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Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations

Nietzsche H.L. Lam, Jan-Mathijs Schoffelen *, Julia Uddén, Annika Hultén [1], Peter Hagoort *

Donders Institute for Brain, Cognition and Behaviour, Centre for Cognitive Neuroimaging, Radboud University Nijmegen, Nijmegen, Netherlands
Max Planck Institute for Psycholinguistics, Nijmegen, Netherlands

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ABSTRACT

We used magnetoencephalography (MEG) to explore the spatiotemporal dynamics of neural oscillations associated with sentence processing in 102 participants. We quantified changes in oscillatory power as the sentence unfolded, and in response to individual words in the sentence. For words early in a sentence compared to those late in the same sentence, we observed differences in left temporal and frontal areas, and bilateral frontal and right parietal regions for the theta, alpha, and beta frequency bands. The neural response to words in a sentence differed from the response to words in scrambled sentences in left-lateralized theta, alpha, beta, and gamma. The theta band effects suggest that a sentential context facilitates lexical retrieval, and that this facilitation is stronger for words late in the sentence. Effects in the alpha and beta bands may reflect the unification of semantic and syntactic information, and are suggestive of easier unification late in a sentence. The gamma oscillations are indicative of predicting the upcoming word during sentence processing. In conclusion, changes in oscillatory neuronal activity capture aspects of sentence processing. Our results support earlier claims that language (sentence) processing recruits areas distributed across both hemispheres, and extends beyond the classical language regions.

Introduction

How are you reading this sentence? Conceptually, the reader needs to retrieve and understand the meaning of individual lexical items (words), and combine these items to derive an interpretation spanning its entirety. The latter process is referred to as unification (Hagoort, 2003, 2005, 2013). At the neural level, the fast and incremental nature of sentence processing likely involves multiple brain regions. Yet, we know little about how the brain orchestrates sentence processing because the majority of neuroimaging studies on language processing have focused on the single word level. Of the studies that focused on sentence processing, most used syntactic or semantic anomalies as an experimental manipulation. Considering daily language exposure, this questions the ecological validity of such stimuli. Moreover, although the experimental designs were well controlled, these studies related neural responses only to specific critical events within a sentence. Consequently, the processing of each word in a sentence, and how it is affected by an incremental context, has not been studied in detail. In the current study, we address these two aspects of sentence processing using natural sentences. We focused on the modulation of neural oscillations in response to individual words in the context of a sentence, and examined how this modulation changed as the sentence unfolded.

Oscillatory neural activity

When studying electrophysiological signals, spectral analysis techniques are aimed at quantifying frequency-specific neural activity. These techniques were initially used to study rhythmic activity during visual processing, or low-level motor behavior, and then gained popularity in the 2000s to study higher order cognition, such as language (Hari and Salmelin, 2012). Beyond capturing the transient response to external events, estimates of frequency-specific activity reflect oscillatory neural activity that is not necessarily time- or phase-locked to an event, as opposed to event-related averages. Thus, it may provide a different but complimentary perspective on how the brain orchestrates language (including sentence) processing. Furthermore, this technique allows us to investigate the relationship between aspects of sentence processing and the spatiotemporal dynamics of oscillatory activity.

The power of oscillatory activity has been observed to be modulated in many cognitive tasks. These modulations are typically described as relative decreases (event-related desynchronization, ERD; Pfurtscheller and Aranibar, 1977) or relative increases (event-related sychronization, ERS; Pfurtscheller, 1992). Depending on the frequency band, such power

* Corresponding authors at: Donders Centre for Cognitive Neuroimaging, Kapittelweg 29, 6525 EN, Nijmegen, Netherlands.
E-mail addresses: jan.schoffelen@donders.ru.nl (J.-M. Schoffelen), p.hagoort@donders.ru.nl (P. Hagoort).
[1] Current affiliation: The Department of Neuroscience and Biomedical Engineering, Aalto University, Helsinki, Finland.

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changes may indicate either activation or deactivation of a brain region. An ERD in the gamma band (>40 Hz) reflects a reduction in processing in underlying cortical regions, but would reflect increased processing when observed in the alpha (8–12 Hz) or beta (13–30 Hz) bands (Jensen and Mazaheri, 2010; Klimesch et al., 1997; Osipova et al., 2006; Klimesch et al., 2001). For the theta frequencies, however, it is equivocal as to whether an ERD reflects activation or deactivation. Oscillatory neural activity can be productively studied using MEG. This method has good spatial resolution and excellent temporal resolution (in the order of milliseconds), which enables it to capture rapid (tens of milliseconds) changes associated with cognitive processes in the brain.

Studying sentence processing with oscillations

Both ERS and ERD have been observed in studies concerned with sentence processing, but most studies analyzed the data on the sensor-level which provided poor spatial localization of the effects, and most of them focused on a single word (that produced a grammatical violation) in the sentence (e.g., Bastiaansen et al., 2010; Davidson and Indefrey, 2007). Across these studies, different frequency bands have been associated with different functional explanations. The theta and alpha bands, for example, have been associated with the lexical-semantic retrieval of words (Bastiaansen et al., 2005; Klimesch et al., 1997). Beta and gamma band ERS has been suggested to reflect unification of the semantic and syntactic information in sentences, respectively (Bastiaansen and Hagoort, 2015; Bastiaansen et al., 2010; Hald et al., 2006). The alpha and beta bands have also been demonstrated to be involved in syntactic processing (Bastiaansen et al., 2010; Davidson and Indefrey, 2007; Kielar et al., 2015). Overall, these results, whilst suggestive, highlight the need for further study of oscillations in sentence processing, specifically to study multiple frequency bands in one dataset, and to understand their relation to each other.

In sentence processing, words are retrieved from memory and combined into an interpretation of the larger phrase, regulated by semantic and grammatical constraints (Hagoort, 2013). A recent fMRI meta-analysis revealed consistent involvement of the left inferior frontal gyrus (BA 45 and BA 47), left middle temporal gyrus (MTG), and left superior temporal gyrus in sentence processing (Hagoort and Indefrey, 2014). The memory, unification, and control (MUC) model of sentence processing also focuses on these areas (Hagoort, 2003, 2005, 2013). It proposes that the left temporal cortex and angular gyrus are implicated in word retrieval from memory, while unification (maintenance and integration of words) involves the left inferior frontal cortex. Furthermore, as the sentence unfolds, a predictive context results from the interaction between these areas, and this context facilitates the processing of upcoming words. Previous oscillatory studies on sentence processing have, to our knowledge, been restricted to the sensor level. It is therefore unclear whether oscillations localize to similar brain regions as found in event-related M/EEG and fMRI studies. The current study, presenting a thorough source-level analysis of oscillatory activity during sentence processing, addresses this shortcoming.

Current study

In the present study, we investigated oscillatory power changes during sentence processing. We obtained MEG data while participants read sentences. As a control condition, participants also read lists of words (created by scrambling sentences). Our study focused on exploring which neural areas, at which frequencies are involved in sentence processing. We analyzed the spatiotemporal dynamics of the oscillatory activity by using a beamformer in the frequency domain. This allowed us to better quantify the spatial aspects of the effects, and to improve on the previous studies that could only report results at the sensor-level.

To obtain a complete picture of oscillations at various frequencies, we investigated five frequency bands: theta, alpha, beta, low gamma, and high gamma. We chose to divide the gamma band because previous studies have shown a distinction between low gamma (around 30 to 60 Hz) and high gamma (above 80 Hz); the precise frequencies for low and high gamma differ between cortical regions and the cognitive task (Crone et al., 1998; Dalal et al., 2008; Hauck et al., 2007). Furthermore, previous sentence-processing studies have only shown effects at around 40–60 Hz, and we were interested in whether effects in higher frequencies were also present. In the current study, we investigated two aspects of sentence processing: The *word analysis* sought to reveal how single words are integrated into a representation of the entire sentence, and the *context analysis* assessed the effect of the incremental context on single word processing.

Word analysis

In order to investigate the oscillatory response to single words within the context of a sentence, we analyzed the responses to each of the single words in a sentence and contrasted them to single words in a random order (word list). Sentences have a structured and meaningful context—semantic and syntactic information that goes beyond the level of the individual words. Word lists on the other hand have no structure and only a weak overarching semantic context (because each word list was created by scrambling a sentence). We hypothesized the sentence context to have a facilitatory effect, since the syntactic and semantic information in preceding words constrain the possibilities of the upcoming word both syntactically and semantically. The effect of the context may be observed in memory retrieval, unification, and prediction (Hagoort and Poeppel, 2013). The sentence context should make memory retrieval easier for sentences than word lists, and because previous studies associated theta power with memory retrieval (Bastiaansen et al., 2005; Hagoort, 2013), we expected differences between the conditions in this frequency band. Since the prediction of the upcoming word within a context has been associated with gamma ERS (Wang et al., 2012), we expected to observe this pattern for sentences but not word lists. Finally, the alpha, beta, and gamma bands have been implicated in unification (e.g., Bastiaansen and Hagoort, 2015; Bastiaansen et al., 2010; Hald et al., 2006); therefore, we expected differences between sentences and word lists in one or more of these frequencies.

Context analysis

To analyze how the unfolding sentence context affects oscillatory activity over time we quantified the modulation of the oscillatory response between words at early and late positions in a sentence. This provides a view of the long-term changes in power as the sentence progresses. As the sentence unfolds, memory should become taxed because more words need to be retained for unification. As ERS in the theta band has been associated with memory maintenance, we expected an increase in theta power for words in late versus early positions in the sentence. An incremental context can also impose more constraints on how words are being combined, which could facilitate unification as the sentence unfolds. Changes in power across a sentence but not a word list have previously been associated with the beta and gamma bands (Bastiaansen et al., 2010; Hald et al., 2006). Effects in these frequency bands are suggested to reflect unification. Therefore, we hypothesized that a change in beta and/or gamma oscillations would also be observed as the sentence unfolded.

Methods

Participants

A total of 102 native Dutch speakers (51 males), with an age range of 18 to 33 years (mean of 22 years), participated in the experiment. These participants formed part of a larger study—MOUS (Mother of all Unification Studies; $N = 204$), where all participants took part in an fMRI and a MEG session. Half of these participants completed both sessions where they read the stimuli, and the other half listened to recordings of the