



Localization of electrophysiological responses to semantic and syntactic anomalies in language comprehension with MEG



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ABSTRACT

Syntactically and semantically anomalous words encountered during sentence comprehension are known to elicit dissociable electrophysiological responses, which are thought to reflect distinct aspects of language processing. However, the sources of these responses have not been well characterized. We used beamforming analysis of magnetoencephalography (MEG) data to map generators of electrophysiological responses to linguistic anomalies. Anomalous words occurred in the context of a sentence acceptability judgement task conducted in both visual and auditory modalities. Time–frequency analysis revealed that both kinds of violations elicited event-related synchronization (ERS) in the delta–theta frequency range (1–5 Hz), and desynchronization (ERD) in the alpha–beta range (8–30 Hz). In addition, these responses were differentially modulated by violation type and presentation modality. 1–5 Hz responses were consistently localized within medial prefrontal cortex and did not vary significantly across violation types, but were stronger for visual presentation. In contrast, 8–30 Hz ERD occurred in different regions for different violation types. For semantic violations the distribution was predominantly in the bilateral occipital cortex and left temporal and inferior frontal regions, and these effects did not differ for visual and auditory presentation. In contrast, syntactic responses were strongly affected by presentation modality. Under visual presentation, syntactic violations elicited bilateral 8–30 Hz ERD extending into dorsal parietal and frontal regions, whereas effects were much weaker and mostly statistically insignificant in the auditory modality. These results suggest that delta–theta ERS reflects generalized increases in working memory demands related to linguistic anomaly detection, while alpha–beta ERD reflects specific activation of cortical regions involved in distinct aspects of linguistic processing, such as semantic vs. phonological short-term memory. Beamforming analysis of time-domain average signals (ERFs) revealed an N400m effect for semantic anomalies in both modalities, localized to left superior temporal and posterior frontal regions, and a later P600-like effect for syntactic anomalies in both modalities, widespread over bilateral frontal, posterior temporal, and parietal regions. These results indicate that time-domain averaged responses and induced oscillatory responses have distinct properties, including localization and modality dependence, and likely reflect dissociable and complementary aspects of neural activity related to language comprehension and additional task-related processes.

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Introduction

Neuroimaging evidence and lesion data indicate that language processing depends on dynamic interactions between anterior and posterior brain regions. Areas critical for language use have been grouped into functionally connected networks responsible for processing distinct kinds of linguistic information. For example, brain regions comprising a ventral language network are selectively involved in lexical–semantic aspects of language (Saur et al., 2008; Turken and Dronkers, 2011), whereas more dorsal frontal–parietal regions have been found to participate in computation of syntactic structure (Friederici et al., 2006), in

phonological short-term memory (Buchsbaum et al., 2011; Kellmeyer et al., 2009; Majerus, 2013), and mapping of sound to articulation (Saur et al., 2008, 2010). The white matter pathways connecting the temporal and inferior parietal lobes with the frontal lobe have been mapped with diffusion tensor imaging (Catani et al., 2005, 2007; Glasser and Rilling, 2008). There is currently great interest in linking these distinct anatomical networks to electrophysiological responses that have long been known to correspond to separate aspects of language processing.

Semantic and syntactic processing have been successfully dissociated with scalp-recorded event-related potentials (ERPs). Semantically anomalous words elicit a central–parietal negativity at about 400 ms known as the N400 (Friederici et al., 1993, 2004; Kutas and Federmeier, 2000; Kutas and Hillyard, 1980). In sentences, N400 amplitude is modulated by the expectedness of a single word or the ease with which a word is integrated

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with the preceding portion of the sentence. Modulation of this component has been used as a marker of semantic processing in various clinical populations (Ford et al., 1996; Kawohl et al., 2010; Kielar et al., 2012; Kumar and Debruille, 2004; Ruchow et al., 2003).

In contrast, syntactic anomalies have been associated with a left anterior negativity (LAN, about 400 ms post-stimulus) and a centro-parietal positive component, beginning at approximately 600 ms after word onset, referred to as the P600 (Coulson et al., 1998; Friederici et al., 1993; Münte et al., 1993). The P600 effect has most often been reported in response to syntactic or morphosyntactic violations to sentence structure (Friederici et al., 1993; Kuperberg et al., 2003; Osterhout, 1997; Osterhout and Mobley, 1995; Osterhout and Nicol, 1999), but has also been found in fully grammatical but ambiguous or complex sentences (Osterhout and Holcomb, 1992; Osterhout et al., 1997). Although the P600 response has been replicated multiple times, there is no consensus on its exact functional role. It has been suggested to reflect second-pass reanalysis and repair of syntactic structure after a violation has been detected (Friederici, 2002), or difficulty in syntactic integration (Frisch et al., 2002; Kaan et al., 2000).

One way to identify the brain networks involved in different aspects of language comprehension would be to identify the sources of electrophysiological responses related to semantic and syntactic aspects of sentence processing. The distinct polarity but similar central-parietal scalp distribution of the N400 and P600 suggests the engagement of different but likely overlapping populations of neurons in processing semantic and syntactic anomalies. In addition, patients with left temporal-parietal lesions show dissociations between N400 and P600 components, suggesting involvement of distinct functional neural networks for these two responses (Friederici et al., 1998). However, accurate localization of neural generators from scalp-recorded EEG is difficult because the same scalp topography can result from different intracranial generators. Thus, it is possible that the similar centro-parietal scalp topography for N400 and P600 components arises from activity in substantially different brain regions. Any mathematical technique attempting to map the generators of electromagnetic fields detected on the surface (i.e. an inverse solution) depends first on an accurate “forward solution” that models the projection of internal sources to the sensors. Magnetoencephalography (MEG) offers more accuracy in this respect, because magnetic fields are not distorted by passing through the skull (Hamalainen, 1993).

MEG studies have localized a magnetic equivalent of the N400 ERP component (N400m) to left superior temporal regions in both visual (Service et al., 2007; Halgren et al., 2002) and auditory modalities (Helenius et al., 2002; Wang et al., 2012). In contrast to N400 sources, the generators of P600 responses have been less well characterized. In some studies, MEG responses to syntactic violations embedded in visually presented sentences have been localized to the bilateral temporal lobes, posterior to the N400 sources (Service et al., 2007), whereas auditory presentation elicited responses in the left anterior temporal and fronto-lateral cortices (Friederici et al., 2000).

The utility of MEG in the study of language processing is enhanced by analysis of data in the frequency domain. The classical method of signal analysis is to derive event-related responses — event-related fields (ERFs) in MEG and corresponding event-related potentials (ERPs) in electroencephalography (EEG). These measures are obtained by averaging the signal obtained over repeated trials in a specific time window that is time-locked to the external stimulus event. Although this method has been extensively explored in psycholinguistic research, ERFs are only sensitive to neural activity that is phase-locked to the event onset, ignoring non-phase-locked activity that is cancelled out by the averaging procedure (Mouraux and Lannetti, 2008).

Non-phase-locked activity is also detectable in cognitive paradigms, most frequently as changes in oscillatory power in certain frequency ranges. Analysis of oscillatory responses can reveal neural activity that is reliably induced by an event, but exhibits more temporal variability across trials and participants. Recent data indicates a close coupling

between oscillatory reactivity measured with EEG/MEG and the blood-oxygen-level-dependent (BOLD) response in fMRI. Specifically, the power of high-frequency oscillations (>40 Hz) tends to increase with neural firing and BOLD signal, resulting in event-related synchronization (ERS). In contrast, lower frequencies (<30 Hz) tend to show reduction in power in activated cortex, resulting in event-related desynchronization (ERD; Meltzer et al., 2007; Pfurtscheller and Lopes da Silva, 1999; Singer, 1993).

In recent years, oscillatory reactivity in MEG has been extensively studied using beamforming techniques for source analysis (Vrba, 2002; Vrba and Robinson, 2001). This method estimates a virtual signal at a particular location in the brain while attenuating activity arising from other brain areas and extracranial sources, such as ocular artifacts (Cheyne et al., 2006; Robinson, 2004). This technique offers the necessary combination of spatial and temporal resolution to reveal neural activation in specific brain regions during language comprehension on a realistic time scale. For example, it allows one to measure responses to individual words within a sentence in either the frequency or time domain. Increasingly, power decreases in the alpha and beta ranges are being identified as a reliable indicator of increased neural activity, with close correspondence to the BOLD responses in diverse parts of the cortex (Brookes et al., 2005; Hillebrand et al., 2005; Hanslmayr et al., 2012). Changes in oscillatory power in these frequency bands have been induced in a wide range of cognitive paradigms including language processing, most commonly in a block design (Singh et al., 2002; Kim and Chung, 2008). In a recent study, Meltzer and Braun (2011) used MEG beamforming to measure the temporal dynamics of neural activity involved in language comprehension for a sentence-picture matching task. They observed 8–30 Hz ERD in response to two different factors that affect comprehension difficulty: semantic reversibility and syntactic complexity. However, the two factors influenced neural activity in different brain regions and in different time periods, with effects of syntactic complexity emerging only during a memory delay after sentence presentation was complete. These findings illustrate the sensitivity afforded by MEG beamforming in the frequency domain, as language activity can be tracked at much finer temporal resolution than that afforded by fMRI, with reasonable spatial resolution.

To date, one study has used MEG to map neural activity in the frequency domain related to perceiving semantically anomalous words. Wang et al. (2012) showed that, compared to semantically congruent words at the end of sentences, incongruent words induced suppression of alpha and beta power over the left hemisphere. Similarly, in an EEG study, Willems et al. (2008) observed decreases in alpha band power in response to sentence-embedded semantic anomalies. However, in other EEG studies, semantic anomalies were associated with reactivity in the theta band (desynchronization: Allefeld et al., 2005; synchronization: Davidson and Indefrey, 2007; Hald et al., 2006).

Syntactic violations have received less attention in MEG research, especially in the frequency domain. Although no such studies have attempted to localize generators of oscillatory activity using MEG, at least two studies have reported ERD in the alpha and beta bands in response to syntactic violations. In a MEG study, Bastiaansen et al. (2009) detected beta band ERD that was strongest over left frontal sensors, while in an EEG study Davidson and Indefrey (2007) reported alpha and beta power decrease in response to grammatical violations. In several other EEG studies, syntactic violations elicited theta power increases (Bastiaansen et al., 2002a; Roehm et al., 2004).

More recently, we examined oscillatory responses to sentence-embedded semantic and syntactic violations within the same paradigm (Kielar et al., 2014). The results showed that both types of violations elicited power decreases in alpha and beta frequency bands (8–30 Hz), most likely reflecting increased neural processing associated with reanalysis of the sentence after the violation is encountered. In addition, semantic anomalies elicited fronto-central power increases in the 1–5 Hz frequency range.

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