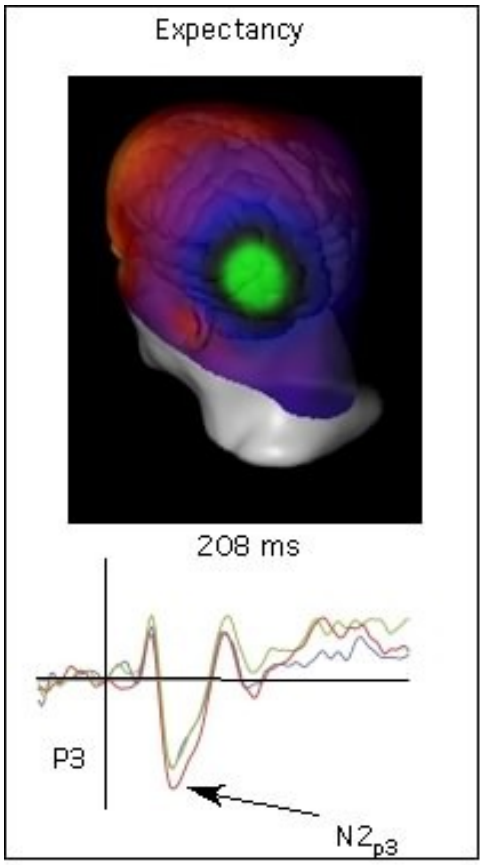
Cluster p	k_E	Voxel p	Voxel T	Coords	BA	Anatomical Landmark
Positive Unexpectedness						
0.031	403	0.726	6.40	-24 -30 -12	27	L Collateral Sulcus
		0.999	4.76	-22 -40 -8	30	L Fusiform Gyrus
		1.000	3.47	-14 -20 -10	27	L Parahippocampal Gyrus
0.040	381	0.904	5.83	26 -38 -16	-	R Cerebellum
		0.998	4.90	44 -42 -20	-	R Cerebellum
		0.999	4.81	54 -36 -20	37	R Inferior Temporal Gyrus
Negative Cloze						
0.003	502	0.444	7.45	50 30 28	46	R Inferior Frontal Gyrus
		0.993	5.35	54 24 32	9	R Inferior Frontal Gyrus
		1.000	4.37	58 14 32	9	R Inferior Frontal Gyrus
0.007	427	1.000	4.35	-54 14 28	44	L Inferior Frontal Gyrus
		1.000	3.72	-42 0 30	44	L Inferior Frontal Gyrus
		1.000	3.60	-52 10 40	9	L Precentral Gyrus
0.035	318	0.974	5.65	-14 6 70	6	L Superior Frontal Gyrus
		1.000	3.42	2 8 64	6	R Superior Frontal Gyrus
Positive Meaning						
0.001	533	0.748	6.67	-44 14 28	9	L Inferior Frontal Gyrus
		1.000	4.41	-54 18 26	44	L Inferior Frontal Gyrus
		1.000	3.69	-52 14 38	9	L Inferior Frontal Gyrus
Negative Word Length						
0.000	743	0.733	6.67	-12 46 -4	32	L Orbital Sulcus
		0.998	5.20	-22 36 -12	10	L Orbital Sulcus
		1.000	4.91	-16 42 -10	10	L Orbital Sulcus

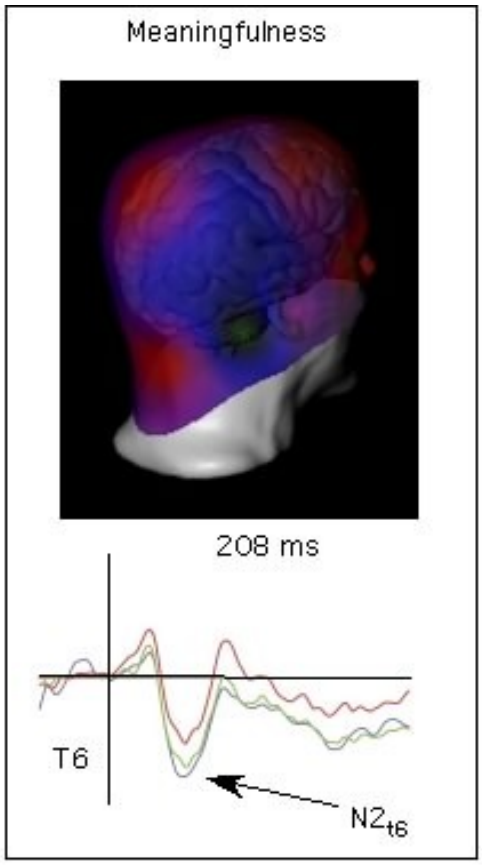
Table 2. Results of Parametric Analyses. Cluster p-values are corrected. BA is Brodmann Area. Voxel p-values are FWE-corrected. Coordinates are MNI coordinates.

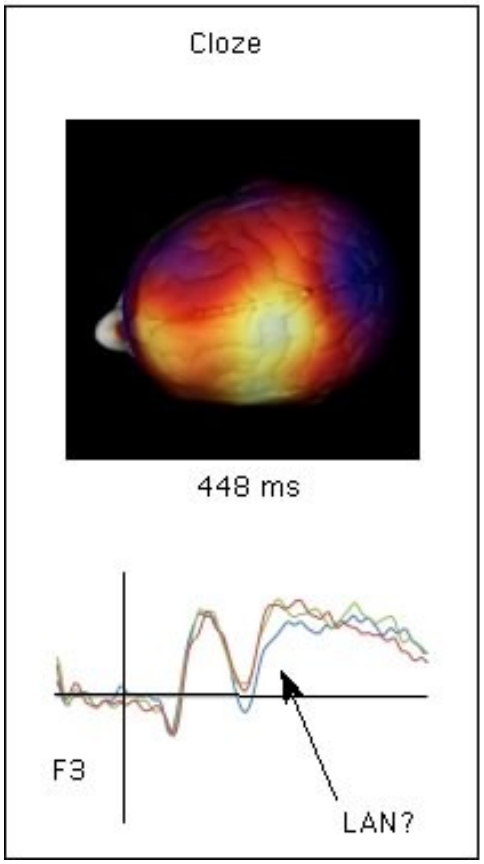
Parameters	Order	Freq	WL	SL	Unx	Mng
Congruent	61.37 (35.25)	184.48 (305.53)	4.73 (1.48)	7.87 (1.20)	3.43 (.18)	6.53 (.26)
Sem Inc	50.63 (33.03)	156.57 (192.02)	5.53 (1.61)	8.10 (1.12)	4.29 (.15)	2.26 (.47)
Sem+Syn Inc	68.63 (34.28)	113.20 (176.15)	6.17 (1.53)	7.70 (1.26)	4.35 (.20)	1.93 (.43)
	#		*		*#	*#

Table 3. Mean Stimulus Parameters. Order = Sentence Presentation Order. Freq = Word Frequency. WL = Word Length. SL = Sentence Length. Unx = Unexpectedness. Mng = Meaningfulness. * indicates significant difference between the congruent endings and the combined incongruent endings. # indicates significant difference between the two types of incongruent endings.

Figure Legends


Expectancy
208 ms
P3
N2p3


Meaningfulness
208 ms
T6
N2t6


Cloze
448 ms
F3
LAN?

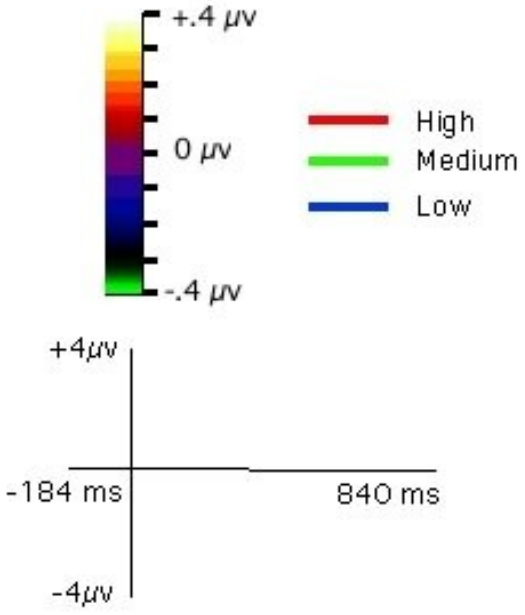

+.4 μv
0 μv
-.4 μv
High
Medium
Low
+4μv
-184 ms
840 ms
-4μv

Figure 1. Event-Related Potential Effects. The relevant ERP effects from Dien, Frishkoff, Cerbone, and Tucker (2003). The heads depict the parametric maps of the scalp topographies of the ERP factors that correlated with the each of the parameters of interest; the amplitudes indicate the microvolt change associated with a one standard deviation change in the parameter (at the peak time point of the factor, as indicated). The waveforms depict the grand average time course at the peak electrode for each effect, binned into high, medium, and low thirds for the indicated parameter.

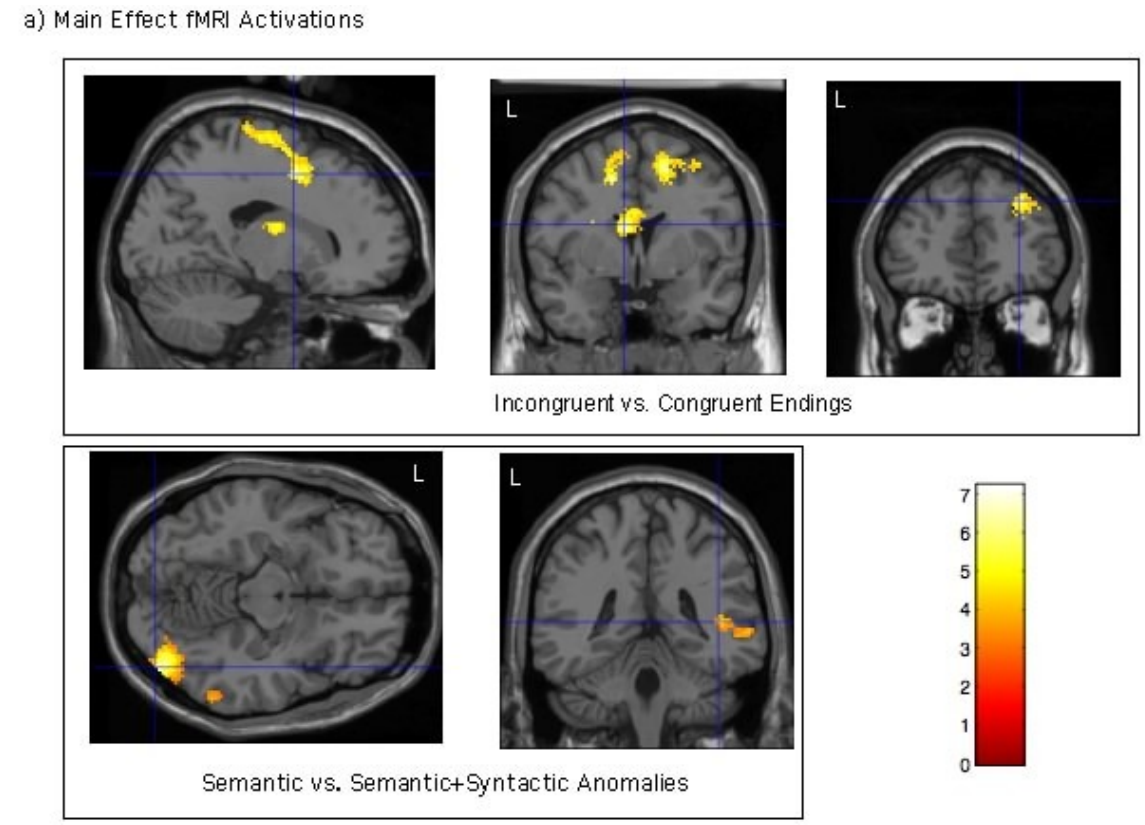


Figure 2. Haemodynamic Effects. a) The co-registration results for the ERP and the fMRI data. The blue crosshairs for unexpectedness and cloze indicate the source solution locations for the $N2_{p3}$ and the frontal N400 effects respectively. The circle for Cloze indicates the correct source solution that would be obtained for an equal weighting

of the two fMRI source activations. Only the relevant fMRI activations are shown. b) Activations for the main effect contrasts are shown.

Acknowledgements

This study was supported by a grant from the University of Kansas General Research Fund and pilot funding from the Hoglund Brain Imaging Center. Thanks to the reviewers and to Ron Mangun, the editor, for their very helpful and thoughtful comments.

Appendix A

Congruent

My aunt adores reading the daily paper.

Sam went to the factory where the toys were made.

Nothing can beat a bowl of hot soup.

Ron wondered if the storm would be over.

Terry wiped the bowls with a towel.

New York is a very busy city.

You'll never achieve anything if you don't try.

Andy sprayed the yard to keep away the bugs.

Mickey ordered a salad and a sirloin steak.

The grocer surveyed his stock before going home.

The Smiths had never visited that place.

Ira turned on the radio and danced to the music.

The mail should get here soon.

Peter won the cross country race.

The difficult concept was beyond his comprehension.

To find the corpse they had to drain the lake.

The cigar burned a hole in the couch.

Dick waited and read a book.

Sharon liked to sleep under the stars.

The old cabin was built entirely of wood.

Not even the cast liked the play.

Jackson disappeared last year and has not been seen.

You can't take the test without a pencil.

Cheryl is cherished by all her friends.

The child learned to count to ten.

The drums were so loud he couldn't hear himself think.

The florist sent a single red rose.

We used to get company every night.

Don found that he had no spare tire.

The sail got loose so they tightened the ropes.

Lois is taller than most girls.

It was important to be on time.

Billy slapped his sister in the face.

Starting a business demands a lot of money.

At the track the handicapper gave me a handy tip.

The child soared even higher on the swing.

Next year my little boy will be going to school.

It was clear that his thumb was broken.

Joe had to fill his truck with gas.

The rabbit hid in the tall grass.

Betsy couldn't tell what she was doing.

A direct attack failed so they changed their strategy.

The crows in the yard ate every last crumb.

Mary's vest was made of very fine silk.

Jeff was sent to bed without dinner.

Barbara's money was divided by the banker.

Mark was knocked off his board by the first wave.

Rob disliked having to commute to the city.

The ruby was so big it looked like a rock.

Suzy liked to play with her toy dolls.

The surgeon tried vainly to save his patient.

For a runner Ted is rather slow.

As soon as they got in they turned on the lights.

Fred put the worm on a hook.

Kelly rested under a tree in the shade.

The little girl was afraid of the dark.

Virginia punched him right in the nose.

Liz locked the valuables in the safe.

Kathrine was stung by a bee.

Tammy smashed a glass and woke up the baby.

Incongruent Semantics

The hero who caught the thief deserves our domestic.

Jock bet all he had on the last intensity.

Stan slowed down going around the digest.

The pimp was caught selling an illegal circle.

The mole lived in a hole in the tax.

Marie gazed back through the peace.

Too many men are out of dusk.

A hound has a good sense of knife.

George had been fired but he couldn't tell his room.

Jade's new green car blocked the narrow alibi.

Sondra was startled by a sudden surface.

Denny got off the freeway at the first rat.

Harriet sang while my brother played the clothes.

A large stone obstructed the entrance to the might.

Sally took short trips during the basis.

Some of the ashes dropped on the find.

Through the rain it was hard to read the burn.

A future energy source is the caller.

Dean's leg was broken so Ed went to get war.

After speaking Allen left the noisy finger.

During the class Jack had to borrow some grind.

Paul has always wanted to be a chain.

Dan caught the ball with his mustard.

Scott licked the bottom of the year.

The pill contained a powerful group.

In the park the hippie touched the calorie.

George could not believe his son stole a situation.

Fred relaxed in his chair on the back throat.

The front was clearly marked on the weather freedom.

Plants will not grow in dry murder.

Incongruent Semantics+Syntax

In the morning Jake took out the fiscal.

The thick mud stuck to her give.

One of the scouts got area.

Surgery was needed to repair his failing agree.

My father and mother are getting capacity.

The kids were given hamburgers for maid.

The puppy chewed on the those.

The actor was praised for being very teach.

When the shooting started they ran for lady.

Getting the shot didn't really valve.

The ache she felt was all in her leaved.

Seals can swim better than they can nameless.

Bob thought that she had such a friendly continue.

At night they often took a short spend.

Jon and Sue wanted their parents to come navigator.

The dog chased our cat up the retire.

Most students prefer to work during the knocked.

The sun turned his hair seafood.

Jill decided against the car when she learned the devote.

The earth is shaped like a develop.

The train was still on knowing.

Walter wanted to buy a beer but he was too department.

Motorcycles can emit a lot of sentence.

On his vacation he got some needed early.

Matt was wild when he was artery.

Helen liked to season her food with crisis.

At each table I had to fill in another bright.

David frowned and sat down at the untie.

The pamphlet was missing its listen.

Before jogging it's a good idea to century.

References

Achim, A., Richer, F., & Saint-Hilaire, J.-M. (1991). Methodological considerations for the evaluation of spatio-temporal source models. *Electroencephalography and Clinical Neurophysiology*, *79*, 227-240.

Becker, C. A. (1980). Semantic context effects in visual word recognition: An analysis of semantic strategies. *Memory and Cognition*, *8*(6), 493-512.

Bentin, S., Mouchetant-Rostaing, Y., Giard, M. H., Echallier, J. F., & Pernier, J. (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience*, *11*(3), 235-260.

Bihrle, A. M., Brownell, H. H., Powelson, J. A., & Gardner, H. (1986). Comprehension of humorous and nonhumorous materials by left and right brain-damaged patients. *Brain and Cognition*, *5*, 399-411.

Binder, J. R., Medler, D. A., Westbury, C. F., Liebenthal, E., & Buchanan, L. (2006). Tuning of the human left fusiform gyrus to sublexical orthographic structure. *Neuroimage*, *33*(2), 739-748.

Bloom, P. A. & Fischler, I. (1980). Completion norms for 329 sentence contexts. *Memory and Cognition*, *8*(6), 631-642.

Broca, M. P. (1865). Sur la siege de la faculté langage articulé. *Bulletin of the Society of Anthropology*, *6*, 377-396.

Brownell, H. H., Michel, D., Powelson, J., & Gardner, H. (1983). Surprise but not coherence: Sensitivity to verbal humor in right-hemisphere patients. *Brain and Language*, *18*, 20-27.

Cohen, D., Cuffin, B. N., Yunokuchi, K., Maniewski, R., Purcell, C., Cosgrove, G. R. et al. (1990). MEG versus EEG localization test using implanted sources in the human brain. *Annals of Neurology*, *28*, 811-817.

Cohen, L., Lehéricy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the Visual Word Form Area. *Brain*, *125*, 1054-1069.

Collins, A. M. & Loftus, E. F. (1975). A spreading activation theory of semantic processing. *Psychological Review*, *82*, 407-428.

Compton, P. E., Grossenbacher, P., Posner, M. I., & Tucker, D. M. (1991). A cognitive-anatomical approach to attention in lexical access. *Journal of Cognitive Neuroscience*, *3*(4), 304-312.

Cuffin, B. N., Schomer, D. L., Ives, J. R., & Blume, H. (2001). Experimental tests of EEG source localization accuracy in realistically shaped head models. *Clin Neurophysiol*, *112*(12), 2288-2292.

Curran, T., Tucker, D. M., Kutas, M., & Posner, M. I. (1993). Topography of the N400: Brain electrical activity reflecting semantic expectation. *Electroencephalography and Clinical Neurophysiology*, *88*(3), 188-209.

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends Cogn Sci*, *9*(7), 335-341.

Desjardins, A. E., Kiehl, K. A., & Liddle, P. F. (2001). Removal of confounding effects of global signal in functional MRI analyses. *Neuroimage*, *13*, 751-758.

Devlin, J. T., Russell, R. P., Davis, M. H., Price, C. J., Wilson, J., Moss, H. E. et al. (2000). Susceptibility-induced loss of signal: Comparing PET and fMRI on a semantic task. *Neuroimage*, *11*(6), 589-600.

Dick, F., Bates, E., Wulfeck, B., Utman, J. A., Dronkers, N., & Gernsbacher, M. A. (2001). Language deficits, localization, and grammar: evidence for a distributive model of language breakdown in aphasic patients and neurologically intact individuals. *Psychol Rev*, *108*(4), 759-788.

Dien, J. (in press). A Tale Of Two Recognition Systems: Implications Of The Fusiform Face Area And The Visual Word Form Area For Lateralized Object Recognition Models. *Neuropsychologia*.

Dien, J. (in press). The Neurocognitive Basis of Reading Single Words As Seen Through Early Latency ERPs: A Model of Converging Pathways. *Biological Psychology*.

Dien, J., Franklin, M., & May, C. (2006). Is "blank" a suitable neutral prime for event-related potential experiments? *Brain and Language*, *97*, 91-101.

Dien, J., Franklin, M. S., Michelson, C. A., Lemen, L. C., Adams, C. L., & Kiehl, K. A. (2008). fMRI Characterization of the Language Formulation Area. *Brain Research*, *1229*, 179-192.

Dien, J., Frishkoff, G. A., Cerbone, A., & Tucker, D. M. (2003). Parametric analysis of event-related potentials in semantic comprehension: Evidence for parallel brain mechanisms. *Cognitive Brain Research*, *15*, 137-153.

Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: high resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, *130*(Pt 5), 1432-1441.

Dronkers, N. F., Wilkins, D. P., Van Valin, R. D. J., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, *92*(1-2), 145-177.

Fiez, J. A. & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proc Natl Acad Sci U S A*, *95*(3), 914-921.

Francis, W. N. & Kucera, H. (1982). *Frequency Analysis of English Usage.* Boston: Houghton Mifflin.

Friederici, A. D. (2002). Towards a neural basis of auditory sentence processing. *Trends in Cognitive Sciences*, *6*(2), 78-84.

Friederici, A. D., Gunter, T. C., Hahne, A., & Mauth, K. (2004). The relative timing of syntactic and semantic processes in sentence comprehension. *NeuroReport*, *15*(1), 165-169.

Friederici, A. D., Pfeifer, E., & Hahne, A. (1993). Event-related brain potentials during natural speech processing: effects of semantic, morphological and syntactic violations. *Brain Res Cogn Brain Res*, *1*(3), 183-92.

Friederici, A. D. & Kotz, S. A. (2003). The brain basis of syntactic processes: functional imaging and lesion studies. *Neuroimage*, *20 Suppl 1*, S8-17.

Gold, B. T., Balota, D. A., Jones, S. J., Powell, D. K., Smith, C. D., & Andersen, A. H. (2006). Dissociation of automatic and strategic lexical-semantics: functional magnetic resonance imaging evidence for differing roles of multiple frontotemporal regions. *J Neurosci*, *26*(24), 6523-6532.

Hopfinger, J. B., Buchel, C., Holmes, A. P., & Friston, K. J. (2000). A study of analysis parameters that influence the sensitivity of event-related fMRI analyses. *Neuroimage*, *11*(4), 326-333.

Huettel, S. A., McKeown, M. J., Song, A. W., Hart, S., Spencer, D. D., Allison, T. et al. (2004). Linking hemodynamics and electrophysiological measures of brain activity: Evidence from functional MRI and intracranial field potentials. *Cerebral Cortex*, *14*(2), 165-173.

Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. *Neuroimage*, *20*(2), 693-712.

Joseph, J., Noble, K., & Eden, G. (2001). The neurobiological basis of reading. *J Learn Disabil*, *34*(6), 566-579.

Josephs, O., Turner, R., & Friston, K. J. (1997). Event-related fMRI. *Human Brain Mapping*, *5*, 243-248.

Keselman, H. J., Wilcox, R. R., & Lix, L. M. (2003). A generally robust approach to hypothesis testing in independent and correlated groups designs. *Psychophysiology*, *40*, 586-596.

Kiehl, K. A., Laurens, K. R., & Liddle, P. F. (2002). Reading anomalous sentences: An event-related fMRI study of semantic processing. *Neuroimage*, *17*, 842-850.

Krings, T., Chiappa, K. H., Cuffin, B. N., Cochius, J. I., Connolly, S., & Cosgrove, G. R. (1999). Accuracy of EEG dipole source localization using implanted sources in the human brain. *Clin Neurophysiol*, *110*(1), 106-114.

Kutas, M. (1987). Event-related brain potentials (ERPs) elicited during rapid serial visual presentation of congruous and incongruous sentences. In R. Johnson, J. W. Rohrbaugh, & R. Parasuraman (Eds.), *Current trends in event-related potential research. Electroencephalography and Clinical Neurophysiology, supplement 40*. (pp. 406-411). Amsterdam: Elsevier.

Kutas, M. & Hillyard, S. A. (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, *207*, 203-205.

Kutas, M. & Schmitt, B. M. (2003). Language in microvolts. In M. T. Banich & M. Mack (Eds.), *Mind, brain, and language*. (pp. 171-209). Mahwah, New Jersey: Lawrence Erlbaum Associates.

Leahy, R. M., Mosher, J. C., Spencer, M. E., Huang, M. X., & Lewine, J. D. (1998). A study of dipole localization accuracy for MEG and EEG using a human skull phantom. *Electroencephalography and Clinical Neurophysiology*, *107*(2), 159-173.

Leiner, H. C., Leiner, A. L., & Dow, R. S. (1995). The underestimated cerebellum. *Human Brain Mapping*, *2*(4), 244-254.

Lewis, M. B. (2006). Chasing psycholinguistic effects: A cautionary tale. *Visual Cognition*, *13*(7/8), 1012-1026.

Logothetis, N. K., Pauls, J., Augath, M., Trinath, T., & Oeltermann, A. (2001). Neurophysiological investigation of the basis of the fMRI signal. *Nature*, *412*, 150 - 157.

Lüders, H., Lesser, R. P., Hahn, J., Dinner, D. S., Morris, H., Resor, S. et al. (1986). Basal temporal language area demonstrated by electrical stimulation. *Neurology*, *36*(4), 505-510.

Lüders, H., Lesser, R. P., Hahn, J., Dinner, D. S., Morris, H. H., Wyllie, E. et al. (1991). Basal temporal language area. *Brain*, *114(*Pt 2), 743-754.

Mangun, G. R., Hopfinger, J., & Jha, A. J. (2000). Integrating electrophysiology and neuroimaging in the study of brain function. *Advances in Neurology*, *84*, 35-49.

Mangun, G. R. & Heinze, H. J. (1995). Combining electrophysiology with neuroimaging in the study of human cognition. In H. Mueller-Gartner (Ed.), *Supercomputers in Brain Research: From Tomography to Neural Networks*. (pp. 61-74). New Jersey: World Scientific Pub.

Marien, P., Engelborghs, S., Fabbro, F., & De Deyn, P. P. (2001). The lateralized linguistic cerebellum: a review and a new hypothesis. *Brain Lang*, *79*(3), 580-600.

Martín-Loeches, M. (2007). The gate for reading: reflections on the recognition potential. *Brain Res Rev*, *53*(1), 89-97.

Martinez, A., Anllo-Vento, L., Sereno, M. I., Frank, L. R., Buxton, R. B., Dubowitz, D. J. et al. (1999). Involvement of striate and extrastriate visual cortical areas in spatial attention. *Nature Neuroscience*, *2*(4), 364-369.

McCandliss, B. D., Cohen, L., & Dehaene, S. (2003). The visual word form area: Expertise for reading in the fusiform gyrus. *Trends in Cognitive Sciences*, *7*(7), 293-299.

McCandliss, B. D., Posner, M. I., & Givon, T. (1997). Brain plasticity in learning visual words. *Cognitive Psychology*, *33*(1), 88-110.

McCarthy, G., Nobre, A. C., Bentin, S., & Spencer, D. D. (1995). Language-related field potentials in the anterior-medial temporal lobe: I. Intracranial distribution and neural generators. *Journal of Neuroscience*, *15*(2), 1080-1089.

Mechelli, A., Gorno-Tempini, M. L., & Price, C. J. (2003). Neuroimaging studies of word and pseudoword reading: consistencies, inconsistencies, and limitations. *J Cogn Neurosci*, *15*(2), 260-271.

Moore, C. J. & Price, C. J. (1999). Three distinct ventral occipitotemporal regions for reading and object naming. *Neuroimage*, *10*(2), 181-192.

Morrison, C. M. & Ellis, A. W. (1995). Roles of word frequency and age of acquisition in word naming and lexical decision. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *21*(1), 116-133.

Neville, H., Nicol, J. L., Barss, A., Forster, K. I., & Garrett, M. F. (1991). Syntactically based sentence processing classes: Evidence from event-related brain potentials. *Journal of Cognitive Neuroscience*, *3*(2), 151-165.

Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, *372*, 260-263.

Nobre, A. C. & McCarthy, G. (1995). Language-related field potentials in the anterior-medial temporal lobe: II. Effects of word type and semantic priming. *Journal of Neuroscience*, *15*(2), 1090-1098.

Noppeney, U. & Price, C. J. (2002). A PET study of stimulus- and task-induced semantic processing. *Neuroimage*, *15*(4), 927-935.

Paulesu, E., Frith, C. D., & Frackowiak, R. S. J. (1993). The neural correlates of the verbal component of working memory. *Nature*, *362*, 342-345.

Petersen, S. E. & Fiez, J. A. (1993). The processing of single words studied with positron emission tomography. *Annual Review of Neuroscience*, *16*, 509-530.

Price, C. J. (2000). The anatomy of language: Contributions from functional neuroimaging. *Journal of Anatomy*, *197*(3), 335-359.

Price, C. J. & Friston, K. J. (1997). Cognitive conjunction: a new approach to brain activation experiments. *Neuroimage*, *5*(4 Pt 1), 261-270.

Price, C. J. & Mechelli, A. (2005). Reading and reading disturbance. *Curr Opin Neurobiol*, *15*(2), 231-238.

Price, C. J., Winterburn, D., Giraud, A. L., Moore, C. J., & Noppeney, U. (2003). Cortical localisation of the visual and auditory word form areas: a reconsideration of the evidence. *Brain Lang*, *86*(2), 272-286.

Puce, A., Allison, T., Spencer, S. S., Spencer, D. D., & McCarthy, G. (1997). Comparison of cortical activation evoked by faces measured by intracranial field potentials and functional MRI: Two case studies. *Hum Brain Mapp*, *5*, 298-305.

Rudell, A. P. (1991). The recognition potential contrasted with the P300. *International Journal of Neuroscience*, *60*, 85-111.

Schmahmann, J. D. (1996). From movement to thought: Anatomic substrates of the cerebellar contribution to cognitive processing. *Human Brain Mapping*, *4*(3), 174-198.

Seger, C. A., Desmond, J. E., Glover, G. H., & Gabrieli, J. D. (2000). Functional magnetic resonance imaging evidence for right-hemisphere involvement in processing unusual semantic relationships. *Neuropsychology*, *14*(3), 361-369.

Sheth, S. A., Nemoto, M., Guiou, M., Walker, M., Pouratian, N., & Toga, A. W. (2004). Linear and nonlinear relationships between neuronal activity, oxygen metabolism, and hemodynamic responses. *Neuron*, *42*(2), 347-355.

Smith, A. T., Singh, K. D., & Balsters, J. H. (2007). A comment on the severity of the effects of non-white noise in fMRI time-series. *Neuroimage*, *36*(2), 282-288.

Spironelli, C. & Angrilli, A. (2007). Influence of Phonological, Semantic and Orthographic tasks on the early linguistic components N150 and N350. *Int J Psychophysiol*, *64*(2), 190-198.

Suls, J. M. (1972). A two-stage model for the appreciation of jokes and cartoons: An information-processing analysis. In J. H. Goldstein & P. E. McGhee (Eds.), *The psychology of humor: Theoretical perspectives and empirical issues*. (pp. 81-100). New York: Academic Press.

Tan, L. H., Spinks, J. A., Gao, J. H., Liu, H. L., Perfetti, C. A., Xiong, J. et al. (2000). Brain activation in the processing of Chinese characters and words: a functional MRI study. *Hum Brain Mapp*, *10*(1), 16-27.

Taylor, W. L. (1953). "Cloze" procedure: A new tool for measuring readability. *Journalism Quarterly*, *30*, 415.

Thompson-Schill, S. L., Bedny, M., & Goldberg, R. F. (2005). The frontal lobes and the regulation of mental activity. *Curr Opin Neurobiol*, *15*(2), 219-224.

Thompson-Schill, S. L. & Botvinick, M. M. (2006). Resolving conflict: a response to Martin and Cheng (2006). *Psychon Bull Rev*, *13*(3), 402-8; discussion 409-11.

Thompson-Schill, S. L., D'Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proc Natl Acad Sci U S A*, *94*(26), 14792-14797.

Thompson-Schill, S. L., D'Esposito, M., & Kan, I. P. (1999). Effects of repetition and competition on activity in left prefrontal cortex during word generation. *Neuron*, *23*(3), 513-522.

Van Petten, C. & Luka, B. J. (2006). Neural localization of semantic context effects in electromagnetic and hemodynamic studies. *Brain Lang*, *97*(3), 279-293.

Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O. et al. (2006). Meta-analyzing left hemisphere language areas: phonology, semantics, and sentence processing. *Neuroimage*, *30*(4), 1414-1432.

Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: dissecting the inner organization of the visual word-form system. *Neuron*, *55*(1), 143-156.

Wernicke, C. (1874). *Der aphasiche symptomenkomplex.* Breslau, Poland: Cohen and Weigert.

Wheatley, T., Weisberg, J., Beauchamp, M. S., & Martin, A. (2005). Automatic priming of semantically related words reduces activity in the fusiform gyrus. *J Cogn Neurosci*, *17*(12), 1871-1885.