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Separable Processes Before, During, and After the N400 Elicited by Previously Inferred and New Information: Evidence from Time-Frequency Decompositions

Vaughn R. Steele[a,b,c,*], **Edward M. Bernat**[d], **Paul van den Broek**[e,f], **Paul F. Collins**[e], **Christopher J. Patrick**[d], and **Chad J. Marsolek**[e]

[a]The Mind Research Network [b]Lovelace Biomedical and Environmental Research Institute [c]University of New Mexico [d]Florida State University [e]University of Minnesota [f]Leiden University, the Netherlands

Abstract

Successful comprehension during reading often requires inferring information not explicitly presented. This information is readily accessible when subsequently encountered, and a neural correlate of this is an attenuation of the N400 event-related potential (ERP). We used ERPs and time-frequency (TF) analysis to investigate neural correlates of processing inferred information after a causal coherence inference had been generated during text comprehension. Participants read short texts, some of which promoted inference generation. After each text, they performed lexical decisions to target words that were unrelated or inference-related to the preceding text. Consistent with previous findings, inference-related words elicited an attenuated N400 relative to unrelated words. TF analyses revealed unique contributions to the N400 from activity occurring at 1–6 Hz (theta) and 0–2 Hz (delta), supporting the view that multiple, sequential processes underlie the N400.

Keywords

Event-related potentials; N400; inference-priming; time-frequency

1. Introduction

When comprehending stories, readers often use background knowledge to infer information that is not explicitly stated in the text. When they do this, the accessibility of the inferred information is increased, as evident in behavior measures (e.g., Potts, Keenan, & Golding, 1988). An important neural correlate of this enhanced accessibility of information is an attenuation of the N400 event-related potential (ERP) component elicited by reading such information when it is later explicitly presented in the text. However, the process(es) associated with the attenuation of the N400 when encountering inference-primed information are not clear. In the current study, we used time-frequency analysis of the N400

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[*]Corresponding author: Vaughn R. Steele, The Mind Research Network, Lovelace Biomedical and Environmental Research Institute, Department of Psychology, University of New Mexico, 1101 Yale Blvd NE, Albuquerque, NM 87106, vsteele@mrn.org.

to dissociate underlying operations involved in processing recently inferred and non-inferred information during reading.

Readers use background knowledge to infer information when breaks in the causal coherence between events in the text are encountered. For example, when reading "*With his exam coming up, the student opened his book. After three hours, he was sure he knew the material quite well for the exam,"* background knowledge of exams and the need to *study* prior to knowing the material is accessed. This background knowledge is used to generate an inference that the student spent the three hours studying. In this manner, information not explicitly presented in the text, but inferred, provides a bridge for the break in causal coherence (Fletcher & Bloom, 1988; Graesser, Bertus, & Magliano, 1995; Graesser, Haberlandt, & Koizumi, 1987; McKoon & Ratcliff, 1986, 1989; Myers, Shinjo, & Duffy, 1987; Potts et al., 1988; van den Broek, 1990, 1994). When an inference is generated online to bridge a causal gap, this inferred information can be incorporated into the long-term memory representation of the text (Kintsch, 1988; Singer, 1994; van den Broek, Young, Tzeng, & Linderholm, 1998).

Behavioral evidence that an inference has been generated during reading comes from 'inference-priming' effects. For example, participants make faster lexical decisions to target words that are related to inferences that have been made when reading a preceding text (e.g., *study*), compared with lexical decisions to unrelated target words (e.g., Keenan, Golding, Potts, Jennings, & Aman, 1989; Potts et al., 1988; Sundermeier, Virtue, Marsolek, & van den Broek, 2005). In addition to such behavioral evidence, a neural correlate of processing previously inferred information while reading for comprehension involves an attenuation of the N400 that is similar to the attenuation observed in classic N400 work (Kutas & Hillyard, 1980). In one study (St. George, Mannes, & Hoffman, 1997), participants read short narrative stories and ERPs were extracted in relation to processing of the final sentence of each scenario. The context of some scenarios encouraged generating a causal coherence inference prior to reading the final sentence. Some of the final sentences explicitly stated the information that could have been inferred from the preceding text. N400s were attenuated for sentences that explicitly stated information that had been inferred from comprehending the preceding text relative to sentences that followed scenarios that had not encouraged generating a causal coherence inference.

What memory and comprehension processes are engaged when processing inference-primed information? Comprehension theories have posited multiple processes involved in generating inferences and integrating them into text representations (e.g., Kintsch, 1988; Mason & Just, 2004; Myers & O'Brien, 1998; Singer, 1994; Singer & Halldorson, 1996; van den Broek et al, 1998), although single-process perspectives exist as well (e.g., McKoon & Ratcliff, 1992; Ratcliff & McKoon, 1988). The question of whether multiple processes are involved is notoriously difficult to test using only behavioral evidence (different theories often can account for the same set of behavioral results). Thus, in addition to collecting behavioral evidence, we recorded event-related potentials and used the technique of time-frequency analysis, in which information from both temporal and spectral (frequency) domains is used to decompose ERP signals,[1] to investigate the neural correlates of processing recently inferred information and non-inferred information during reading.

Previous results using time-frequency analyses of ERP data suggest that multiple processes may underlie the N400 (Hald, Bastiaansen, & Hagoort, 2006; Roehm, Schlesewsky, Bonrkessel, Frisch, & Haider, 2004). Roehm et al. (2004) decomposed the N400 elicited by individually presented words of single sentences during a reading task. The sentences were grammatical and ungrammatical German sentences. Roehm et al. reported that ERP activity in a theta frequency band (3.5–5 Hz), reflecting what they called linguistic problem detection[2], coincided with the early part of the N400. Roehm et al. found a delta band (1–2.33 Hz) component, reflecting what they called a form of conflict resolution[3], occurring within a later time window (i.e., 600–1000 ms post stimulus presentation). Therefore, an initial linguistic problem detection process was associated with the N400 and a later conflict resolution process was associated with a later time window.

A different research group also used time-frequency methods to decompose the N400 elicited by individually presented words of single sentences (Hald et al., 2006). Two time-frequency bands were extracted for analysis, a lower theta band (~3–7 Hz) and a higher gamma band (35–45 Hz). Most important for the current study, during the N400 window greater activation in the theta frequency band was found for sentences with semantic violations (e.g., the Dutch translation of “The Dutch trains are sour and blue.”) compared with sentences that did not have semantic violations (e.g., the Dutch translation of “The Dutch trains are yellow and blue.”). In particular, maximal theta activity during semantic violations was evident at the fronto-central midline electrode Fz. This increased theta activity for semantic violations was interpreted as reflecting either an increase in verbal working memory load due to online evaluation of the current context and the current word, or an error monitoring process similar to the error-related negativity (ERN; Gehring, Goss, Coles, Meyer, & Donchin, 1993).

In our study, because both theta and delta frequencies have been observed during the N400, we focused primarily on these frequency bands. For our purposes here, we used a Cohen’s class reduced inference distribution (RID) time-frequency transform (Cohen, 1995). This approach has the advantage of providing uniform time-frequency resolution, thus offering greater time-frequency specification[4] of effects relative to previously reported effects (see

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[1] Time-frequency analysis has been utilized to assess ERP activity that overlaps in time, but that is distinguishable in terms of frequency characteristics (for reviews of ERP frequency analysis, see Basar 1998, 1999,). Such activity is often difficult to separate in the time-domain. Theta (3–7 Hz) and delta (0–3 Hz) bands have been shown to contain separable time-frequency representations of common stimulus-locked ERP components such as the error-related negativity (ERN; see e.g., Bernat et al, 2005; Gehring & Willoughby, 2004; Hall et al., 2007) and P300 (see e.g., Bernat et al., 2007; Demiralp, Ademoglu, Comerchero, & Polich, 2001). The technique of time-frequency decomposition has the potential to disentangle underlying brain activity components that overlap with one another in the standard time-domain signal representation. Work of this kind points to the possibility that the stimulus-locked N400 ERP could contain separable time-frequency components.

[2] Linguistic problem detection was operationalized by Roehm et al. (2004) as detection of the syntactic violation that occurs when a subject follows another subject (ungrammatical). The syntactic violation is analogous to, but not the same as, for example, “She hit he” in English, in which the object is in a form that is only applicable to subjects.

[3] Conflict resolution, as defined by Roehm et al. (2004), was indexed by comparing processing between the two ungrammatical conditions (the second subject was animate versus inanimate). Greater activity in the delta frequency range was found for sentences when the second subject was inanimate (which enabled a possible resolution for understanding what occurred, given that inanimate things are not likely to realize subject functions) compared with when the second subject was animate (which did not enable a possible resolution for understanding what occurred). The important difference was that in the ungrammatical inanimate condition it was possible to decipher who was likely doing what to whom, whereas in the ungrammatical animate condition this was not achievable.

[4] The Cohen’s class RID (Cohen, (1995) time-frequency transform provided a uniform time-frequency resolution, unlike the wavelet transform. There are advantages to each method, as well as distinct differences between them (see Bernat, Williams, & Gehring, 2005 for further discussion). In particular, wavelet transforms are inherently susceptible to tradeoffs in measurement resolution between time and frequency, unlike the RID. At higher frequency ranges, wavelet transforms have high time resolution coupled with low frequency resolution, and at low frequency ranges, wavelet transforms have high frequency resolution coupled with low time resolution.

Bernat et al., 2005). In particular, previously reported time-frequency N400 effects (Hald et al., 2006; Roehm et al., 2004) were based on wavelet time-frequency transforms to decompose ERP waveforms, as opposed to the Cohen's RID. There are advantages to each method, as well as distinct differences between them (see Bernat, Williams, & Gehring, 2005 for further discussion). In both of these studies, time-frequency effects were measured to incongruities within single sentences that elicited a time-domain N400. These N400 effects are similar to classic effects reported by Kutas and Hillyard (1980) albeit with the incongruities either being semantic or syntactic, rather than only semantic.

The potential finding of separate dissociable processes associated with theta and delta frequency bands may be crucial for understanding mechanisms underlying the processing of previously inferred information following comprehension of multiple sentence scenarios. For example, if dissociable processes are involved, one distinct process may underlie the detection of greater incoherence when incoming information is not inference-related to the preceding text than when it is. This effect may be associated with enhanced theta activity for non-inference-related information versus inference-related information (cf. Hald et al., 2006). High incoherence between incoming information and the preceding context may be similar to other forms of conflict that have been associated with increased theta activity (e.g., Bernat, Malone, Williams, Patrick, & Iacono 2007; Bernat et al., 2005; Hall, Bernat, & Patrick 2007; Luu, Tucker, & Makieg, 2004). In addition, another process may underlie improved integration of incoming information and affiliated text representations when incoming information is related to a preceding inference versus when it is not. This effect may be associated with enhanced delta activity for inference-related information in comparison with non-inference-related information (cf. Roehm et al., 2004). Furthermore, the processing of inferences in highly familiar scenarios may differ from the processing of inferences in less familiar scenarios (see Sundermeier et al., 2005), thus we also manipulated level of familiarity of the inference scenarios. Finally, we also examined potential effects on the P600 because it has been associated with other kinds of non-semantic violations (Osterhout, McLaughlin, & Bersick, 1997).

In summary, the current study extended previous work on inference-priming effects (Sundermeier et al., 2005) by including ERP measurements and time-frequency analysis to test hypotheses regarding the N400 elicited by information either inferred (in highly familiar or less familiar scenarios) or not inferred when reading preceding narrative texts. Participants read two-sentence texts, some of which required generating causal coherence inferences to comprehend the second sentence, and some of which did not. After each text, subjects performed a lexical decision. In some trials, the target word reflected an inference that would have been made when reading the just-preceding text, and in other trials the target word was not inference-related to the preceding text. We hypothesized that lexical decisions to inference-primed targets would be faster than lexical decisions to unprimed (neutral) targets. This would provide behavioral evidence that the inferences were generated and the accessibility of relevant concepts was enhanced. We hypothesized that N400s would be attenuated for inference-primed target words relative to unprimed target words (St. George et al., 1997). Because time-frequency analysis allows for separation of overlapping cognitive processes, we additionally hypothesized that different time-frequency measures would be associated with different processes that occur before, during, and after the N400 elicited when reading inference-primed information or neutral (i.e., unprimed) information. Specifically, following the aforementioned reasoning, we predicted that: (1) theta activity occurring relatively early in the N400 time window would be greater for neutral target words than for inference-primed target words, reflecting differing degrees of coherence, (2) delta activity occurring relatively late in the N400 time window would be greater for inference-primed target words than for neutral target words, reflecting differing degrees of integration of incoming information with the text representation and (3) these two processes would be separable from later (e.g., P600) time-domain and time-frequency measures that perhaps could be attributed to further integrative, familiarity, or syntactically based processes.

2. Results

Repeated-measures ANOVAs were conducted to analyze behavioral performance, ERP time-domain (TD) effects, and ERP time-frequency (TF) decompositions. Pseudowords were not included in these analyses because we were interested in processing differences in the three word conditions (familiar, less-familiar, and neutral). When significant violations of sphericity were detected, Greenhouse-Geisser corrected effects and epsilon (ε) are reported, as recommended by Jennings and Wood (1976; see also Picton et al., 2000). Simple effects *t*-tests as well as orthogonal linear and quadratic contrasts were calculated to clarify significant main effects and interactions. Regression analyses were carried out with TD components as the criterion variable and the TF components as the predictor variables to better explain TD components with TF components. Effects that did not reach statistical trend ($p > .10$) are not reported.

2.1 Behavioral Results

Separate repeated-measures ANOVAs were conducted using response times for correct lexical decisions and lexical decision error rates as the dependent variables. In each analysis, experimental condition (familiar, less-familiar, or neutral) was the (within-participants) independent variable, and the random variable was participant.

In the analysis of lexical decision response times, the main effect of experimental condition was significant, $F(2,56) = 12.41$, $MSe = 3481.07$, $p < .001$ (see Figure 1). In line with a priori predictions that inferences would be generated and facilitate lexical decisions in the inference conditions, lexical decisions were significantly faster in the familiar inference condition (570 ms) than in the neutral condition (629 ms), $t(29) = -3.83$, $p = .001$, and lexical decisions were significantly faster in the less-familiar inference condition (558 ms) than in the neutral condition (629 ms), $t(29) = -4.54$, $p < .001$. No response time difference was found between the two inference conditions, $t < 1$. In the error rate analysis, the main effect of experimental condition did not approach significance, $F < 1$; the error rates were uniformly low throughout (means between 1% and 2%). Most important, this indicates that the response time effects were not compromised by tradeoffs between speed and accuracy performance.

Our interpretation of the behavioral results is that inferences were generated when reading the inference-condition scenarios and this primed the lexical decisions that were made to the inference-primed probes. However, it is possible that inferences were not generated before the appearance of the probes but that the facilitation in lexical decision times may have been due to backward integration of a probe with its preceding context. By that account and by the compound cue theory more generally (McKoon & Ratcliff, 1992; Ratcliff & McKoon, 1988), the magnitude of the facilitation in lexical decision times should be greater when the probes fit especially well or integrate easily with their preceding contexts. Therefore, this account would predict that if the probes and their contexts in the familiar scenarios condition have greater semantic similarity than the probes and their contexts in the less-familiar scenarios condition, then the facilitation in lexical decision times should be greater in the familiar condition than in the less-familiar condition. To test that prediction, we measured the strengths of semantic association between the probes and their preceding contexts using Latent Semantic Analysis (LSA; LSASS1 “LSA overlap, adjacent sentences, mean”) via a web interface (Coh-Metrix 3.0, McNamara, Louwerse, Cai, & Graesser, 2005, http://cohmetrix.memphis.edu, accessed on September 11th and 12th 2012). LSA is a mathematical method for representing the semantic similarities between words and passages by using their co-occurrences in large corpora of texts. We conducted a one-way ANOVA with probe word as the random variable, semantic similarities as the dependent variable, and condition (familiar, less-familiar, and neutral scenario) as the independent variable. The main effect of condition was significant $F(2,95) = 11.24$, $p = .0001$. Simple effect contrasts indicated that semantic similarities were higher in the familiar condition than in both the less-familiar condition, $F = 4.046$, $p = .0454$, and the neutral condition, $F = 22.323$, $p = .0001$, and higher in the less-familiar condition than in the neutral condition, $F = 7.348$, $p = .0073$. According to these semantic similarity effects, the facilitation in lexical decision times should be greater in the familiar condition than in the less-familiar condition, but this was not observed (see Figure 1). In fact, response times in the less-familiar condition were numerically faster than response times in the familiar condition, providing evidence against backward integration of the probes and their preceding contexts.

2.2 Time-Domain Results

In the TD analyses, a subset of electrode sites representing three coronal levels of location crossed with three lateral levels of location was examined (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4; see Figure 2). A repeated-measures ANOVA was conducted in which mean amplitude of the TD component comprised the dependent variable and participant comprised the random variable. The (within-participants) independent variables were experimental condition (familiar, less-familiar, or neutral), coronal level of electrode location (F electrode row, C electrode row, P electrode row), and lateral level of electrode location (left, midline, right). Interactions involving this lateral factor, which had a quadratic distribution with an uninteresting increase in activation over midline electrodes, were not of theoretical interest and are not reported here. When significant violations of sphericity were detected in the ANOVAs, as mentioned above, Greenhouse-Geisser corrected effects and epsilon (ε) are reported.

N400—In the analysis of the N400 component, the main effect of experimental condition was significant, $F(2,56) = 10.72$, $MSe = 83.52$, $p < .001$, $\varepsilon = .81$. Consistent with evidence indicating that the N400 is attenuated when processing information inferred from the preceding text (St. George et al., 1997), simple-effect t-tests revealed that N400 mean amplitude in the familiar (inference) condition ($M = 6.80$ μV) was attenuated relative to N400 mean amplitude in the neutral condition ($M = 3.60$ μV), $t(29) = 3.87$, $p = .001$. Similarly, the N400 mean amplitude in the less-familiar (inference) condition ($M = 5.84$ μV) was attenuated relative to N400 mean amplitude in the neutral condition ($M = 3.60$ μV), $t(29) = 4.24$, $p < .001$. Mean N400 amplitudes for the familiar condition ($M = 6.69$ μV) and the less-familiar ($M = 5.88$ μV) conditions were not different from each other, $t(29) = 1.37$, $p = .180$.

There was a trend main effect of mean amplitude for lateral electrode location, $F(2,56) = 3.08$, $MSe = 11.46$, $p = .054$. In particular, there was a quadratic effect, $F(1,28) = 5.97$, $MSe = 9.84$, $p = .021$, indicating enhanced N400 at midline sites ($M = 5.74$ μV) compared with left ($M = 5.31$ μV) and right ($M = 5.00$ μV) electrode sites. In addition, there was a main effect for coronal electrode location, $F(2,56) = 23.52$, $MSe = 89.15$, $p < .001$, $\varepsilon = 0.62$. A priori linear contrasts indicated that the N400 was reduced towards posterior electrode locations relative to anterior sites, $F(1,28) = 26.51$, $MSe = 97.39$, $p < .001$ (i.e., less of a negative deflection from the F row, $M = 2.97$ μV, to the P row, $M = 7.41$ μV, with the C row falling numerically between the two, $M = 5.67$ μV). Also, the experimental condition by coronal location interaction was significant, $F(4,112) = 3.61$, $MSe = 8.55$, $p = .008$, $\varepsilon = 0.69$. In particular, the difference between the inference conditions compared against the neutral condition was greater at the central and parietal electrode locations combined (M = 3.17 μV), than at the frontal electrode locations (M = 1.80 μV), $t(29) = 3.10$, $p = .004$.

P600—In the analysis of the P600 component, the main effect of experimental condition was significant, $F(2,56) = 6.76$, $MSe = 78.83$, $p = .002$, $\varepsilon = .82$. Simple-effect *t*-tests revealed that P600 mean amplitude in the familiar condition (M = 9.38 μV) was more positive relative to the P600 mean amplitude in the neutral condition (M = 6.87 μV), $t(29) = 3.11$, $p = .004$. Similarly, the P600 mean amplitude in the less-familiar condition (M = 8.92 μV) was more positive relative to the P600 mean amplitude in the neutral condition (M = 6.87 μV), $t(29) = 3.99$, $p < .001$. Mean P600 amplitudes for the familiar condition (M = 9.38 μV) and the less-familiar (M = 8.92 μV) condition were not different from each other, $t < 1$.

There was a main effect of mean amplitude for lateral electrode location, $F(2,56) = 7.12$, $MSe = 19.79$, $p = .025$. In particular, there was a quadratic effect, $F(1,28) = 14.41$, $MSe = 18.19$, $p = .001$, indicating more positive P600 at midline sites (M = 9.21 μV) compared with left (M = 8.17 μV) and right (M = 7.79 μV) electrode sites. In addition, there was a main effect for coronal electrode location, $F(2,56) = 44.22$, $MSe = 50.19$, $p < .001$, $\varepsilon = 0.77$. Predictably, P600 amplitude was more positive at posterior electrode locations relative to anterior electrode locations, $F(1,28) = 45.49$, $MSe = 58.79$, $p < .001$ (F row, M = 5.44 μV, C row M = 9.77 μV, and the P row, and M = 9.96 μV).

2.3 Time-Frequency Decompositions

All electrodes were utilized for the TF-PCA (AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC3, FC1, FCz, FC2, FC4, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP3, CP1, CPz, CP2, CP4, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO5, PO3, POz, PO4, PO6, O1, Oz, and O2), and 9 of these electrodes were selected for statistical analysis (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4; these were the same 9 electrodes that were used in the TD analyses). As in the TD analysis, the (within-participants) independent variables were experimental condition, coronal level of electrode location, and lateral level of electrode location. Separate repeated measures ANOVAs were conducted in which activity measured on the TF surface comprised the dependent variables, and participant comprised the random variable; significant main effects and interactions were again clarified using simple effect *t*-tests. A three-component theta decomposition and a three-component delta decomposition best fit the data (see scree plots of singular values in Figure 3D and Figure 4D, respectively); thus theta and delta decompositions were analyzed in separate ANOVAs. Both decompositions accounted for a substantial amount of variance (theta, 39.65%; delta, 93.69%). For similar reasons as in the TD analysis, interactions involving the lateral electrode location variable are not reported here. When significant violations of sphericity were detected in the ANOVAs, as mentioned above, Greenhouse-Geisser corrected effects and epsilon (ε) are reported.

Theta Activity Decomposition—Only principal component number 2 indicated a significant difference between experimental conditions, thus it was selected for further analysis (see Figure 3).

The main effect for experimental condition was significant, $F(2,58) = 7.45$, $MSe = 0.01$, $p = .001$. Theta activation in the familiar condition and less-familiar condition did not differ significantly from one another, $t(29) = -1.14$, $p = .266$. There were some significant differences in theta activation between these experimental conditions at some electrodes (see Figure 3) even though the *t*-test for the selected 9 electrodes did not reach significance. More important, theta activity was significantly greater in the neutral condition than in the familiar condition, $t(29) = -3.24$, $p = .003$ and in the less-familiar condition, $t(29) = -2.71$, $p = .011$.

Additionally, a trend main effect of coronal electrode location on theta activity was found, $F(2,56) = 3.05$, $MSe = 0.02$, $p = .056$. This coronal main effect is in line with previous research in which theta activity is maximal over anterior electrode locations during detections of incoherence (e.g., Bastiaanses, van Berkum, & Hagoort, 2002; Hald et al., 2006).

Delta Activity Decomposition—All three delta principal components indicated significant condition effects and were selected for further analysis (see Figure 4).

Delta Component 1: The main effect of experimental condition was significant, $F(2,56) = 3.26$ $MSe = 0.23$, $p = .046$, $\varepsilon = 0.74$. Delta activty in the familiar condition and the less-familiar condition were not different, $t < 1$. Delta activity for the familiar and less-familiar conditions were both significantly greater than for the neutral condition, $t(29) = 2.16$, $p = .039$, $t(29) = 3.42$, $p = .002$, respectively.

The main effect of coronal electrode locations was significant, $F(2,56) = 14.72$ $MSe = 0.142$, $p < .001$. In particular, delta activation increased for more posterior versus anterior electrode locations, as evidenced by a significant linear contrast, $F(1,28) = 12.81$ $MSe = 0.19$, $p = .001$. The main effect of lateral location was also significant, $F(2,56) = 5.98$, $MSe = 0.09$, $p = .004$. As in previous analyses, the quadratic contrast effect was significant, with greater activation over the midline electrode locations than over the lateral locations, $F(1,28) = 14.19$, $MSe = 0.07$, $p = .001$.

Delta Component 2: The main effect of experimental condition was significant, $F(2,56) = 5.41$ $MSe = 0.76$, $p = .007$, $\varepsilon = 0.60$. Delta activity in the familiar condition and the less-familiar condition were significantly different, $t(29) = 2.06$, $p = .049$ (see Figure 4). Delta activity for the familiar and less-familiar conditions were both significantly greater than for the neutral condition, $t(29) = 2.59$, $p = .015$, $t(29) = 2.44$, $p = .021 < .05$, respectively.

The main effect of coronal electrode locations was significant, $F(2,56) = 12.74$ $MSe = 0.29$, $p < .001$, $\varepsilon = 0.83$. In particular, delta increased for more posterior versus anterior electrode locations, as evidenced by a significant linear contrast, $F(1,28) = 13.36$ $MSe = 0.35$, $p = .001$. The main effect of lateral location was also significant, $F(2,56) = 11.27$, $MSe = 0.09$, $p < .001$. As in previous analyses, the quadratic contrast effect was significant, with greater activation over the midline electrode locations than over the lateral locations, $F(1,28) = 19.55$, $MSe = 0.08$, $p < .001$.

Also, the interaction between experimental condition and coronal electrode location was significant, $F(4,112) = 5.29$, MSe = 0.13, $p = .001$, $\varepsilon = 0.47$. In particular, the delta activity difference between frontal and posterior electrode sites was greater in the two inference conditions than in the neutral condition, $t(29) = 3.90$, $p = .001$.

Delta Component 3: The main effect of experimental condition was significant, $F(2,56) = 4.96$ $MSe = 0.09$, $p = .010$. Delta activity in the familiar condition and the less-familiar condition were not different $t < 1$ (see Figure 4). There were some significant differences in delta activity between these experimental conditions at some elecrtodes (see Figure 4) even though the t-test for the selected 9 electrodes did not reach significance. Delta activity for the familiar and less-familiar conditions were both significantly greater than for the neutral condition, $t(29) = 2.73$, $p = .011$, $t(29) = 2.80$, $p = .009$, respectively.

The main effect of coronal electrode locations was significant, $F(2,56) = 22.83$ $MSe = 0.15$, $p < .001$. In particular, delta activity increased for more posterior versus anterior electrode locations, as evidenced by a significant linear contrast, $F(1,28) = 31.30$ $MSe = 0.18$, $p < .001$. The main effect of lateral location was also significant, $F(2,56) = 7.57$, $MSe = 0.06$, $p = .001$. As in previous analyses, the quadratic contrast effect was significant, with greater activation over the midline electrode locations than over the lateral locations, $F(1,28) = 8.02$ $MSe = 0.07$, $p = .008$

Finally, the interaction between experimental condition and coronal electrode location was significant, $F(4,112) = 2.55$, MSe = 0.04, p = .043, $\varepsilon = 0.55$. In particular, the delta activity difference between frontal and posterior electrode sites was greater in the two inference conditions than in the neutral condition, $t(29) = 2.19$, $p = .037$.

2.4 Regression Analyses

To directly assess the relationship between the TD and TF components, regression analyses were performed. In these regressions, TD components served as the criterion variables and TF components served as predictors. The TD components used in separate regressions were the peak difference between the P2 and N400 amplitude, mean N400 amplitude, and mean P600 amplitude. Only the TF components that carried condition effects were used in these regression analyses (i.e., theta component 2 and all three delta components). For both the criterion and predictor variables, a difference score between the inference condition (mean of familiar and less-familiar conditions) and the neutral condition was calculated. Therefore, the differences between the inference condition and the neutral condition in the TD measures were predicted by the same differences in the TF component measure.

Two regression models were calculated for each dependent variable, and each was a 2-step regression model. In one model (denoted as model a), the theta component 2 was included in the first step and the 3 delta components were added to the overall model at step 2 (see Table 2). In the other model (denoted as model b), the 3 delta components were included in the first step and the theta component 2 was added to the overall model at step 2 (see Table 3).

P2 to N400 Peak Difference—The regression model 1a predicting the difference between the P2 and N400 peak amplitude from TF components was significant at both steps: step 1 $R^2 = .34$, $F(1,28) = 14.44$, $p = .001$; step 2 $R^2 = .56$; $\Delta R^2 = .22$, $F(4,25) = 7.81$, $p < .001$ (see Table 2). There was a significant ΔR^2 in step 2, $p = .018$. The theta component was a unique predictor in both steps and delta components 1 and 3 were unique predictors in step 2 of the model, *ps* < .05. The regression model 1b predicting the difference between P2 and N400 peak amplitude from TF components was only significant at step 2: step 1 $R^2 = .23$, $F(3,26) = 2.64$, $p = .070$; step 2 $R^2 = .56$; $\Delta R^2 = .32$, $F(4,25) = 7.81$, $p < .001$ (see Table 3). There was a significant ΔR^2 in step 2, $p < .001$. Only delta component 1 was a significant predictor in step 1 and the theta component and delta components 1 and 3 were unique predictors in step 2 of the model, *ps* < .05. Therefore, the theta component significantly predicted the peak to peak amplitude difference between the P2 and N400 on its own or in combination with delta components 1 and 3.

N400—Only step 2 of the regression model 2a predicting mean N400 amplitude from TF components was significant: step 1 $R^2 = .08$, $F(1,28) = 2.57$, $p = .120$; step 2 $R^2 = .72$; $\Delta R^2 = .63$, $F(4,25) = 15.86$, $p < .001$, (see Table 2). The ΔR^2 in step 2 was significant, $p < .001$. The delta component 2 was a unique predictor in model step 2, $p < .001$. The regression model 2b predicting mean N400 amplitude from TF components was significant: step 1 $R^2 = .71$, $F(3,26) = 21.63$, $p < .001$; step 2 $R^2 = .72$; $\Delta R^2 = .003$, $F(4,25) = 15.86$, $p < .001$, (see Table 3). The Δ R^2 in step 2 did not reach significance, $p = .588$. The delta component 2 was a unique predictor in both model steps, $ps < .001$, and delta component 3 was only marginally significant in step 1 of the model, $p < .10$. Therefore, the delta component 2 was the only TF component that significantly predicted the TD mean N400 measure.

P600—Only step 2 of the regression model 3a predicting mean P600 amplitude from TF components was significant: step 1 $R^2 = .03$, $F(1,28) = 0.75$, $p = .394$; step 2 $R^2 = .62$; Δ $R^2 = .59$, $F(4,25) = 10.12$, $p < .001$, (see Table 2). The Δ R^2 in step 2 was significant, $p < .001$. In step 2, the delta component 1 was a unique predictor, $p < .005$, and the delta component 2 was marginally significant as a unique predictor, $p = .086$. Both steps in regression model 3b predicting mean P600 amplitude from TF components were significant, step 1 $R^2 = .61$, $F(3,26) = 13.64$, $p < .001$; step 2 $R^2 = .62$; Δ $R^2 = .007$, $F(4,25) = 10.12$, $p < .001$ (see Table 2). The Δ R^2 in step 2 did not reach significance, $p = .514$. The delta component 1 was a unique predictor in both model steps, $ps < .005$. Therefore, delta component 1 was the only TF component that significantly predicted the TD mean measure of the P600.

2.5 Additional Correlations

Pearson correlations also were calculated to further dissociate the theta and delta components. When mean TF measures were used, the theta component was negatively correlated with the second delta component, $r(28) = -.435$, $p = .016$, but was not correlated with the other two delta components ($ps > .10$).

Taken together, the regression and correlation analyses can be used to dissociate activity occurring before, during, and after the N400. Specifically, (1) the peak to peak difference between the P2 and N400 was best characterized by the theta component; (2) the TD measure of the N400 was best characterized by a single delta component; (3) the TD measure of the P600 was best characterized by a single delta component that is separable from the delta component that best characterizes the N400. Finally, the early theta activity was negatively related to the two later delta component but was not significantly contribute to the regression models predicting the N400 and P600 TD measures.

3. Discussion

In this study, the goal was to examine the possibility of dissociable processes that may occur before, during, and after the N400 attenuation that has been associated with processing inference-primed information. Increased accessibility of inference-primed information has been quantified as speeded lexical decisions to words corresponding to that information (e.g., Keenan et al., 1989; Potts et al., 1988; Sundermeier et al., 2005) and can now also be linked to decreased theta activity (cf. Hald et al., 2006; Roehm et al., 2004) and increased delta activity (cf. Roehm et al.) when reading inference-primed words.

After short scenarios were read, lexical decisions to inference-primed target words were faster than lexical decisions to words that were not inference-primed (neutral). In the ERP TD, the N400 elicited by inference-primed words was attenuated compared with the N400 elicited by neutral words. In addition, the P600 elicited by inference-primed words was more positive than the P600 elicited by neutral words. There is a surface similarity between these TD effects, with inference-primed words eliciting activity more in the positive direction than neutral words in both the N400 and P600. However, this surface similarity appears to be misleading, given our additional findings.

Our time-frequency analysis of the N400 provides evidence for dissociable and sequential time-frequency measures. Specifically, an initial activation in the theta range and a subsequent activation in the delta range were found during the N400 time window. Also, a delta activation was found during the P600 time window that was separable from the two components found during the N400 time window. Greater theta activation was produced in the neutral condition than in the inference-primed conditions, whereas greater delta activation was measured in the inference-primed conditions than in the neutral condition. This provides evidence for functional differences associated with the theta and delta activity. Our logic is as follows. At the functional level, it is not controversial that detection of incoherence should be greater in the neutral condition than in the inference-primed condition, and it is not controversial that integration of incoming information with text representations should be greater in the inference-primed condition than in the neural condition. We found significantly greater theta in the neutral condition than in the inference-primed condition (potentially a correlate of greater detection of incoherence in the former than in the latter) and significantly greater delta in the inference-primed condition than in the neutral condition (potentially a correlate of greater integration of incoming information in the former than in the latter). This is a double dissociation that supports multiple-process theories to a greater degree than single-process theories. Single-process theories would need to be revised to account for our double dissociation.

We also used regression analyses to test whether different TD components could be predicted by different TF components. Indeed, the negativity of the N400 (peak difference between P2 and N400) was best predicted by the theta component, the later portion of the N400 was best predicted by delta component 2, and the P600 was best predicted by delta component 1. Thus, an important finding in these data is that the N400 is best predicted by a single delta component and not the theta component. The theta component best predicted the peak-to-peak difference of the P2 to N400 which was statistically separate from the N400. Also, the delta component that best predicted the later portion of the N400 was statistically separate from the delta component that best predicted the later P600 component. Therefore, the initial negativity of the N400 can be accounted for by theta power. Also, the attenuation of the N400 and the increased amplitude of the P600 can be accounted for by two delta components that, in both cases, drive the ERP waveform more positive. These distinctions may be very beneficial when interpreting future TD N400 and P600 condition effects. Given the functional differences associated with the theta and delta activations, we conclude from this data driven analysis that dissociable processes occur before, during, and after the N400.

Our finding of faster responding to inferred information compared with non-inferred (neutral stimulus) information is in line with findings from previous inference-priming studies (e.g., Keenan et al., 1989; Potts et al., 1988; Sundermeier et al., 2005). The attenuation of N400 evident for inference-primed compared with neutral stimuli is in line with previously observed N400 attenuation reflecting facilitation in processing information due to reading preceding texts (e.g., Curran, Tucker, Kutas, & Posner, 1993; Frisch & Schlesewsky, 2001; van Berkum, Hagoort, & Brown, 1999). More importantly, it is consistent with previous N400 measures of inference-priming during reading (St. George et al., 1997). Finally, our results are consistent with previous ERP research on processing coherent and incoherent information (e.g., Bastiaanses et al., 2002; Federmeier & Kutas, 1999; Hald et al., 2006; Lee & Federmeier, 2006; van Berkum et al., 1999). For example, Lee and Federmeier (2006) presented words with high levels of ambiguity (e.g., 'duck'), such that contextual information was needed to specify a particular meaning, as well as other words with low levels of ambiguity (e.g., 'vote'). They observed greater frontal negativity for highly ambiguous than for low ambiguous words, suggesting that the negativity could be attributed to detection of semantic ambiguity.

Of primary interest here is the finding that dissociable frequencies underlie the N400. Theta activity was evident during the initial negativity of the N400 (peak difference between the P2 and the N400), followed by delta activity later in the N400 time window. Greater theta activity was evident for target words that were neutral than for words that were inference-primed. In contrast, greater delta activity was evident for inference-primed target words compared with neutral target words. The observed theta effect may be due to greater incoherence between the preceding text and the incoming information (i.e., the target word) when the incoming information is neutral than when it is inference-primed. One speculation is that this is the kind of incoherence that can signal perceived event boundaries (Zacks, Speer, Swallow, Braver, & Reynolds, 2007). Considering this finding in relation to other reported N400 theta effects (Hald et al., 2006; Roehmn et al., 2004), it appears that increased anterior theta activity reflects processing of incoherent information. Note however, that each condition elicited some anterior theta activity and therefore not all theta activity can be interpreted as reflecting solely incoherence monitoring. One important distinction highlighted in the current study however, is that the theta component was not a significant predictor of the TD N400 (the N400 is best described as delta activity that is separate from the earlier theta and the later P600 delta component).

Other tasks elicit similar anterior theta activity associated with incoherence, referred to as error detection (e.g., the error-related negativity [ERN]; Gehring et al., 1993). This error detection process associated with the ERN, reflected by an increase in midline-frontal theta activity, is well established (e.g., Bernat et al., 2007; Bernat et al., 2005; Gehring & Willoughby, 2004; Hall et al., 2007; Luu et al., 2004). One key brain region that has been implicated in such an incoherence monitoring process is the anterior cingulate cortex (ACC; Botvinick, Cohen, & Carter, 2004; Carter, Braver, Barch, Botvinick, Noll, & Cohen, 1998). In view of data indicating ACC activation is greater when greater response conflict occurs (e.g., Carter et al., 1998), the ACC is considered by some to operate as a conflict detector. Together with the present findings, an incoherence monitoring process can account for greater theta activity elicited by the neutral condition compared with the inference-primed conditions. Further explorations of this theta component and how it relates to the N400 are necessary to fully understand how and when it is related to the N400.

The observed delta activity associated with the N400 may reflect integration of information (i.e., the target word) with the preceding text and was greatest for the inference-primed compared with the neutral condition. This delta activity was greater at posterior than at anterior electrode sites and was found later than the theta activity, but still within the N400 time window. There was an increased ability to integrate the incoming information with representations of the texts in the inference conditions compared to the neutral condition. This greater integration was highest in the familiar inference condition, in which the target words were most readily integrated with the representations of the previous texts. As the potential for integration decreased in a linear fashion across conditions, activity in the delta frequency range also decreased (familiar > less-familiar > neutral). These findings are in line with previous research supporting the notion that when information is encountered that is only distantly causally related to preceding text; it is not effectively stored in memory (Keenan, Baillet, & Brown, 1984; Myers et al., 1987; van den Broek, Rapp, & Kendeou, 2005). Difficulty integrating the neutral stimuli into the preceding texts can account for the reduced delta activity compared with both of the inference-primed conditions.

A secondary finding was that condition effects were found after the N400 and during the P600 time window. Effects during the P600 time window are often interpreted as processing of syntactic ambiguities or violation (Osterhout et al., 1997). For example, when reading the sentences '*The cats won't eat the food*' and '*The cats won't eating the food*' a more positive P600 will be measured to the critical word '*eating*' compared to the critical word '*eat*'. Another possible interpretation is that the P600 is similar to the P300 which is sensitive to infrequent stimuli or "odd-balls" (Coulson, King, & Kutas, 1998). However, no syntactic violation occurred in the present experiment and the present effects are not likely explained as a P300 type of odd-ball effect. One thing that is clear from the present results is that the P600 effect was separate from the N400 effect. Regression analyses indicated that one delta TF component uniquely predicted the N400 and a separate delta TF component uniquely predicted the P600. Further exploration is needed to sufficiently identify the separate and co-occurring processes that underlie the P600 and N400.

Several factors of our procedure allowed for greater ecological validity and isolation of operations needed to process inferred and non-inferred information. Participants read each scenario at their own pace, unlike in language studies in which individual words are presented one at a time for a predetermined duration (e.g., St. George et al., 1997; van Berkum et al., 1999). Additionally, we measured physiological responses to a single word and not to an entire sentence (cf. St. George et al.), which increased our precision of measuring the neural processes associated with semantic incoherence and integration. Such specificity allowed for isolation and dissociation of processes associated with reading and integrating individual words into a greater context. This initial exploration of underlying operations before, during, and after the N400 associated with processing individual words (either inference-primed or neutral) may have benefitted from these aspects of our procedure.

By using ERPs, time-frequency analysis, and regression analyses, we found evidence for dissociable TF components before, during, and after the TD N400. An early process, indexed by theta frequency activity, appears to have been associated with detecting incoherence between inferred information and the incoming text. In addition, a later N400 process, indexed by delta frequency activity, appears to have been associated with integrating incoming information with the preceding text representation. These processes proved statistically separate from the P600. These results support comprehension theories that have posited multiple processes involved in generating inferences and integrating them into text representations (e.g., Kintsch, 1988; Mason & Just, 2004; Myers & O’Brien, 1998; Singer, 1994; Singer & Halldorson, 1996; van den Broek et al., 1998) more than theories that posit a single or unified process for those aspects of comprehension (e.g., McKoon & Ratcliff, 1992; Ratcliff & McKoon, 1988). Taken together, theta and delta TF components measured here reflect sequential processes that are quite useful to bridge theories of text comprehension and the underlying neural generators required for text comprehension.

4. Experimental Procedure

4.1 Participants

Thirty native English speakers (15 females) participated in exchange for either introductory psychology course credit or monetary compensation. Participants were recruited by newspaper advertisements in the University of Minnesota student newspaper and a local Minneapolis newspaper. All participants had normal or corrected to normal vision and reported no history of traumatic head injuries. All participants gave informed consent before participating and ranged in age from 18 to 27 (*Mage* = 20.8).

4.2 Materials

The two-sentence scenarios, words, and pseudowords used by Sundermeier et al. (2005) and available online (http://levels.psych.umn.edu/stimuli/inference.pdf) were used in this experiment. For each participant, 48 experimental scenarios were followed by words, and 48 filler scenarios were followed by pseudowords (pronounceable nonwords).

The same set of 48 probe words was presented to each participant, but each of these 48 words was preceded either by a high-familiarity inference scenario, a low-familiarity inference scenario, or a neutral, non-inference scenario. Coherence breaks occurred in the inference scenarios so that comprehension of the second sentence required making a causal inference to bridge the coherence break. More specifically, the first sentence for an inference scenario created a story foundation by introducing a protagonist, conflict, or goal. Between the first and second sentence a causal coherence gap occurred, such that for full comprehension the reader was required to draw upon background knowledge to make an inference that bridged the gap between the two sentences, and the word that followed such a scenario matched a concept essential to the bridging inference. The level of pre-experimental familiarity of the inference scenarios (assuming their inference words occurred with them) was manipulated across two conditions. In the high-familiarity condition, the scenarios were familiar in that they had been seen, read about, thought about, or experienced frequently in the past, and in the low-familiarity condition, the scenarios were less-familiar in that they had not been seen, read about, thought about, or experienced frequently in the past.

Ratings reported by Sundermeier et al. (2005) confirmed this manipulation. Scenarios in the neutral condition did not require making a bridging inference to comprehend the second sentence, but like the inference-promoting scenarios they involved general semantic contexts that were consistent with their probe words. Thus, the main manipulation was that only in the inference conditions (high and low familiarity) did the scenario support generation of a bridging inference involving the target word. As an example, the familiar inference, less-familiar inference, and neutral scenarios for one of the target words are presented in Table 1. Eight additional scenarios and words/pseudowords were used for practice and warm-up trials, and data from these trials were not included in the analyses.

The critical scenarios had an average of 19 syllables, with a range of 14 to 28. The 48 probe words consisted of 44 verbs and 4 nouns and were equated in number of letters with the 48 pseudowords. Three lists of sixteen probe words were created and were balanced on number of letters (overall $M = 4.98$) and word frequency (overall $M = 85$ per million; Carroll, Davies & Richman, 1971). These lists were assigned to the three experimental conditions (familiar, less-familiar, and neutral) in a rotation across participants that assured that each probe word was used to represent each of those conditions an equal number of times for female and male participants.

4.3 Procedure

Participants sat in a reclining chair in a dimly lit, sound-attenuated room and viewed stimuli on a computer screen from a distance of approximately 100 cm. Stimuli were presented centrally on a 21″ Dell high-definition computer screen one sentence at a time**,** using E-Prime software and a serial response box (Psychology Software Tools, Inc. www.pstnet.com). Sentences were displayed in Times New Roman 16 pt font, with clauses occupying separate lines. Participants were instructed to read each scenario at their own reading pace. Once the first sentence was read, the participant pressed a button with their thumb to advance to the second sentence. Immediately after the second sentence was read and the button press was made, a fixation point was presented centrally in bold Arial 24 pt font for 1000 ms, followed by a letter string in Arial 24 pt font for 170 ms. Participants were instructed to make a lexical decision to each letter string as quickly and accurately as they could. To make a lexical decision response, the participant either pressed a button with their index finger, identifying that the letter string formed an English word, or a different button with their middle finger, identifying that the letter string did not form an English word. All responses were made with the right hand. An intertrial interval of 1000 ms (with a blank display) was initiated after the response to the lexical decision was registered.

When the task was explained to participants, it was stressed that reading and comprehending the sentences was needed in order to do well on a memory test that would follow the experiment. This was done to motivate good comprehension, but the memory test was not actually administered due to session timing constraints. Also, it was stressed that each sentence should be read only once, without going back to re-read any part of the sentence.

Participants were given five practice trials before they began what appeared to be the experimental trials. The first three of the putative experimental trials were not analyzed; instead, these trials tested understanding of the procedure in the following way. If two or more of these three preliminary lexical decisions were incorrect, the experiment would loop back to the beginning and the experimenter would re-enter the testing room to reiterate the instructions to the participant. Once the participant understood the instructions, the experiment was restarted. When two or more of the three preliminary lexical decisions were correct, the experiment transitioned directly into presenting each of the 96 experimental trials. Of these, 48 were trials in which pseudowords were presented, and 16 trials represented each of the familiar inference, less-familiar inference, and neutral conditions (words were presented after the scenarios for these conditions). Trial orders were pseudorandom; they were random with the constraint that no more than 3 consecutive trials represented the same condition.

4.4 Electroencephalographic Recordings

Electrophysiological data were collected using two IBM-compatible computers and a 64-channel Neuroscan Synamps Amplifier. The first computer used E-Prime version 1.1 software (Psychology Software Tools, Inc.) to deliver the stimuli, accept responses, and send digital triggers to the other computer indicating when stimulus events occurred. The second computer acquired physiological data using Neuroscan Acquire version 4.2 software in conjunction with the 64-channel Neuroscan amplifier. All signals collected with the Neuroscan system were digitized at 1000 Hz during data collection. During data acquisition, a high pass filter of 0.05 Hz and a low pass filter of 200 Hz were applied. A 64-channel cap (AF3, AF4, F7, F5, F3, F1, Fz, F2, F4, F6, F8, FT7, FC3, FC1, FCz, FC2, FC4, FT8, T7, C5, C3, C1, Cz, C2, C4, C6, T8, TP7, CP3, CP1, CPz, CP2, CP4, TP8, P7, P5, P3, P1, Pz, P2, P4, P6, P8, PO5, PO3, POz, PO4, PO6, O1, Oz, and O2) collected EEG activity using sintered Ag-AgCl electrodes placed in accordance with the 10–20 International System (Jasper, 1958). EEG activity was recorded using CPz as the reference, and then re-referenced offline to averaged mastoids. Electrodes were placed on each participant's face to measure electro-oculogram (EOG) data, which were used later to correct for eye blink artifacts. Horizontal EOG was measured with electrodes placed on either canthus and vertical EOG was measured with electrodes placed sub- and supra-orbital ridge of the left eye. All impedances were kept below 8 kΩ. All electrodes were used when plotting the distribution of activation for all subsequent decompositions; however, for simplicity, 9 electrodes from the overall montage were selected for the main statistical analyses (F3, Fz, F4, C3, Cz, C4, P3, Pz, and P4).

4.5 Behavioral Data Analysis

Response times for correct lexical decisions and lexical-decision accuracy rates were analyzed. Cutoff criteria were used to identify response time outliers. Trials in which response times were faster than 300 ms or greater than 2.5 standard deviations from the participant's mean response time were eliminated from the analyses. Also, any sentences with reading times faster than 1000 ms were deemed too rapid to actually have been read for comprehension; therefore, these trials were excluded from the analyses.

4.6 Event-Related Potential (ERP) Data Reduction

ERP epochs were defined in relation to the onset of the lexical decision stimulus, from 1000 ms pre- to 2000 ms post-stimulus. The epoched data were corrected for eye movement artifacts using an algorithm developed by Semlitsch, Anderer, Schuster, and Presslich, (1986), as implemented in the Neuroscan Acquire version 4.2 software. The resultant epochs were baseline corrected for the 150 ms preceding the stimulus. Within each trial, individual electrodes in which activity exceeded ± 75 μV were omitted from analysis. Additionally, only trials accepted for behavioral data analysis were selected for ERP data analysis. Applying these criteria, 12.5 % of trials were excluded. On average, 1.5% of trials per condition (or .25 out of 16 total trials per condition) were excluded per participant because of response errors and 11 % of electrode-trials (or 1.75 out of 16 total trials per condition) per participant were excluded because activity exceeded ± 75 μV. The N400 component was defined by the negative-going deflection between 250 and 500 ms post-stimulus onset. A later component, the P600, was defined as the positive-doing deflection between 400 and 800 ms post-stimulus onset. Condition averages for each participant were used for statistical analyses, and condition grand averages were computed and used for plotting ERP waves.

4.7 Time-Frequency Decomposition

A time-frequency (TF) principal components analysis (PCA) provided a data driven approach to defining TF components for analysis (Bernat et al., 2005). Ranges of time-frequency activity were delineated, and relevant principal components were extracted. Because previous work (described earlier) indicates that theta and delta can contribute distinctively to the assessed processes, and to better isolate the temporal characteristics of these signals, time-frequency decompositions were carried out separately for theta and delta band-pass filtered signals. Theta activity was defined by a 3^{rd} order highpass Butterworth filter at 1 Hz and a lowpass at 6 Hz. Delta activity was defined with a 3^{rd} order lowpass Butterworth filter at 2 Hz applied to each participant's experimental condition average ERP waveforms (butter function, Matlab, Inc.). Overlapping theta and delta filters were employed to avoid artifactually forcing activity into one or the other band, and rather allowing the PCA to determine where the overlapping activity was best characterized. To avoid filter edge effects, which are potential distortions caused when a time-frequency surface has the same beginning or end as the relevant ERP waveform epoch, time-frequency activity was computed for the entire epoch (-1000 to 2000 ms relative to stimulus onset), but time-frequency decompositions and analyses were conducted on data in the range from stimulus onset to 812.5 ms post-stimulus onset. All Cohen's class (Cohen, 1995) time-frequency transforms and PCA data reduction were conducted following the methods detailed by Bernat et al. (2005).

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References

Basar, E. Principles and Approaches. Berlin, Germany: Springer; 1998. Brain Functions and Oscillations. Volume I: Brain Oscillations.

Basar, E. Brain Functions and Oscillations. Volume 2: Integrative Brain Function. Berlin, Germany: Springer; 1999.

Bastiaanses MCM, van Berkum JJA, Hagoort P. Syntactic processing modulates the theta rhythm of human EEG. NeuroImage. 2002; 17:1479–1492.10.1006/nimg.2002.1275 [PubMed: 12414287]

Beeman MJ, Bowden EM, Gernsbacher MA. Right and left hemisphere cooperation for drawing predictive and coherence inferences during normal story comprehension. Brain Lang. 2000; 71:310–336.10.1006/brln.1999.2268. [PubMed: 10716864]

Bernat EM, Malone SM, Williams WJ, Patrick CJ, Iacono WG. Decomposing delta, theta, and alpha time-frequency ERP activity from a visual oddball task using PCA. Int J Psychol. 2007; 64:62–74.10.1016/j.ijpsycho.2006.07.015.

Bernat EM, Williams WJ, Gehring WJ. Decomposing ERP time-frequency energy using PCA. Clin Neurophysiol. 2005; 116:1314–1334.10.1016/j.clinph.2005.01.019. [PubMed: 15978494]

Botvinick MM, Cohen JD, Carter CS. Conflict monitoring and anterior cingulate cortex: An update. Trends Cogn Sci. 2004; 8:539–546.10.1016/j.tics.2004.10.003. [PubMed: 15556023]

Carrol, JB.; Davies, P.; Richman, B. The American Heritage Word Frequency Book. Boston: Houghton Mifflin Company; 1971.

Carter CS, Braver TS, Barch DM, Botvinick MM, Noll D, Cohen JD. Anterior cingulate cortex, error detection, and the online monitoring of performance. Science. 1998; 280:747–749.10.1126/science.280.5364.747. [PubMed: 9563953]

Cohen, L. Time-Frequency Analysis. Prentice Hall PTR; Englewood Cliffs, NJ: 1995.

Coulson S, Federmeier KD, Van Patten C, Kutas M. Right hemisphere sensitivity for word- and sentence-level context: Evidence from event-related potentials. J Exp Psychol Learn. 2005; 31:129–147.10.1037/0278-7393.31.1.129.

Coulson S, King JW, Kutas M. Expect the unexpected: Event-related brain response to morphosyntactic violations. Lang Cognitive Proc. 1998; 13:21–58.10.1080/016909698386582.

Curran T, Tucker DM, Kutas M, Posner MI. Topography of the N400: Brain electrical activity reflecting semantic expectancy. Electroen Clin Neuro. 1993; 88:188–209.10.1016/0168-5597(93)90004-9.

Demiralp T, Ademoglu A, Comerchero M, Polich J. Wavelet analysis of P3a and P3b. Brain Topogr. 2001; 13:251–267.10.1023/A:1011102628306. [PubMed: 11545154]

Federmeier KD. Thinking ahead: The role and roots of prediction on language comprehension. Psychophysiology. 2007; 44:491–505.10.1111/j.1469-8986.2007.00531.x. [PubMed: 17521377]

Federmeier KD, Kutas M. Right words and left words: Electrophysiological evidence for hemispheric differences in meaning processing. Cognitive Brain Res. 1999; 8:373–392.10.1016/S0926-6410(99)00036-1.

Federmeier KD, Segal JB, Lombrozo T, Kutas M. Brain responses to nouns, verbs, and class-ambiguous words in context. Brain. 2000; 123:2552–2566.10.1093/brain/123.12.2552. [PubMed: 11099456]

Fletcher CR, Bloom CP. Causal reasoning in the comprehension of simple narrative texts. J Mem Lang. 1988; 27:236–244.10.1016/0749-596X(88)90052-6.

Frisch S, Schlesewsky M. The N400 reflects problems of thematic hierarchizing. NeuroReport. 2001; 12:3391–3394.10.1097/00001756-200110290-00048. [PubMed: 11711892]

Gehring WJ, Goss B, Coles MG, Meyer DE, Donchin E. A neural system for error detection and compensation. Psychol Sci. 1993; 4:385–390.10.1111/j.1467-9280.1993.tb00586.x.

Gehring WJ, Willoughby AR. The medial frontal cortex and the rapid processing of monetary gains and losses. Science. 2004; 295:2279–2282.10.1126/science.1066893. [PubMed: 11910116]

Graesser, AC.; Bertus, E.; Magliano, JP. Knowledge based inferences. In: Lorch, RF., Jr; O'Brien, EJ., editors. Sources of Coherence in Reading. Lawrence Erlbaum Associates; Hillsdale: 1995. p. 295-320.

Graesser, AC.; Haberlandt, K.; Koizumi, D. How is reading time influenced by knowledge-based inferences and world knowledge. In: Britton, BK.; Glynn, SM., editors. Executive Control Processes in Reading. Lawrence Erlbaum Associates; Hillsdale: 1987. p. 217-251.

Hald LA, Bastiaansen MCM, Hagoort P. EEG theta and gamma response to semantic violations in online sentence processing. Brain Lang. 2006; 96:90–105.10.1016/j.bandl.2005.06.007. [PubMed: 16083953]

Hall JR, Bernat EM, Patrick CJ. Externalizing psychopathology and the error-related negativity. Psychol Sci. 2007; 18:326–333.10.1111/j.1467-9280.2007.01899.x. [PubMed: 17470258]

Jasper HH. The ten-twenty electrode system of the International Federation. Electroen Clin Neuro. 1958; 10:371–375.

Jennings JR, Wood CC. The ε - adjustment procedure for repeated-measures analysis of variance. Psychophysiology. 1976; 13:277–278.10.1111/j.1469-8986.1976.tb00116.x [PubMed: 1273235]

Keenan JM, Baillet SD, Brown P. The effects of causal cohesion on comprehension and memory. J Verb Learn Verb Be. 1984; 23:115–126.10.1016/S0022-5371(84)90082-3.

Keenan, JM.; Golding, JM.; Potts, GR.; Jennings, TM.; Aman, CJ. Methodological issues in evaluating the occurrence of inferences. In: Graesser, AC.; Bower, GJ., editors. The Psychology of Learning and Motivation. Academic Press; New York: 1989. p. 295-312.

Kintsch W. The role of knowledge in discourse comprehension: A construction-integration model. Psychol Rev. 1988; 95:163–182.10.1037/0033-295X.95.2.163. [PubMed: 3375398]

Kutas M, Hillyard SA. Reading senseless sentences: Brain potentials reflect semantic incongruity. Science. 1980; 207:203–205.10.1126/science.7350657. [PubMed: 7350657]

Lee C, Federmeier KD. To mind the mind: An event-related potential study of word class and semantic ambiguity. Brain Res. 2006; 1081:191–202.10.1016/j.brainres.2006.01.058. [PubMed: 16516169]

Luu P, Tucker DM, Makieg S. Frontal-midline theta and the error-related negativity: Neurophysiological mechanisms of action regulation. Clin Neurophysiol. 2004; 115:1821–1835.10.1016/j.clinph.2004.03.031. [PubMed: 15261861]

Mason RA, Just MA. How the brain processes causal inferences in text. Psychol Sci. 2004; 15:1–7.10.1111/j.0963-7214.2004.01501001.x. [PubMed: 14717824]

McKoon G, Ratcliff R. Inferences about predictable events. J Exp Psychol Learn. 1986; 12:82–91.10.1037/0278-7393.12.1.82.

McKoon G, Ratcliff R. Semantic associations and elaborative inference. J Exp Learn. 1989; 15:326–338.10.1037/0278-7393.15.2.326.

McKoon G, Ratcliff R. Inference during reading. Psychol Rev. 1992; 99:440–466.10.1037/0033-295X.99.3.440. [PubMed: 1502273]

McNamara, DS.; Louwerse, MM.; Cai, Z.; Graesser, A. Coh-Metrix version 1.4. 2005. Retrieved September, 11th and 12, 2012, from http//:cohmetrix.memphis.edu

Myers JL, O'Brien J. Accessing the discourse representation during reading. Discourse Process. 1998; 26:131–157.10.1080/01638539809545042.

Myers JL, Shinjo M, Duffy SA. Degree of causal relatedness and memory. J Mem Lang. 1987; 26:453–465.10.1016/0749-596X(87)90101-X.

Osterhout L, McLaughlin J, Bersick M. Event-related brain potentials and human language. Trends Cogn Sci. 1997; 6:203–209.10.1016/S1364-6613(97)01073-5. [PubMed: 21223908]

Picton TW, Bentin S, Berg P, Donchin E, Hillyard SA, Johnson R Jr, Taylor JM. Guidelines for using human event-related potentials to study cognition: Recording standards and publication criteria. Psychophysiology. 2000; 37:127–152.10.1111/1469-8986.3720127. [PubMed: 10731765]

Potts GR, Keenan JM, Golding JM. Assessing the occurrence of elaborative inferences: Lexical decision versus naming. J Mem Lang. 1988; 27:399–415.10.1016/0749-596X(88)90064-2.

Ratcliff R, McKoon G. A retrieval theory of priming and memory. Psychol Rev. 1988; 95:385–408.10.1037/0033-295X.95.3.385. [PubMed: 3406246]

Roehm D, Schlesewsky M, Bornkessel I, Frisch S, Haider H. Fractionating language comprehension via frequency characteristics of the human EEG. NeuroReport. 2004; 15:409–412.10.1097/00001756-200403010-00005. [PubMed: 15094493]

Semlitsch HV, Anderer P, Schuster P, Presslich O. A solution for reliable and valid reduction of ocular artifacts, applied to the P300 ERP. Psychophysiology. 1986; 23:695–703.10.1111/j.1469-8986.1986.tb00696.x. [PubMed: 3823345]

Singer, M. Discourse inference processes. In: Gernsbacher, MA., editor. Handbook of Psycholinguistic. Academic Press; San Diego: 1994. p. 479-515.

Singer M, Halldorson M. Constructing and validating motive bridging inferences. Cognitive Psychol. 1996; 30:1–38.10.1006/cogp.1996.0001.

StGeorge M, Mannes S, Hoffman JE. Individual differences in inference generation: An ERP analysis. J Cognitive Neurosci. 1997; 9:776–787.10.1162/jocn.1997.9.6.776.

Sundermeier BA, Virtue SM, Marsolek CJ, van den Broek P. Evidence for dissociable neural mechanisms underlying inference generation in familiar and less-familiar scenarios. Brain Lang. 2005; 95:402–413.10.1016/j.bandl.2005.03.005. [PubMed: 16298670]

van Berkum JJA, Hagoort P, Brown CM. Semantic integration in sentences and discourse: Evidence from the N400. J Cognitive Neurosci. 1999; 11:657–671.10.1162/089892999563724.

van den Broek, P. The causal inference maker: Towards a process model of inference generation in text comprehension. In: Balota, DA.; Flores d'Arcais, GB.; Rayner, K., editors. Comprehension Processes in Reading. Lawrence Erlbaum Associates; Hillsdale: 1990. p. 423-445.

van den Broek, P. Comprehension and memory for narrative texts: Inferences and coherence. In: Gernsbacher, MA., editor. Handbook of Psycholinguistic. Academic Press; San Diego: 1994. p. 539-588.

van den Broek P, Rapp DN, Kendeou P. Integrating memory-based and constructionist processes in accounts of reading comprehension. Discourse Process. 2005; 39:299–316.10.1207/s15326950dp3902&3_11.

van den Broek, P.; Young, M.; Tzeng, Y.; Linderholm, T. The landscape model of reading: Inferences and the on-line construction of a memory representation. In: van Oestendorp, H.; Goldman, SR., editors. The Construction of Mental Representations during Reading. Erlbaum; Mahwah: 1998. p. 91-98.(Reprinted in *Theoretical Models and Processes of Reading,* pp. 1244–1269, by R.B. Ruddel & N.J. Unrau. Eds. 2004, International Reading Association, Newark)

Zacks JM, Speer NK, Swallow KM, Braver TS, Reynolds JR. Event perception: A mind-brain perspective. Psychol Bull. 2007; 133:273–293.10.1037/0033-2909.133.2.273. [PubMed: 17338600]

Highlights

- We examine processing of inference-primed information with event-related potentials.
- We examine dissociable processes that occur before, during, and after the N400.
- Time-frequency analysis identifies dissociable processes that underlie the N400.
- Functional differences are associated with theta and delta time-frequency activity.

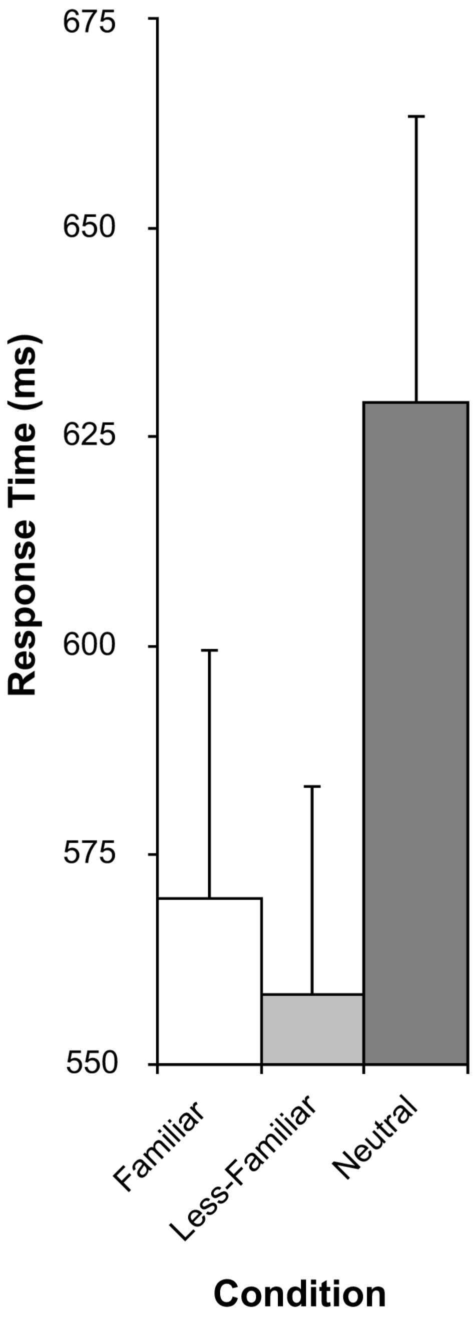

Figure 1.

Mean lexical decision response times in ms (*+SEM*) are depicted for the three experimental conditions of interest (familiar inference scenario, less-familiar inference scenario, and neutral scenario).

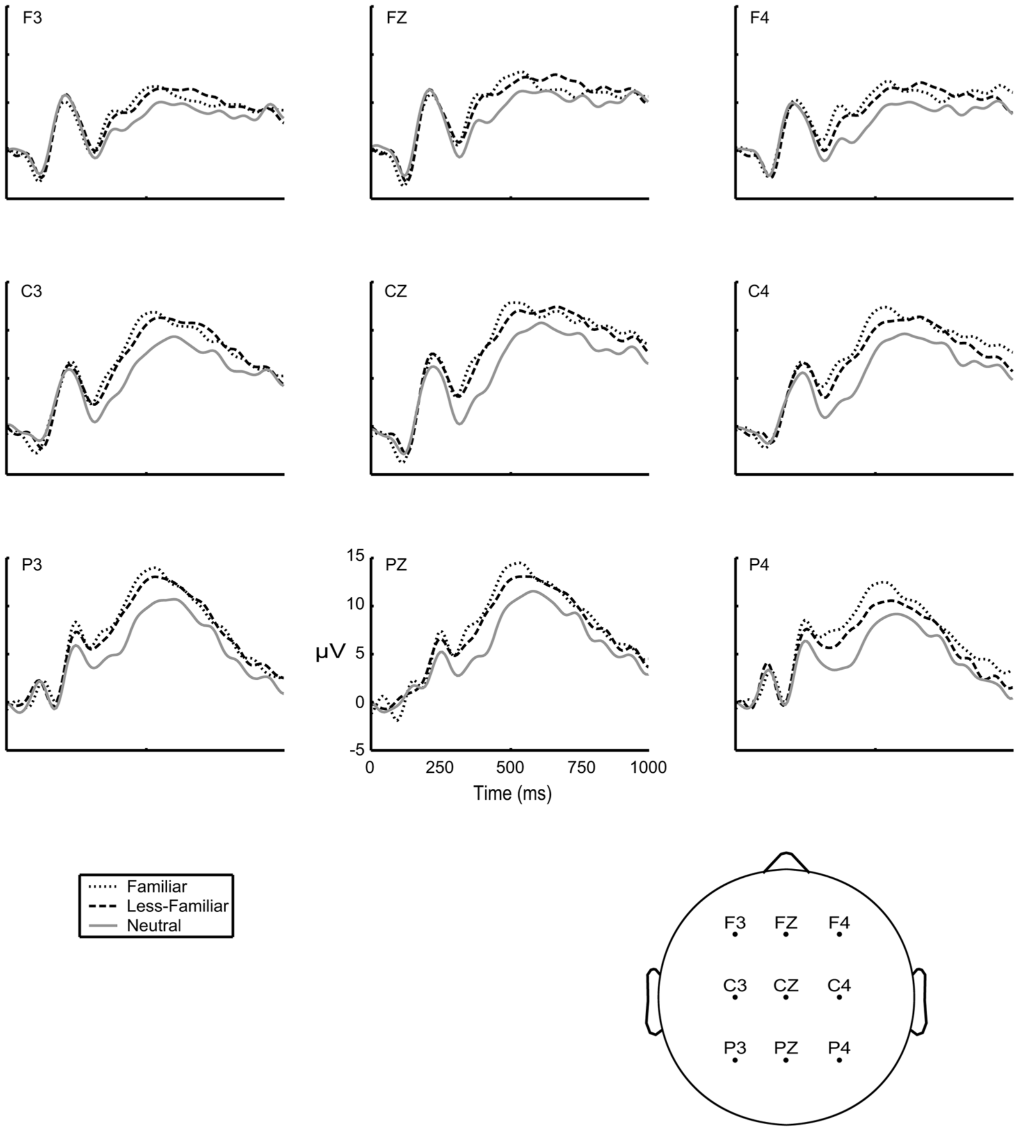

Figure 2.
ERP waveforms (amplitude in μV, and time in ms) for the three experimental conditions of interest (familiar inference scenario, less-familiar inference scenario, and neutral scenario) across nine electrodes used in the ANOVA computations.

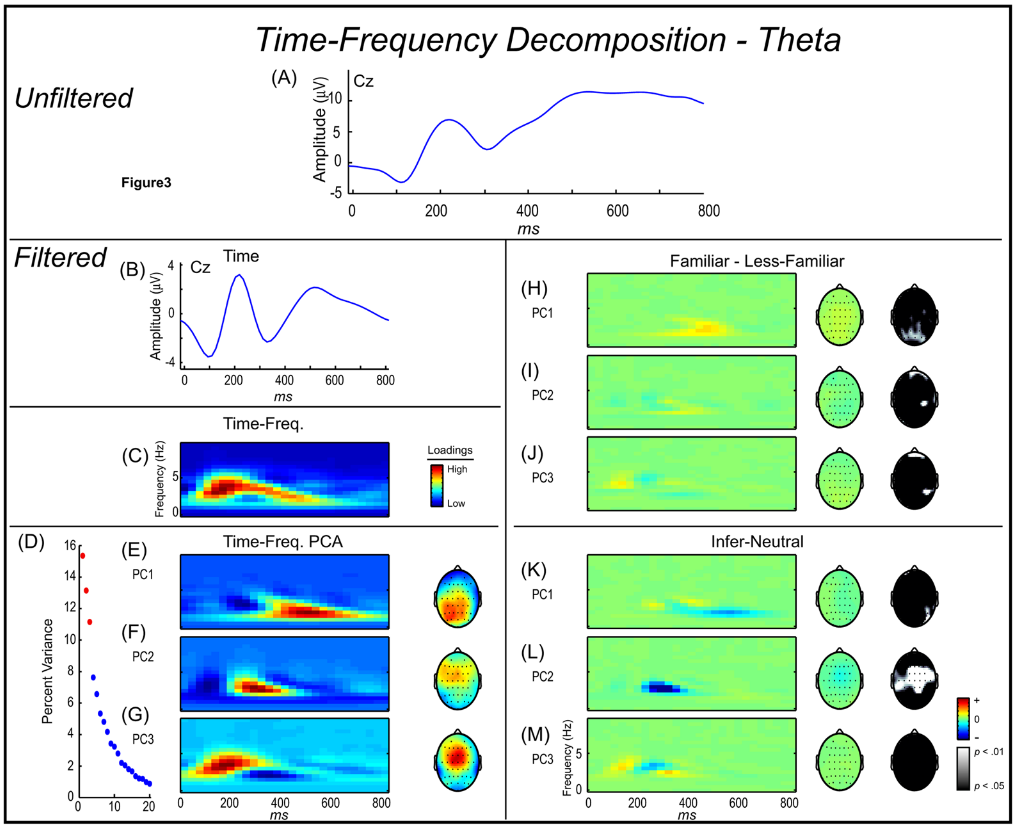

Figure 3.

Time-frequency (TF) decomposition: Theta. (A) Grand average waveform plotted at Cz. (B-G) TF-PCA decomposition of theta band pass filtered data. (H-M) Theta time-frequency condition differences: Time-frequency surfaces and headmaps are plotted with a midpoint of 0, red reflecting a positive difference, and blue reflecting a negative difference. (B) Theta filtered (1–6 Hz) grand average ERP time-domain waveform. (C) TF grand average of the theta filtered data. (D) Scree plot of singular values which was used to determine a three factor theta solution (red circles depict extracted components that account for 39.65% of the variance). (E) TF theta principal component 1, reflecting post N400 theta activity (e.g., theta activity concomitant with the P300). (F) TF theta principal component 2, reflecting theta activity corresponding to the initial N400 negativity. This component was selected for further analysis. (G) TF theta principal component 3, reflecting pre - N400 theta activity (e.g., theta activity concomitant with the the N1 or P2). (H) Largely non-significant differences in activation for theta component 1 between familiar and less-familiar condition. Topographical depiction of mean theta activation differences (amplitude and statistical maps) between familiar and less-familiar conditions. (I) Largely non-significant differences in activation for theta component 2 between familiar and less-familiar condition. (J) Largely non-significant differences in activation for theta component 3 between familiar and less-familiar condition. (K) Non-significant differences in activation for theta component 1 between inferred and neutral condition. (L) Significant differences in activation for theta component 2 between inferred and neutral condition. (M) Non-significant differences in activation for theta component 3 between inferred and neutral condition.

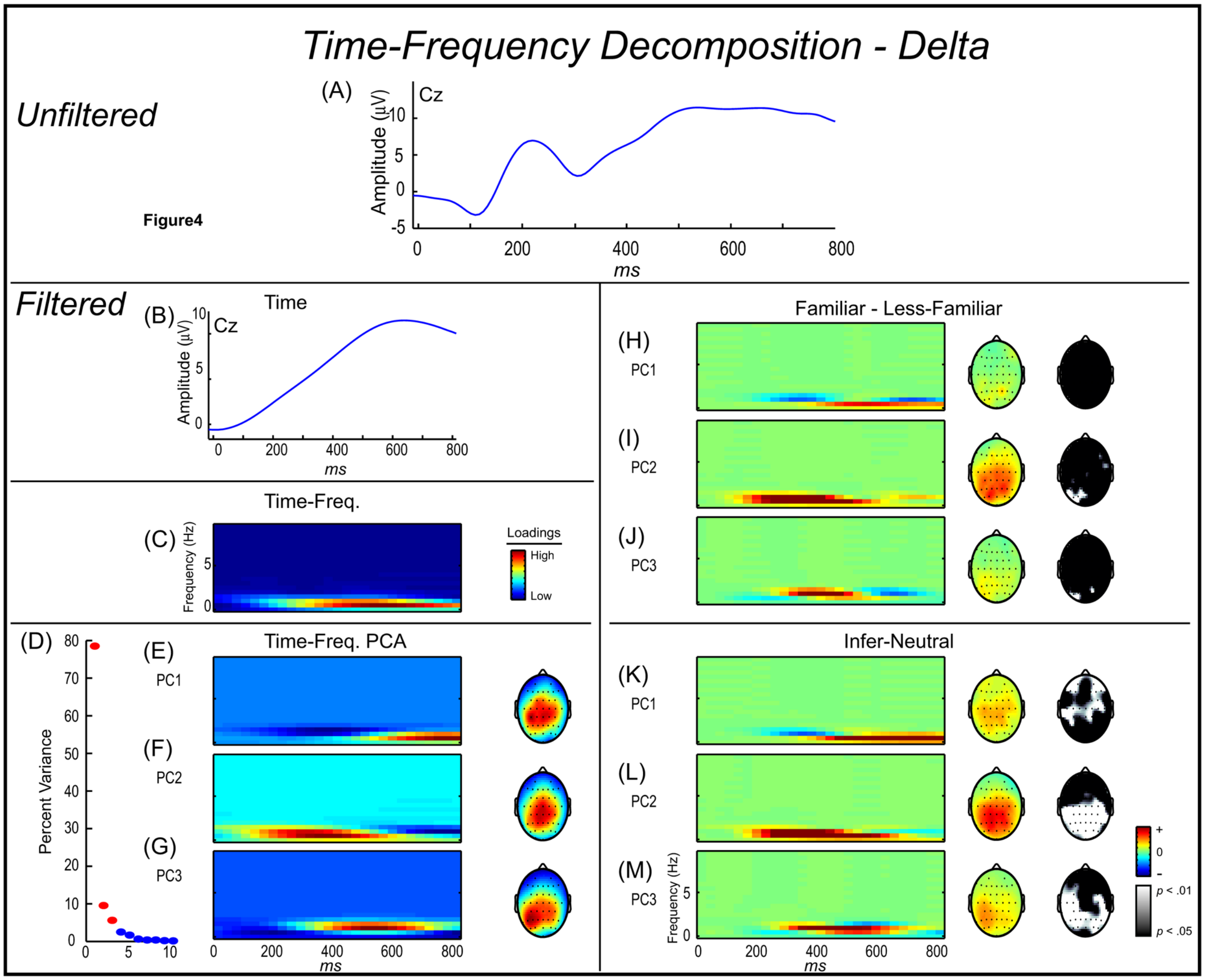

Figure 4.

Time-frequency (TF) decomposition: Delta. (A) Grand average waveform plotted at Cz. (B-G) TF-PCA decomposition of delta low pass filtered data. (H-M) Delta time-frequency condition differences: Time-frequency surfaces and headmaps are plotted with a midpoint of 0, red reflecting a positive difference, and blue reflecting a negative difference. (B) Delta filtered (below 2 Hz) grand average ERP time-domain waveform. (C) TF grand average of the delta filtered data. (D) Scree plot of singular values which was used to determine a three factor delta solution (red circles depict extracted components that account for 93.69% of the variance). (E) TF delta principal component 1, reflecting post N400 delta activity (e.g., delta activity concomitant with the P300). (F) TF delta principal component 2, reflecting delta activity corresponding to the initial N400 negativity. (G) TF delta principal component 3, reflecting post N400 delta activity (using regression analysis, this TF component was linked to the P600). (H) Largely non-significant differences in activation for delta component 1 between familiar and less-familiar condition. Topographical depiction of mean theta activation differences (amplitude and statistical maps) between familiar and less-familiar conditions. (I) Largely non-significant differences in activation for delta component 2 between familiar and less-familiar condition. (J) Largely non-significant differences in activation for delta component 3 between familiar and less-familiar condition. (K) Sparsely significant differences in activation for delta component 1 between inferred and neutral condition. (L) Significant differences in activation for delta component 2 between inferred and neutral condition. (M) Significant differences in activation for theta component 3 between inferred and neutral condition.

Table 1

The scenarios that preceded one of the target words used in the experiment, STUDY.

Condition	Sentence Number	Sentences
Familiar (High Familiarity)	1	With his exam coming up, the student opened his book.
	2	After three hours, he was sure he knew the material quite well for the exam.
Less-Familiar (Low Familiarity)	1	The CIA agent picked up the photograph of the suspect.
	2	After a few minutes, he felt confident that he could identify the man on the street.
Neutral	1	The children arrived for their first day of elementary school dressed in new clothes.
	2	They were so excited to meet their new teacher, see their old friends, and play outside.

Table 2

Summary of Regression Analysis for Time-Frequency Components Predicting Time-Domain Components when the Theta Component is used in Step 1 (N=30)

Regression 1a†	**-**	**-**	**B**	**SE B**	**B**
DV = P200 to N400 peak					
	Predictors				
Step 1					
	Theta 2 mean		25.158	6.620	0.583^{*}
Step 2					
	Theta 2 mean		27.399	6.411	0.635^{*}
	Delta 1 mean		−7.390	2.365	-0.525^{*}
	Delta 2 mean		0.797	1.529	0.098
	Delta 3 mean		6.149	2.795	0.361^{*}
Regression 2a	-	-	B	SE B	B
DV = N400 mean					
	Predictors				
Step 1					
	Theta 2 mean		−19.205	11.983	−0.290
Step 2					
	Theta 2 mean		4.325	7.890	0.065
	Delta 1 mean		1.405	2.897	0.065
	Delta 2 mean		11.659	1.873	0.936^{*}
	Delta 3 mean		−5.742	3.424	−0.220
Regression 3a	-	-	B	SE B	B
DV = P600 mean					
	Predictors				
Step 1					
	Theta 2 mean		−10.259	11.840	−0.162
Step 2					
	Theta 2 mean		5.814	8.787	0.092

Regression 1a[†]	-	-	B	SE B	B
	Delta 1 mean		11.574	3.226	0.558*
	Delta 2 mean		3.728	2.086	0.312^
	Delta 3 mean		1.299	3.814	0.052

Note. Regression 1a: $R^2 = .34$ $R = .58$ for step 1 ($p = .001$); Δ $R^2 = .22$ for step 2 ($p = .018$); Regression 2a: $R^2 = .08$ $R = .29$ for step 1 ($p = .120$); Δ $R^2 = .63$ for step 2 ($p < .001$); Regression 3a: $R^2 = .03$ $R = .16$ for step 1 ($p = .395$); Δ $R^2 = .592$ for step 2 ($p < .001$)

^ $p < .10$

[†] Dependant measure for regression 1a is the peak to peak difference between P200 and N400.

Table 3

Summary of Regression Analysis for Time-Frequency Components Predicting Time-Domain Components when the all three Delta Components are used in Step 1 (N=30)

Regression 1b	-	-	**B**	**SE B**	**B**
DV = P200 to N400 peak					
	Predictors				
Step 1					
	Delta 1 mean		−6.303	3.027	-0.448^{*}
	Delta 2 mean		−1.514	1.840	−0.187
	Delta 3 mean		5.042	3.583	0.296
Step 2					
	Theta 2 mean		27.399	6.441	0.635^{*}
	Delta 1 mean		−7.390	2.365	-0.525^{*}
	Delta 2 mean		0.797	1.529	0.098
	Delta 3 mean		6.149	2.795	0.361^{*}
Regression 2b	-	-	B	SE B	B
DV = N400 mean					
	Predictors				
Step 1					
	Delta 1 mean		1.577	2.841	0.073
	Delta 2 mean		11.295	1.727	0.907^{*}
	Delta 3 mean		−5.916	3.363	$-0.226^{\wedge}$
Step 2					
	Theta 2 mean		4.325	7.890	0.065
	Delta 1 mean		1.405	2.897	0.065
	Delta 2 mean		11.659	1.873	0.936^{*}
	Delta 3 mean		−5.742	3.424	−0.220
Regression 3b	-	-	B	SE B	B
DV = P600 mean					
	Predictors				

Regression 1b	**-**	**-**	**B**	**SE B**	**B**
Step 1					
	Delta 1 mean		11.805	3.172	0.569^{*}
	Delta 2 mean		3.238	1.928	0.271
	Delta 3 mean		1.064	3.756	0.042
Step 2					
	Theta 2 mean		5.814	8.787	0.092
	Delta 1 mean		11.574	3.226	0.558^{*}
	Delta 2 mean		3.728	2.086	$0.312^{\wedge}$
	Delta 3 mean		1.299	3.814	0.052

Note. Regression 1b: $R^2 = .23$ $R = .48$ for step 1 ($p = .070$); Δ $R^2 = .32$ for step 2 ($p < .001$); Regression 2b: $R^2 = .71$ $R = .85$ for step 1 ($p < .001$); Δ $R^2 = .003$ for step 2 ($p = .588$); Regression 3b: $R^2 = .61$ $R = .78$ for step 1 ($p < .001$); Δ $R^2 = .007$ for step 2 ($p = .514$)

[^] $p < .10$

[†] Dependant measure for regression 1b is the peak to peak difference between P200 and N400.