Exploring Oscillatory Signatures of Prediction and Prediction Error in Language Processing

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Abstract

Language comprehension is a quick and dynamic process. The predictive coding theory suggests that we regularly make use of contextual clues in order to predict the upcoming content. In this study, we have used magnetoencephalography (MEG) to investigate oscillatory changes connected to predictions and prediction errors in discourse comprehension. While participants read short, semantically manipulated stories, we measured beta and gamma oscillatory powers as respective indicators of adaptation and prediction strengthening throughout the stories, and the one-off surprise, error-triggering effect, at the very end of the story. As hypothesized, we found evidence of adaptation and prediction strengthening, reflected in the significant beta band power increase as the reader becomes familiar with the content of the story. Furthermore, contrary to our expectations, we found a significant increase in both low and high gamma power in the same direction as beta band finding. This finding, while failed to confirm gamma frequencies as indicators of surprise in language comprehension, were in line with previous sentence comprehension studies that suggested gamma band to be indicative of the match between our expectations and input. Finally, we failed to find any difference in gamma power at the occurrence of the one-off surprise factor incongruent with the rest of the story. Our findings confirm partial, yet consistent discrepancy between the predictive coding hypothesis on prediction and prediction errors oscillatory signatures, and evidence from the language comprehension research.

Keywords: *language comprehension, neural oscillations, MEG, beta, gamma, predictive coding*

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1. Introduction

Language comprehension is an extremely fast and dynamic process. It entails a quick and efficient retrieval of the lexical building blocks, and their effectively immediate integration into a meaningful whole. These building blocks contain information on various levels and timescales of linguistic representation, ranging from orthographic and phonological to syntactic and semantic word properties. Yet, despite the clearly complex dynamics of the system, we manage to regularly construct meaningful interpretations of the linguistic input (Hagoort, 2005; Jackendoff, 2007).

Keeping in mind the intricacy and speed of our comprehension system, various studies have set out to investigate the tools and methods our neural system employs in order to navigate through such a sophisticated combinatorial process. One plausible explanation is that the language system constantly makes use of contextual clues in order to generate predictions about the upcoming linguistic input, and thus, facilitate the linguistic interpretation process (van den Brink, Brown, & Hagoort., 2001; Federmeier & Kutas, 1999; Knoeferle, Crocker, Scheepers, & Pickering, 2005).

Conversely, a number of theories deny the likelihood of such predictions being successfully implemented into the processing steps, claiming that the system itself is too vast and complex to steadily generate an accurate prognosis of what is to follow (van Petten & Luka, 2012). This counterargument is based on the assumption that, at any point during the incoming stream of linguistic input, there is always a number of different continuations one might employ, regardless of the amount of contextual clues provided beforehand (van Petten & Luka, 2012).

Nevertheless, presently there is an abundance of studies confirming the crucial role that the linguistic context, and predictions derived from such contextual clues, play in facilitating and speeding up language comprehension (van den Brink, Brown, & Hagoort., 2001; Federmeier & Kutas, 1999; Kamide, Altmann, & Haywood., 2003; Kamide, Scheepers, & Altmann, 2003; Knoeferle, Crocker, Scheepers, & Pickering, 2005). The evidence coming from these studies has made the predictive coding framework, which put forward the notion of predictions guiding our everyday actions and reactions to the incoming stimuli, grow in popularity and soon become a broadly accepted view in neuroscientific research community (Pickering & Garrod, 2007).

From the predictive coding perspective, predictions are based on our prior experiences and regularly sent from higher cortical levels to lower ones via top-down processes. These feedback processes are propagated over slower timescales by means of oscillatory neural activity in the beta range (12-30Hz) and can travel over larger distances in the brain. Prediction errors, on the other hand, are transmitted in the bottom-up hierarchical direction every time an unexpected stimulus is encountered, thus contributing to the process of updating of the system and optimization of future predictions. They are propagated more locally in a feed-forward fashion over faster time scales via neural oscillations in the gamma range (> 30Hz) (Friston, 2002, 2005).

Despite the popularity and the constantly growing body of evidence supporting the predictive coding framework, there is still some unexplored ground to cover, especially when it comes to language cognition. Even though language comprehension has been vastly investigated (Bookheimer, 2002; Cabeza & Nyberg, 2000; Friederici, 2002; Hagoort, 2005, 2013; Hagoort & Indefrey, 2014; Indefrey & Cutler, 2004; Jung-Beeman, 2005; Lau, Phillips, & Poeppel, 2008; Price, 2010), there is still a distinct lack of studies about discourse comprehension, mainly due to a number of obstacles that need to be overcome in order to get reliable results.

A written or spoken discourse, such as a story, can provide a structured medium for the build-up of the linguistic load that can readily be used to track and facilitate the processing of its constituent lexical units. Creating this type of linguistic environment enables us to introduce and investigate the potential surprise elements and system adaptation opportunities, as the content of the discourse unravels before our eyes.

Solid confirmation on how linguistic units beyond a sentence can be used to investigate language comprehension comes from the study by Nieuwland and van Berkum (2006). Their stimuli consisted of short stories depicting interaction between human characters and inanimate objects, which serves to investigate the influence of discourse context on semantic interpretation. By manipulating the stories through the introduction of animacy-violating but context appropriate elements, they set out to look at the N400 ERP effect, known to be a sign of interpretive problems. Their findings indicate that we not only use the discourse contextual model at hand to anticipate further stimuli, but this model can completely overrule our real-world knowledge and expectations, thus leaving us surprised when the 'canonical' realistic properties that clash with the story context are introduced in the discourse.

We used a very similar type of stimuli for our study in order to investigate the relationship between the top-down and bottom-up activations, measured as oscillatory powers, in discourse comprehension. The stories used in this study were taken over from Nieuwland and van Berkum (2006) and slightly modified in terms of length and target words placement, but the premise remained essentially the same. Each story revolved around the interaction between a human character and an inanimate object. Such interaction between the inanimate and animate characters was consistent throughout the story, and appropriate for its content, but violated our real-life expectations and knowledge about inanimate objects and their behavior. Furthermore, at the very end of each story, a potential surprise factor was introduced in the form of an adjective, which was either congruent or incongruent with the rest of the story.

This paradigm allowed us to use magnetoencephalography (MEG) in order to study top-down beta and bottom-up gamma oscillatory activity as potential indicators of predictions and prediction errors in discourse comprehension.

Specifically, we studied the quantitative relationship between the beta and gamma bands at the beginning and at the end of each story, time-locked to the target words therein, in order to investigate the adaptation and prediction consolidation throughout the story with respect to the alternative context that goes against our real-world knowledge. Additionally, we looked at the gamma band activity at the one-off target word occurrence at the very end of the story, with the aim of finding the evidence of surprise in the case of story-incongruent item.

For the animacy-violation analysis of target nouns in the stories, we expected to find quantitative evidence in the form of changes in the beta and gamma power spectra respectively, that reflect adaptation and prediction consolidation of the language system throughout the course of the story. We further expected the changes in the two bands to occur in opposite direction, with the beta band activity increasing towards the end of the story, and the gamma band activity decreasing in that same direction. In other words, we anticipated the increase in beta band synchronization to be quantitatively correlated with the gamma band desynchronization and vice versa.

For the one-off surprise adjective analysis, we were interested in the element of surprise without further incentive to update the model. In accordance with the predictive coding theory, we expected to find an increase in the gamma band synchronization in incongruent endings as compared to the congruent ones.

In summary, we hypothesize that beta and gamma powers will be closely correlated, reflecting the fact that the more the system updates itself and solidifies further predictions throughout the story, the higher the surprise factor will be once an unexpected story ending is encountered that does not match the updated model.

1.1. Predictive Coding

As mentioned in the introduction, the view that the constant stream of predictions about the upcoming stimuli facilitates language comprehension is in line with the predictive coding framework (Friston, 2002, 2005). According to the theory, the brain is seen as a hierarchical structure, with higher cortical levels creating probabilistic models designed to explain neural activity at lower levels. In other words, the brain is believed to have an internal model, which steadily generates predictions about our sensory inputs based on assumptions about the world, with the ultimate aim of keeping the average surprise levels at a minimum (Friston, 2005).

More specifically, the predictions are formed by means of top-down processing, in which higher order hypotheses are transformed to lower levels of stimuli reception. This top-down processing, in turn, facilitates the bottom-up processing in which sensory inputs are received and further transferred to higher, more abstract, cortical levels. This system allows for the predictions at each level to be tested against the actual observations at the same level in the hierarchy, and determine the extent to which they match. In case of a mismatch, a prediction error is sent back up the hierarchy with the objective of updating the internal model of expectations (Friston, 2002). Prediction errors, therefore, effectively become the input for the higher-level system, while the feedback from the higher-level system provides the set of prior beliefs guiding the lower-level system. They indicate the failure of the inner model to fully account for the sensory input and prompt the adjustment of the priors that ultimately leads to a more accurate inner system and entropy minimisation (Friston, 2002).

While the predictive coding framework has received much experimental support from studies covering low-level perception (Bastos et al., 2015; Colby et al., 1996; Summerfield and de Lange, 2014; Wacongne et al., 2012; Wolpert et al., 2003;), solid experimental evidence from more abstract, higher-order cognitive domains still remains fairly elusive (Clarke, 2013).

1.2. Oscillatory Activity: Beta and Gamma

The view that there is an exclusive and fixed link between specific brain areas and cognitive functions has long been replaced by the concept of spatially distributed, yet functionally coherent networks, dynamically recruiting a variety of cortical areas for different (components of) cognitive functions **(**Bastiaansen & Hagoort, 2006; Bastiaansen, Mazaheri, & Jensen, 2012**)**. The coupling and uncoupling of these functional networks has been closely related to the patterns of synchronization and desynchronization of neuronal activity (Bastiaansen & Hagoort, 2006; Bastiaansen et al., 2012). Synchronous firing of neurons at a given frequency is today understood to be crucial in activating functional networks. Correspondingly, neurons are recognized as belonging to a network by virtue of their synchronization activity with other neurons within the same network, thus allowing a neuron or neuronal pool to participate at different times in different representations (Bastiaansen et al., 2012).

When studying cortical hierarchies, we distinguish between bottom- up, feed-forward influences and top-down, feedback activations. Looking at the neurocortical layers, feed-forward and feedback influences are characterised by functionally distinct processing streams: superficial layers (L2/3) generate mainly feed-forward connections, while deeper layers (L4/5) generate feedback connections (Bastos et al., 2012). Correspondingly, Maier et al. (2010) reported that gamma oscillations are most noticeably expressed in superficial supragranular cortical layers (L2/3), whereas beta oscillations are most prominent in deep infragranular layers (L4/5). This different spectral behaviour of superficial and deep cortical layers suggests that feedforward and feedback influences may be mediated by distinct frequencies: feed-forward signaling is believed to be transmitted via higher-frequency (gamma) oscillations, and feedback signaling is taken to be propagated by lower (beta) frequencies.

Furthermore, experimental and modeling efforts suggest that beta and gamma oscillations have different dynamical structure. While beta frequencies are able to synchronize over longer conduction delays (corresponding to signals travelling longer distances in the brain), gamma frequencies tend to synchronize over shorter intervals. These synchronization properties are consistent with the data suggesting that beta oscillations are more active in higher-level interactions over more distant brain regions, while gamma oscillations are activated during more local computations (Kopell et al., 1999).

When investigating certain aspects of human cognition by means of oscillatory activity, it is important to keep in mind that neural oscillations reflect network dynamics and information flow across them, and not specific cognitive functions. Neural networks are recruited differently depending on the cognitive process at hand, so there is rarely, if ever, a one-to-one mapping between the oscillatory neural dynamics and cognitive function (Lewis & Bastiaansen, 2015).

With this in mind, we will now take a close look at different findings connecting language comprehension and neural dynamics pattern as reflected by beta and gamma oscillations.

1.2.1 Beta Oscillations in Language Processing

In accordance with the predictive coding framework, Engel and Fries (2010) argue that the beta band activity may reflect active maintenance of the cognitive set at hand. Namely, the assumption is that higher levels of beta synchronization appear when the existing network configuration is being actively maintained, whereas beta desynchronization occurs when the said configuration is under revision or undergoing some kind of change. Additionally, Bressler and Richter (2015) propose that, apart from the maintenance role, the beta band may also be indicative of the top-down predictions propagation from higher to lower cortical levels in the brain.

A number of studies have shown higher beta power at the target word for syntactically legal sentences than for sentences with syntactic violation or words in random order (Bastaansen, Magyari, & Hagoort., 2010; Perez et al., 2012). Furthermore, Bastiaansen et al. (2010) have shown a linear increase in beta power over the course of syntactically legal sentences, as opposed to a steady low beta power observed in random word lists. Correspondingly, beta activity has been shown to be higher for syntactically more demanding sentences than for those with lighter syntactic load (Bastaansen & Hagoort, 2006). All these findings therefore show that an increase in beta frequency ranges might be related to the increase in linguistic load at syntactic level, and therefore reflect higher syntactic processing demands.

Beta activity, however, transcends the role of syntactic binding in language cognition and can be affected by a number of linguistic processes at other levels. Accordingly, a decrease in beta power has been found in sentences with semantic violations compared to semantically correct sentences (Kielar et al., 2014; Wang et al. 2012), rhythmically abnormal nouns in Chinese compared to their rhythmically correct counterparts (Luo et al., 2010), and grammatically incorrect sentences with respect to subject-verb person marking in Spanish (Perez et al., 2012).

Lewis and Bastiaansen (2015) have, therefore, proposed a more general explanation for beta activity, which supports and builds upon the Engel and Fries (2010) hypothesis. They suggest that the beta power increase reflects active maintenance of a cognitive set, which in the language context corresponds to any meaningful linguistic unit bound together under a construction. The decrease in beta power, on the other hand, may signal a call for a change in that set, thus indicating the need to revise the linguistic representation at hand. In other words, the language comprehension system is believed to use linguistic input cues to either change, maintain or actively maintain the cognitive processing set, and this is directly reflected in the power of the beta oscillations. The need for a change should be reflected in a decrease in beta activity, maintenance should require no change in beta activity, and active maintenance should indicate an increase in beta activity.

As mentioned above, it has also been suggested that beta power synchronization reflects the top-down flow of predictions (Bressler & Richter, 2015). This hypothesis states that when the integration of information proceeds normally, the transmission is unobstructed and the beta activity is therefore high. However, when the sentence input can no longer provide reliable predictions due to an unexpected event, the system supresses the flow of such top-down information, thus decreasing beta power oscillations, until the expectations are strengthened and can flow uninhibitedly again (Bressler & Richter, 2015).

Taken together, the broader view that the beta band synchronization indicates both active maintenance of a current cognitive set and top-down prediction propagation can account for a large number of findings that may not be fully accommodated by the research restricted to a single linguistic level. It also fits well into the larger framework of the predictive coding theory and its argument that beta band is indicative of the top-down prediction propagations.

1.2.2. Gamma Oscillations in Language Processing

The main function of the gamma band activity in the language setting, as proposed by Lewis and Bastiaansen (2015), may be that of matching strong top-down predictions and bottom-up sensory input. Namely, the argument here is that the increase in gamma band activity reflects the strong match between the pre-activated lexical representations and the linguistic input we are about to receive. Should the incoming input, therefore, be incongruent with the preceding linguistic content, no synchronization occurs due to its mismatch with the top-down predictions. Similarly, if the incoming input is congruent with the preceding content, but less predictable, gamma oscillations are expected to remain weak. This is argued to happen due to the lack of the strong prediction in said context to begin with, which would then lead to a strong match with the input.

This proposal clashes considerably with the predictive coding theory and the hypothesis outlined by Bastos et al. (2012), where gamma frequencies are argued to be carriers of prediction errors up the cortical hierarchy. Lewis and Bastiaansen (2015), however clarify that the proposal conflicting with the predictive coding framework could refer only to low and middle gamma ranges (35-75Hz), while prediction errors might still be propagated by gamma oscillations of higher frequencies (80-130Hz). The data supporting this view comes mainly from the speech processing studies, which have reported feed-forward prediction error propagation up the hierarchy of the auditory cortex (Arnal & Giraud, 2012; Arnal, Wyart & Giraud, 2011; Giraud & Poeppel, 2012).

As a possible alternative explanation of gamma activity in language processing, research has shown a strong link between gamma power and semantic binding. A number of studies found an increased gamma power throughout the sentence for semantically correct sentences compared to semantic violations (Hald, Bastiaansen, & Hagoort, 2006; Rommers, Dijkstra, & Bastiaansen, 2013). Gamma power was also found to be higher for semantically legal sentences than for syntactically acceptable ones (Bastiaansen & Hagoort, 2010). Finally, gamma power was reported to be higher when listening to sentences in native language as opposed to those in foreign language (Pena & Melloni, 2012).

Still, some reports remain inconsistent with the semantic binding proposal. In an isolated report, an increase in gamma range has been found at the target word that violated participants' world knowledge, but not in semantically legal or violated sentences (Hagoort et al., 2004). A number of studies showed gamma increase for semantically congruent and highly predictable words, but no increase for congruent but less predictable words (low cloze probability scores) or semantic violations (Molinaro, Barazza, & Carreiras, 2013; Monsalve, Perez, & Molinaro, 2014). These findings may indicate that gamma is, after all, mainly involved in signalling the predictability of the upcoming word rather than semantic unification.

Given the overall evidence, Lewis and Bastiaansen (2015) suggest a more general view of gamma band function originally proposed by Herrmann et al. (2004). An increase in gamma power is, therefore, taken to indicate a strong match between the bottom-up linguistic input and a pre-activated lexical item, whereas the lack of said increase is understood as a sign of absence of any lexical pre-activation or strong prediction, as well as the indication of the mismatch between the linguistic input and the prediction.

2. Methodology

2.1. Participants

A total of 25 native Dutch speakers (7 men, mean age: 24, age range: 19-35) participated in this study and received monetary compensation for their participation. The data of three participants was removed from the analysis due to the technical errors that occurred during the data acquisition. All participants were right-handed, had normal or corrected-to-normal vision, and reported no neurological or language impairments.

2.2. Materials

The stimuli used in this study were taken over from Nieuwland and van Berkum (2006) and slightly modified in terms of length, content, and strategic placement of target words. The stories depicted an interaction between two characters, and the content of the stories were designed to be as engaging as possible under the constraints of the present design. Each story consisted of five sentences, and to consolidate the potentially atypical content of the story, the target noun (TN), referring to the main character of the story, was repeated once in each of the five sentences. This resulted in five TN repetitions per story. Additionally, each story had a potential surprise element in the form of a target adjective (TA) in the fifth sentence of the story, after the last occurrence of the story's target noun (see *Table 1*).

Table 1

Example story

1.	Een vrouw zag op straat een dansende **pinda/bloemist** met een grote glimlach op zijn gezicht. *A woman saw a dancing **peanut/florist** on the street with a big smile on his face.*
2.	De **pinda/bloemist** zong namelijk over een meisje dat hij net had ontmoet. ***The peanut/florist** was singing about a girl he had just met.*
3.	De **pinda/bloemist** was helemaal gek van haar, zijn liedje loog er niet om. *Judging by the song, the **peanut/florist** was totally crazy about her.*
4.	De vrouw vond het schattig om de **pinda/bloemist** zo te zien en zo te horen zingen. *The woman thought it was really cute to see the **peanut/florist** singing like that.*
5.	De **pinda/bloemist** was gezouten/verliefd en zo te horen was het ook wederzijds. ***The peanut/florist** was **salty/in love**, and by the sounds of it, the feeling was mutual.*

Note. Original story in Dutch and an approximate translation to English (in italics). Bolded nouns: **IC TN/AC TN**; Underlined adjectives: **IC ITA/IC CTA**

We used a total of 60 stories, divided in four different conditions (see *Table 2*). 40 stories belonged to the inanimate condition (IC), and portrayed an interaction between an animate character and an inanimate object. The remaining 20 stories belonged to the animate condition (AC), narrating the interaction between two animate characters. Furthermore, half of the stories in each of the two conditions had a congruent ending and half of them had an incongruent ending The congruency was reflected in the target adjective content in the last sentence of the story. We focused mostly on the IC condition stories in our analyses, while the AC stories served as the 'filler' stories, distracting the readers from the overall pattern of story manipulations throughout the experiment.

Table 2

Story Conditions

	Inanimate condition (IC): target noun (TN)	Animate condition (AC): target noun (TN)
Incongruent condition: target adjective (ITA)	20 stories	10 stories
Congruent condition: target adjective (CTA)	20 stories	10 stories

Note. IC stories used in the analysis. AC stories used as 'filler' stories.

As mentioned, the IC stories portrayed a relationship or an interaction between a human, animate character (e.g. *journalist, student*) and an inanimate object acting as a human-like, animate being (e.g. *peanut, peach*). In this condition, the inanimate object served as the target noun (TN). The interaction between the characters was consistent throughout the story, and appropriate for its content, but violated our real-life expectations and knowledge about inanimate objects and their properties or behavior. In line with our discourse design, each story had five repetition of the inanimate object TN.

Further, 20 out of 40 IC stories had an incongruent ending, and 20 had a congruent ending. Specifically, this means that at the very end of each story, a potential surprise element was introduced in the form of a target adjective (TA) that occurred after the last (fifth) repetition of the target noun and referred back to it in some way. The object's property described by the TA was either congruent (CTA) with the rest of the story, but went against our real-life knowledge (e.g. *the peach was tired*), or was incongruent (ITA) with the rest of the story but depicted a 'canonical' inanimate property of the object (e.g. *the peach was sweet*).

In addition to the 40 stories used in the analyses, 20 'filler' stories were introduced to mask the pattern of the story structure across the experiment. All the 'filler' stories depicted an interaction between two human characters, thus making them an animate condition (AC) stories. They had the same structure as the IC stories, with five sentences each, and five TN repetitions that here represented a human character. Ten of the 'filler' stories had an incongruent ending with a surprising target adjective describing the animate human character as an inanimate object (e.g. *the artist was sweet*), and ten had an adjective describing a 'canon' expected property of the target noun (e.g. *the artist was tired*).

All target words were matched for length and lexical frequency values using the SUBTLEX-NL database of Dutch word frequencies (Keuleers et al., 2010). The target nouns were matched across animate and inanimate conditions, and the target adjectives were matched across congruent and incongruent conditions.

2.3. Experimental design and procedure

The 60 stories were randomized across the four conditions and across participants. Each story was presented word-by-word in the middle of the screen using Presentation software (Version 16.0, Neurobehavioral Systems, Inc.). Each word was presented for 350ms and was followed by 250ms of blank screen. The break between each sentence was 500ms, and the break between two stories was 2000ms. The stories were divided into 6 blocks (10 stories per block), in between which the participants were able to take a break for a period of time of their choosing. The participants were instructed to read the stories silently and attentively, and blink as they normally do.

2.4. MEG Data Acquisition

The magnetic brain activity was recorded using the whole-head MEG (275 axial gradiometers, VSM/CTF Systems) in a magnetically shielded room at the Donders Centre for Cognitive Neuroimaging in Nijmegen. Participants sat upright and were instructed to sit comfortably and remain as still as possible throughout the experiment. Their head position relative to the MEG sensors was monitored during the experiment using coils placed at the left and right ear canal and the nasion, and was corrected during breaks if needed. The horizontal and vertical electrooculogram (EOG) was recorded using 10mm Ag-AgCl surface electrodes in order to subsequently discard trials contaminated by eye movements. An online low-pass filter (cutoff 300Hz) was applied and all signals were sampled at 1200Hz and stored for offline analysis.

2.5. MEG Data Analysis

The MEG data was preprocessed and analyzed using the FieldTrip toolbox (Oostenveld, Fries, Maris & Schoffelen, 2011) and custom-written scripts for Matlab, version R2012b (MathWorks).

2.6. MEG Data Preprocessing

During the preprocessing of the data, artifact rejection was done for each subject individually. First, trials with SQUID jump or muscle movement artifacts were identified and removed from the data using a semi-automatic procedure. Then, we down-sampled the data to a 600Hz sampling frequency and performed independent component analysis (ICA; Bell and Sejnowski 1995; Jung et al. 2000) in order to remove eye movements and cardiac related activity from the remaining MEG signals. Finally, the trials were reviewed visually to remove any residual artifacts overlooked by the previous automated procedures.

For the sensory-level analysis, we calculated planar gradients of the MEG field distribution by using a nearest neighbor method, where the horizontal and vertical components of the estimated planar gradients were derived. In doing this, we were able to approximate the signal measured by the MEG with planar gradiometers. This planar gradient representation facilitated the interpretation of the sensory-level data, given that the largest signal of the planar gradient is normally located right above the source (**Bastiaansen & Knosche, 2000)**.

2.7. Time-Frequency Analysis

Time-frequency representations (TFR) of power were calculated for each trial using a Fourier transform approach applied to short sliding time windows. The trials were time-locked to the target nouns and adjectives in the stories. The trial duration was determined as beginning 250ms before the target word onset and lasted for 600ms after words onset (350ms of the word being presented on the screen and 250ms of the blank space between two words), resulting in the overall 850ms time window of interest.

Oscillations analyzed in this study were beta band and low/high gamma band. The frequency bands were selected based on previous studies. For beta frequencies, the band was centered at the frequency of 15Hz (12-18Hz), for lower gamma at 50Hz (40-60Hz), and for higher gamma at 80Hz (60-100Hz).

Beta frequency band was analyzed in 50ms time steps and 2Hz frequency steps from -250ms to 600ms, using an adaptive sliding time window four cycles long in combination with a Hanning taper. For gamma frequencies, the analysis was performed in 50ms time steps and 4Hz frequency steps from -250ms to 600ms in combination with multitapers (Mitra & Pesaran, 1999), effectively achieving a bandwidth of 16Hz.

2.8. Statistical Analysis

In order to establish whether the differences in TFRs of power between conditions were significant, we performed cluster-based non-parametric permutation statistics (Maris & Oostenveld, 2007; Nichols & Holmes, 2002). This test efficiently controls for the Type I error rate in situations involving multiple comparisons over sensors, frequencies and times, by clustering neighboring sensor, time or frequency pairs with the same effect. The randomization method identified sensors whose t-statistics exceeded an a priori determined critical value ($p < 0.05$) when comparing the sensors of the two conditions. This is done in order to identify sensors with effects exceeding the threshold for the subsequent cluster analysis. The sum of the t-values of the sensors within a given cluster was used as cluster level statistic. The cluster with the maximum sum was used in the test statistics. The Type I error rate for the complete set of sensors was, therefore, controlled by evaluating the cluster-level test statistic under the randomization null distribution of the maximum cluster-level test statistic. This, in turn, was obtained by randomly permuting the data across the two conditions 1000 times, and re-computing the test statistic for the new set of clusters. The end result was the Monte Carlo p-value, estimated according to the proportion of the randomization null distribution exceeding the observed maximum cluster-level test statistic.

For the target noun (TN) analysis, we quantified the neural responses in both beta and gamma bands to first (TN1) and last (TN5) occurrence of the target nouns across all IC stories. Upon extracting all TN1 and TN5 occurrences across stories, we calculated the average power for each of the two conditions across participants and performed cluster statistical analyses as described in the previous paragraph. For the target adjective (TA) analysis, we looked at the neural activity in gamma band congruent (CTA) versus incongruent (ITA) story endings across the IC stories. Upon extracting the TA occurrences for the two conditions, we computed the average power for each of the two conditions across participants and performed statistical analyses as stated in the first paragraph of this section.

For the TN analysis, 17-38% of trials were discarded after the artifact rejection, which left approximately 25 and 30 respective trials per condition (TN1 vs. TN5) per participant. For TA analysis, 14-20% of trials were discarded after artifact rejection, leaving respectively 17 and 16 trials per condition (ITA vs. CTA) per participant.

3. Results

3.1. Target Nouns Analysis: Inanimate condition

In our inanimate TN analysis, we measured the changes in oscillatory activity of beta and gamma band, respectively, at the beginnings and endings of the stories time-locked to the TN occurrences. Concretely, we analyzed 40 IC stories, and measured the oscillatory activity at TN5 against the oscillatory activity at TN1 occurrence.

3.1.1. Inanimate Target Nouns Analysis: Beta

When measuring beta oscillatory activity at TN5 occurrence against that at the TN1 occurrence, the cluster-based permutation test revealed a significant difference (TN5 > TN1; $p = 0.002$) in the power of beta band activity in between the TN5 and TN1 occurrence (see *Fig. 1A*). In this frequency range, the difference starts around 0ms (right around the TN-onset time) and is most pronounced over the right temporo-parietal regions (see *Fig. 2A)*, and left occipito-parietal regions (see *Fig. 2B)* initially. Subsequently it moves to the bilateral occipital and frontal areas and the right temporal cortex, as it becomes stronger over time.

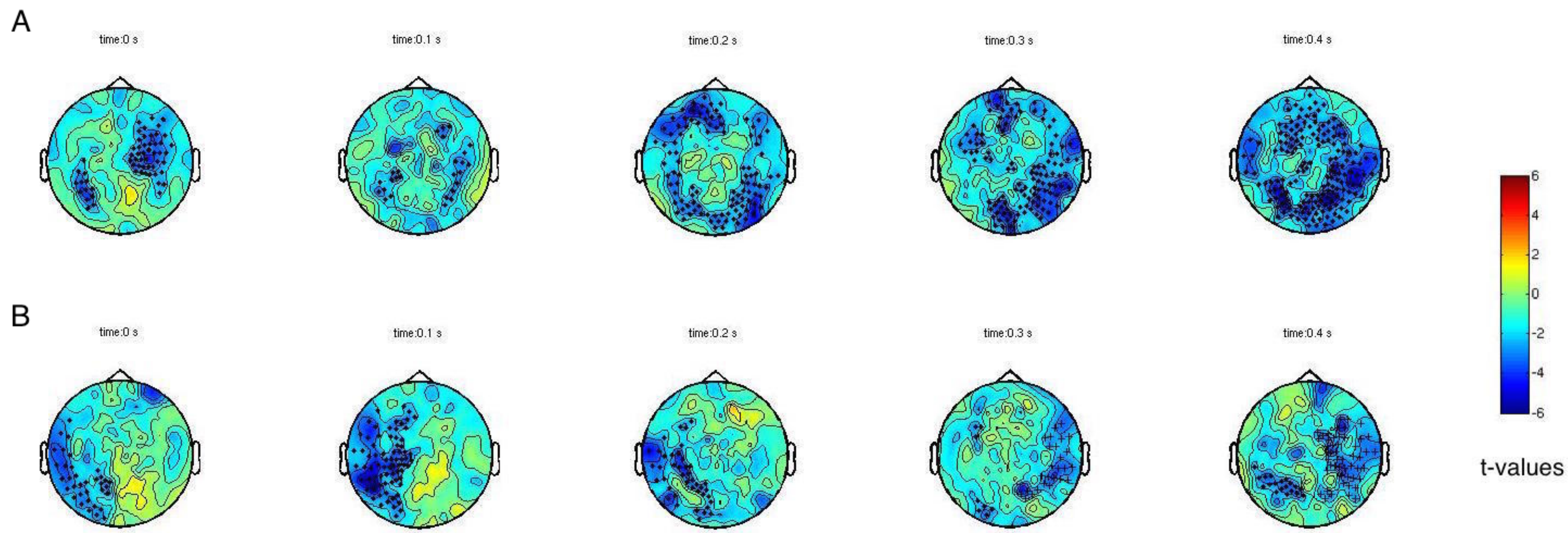

Figure 1 Cluster-based permutation test. Beta frequency band (12-18Hz). **A.** TN1 vs. TN5 IC contrast, one statistically significant negative cluster found (TN5>TN1; $p = 0.002$). The difference begins at the time of the TN onset (0ms). 0-100ms post-TN onset the difference is strongest in the right temporo-parietal, and left posterior parietal and occipital regions. Around 150-200ms post-TN onset, the effect moves to the bilateral occipital and left temporal and prefrontal regions. At 200-400ms post-TN onset the effect spreads out to the right prefrontal, right temporal, right parietal, and bilateral occipital regions, becoming stronger over time. **B.** TN1 vs. TN5 AC contrast, two significant negative clusters (TN5>TN1; $p = 0.006$, $p = 0.032$). The difference begins at the time of the TN onset (0ms). 0-200ms post-TN onset the difference is strongest in the left occipito-temporal regions. 200ms post-TN onset, the effect moves to the right temporal and parietal regions.

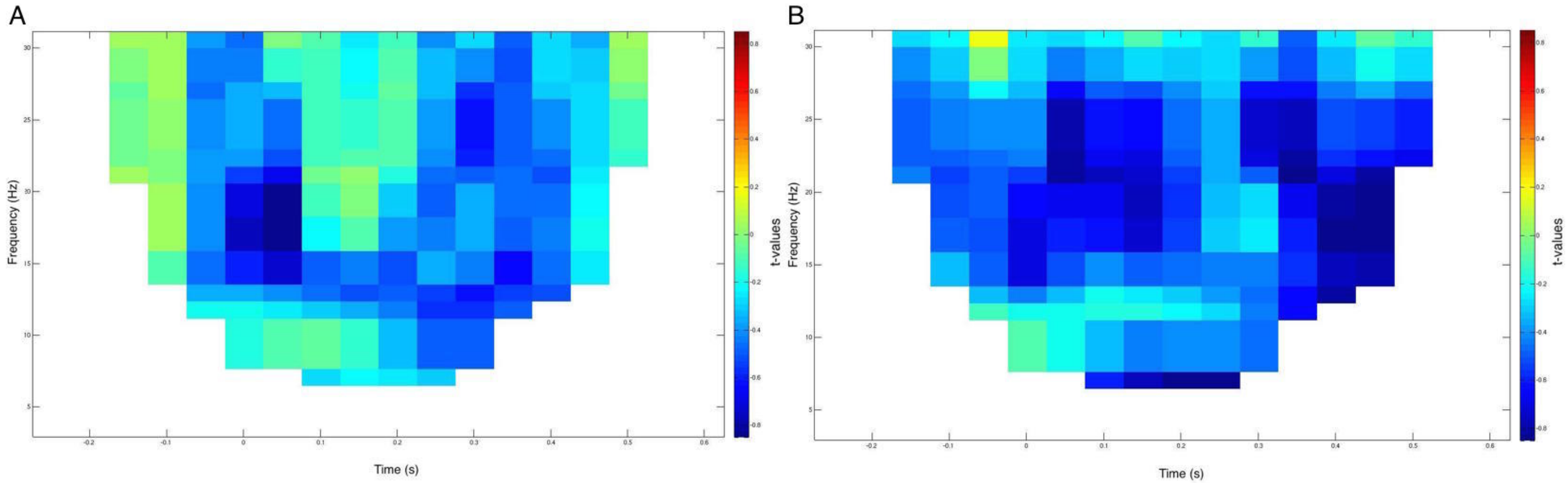

Figure 2. Time-frequency representation of beta band activity (12-30Hz) over time. IC condition, TN1-TN5 contrast**. A.** Averaged over right temporo-parietal channels (MRF35, MRF46, MRT11, MRT21, MRT32). Maximum synchronization around 0 - 100ms at around 15-20Hz. **B**. Averaged over left occipito-parietal channels (MLO34, MLT26, MLT27, MLT37). Maximum synchronization around 400-450ms at around 15-20Hz.

3.1.2. Inanimate Target Nouns Analysis: Gamma

When measuring both low and high gamma oscillatory activities at TN5 occurrence against that at the TN1 occurrence, the cluster-based permutation test revealed a significant difference in the power of both low and high gamma band activity in between the TN1 and TN5 occurrence (low gamma: N5 > N1; $p = 0.002$; high gamma: N5 > N1; $p = 0.002$). For both low and high gamma bands, the difference starts about 100ms prior to the TN-onset and lasts up until 450ms post TN-onset (see *Fig. 5*). In the low gamma frequency range the biggest difference was vastly spread over the bilateral occipital, parietal and frontal regions (see *Fig. 2A*), while in the high gamma frequency range, the difference was most prominent in the bilateral parietal and frontal areas (see *Fig. 3A*). The effect seems to be much stronger spatially for lower than for higher gamma frequencies.

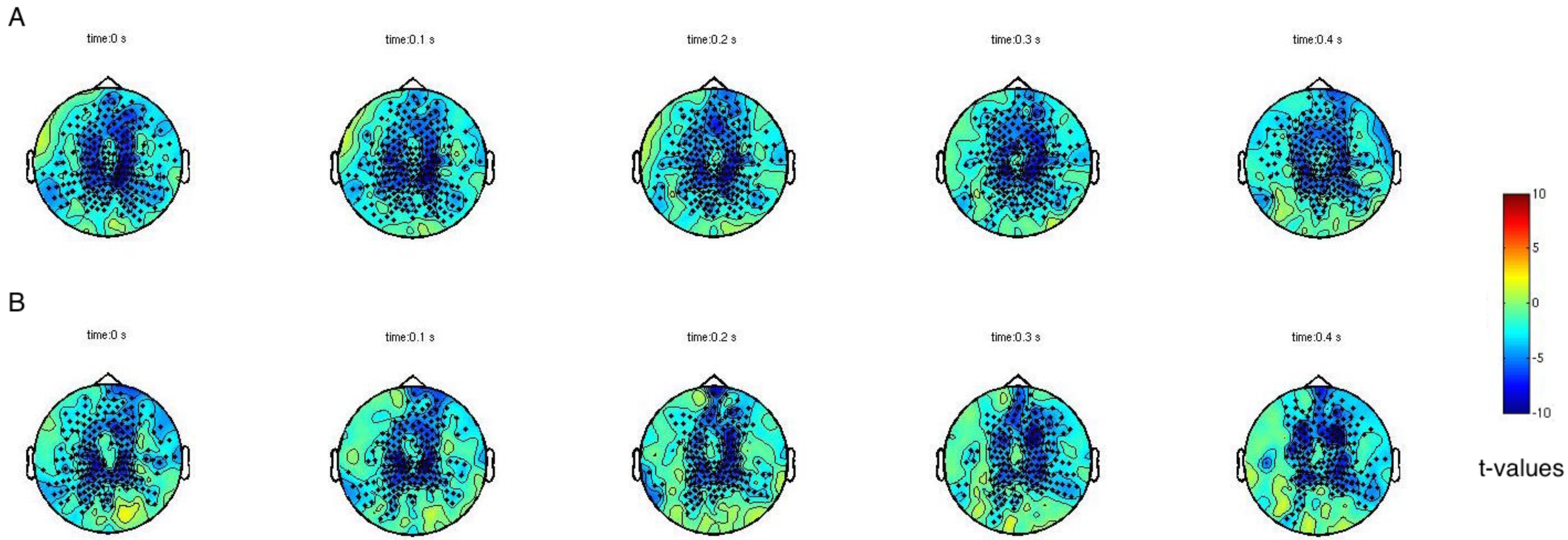

Figure 3 Cluster-based permutation test. Low gamma frequency band (40-60Hz). **A.** TN1 vs. TN5 IC contrast, one statistically significant negative cluster found (TN5>TN1; p = 0.002). The difference starts at 100 prior to the TN onset and lasts up to 450ms post-TN onset. The effect is most prominent along the bilateral parietal and frontal lobes. **B.** TN1 vs. TN5 AC contrast, one statistically significant negative cluster found (TN5>TN1; p = 0.002). The difference starts at 100 prior to the TN onset and lasts up to 450ms post-TN onset. The effect is most prominent along the bilateral parietal and frontal lobes.

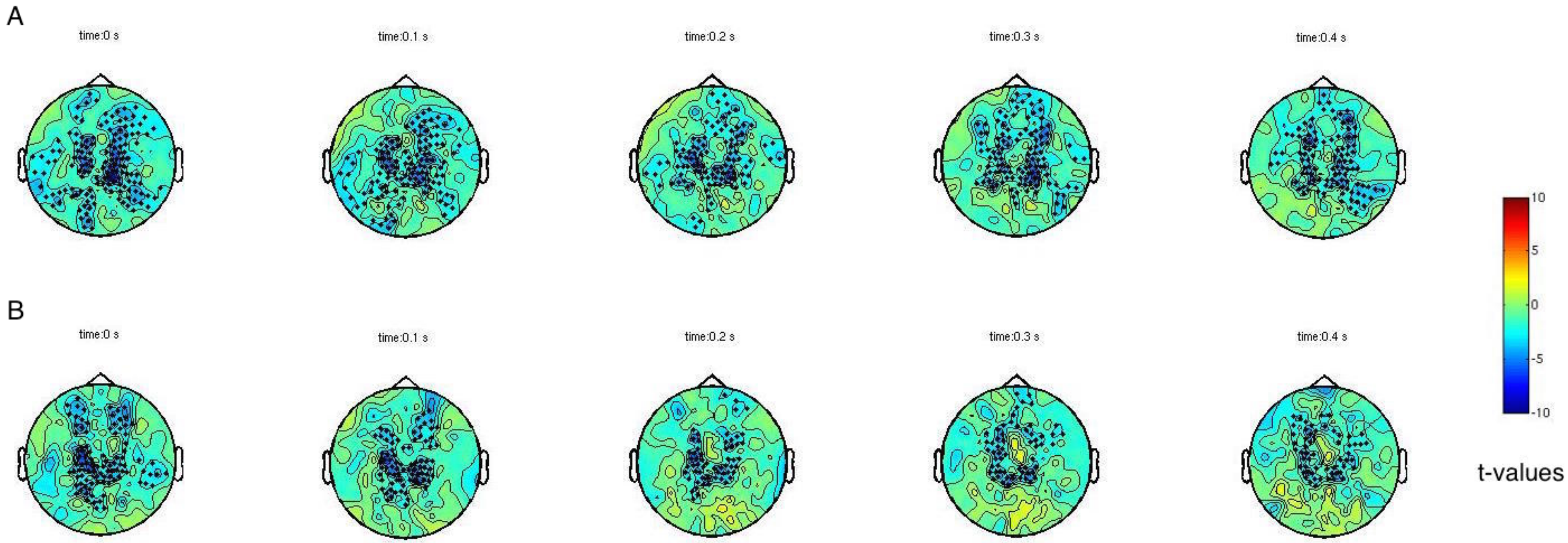

Figure 4 Cluster-based permutation test. High gamma frequency band (60-100Hz). **A.** TN1 vs. TN5 IC contrast, one statistically significant negative cluster found (TN5>TN1; p = 0.002). The difference begins 100 prior TN onset and lasts until-450ms post-TN onset. It encompasses the bilateral parietal and frontal regions and is less spatially spread than low gamma frequency band. **B.** TN1 vs. TN5 AC contrast, one statistically significant negative cluster found (TN5>TN1; p = 0.002). The difference begins 100 prior-TN onset and lasts until 450ms post-TN onset. It encompasses the bilateral parietal and frontal regions and is less spatially spread than low gamma frequency band.

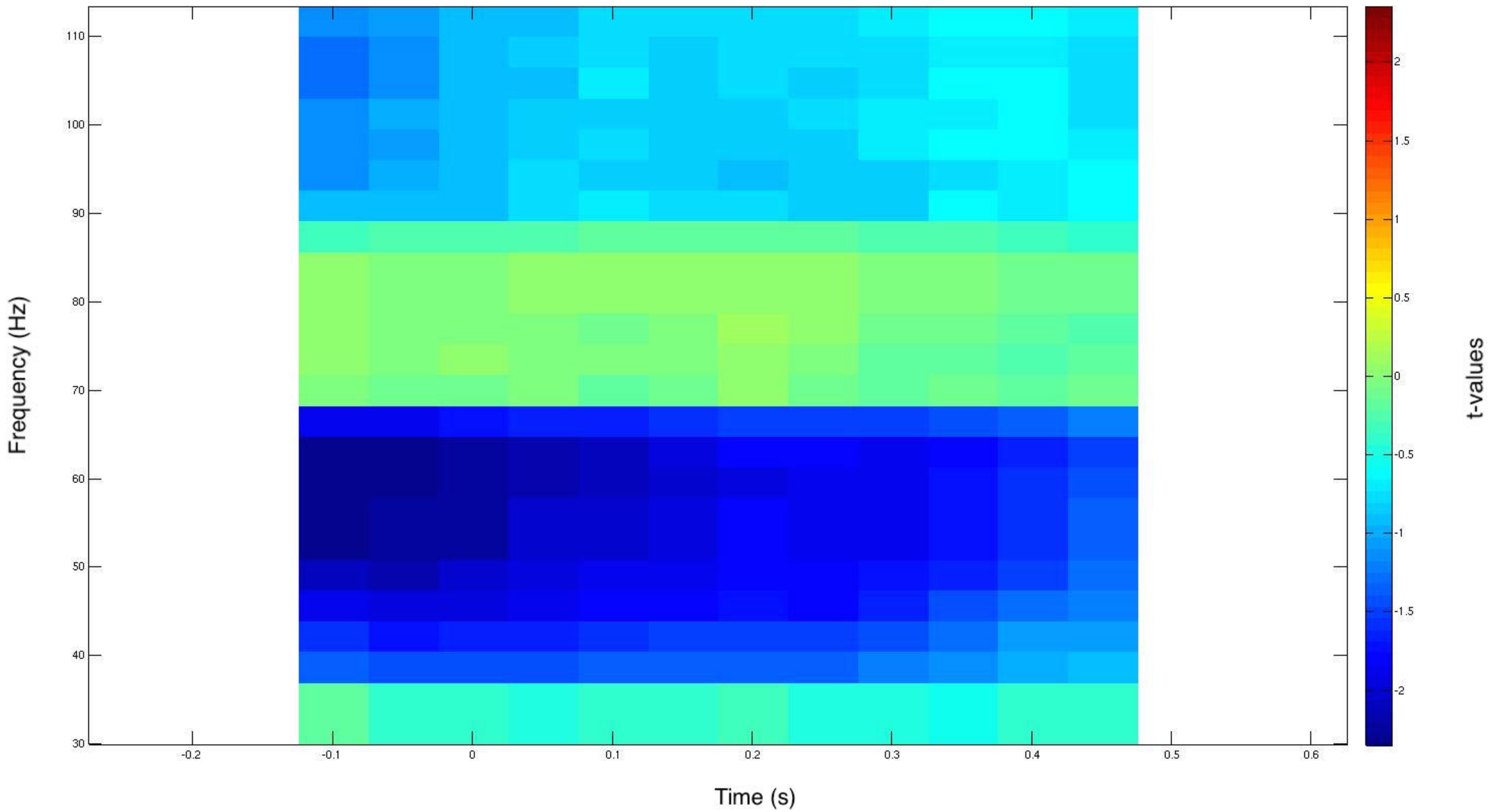

Figure 5. Time-frequency representation of gamma band activity (32-112Hz) over time measured at central parietal channels (MLC42, MLP12, MRC32, MRC42, MRP23). IC condition, TN1-TN5 contrast. Visual effects enhanced due to the temporal smoothing. Maximum synchronization between -100 - 0ms, prior to the TN-onset. Two visible effects, 40 – 70Hz and <90Hz.

3.2. Target Nouns Analysis: Animate condition

In the TN analysis, we additionally measured the beta and gamma oscillatory activity at the beginning and ending of each AC 'filler' story, time-locked to the TN occurrences therein. In this condition, we had 20 stories at our disposal.

3.2.1. Animate Target Nouns Analysis: Beta

When measuring beta oscillatory activity between TN1 and TN5 occurrences, the cluster-based permutation test revealed a significant difference in the power of beta band activity in between the two conditions (TN5 > TN1; $p = 0.006$, $p = 0.032$). In this frequency range, the difference starts around around the TN-onset time at 0ms and is most pronounced over the left occipito-temporal regions for the first 200ms and the right temporal and occipital regions after that (see *Fig 1B*).

3.2.2. Animate Target Nouns Analysis: Gamma

When measuring both low and high gamma oscillatory activities between TN1 and TN5 occurrences, the cluster-based permutation test revealed a significant difference in the power of both low and high gamma band activity in between the conditions (low gamma: N5 > N1; $p = 0.002$; high gamma: N5 > N1; $p = 0.002$). For both low and high gamma bands, the difference starts about 100ms prior to the TN onset and lasts until 450ms post-TN onset. In the low gamma frequency range the biggest difference can be spotted over the bilateral parietal and frontal regions (see *Fig. 3B*), and is very similar to the high gamma frequency range, with the difference showing in the same areas (see *Fig. 4B*). The effect seems to be much stronger for lower than for higher gamma frequencies.

3.3. Target Adjectives Analysis

For our TA analysis, we measured the changes in oscillatory activity of the low and high gamma frequency bands at the one-off occurrence of the TA in congruent and incongruent ending conditions. We analyzed 40 IC stories, and measured the oscillatory activity at the ITA against the oscillatory activity at the CTA occurrence.

3.3.1. Target Adjectives Analysis: Gamma

In this analysis, the cluster-based permutation test revealed no significant difference in the power of either low or high gamma frequency bands (low gamma: $p = 0.959$; high gamma: $p = 1$) between the ITA and the CTA conditions.

4. Discussion

In this study, we used MEG to investigate neuronal oscillatory activity signaling predictions and prediction errors during sentence and discourse processing. In particular, we focused on the quantitative relationship between feedback beta and feed-forward gamma oscillations to study the updating and prediction strengthening throughout the story. We then further looked at the gamma activity as potential representative of prediction errors tied to the one-off surprise element in the last sentence of the story.

During the target noun analysis, we primarily looked at the target nouns semantically manipulated to denote inanimate objects acting like human characters in short stories. The first occurrence of the target nouns (TN1) in the stories served as a surprise factor for the reader. However, after the initial surprise, the target nouns were steadily repeated four more times throughout the story, thus presumably eliciting the weakening of the readers' surprise effect by the time the last (TN5) occurrence was reached. This kind of repetitive animacy-manipulation gave the readers enough room to adjust their expectations and adapt to the story plot.

We measured both beta and gamma band oscillations at the TN1 and TN5 occurrences, in order to test the levels of adaptation as the story unfolds. As expected, we found a significant increase in the beta band oscillations at the TN5 occurrence as compared to its power at the TN1 occurrence. This difference was seen mostly in the right fronto-parietal cortex, as well as in the left occipito-parietal cortex in the first 100ms after the target word onset, subsequently spreading to the bilateral occipital and frontal areas and the right temporal cortex and becoming stronger over time. The spatial pattern of the beta oscillations seems to reflect the synchronization over longer cortical distances, encompassing both frontal and occipital regions. It also shows activations in left temporal and frontal regions after the TN-onset, which agrees with our expectations and the predictive coding literature.

These findings are also in line with the hypothesis proposed by Engel and Fries (2010), claiming that the increase in beta band power indicates active maintenance, and the absence of undergoing change in the cognitive set under observation, i.e. a story. They also reflect the fact that the increase in the beta band strength signals a decrease in neural population activation. As the story unfolds, more constraints are imposed upon our predictions and less general neuronal population activity is necessary for the language processing.

This result follows the findings of the original Neuwland and van Berkum (2006) study, where the authors found a decreased N400 effect at the end of the story as compared to the beginning, manipulated in the similar manner to our stimuli. This shows that the participants are indeed successful in adapting to the discourse topic at hand, even when it goes against their real-world knowledge, narrowing their predictions as they become more secure in their expectations.

Moreover, the upgraded version of Engel and Fries hypothesis proposed by Bressler and Richter (2015) fits into this framework. They claim that, in addition to keeping up the active maintenance of a cognitive set, the beta band oscillations are also involved in the top-down prediction propagation from higher to lower cortical areas. Given that the stories were manipulated in such a way that the readers are given the opportunity to systematically keep updating and narrowing their expectations after the initial surprise at the beginning, this hypothesis can be applied to our findings as well. With each TN repetition throughout the stories, the reaction to animacy-violation is further neutralized by the plot at hand, and the newly adjusted priors are becoming stronger, thus reflecting the increasing certainty in our predictions. The increase in beta power at the TN5 occurrence as compared to the TN1 occurrence may reflect precisely this strengthening of predictions as the story unfolds.

Finally, all these interpretations of our beta band activity increase fit under the framework of the predictive coding theory and are consistent with both previous findings on beta frequencies in cognitive processing (Brinkman et al., 2014; Lewis et al., 2016) and our expectations for this study.

Contrary to our expectations, however, we found the same direction of significant increase in the oscillatory activity of both low and high gamma frequencies at the TN5 as compared to the TN1 occurrence. These differences started around 100ms prior to the target noun onset for both low and high gamma bands, and were spread across the bilateral occipital, parietal and frontal regions. We should be careful about this spatial activation pattern, due to the fact that these regions are involved more in lower-level memory and attention tasks, and not in higher-level language tasks, which are usually left lateralized to the more temporal cortical regions. Therefore, while the distribution pattern of gamma synchronization is more spatially localized and contained, it does not reach language-specific processing areas relevant for this experiment.

Looking closely at the low and high gamma band activity, we found the same pattern of significant increase in both lower and higher ranges of gamma power at the TN5 occurrence as measured against the TN1 occurrence, with a slightly more restricted spatial pattern of the higher gamma band across bilateral parietal and frontal cortical areas. This outcome, while comparable to the previous findings of gamma band activity in language comprehension studies, is not in accordance with the predictive coding framework and our hypothesis for this study.

Namely, in line with the predictive coding framework, Bastos et al. (2012) claimed gamma oscillations to be the indicators of bottom-up prediction errors. In agreement with their hypothesis, we expected to find an increase in the gamma band power at the TN1 occurrence in the story, followed then by the decrease in the gamma activity as the reader approaches the end of the story.

But while our results do not fit into the predictive coding framework, they are consistent with most finding reported on the topic of sentence comprehension. Herrmann et al. (2004), and later Lewis and Bastiaansen (2015), suggested that the increase in gamma power could be observed when there is a strong match between the bottom-up linguistic input and the top-down pre-activated lexical item. Conversely, the increase is absent when there is either no strong prediction about the upcoming input or there is a mismatch between the prediction and the actual input.

To put this hypothesis in the context of our study, we can follow the same line of argument and tentatively claim that, the mismatch between the prediction and the incoming linguistic input at the TN1 occurrence is precisely the reason we found no increase in gamma power at the beginning of the story compared to the ending. By the time the last sentence has been reached, the significant portion of the story is already behind the reader and their priors have been updated, thus strengthening the new predictions. These strong predictions are met by the time the TN5 is reached, which results in a significant increase in the gamma band synchronization.

Furthermore, due to the similarities in the low and high gamma band activities, our results failed to give substance to the Lewis and Bastiaansen (2015) claim that higher gamma frequency ranges might have a different role than lower gamma frequencies, and reflect the prediction error propagation.

The fact that a very similar pattern of oscillatory activity was found for our animate condition ‘filler’ stories, further shows that both beta and gamma bands may be indicators of becoming more adjusted to and familiar with the cognitive set at hand, i.e. the story plot. Given our current results, we are unable to claim with certainty to have found oscillatory signatures of prediction strengthening effect, as opposed to the general effects of lexical repetition in language comprehension over a period of time.

This absence of prediction error propagation extends to our final analysis as well. We looked at a single occurrence of the target adjective (TA) across congruent and incongruent ending IC condition stories, in the context of low and high gamma oscillatory power. The target adjective appears only once per story, at the very end of the story after the TN5 occurrence, and refers back to it in one of two ways. The description is either congruent with the story plot, but clashes with our world-knowledge (CTA), or it is incongruent with the story plot, but in agreement with or canonical beliefs about the world (ITA). We examined lower and higher gamma band frequencies at the ITA and CTA, and found no significant difference between the two conditions.

This lack of any significant finding again went against our expectations, as we hypothesized we would find an increase in gamma activity at this point in the story. While going against the predictive coding theory, this result, or lack thereof, once again falls in line with the previous language comprehension findings and the hypothesis of the gamma band as an indicator of a strong match between our predictions and the input (Hermann et al., 2004; Lewis & Bastiaansen, 2015).

In summary, for the TN analysis, we expected to find quantitative evidence in the form of changes in beta and gamma power spectra respectively, that would reflect adaptation and prediction consolidation of the language system throughout the course of the story. While we did find significant changes in both bands, the changes in the two bands did not happen in the expected opposite directions.

Instead of finding an expected negative correlation between the increase in beta band synchronization and gamma band synchronizations, we found a significant change in power for both of them in the same direction – higher at the end of the story as compared to the beginning of the story. Following the same line of argument as the previous studies on the topic of language comprehension, we explain our findings by assigning beta band the role of signaling the processing state of the language comprehension and any potential changes over time, while gamma changes reflect predictions about linguistic input that the language comprehension system expects to receive. Furthermore, we found no difference in the directionality of the low and high gamma bands, thus failing to provide evidence for prediction error propagation in any frequency range of the gamma band.

For the TA analysis, we were interested in the element of surprise without further incentive to update the model. In accordance with the predictive coding theory, we expected to find an increase in the gamma band synchronization in incongruent versus congruent endings of the IC stories. We failed to find any significant difference in between the two conditions, once again challenging the predictive coding view of the gamma band role in language processing.

There is still a distinct lack of studies investigating language comprehension at a discourse level, mainly due to a number of challenges that need to be overcome in order to get reliable results. Finding the compromise between the duration of the experiment and gathering enough data for statistical analysis, as well as creating an optimal environment to measure the neural activities of interest are just a few of them. Because of that, the majority of the theories and interpretations of oscillatory activity in the context of discourse comprehension have been derived from the studies done on sentence processing.

In this study, we were unable to isolate the oscillatory signatures of prediction propagation from the general repetition and increasing familiarity with the stimulus at hand effect. This may be due to the fact that the stories, employed for the purpose of this study was too short for a proper adaptation effect or too predictable to be able to detect a strong enough element of surprise or adjustment connected to language comprehension.

A further investigation of the potential linear growth in oscillatory synchronizations over all five TN repetitions in the story might shed more light on the topic. Furthermore, the N400 ERP effect measure might give a better insight into the issue of a strong enough surprise and the brain's oscillatory reaction to it.

5. Conclusion

In this study, we used semantically manipulated short stories to look at the oscillatory activity signaling predictions and prediction errors in language comprehension. First, we investigated the process of adaptation and strengthening of predictions as the reader becomes familiar with a meaningful discourse that clashes with their real-world knowledge. We observed the oscillatory activity of beta and gamma bands at the beginning and end of the stories containing animacy-violations, and measured the quantitative relationship between the two bands. We found evidence of adaptation and prediction strengthening in the form of an increase in beta activation at the end of the story, supporting the hypothesis that we indeed update our inner system of expectations to the content before us, even when it goes against our real-life beliefs. However, instead of finding the accompanying decrease in gamma oscillations that would indicate the gradual drop in the surprise levels as the story unravels, we found the exact opposite. Gamma band activation grew towards the end of the story in the same manner as beta band activation, thus clashing with the premise that the surprise levels will go down as the system is updated and adapted to the new condition. Finally, we looked for the evidence of surprise when faced with an unexpected lexical input in an otherwise meaningful sentence consistent with the rest of the story, as signaled by the increase in the gamma band activity. We found no evidence of such surprise, thus failing to encounter any indication of prediction error signaling when faced with semantic violation of expected linguistic input. Further studies are necessary on the topic of discourse comprehension within the predictive coding framework, seeing as there is a discrepancy between the language cognition findings and the predictive coding hypotheses.

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