Separating the Visual Sentence N400 Effect from the P400 Sequential Expectancy Effect: Cognitive and Neuroanatomical Implications

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Running Head: N400 Localization

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Abstract

The N400 is an event-related potential (ERP) component that is elicited by semantically meaningful stimuli; one of its defining characteristics is that it is amplified for sentence completions that are semantically unexpected or incongruous with the preceding context. Some prior reports using visual sentence reading paradigms have suggested there may also be a Cz-centered P400 (a P400cz) that is also responding to semantic congruity manipulations, distinct from the classic Pz-centered N400 (the N400pz). In the present experiment, sentences were presented visually one word at a time, and half of the sentences ended with a semantically incongruent ending. High-density 129-channel event-related potential data were recorded from 26 participants. A combination of temporo-spatial principal components analysis (PCA) and item-averaging was applied to decompose the waveforms. The presence of the P400cz was confirmed. The P400cz was much more sensitive to congruity and somewhat more sensitive to cloze probability than the N400pz. The separation of the N400 semantic effect into these two portions is consistent with both MEG studies and intracranial studies. The data suggest that the N400pz has its major source in the bilateral anterior medial temporal lobe (AMTL) whereas it is suggested that the P400cz has its major source in the medial parietal region. It is further suggested that whereas the N400pz process appears to be semantic in nature, some prior reports suggest that the P400cz reflects a general sequential expectancy system.

1. **Introduction**

An event-related potential (ERP) component termed the N400 (a negativity that peaks at about 400 ms) over posterior (temporo-parietal) scalp regions is enhanced by semantic incongruities like "I drink coffee with milk and socks" (Kutas & Hillyard, 1980; Kutas & Schmitt, 2003). This response therefore appears to provide entree into the workings of semantics, a central concern of cognitive psychology, and its neural substrate. For this reason, it has drawn widespread interest and has been examined in hundreds of studies.

Two views have dominated theoretical thinking about the N400, namely the lexical access view that the N400 reflects the retrieval of the lexical and/or semantic information associated with a word form, as in automatic spreading activation (Kutas, Lindamood, & Hillyard, 1984), and the semantic integration view that the N400 reflects the integration of the word semantics into the broader semantic context (Brown & Hagoort, 1993). The latter view obtained compelling support in the form of the finding that masked subliminal priming could produce behavioral priming (evidence of lexical access) without an accompanying N400 effect (Brown & Hagoort, 1993), resulting in the integration account becoming "the prevalent view of the N400" (Kutas & Federmeier, 2000, p. 464). However, a subsequent study (Deacon, Hewitt, Yang, & Nagata, 2000) did not support this finding.

As a result, the lexical access view has regained ascendance, as can be seen in five recently presented versions. One version (Lau, Phillips, & Poeppel, 2008) is that the N400 reflects access from an amodal lexicon localized to the posterior middle temporal gyrus and its environs, with congruent semantic context helping facilitate retrieval. Another version (Federmeier & Laszlo, 2009; Kutas & Federmeier, 2000) is that the

N400 reflects the difficulty of a temporally based binding of a distributed semantic representation (with no intermediate lexical representation), with an incongruent semantic context being of less help for preparing the semantic features in advance (and hence resulting in a larger N400 as more effort is required to activate and bind together the semantic representation). A third version (Van Berkum, 2009) is that the N400 reflects the degree of effort in retrieving a semantic representation, with the effort being determined by multiple cueing factors, including consistency with high-level pragmatics. A fourth version (Debruille, 2007) is that the N400 reflects a semantic inhibition process wherein disfavored alternatives are suppressed to allow for access of the favored alternative, with an incongruent semantic context requiring the predicted word choices to be suppressed (resulting in a larger N400). A fifth version (Franklin, Dien, Neely, Waterson, & Huber, 2007) suggests that the N400 does not reflect lexical access per se but rather an updating of semantic expectations (as in associative relationships) to improve future lexical access, with an incongruent semantic context resulting in the need for greater updating changes and hence a larger N400 (for a related theory of the P300, see Donchin, 1981; Donchin & Coles, 1988).

A possibility that has not yet been discussed in this literature is that in some sense both views of the N400 might be correct in that multiple "N400" components might be involved, some corresponding to lexical access and some to semantic integration. There is already a well-documented precedent for N400 subcomponents. A more frontal N400 for concrete words than abstract words has been reported (Kounios & Holcomb, 1994; Swaab, Baynes, & Knight, 2002; Zhang, Guo, Ding, & Wang, 2006), especially when they are incongruent with a preceding sentence stem (Holcomb, Kounios, Anderson, & West, 1999). Some careful manipulations clarified that this "frontal N400" effect, was due to a combination of an N400 component and a frontal N700 component (for a review of pre-N400 frontal negativities that can also appear to contribute to a frontal N400, see Dien, 2009). A series of papers (Frishkoff, Tucker, Davey, & Scherg, 2004; Frishkoff, Perfetti, & Westbury, 2009; Frishkoff, Perfetti, & Collins-Thompson, 2010) have reported on a medial frontal negativity (MFN) that could also be related to this effect.

Sentence paradigms, where the N400 effect was first identified, provide the prototypical N400. In such data, it is suggested that there might be two ERP components contributing to the typical N400 effect. We suggest that the first ERP component is an N400pz reflecting some version of the lexical access view and the second is a P400cz reflecting some aspect of semantic integration, using a naming convention suggested elsewhere (Dien, 2009) in which the peak electrode is added as a suffix. Support for the P400 comes from data (O'Hare, Wolcott, and Dien, November, 2008), which replicates and extends an earlier experiment (Jentzsch & Sommer, 2001), suggesting that expectancy effects in oddball tasks can be divided into a P300 which responds primarily to the global expectancies (overall probability) of a stimulus and a P400cz-like ERP component that responds most to the local expectancy (expectation for a specific event to occur at a specific time) of a stimulus, as in sequential probabilities. Given that a sentence can be thought of as being a sequential set of stimuli, it is unsurprising that the same cognitive expectancy process operating on sequences of tones might also operate on sequences of word stimuli. One might view such sequential representations as being a kind of context into which the words of a sentence can be integrated and the P400 as indexing this operation, although it would not be restricted to semantics given its appearance in simple oddball tasks.

A promising tool for separating and characterizing subcomponents (such as the N400 and the P400) is principal components analysis or PCA (Dien & Frishkoff, 2005;

Donchin & Heffley, 1979; Glaser & Ruchkin, 1976; Möcks & Verleger, 1991). For example, it has been shown that it can meaningfully improve source analysis efforts (Carretie et al., 2004; Dien, Tucker, Potts, & Hartry, 1997; Dien, Frishkoff, Cerbone, & Tucker, 2003; Dien, Spencer, & Donchin, 2003; Dien & O'Hare, 2008; Dien, 2010a; O'Hare & Dien, 2008; O'Hare, Dien, Waterson, & Savage, 2008; Pourtois, Delplanque, Michel, & Vuilleumier, 2008) by separating overlapping ERP components and by estimating the number of sources to be localized. By PCA, the authors include the use of independent components analysis or ICA (Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997) as an oblique rotation for PCA. The technical issues involved in their application to ERP data and the evaluation of its effectiveness for this purpose are out of the scope of the present paper and interested readers are directed to the appropriate papers.

The only published N400 study we are aware of that sought to separate N400 subcomponents by applying PCA to a visual sentence paradigm was a previous effort by our lab (Dien et al., 2003). In this study, the N400 was first isolated from activity with differing time courses with a conventional temporal PCA, in which the variables were the time points; however, such a procedure would not separate ERP components with similar time courses. The N400 was further isolated by making use of the well-known finding that the N400 is larger for smaller cloze probabilities in sentence paradigms (Kutas & Hillyard, 1984). Cloze probability is the percentage of norming groups that spontaneously generate a specific ending word given a sentence stem (Bloom & Fischler, 1980; Taylor, 1953). In principle, it should be possible to separate ERP activity that is correlated with cloze probability from ERP activity that is not, if multiple ERP components are present. To accomplish this, we generated item averages (averaging over 78 subjects, thus yielding a separate average for each sentence) and correlating the N400 window factor with cloze ratings separately for each channel, thus determining what portion of the N400 effect was responsive to the cloze value. This procedure suggested there were indeed at least two ERP components present since the topography of the overall "N400 effect" was not the same as the topography of the cloze effect; results suggested the presence of both a posterior negativity resembling the conventional N400 and a more frontal positivity that was more responsive to cloze probability.

A potential problem with this prior study (Dien et al., 2003) is that half of the incongruent endings were syntactic anomalies. Syntactic anomalies are known to produce a left anterior negativity (LAN) effect (Friederici, 1995; Kluender & Kutas, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991) that is also active in the N400 window. It is therefore possible that the left-lateralized fronto-central topography was more reflective of a LAN than of the N400. If, for example, both the LAN and the N400 respond to the cloze probability then they would not be successfully separated.

Concern is deepened by the observation of an apparent enhanced P600 to the incongruent endings, an effect more normally associated with syntactic anomalies (Friederici, 2002; Hagoort, 2003; Neville et al., 1991; Newman, Ullman, Pancheva, Waligura, & Neville, 2007; Osterhout & Holcomb, 1992; Osterhout & Nicol, 1999), although the study (Dien et al., 2003) did demonstrate that the effects remained even after most of the syntactic errors were excluded. Recent work has suggested that the P600 may reflect a general process of resolving conflicts between separate meaning analysis systems and therefore is not limited to syntactic anomalies (Kuperberg, 2007; van Herten, Chwilla, & Kolk, 2006). Regardless, it would be preferable to not have the additional complication of syntactic anomalies present.

In order to address these issues, a new study was undertaken[1], using a new stimulus set that excluded syntactic errors. The primary goal was to verify the basic finding of there being two separate ERP components in the N400 window (for visual sentence comprehension), a classic parietal N400 and a more central P400, that are differentially sensitive to cloze probability and to semantic congruity. As a further refinement, in order to facilitate the parametric analysis, the congruent sentence endings were chosen to represent a full, evenly distributed range of cloze probabilities. If there are multiple ERP components present, the secondary goal is to examine the consequences for N400 source analysis; efforts to model two separate sources with a single dipole is likely to result in a location in between both of them, corresponding to neither of them. The P600, if again present, will also be examined as the question of whether and how it responds to semantics is of current interest (Kuperberg, 2007; van Herten et al., 2006).

The analysis will consist first of the conventional windowed measures to verify the presence of the standard N400 and P600 effects. The primary analysis was a combination of a temporo-spatial two-step PCA and item-averaged data to determine if the N400 and the P600 could be decomposed and to better separate the ERP components from embedded noise. Although the item-averaged data (as opposed to the subject-averaged data) could have been analyzed with windowed measures as well, it was not for reasons of conciseness.

2. Results

BEHAVIOR RESULTS

The average recognition performance was 89% with a standard deviation of 7%.

ERP RESULTS

Windowed N400: The robust statistics for the N400 window yielded only one effect that interacted with semantics, semantics by DV: $T_{WJt}/c[2,18.67]=8.52,p=.0040$. This effect indicated a relative negativity along the top surface and a relative positivity along the bottom surface of the head to incongruent endings, reflecting the two ends of the N400 dipoles. The classic N400 and P600 effects can be seen at Pz.

Comparison of the topography of the posterior negativity in the incongruent condition (Figure 2a) reveals the same slightly right-lateralized topography previously reported by the first high-density electrode report of the N400 (Nobre & McCarthy, 1994). The difference map yields a more Pz-centered topography (Figure 2b), one more typical of the N400 than seen in the prior ERP study (Dien et al., 2003). Thus, the present N400 appears to be a classic N400 effect, as intended.

Windowed P600: The robust statistics for the P600 window yielded only one effect that interacted with semantics, semantics by AP: $T_{WJt}/c[1,21]=10.82,p=.0031$. This effect indicated a relative negativity along the anterior surface and a relative positivity along the posterior surface of the head to incongruent endings (reflecting the two ends of the P600 dipole).

The Temporo-Spatial PCA: In the initial step, a temporal PCA was conducted on the item-averaged data. The Scree test suggested that fourteen factors should be retained, accounting for 72.5% of the variance for the Promax solution. The two temporal factors of a priori interest were one peaking at 420 ms (N400 window) and one peaking at 616 ms (P600 window). A spatial PCA was conducted on each of these temporal factors. A Scree test suggested five factors for both of them, accounting for

63.5% and 63.2% respectively. Of the resulting ten factors, three in the N400 window and four in the P600 window accounted for at least .5% of the variance.

Three of these seven factors (Figure 3) proved to be of interest because they displayed statistically significant sensitivity to the semantic manipulation (Figure 4). Using a naming convention suggested elsewhere (Dien, 2009) in which the peak electrode is added as a suffix, the P400cz factor (which is to say, a positivity peaking at 400 ms and centered on Cz) was more positive to congruent endings: $T_{WJt}/c(1,130.2)=23.87$ $p<.00000001$. The N400pz factor was more negative to incongruent endings: $T_{WJt}/c(1,133.1)=4.70$, $p=.032$. The P600oz factor was more positive for incongruent endings: $T_{WJt}/c(1,135.1)=7.52$, $p=.0064$. Furthermore, both the P400cz ($r=.34$, $p=.0025$) and the N400pz ($r=.29$, $p=.012$) factors were enhanced by smaller cloze probabilities (as residualized for letter length).

In order to verify that the N400pz and the P400cz congruity effects were indeed due to congruity and not the confounded orthographic neighborhood parameter, a matched subset of stimuli (64 each of congruent and incongruent endings, both with a mean of 4.4 and still matched for word frequency and word length) were tested and still found to respond to congruity. The P400cz factor was more positive to congruent endings: $T_{WJt}/c(1,106.4)=23.94$, $p<0.00000001$. The N400pz factor was more negative to incongruent endings: $T_{WJt}/c(1,113.9)=6.09$, $p=.015$. Orthographic neighborhood was not confounded with cloze so no further analysis was necessary.

Source Analysis: Source analyses were carried out on the incongruent-congruent difference waves of the grand average and on the portion of the grand average accounted for by the factors of interest (Figure 5). The source analysis of the N400 window resulted in coordinates somewhat medial to the STG [+/-23.4 -42.5 22.4] but an unacceptably large residual variance (RV) of 25.6%. The P600 window resulted in coordinates along the middle of the ventral temporal lobe [+/-46.0 -28.4 -9.5] and an RV of 21.9%. The N400pz factor yielded results [+/-24.5 1.1 15.1] located above the anterior medial temporal lobe and an RV of 1.3%. The P400cz factor yielded results consistent with the medial parietal region or possibly the inferior parietal region [+/-20.5 -34.2 6.5] and an RV of 3.4%. The P600oz factor suggested a generator site in the region of the anterior temporal lobe or inferior frontal cortex [+/-23.6 7.0 4.8], below that of the N400pz factor, and an RV of 2.1%. All source solutions were robust to starting location, with variations of no more than +/- .3 mm. The right hemisphere dipole was somewhat stronger for all three factors, although the two-step PCA process does not allow for the individual difference variance needed for a statistical test.

3. Discussion

The present experiment produced a more typical N400 effect than that seen in the prior parametric ERP experiment (Dien et al., 2003). The PCA confirmed that even with a more typical N400 effect, the N400 window contains at least two different ERP components sensitive to the semantic manipulation, a conventional N400pz and a central P400cz. Both the N400pz and the P400cz were positively correlated (meaning stronger absolute amplitude) with cloze probability and responded to semantic congruity (Figure 4). A P600oz effect was also found to semantic congruity but not cloze probability. The N400pz point equivalent dipoles were located above the anterior medial temporal lobe region, the P400cz point equivalent dipole was placed closer to the medial parietal region or possibly the pMTG, and the P600oz in the anterior temporal lobe or inferior frontal regions.

The most noteworthy finding is the evidence that two separate ERP components can contribute to the sentence N400 semantic congruity effect, what is here termed the N400pz and the P400cz. We feel comfortable labeling the latter component a positivity because this is how it is characterized by the PCA and because in the grand average at Cz the semantic effect does in fact have the appearance of being primarily due to a positivity in the congruent condition (with a small negativity in the incongruent condition from the neighboring N400pz), in contrast to Pz where it is clearly due to a negativity in the incongruent condition (with a small positivity in the congruent condition from the neighboring P400cz). The present results suggest that the more central N400 topography of the prior study (Dien et al., 2003) may have occurred because the P400cz contributed more strongly to it. On the other hand, in the 2003 study the frontal positive effect was more frontal, centered on F3 rather than Cz. One possibility is that the N400 effect actually consisted of three ERP components, an N400pz, a P400cz, and a LAN responding to the presence of the syntactic anomalies.

The observation that the P400cz responds more to congruity than to cloze also suggests that it is less sensitive to the subtleties of semantics than is the N400pz. If the P400cz reflects an integration of the word into the ongoing sequential representation of events, the integration process is stronger for less consistent low cloze endings than for high cloze endings; conversely, the integration process is larger for congruent vs. incongruent endings because the subjects presumably recognize that the incongruent endings are largely nonsense endings and therefore decline to integrate the ending into the sentence representation. Alternatively, the P400cz might reflect an expectancy updating process for sequential probabilities, just as the P300 is thought to do for global probabilities (Donchin, 1981; Donchin & Coles, 1988), in which case the lack of a P400cz to the nonsense endings would reflect an activate avoidance of learning them, just as a college professor grading C papers must suppress any learning of the copious mistakes in poor writing.

The present findings may also help clarify N400 source localization issues. Source analyses of the N400 (e.g., Frishkoff et al., 2004; Maess, Herrmann, Hahne, Nakamura, & Friederici, 2006; Silva-Pereyra et al., 2003) have yielded a variety of potential sources (produced by visual sentences, auditory sentences, and by series of single visual words respectively). Furthermore, intracranial electroencephalography (EEG) studies (Dietl et al., 2008; Elger et al., 1997; Fell et al., 2004; Guillem, N'Kaoua, Rougier, & Claverie, 1995; McCarthy, Nobre, Bentin, & Spencer, 1995; Meyer et al., 2005; Nobre & McCarthy, 1995), which have much better spatial resolution but are typically limited in their coverage, have tended to highlight potential N400 sources in the bilateral anterior medial temporal lobes or AMTL (using auditory and visual sentences and repetition priming of visual words). In contrast, magnetoencephalography (MEG) studies (Helenius et al., 2002; Helenius, Salmelin, Service, & Connolly, 1998; Helenius, Salmelin, Service, & Connolly, 1999; Laine, Salmelin, Helenius, & Marttila, 2000; Maess et al., 2006; Mäkelä, Mäkinen, Nikkilä, Ilmoniemi, & Tiitinen, 2001; Service, Helenius, Maury, & Salmelin, 2007; Simos, Basile, & Papanicolaou, 1997; Simos et al., 2002) have consistently pointed towards the middle temporal gyrus (MTG)/superior temporal gyrus (STG) region.

Some reports, both MEG and intracranial EEG, have suggested that both the AMTL and the MTG/STG could be sources of the N400 effect, just as the present report finds two N400 subcomponents. A series of three MEG papers (Helenius et al., 1998; Helenius et al., 1999; Laine et al., 2000) reported finding sources in both anterior to the MTG/STG region and posterior to it. The MTG/STG solutions reported in the other papers could be understood as what happens when one tries to account for two sources with a single dipole (a location midway between the two). A particularly striking correspondence is provided by one such MEG study (Figure 2, Helenius et al., 1998) which reported two clusters of congruity effects, one which appears to correspond to the present N400pz solution and one which appears to correspond to the P400cz solution.

The N400pz source solution is not conclusive but does point most strongly towards the AMTL. The intracranial ERP studies were unable to be precise about the locations of their electrodes but generally described the maximal intracranial N400 effects as being recorded in the rhinal cortex near the amygdala. According to the Talairach and Tournoux atlas (1988), the amygdala has roughly coordinates of X=15 to 30 (with the rhinal cortex overlying the amygdala being about X=15), Y = 0 to -10, Z = -8 to -20 so the intracranial N400 coordinates can be estimated as being roughly [-15,-5,-14]. By this estimate, the N400pz source solution [+/-24.5 1.1 15.1] is very close (within 1 cm) along the x and y axes but about 3 cm too high along the z-axis (the imprecision of EEG source analysis is about 1-2 cm even under ideal conditions, Krings et al., 1999). Given that the z-axis (up-down) is the one that is least accurate due to the absence of electrodes along the bottom surface of the head, the AMTL seems to be the best candidate for the N400pz source; the superior temporal gyrus cannot be excluded on the basis of the coordinates alone but it lacks the supporting intracranial ERP evidence.

The source solution for the P400cz [+/-20.5 -34.2 6.5] is more ambiguous. One possibility is a putative N400 source location (Lau et al., 2008), the posterior middle temporal gyrus (pMTG), as noted earlier. Three sentence studies who have reported pMTG activations (Baumgaertner, Weiller, & Buchel, 2002; Kuperberg et al., 2000; Stringaris, Medford, Giampietro, Brammer, & David, 2007) reported an averaged coordinate of [-47 -54 6], which is close enough to be plausible but different enough to not be conclusive. An equally plausible source region would be the medial parietal. For example, the medial parietal region [−12 −45 33] was one of the areas found to respond to semantic incongruence in a child ERP/fMRI study (Schulz et al., 2008) and was one of only two semantic incongruence areas that distinguished dyslexic readers from controls (the other being inferior parietal). This medial parietal area is a reasonably good fit along the x and y axes but too high along the z-axis. As noted earlier, the z-axis is the one most likely to be inaccurate due to the absence of electrodes on the underside of the braincase.

Although the medial parietal is not considered to be a semantic region, it is thought to be involved in evaluating various aspects of the environment, some areas having to do with spatial locations and some having to do with one's goal-oriented navigation of these locations (Cavanna & Trimble, 2006; Nielsen, Balslev, & Hansen, 2005; Vogt, Vogt, & Laureys, 2006), and therefore could reflect a more general cognitive process than language per se (e.g., O'Hare et al., 2008; Vitacco, Brandeis, Pascual-Marqui, & Martin, 2002). The hypotheses that the P400cz reflects integration into a sequential representation or updating of general sequential expectancies is therefore not inconsistent with what is known of this region. However, given the imprecision of source analyses, the pMTG source location cannot be ruled out, and indeed both regions have been implicated in a recent meta-analysis of functional imaging studies (Binder, Desai, Graves, & Conant, 2009).

The P600oz effect was once again observed even though the syntactic anomalies were eliminated from the stimulus set. Although the P600 is usually linked to syntactic anomalies (Friederici, 2002; Hagoort, 2003; Neville et al., 1991; Newman et al., 2007; Osterhout & Holcomb, 1992; Osterhout & Nicol, 1999), there is increasing evidence that it can be evoked by semantic anomalies as well (Kolk, Chwilla, van Herten, & Oor, 2003; van Herten, Kolk, & Chwilla, 2005; van Herten et al., 2006). It has been proposed (van Herten et al., 2006) that the P600 reflects the operation of a monitoring mechanism triggered by a conflict between a heuristic word-based comprehension system and a syntactically based algorithmic comprehension system. In the present case, it could have been triggered by the anomalous sentences if the two systems generated competing interpretations, as where the final word is appropriate at the level of individual word associations (e.g., in "His view was blocked by the music", having one's view blocked does occur in the context of attending an opera or concert so the individual words do belong together) but not when processed grammatically. Thus, whether a P600 is elicited by semantic anomalies may depend on the nature of the incongruent sentences in the stimulus set. Further support for this reasoning is that the prior study (Dien et al., 2003) did have syntactic anomalies and they elicited a similar ERP component with a scalp topography that was so similar that it localized in approximately the same anterior temporal region (localization is a function of scalp topography and can therefore serve as a summary measure of overall topography).

In any case, the P600oz source analysis indicated a point equivalent dipole location that could be taken as implicating the AMTL, replicating a prior study (Dien et al., 2003), but could also implicate the inferior frontal cortex. An intracranial ERP study (McCarthy et al., 1995) reported evidence for two areas sensitive to semantic incongruity in visual sentences, one in the hippocampal area peaking at about 400 ms and one anterior to it peaking later at perhaps 500 to 600 ms; it may be that these two signals correspond to the N400pz and the P600oz respectively. However, if this P600z is indeed the classic P600, then it is most reliably associated with syntactic sensitivity (Friederici, 2002; Hagoort, 2003; Neville et al., 1991; Newman et al., 2007; Osterhout & Holcomb, 1992; Osterhout & Nicol, 1999) and PET studies, which can image the AMTL (Devlin et al., 2000), show no evidence of the AMTL responding to such manipulations

(Caplan, Alpert, & Waters, 1998; Caplan, Alpert, & Waters, 1999; Caplan, Alpert, Waters, & Olivieri, 2000; Indefrey, Hagoort, Herzog, Seitz, & Brown, 2001; Indefrey, Hellwig, Herzog, Seitz, & Hagoort, 2004; Moro et al., 2001; Stromswold, Caplan, Alpert, & Rauch, 1996).

It is therefore argued that the P600oz solution is more consistent with a frontal source (see also Matsumoto, Iidaka, Haneda, Okada, & Sadato, 2005; Van Petten & Luka, 2006). The left inferior frontal cortex has repeatedly been implicated in executive level language processes, both semantic and syntactic (Cardillo, Aydelott, Matthews, & Devlin, 2004; Fiez, 1997; Gold, Balota, Kirchhoff, & Buckner, 2005; Just, Carpenter, Keller, Eddy, & Thulborn, 1996; Poldrack et al., 1999; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997; Vigneau et al., 2006; Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Furthermore, the companion fMRI study (Dien et al., 2008) did detect a semantic activation in this region that, like the P600oz, was not sensitive to cloze value. Since the P600oz in the prior ERP study (Dien et al., 2003) was sensitive to both semantic and syntactic incongruity and the left IFG has been shown to be sensitive to both as well, we suggest tentatively that this is the most likely source of the P600oz effect.

A final aspect to this dataset, not relevant to the questions regarding the nature of the late N400 and P600 effects, is that of two lateralized N200 effects reported in the original study (Dien et al., 2003). No evidence was seen for the left-lateralized N200 effect (correlated with Expectancy ratings) or the right-lateralized N200 effect (correlated with Meaningfulness ratings). One possibility is that the effects were unreliable or due to a confound of some sort. Another possibility is that the effects disappeared because one of the changes in the stimulus set changed a volitional aspect of how the participants processed the sentences. For example, the elimination of the syntactic anomalies, the lower predictability of the congruent endings, and the less bizarre nature of the incongruent endings could all have led the participants to approach the sentence reading differently. Additional studies, now in preparation, have provided some suggestive results in this respect that could support either conclusion and so the matter must, for now, be considered inconclusive. In contrast, the N400 and P600 results discussed in this present report are also consistent with the earlier report.

Conclusion

The present results indicate that the "N400 effect", at least for visual sentences, consists of at least two distinct ERP components, an N400pz and a P400cz. Both components were responsive to cloze probability and congruity, although the P400cz was relatively more sensitive to congruity than cloze. It is suggested that the P400cz might reflect a non-language sequential expectancy process and that studies of the N400pz might benefit from separating the two ERP components. For example, separating the P400cz from the N400pz improved the convergence with MEG reports. The data also supported other reports that the P600 can respond to semantics and that it appears to emanate from the frontal cortex.

4. Experimental Procedure

Participants: Forty-six participants engaged in the ERP experiment either on a volunteer basis or for course credit. All had corrected-to-normal vision, were right-handed (three with familial left-handedness), and were native English speakers. None had any history of brain injury, attention deficit disorder, or dyslexia. After data processing, 26 participants remained (15 female), ranging in age from 18 to 25 (mean = 19.4).

Stimuli: The stimuli consisted of 150 sentences (listed in Dien et al., 2008) derived from a published stimulus set (Bloom & Fischler, 1980). The incongruent group (cloze probabilities equal zero) contains 75 sentences. The 75 congruent sentences were chosen to provide an even distribution of cloze probabilities ranging from 0.02 to 0.99 in order to facilitate correlational analyses (mean of .39 and standard deviation of .34). Of the 75 congruent sentences, 39 matched the most commonly chosen ending and 36 did not. The incongruous endings were chosen to be roughly matched (no statistically significant difference) to the congruous endings in terms of mean sentence length (7.8 vs. 7.7), word length (5.0 vs. 5.5), and word frequency (Francis & Kucera, 1982) (94.9 vs. 125.0).

Subsequent analysis indicated that within the set of congruent stimuli, cloze was significantly correlated with word length: $r(73)=.26$, $p=.03$. For correlational analyses, a regression equation was used to partial out the portion of the cloze variable predictable from word length and the resulting residual was utilized for parametric analysis.

Subsequent analysis using norms from the English Lexicon Project (Balota et al., 2007) also indicated that although the congruent and incongruent endings were matched for mean bigram frequency (1835.5 vs. 1848.5), they were not matched for orthographic neighborhood (3.8 vs. 5.9), T_{WJt}/c (1.0,118.0)=8.15, $p=0.0046$. Critically, neither measure was correlated with cloze probability. Although orthographic neighborhood size can affect the N400 (Debruille, 1998; Holcomb, Grainger, & O'Rourke, 2002), as the purpose of this study is to study the neural basis of the N400 effect, it should not matter to what degree it is being elicited by semantic incongruity and to what extent it is being elicited by orthographic neighborhood size.

Procedure: The session started with a practice section with ten sentences. The experiment was then divided into four blocks, each lasting about six minutes. Participants were instructed to read the sentences for comprehension, as a recognition quiz was given at the end of each block for the full sentences. The recognition test consisted of twenty complete sentences, half new and half old. In order to match stimulus presentation conditions with a companion fMRI study[1], stimuli were presented via an fMRI Devices IFIS LCD stimulus hood (Invivo Corporation, Orlando, Florida), wherein the contents of the LCD screen were conveyed to the eyes via mirrors in a periscope-like apparatus. Each word was displayed for 105 ms, and immediately replaced by a fixation mark (a "+" sign), and then the next word was displayed following a 900 ms delay, until each word in the sentence was shown. The inter-trial interval was one second. These parameters were chosen to maintain comparability with a prior study (Dien et al., 2003). The sentences were presented in the same randomized sequence to all participants. There was no significant correlation between order and sentence types or sentence parameters. The experiment was approved by the Tulane University Medical Center Institutional Review Board and were in compliance with the Code of Ethics of the World Medical Association (Declaration of Helsinki).

Data Collection: ERPs were recorded at a 250 Hz sampling rate in a shielded room using a 129-channel GSN200 geodesic net system (Electrical Geodesics, Incorporated) referenced to Cz (the recording reference is irrelevant as data can be mathematically referenced, see Dien, 1998). The impedance criterion was 50k ohms, which according to the vendor is appropriate for the system, which has been designed to accommodate high impedances (via the use of high amplifier input impedances).

Data Analysis: The raw waveforms were segmented 212 ms before stimulus onset to 1012 ms after stimulus onset (sentence endings only). Eye blinks were removed using an automated independent components analysis (ICA) routine using the EP Toolkit (Dien, 2010b), available for download at http://homepage.mac.com/jdien07/), which in turn uses EEGLAB (Delorme & Makeig, 2004). In this procedure (Frank & Frishkoff, 2007), ICA components correlating at least .9 with the scalp topography of a blink template generated by averaging together eight blinks were removed and the data reconstituted from the remaining ICA components. Bad channels were identified by software procedures (Net Station 4.0) and by visual inspection. Automatic criteria were to mark a trial's channel as bad if the fast average amplitude exceeds 100 μv or if differential average amplitude exceeds 50 μv. A channel was marked as bad for the entire session if more than 20% of the trials were deemed bad. A trial was marked bad if it contained more than 10 bad channels, if the vertical electro-oculographic (VEOG) differential exceeded 70 μv, or if any EOG amplitude exceeded 70 μv. Bad channels were corrected using spline interpolation based on neighboring channels.

Participants without at least thirty trials per cell were excluded from the analysis, resulting in 26 participants (reflecting the opinion that item averaging is best done with participants that are contributing to most of the item averages). No trials were excluded due to behavioral performance (based on the reasoning that performance on the intra-break recognition task would not be sufficiently related to the participant's attentiveness during the reading process for such removal to have a favorable cost-benefit ratio) and all participants met the minimum performance criterion of 60%. No participants were excluded on any other grounds. It is likely that the unusually high data loss rate was due to the use of the fMRI stimulus presentation system. It was designed to be used by a prone participant in the scanner but since the ERP participants were seated upright, it was necessary to prop the viewer vertically and have the participant lean forward to squint into it; the resulting awkwardness appears to have produced a higher than normal level of movement artifact.

The data were re-referenced to the average reference (Bertrand, Perrin, & Pernier, 1985; Dien, 1998) using the polar average reference effect (PARE) correction to correct for the undersampling of the undersurface of the head (Junghöfer, Elbert, Tucker, & Braun, 1999). Next, the waveforms were low-pass filtered at 30 Hz and the first and last 12 ms with filter artifact were dropped. Finally, the data were baseline corrected using the 200 ms pre-stimulus period. In order to conduct parametric ERP analyses, item averages were generated by averaging across subjects, generating a unique waveform for each of the 150 sentences (see Dien et al., 2003). The mean number of trials per average was 22.8, ranging from 18 to 26.

A conventional windowed analysis was performed to enable direct comparison of the results to non-PCA studies. For the N400 analysis, a window from 352 to 448 ms was chosen to minimize overlap with preceding and succeeding ERP components, reflecting this missive's core concern with isolating the N400. For the P600 effect, a window was set for 600 to 800 ms. The windows were chosen on the basis of what the literature indicates is a generally appropriate period for these ERP components. More customized fitting (e.g., 652 to 824) was not done to avoid giving the appearance, whether true or otherwise, of capitalizing on chance variations in the data. For scalp topography analyses, the montage was divided into 12 regions (Dien & Santuzzi, 2005) with roughly equal numbers of electrodes (8-10 each), excluding midline electrodes along the division between the left and right sides and the front and back sides. Thus, each ANOVA included three spatial factors: Hemisphere (left, right), AP (anterior, posterior), and DV (dorsal, middle, ventral).

A temporo-spatial PCA was conducted using the ERP PCA Matlab Toolbox 1.23 (Dien, 2010b)[2]. The subject averages were analyzed, using a covariance matrix as the relational matrix (Dien, Beal, & Berg, 2005; Kayser & Tenke, 2003). As suggested by simulation analyses (Dien, Khoe, & Mangun, 2007; Dien, 2010a), Promax rotation (Hendrickson & White, 1964) was used for the temporal step and the Infomax rotation (Bell & Sejnowski, 1995), a type of ICA, as implemented by EEGLab (Delorme & Makeig, 2004), was used for the spatial step. Based on simulation data (Dien, 2010a), the temporal step was taken first and the spatial step was taken second. For source analysis and figures, the portion of the grand average waveforms accounted for by each factor was computed (Dien et al., 1997). Following the recommended guidelines for the EP Toolkit (Dien, 2010b), factors accounting for less than .5% variance were ignored (Dien, submitted).

Source Analysis: Source analyses were conducted with BESA 5.2.4.8 using an elliptical four-shell model. A pair of hemispheric dipoles (the second dipole mirroring position but not orientation or amplitude) was used for the analyses. Such mirrored dipoles are justified because the neuroimaging literature indicates that even lateralized language activity often involves both homologous hemispheric locations (Just et al., 1996); furthermore, a recent review (Van Petten & Luka, 2006) concluded that the N400 involves bilateral activity, although stronger in the left hemisphere. Observations such as this have resulted in the recommendation to use mirrored symmetric dipoles (Wibral, Turi, Linden, Kaiser, & Bledowski, 2008). In the event that the two paired dipoles are drawn to the midline by the fitting process such that they are separated only by the minimum inter-dipole distance of 6 mm, a dipole solution with only a single dipole will be attempted. Note that the amplitudes of the two dipoles are independently determined and so a situation with only a single hemispheric dipole will largely be modeled by a dipole pair as being a large amplitude in the appropriate hemispheric dipole and a negligible amplitude in the other hemisphere, all things being equal.

The use of more than a pair of dipoles was avoided because of findings that localization accuracy suffers when trying to model simultaneous dipoles (Zhang, Jewett, & Goodwill, 1994) and indeed a major impetus for the use of the PCA was to avoid having to do so. The problem is that the dipoles need to be added serially. The first dipole (or dipole pair) added in moves to account for all the possible variance, which means positioning itself in between the coordinates for all the ERP components present. It would therefore not be situated in a meaningful location. The next dipole (or dipole pair) to be added likewise would be set to account for the maximum possible variance, which again means accounting for as much of the remaining ERP activity as possible, again resulting in a position that is not meaningful. The standard technique for addressing this problem is to identify a window where only one of the ERP components is present, adding the appropriate dipole(s), and then moving on to the part of the window where both ERP components are present and adding an additional dipole(s) to account for the second ERP component. In the present case, examination of the scalp topography difference maps suggests no such window exists for the N400 effect.

Successfully meeting the generally accepted guideline for a good quality solution (residual variance or RV no more than 10% residual variance) was taken as evidence that no more dipoles were needed for a given solution. Not meeting this criterion was accepted as a sign that the source analysis procedure had failed. Meeting the criterion was not taken as indicating success but rather that the solution was worthy of further consideration. Time windows were not specified because the spatial distribution of two-step PCA factors is identical across the entire time course (insofar as each temporo-spatial factor is characterized by a single set of temporal factor loadings and a single set of spatial factor loadings). The entire epoch was therefore selected for the fitting process. Channels 125-128 were excluded from the analysis because in the GSN200 system these electrodes are not as constrained as the rest of the montage and their positioning is therefore not as reliable. Including them in the analyses made little difference in any case.

An iterative algorithm was utilized in which the program automatically shifted the position of the dipoles until it found a position of maximum fit. The fitting criteria were an equal weighting of maximizing variance accounted for and minimizing total energy (to reduce unwanted interaction effects between the two dipoles). The regularization constant was 1%. Minimum inter-dipole distance was set at 6 mm. To maintain uniformity, all reported solutions were based on a central starting position. Solutions were rechecked against front and rear starting locations to ensure the solution was not dependent on the starting location. The present dataset is not suited for the alternative approach of trying to separate such components based on different condition effects and, indeed, would pose a chicken-and-egg situation in that it is the goal of the present experiment to determine whether such overlapping ERP components are present in the first place, let alone what manipulations might differentiate them. Finally, seeded solutions were not used because the point equivalent nature of point equivalent dipoles means that seeding them in anything other than a dimensionless activation is questionable (and, of course, significant PET/fMRI activations used for seeding are by their nature anything but dimensionless) and because personal experience has shown that oftentimes a wide portion of the head meets the 10% criterion, making a seeded solution of low value; for this reason, only the best fitting location was utilized and success or failure was evaluated on that basis.

Statistical Tests: Following standard lab procedure, robust ANOVAs were used to test effects (Keselman, Wilcox, & Lix, 2003), as implemented in the EP Toolkit (Dien, 2010b). The purpose of the robust ANOVA is to achieve a Type I error rate that more closely complies to the nominal alpha rate than the conventional ANOVA by: 1) using bootstrapping to estimate the population distribution rather than assuming a normal distribution, 2) using trimmed means to be more resistant to outliers, and 3) using a Welch-James statistic to not assume a homogenous variance-covariance structure. Further discussion of the limitations of conventional ANOVAs, as they apply to ERPs, is available elsewhere (Dien & Santuzzi, 2005). The experience of the authors is that the robust statistic is generally more conservative than conventional F-tests (for side-by-side comparisons, see Dien, Franklin, & May, 2006). Aside from being more robust to violations of assumptions, the statistic is otherwise comparable to a conventional t-statistic and p-values are interpreted in the usual manner. Note that robust statistics (specifically the use of non-pooled error variance estimates) is endorsed by the journal Psychophysiology in their Guidance to Authors (as of December, 2009). A 10% symmetric trim rule was used. The seed for the number generation was set at 1000. The number of iterations used for the bootstrapping function was 50000. P-values are rounded to the second significant digit (where available).

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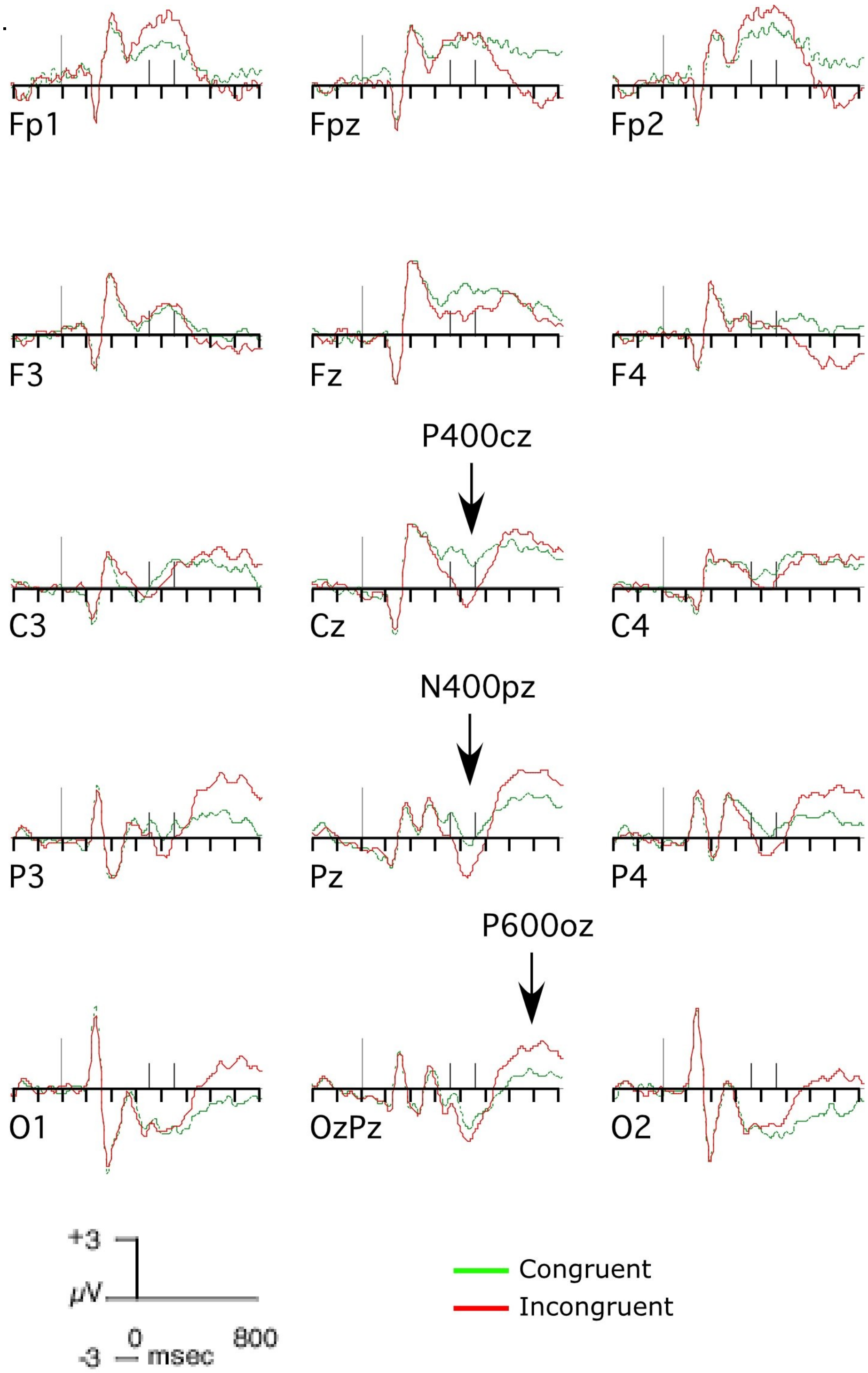
Footnotes

1) A companion fMRI study with a separate sample of subjects was conducted at the same time. Unfortunately, the fMRI component of the study apparently had insufficient statistical power. The fMRI dataset had a sample size of eleven whereas a recent study (Seghier, Lazeyras, Pegna, Annoni, & Khateb, 2008) has concluded that at least sixteen are needed to reliably detect strong language effects and at least thirty are needed for weak effects. It is therefore not surprising that poor convergence was found between the ERP effects and the fMRI effects, especially since there is a good possibility that at least some of the ERP semantic effects emanate from the anterior temporal pole, where fMRI is largely blind (Devlin et al., 2000). Following advice of the reviewers, the fMRI study was published as a separate report (Dien et al., 2008), focusing on an effect in the posterior inferior temporal gyrus that appears to be unrelated to both the N400 and the P600 processes (the ERP data has a trend towards an N250 effect above this portion of the cortex but just misses significance and so it will not be discussed).

2) Note that although the use of the PARE correction means that the mean across the recording electrodes will not equal zero, a PCA factor corresponding to the mean will not be generated because the use of a covariance matrix eliminates the mean; such a factor would only be generated for a sum-of-squares-cross-products matrix (see Curry et al., 1983). In essence, both the PCA and the BESA are using a conventional average reference (since BESA always average references its data). The difference between the average reference and the PARE average reference should only be relevant for direct comparisons between the scalp voltage maps of the grand average data and that of the PCA factors and does not affect the conclusions made in this paper.

Figure Captions

Figure 1.



Grand Average Waveforms. Vertical lines above the baseline indicate the 350-450 ms window.

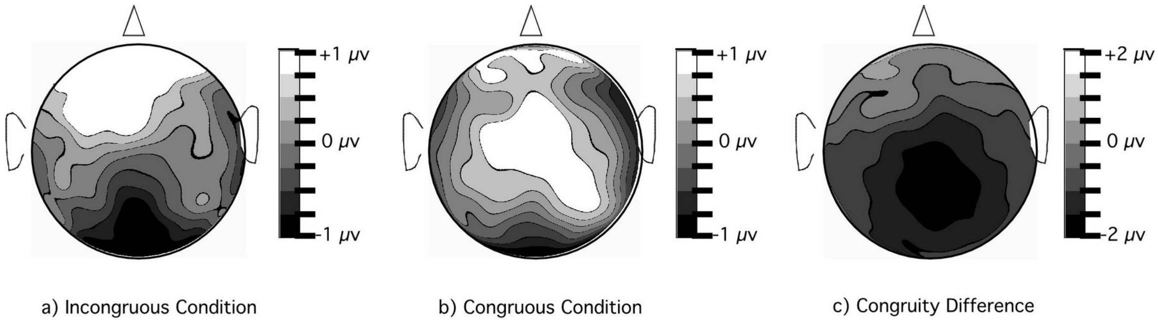


Figure 2. N400 Scalp Topography at 400 Milliseconds. A) The scalp topography of the incongruent grand average data. B) The scalp topography of the incongruent grand average data. C) The scalp topography of the grand average difference map of the incongruent condition minus the congruent condition.

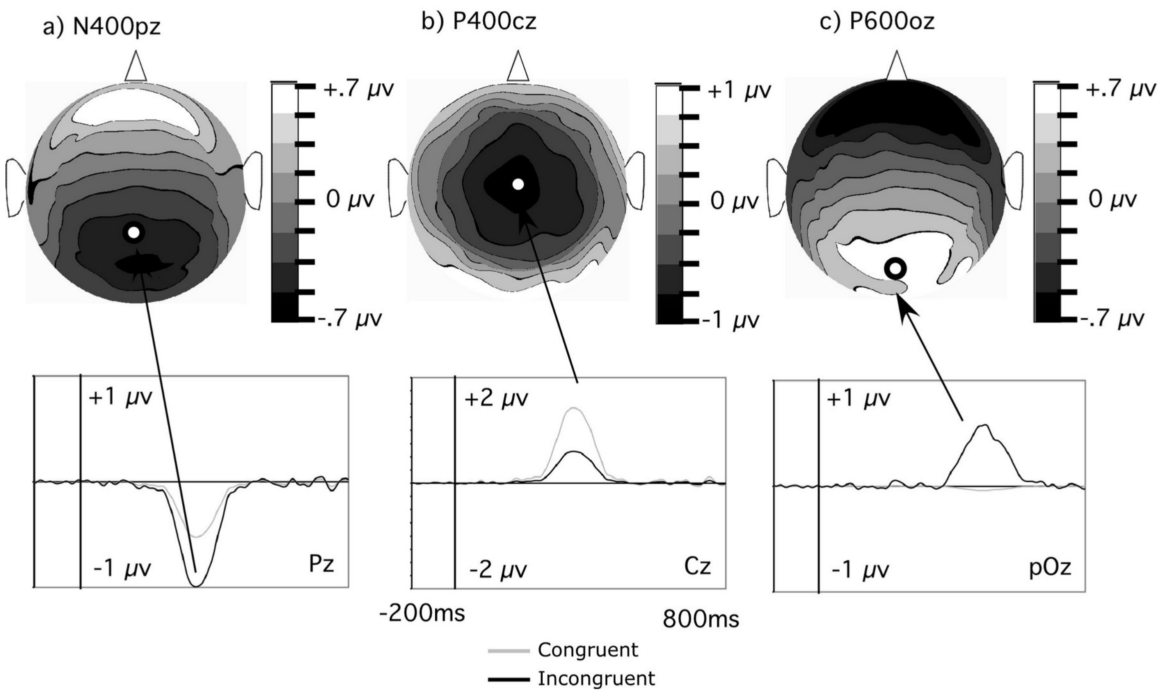


Figure 3. Factor Scalp Topography and Waveforms. The pOZ electrode stands for just posterior to Oz. The figure shows the scalp topography and the time course of the latent PCA factors, projected back into channel space so that they can be compared against other datasets. The topographical maps are difference maps (incongruent-congruent).

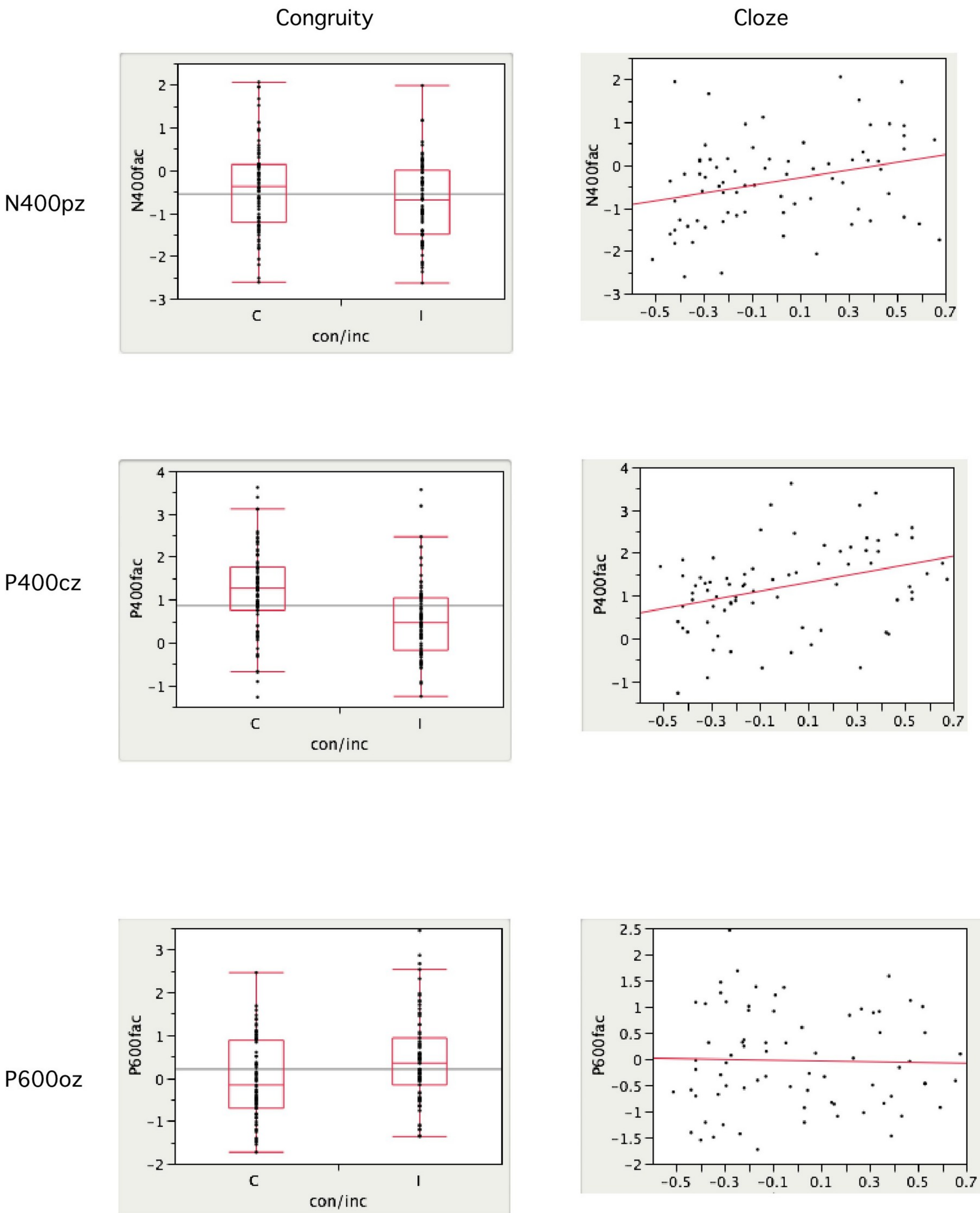
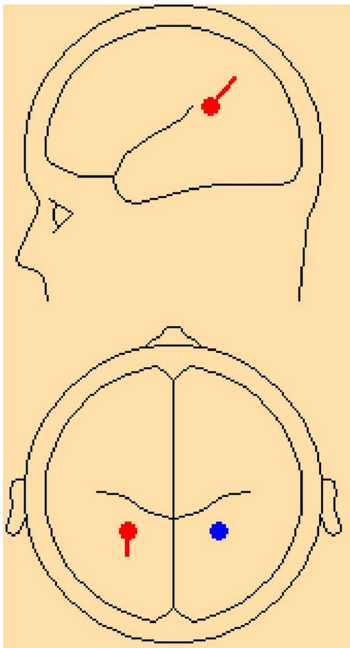
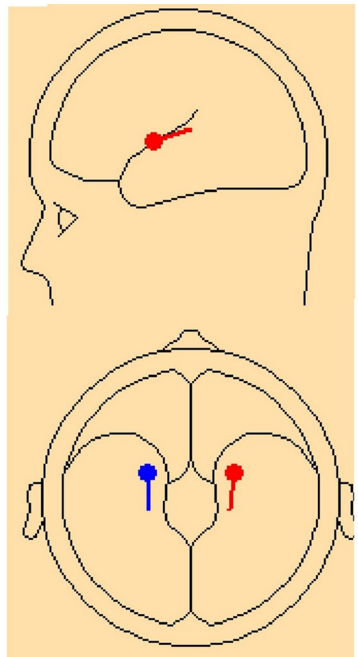


Figure 4. Scatterplots for N400pz, P400cz, and P600oz Factor Congruity and Cloze Effects. Each black dot indicates one of the observations. The grey line is the grand mean. The box plots for the congruity effect indicate the median, the 25th and 75th percentiles in the middle and the whiskers extend to a distance of 1.5

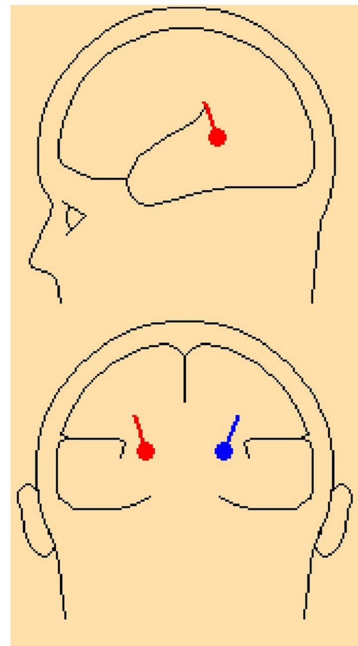
times the interquartile distance between the 25th and 75th percentiles (by way of highlighting possible outliers). The cloze effect scatterplot is for the measure as residualized for letter length. The red line indicates the least-squares linear fit.



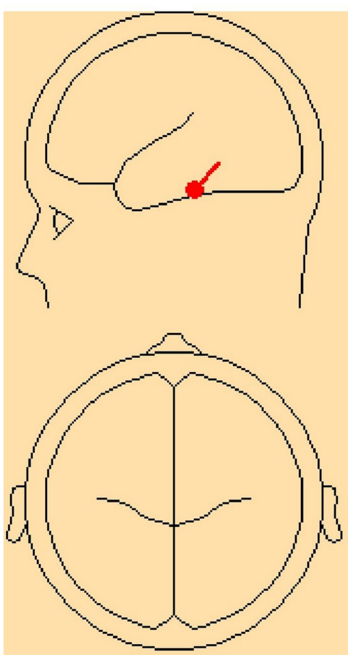
N400 Window



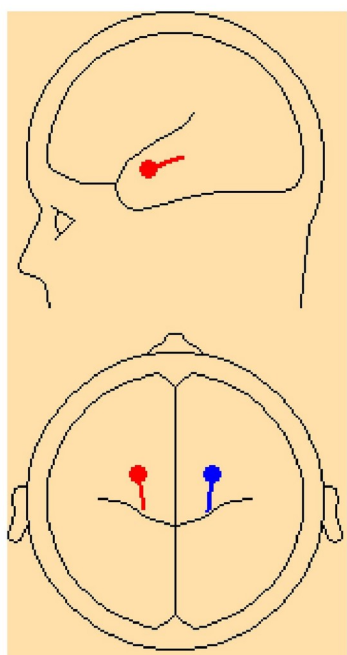
N400Pz Factor



P400Cz Factor



P600 Window



P600Oz Factor

Figure 5. Source Analyses for the N400 and P600 Windows and the N400pz, P400cz, and P600oz Factors. The residual variance of the source analyses for the N400 and P600 windows of the grand average were much too high to interpret the dipole locations but are presented so they can be compared against the source analyses for the factors. Note how the N400 window dipole localizes to the vicinity of the STG only when an effort is made to separate the N400pz and the P400cz. The red dipole is the left hemisphere dipole and the blue dipole is the right hemisphere dipole. The direction of the dipole stem has been set to be consistent with the labeling for the ERP component (positive for "positive" components and negative for "negative" components).

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