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Localization of Syntactic and Semantic Brain Responses using Magnetoencephalography

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Abstract

■ Electrophysiological methods have been used to study the temporal sequence of syntactic and semantic processing during sentence comprehension. Two responses associated with syntactic violations are the left anterior negativity (LAN) and the P600. A response to semantic violation is the N400. Although the sources of the N400 response have been identified in the left (and right) temporal lobe, the neural signatures of the LAN and P600 have not been revealed. The present study used magnetoencephalography to localize sources of syntactic and semantic activation in Finnish sentence reading. Participants were presented with sentences that ended in normally inflected nouns, nouns in an unacceptable case, verbs instead of nouns, or nouns that were correctly inflected but made no sense in the context. Around 400 msec, semantically anomalous last words evoked strong activation in the left superior temporal lobe with significant activation also for word class errors (N400). Weaker activation was seen for the semantic errors in the right hemisphere. Later, 600–800 msec after word onset, the strongest activation was seen to word class and morphosyntactic errors (P600). Activation was significantly weaker to semantically anomalous and correct words. The P600 syntactic activation was localized to bilateral sources in the temporal lobe, posterior to the N400 sources. The results suggest that the same general region of the superior temporal cortex gives rise to both LAN and N400 with bilateral reactivity to semantic manipulation and a left hemisphere effect to syntactic manipulation. The bilateral P600 response was sensitive to syntactic but not semantic factors. ■

INTRODUCTION

For the last two decades, one of the central questions in psycholinguistics has been whether sentences are comprehended by the serial deployment of modular linguistic devices, syntactic and semantic processors, respectively (e.g., Frazier, 1987), or whether semantic and syntactic (and other) constraints to sentence interpretation are processed interactively to produce a parsing (e.g., MacDonald, 1994; Boland, Tanenhaus, & Garnsey, 1990; Tanenhaus, Carlson, & Trueswell, 1989). In the last 10 years, scalp-recorded brain activity, tagged to the presentation of specific stimuli in so-called event-related designs, has emerged as a promising tool to try to answer this question. The rationale has been that if brain responses reflecting semantic and syntactic processing can be identified, their activation in time can be inspected and possible interactions can be observed. The value of this tool depends on the functional interpretation of identifiable brain responses. In this study, we use magnetoencephalography (MEG) to localize the sources of commonly reported semantic and syntactic responses in order to add spatial information to the constraints by which these components are identified.

A response generally agreed on to reflect the semantic integration of single words to sentential contexts is a negativity that can be recorded from the scalp, peaking approximately 400 msec after stimulus presentation, the so-called N400, originally discovered by Kutas and Hillyard (1980). This response was first seen when event-related potentials (ERPs) were recorded to last words that made little sense as sentence endings, as compared to highly expected and meaningful last words. Since the first report, this response has been recorded in a great number of experiments, in which a word and its meaning, or even a picture, are not highly expected (see Kutas & Van Petten, 1994). The accumulated data suggest that the N400 reflects semantic processing associated with a word, or other meaningful stimulus, in a larger context. Modulation of this response has been used as a marker of semantic processing effects in sentence comprehension experiments.

A little over a decade ago, the first reports of scalp-recorded positivities that were sensitive to syntactic violations (Hagoort, Brown, & Groothusen, 1993; Osterhout & Holcomb, 1992) appeared. The response, called the P600 or syntactic positive shift, is typically recorded after 500 msec from stimulus presentation in an extended time window of 2 msec to a few hundred milliseconds. The P600 has repeatedly been reported to words that contain a syntactic (for instance, a verb instead of a noun) or

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morphosyntactic (for instance, a plural instead of a singular form) violation to sentence structure. This response gave cognitive neuroscientists the second necessary tool to address the question of independence versus interactivity of semantic and syntactic processes in sentence comprehension.

In addition to the P600, other ERP responses, thought to be sensitive to syntactic violations, have been reported. A negativity recorded between 300 and 500 msec after stimulus presentation, in the same time window as the N400 but with a more anterior temporal distribution on left-side electrodes (King & Kutas, 1995; Friederici, Pfeifer, & Hahne, 1993; Neville, Nicol, Barss, Forster, & Garrett, 1991), the so-called LAN, has been suggested to be sensitive to morphosyntactic violations in first-pass syntactic analysis, for instance, to lack of agreement in number or gender (Barber & Carreiras, 2005; Angrilli et al., 2002; Gunter, Friederici, & Schriefers, 2000). Some researchers have also suggested that it reflects additional working memory (WM) load as a result of syntactic processing difficulty. An even earlier negativity, reported in a few, mostly auditory, studies, the so-called early left anterior negativity (ELAN), recorded as early as 150–200 msec after stimulus presentation, has been proposed to be sensitive to gross violations of word category (for instance, a verb in a sentence position requiring a noun) (Friederici, 2002; Hahne & Friederici, 1999). An early response, overlapping in time with word recognition, could, however, also reflect identification processes at the word level. Such an explanation would be plausible especially if the lexicon is organized according to word category.

Although the ELAN and the LAN have been recorded in a number of studies, the P600 remains the most robust response associated with syntactic anomalies. This is also the response whose interaction with the N400 has been studied the most. Despite the many replications of the P600 response, there is no consensus on its exact functional role. It has been suggested to reflect second-pass syntactic analysis, including reanalysis and repair (Friederici, 2002), or difficulty of syntactic processing (Kaan, Harris, Gibson, & Holcomb, 2000), with a posterior component, perhaps, specializing in revision and an anterior one reflecting complexity of the processed material (Kaan & Swaab, 2003), or first-pass syntactic analysis (Deutsch & Bentin, 2001). Finally, the P600 has also been suggested to belong to the P300 family, marking a general reaction to rare and salient events (Coulson, King, & Kutas, 1998). The puzzle of the P600 is its latency. It only appears after 500 msec, and can then last over a second (Osterhout, Allen, McLaughlin, & Inoue, 2002). As normal reading rates vary between 200 and 300 msec per word, such effects have to stretch over several words, perhaps only wrapping up after the last word of the sentence. In contrast, the semantic N400 effect for visual stimuli appears to return to baseline 100–200 msec after peaking at approximately 400 msec.

When both syntactic and semantic violations are present, interactions between the two types of manipulations have been observed in a number of earlier experiments. The results show many different patterns. We present here examples of the observed effects. Ainsworth-Darnell, Shulman, and Boland (1998) found an N400 response when nouns were semantically inappropriate, a P600 response when they occurred in a syntactically inappropriate position, and both when the violations were combined. In their study, the combined violations showed similar N400 and P600 responses as the separate violations, respectively. Osterhout and Nicol (1999) found semantically anomalous verbs to give rise to an N400. Syntactically anomalous verb forms were associated with a nonsignificant negativity in the same time window as the N400 as well as a very clear P600. Verbs with a combined violation showed both responses. In these data, the combined waveform quite closely approximated a linear summation of the two separate responses, suggesting independent contributions from syntactic and semantic violations.

Friederici, Steinhauer, and Frisch (1999) manipulated the acceptability of a sentence terminal verb in visually presented sentences in German. In a syntactic anomaly condition, the past participle of a verb replaced a noun that should have been part of a prepositional phrase. In a semantic anomaly condition, a selection restriction for a verb was violated. Finally, in a combined anomaly condition, both phrase structure and a selection restriction were violated. The syntactic anomaly alone gave rise to a robust P600 effect but no N400. The semantic anomaly alone was accompanied by a large N400 effect but no P600. The combined syntactic and semantic anomalies showed only a P600 effect and no N400. This pattern of effects would suggest that an early syntactic process (the authors thought this would be ELAN, although this was not statistically reliable) detected the phrase structure anomaly and blocked semantic analysis. It should be pointed out that, in this study, it was not really possible to construct a mental model of the meaning of the syntactically anomalous sentences. A pronounced N400 is typically elicited by low-probability or semantically anomalous words within otherwise meaningful sentences.

Gunter et al. (2000) studied ERPs to visually presented German sentences with an article–noun gender violation. They found a LAN for the morphosyntactic violations and an elevated N400 for unexpected nouns. The N400 was not affected by the morphosyntactic violation. A P600 was seen to gender violations for highly expected nouns (with a small N400) but was greatly attenuated and delayed to unexpected nouns (with a prominent N400). The authors interpreted this to mean that there is early autonomy between syntactic and semantic analysis (during LAN and N400) but later interaction (during P600).

Hagoort (2003) used a fully factorial design, studying the separate and combined effects of syntactic and

semantic anomaly on the same visually presented words in determiner–adjective–noun phrases. N400 and P600 effects were found for semantic and syntactic violations, respectively. In sentence-final position, all violation conditions resulted in an enhancement of the N400. Semantic violations did not produce significant P600 responses in either sentence position. The author's conclusion was diametrically opposite to that of Gunter et al. (2000) (i.e., of early interaction between syntactic and semantic analysis in the N400 window and late independence in the P600 window).

In the only published study based on the morphologically rich Finnish, Palolahti, Leino, Jokela, Kopra, and Paavilainen (2005) systematically varied the morphosyntactic and semantic acceptability of verb forms in visually presented sentences. The critical verbs either agreed in number with their subjects or did not (morphosyntactic violation) and were either semantically acceptable or broke a selection restriction (semantic violation). The semantic and syntactic factors were fully crossed for the same verbs. The authors reported a LAN and a P600 for the syntactic violations, an N400 but no P600 for the semantic violations, and a negativity in the LAN/N400 window and a P600 for the combined syntactic and semantic violations. The negativity in the combined condition was smaller than the sum of the LAN in the syntactic violation condition and the N400 in the semantic violation condition. In contrast, the P600 in the combined condition was identical to the P600 in the sum of the separate syntactic and semantic violation conditions. The authors concluded that their results pointed to an interaction between syntactic and semantic processes already in the LAN/N400 time window, thus, echoing the conclusion by Hagoort.

The contradictions in the results above may depend on different stimulus materials and presentation conditions. However, it is also possible that the responses have not always been optimally identified. The neurophysiological and functional independence of different ERP components is not always easy to show. This is exemplified by Osterhout's (1997) speculation that the LAN could be a modulation of the N400 interacting with a P600. Also, Thierry, Cardebat, and Démonet (2003) reported a very similar, slightly left-lateralized response, described as topographically intermediate between an N400 and a LAN, in both semantic and gender categorization tasks. In ERP work, components are identified by their behavior as a response to stimulus manipulation, their timing, and the electrodes that show the strongest response. As the review of results cited above reveals, this is not always enough to distinguish between different responses. One way of further constraining the identification of ERP components related to sentence processing would be to identify their neural sources. Here different brain imaging techniques have different strengths. MEG can easily be mapped onto ERPs as it has the same temporal resolution. However, localization is

not as accurate as with blood-flow based techniques such as positron emission tomography (PET) or functional magnetic resonance imaging (fMRI). These techniques, on the other hand, have the drawback that they sum activity over a wider time window of several seconds, making it difficult to distinguish between transient responses following each other in a rapid succession. For source analysis of relatively short-lived responses such as the N400, Electroencephalography (EEG) and MEG presently appear to be the most efficient methods.

The sources of the N400 were first studied using intracranial recordings, which suggested generators in the anterior basal temporal lobe (Nobre & McCarthy, 1995; Nobre, Allison, & McCarthy, 1994). Interpretation of intracranial EEG registration is limited by patient pathology and available electrode sites. Source localization based on recording ERPs with high-density electrode set-ups would be a more direct way to try to find neural generators for scalp-recorded responses but, in practice, it is complicated by spatial smearing of the electrical potential as electric current passes through layers with different conductivities. This technique has been applied to finding the generators of the N400. For instance, D'Arcy, Connolly, Service, Hawco, and Houlihan (2004) found N400 sources in an auditory experiment in Wernicke's area and its right homologue in the posterior superior temporal gyrus, as well as in the left supratemporal plane and the left temporo-parieto-occipital region. Frishkoff, Tucker, Davey, and Scherg (2004) reported sources responding to semantic manipulation of written sentences in the 300–500 msec window in both the left and right lateral prefrontal cortex, the right temporal cortex and both anterior and posterior cingulates. Thus, the results from localization based on high-density EEG recordings are somewhat conflicting, perhaps partly due to different stimulus presentation modalities and different source localization algorithms.

MEG studies using equivalent current dipole (ECD) modeling have repeatedly localized a component behaving like the electrical N400 to bilateral sites in the superior temporal cortex, with earlier and stronger activation occurring in the left hemisphere in both visual (see, e.g., Marinkovic et al., 2003; Halgren et al., 2002; Helenius, Salmelin, Service, & Connolly, 1998) and auditory (Helenius et al., 2002) experiments. A distributed solution employing dynamic statistical parametric maps (Halgren et al., 2002) was interpreted to suggest that the typical N400 effect to semantically anomalous words is first generated in Wernicke's area at about 250 msec after the onset of a visually presented word. Thereafter, activity is thought to spread to the left superior and inferior sulci, anteroventral temporal lobe, insula, and collateral sulcus at the occipito-temporal junction. At 300 msec, the orbital prefrontal cortex gets activated, shortly followed by Broca's area. Finally, after approximately 370 msec, the dorsolateral and

frontopolar cortices are also activated. Activation in the right hemisphere was weaker and not apparent until 370 msec after stimulus onset.

The generators of the P600 have been sought in hemodynamic studies of brain activation. Earlier PET (e.g., Stromswold, Caplan, Alpert, & Rauch, 1996) and fMRI (e.g., Keller, Carpenter, & Just, 2001; Bavelier et al., 1997) studies of visual sentence processing detected widespread left-dominant activation patterns. However, these studies could not discriminate between different levels of language processing, for instance, syntactic, semantic, and WM load effects. An early study (Dapretto & Bookheimer, 1999) attempting to dissociate use of syntactic and semantic information during auditory sentence processing found part of Broca's area (BA 44) to be implicated in detecting differences between sentence pairs based on word order and sentence structure (syntactic processing). In contrast, a more inferior part of the left frontal gyrus (BA 47) appeared to be involved in comparing auditory sentence pairs based on the meanings of single critical words (lexical–semantic processing).

Recent fMRI studies have employed event-related designs that provide a better opportunity to focus on activity related to the processing of specific sentences. For instance, Ni et al. (2000) found that semantic anomalies yielded more activity in the middle and superior frontal cortex as well as in the left posterior superior temporal and parietal cortex. Syntactic anomalies were associated with more activity in the left inferior frontal region (Broca's area). Kuperberg et al. (2003) presented the same sentences to their subjects in an ERP experiment and then in an event-related fMRI paradigm. Morphosyntactic agreement violations gave rise to a P600. Pragmatic violations elicited an N400. In their fMRI paradigm, the two types of violations appeared to modulate activity in the same extensive neural network, but in different directions (an increased hemodynamic response in the left temporal and inferior frontal region for pragmatic violations and a decreased response for morphosyntactic violations). Humphries, Binder, Medler, and Liebenthal (2006) studied two types of stimuli: word lists and sentences, and varied their semantic meaningfulness (based on the relatedness of the content words) and syntactic meaningfulness (depending on word order). Effects of syntactic structure were seen in the left anterior superior temporal sulcus and left angular gyrus. Semantic effects were seen in widespread bilateral temporal lobe areas and in the angular gyrus. The anterior temporal region was relatively insensitive to semantic structure, whereas the angular gyrus was more sensitive to semantic than syntactic structure. In line with other studies comparing sentences with word lists, this study did not show Broca's area or other left inferior frontal gyrus activation associated with processing of sentence structure. One suggestion is that the role of the left inferior frontal cortex is not specific to syntactic process-

ing but is shared among a number of verbal tasks with graded task demands (Kaan & Swaab, 2002).

Although the time resolution of fMRI techniques has improved, it is not possible to directly map results from them to transient ERP components. The present study therefore employed MEG to localize the neural sources of brain responses associated with reading semantically and syntactically/morphosyntactically anomalous words in Finnish sentences. Finnish is a highly inflected language that uses case inflections on nouns and their modifiers to signal both grammatical functions (e.g., subject vs. object) and semantic relations (e.g., location on a surface, expressed by a prepositional phrase in English: *tuoli + lla*, literal translation: on chair). We were especially interested in the possibility of finding sources for ERP components associated with syntactic processing: the ELAN, the LAN, and the P600. For this purpose, we studied four kinds of sentences (see Table 1). Semantic congruity was varied by presenting sentences with critical ending words that were perfectly comprehensible compared to ones that made no pragmatic sense in their context (i.e., *semantic errors*). Syntactic anomalies were contrasted with acceptable word forms on two levels. *Word class errors* replaced an expected noun head of a noun phrase with a verb in past participle form, creating a phrase structure violation. *Morphosyntactic errors* vio-

Table 1. Examples of Sentence Types and Their Translations

Correct

Poika (boy, nominative case) *kiipesi* (climbed) *jyrkälle* (steep, allative case ≈ onto) *katolle* (roof, allative case ≈ onto).

English translation: *The boy climbed onto a steep roof.*

Semantic Error

Kissa (cat, nominative case) *kiipesi* (climbed) *jyrkälle* (steep, allative case, ≈ onto) **auringolle* (sun, allative case ≈ onto).

English translation: *The cat climbed onto a steep *sun.*

Word Class Error

Tyttö (girl, nominative case) *kiipesi* (climbed) *jyrkälle* (steep, allative case ≈ onto) **uinut* (swim, past participle).

English translation: *The girl climbed onto the steep *swum.*

Morphosyntactic Error

Mies (man, nominative case) *kiipesi* (climbed) *jyrkälle* (steep, allative case ≈ onto) **kattoa* (roof, partitive case, one of the object cases).

Approximation of English equivalent: *The man climbed onto a steep *of roof.*

lated case agreement between an adjective attribute and its head noun.

According to the proposal by Friederici (2002) as well as previous studies (e.g., Friederici et al., 1999), the word class errors should elicit an ELAN or LAN as well as the later repair response P600, whereas the morphosyntactic errors are expected to affect the later LAN and the P600. Semantic anomalies should elicit an N400. Possible interactions between syntactic and semantic processing should be seen as modulations of the same neural networks in the syntactic and semantic anomaly conditions.

METHODS

Participants

We recorded data from nine subjects (3 women) 19–34 years old at the time of the measurement (average 26.4 years). Eight subjects were right-handed and one subject was ambidextral according to their own report. All spoke Finnish as their first language. Informed consent was obtained from all subjects, in agreement with the prior approval of the Helsinki and Uusimaa Ethics Committee.

Stimuli

There were altogether 500 Finnish sentences, consisting of four to five words each. The 400 test sentences (cf. Table 1) were constructed in groups of four so that all four started with a different noun (N), which was followed by a shared main verb (V), and ended in either an object or locative noun phrase (NP) that started with an adjective (Adj.) attribute common to all four sentences. Thus, affirmative sentences were of the form NP_1 VP NP_2, where $NP_1 \rightarrow N_1$ and $NP_2 \rightarrow$ Adj. + N_2. To add to the plausibility of the sentences, the adjective was occasionally modified by an uninflected adverb (e.g., *fairly big tree*). One hundred sentences were perfectly normal (correct). One hundred sentences were syntactically well-formed but ended in a semantically peculiar way, violating pragmatic expectations (semantic error). One hundred sentences broke the NP structure and ended with a verb when a noun or noun phrase would have been required (word class error). The verb was always a past participle. One hundred sentences included a violation of the obligatory agreement of case between a modifier and its head noun, ending with a noun in an ungrammatical inflectional form (morphosyntactic error). Lastly, there were 100 filler sentences consisting of variable acceptable grammatical structures made up from four to five words. The same sentence-final nouns were used once in each of the three conditions that ended with a noun. The frequencies of the sentence-ending words did not significantly differ between conditions (187 per million for correct, semantic, and morphosyntactic errors; 301 per million for word class errors; paired

comparisons between word class error and other conditions *ns*). This frequency analysis included 317 words (79% of the total 400). The number of less frequent words, not included in the available frequency count (Suomen taajuussanasto, Scientific Computing, 2004), was approximately equally distributed among the different sentence types (11 words for the word class error and 24 for each of the other three conditions). A Chi-square goodness-of-fit test failed to show a statistically significant difference among conditions.

In Finnish, inflections are used to signal grammatical functions, such as subject or object, as well as many prepositional phrases. Modifiers in Finnish take the same inflection as their heads. Our inflectional violations involved replacing an object inflection (accusative or partitive case) with a locative inflection (inessive or allative case), or vice versa. This was always after an NP-initial adjective modifier that was in the correct, expected form. The noun case, thus, did not agree with the adjective case, resulting in a local agreement error.

Procedure

The participants sat in a shielded, dimly lit, room under a measurement helmet. The sentences were visually presented one word at a time. The words were printed in black Helvetica font on a light gray area and shown via a data projector on a rear-projection screen. Each word was shown for 300 msec, followed by a pause (interstimulus interval, ISI) of 400 msec. Each sentence was followed by a 2000-msec pause. After this, a fixation point appeared in the middle of the screen for 400 msec. This was followed by a 300-msec blank screen before the next sentence was presented. The experiment lasted about 50 min, divided into approximately 10-min sessions with short breaks in between. The participants were instructed to read the sentences for comprehension. No other specific task was given. Stimulus presentation was controlled by a Macintosh Quadra 800 computer.

MEG Recording and Analysis

Brain responses were registered using a 306-channel Vectorview neuromagnetometer (Neuromag, Helsinki, Finland), measuring magnetic field strength in 102 locations over the head, with each location covered by a triplet of sensors (two planar gradiometers and one magnetometer). The planar gradiometers detect the maximum signal directly above an active cortical area. Source localization was carried out in three-dimensional space with the x-axis directed from left to right in front of the ear canals (pre-auricular points), the y-axis toward the nasion, and the z-axis toward the vertex. The locations of four head-position indicator coils were determined by a 3-D digitizer with respect to the pre-auricular and nasion reference points. At the beginning of the

experimental session, an electric current was fed to the coils and their location with respect to the recording helmet was established. Afterward, the localization information was used to relate the sources to the anatomic structure of the individual participants with the help of MR images of each brain.

The MEG signals were band-pass filtered at 0.1–200 Hz and sampled at 600 Hz. Responses were averaged online across trials from 200 msec before the onset of the sentence-final critical word to 1000 msec after onset. Vertical and horizontal eye movements were continuously registered, and epochs contaminated by ocular signals were rejected.

The results were first visualized by depicting the responses over groups of sensors, averaged across participants. Areal mean signal (AMS) averaging in MEG is closest to what is typically reported in ERP experiments (sensor/electrode level). However, as the sensors are attached to a fixed helmet, individual variability in head position does not allow simple, uncorrected, averaging over each channel as is done in EEG analysis. Instead, nearby sensors were combined to provide an overview of active brain areas. The whole-head sensor array was divided into 10 areas of interest. We first computed vector sums of each gradiometer pair by squaring the MEG signals, summing them together, and calculating the square root of this sum. The AMSs were computed by averaging these vector sums for each area of interest, individually for each subject. Finally, the AMSs were averaged across subjects. Because of the way the sensor-level AMSs are calculated (square root of sum of squared signals), they always have a positive value (>0). The AMS inspection provides an initial overview of the data but not the location of the active brain areas or the direction of current flow in those areas.

The main data analysis involved localizing the active source areas in the individual subjects in each of the four experimental conditions and determined their time courses of activation. The analysis allowed identification of source areas with specific functional properties (corresponding to N400, P600, LAN/ELAN). We modeled the source areas as focal ECDs (Hämäläinen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). ECD analysis reduces the signals detected by the MEG sensors into the time behavior of distinct cortical areas. Each ECD represents the center of an active cortical patch and the strength and direction of electric current in that area. The ECD modeling was done following the procedure by Salmelin and colleagues (Salmelin, Service, Kiesilä, Uutela, & Salonen, 1996). The whole-head magnetic field patterns were inspected individually for each subject, and a cluster of channels were selected that optimally covered distinct dipolar field patterns (thus, reflecting neural activity that can be reasonably modeled with an ECD). Thereafter, time courses of activation in those brain areas (represented by the ECDs) were obtained by including the ECDs simultaneously in a

multidipole model: The locations and orientations of the ECDs were fixed while their amplitudes were allowed to vary to achieve maximum explanation of the recorded whole-head data. A single set of seven to eight ECDs per subject accounted for the MEG signals in all experimental conditions. The ECDs were displayed on an average MR image created using elastic transformation (Schormann, Henn, & Zilles, 1996).

In the following step, those ECDs were identified that displayed behavior similar to the electrophysiological N400 and P600 responses. Adopting the procedure originally described by Tarkiainen, Helenius, Hansen, Cornelissen, and Salmelin (1999), activation of a source area was considered to differ significantly between experimental conditions when the difference exceeded 2.58 times the standard deviation (corresponding to $p < .01$) of activity in that source area during the prestimulus baseline interval ($-200 \ldots 0$ msec) and lasted for at least 100 msec, and peak activity exceeded 5 nAm (nanoamperemeters). ECDs that showed significant ($p < .01$) activation in the semantic error condition compared to the correct condition between 200 and 500 msec after word onset for a minimal total duration of 100 msec were identified as N400 ECDs. ECDs that showed significantly stronger activation in the word class error condition than in either of the two conditions that were syntactically well-formed (correct and semantic error conditions) between 500 and 900 msec poststimulus, for at least 100 msec, were identified as P600 ECDs. In group-level analyses, the peak strength of the identified dipoles was further subjected to a series of one-way within-subjects analyses of variance (ANOVAs) and planned single-degree-of-freedom pairwise comparisons, with condition as the repeated variable. In cases of sphericity violation, Huynh–Feldt correction on degrees of freedom was used.

RESULTS

Areal Mean Signals

Figure 1 illustrates the grand-average AMSs calculated for correct, semantic error, word class error, and morphosyntactic error conditions. Two functionally different response patterns can be seen centering over the temporal areas. Around 400 msec, semantic errors evoked stronger responses than the last word in the correct condition over the left ($p < .001$) and right temporal areas ($p < .03$; paired t test at the time point when the response peaked for the semantic errors). This response pattern will be referred to as the N400 response. Between 600 and 800 msec, the word class errors, but not the semantic errors, evoked stronger responses than the correct condition in the left ($p < .003$) and right hemispheres ($p < .05$; paired t test at the time point when the response peaked for the word class errors). It is also worth noting that, in the left hemisphere, the peak

Figure 1. Grand-average AMSs of nine participants in 10 areas of interest in the four experimental conditions. The temporal areas, specially marked, were included in comparisons between hemispheres.
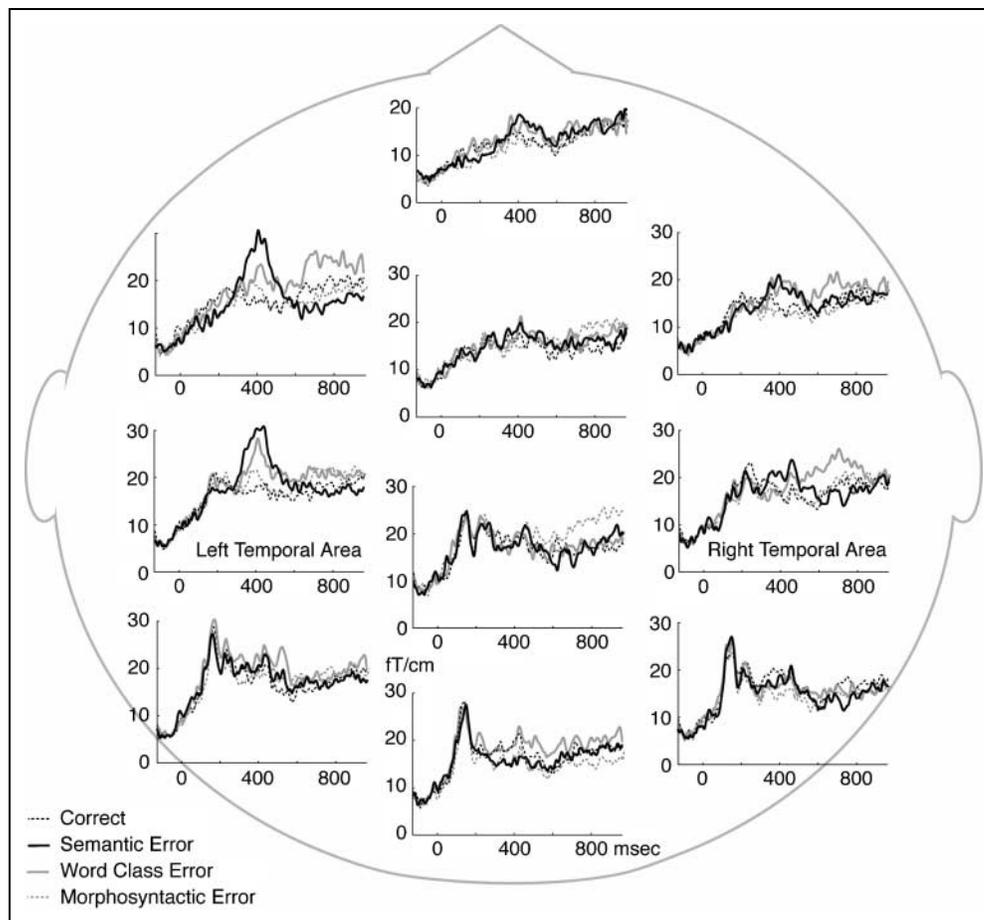
response for the word class errors around 400 msec was stronger than for the correct condition ($p < .003$).

## Cortical Sources

N400 Response

The ECDs displaying N400-type behavior in each subject were identified as those that showed significantly stronger activation in the semantic error than in the correct condition between 200 and 500 msec ($p < .01$, with respect to signal variation during the prestimulus baseline interval).

Figure 2 (upper row) depicts the spatial distribution of the N400 sources collected from all nine subjects. The sources were clustered to the temporal lobe. In the left hemisphere, the black ellipse marks the area in which each participant had exactly one source. In addition, one subject had two other posterior sources and one subject an anterior source. In the right hemisphere, five participants had one ECD each, four of which fell into the right temporal lobe shown as a circled area. The mean orientation of the current flow in these left and right hemisphere regions of interest (ROIs) was downward, perpendicular to the course of the superior temporal

sulcus and sylvian fissure (see the arrow in Figure 2). The mean time course of activation within the left and right hemisphere ROIs is shown in Figure 2. On average, the N400 activation peaked at 409 msec (± 12 msec *SEM*) for semantic errors in the left and at 392 msec (± 25 msec *SEM*) in the right hemisphere. All N400 peaks in individuals occurred before 500 msec (range: 350–450 msec).

The data were analyzed at group level by one-way within-subjects ANOVAs with the strength and time behavior of the activation as dependent variables, using the values gathered from the individual responses within the ROIs. For maximal statistical power, a within-subjects analysis of the peak strength of the activation was conducted using the values gathered from individual responses within both the left and the right hemisphere ROIs (altogether 13 sources). An omnibus ANOVA showed a significant effect of condition [$F(3, 36) = 18.2, p < .001$]. Semantic errors evoked stronger activation than any other condition [$F(1, 12) = 33.6, p < .001$ compared to correct, $F(1, 12) = 7.6, p < .02$ compared to word class error, and $F(1, 12) = 8.3, p < .01$ compared to morphosyntactic error conditions]. The activation also lasted longer for semantic errors than for correct and word class error conditions [tested at

Figure 2. All ECDs in nine participants that showed significant activation in the semantic error condition compared to the correct condition, shown on an average brain. The black ellipsoids indicate ECDs localized to the temporal lobe in individual participants. The black arrows indicate the estimated direction of current flow. The lower row shows the average time course of activation of the temporal sources in the correct, semantic error, word class error, and morphosyntactic error conditions.
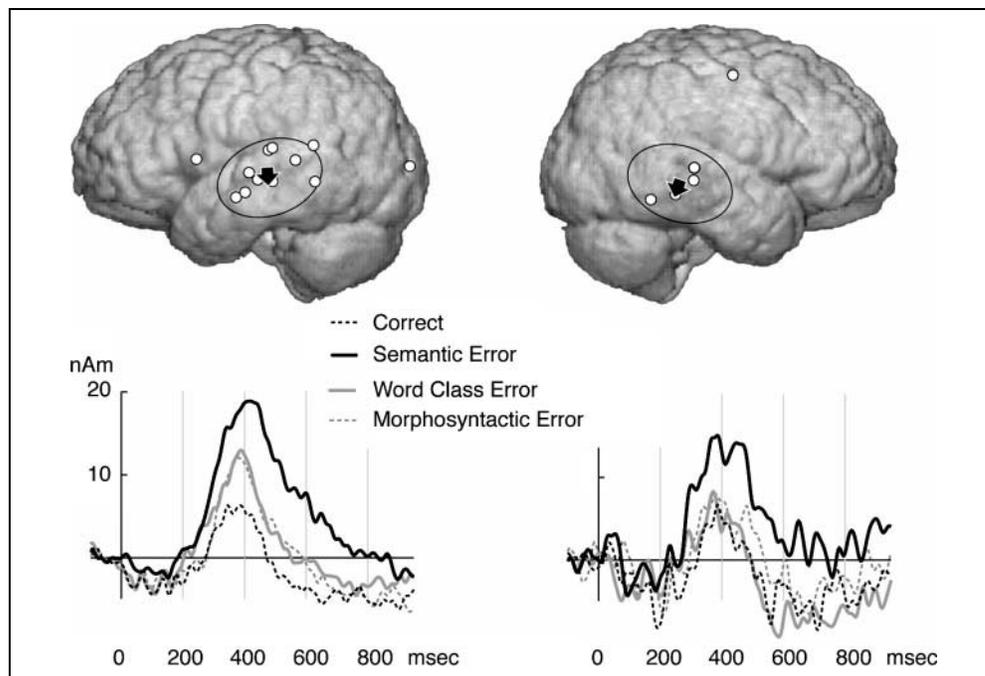
the time point when the strength of the activation had dropped to 80% from the maximum activation; $F(1, 12) = 10.7, p < .007$ for correct; $F(1, 12) = 14.7, p < .002$ for word class errors; $F(1, 12) = 2.7,$ *ns* for morphosyntactic errors]. The activation strength and duration did not differ significantly between the word class and morphosyntactic error conditions. However, both these conditions evoked stronger activation than the correct condition [$F(1, 12) = 7.6, p < .02$ for word class and $F(1, 12) = 8.3, p < .01$ for morphosyntactic errors].

An analysis of the strength of activation including only left-hemisphere sources resulted in exactly the same significant effects as the analysis including all ECDs irrespective of laterality. As only four ECDs were localized to the right temporal lobe, a separate group-level statistical analysis was not carried out on these sources. It can be noted, though, that the right-hemisphere dipoles were not visibly sensitive to either of the two syntactic violation conditions. Thus, N400 activation in the left, but possibly not the right, superior temporal cortex during reading appears to be sensitive not only to semantic but also to syntactic and morphosyntactic variables, around 400 msec after word onset.

P600 Response

The ECDs displaying P600-type behavior in each subject were identified as showing significantly stronger activation ($p < .01$, with respect to signal variation during the prestimulus baseline interval) in the word class error than in either the correct or semantic error condition between 500 and 900 msec for a minimal duration of 100 msec.

Figure 3 (upper row) depicts the spatial distribution of the P600 sources collected from all nine subjects. In the left hemisphere, four participants had temporal sources (marked circle). One of these subjects also had a frontal source. A fifth participant had only a posterior source. In the right temporal lobe, seven subjects had an ECD showing P600-type behavior. The mean orientation of the current flow in the left and right hemisphere ROIs was along the superior temporal sulcus pointing to the occipito-temporal border. The mean difference between the orientation of all the P600 dipoles and all the N400 dipoles was $123°$ ($p < .001$).

On average, the P600 activation peaked for the word class errors at 673 msec (± 50 msec *SEM*) in the left and at 720 msec (± 18 msec *SEM*) in the right hemisphere. There was no sufficient number of sources in the left hemisphere for statistical analysis. Therefore, for maximal statistical power, a within-subjects analysis of the strength of the activation was conducted using the values gathered from individual responses within both the left and the right hemisphere ROIs (altogether 11 sources). An omnibus one-way ANOVA showed a main effect of condition [$F(3, 30) = 19.0, p < .001$]. In planned pairwise comparisons, word class errors evoked stronger activation than both the correct words [$F(1, 10) = 63.3, p < .001$] and the semantic errors [$F(1, 10) = 32.1, p < .001$], as expected on the basis of ECD identification. This activation was also stronger than that for the morphosyntactic errors [$F(1, 10) = 7.5, p < .02$]. The responses to correct and semantic error conditions did not show any difference. However, the response evoked by the morphosyntactic errors was stronger than that evoked by the correct condition [$F(1, 10) = 14.3,$

Figure 3. All ECDs in nine participants that showed significant activation in the word class error condition compared to the correct condition and the semantic error condition shown on an average brain. The black ellipsoids indicate ECDs localized to the temporal lobe in individual participants. The black arrows indicate the estimated direction of current flow. The lower row shows the average time course of activation of the temporal sources in the correct, semantic error, word class error, and morphosyntactic conditions.
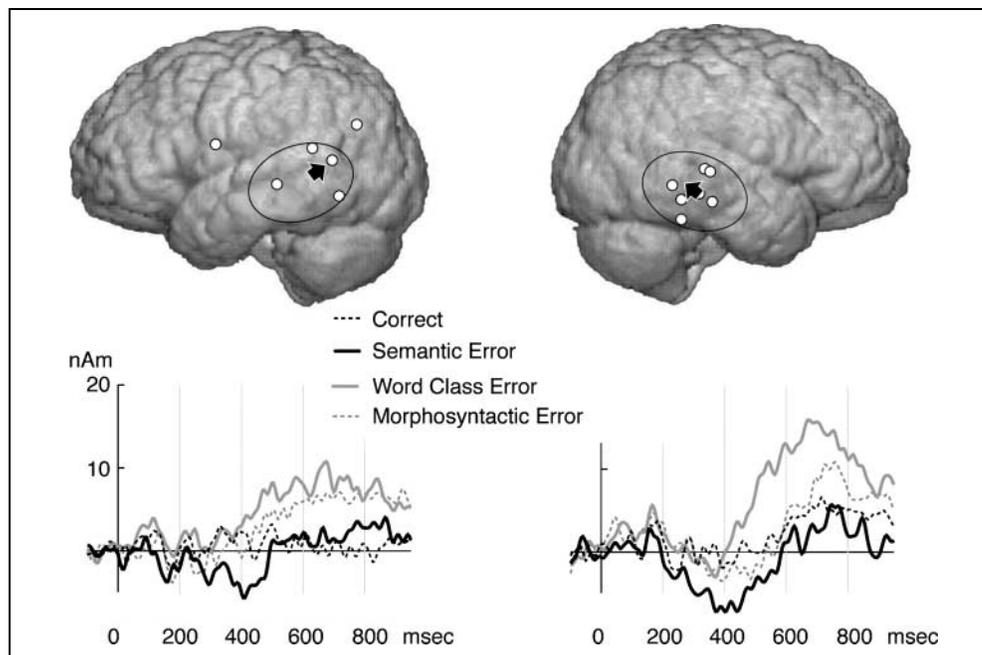
$p < .004$]. When the analysis was conducted using only values from the right hemisphere (which had a greater number of sources), the above results were replicated: Word class errors evoked stronger activation than either the correct [$F(1, 6) = 28.7$, $p < .002$] or the semantic errors [$F(1, 6) = 18.7, p < .005$]. The difference between the morphosyntactic errors and the word class errors approached significance ($p < .06$).

When the locations of the P600 and the N400 sources were compared across all subjects and both hemispheres, the N400 sources tended to be more anterior than the P600 sources (mean difference = 12 mm), as shown by a marginally significant effect ($p < .058$). However, the uneven distribution of the N400/P600 sources across the two anatomically different hemispheres could distort this figure. Measured across those subjects that had both N400 and P600 sources in the left hemisphere ($n = 4$) or in the right hemisphere ($n = 1$), the N400 responses were generated 29 mm anterior to the P600 responses ($p < .01$).

Thus, during a reading task, we found bilateral P600 activation in the superior temporal cortex around 600 to 800 msec after word onset. This activation was sensitive to syntactic phrase structure violations and, to some degree, also to local morphological agreement violations. The generators of the P600 response were located 12–29 mm posterior to those of the N400 response, probably originating in the posterior superior temporal sulcus/middle temporal gyrus.

Hemispheric Differences

Visual inspection of the mean time behavior of the N400 and P600 dipoles (Figures 2 and 3) in the left and right hemispheres suggests that the two hemispheres could react differently to the presence of syntactic error. However, the limited number of localizable sources did not allow a direct statistical comparison of the hemispheres. We therefore analyzed the AMSs registered over the temporal areas (see Figure 1). For each individual subject, we measured the mean signal strength in each of the four conditions between 375 and 425 msec as well as between 675 and 725 msec over the left and right temporal lobes. The values were then subjected to a 4×2 repeated-measures ANOVA (within-subjects factors: sentence type and hemisphere), separately for each time window.

In the 375–425 msec time window, there was a main effect of hemisphere [$F(1, 8) = 8.34, p < .02$]. The main effect of condition was also significant [$F(3, 24) = 9.71$, $p < .0001$]. The interaction between hemisphere and condition did not reach significance [$F(3, 24) = 2.34$, $p = .099$]. However, planned comparisons between the correct condition and the other conditions showed that semantic error was significantly different from correct both in the left hemisphere [$F(1, 8) = 12.65$, $p < .01$] and in the right hemisphere [$F(1, 8) = 6.44$, $p < .05$]. Word class error also significantly differed from the correct word in the left hemisphere [$F(1, 8) = 13.26$, $p < .01$], but not in the right hemisphere [$F(1, 8) = 0.21$, $p = .657$]. The difference between morphosyntactic error and correct word was not statistically significant in either the left [$F(1, 8) = 1.91$, $p = .204$] or the right hemisphere [$F(1, 8) = 0.002$, $p = .966$]. Thus, N400 activation recorded over the left temporal area was sensitive to a major phrase structure error, whereas activity recorded over the right temporal area was not.

A similar ANOVA in the 675–725 msec window showed a main effect of condition [$F(3, 24) = 6.51, p < .002$], but not hemisphere [$F(1, 8) = 0.60, p = .461$]. There was no interaction between the two variables [$F(3, 24) = 0.60, p = .561$]. Planned comparisons revealed a significant difference between word class error and correct word [$F(1, 8) = 13.59, p < .01$]. The difference between morphosyntactic error and correct did not reach significance [$F(1, 8) = 2.77, p = .135$], nor was there any statistically reliable difference between the semantic error and the correct conditions [$F(1, 8) = 0.243, p = .635$]. Thus, activation in the later time window was equally sensitive to syntactic error over the left and right temporal areas.

DISCUSSION

Localization of Language Responses

This study set out to use the MEG method to localize and compare the generators of commonly reported brain responses during the reading of semantically and/or syntactically ill-formed sentences: the N400, the (E)LAN, and the P600. Inspection of AMSs, combining the signal in nearby MEG sensors and averaging this over subjects, confirmed that our experimental manipulations produced similar effects as those seen in ERP experiments manipulating the syntactic and semantic well-formedness of sentences. Both semantic errors and word class errors resulted in an increased signal during the N400/LAN time window over the temporal and fronto-temporal areas, dominant on the left. In addition, word class errors, but not semantic errors, showed bilaterally increased signal in the P600 time window.

A fine-grained analysis was accomplished by modeling the source areas as a set of ECDs. Around 400 msec after word onset, in the N400/LAN time range, analysis revealed ECDs only in the left superior temporal cortex, reacting to both semantic and syntactic anomaly, and in the right superior temporal cortex, apparently sensitive to semantic violations. The spatial distribution of the N400 activation is in line with previous MEG reports on semantic processing (Marinkovic et al., 2003; Halgren et al., 2002; Helenius et al., 1998). The left-hemisphere N400 sources showed a gradation between conditions with the strongest activation to semantic anomaly, somewhat weaker activation to phrase structure violations and local morphosyntactic violations, and the weakest activation to acceptable last words. Activity in the later P600 time window between 600 and 800 msec was best modeled by slightly more posterior temporal sources in both hemispheres, with direction of current flow practically orthogonal to that in the N400 source areas. The analyses, thus, suggested that up to 400 msec after visual word presentation, the left hemisphere plays a role in both syntactic and semantic word processing, whereas the right hemisphere may be limited to seman-

tic analysis. In the later P600 time window, responses were sensitive to syntactic violations bilaterally.

The results suggest that, around 400 msec poststimulus, both global syntactic and local morphosyntactic LAN effects may be created by essentially the same neural network in the left temporal lobe that also produces semantic N400 effects. However, the right temporal lobe appears to be sensitive to semantic violations only. Thus, the different scalp distributions of the semantic N400 and the syntactic LAN in ERP studies could, at least partly, depend on the differential contribution of left- and right-hemisphere sources (for a similar argument in single-word processing, see Thierry et al., 2003).

P600 activity was dissociated from N400 activity in the sense that no semantic violation effects could be detected in it. Although generators of the P600 response were located approximately 2 cm posterior to the sources of the N400 response, these two populations showed some spatial overlap. However, the orientations were clearly different, pointing to involvement of distinct neuronal populations. All in all, the spatial analysis lends support to the idea that the LAN is a (left-hemisphere) N400-like response that is modulated by syntactic and morphosyntactic variables (cf. Osterhout, 1997).

There is an ongoing debate about the functional interpretation of the electrical P600 response. Although it is reliably found in connection with syntactically anomalous sentences, it has variably been interpreted as a first- (Deutsch & Bentin, 2001) or second-pass (Friederici, 2002) syntactic parsing response, a repair and reanalysis response (Kaan & Swaab, 2003; Friederici, 2002), a response reflecting the difficulty of syntactic processing (Kaan et al., 2000), or just a response to a salient stimulus (Coulson et al., 1998). The bilateral scalp distribution of the P600 response reported in previous ERP studies was, in the present study, complemented with a bilateral distribution of ECD sources. If the neural generators of P600 activation are bilateral, it follows that interpretations in terms of complex syntactic analysis and repair processes would have to accommodate the idea that such processes are not necessarily left-lateralized. An alternative is to attribute the P600 activation to a nonlinguistic process, for instance, attention or context updating (Coulson et al., 1998), monitoring (van Herten, Kolk, & Chwilla, 2005), or WM load. A bilateral medial and lateral parietal change in activation seen in an event-related fMRI study in response to syntactic anomalies was suggested to possibly reflect changes in focused attention (Kuperberg et al., 2003).

Contrary to expectations derived from many fMRI studies (e.g., Ni et al., 2000), this study only found one anterior dipole in one single subject in the N400/LAN window and one (for a different participant) in the P600 window, compatible with a source in Broca's area. A lack of activation in Broca's area lends support to views that the role of this area is more related to the cognitive demands of many different tasks with language or

musical content than specifically syntactic processing (Kaan & Swaab, 2002).

The Time Course of Syntactic and Semantic Analysis

Our study did not directly address possible interactions between syntactic and semantic processes. However, the results do not easily fit views that categorically assume early independence and late interaction between syntax and semantics (Gunter et al., 2000). Instead, they are largely in agreement with another recent Finnish study (Palolahti et al., 2005), using ERPs. In that study, syntactic and semantic violations separately gave rise to very similar left-dominant negativities between 300 and 500 msec from word onset. The only difference in the ERPs was that the syntactic effect could only be seen on left frontal electrodes. A combined syntactic and semantic violation also gave rise to a left-dominant N400/LAN response in combination with a large P600. An analysis including syntactic, semantic, hemisphere, and front–back location factors showed an early interaction between the syntactic and semantic violation factors in the N400/LAN time window, and suggested that syntactic and semantic violation effects were not additive on left hemisphere electrodes.

In our study, the overlapping effects of semantic and syntactic manipulations in the left temporal cortex during the N400/LAN window suggest a shared neural substrate for these processes at 300–500 msec poststimulus. It is tempting to think that interactions, for instance, dampening of semantic processing of syntactically ill-formed structures, may occur here. The left temporal activation in our study is, therefore, tentatively interpreted as a comprehension response that is enhanced by syntactic and semantic ill-formedness in different shapes, that is, it is both an N400 and a LAN.

Note that although it is conceivable that the word class error could have resulted in a separate semantic effect in addition to a syntactic effect, and therefore, generated a ''purely'' semantic N400, a similar manipulation in a study by Friederici et al. (1999) did not show any detectable N400 to a past participle replacing a noun. Rossi, Gugler, Hahne, and Friederici (2005) reviewed eight similar studies that all produced an ELAN and a P600 but no N400 to a word category violation. The Rossi et al. study had a pattern of ELAN, followed by a negativity in the LAN/N400 window, and a P600. The authors speculated that this additional negativity could be related to mentally inserting a missing noun into a subject noun phrase. Such an interpretation is quite compatible with our suggestion of a combined N400 and LAN. Note also that, in the right hemisphere, we were unable to detect ECDs sensitive to category or morphosyntactic violations in the N400 window. In a recent study (Kim & Osterhout, 2004), a somewhat different pattern was reported, namely, one in which conflicts between semantic and syntactic cues were sometimes solved in favor of the semantic information, thus, forcing later syntactic repair and resulting in P600 responses. The study by Kim and Osterhout underlines the fact that interaction between syntax and semantics can happen early but is still not very well understood.

The results of the present study also agreed with Palolahti et al. (2005), in that we found P600 sources that were affected by morphosyntactic, but not semantic, violations. This is also in line with results reported by Hagoort (2003). They are in contradiction with findings by Gunter et al. (2000), who found an effect of semantic anomaly on the P600 (i.e., that it was abolished for low-probability words that elicited a large N400). As the N400 and the P600 were both maximal on posterior electrodes in the Gunter et al. study, it is possible that the larger N400 for the low-probability nouns overlapped in time with, and therefore attenuated, the scalp-recorded positivity for these words in the morphosyntactic violation condition.

To summarize, we were able to localize both N400 and P600 responses to the middle/posterior temporal cortex. The P600 response was characterized by a distribution of sources, on average, 2 cm posterior to the N400 sources and with a different direction of current flow. Activation sensitive to semantic errors around 400 msec after word onset in the left hemisphere also responded to syntactic and morphosyntactic violations, suggesting that LAN and N400 may have common, or considerably overlapping, neural representations. P600 activation, however, was more balanced across hemispheres as both the left and right hemispheres were sensitive to word class and morphosyntactic violations.

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