Neural representations of sentence processing: event-related components and oscillations

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Keywords: Sentence Processing, Magnetoencephalography (MEG), neuronal oscillations, evoked-responses, Memory, Unification and Control Model.

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Abstract

Event-related fields (ERFs) and rhythmic oscillations represent two measures that quantify the electrophysiological brain activity in response to a stimulus. Using MEG, we analyzed both measures in a sentence processing task to clarify the relationship between these measures. We presented participants with sentences and matched word sequences. Results indicated a partial spatial overlap on the sensor level between the two measures, with a wider area of activity present for oscillations. Within the common region, the effect for each measure was in a different time window. Relating the results to the literature reveals furthermore a functional distinction between the results observed in the two respective measures. The sustained left dominant event-related field peaking around 400 ms is most likely related to lexical processing whereas the rhythmic activity of 13-30 Hz (beta rhythm) captures some aspects of sentence unification. We conclude that the ERFs and the rhythmic activity provide a complementary view of brain function during sentence level language processing.

Introduction

Human language is a dynamic form of communication and its expressive power stems from the combination of words with grammar. Given the vast vocabulary and various possible combinations, the speed and fluency at which communication operates is impressive. Nevertheless, the cognitive processes and neural substrates underlying this communication system remain unresolved. Many neuroimaging studies have sought to understand how sentence processing is implemented in the brain. A majority of the studies have focussed on the spatial localization of the neural correlates of language processing, with methods such as functional Magnetic Resonance Imaging (fMRI) (Booth et al., 2002; Friederici, Meyer, & von Cramon, 2000; Friederici, Ruschemeyer, Hahne, & Fiebach, 2003) and they suggest that several areas of the brain (e.g., left inferior frontal and left temporal areas) are involved in language comprehension.

Sentence processing extends over a relatively long period in which the earlier words are kept in working memory and then combined with the incoming words to form a coherent sentence. On this basis, it is equally important to understand the temporal dynamics of language-related brain areas. In reading, the analysis of visual features occurs in the occipital cortex around 100ms after word onset (Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999). Around 150ms letter-string analyses occur in the left occipitotemporal cortex, (Dehaene, Le Clec, Poline, Le Bihan, & Cohen, 2002). This is followed by the analysis of lexical-semantic properties in the left superior temporal cortex around 300 to 450ms, and thereafter activity spreads to nearby regions and to both hemispheres (Vartiainen, Parviainen, & Salmelin, 2009). At the sentence level, the combination of the current word with the context (from previous words) begins around 375ms (Federmeier & Kutas, 1999). The multiple linguistic processes occurring at various (overlapping) times indicate the complexity of language processing. To contribute to our understanding of how the brain processes language, the current project investigated the temporal dynamics of sentence-level processing.

Magnetoencephalography

To understand the temporal dynamics of neural activity involved in sentence processing, suitable methods are non-invasive electrophysiological techniques such as Electroencephalography (EEG) and Magnetoencephalography (MEG) which have high temporal resolution in the millisecond range.

Brain activity takes the form of electric currents, and MEG measures the magnetic fields generated mainly from electric currents of post-synaptic potentials in the pyramidal neurons of the cortex (Hämalainen, Hari, Ilmoniemi, Knuutila, & Lounasmaa, 1993). As the magnetic fields produced by the brain (about 10^{-13} Tesla) are much weaker than the earth's magnetic field (10^{-4} Tesla), in order for a signal to be detectable outside the head neuronal populations of tens of thousands of neurons need to be simultaneously active (Murakami & Okada, 2006). MEG is most sensitive to magnetic fields arising from currents with tangential orientations close to the scalp surface (i.e. the sulci of the cortex), whereas radial sources are less strongly detected. This is because primary currents with radial orientations generate volume currents that lead to magnetic fields which are largely attenuated by the magnetic fields generated from the primary currents themselves. As two thirds of the brain consists of sulci, the majority of brain activity is well detected; only sources that are strictly radial cannot be detected. In practice, however, the depth of a source poses much stronger limitations on the sensitivity of the MEG signal than the orientation of the sources (Hillebrand & Barnes, 2002). Although EEG also has high temporal resolution, MEG is favoured because the magnetic fields are not perturbed by the different tissue boundaries between skin, skull and dura, which make source localization easier.

Event-related components and rhythmic oscillatory activity

In this study we used MEG to track the neural underpinnings of linguistic processing in terms of their temporal dynamics to delineate the time course of various processes involved in sentence comprehension. The raw MEG signal captures information that can be expressed along various dimensions: frequency, power, phase and time (Makeig, Debener, Onton, & Delorme, 2004). Two common measures derived from this signal are event-related components and oscillations. Event-related components are the part of the signal that is time-locked to an event and averaged across several trials or epochs. These components can be modulated in terms of latency onset, duration, and amplitude. Oscillations, on the other hand, capture rhythmic activity in the frequency domain. In comparison to event-related components, oscillations are related but less time-locked to an event or stimulus (cf. Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998). Oscillations can be studied in terms of power (amplitude square) and phase (degree of synchronization between two oscillations in terms of their features with respect to an event), both of which are induced more slowly than event-related components.

Memory, Unification and Control Model

One particular model on sentence processing is the Memory, Unification and Control Model (MUC; Hagoort, 2003; 2005). As indicated in its name this model consists of three components. The Memory component is the retrieval of words from long-term memory (referred to as the Mental Lexicon, Levelt, 1992). Subsequently, these words are combined to represent a coherent sequence to achieve comprehension of the utterance as a whole, a process referred to as unification. Control, the third component, monitors sentence processing in terms of actions and intention involved in communication e.g., directing attention to the relevant object(s) and speaker or taking-turns to speak in a conversation. Based on a meta-analytical review that the left posterior temporal cortex (LPTC) is involved in processing lexical information (Indefrey & Cutler, 2003), Hagoort proposed that this area could be the location of lexical item storage and retrieval. In 2002, Mesulam demonstrated that the left prefrontal cortex (LPFC) is associated with the maintenance and combination of information. This area was considered by Hagoort as a strong candidate for unification – to hold and combine words in a sentence. These two areas form the core of the neural implementation of the MUC model, but both are modulated by the control unit localized in the anterior cingulated cortex and dorsolateral prefrontal cortex (figure 1).

Although our study is primarily exploratory and data-driven, we aim to relate both the oscillatory and event-related activity to processes of retrieval and unification. Below, we review the existing literature on language processing while keeping in mind the processes involved in the MUC model.

Event-related components in language processing

The language literature has focussed on several components. The N400 is a negative deflection in the EEG signal that begins around 200-300ms and peaks around 400ms after the onset of the word (first discovered by Kutas & Hillyard, 1980) and is associated with semantic processing. The amplitude of the N400 is larger for violations compared to correct words, and is also sensitive to (modulated by) context (Kutas & Hillyard, 1984).

Osterhout and Holcomb (1992) discovered the P600, a positive component peaking around 600ms, which was associated with syntactic processing. Two other components have also been associated with syntactic processing. The left anterior negativity (LAN) from about 350 to 500ms (e.g., Neville, Nicol, Barss, Forster, & Garrett, 1991) is related to morphosyntactic errors. Word-category errors are correlated with an earlier form of the LAN, the early left anterior negativity (ELAN) around 150-200m (e.g., Osterhout & Mobley, 1995). All the above event-related components have been reliably found in many studies, both in the visual (Hagoort, Wassenaar, & Brown, 2003) and auditory modalities (Hahne & Jescheniak, 2001) and have been replicated in many languages (e.g., (Hagoort & Brown, 2000a, 2000b; Hahne & Jescheniak, 2001; Wolff, Schlesewsky, Hirotani, & Bornkessel-Schlesewsky, 2008)). Yet, debates remain on what each component reflects (see Lau, Phillips, & Poeppel, 2008 and Kutas & Federmeier, 2011 for a detailed discussion on the N400; see Kuperberg, 2007 for a discussion on the P600).

It should be noted that MEG and EEG signals cannot be compared directly because they do not measure the exact same activity. For the same source, MEG and EEG detect mutually orthogonal (different) field electric/magnetic field patterns. Nevertheless, it is of interest to understand the extent in which spatial and temporal dynamics are similar, using the same tasks with both methods. Currently, studies suggest that the MEG counterparts of the ERPs generally depict similar characteristics. However, as in the EEG literature, the details of how these components are modulated and what they reflect remain debated (Halgren et al., 2002; Service, Helenius, Maury, & Salmelin, 2007).

Importantly, most studies on event-related components employed some form of a violation paradigm: semantic violation or incongruity ("*The mountain was eaten.", "The hikers arrived at* *the top of the flower."*), syntactic violation ("*The girl was believed was happy."*) or both ("*Today she sail to the cupboard."*). These violations are typically compared to grammatically correct sentences ("*The mountain was green.", "The hikers arrived at the top of the hill."*), which are otherwise identical except for the critical word, which would be incorrect in the violation condition. Thus the critical word is in the same position in both sentences and usually controlled for word frequency and word length. These studies have provided much insight into language processing but they tend to draw inferences on the processing of normal sentences based on neural processes capture during a violation. In the present study we sought to determine whether similar conclusions could be drawn by studying sentences that did not contain any form of violation.

Oscillatory activity in language processing

Neural oscillations have been studied in many fields which include sensory and motor tasks (e.g., Hari et al., 1998; Samelin, Hämalainen, Kajola, & Hari, 1995), tasks involving attention (e.g., van Gerven & Jensen, 2009), memory (e.g., Jensen & Tesche, 2002), and to a lesser extent, language (e.g., Saarinen, Laaksonen, Parviainen, & Salmelin, 2006). The classical categorization of oscillations is: delta (0.5-3.5Hz), alpha (8-12Hz), beta (13-30Hz) and Gamma (greater than 30Hz), and prominent questions in oscillatory research are whether different frequencies underlie distinct functional roles, or interact with each other for certain neural functions.

Within the language literature, compared to studies on event-related components, oscillatory studies have used a wider variety of stimuli (not just different types of violation paradigms) and more variation in the types of sentence constructions. Furthermore, oscillatory research in language has looked at individual words, single words within a sentence, and how oscillatory rhythms are modulate over the course of a sentence.

We proceed to review the oscillatory literature specific to language, beginning with the beta band (12-30Hz) which is associated with syntactic unification. Most recently, Bastiaansen, Magyari & Hagoort (2010) had participants read three types of sentences which differed at the critical word. The critical word was either a grammatically correct continuation of the sentence, a category violation (verb instead of noun), or the same word as in the correct condition but all words were scrambled into a meaningless sequence. Beta activity as measured for the entire sentence was found to increase over the course of the sentence only in the correct condition. Focusing on the critical word, beta power (13-18Hz) increased for the correct condition, but was disrupted (and returned to baseline) for the incorrect condition. No significant change in power was found for the sequence condition. Together, this suggested that beta may be sensitive to changes in syntactic structure.

Similar findings were demonstrated in another study. Participants read two types of sentences, those that contained a filler-gap and those that did not (Haarmann, Cameron, & Ruchkin, 2002). A filler-gap is the event in which the object and the main verb of a sentence are separated by several words, and in order to comprehend this sentence the reader needs to keep the object in mind during this ‘gap’ and syntactically integrated it with the verb when it appears. The authors found an increase in beta (15-18Hz) for the sentences with a filler-gap in comparison to those without. In the latter study, working memory was strongly related to the syntactic operations; therefore, it seems that modulation of the beta activity is associated with syntactic unification but not necessarily independent of working memory processes.

The process of lexical-retrieval has been associated with theta activity. In one study, Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort (2005) had participants read short stories. They found that open class (OC) words (those carrying the majority of semantic information: nouns, verbs and adjectives) had a larger power increase in the theta band (4-7Hz) than closed class words (articles, determiners, preposition.This increase was found in left occipital, midfrontal and temporal sensors. As this effect was largest for OC words in the left temporal sensors, and Indefrey and Cutler’s (2003) review suggested the LPTC to be involved in lexical retrieval, Bastiaansen et al. proposed that the theta band is involved in lexical-semantic retrieval. Further evidence for theta’s involvement in lexical retrieval was found by in a lexical decision task performed on words and nonwords (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008).

The alpha band may also be related to lexical-retrieval. In two studies a decrease in alpha power was found when participant performed semantic-lexical operations. Klimesch, Doppelmayr, Pachinger, & Russegger (1997) had participants judge whether pairs of words were semantically related, while Rohm, Klimesch, Haider, & Doppelmayr (2001) had participants determine the superordinate category of a word within a sentence (semantic retrieval). However, there is also evidence for alpha to be associated with attention. Bastiaansen et al.(2010).

Another process, semantic unification, has been mainly associated with the gamma band (around 40Hz). Hald, Bastiaansen, & Hagoort (2006) / Hagoort, Hald, Bastiaansen, & Petersson (2004) had participants read sentences in three versions which differed at the critical word (here shown in italics), such as the following "The Dutch trains are *yellow/white/sour* and very crowded". Dutch trains are in fact yellow, and is therefore correct and meaningful in terms of world knowledge. The word *white* on the other hand, although semantically plausible, violates world knowledge, while *sour* is an outright violation as trains do not have taste, nor are they a type of food. A parametric relationship was found between the three conditions. For the critical word, in comparison to baseline, the correct condition had a small increase in gamma, the world knowledge violation condition had a larger increase in gamma, and the incorrect condition had no increase (Hald et al., 2006). Decrease of the gamma rhythm only in the incorrect condition led to the hypothesis that gamma is part of the normal processing pattern for language (Hald et al., 2006). In support of this, another study using a lexical decision task on words and pseudowords (matched for word length and frequency) found a decrease in gamma following the onset of pseudowords but no attenuation for words (Pulvermuller, 1996).

Importantly, it should be noted that the detection of gamma activity in general, and in language tasks in particular, has been difficult. Rather it is more commonly recorded from areas involved in lower-level processing, and predominantly from the visual cortices during low-level perceptual tasks. The complexity with gamma activity is (partially) inherent to the issue that electromyographic activity associated with movements of the mouth (including swallowing), eyes and neck contains strong signal components in the gamma frequency range. For example, Laaksonen, Kujala, Hultén, Liljestrom, & Salmelin (2012) found gamma in a language task but when localized the sources were situated in the region of the eyes, and as such great caution should be exercised in interpreting gamma activity. On the basis of the current literature we can only conclude that (de)synchronization in the gamma band is potentially associated with semantic unification.

In summary, the main trend across studies suggests that power changes in the theta band and alpha band potentially reflect lexical-semantic retrieval of words to construct a working memory trace of linguistic for unification. Furthermore, activity in the beta band and gamma bands are related to semantic and syntactic unification of words in sentences, respectively. However, caution should be taken with gamma as past literature has not reliably found gamma activity in language tasks.

Theories on the relationship between event-related components and oscillatory activity

Previous studies have focused on either event-related components or rhythmic oscillations. With few studies using both measures, little is known about whether event-related components and rhythmic oscillations highlight the same or different aspects of cognitive processing. A few different hypotheses have been offered on the relationship between these two phenomena. According to one account, evoked responses arise from stimulus-induced changes in the phase of the rhythmic activity (Makeig et al., 2002; Penny, Kiebel, Kilner, & Rugg, 2002). In a visual selective attention task, the N1 component was found to be generated by partial phase resetting of eight oscillating components which include left posterior alpha, mu, and theta rhythms (Makeig et al., 2002). When an incoming stimulus consistently resets the phase of an ongoing rhythm, shifting this phase to a certain value, the post-stimulus phase distribution, observed at a fixed latency after stimulus onset, peaks around a particular value (Penny et al., 2002). Prior to the stimulus, however, the distribution of the observed phase will be uniform.

Another account proposes that event-related components arise from asymmetry in the amplitude of the peaks and troughs in the rhythmic activity, with peaks being modulated more by the stimulus. Neural oscillations in the alpha band have been reported to give rise to slow event-related fields in two simple visual tasks (Mazaheri & Jensen, 2008) and to event-related fields during working memory maintenance (van Dijk, van der Werf, Mazaheri, Medendorp, & Jensen, 2010). A third account proposes that transient brain activity generates evoked responses but that this transient activity does not affect ongoing rhythmic oscillations (Mäkinen, Tiitinen, & May, 2005; Mazaheri & Jensen, 2006; Shah et al., 2004). Although informative, all these studies were limited to visual attention and somatosensory processing, and it is unclear whether this relationship applies to other types of cognitive processing.

Studies comparing event-related components and oscillatory activity

Only a handful of language studies have looked at event-related components and oscillations together. Most recently, Wang et al. (2012) had participants read sentences with the final (critical) word that was congruent or incongruent (*the climbers finally reached the top of the mountain/tulip*). The authors found a larger N400m for congruent compared to incongruent words and this component was localized to the left superior temporal region at the source level, and the authors interpreted the result as indexing lexical-semantic retrieval. They also found a decrease in alpha (8-11 Hz) and beta (16-19 Hz) activity for the incongruent sentences compared to congruent sentences. Furthermore, they discovered a linear trend in the incongruent condition: a smaller N400m amplitude was associated with a greater decrease in the beta band. Interestingly, the beta activity was localized to left inferior frontal gyrus, an area that according to the MUC model is proposed to be involved in semantic unification (Hagoort, 2005). Wang et al. concluded that the alpha activity was related to attention, while the relationship between the N400 and beta could be interpreted as more engagement in unification areas (beta increase) which facilitates lexical retrieval (smaller N400m), a proposal that is in line with the predictions of the MUC model. Crucially, these findings suggest that event-related components and oscillations do not capture identical brain functions in language processing.

In an EEG studyon semantic congruity, Hald et al.(2006) found that gamma power increased for semantically correct sentences and sentences that violated world knowledge violated (but were semantically plausible), but was attenuated for semantically incorrect sentences. In the theta band, only a power increase was present for the semantically incorrect sentences. For event-related activity, the N400 in the correct and world knowledge violation condition were identical in onset and peak latency and similar in topography and amplitude. Furthermore, the oscillatory activity occurred at a similar time to the N400. The authors concluded that lexical-semantic and world knowledge are processed in parallel during sentence comprehension, and that gamma reflected a post-integration process.

Laaksonen, Kujala, Hulten, Liljestrom, & Salmelin (2012) also recently compared the event-related components to oscillations from three separate studies on picture naming. The authors found an overlap between the two electrophysiological measures at the sensor-level (sensorimotor and occipital regions) but when decomposed to the source level, overlap of active areas was fairly low (30%) as was the convergence on functionality. Although this is a language production study, their findings also suggest that event-related components and oscillatory activity are complementary measures of the neural processing underlying high-level cognitive processing. Thus far, most studies on language comprehension have focused either on event-related components or oscillatory activity. The majority of these studies favoured the use of violation paradigms and short sentences, and some isolated words. The few studies that have looked at the spatiotemporal relationship between event-related components and oscillations suggest that they capture complementary aspects of sentence processing in the brain.

Current study

In the present study, we aimed to determine how natural language processing is reflected in the electrophysiological signal. We established that MEG is a good measure for doing this because it captures neural changes in the millisecond range. From this MEG signal we chose to focus on event-related components and rhythmic oscillations, and to determine whether they provide a complementary view on sentence processing in the brain. Previous studies using low-level cognitive tasks suggested that event-related fields (ERFs) and oscillations capture similar functionality of the brain and certain models have been proposed on how they are tightly related. Nevertheless, results from high-level cognitive studies suggest that these two measures may capture functionally different aspects of cognitive processes, in particular in language processing. Therefore, the current study aimed to clarify the relationship between these two measures in a sentence processing task.

Sentence processing involves lexical retrieval of each word, as well as the unification of the words over the course of the sentence. On this basis, we were motivated to capture lexical retrieval at the single word level using ERFs (time-locked to the onset of a single word), as well as oscillatory rhythms to capture the ongoing unification. To do this we used normal sentences that were absent of syntactic or semantic violations but encompassed a range of syntactic structures (i.e. independent and relative clauses) in order to capture language processing as naturally as possible. To tap into the influence of structure, and by extension predictability, in sentence processing, we had a second condition – sequences of words. Each sequence was created by randomizing the words within each sentence. Crucially, one word remained in the same position in sentences and sequences; we refer to this as the fixed word. In order to compare ERFs and oscillations we looked at each measure time-locked to the fixed word, albeit acknowledging that this might limit the extent to which unification is captured by rhythmic activity. In sum, we compared the sentence condition to the sequence condition to determine how the syntactic and semantic structure of the sentence influences the processing of the fixed word using two neural measures.

Predictions Our study is largely exploratory and data driven because only a few studies have focused on sentence-level processing without using violations paradigms. Another reason is the limited number of studies done on the topic of event-related and oscillatory activity. Nevertheless, we propose a few tentative predictions based on the available literature.

Across the various language studies reviewed the N400(m) has been most reliably found in various paradigms, whereas other event-related components were less reliable, especially at the sentence level. Therefore, we hypothesized that sustained activity between 200 – 800ms, peaking around 400ms could be modulated across conditions. Activity in this latency was proposed to indicate lexical-retrieval. Therefore, compared to sequences, we may observe higher amplitude for sentences, which could reflect facilitation of lexical retrieval because of the available sentence context. However, an alternative could be that the absence of a context in sequences could lead to a larger amplitude reflecting the increase in neural processing power needed to retrieve the appropriate word from the lexicon.

For the oscillatory activity, beta activity has been found most reliably during sentence processing. In addition, there has been a trend to observe an increase in beta activity for correct sentences, but lower beta power for sequences, or when the sentence is disrupted by a violation (Bastiaansen et al., 2010; Wang et al., 2012). Therefore, we hypothesize larger beta activity for sentences than sequences.

Theta and alpha activity have been associated with lexical-retrieval (e.g., Bastiaansen et al., 2008; Rohm et al., 2001) but the majority of these studies having been performed at the single word level. Although we our studying sentence level processing, we may observe changes in alpha and theta activity for individual words as a function of context (sentences create a context for the upcoming word but context is absent in sequences). Gamma activity has been observed in sentence-level processing (Bastiaansen et al., 2010), albeit not reliably. Therefore, we may observe an increase in gamma for sentences which reflects unification but a decrease or absence of gamma in sequences where unification is not required.

Methods

Participants

Sixteen native Dutch speakers (4 males, 12 females) with a mean age of 21 years (range: 18 to 25 years) participated in the experiment. These participants belonged to a sample of a larger study in which participants were measured in two separate sessions, one with fMRI and the other with MEG. Furthermore, the task could be presented in the visual or auditory modality, but the same modality was used for both sessions for each participant. This paper is only concerned with the visual modality of the MEG session.

All participants were right-handed, and all had normal or corrected-to-normal vision. In addition they were screened for neurological, developmental and psychiatric disorders, claustrophobia, active implants (e.g., pacemaker) or non-removable metal parts, and head injury or surgery. Participants were compensated for their participation and provided informed consent in accordance with the CMO (the local “Committee on Research Involving Human Subjects” in the Arnhem-Nijmegen region) ethics committee.

Stimuli

The stimuli consisted of 408 sentences and their sequence counterpart, which was created by scrambling the words in the sentence with the criteria that three or more consecutive words must not form a coherent sentence fragment. The stimuli was randomly divided into six sets each containing 120 unique sentences (S) and 120 unique sequences (W). That is, within each set only the sentence or its sequence counterpart would appear once, but not both. These sentences and sequences were then presented in blocks of 5 sentences and 5 sequences. Each set was accompanied by 24, Yes or No comprehension questions about the most recent sentence or sequence (e.g., *Werd er iets eetbaars genoemd?* 'Was something edible mentioned?') These questions were randomly embedded to maintain and check participants' attentiveness during the experiment.

The sentences (and subsequently also the scrambled sequences) ranged between 9 to 15 words. The grammatical structure of the sentences included both relative clauses (RC) and a group of various simpler structures (M) such as *'De wrede president die de onderdaan beveelt is boos'* ('The cruel president who commands his people is angry.')**.** Table 1 provides a sample of the four types of stimuli.

	Sentence	**Sequence**
Relative Clause	Het is een schrijnende situatie waaraan de Nederlandse **politiek** nauwelijks iets doet.	schrijnende de is waaraan nauwelijks het iets een **politiek** situatie doet Nederlandse
Mix	Dit zijn geen regionale **problemen** zoals die op de Antillen.	zoals geen die Antillen **problemen** regionale zijn de dit op

Note. The fixed word is in bold

Each sentence and its sequence counterpart had one word, which was the same word in the same position, referred to as the *fixed word*. This word allowed us to compare the processing of the same word in the context of a sentence versus that of a sequence. For the context to be of a sufficient size and there to be enough data to be acquired before and after the word, the fixed word appeared between the third to the thirteenth word position of the sentence and across sentences the position of the fixed word was evenly distributed.

All fixed words were nouns with length ranging from 5 to 12 letters. The fixed words were matched for word (lemma) frequency between the RC sentences (*Mean*: 37.05) and M sentences (*Mean:* 18.22), $t_{(196)} = 3.14$, $p = .002$, and the maximum frequency was 510.78 (SUBTLEX-NL database of Dutch word frequencies, Keuleers, Brysbaert & New, 2010). In order to normalize the baseline measure for the target word, the word preceding the target was constrained to being in the range of 5 to 12 letters. In addition, the word preceding the target in the sequences must not differ from that in the sentences by more than two letters.

Experimental design and procedure

The six sets of sentence and sequences items were counterbalanced across participants, with each participant encountering only one set. Hence, participants only saw the sentence or sequence version of a sentence-sequence pair.

All stimuli were presented at the centre of the screen within a visual angle of 4 degrees using the Presentation software (Version 16.0, Neurobehavioral Systems, Inc). Each block began with a description of the block type: *zinnen* (Sentence) for sentences, and *worden (*words) for sequences, which lasted for 1500ms. We did this to encourage participants attempt to semantically/syntactically integrate for sentences but discourage this behaviour for sequences. Participants were presented with a total of 48 blocks, alternating between a sentence block and sequence block.

Each sentence or sequence began with a fixation cross of 2000ms with a jitter varying from 3200 to 4200ms, followed by a word-by-word presentation of the sentence or sequence. To simulate the appearance of a real sentence each sentence began with a capital letter and the last word was presented with a full stop. The interval between the offset of the previous word and the onset of the next word was 300ms. The duration of each word was determined with respect to the stimuli's length from the spoken recording made for the auditory version of this task. The average presentation time for a word was 351ms, with a minimum of 300ms and maximum of 1400ms.

Participants were instructed to fixate on the cross and then read the individual words as they appeared on the screen. When the questions appeared they answered by pressing the button for 'Yes' or the button for 'No' with the left hand index and middle finger respectively.

Data Acquisition

Data was recorded in a magnetically shielded room with the MEG system (CTF MEG TM Systems, Inc., Port Coquitlam, Canada) which contains 275 axial gradiometers. Participants sat upright and were instructed to sit as comfortable as possible but to remain still throughout the experiment. We used the electrooculogram (EOG) to subsequently discard trials contaminated by horizontal and vertical eye movements. The position of the head with respect to the MEG sensors was determined by measuring the current passing through three coils attached to on the outer rim of the left and right ear canal, and the nasion. All signals were sampled at 1200Hz and stored for offline analysis. We chose a high sample rate in order to be able to study the higher frequencies.

Data Analysis

We analyzed all MEG data using the Fieldtrip open source Matlab toolbox (Oostenveld, Fries, Maris, & Schoffelen, 2011), developed for the analysis of electrophysiological data. Statistics were partly performed using PASW Statistics, version 18 (SPSS Inc.,Chicago, IL, USA).

Artefacts were defined as blinks, saccades, muscle artifacts and sensor jumps and the threshold for each type of artefact was determined individually for each participant. We defined the trials of interest as 500ms prior to onset of the fixed word until 1000ms following onset. This long baseline was chosen in order to have the same window length for ERFs and oscillations, and was based on oscillations requiring a longer baseline. Subsequently, trials which contained artefacts within this duration were discarded from further analyses. Across participants we retained an average of 97 sentences (*SD* 7.11) and 89 sequences (*SD* 13.1).

For the ERF analysis, we applied a high-pass-filter of 0.5Hz and a low-pass-filter of 40Hz. For the time-frequency representation (TFR) analysis of the oscillations, a 50Hz band-stop filter was applied to remove the power line noise. Furthermore, the data was detrended to remove the slow drift in the signal, as well as to prevent edge artifacts arising from the subsequent application of filters. To speed up computations, the epoched and filtered data were downsampled to 300Hz.

The data was collected with axial gradiometers but axial gradient data are difficult to interpret in topography. Planar gradient topographies, on the other hand, can be interpreted such that signal strength of the source is strongest when located directly below the gradiometer (Hämäläinen et al., 1993). Therefore, to achieve a more easily interpretable topography of the ERFs and TFRs, we computed synthetic planar gradients by determining the average of the absolute values of the first spatial derivatives in two orthogonal directions of the axial-gradiometer data mathematically transforming the axial gradiometer data.

The analyses for the current study focused on the sensor level. However, it is difficult to determine the source of the signal at the sensor level, because activity from any source is usually picked up by most sensors (independent of the gradiometer configuration). As individuals vary in head shape, and therefore head (source) position with respect to the MEG sensors, sensor analyses at the group-level (as oppose to single-subject analysis) are further complicated. Even if a particular sensor captured a dominant effect in the MEG signal, it may not have stemmed from the same source (brain area) across participants because of individual variation. To overcome this matter we pre-defined 8 groups of sensors (spanning several centimetres): 4 groups on each hemisphere: anterior, lateral, medial and posterior, with an average of 32 sensors for each group (see figure 1). In this way, any effect found spanned a sufficient distance that mitigated the issue of finding significant activity at the sensor level to be confounded by varying head position.

Importantly, no assumptions can be made about the source of the signal because for any activity captured at the sensor-level there are an infinitive number of potential source(s) that could be defined**.** In general, to determine the reliability of sensor-level results, source-level analyses should be performed to determine whether the signal derives from one or more sources. This approach however adds another level of complexity to the analysis, and we refrained from this step in the initial analysis (the current paper) but plan to do so subsequently.

To calculate the activity in each sensor groups, the activity (separately for ERFs and TFRs) was first calculated at each sensor. Following this, the activity at each sensor was averaged with all other sensors in its group, which reduced the spatial dimension from 275 sensors to 8 sensor groups, producing for each sensor group 2D data for the time-frequency analysis, and 1D data for the event-related analysis. Subsequently, statistical analyses were performed on the difference in activity between sentences and sequences.

Event-related Fields

The event-related activity for the sentence and sequence conditions was obtained by averaging the trials for each condition, using a 500ms baseline. This was done for each sensor, and then an average ERF was computed for each sensor group. For the visual depiction of each condition, we choose a base from -250ms to -150ms for the topographies. We did this because we wanted to use the same baseline for visual depictions for event-related data and oscillatory data. The reason for this interval was based on the oscillatory data which we explain in the section on *Time-Frequency Representations.*

We performed 8 dependent t-tests to compare the two conditions (sentences vs. sequences) for each sensor group (left anterior, left lateral, left medial, left posterior, right anterior, right lateral, right medial, and right posterior). A Bonferroni correction was performed to account for multiple comparisons. The dependent variable was the mean amplitude calculated for the interval of interest: 250 to 500ms. This interval was motivated by previous literature in which the interval of interest ranged from 200 to 1000ms, and because it corresponded well with the visual inspection of the data.

Time-Frequency Representations

To investigate the time-frequency representation of power changes associated with the target word, we obtained an estimate of oscillatory power. In addition, we chose to depict the power changes over time for each of the four classical frequency bands (theta, alpha, beta and gamma) because they provide a general picture of the neural activity progression, as well as the opportunity to relate our findings to previous literature. For the visual depiction of this data we chose the a baseline interval from -250ms to -150ms. We did not extend this prior to -250ms because this might include neural activity from the word prior to the fixed word. Neither did we extend the interval beyond -150ms because this would include activity from the fixed word itself. For the statistical analyses, the frequency bands and clusters of interest remained data-driven but no baseline correction was applied.

The following steps were performed for calculating the estimate of oscillatory power. We applied a Hanning taper for the lower frequencies (2.5 to 30Hz), and multitapers for the higher frequencies (28 to 100Hz) in order to reduce spectral leakage and smooth the spectral representation of the data. The number of tapers applied determines the extent of smoothing. To account for the fact that higher frequency oscillations have a broader bandwidth, and thus the spectral representation of the signal of interest is more spread out, several orthogonal taper were applied to improve the signal to noise ratio and better capture the signal of interest.

For the lower frequencies we used a frequency-dependent sliding time window with a time window of 400ms, and a frequency window of 2.5Hz. The window was applied in steps of 50ms for frequencies ranging from 2.5 to 30Hz, in steps of 2.5Hz. In this way, individual time points in the TFR were in fact estimates obtained from data that extended 200ms before and 200ms after the time point itself. For the higher frequencies, we used a frequency-dependent sliding time window with a time window of 400ms, and a frequency window of 4Hz. The window was applied in steps of 50ms for frequencies ranging from 28 to 100Hz in steps of 4Hz.

With the resulting TFRs, for each sensor group, an average for each time-frequency point was calculated across all sensors within the group. Subsequently, at the group level, averaging across participants, we evaluated the difference between sentences and sequences for each sensor group by performing a cluster-based random permutation test (Maris & Oostenveld, 2007). This approach tests the null hypothesis of no difference between conditions, while controlling for the Type-I error rate in the presence of performing multiple-comparisons, which is inherent to the structure of the data given many frequency-time points. For each sensor group the following steps were taken. First, at the sample level, a dependent samples t-test was performed at each sample (frequency-time point) to quantify the difference effect between sentences and sequences. Samples that exceed the significance level of 5%, and were adjacent to each other in time and frequency were clustered together. For each cluster, the cluster-level t-statistic was calculated by summing the t-statistic from each sample. Next, a null distribution with the assumption that there is no difference between conditions was created for the permutation. Each point in the distribution was created by combining data from both conditions, randomly reassigning them to each condition, and then calculating a cluster-level statistic. This was performed 2000 times. Finally, the actual observed cluster-level t-statistics were located in the created null distribution. Clusters located on the highest or lowest 2.5th percentile of the distribution were considered as significant for this test.

Results

No participant answered less than 92% of the questions correctly which indicated that they paid attention during the experiment. Therefore, all participants were included in the analyses. The results are presented separately for the event-related signal and the oscillatory activity, each beginning with a descriptive account of the progression of neural activity for the fixed word, in each condition.

ERFs

Sequence of cortical activation in reading Figure 3 illustrates the ERFs with topographical plots in 250ms intervals. At the onset of the fixed word, activity was concentrated bilaterally, in the posterior (occipital) sensors. This then spread across to lateral, anterior and medial sensors between 250 – 500ms, with stronger activity in the left hemisphere. Between 500 and 750ms the activity decreased, but then increased again in the left posterior and central areas, beginning around 750ms.

The grand-averaged ERF waveforms for each sensor group are depicted in figure 4. These signals further complement the pattern in the topographies. In both sentences and sequences, an early transient deflection (around 120 to 200ms) is seen bilaterally in the posterior (occipital) sensor groups. Subsequently, sustained activity from around 200 to 500ms, peaking around 400ms, was present in both hemispheres for the lateral, central and anterior sensor groups. Importantly, the amplitude for this sustained activity across the left hemisphere appeared larger for sentences compared to sequences. In the right hemisphere, the sustained activity appeared to be of lower amplitude. Overall, this suggested a left lateralization of the difference between sentences and sequences in the sustained activity between 200-500 ms.

With exception of the posterior sensor groups, from 500ms onwards we observed the signal to decrease in amplitude and return to baseline. Around 800ms was a small deflection peaking around 800ms.

Analysis Previous literature have found effects for the N400(m) between 200 and 1000ms e.g., (Bastiaansen et al., 2010; Liljeström, Hulten, Parkkonen, & Salmelin, 2009; Vartiainen et al., 2009; Wang, Bastiaansen, Yang, & Hagoort, 2011). To determine whether our sustained activity might be similar to the N400m, we performed dependent t-tests on the mean ERF signal from 250 to 500ms, between sentence and sequences, for the 8 sensor groups. Prior to doing a Bonferroni correction for multiple comparisons the difference in amplitude between sentences and sequences was significant in the left anterior ($p < 0.02$), left medial ($p < 0.01$), left posterior ($p < 0.04$) and right posterior sensor groups ($p < 0.03$). However, only the left medial sensor group survived the corrected threshold.

TFRs

Sequence of Cortical Activation in reading Figure 5 depicts the four frequency bands (theta, alpha, beta and gamma) that were analysed in the present study (note that the scales are tailored to each frequency band). We begin with the theta band (4-7Hz) where an apparent similarity in power change is observed in sentences and sequences. We observed strong activity bilaterally in the posterior sensors at the onset of the fixed word. From 250ms onwards, the power remained positive but weaker and more focused on the left occipital and lower lateral sensors. A decrease in the posterior sensors occurred between 500 and 750ms, which was was followed by an increase in the posterior sensors.

In the alpha band (8-12Hz), for the sentences, a prominent power increase was observed at the onset of the fixed word in bilateral posterior sensors, as well as right lateral and anterior sensors. Most activity in these aforementioned areas then decreased between 250-500ms. 500ms onwards was a gradual increase in power, which began at the frontal sensors and spread to the posterior sensors. For the sequences, the onset of the fixed word was also met with a power increase in the posterior sensors. Between 250 and 750ms was mainly a power decrease. From 750ms onwards was a power increase in the left lateral, left frontal and right posterior sensors.

In the beta band (13-30Hz) there was a clear alternation between power increase and power decrease, in both sentences and sequences. At baseline, there was already an increase in power, which continues through word onset. From 250 to 500ms was a large power decrease in bilateral posterior sensors and lateral/central sensors. This decrease remained between 500 and 750ms but was much weaker and concentrated in the posterior sensors. In the last time interval was a power increase, mainly in the posterior sensors.

For the gamma band (30-100Hz), the sentence condition wass dominated by a power decrease at all time intervals, scattered across different sensors. Power increases were seen in at word onset in a few sensor located in the bilateral posterior and right lateral areas. Between 250 to 500ms this activity increased in strength and spread further, subsequently this activity decreased. In the sequence condition, for the entire duration, we observed a power increase in the bilateral posterior sensors and left lateral, and in parallel, a power decrease in the bilateral central areas and right lateral areas. Furthermore, the relative power changes here were much smaller (about 3%) than the lower frequencies.

Overall, theta, alpha and beta frequency bands showed a similar pattern in sentences and sequence: an alternation between power increase and decrease, in well defined areas. However, the theta band had a longer duration for the initial power increase than the other two frequency bands. Interestingly, the beta band was the only frequency band with a relative power increase prior to word onset (the increase in the alpha band was very weak).The power changes in the higher frequencies are smaller and the pattern differs between sentences and sequences. Sensor-level depictions of activity are blurred and multiple sensors can pick up activity from the same source, therefore no conclusions can be made on whether the activity in two distinct sensor areas arises from two distinct sources.

Analysis The cluster-permutation test was performed for the entire window of 1000ms beginning at the onset of the fixed word. We chose a longer duration for the TFRs because trends in oscillatory activity tend to be depicted over longer durations than in ERFs. The statistical test revealed a significant difference in power between sentences and sequences in four of the sensor groups in the lower frequencies. For these four sensor groups, figure 6 depicts the power change from baseline for each condition, the difference in power change between conditions, and the corresponding topography for the duration in which the difference effect was significant. A positive cluster was found in each anterior sensor group (left anterior, $p = .0244$, right anterior, $p = 0.004$). Another positive cluster was present in the left lateral sensor group ($p = .0100$). The fourth cluster was found in the left medial sensor group ($p = 0.016$). All these positive clusters indicate a greater power increase for sentences than sequences. The frequency range contributing to these significant clusters was relatively broad band, ranging from 8 to 20Hz. This entailed the classical frequency bands alpha (8 – 12Hz) and beta (13 – 30Hz). In relation to previous language studies, findings have also been observed between13 to 18Hz (Bastiaansen et al., 2010; Wang et al., 2011). No significant clusters were found in the higher frequencies.

Discussion

Event-related activity and oscillatory activity are two neural measures commonly used to study the neural correlates of cognitive processes. In this study, using MEG we investigated the extent to which these measures differed in capturing cognitive aspects in sentence processing. For each measure, we analyzed the spatiotemporal patterns at the sensor level focussing on the fixed word in sentences and matched word sequences. We will discuss the findings for the ERFs and TFRs separately and then attempt to explain the relationship between these two measures.

ERFs

The fixed word elicited two main components: a transient deflection around 150ms in bilateral posterior sensor groups and a sustained response between 250 and 500ms peaking around 400ms in the left and right anterior, central and lateral sensor groups. However, only the left sensor group achieved a significant difference between sentences and sequences. Although not significant, there appeared to be a third component from 750ms onwards that peaked around 800ms. As this activity was limited to the posterior sensor group, and temporally occurs far from fixed word onset, this deflection might reflect the first stages of visual processing of the word following the fixed word which could be

The early component around 150ms in the posterior sensors suggested that the strongest activity was in the visual cortex, which may reflect early visual processing of words. Tarkiainen et al. (1999) compared the processing of four types of stimuli: gaussian noise, single-elements (single letters or geometrical symbols), two-elements (two letter syllables or two symbols) and four-elements (four-letter words or four symbols) and found a left occipito-temporal deflection around 150ms that was only sensitive to words, and proposed this to reflect letter-string analysis. Within this framework, a tentative explanation for the larger amplitude in this early component for sentences compared to the sequences would be that the sentence context provided easier recognition of the visual form of the fixed words. Sentences have by definition a certain clause probability guiding the prediction of the upcoming word, which may include the recognition of the letters in the upcoming word.

The sustained component peaking around 400ms was also in accordance with previous studies. Using word lists of four words Vartiainen et al. (2009) found larger activity in the left temporal sensors for word lists which ended with a semantically incongruous than semantically congruous word. At the source level, the left superior temporal cortex was the location in which semantic priming effects occurred across the first three words, and had a stronger activation for the semantically unrelated compared to the semantically related word. This activity occurred from about 350 to 800ms and peaked around 400ms. From 450ms onwards, this activity spread bilaterally and to neighbouring areas of the superior temporal cortex.

At the sentence level, the majority of studies compared sentences with semantically congruous and incongruous word endings or syntactically correct or violated sentences (Bastiaansen et al., 2010; Halgren et al., 2002; Helenius, Salmelin, Service, & Connolly, 1998; Service et al., 2007; Wang et al., 2011). With the onset of the final word time-locked to 0ms, these studies investigated the sustained activity peaking around 400ms and referred to it as the N400m. These studies found a difference effect – larger amplitude for incongruous than congruous endings – which was bilateral but left dominant in the temporal cortex. One particular study by Snijders et al. (unpublished) compared the processing of sentences to sequences. In their design both sentences and sequences also contained a fixed word (which they called the critical word), which was unambiguous or word-class ambiguous (could be determined as a noun or verb and only disambiguated by the following word). Collapsing across ambiguity, the authors found greater activity for sentences than sequences in the left and right temporal sensors, with an extension to frontal sensors, between 280 and 775ms, with 0ms as critical word onset.

The general trend with all previous ERF studies is finding sustained activity peaking around 400ms that reflects some form of lexical-semantic processing. Despite the difference in experimental paradigm (word versus sentence, comparing grammatical sentences to violated sentences or sequences), the spatiotemporal characteristics of this activity are fairly similar across previous studies and ours. Sentences with a semantic incongruity or syntactic violation resulted in a larger amplitude than correct sentences. In our study (and that of Snijders et al., unpublished), sentences resulted in a larger amplitude than sequences. All previous studies found effects largely concentrated in the left (and only in Snijders et al.'s study, also in the right) temporal area which overlaps with the left medial sensor group in our study.

The difference in amplitude captured across all previous studies and ours may reflect a similar process. With incongruent and congruent sentences, a strong expectation on what the next (last) word should be built up from the context formed by previous words, whereas in sequences there is no expectation for the next word. This suggests that unification, in terms of integrating the next (expected) word, is influenced by top-down processes (prediction) which is guided by context. For integration to take place, lexical-semantic processes such as lexical-retrieval need to take place, this would then imply that lexical-semantic processes are influenced by unification.

One aspect that differs in the sustained activity between our study and previous studies is duration. The onset of our effect (at250ms), does not differ greatly from previous studies which found the onset of the effect between 200 and 300ms. However, the offset of our effect (at 500ms) was earlier than most studies which had offsets varying from 600 to 700ms (Bastiaansen et al., 2010; Halgren et al., 2002; Helenius et al., 1998; Service et al., 2007; Wang et al., 2011) with the exception of one which also an offset of 500ms (Halgren et al., 2002). The reason for an earlier offset in our results could be due to the timing in which the words were presented. From the previous ERF studies using visual presentation, Bastiaansen et al. (2010), Halgren et al. (2002). Helenius, Salmelin, Service, & Connolly (1998), and Snijders et al. (unpublished) all chosed a fixed duration to present words (300, 200, 330, and 300ms, respectively), independent of word length. Within each study the interword interval was constant but varied across studies (300, 133, 750, and 300ms, respectively). In comparison, the duration of each word in our study was determined with respect to the stimuli's length from the spoken recording made for the auditory version of this task, and we had an interword interval of 300ms. Perhaps by presenting word with a duration sensitive to word length this provided a more natural pace of sentence processing which resulted in less lexical-semantic processing time. However, this is only a speculation and further work is necessary to test the influence of presentation time on the durations of ERFs.

We also interested as to why we did not observe a visual difference in the timing of the effect between sentences and sequences. This might be because the sustained activity is not sensitive to timing issues. Alternatively, unification (and how it is affected by top-down processes, specifically prediction) may not influence the timing of lexical-semantic processes, but only the ease at which it takes place (which we hypothesize to be reflected in the amplitude of the ERF). These are questions that we would be interested in pursuing in subsequent studies on sentence processing.

Although not identical, the sustained activity in the left hemisphere found in our results and previous studies are sufficiently similar that we interpret it to reflect lexical-semantic processing, which is in line with the MUC framework (Hagoort 2003, 2005). There are in fact many processes involved in lexical-semantic processing and it remains highly debated which particular aspect(s) are reflected by the sustained activity peaking at 400ms. As our study was not designed to test this question, we will briefly mention the dominant theories on what the sustained activity could reflect. One camp suggests that the N400m predominantly reflects lexical-semantic access but maybe indirectly influenced by integration e.g., (Lau, Phillips, & Poeppel (2008) while other suggests that it reflects the contribution of both processes (e.g., Hauk, Davis, Ford, Pulvermuller & Marslen-Wilson (2006), Pylkkanen, Stringfellow, & Marantz, 2003, Pylkkanen & Marantz, 2002).

In our study, the significant difference in the sustained activity was in the left medial group, which is in the same general region as the left temporal sensors in previous ERF studies (Halgren et al., 2002; Helenius et al., 1998; Service et al., 2007; Wang et al., 2011). Interestingly, these studies observed a bilateral but left dominant pattern. Although visual inspection of our data suggests a greater difference between the two conditions in the left than right sensor groups, no sensor group was significant in the right hemisphere. Unlike the previous studies, because we did not manipulate congruity orambiguity, the absence of the neural activity from these manipulated factors may be why we do not observe activity in the right hemisphere. However, this is unlikely because Snijders et al. (unpublished) did find a significant difference between sentences and sequences (when collapsed for ambiguity). Rather it may be because of difference in statistical analyses. Snijders et al. (unpublished) performed cluster-based permutations on the entire sensor array and found a different in left and right temporal sensors, whereas we used pre-defined sensor groups. Ultimately, it would be beneficial to perform source-level analyses on our data because it provides more reliable results on neural activity.

TFRs

Descriptively, in the lower frequencies (4 – 30Hz) we observed a general alternating pattern of power increase and power decrease from the onset of the fixed word until 1000ms. Analyses revealed a significant difference between sentences and sequences in the frequency range of 8 to 20Hz. This fits in to the common frequency bands alpha (8-12Hz) and beta (13 – 20Hz)..

Beta oscillations Many studies have linked beta activity to motor functions. A primary observation has been that this rhythm is attenuated during engagement in voluntary movements. After the movement is completed an increase in beta (rebound effect) is observed (e.g., Baker 2007; Kilner et al., 1999). In a study by Wang et al., (2012) a strong attenuation of the beta band was found for a sentences ending with an incongruous word but for a congruous one. This effect was localized to left inferior frontal gyrus (LIFG). The authors proposed the incongruent word posed semantic difficulties requiring stronger engagement of the LIFG for integration, and that this was reflected as beta band suppression. In both motor and language studies, there appears to be the general theme that engagement in a particular process is associated with beta decrease. In our study, across the four sensor groups with a significant effect, we observed a beta decrease from 250 to 500ms, and beta increases on either end of this interval (figure 6). Following the idea of beta activity and engagement, the beta decrease in our study may reflect engagement in unification (integrating the fixed word). The power increase from 0 to 250ms could then be interpreted as the beta rebound elicited by the previous word in the sentence/sequence, while the increase from 500ms onwards was the rebound for the fixed word. As the alternating pattern was observed in sentences and sequences, this would suggest that despite the sequences were not semantically or syntactically related, it appeared that the reader nevertheless try to unify. This would imply that unification is a strongly automatic process that is not easily inhibited.

Importantly, the significant difference between conditions occurred in areas in which both the sentences and sequences had a power increase (see individual condition TFRs in figure 6) with a significantly larger increase for sentences. Perhaps, stronger engagement of a neural area was subsequently followed by a stronger rebound. However, this would not explain why greater engagement was limited to the left lateral and central sensor groups but not the anterior groups. Moreover, we did not test whether the beta decrease in either condition was significantly different from baseline, nor did we detect a difference in power decrease between the two conditions (considering that the statistical test was applied from 0 to 1000ms in all frequencies). Therefore, this idea of beta suppression is tentative and we proceed to consider another explanation.

An alternative perspective on beta-band activity is inspired by the finding that the movement related rhythm promotes the current motor set (movement or behaviour taking place) while mitigating neural activity of new (upcoming) movement (Gilbertson et al., 2005; Pogosyan, Gaynor, Eusebio, & Brown, 2009). Engel & Fries (2010) hypothesized that a similar function may be present for, non-motor functions, involved in top-down processing and the contents of the top-down signal. Specifically, an elevation in beta activity is involved in maintaining the current cognitive or perceptual set, otherwise referred to as 'the status quo'. They further hypothesized a decrease in beta activity when the current set is disrupted by unexpected or novel event. Engel & Fries (2010) reviewed a substantial amount of evidence supporting this prediction. In particular, a set of studies show an elevation in beta band activity during delay periods where the current cognitive set must be maintained in working memory tasks (e.g., Deiber et al. 2007; Tallon-Baudry, Bertrand, Peronnet, Pernier, 1998)

According to the MUC model, the unification component in sentence processing involves the integration of the current context (semantics and syntactic structure) from previous words with the upcoming word (Hagoort, 2003, 2005). Importantly, for integration to take place the context from the previous words needs to be maintained, and related to Engel & Fries' (2010) hypothesis, this could be considered as the cognitive set to be maintained. We acknowledge that language processing is a higher, more complicated level of cognitive processing than used in a simple memory or motor task; therefore the maintenance theory may not apply directly. On the other hand, the idea of a general maintenance mechanism used to maintain the current cognitive state is a parsimonious explanation. In this way, the increase in beta activity for words in sentences may reflect the need for them to be maintained in working memory, a process not required for sequences. However, whether maintenance of the status quo also involves the unification process cannot currently be disentangled. As we observe the beta effect in the left anterior, lateral, central sensor groups, this is in accordance with area in which unification takes places – the LIFG – according to the MUC framework.

Further support for this maintenance hypothesis can be found a study by Bastiaansen et al. (2010). The authors found a linear increase in the beta band across the duration of a sentence being processed. Importantly, sentences at which a category violation occurred led to a drop in beta activity (and return to baseline), and no increase was found for sequences. This effect was mainly present over mid-frontal sensors, and left and right parietal sensors. Analyses time-locked to the CW showed a larger beta-band activity in mid-frontal sensors from 0 to 1500ms for sentences compared to sequences. The authors concluded beta oscillations to be a potential candidate for syntactic unification. However, in sentence unification, syntax and semantics both need to be integrated between words, therefore, exclusion of beta-band activity reflecting semantic unification is not possible.

To further test the maintenance hypothesis with our data , we should determine whether the greater beta increase found at the fixed word in sentences compared to sequences was because of a trend at the sentence level. Specifically, whether there was a consistent increase in beta power across the sentence that was absent from sequences. There could be alternative options. In one case, there could be a power decrease for sequences but an increase for sentences. In another case, there could be a linear increase in both conditions but the increase occurs at a slower rate for sequences.

Comparing sentences to sequences, studies have found greater activity for sentences compared to sequences in mid-frontal and right frontal sensors (MEG, Bastiaansen et al., 2010; Snijders et al., unpublished). Based on these previous studies, it is not surprising that we find greater beta activity from 0 to 1000ms in the right anterior sensor groups (figure 6). Rather the question arises as to why greater beta activity is also found in the left anterior, lateral and medial sensor groups but for a shorter duration (figure 6). One reason could be because the left hemisphere is involved in in unification and lexical-semantic processes. The combination of neural activity of these two processes could have produced a different TFR and topography at the sensor level than activity in the right hemisphere which may only reflect maintenance for unification.

In sum, we have observed a similarity between the processing of sentences and sequences in that both show an alternating change in beta power. We also found significantly greater power increase for sentences than sequences. We suggest that the beta band reflects maintenance of words for unification, a hypothesis in line with the MUC framework (Hagoort, 2003, 2005). However, we are limited at this initial stage of the analyses and will later address next steps to clarify the activity reflected by the beta-band in sentence processing.

Alpha oscillations The significant clusters in the TFR also occurred in the 8-12Hz frequency range. This frequency range has been associated with semantic processing. (Bastiaansen et al., 2008; Bastiaansen, et al., 2005; Klimesch, et al., 1997; Rohm et al., 2001). For instance, in comparison to a simple reading task, having to determine a superordinate concept between two words (a process that involved retrieving and comparing lexical-semantic information) was associated with a decrease in alpha band activity (Rohm et al., 2001). Potentially, larger alpha activity for sentences in our study could be because integrating words in a sentence required determining the semantic relationship between words.

There is however an alternative proposal that alpha activity is related to attention (Bastiaansen et al., 2010; Foxe, Simpson, & Ahlfors, 1998; Klimesch, 1999; Klimesch et al., 1997; Wang et al., 2012). For example, attention towards upcoming visual stimuli was accompanied with alpha band attenuation (Foxe et al., 1998). Specific to sentence-processing studies, Bastiaansen et al. (2010) found a decrease in alpha power in sentences when a syntactically violating word was present. Also, Wang et al. (2012) observed a decrease in alpha but when the sentence ended with a semantically incongruous word. As alpha attenuation has been found in syntactic and semantic processing as well as lower-level studies, this suggests that alpha attenuation could reflect a general attention mechanism in cognitive processing.

Looking at the topographies in figure 5, the attenuation of the alpha band occurs in a similar time interval to that of the beta band which we hypothesized to involve maintenance during unification. Also, the alpha band effect was found in left frontal and temporal (and parietal) sensor groups, areas in which the MUC model proposes to reflect unification and lexical-retrieval. From these last two points and the other studies relating alpha and attention, we hypothesize that greater alpha attenuation reflected more attention needed for successful lexical-retrieval and unification in sentences than in sequences (which require little or no unification).

We now briefly discuss the absence of significant effects in other frequencies. For the theta band, some literature (see introduction) suggests it reflects lexico-semantic analysis (Bastiaansen et al., 2010; Bastiaansen et al., 2005; Hald et al., 2006). However, less dominant theories suggest it reflects working memory load (Bastiaansen, van Berkum, & Hagoort, 2002), or error monitoring of violations (Hald et al., 2010) have also been proposed. As we did not provide sentences with grammatical violations we cannot comment on the last theory. In terms of lexical retrieval, because the fixed word is the same word in both sentences and sequences, this may be why lexical retrieval did not differ between conditions. As a next step, we could determine whether theta is significantly difference from baseline at the fixed word, within conditions, as well as how it is modulate over the entire sentence/sequence. In terms of working memory, Bastiaansen, Bocker, & Brunia (2002) related theta to the build up of a memory trace in sentence processing, and similarly Bastiaansen et al (2010) found an increase in theta across sentences but not sequences. As our study was not designed to tap in to working memory per se it is difficult to comment on whether more or less working memory demand was present in sentences compared to sequences.

As mentioned in the introduction, gamma activity has been found in language studies with semantic and syntactic violations (Bastiaansen et al., 2010; Hagoort et al., 2004; Hald et al., 2006). Furthermore, theses studies observed the gamma rhythm in the right frontal areas. Bastiaansen et al. (2010) proposed that normal sentence processing (i.e. correct sentences) is accompanied by gamma activity. On this basis, we should have observed a clear presence of gamma for sentences but not for sequences where semantic unification is not necessary, but we did not. Although we did not detect gamma activity in our study, this does not imply that it is not present. Rather, we may need to use alternative methods such as source localization. We could also apply a type of blind source separation (e.g., independent components analysis) to try to differentiate the gamma activity derived from cortical activity from that generated by muscle and eye movements.

Functional comparison between event-related fields and oscillations

Although both arise from synchronous firing of neurons, ERFs capture activity time-locked to the stimulus, while oscillatory activity is less time-locked and may therefore may better reflect patterns of neural activity that occur over a longer interval.

Individually, the ERFs and TFRs both found significantly more activity for sentences than sequences. This effect was located in four sensor groups for the oscillations but only one for the ERFs. Spatially, both measures found significance in the left central sensor group. However, temporally, the effects are sequential: it is earlier for the ERFs (250 to 500ms) and later for the TFRs (500 and 1000ms). Now, we proceed to discuss how the two measures of brain activity may relate to each other.

Earlier in the discussion we proposed that the event-related activity could reflect lexical-semantic processing. For the rhythmic activity we suggested the effect in the beta band to reflect semantic integration of words or the maintenance of words for integration itself, while alpha activity may reflect lexical-semantic retrieval or attentional processes. Thus, when the rhythmic and event-related activity are interpreted separately our results imply that they do not by and large reflect the same processing functions in sentence processing. This is in line with Wang et al. (2012), who suggested separate cognitive processes for each measure. Specifically, the N400m reflected lexical retrieval, the beta activity reflects semantic unification, and the alpha activity reflected a general attention mechanism. Similarly, in picture naming studies, Laaksonen et al. (2012) found that event-related activity yielded spatiotemporal patterns that were different from those elicited by oscillatory activity.

In the current study we proposed that the event-related fields and oscillations capture different cognitive processes in sentence processing. However, to further clarify this relationship we propose several steps for subsequent analyses and potential improvements for the study. First, in sentence processing, semantic and syntactic unification (processing) are tightly intertwined. Wang et al. (2012) suggested that beta reflects semantic unification but Bastiaansen et al. (2010) has suggested it reflects syntactic unification. As we did not include a semantic or syntactic violation condition we can only conclude that our results support a link between the beta rhythm and unification in general. Second, we need to perform source-level analyses to determine whether these two neural measures derived from the same source or different sources. Third, differences between our study and previous language studies could be due to the part of the stimuli being quantified. Specifically, a complete and proper comparison of our study with previous ones would be to also analyse the power changes across the entire duration of the sentences and sequences. A fourth issue concerns the baseline correction performed for the ERFs. The traditional event-related analysis assumes that the baseline is not affected by the experimental manipulation, and therefore should be similar across conditions. Sentence processing is an on-going process, as our baseline is located in the interval between the fixed word and the preceding word, it is likely that the baseline captures on-line sentence processing for sentences, but does not do so for sequences. Therefore, we should investigate whether the current baseline differs between the two conditions. In addition, we should conduct the same analysis using a pre-sentence/sequence baseline.

As a side note, the increase in amplitude for event-related components and oscillatory power may indeed be due to greater engagement of the neural area due to more frequent firing of neurons. However, it may also be due to a more neurons firing within the general region. Somewhat more specific to event-related components is a third option. The amplitude may be stronger because the variance of the onset of neuronal firing is less jittered. None of these options can be distinguished with MEG; therefore it is important to keep in mind that a wide variety of methods and measurements are needed to test to validity and reliability of any theoretical claim.

Finally, as we did not perform any analysis on phase (coherence), nor did we compared the amplitude between the trough and peaks of the oscillations, it is difficult determine support or challenge the theoretical models on the relationship between event-related components and oscillatory activity, which were mentioned in the introduction. However, this would also provide another topic of interest to pursue with our data.

Conclusion

We compared two neural measures– event-related fields and oscillations – in sentence processing. We propose that the sustained activity peaking around 400ms in the temporal/parietal sensors reflects lexical-retrieval, while the oscillations from 13 – 20Hz reflect maintenance of words for unification, and oscillations from 8 to 12Hz to reflect attentional demands. This proposal is in line with the MUC framework on sentence processing and also with previous literature suggesting that event-related components and rhythmic activity capture different cognitive functions in the brain.

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