

Frequency-based Segregation of Syntactic and Semantic Unification during Online Sentence Level Language Comprehension

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Abstract

■ During sentence level language comprehension, semantic and syntactic unification are functionally distinct operations. Nevertheless, both recruit roughly the same brain areas (spatially overlapping networks in the left frontotemporal cortex) and happen at the same time (in the first few hundred milliseconds after word onset). We tested the hypothesis that semantic and syntactic unification are segregated by means of neuronal synchronization of the functionally relevant networks in different frequency ranges: gamma (40 Hz and up) for semantic unification and lower beta (10–20 Hz) for syntactic unification. EEG power changes were quantified as participants read either correct sentences, syntactically correct though

meaningless sentences (syntactic prose), or sentences that did not contain any syntactic structure (random word lists). Other sentences contained either a semantic anomaly or a syntactic violation at a critical word in the sentence. Larger EEG gamma-band power was observed for semantically coherent than for semantically anomalous sentences. Similarly, beta-band power was larger for syntactically correct sentences than for incorrect ones. These results confirm the existence of a functional dissociation in EEG oscillatory dynamics during sentence level language comprehension that is compatible with the notion of a frequency-based segregation of syntactic and semantic unification. ■

INTRODUCTION

Most current models of language comprehension (e.g., Hagoort, 2005; see also Werning, Hinzen, & Machery, 2012) postulate two main operations that continuously interact and overlap in time: (1) accessing lexical information and (2) incrementally integrating this information with the preceding context, such as to build up a message level representation. The latter process is often referred to as unification (Baggio & Hagoort, 2011). Following Jackendoff's notion of a parallel unification of phonological, syntactic, and semantic information in an abstract "unification space," it has been proposed that the left inferior frontal gyrus (IFG), in close cooperation with the left temporal cortex, constitutes the neuronal correlate of this unification space (Hagoort, 2005, 2009, 2013). Furthermore, a meta-analysis (e.g., Bookheimer, 2002) suggest that within left IFG there is an anterior/posterior "unification gradient," in the sense that semantic unification operations tend to activate anterior IFG (BA 47/45), syntactic unification operations most often activate an area slightly posterior to that (BA 45/44), whereas phonological unification tends to activate posterior IFG (roughly BA 44/6). However, the common observation is that the areas involved in the different types of

unification tend to be largely spatially overlapping (although recently it has been suggested that part of this overlap may be due to differences in individual functional anatomy; Fedorenko & Kanwisher, 2009). The notion of spatial overlap between syntactic and semantic processing has also received support from intracranially recorded EEG data (Sahin, Pinker, Cash, Schomer, & Halgren, 2009).

This raises the following question: How can functionally distinct processes (parallel unification operations at different levels of linguistic analysis) take place at the same time (roughly, in the first few hundredths of milliseconds after word onset) and at spatially overlapping networks in the inferior frontal and temporal cortices. In other words, what are the neuronal dynamics that mediate the functional segregation of semantic, syntactic, and phonological unification in IFG?

We address this question by adopting a "network dynamics" perspective. In the past two decades, consensus has grown among neuroscientists that the neuronal oscillations that are commonly observed in the ongoing scalp EEG and MEG can, by and large, be taken to be a system level reflection of underlying changes in neuronal synchronization (Bastiaansen, Mazaheri, & Jensen, 2012; Bastiaansen & Hagoort, 2006; Varela, Lachaux, Rodriguez, & Martinerie, 2001). Neuronal synchronization, in turn, is a mechanism that is thought to subserve the transient coupling and uncoupling of distinct neuronal populations

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into functional networks (see, among others, Singer, 1999, 2011; Uhlhaas, Roux, Rodriguez, Rotarska-Jagiela, & Singer, 2010; Varela et al., 2001; Singer & Gray, 1995).

Slowly, these insights have percolated into the field of psycholinguistic research, leading to an increasing number of studies that attempt to establish an empirical relationship between event-related changes in EEG and MEG oscillations, on the one hand, and aspects of language comprehension, on the other hand (e.g., Pena & Melloni, 2012; Bastiaansen, Magyari, & Hagoort, 2010; for review, see Bastiaansen et al., 2012; Bastiaansen & Hagoort, 2006; Weiss & Mueller, 2003). At a very general level, the aim of such studies is to provide a window onto the fast temporal dynamics that govern the patterns of coupling and uncoupling within and between the nodes of the brain's language network.

Within this context, a number of studies have focused, among others, on the relationship between oscillatory EEG/MEG dynamics and sentence level unification operations. Several such studies suggest that there is a relationship between gamma-band neuronal synchronization and semantic unification. For example, in one study (Hald, Bastiaansen, & Hagoort, 2006), an increase in gamma power (around 40 Hz) was observed in response to a highly expected word presented in a sentence context. This gamma increase was abolished when, in contrast, the word at the same position in the sentences was semantically anomalous. These results were replicated in a recent study (Rommers, Dijkstra, & Bastiaansen, 2013), which additionally revealed that semantically anomalous words that were nevertheless semantically related to the highly expected word elicited an intermediate increase in gamma power. Furthermore, using EEG coherence analysis, one study (reviewed in Weiss & Mueller, 2003) reported increased gamma-band coherence between left frontal and left temporal electrodes for a semantically correct target word compared to a semantically anomalous target word. In another study (van Berkum, Zwitserlood, Bastiaansen, Brown, & Hagoort, 2004), we observed a gamma power increase for referentially correct words that disappeared when these words were referentially ambiguous or did not have a proper referent. Finally, we found gamma-band activity to be closely associated with cloze probability, rather than with semantic acceptability (Wang, Zhu, & Bastiaansen, 2012). What all these findings have in common is an increase in gamma (~40 Hz) power or coherence when semantic unification can be routinely performed and a disruption of this gamma increase when semantic problems are encountered. On the basis of these findings, we have proposed (Bastiaansen & Hagoort, 2006) that gamma-band neuronal synchronization is related to normal, ongoing semantic unification operations. A recent study (Pena & Melloni, 2012) supports our claim. In that study, gamma power increases were observed only when Spanish or Italian monolinguals listened to sentences in their own language, not when they listened to sentences spoken in a phonologically related or an unre-

lated language. Note however that, in this study, gamma power changes were observed in a higher gamma frequency range (around 70 Hz) than in the previously mentioned studies.

A different strand of studies has investigated the relationship between oscillatory dynamics in the EEG/MEG and syntactic unification. In an initial study (reviewed in Bastiaansen & Hagoort, 2006), we observed a relative increase in MEG power in a frequency band of 15–25 Hz (i.e., the lower part of the beta frequency range) during reading of syntactically complex center-embedded relative clauses, compared to the more straightforward right-branching relative clauses. Similar results were obtained by Weiss et al. (2005), who observed larger coherence in a similar frequency range (13–18 Hz) in response to syntactically more complex, and less preferred, object-relative clauses as compared to the easier and more preferred subject-relatives. In a recent study (Bastiaansen et al., 2010), the temporal evolution of MEG power changes was quantified across the entire sentence. For syntactically legal sentences a gradual increase in lower beta power (13–18 Hz) was observed. This gradual increase was disrupted upon the occurrence of a syntactic word category violation, and the increase was altogether absent when the sentence did not have any syntactic structure (i.e., when word order was randomized). Note that the gradual increase in beta power across the syntactically legal sentences is in close correspondence with the theoretical notion that syntactic unification load increases across sentences, as a syntactic tree has to be built and maintained in unification space/working memory (Jackendoff, 2007; Vosse & Kempen, 2000). Together, these studies suggest a role for neuronal synchronization in the lower beta band in sentence level syntactic unification.

In summary then, there is considerable evidence in the literature that, during sentence level language comprehension, gamma-band neuronal synchronization is predominantly related to semantic unification operations, whereas beta-band synchronization is related to syntactic unification. It is therefore tempting to relate these findings to the riddle that we addressed earlier: how does the brain segregate the parallel processes of semantic and syntactic unification of a given word in its sentence context, given that both operations appear to be subserved by largely overlapping neuronal tissue (the left IFG) and that they occur roughly in the same time frame (within a few hundred milliseconds after word onset)? Tentatively, we therefore propose a frequency-based segregation of syntactic and semantic unification operations in left IFG.

However, there are a number of problems with this proposal. First, not all the literature is compatible with it. For instance, in a previous study we observed a relatively strong gamma power increase in response to violations of world knowledge (Hagoort, Hald, Bastiaansen, & Petersson, 2004), which clearly constitutes a problematic situation at the semantic level and therefore would have been expected to lead to a disruption of the gamma power

increase for the correct sentence condition. In addition, in a recent study (Wang, Jensen, et al., 2012) we observed a beta power decrease in the MEG upon the occurrence of a semantic violation, where a gamma power decrease would have been expected under the assumption of a dissociation between beta and syntax, on the one hand, and gamma and semantics, on the other hand. Second, (with the exception of the study by Wang, Jensen, et al., 2012), all the studies that provide evidence for gamma-band synchronization being related to semantic unification are based on EEG recordings, whereas all the studies addressing the relation between beta-band synchronization and syntactic unification are based on MEG recordings. Third, it is important to realize that unification is an ongoing process that should be engaged throughout the entire sentence. However, although most of the findings pertaining to beta and syntax have been established across the entire sentence or at least across a substantial part of it (e.g., a critical clause), the reports of a relation between gamma and semantics are exclusively based on responses to local semantic violations or violations of semantic expectancies, that is, on responses to one single word.

Despite these apparent problems, we feel that establishing a frequency-based segregation of syntactic and semantic unification operations would constitute an important step forward in understanding the neural underpinnings of language comprehension. Therefore, in this paper we report a within-subject, within-(imaging) modality study on sentence level syntactic and semantic processing.

Participants read sentences that were either syntactically and semantically correct (COR) or that contained a local syntactic violation (a word category violation, SYN) or a semantic anomaly (SEM) on a critical word. In addition, two conditions were included in which the semantics or the syntax was violated across the entire sentence: (i) a syntactic prose condition, consisting of a syntactically correct, but semantically uninterpretable sentence (a “global semantic” violation, hence PROSE) and (ii) a condition in which the sentence’s word order was randomized so as to destroy its syntactic structure (a “global syntactic” violation, RAND). An example item set is given in Table 1. On the concurrently measured EEG, we performed a time–frequency (TF) analysis of power changes, in a wide frequency range (from 1 to 100 Hz). Crucial for a test of our proposal of a frequency-based segregation of different types of unification is the evolution of power changes in the COR, PROSE, and RAND conditions. The SEM and SYN conditions were mainly included in the experiment to allow for a comparison with previously observed results. If our proposal is correct, we should expect relatively larger beta power for syntactically correct sentences (COR, but also PROSE) than for syntactically incorrect sentences (RAND). Similarly, we should expect relatively larger gamma power for semantically correct sentences (COR) compared to semantically anomalous sentences (PROSE, but also RAND, as the word order randomization also renders the

Table 1. An Sample Item Set and Its English Translation

<i>Condition</i>	<i>Example Materials</i>
COR	De ijverige medewerker kopieert het document voor de ongeduldige baas <i>The industrious employee copies the document for the impatient boss</i>
SEM	De ijverige medewerker kopieert het geslacht voor de ongeduldige baas. <i>The industrious employee copies the gender for the impatient boss</i>
SYN	De ijverige medewerker kopieert de document voor de ongeduldige baas. <i>The industrious employee copies the_{COM} document_{NEU} for the impatient boss</i>
PROSE	De stoffige gevangenis graveert het geslacht voor de onschuldige keel. <i>The dusty prison engraves the gender for the innocent throat</i>
RAND	Baas ijverige voor de de document kopieert ongeduldige het medewerker. <i>Boss industrious for the the document copies impatient the employee</i>

Critical words are marked in **boldface**. COM = common gender; NEU = neuter gender.

sentence incomprehensible). Finally, for syntactically legal sentences (COR and PROSE), we expect a gradual (linear) increase in beta power across the sentence compared to illegal ones (RAND), reflecting increasing syntactic unification load because of an incremental extension of the phrasal configuration. We do not necessarily expect such gradual increase in gamma power, however, for semantically correct sentences (COR) compared to semantically anomalous sentences (PROSE and RAND), because the semantic unification load does not seem to be distributed in a linearly increasing fashion across the sentence.

METHODS

Participants

Thirty native speakers of Dutch, 9 men and 21 women, participated in the experiment after having given informed consent. None had neurological impairments, experienced neurological trauma, or had used narcoleptics. The participants were paid a small fee for their participation. Ages ranged from 18 to 26 years (mean: 21 years).

Stimulus Materials

The experimental stimulus materials consisted of 300 quintets of Dutch sentences. A sentence quintet contained the following five conditions (see Table 1 for examples of

the stimulus materials). The correct sentence (COR) condition consisted of grammatically correct Dutch sentences that varied in length from 9 to 11 words. The sentences were constructed such that in each sentence there was a noun occurring either in the seventh, eighth, or ninth position of the sentence, that was preceded by an indefinite article (“de,” for nouns with common syntactic gender, “het” for nouns with neuter syntactic gender). This noun is referred to as the critical word (CW) hereafter. In the second condition (SEM), a semantic anomaly was introduced by replacing the CW with a semantically unrelated noun that was matched for length (100% match) and frequency ($t(299) = -0.95, p = .343$) to the CW. The third condition (SYN) involved a syntactic violation: here we replaced the article preceding the CW by the article with the opposite gender (i.e., not matching with the gender of the CW). This resulted in a syntactic gender agreement violation at the CW (see also Table 1). In a behavioral pretest with 24 participants (different from those participating in the main experiment), we determined the cloze probability of the critical words in the COR condition to be .31, whereas the cloze probabilities in the SEM and SYN conditions were zero.

In the fourth condition (PROSE), we created syntactic prose on the basis of the correct sentences by replacing all nouns, verbs, and adjectives by length- and frequency-matched semantically unrelated ones. This resulted in syntactically correct, but semantically uninterpretable sentences. Finally, in the fifth condition (RAND), all the words of the correct sentence were presented without modification but in a random order (Table 1). Only the CW was kept at the same position as in the correct sentence condition. After randomizing word order, it was verified that the resulting sentence did no longer contain a legitimate syntactic structure. In the rare cases where the randomization procedure did result in a possible syntactic structure, words were manually displaced so as to make this structure illegal.

In addition to the 300 experimental quintets, the stimulus materials also contained 180 correct filler sentences, which varied in length from 6 to 10 words (8 on average). Thus, the number of correct sentences (60 experimental sentences [COR] + 180 filler sentences = 240 correct sentences) was equal to the number of sentences containing violations (120 sentences with local violations [SEM and SYN] and 120 severely violated sentences [PROSE and RAND]).

Experimental Design

We created five different trial lists, consisting of 60 sentences from each condition plus the 180 filler items. The trial lists were created such that an individual participant saw only one sentence of any one quintet. Each list thus contained 480 sentences. For each list, sentence order was randomized separately for each experimental session, so as to avoid any order effects.

Each trial started with a blank screen for 300 msec, which was followed by a word-by-word presentation of the sentences. The words were presented in white fonts on a gray background in the middle of the screen. Each word was on screen for 300 msec, followed by a 300-msec long blank screen. SOA was 600 msec. After the offset of the last word in the sentence and before the onset of the first word of the next sentence, an asterisk was presented for 3000 msec, giving time to the participants to blink.

Procedure

Before the EEG measurement started, participants were asked to read information about the measurement procedure and the instructions about the experiment. Participants were instructed to read the sentences carefully for comprehension. They were told beforehand that some of the sentences would be “strange.” They then filled out an informed consent form.

The measurement took place in 24 short blocks of 20 trials, each block lasting approximately 2.5 min. At the end of each block, participants were allowed to take a short break and could continue with the next block by pressing a response button in front of them. Participants were allowed to leave the EEG recording room in between blocks. Participants were asked to refrain from blinking while reading the sentences. To familiarize the participants with the procedure, a practice block of 11 sentences preceded the first experimental block. The entire session, including subject preparation, instructions, practice block and debriefing took approximately 70 min.

EEG Recordings

The EEG was recorded in an electromagnetically shielded cabin, with 60 surface active electrodes (Acticap, Brain Products, Herrsching, Germany) placed in an equidistant montage. The left mastoid electrode served as the reference, and a forehead electrode served as the ground. A supra- to suborbital bipolar montage was used to monitor vertical (left) eye movements, whereas a right to left canthal bipolar montage was used to monitor horizontal eye movements. All electrode impedances were kept below 10 K Ω during the experiment (which is well below what is recommended for active electrodes). EEG data were digitized at a rate of 500 Hz with a 100-Hz high cut-off filter and a 10-sec time constant.

Data Analysis

Preprocessing

Brain Vision Analyzer software 1.05 (Brain Products) was used to preprocess the raw EEG data. The EEG data were re-referenced offline to the average of both mastoids, and a 1 Hz high-pass filter (48 dB/octave) was applied. Then, the data were segmented in two different ways.

For the conditions that allow for a time-locking to the CW (COR, SEM, and SYN), epochs from 1000 msec before to 2000 msec after CW onset were selected, and a baseline correction from -200 to 0 msec preceding word onset was applied. After that, artifacts were rejected using a semiautomatic rejection procedure. On average, 4% of all trials were rejected, with rejections being equally distributed across the three conditions ($F < 1$).

For the conditions in which we were interested in the evolution of power changes across the entire sentence (again COR, but also PROSE and RAND), we selected epochs from 2000 msec before to 6000 msec (with a SOA of 600 msec, this corresponds to 10 words) after sentence onset, and a baseline from -200 to 0 msec preceding sentence onset was applied. After that, artifacts were rejected using a semiautomatic rejection procedure. On average, 8% of all trials were rejected, with rejections being equally distributed across the three conditions ($F < 1$).

ERP Analysis

For the COR, SEM, and SYN conditions, an ERP analysis was performed by averaging the CW-locked epochs across trials, separately for each participant and each condition. Before averaging, the data were band pass filtered between 0.1 and 30 Hz. A baseline correction was applied, using a baseline interval from -150 to 0 msec preceding CW onset. Finally grand averages across participants were created for each condition for display purposes.

TF Analysis

For a TF analysis of the EEG data and the subsequent statistical analysis, we used the Matlab toolbox Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen, 2011). We analyzed both the CW-locked data and the sentence onset-locked data (see the section on Preprocessing) using the follow strategy: Low-frequency components and high-frequency components were analyzed separately to optimize the analysis protocol for each frequency range. For the lower-frequency range, TF representations were obtained by applying a Hanning taper with a length of 400 msec, followed by an FFT, in 10-msec time steps, in a frequency range from 2 to 30 Hz, in 1-Hz steps. For the higher-frequency range, we used multitapers (Mitra & Pesaran, 1999) with a 400-msec time smoothing and a 5-Hz frequency smoothing (which resulted in the use of three tapers), in a frequency range from 25 to 100 Hz, in steps of 2.5 Hz.

TF transforms were computed for all single trials and subsequently averaged across trials for each participant and condition separately. Power changes were then expressed as the ratio of the increase or decrease relative to a 500-msec pre-CW baseline (for the CW-locked analyses) or a 1000-msec presentence baseline (for the sen-

tence onset-locked analyses). Finally, for each analysis, grand averages across subjects were created for each condition for display purposes.

For the CW-locked analysis, the above procedure pools together both purely phase-locked activity (the frequency contents of the ERP) and non-phase-locked activity. To disentangle these two types of activity, we additionally performed a TF analysis on the subject-averaged ERP data (as opposed to running the analysis on the single-trial data, as one usually does in TF analysis), separately for each condition. Because ERP data only contain phase-locked activity, the TF analysis on the ERP data will only yield TF components that are solely reflecting this phase-locked activity. By qualitatively comparing those results to the results of the standard TF analysis (on the single-trial data), one can then establish which TF components are brought about by the ERP data and which components truly reflect non-phase-locked oscillatory activity, that is, that part of the time-locked EEG response that is not contained in the ERP. The time intervals for analysis and the settings for the multitaper TF decomposition were identical to those used in the TF analysis on the single-trial data.

Regression Analysis

To establish whether power changes across the sentence showed any linear trends, we performed a linear regression analysis on the TF data of the sentence onset-locked data, separately for each condition. First, we defined two frequency ranges of interest based on a priori knowledge (see Introduction), and we further fine-tuned these frequency bands on the basis of a visual inspection of the results (notably the condition contrasts shown in Figures 3–5) to optimize the sensitivity of our analyses. This led to the following frequency ranges of interest: beta: 10–20 Hz; gamma: 40–60 Hz). The differences between these “visual inspection” frequency bands and the “a priori” frequency bands (beta: 13–18 Hz; gamma: around 40 Hz) are so small that we consider this to be a mere fine-tuning of the bands we have observed in previous studies. We are therefore confident that this approach does not result in double dipping. Then, separately for each condition, frequency band, and channel, we fitted a linear regression line to the individual subject averages, where power (beta power for the beta-band analyses and gamma power for the gamma-band analyses) was the dependent variable and time was the independent variable. Finally, we determined whether there were significant differences in the regression coefficients (the beta values or slopes of the regression lines) between conditions at the group level by performing t tests against zero on the individual linear regression coefficients (the slopes or beta values of the regression lines) for each condition and for each frequency band. Significant effects then indicate that linear trends are stronger (i.e., more positive-going or more negative-going) in one condition compared to another condition.

Statistical Analysis

For a statistical analysis of the ERP data, the subject-averaged data were averaged in a time window from 300 to 500 msec after CW onset for the N400 and from 600 to 900 msec post-CW for the P600. Next, channels were grouped into four quadrants (see the inset in Figure 1), and their values were averaged within each quadrant. An ANOVA for repeated measures was performed with the factors Condition (COR, SEM, SYN), Hemisphere (left, right), and Anteriority (anterior, posterior). Degrees of freedom were adjusted using Greenhouse–Geisser's epsilon to correct for violations of the sphericity assumption where necessary.

For the TF data, the statistical significance of the difference between conditions was evaluated by a cluster-based random permutation approach (see Maris & Oostenveld, 2007, for details on the method), implemented in Fieldtrip. This approach elegantly handles the multiple comparisons problem. It naturally takes care of interactions between time points, frequency bins, and channels by identifying clusters of significant differences between conditions in the time, frequency, and space dimensions and effectively controls the Type 1 error rate for multiple comparisons. Here is a brief description of the procedure. (For more details, see Maris & Oostenveld, 2007.)

First, for every data point (time-electrode point), a simple dependent samples *t* test is performed (giving uncorrected *p* values). All data points that do not exceed a preset significance level (here 5%) are zeroed. Clusters of adjacent nonzero data points are computed, and for each cluster, a cluster level test statistic is calculated by taking the sum of all the individual *t* statistics within that cluster. Next, a null distribution is created as follows. Subject

averages are randomly assigned to one of the two conditions several times (here 1000 times), and for each of these randomizations, cluster level statistics are computed. For each randomization, the largest cluster level statistic enters into the null distribution. Finally, the actually observed cluster level test statistics are compared against the null distribution, and clusters falling in the highest or lowest 2.5th percentile are considered significant.

This procedure does not allow for a simultaneous comparison of three conditions. Therefore, a set of two pairwise comparisons was performed for the CW-locked data: COR versus SEM and COR versus SYN. Separate analyses were performed for the low- and high-frequency ranges. For the sentence onset-locked data, the following comparisons were tested (again, separately for the low and the high frequency range): COR versus PROSE, COR versus RAND, and RAND versus PROSE.

RESULTS

ERP Data

The results of the ERP analysis are presented in Figure 1. The semantic anomalies in SEM resulted in a larger N400 compared to COR, whereas the syntactic violations in SYN resulted in a larger P600 compared to COR (Figure 1A). The scalp topographies of these effects are in agreement with the classical distribution of these effects (Figure 1B).

The statistical analysis of the ERP data confirmed the presence of these effects. For reasons of focus, we only present here the effects that involve the factor Condition.

For the N400 time interval, a main effect of Condition ($F(2, 58) = 13.45, p < .001$) and subsequent contrasts indicated that amplitudes in the SEM condition were more negative than in COR ($F(1, 29) = 20.73, p < .001$) and in SYN ($F(1, 29) = 11.91, p = .002$), whereas COR and SYN did not differ ($F(1, 29) = 0.926, p = .344$). Furthermore, a Condition \times Hemisphere interaction indicated that the effects were largest in the right hemisphere ($F(2, 58) = 12.25, p < .001$).

For the P600 time interval, the main effect of condition and the two-way interactions Condition \times Hemisphere and Condition \times Anteriority were not significant (*p* values between .05 and .1). However, a three-way interaction Condition \times Hemisphere \times Anteriority ($F(2, 58) = 3.54, p = .044$) indicated a significant condition effect at right posterior positions only ($F(2, 58) = 3.35, p = .049$). Contrasts further indicated that SYN was more positive than COR ($F(1, 29) = 6.47, p = .017$), whereas SEM did not differ from COR ($F(1, 29) = 0.92, p = .347$). The difference between SYN and SEM did not reach significance, however ($F(1, 29) = 2.25, p = .145$).

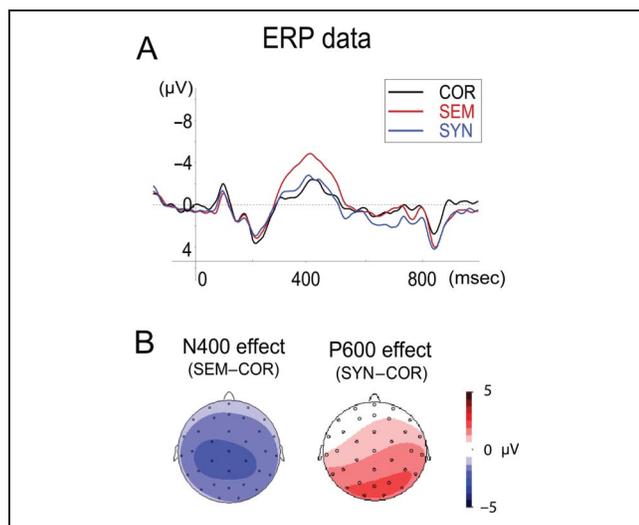


Figure 1. Results of the ERP analysis. (A) ERP time course in three conditions (COR, SEM, and SYN) time-locked to the onset of the critical word at a representative channel (channel 30, corresponding to Cz in the 10–20 system). (B) Topographic distribution of the ERP effects.

TF Data, CW-locked

The results of the TF analysis on the CW-locked data are presented in Figure 2. The only significant cluster

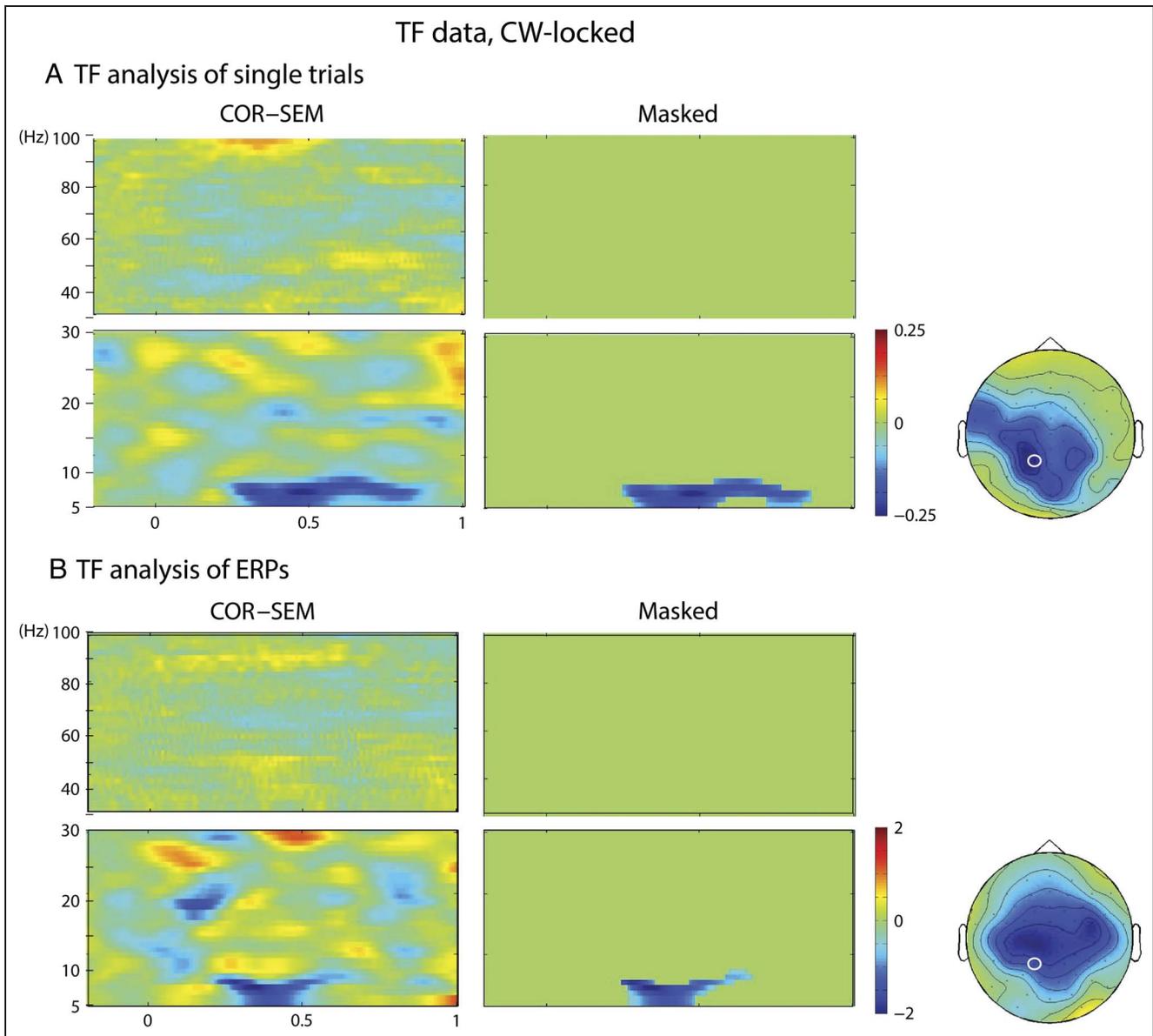


Figure 2. Results of the TF analysis on the CW-locked data. (A) Analysis on the single-trial data (conventional TF analysis). TF representation of the significant COR-SEM contrast, both as the relative difference in power at a representative channel (left-hand column) and with a statistical mask showing only the significant cluster (middle column). Both the low- and high-frequency ranges are shown. The color scale indicates the relative power difference (0 = no difference). The right-hand column shows the scalp topography of the difference in power; the white circle marks the location of the channel shown in the other columns. (B) Same as in A, but now for the TF analysis on the subject-averaged ERP data.

($p = .047$) was found in the contrast between COR and SEM. It consisted of an increase in theta power for the SEM condition compared to the COR condition. This increase was significant from approximately 300 to 800 msec after CW onset, over central and left frontotemporal electrodes. In the TF analysis on the ERP data, a comparable though slightly different cluster was observed ($p = .015$). Here the differential theta power increase lasted shorter (roughly from 300 to 500 msec) and had a postcentral maximum, highly comparable to that of the N400 effect (see Figure 1). There were no significant clusters in the COR-SYN contrast or in the SEM-SYN contrast for the CW-locked data.

TF Data, Sentence Onset-locked

The results of the TF analysis on the sentence onset-locked data, extending over the entire sentence, are shown in Figures 3–5, separately for the three different contrasts: COR-PROSE, COR-RAND, and PROSE-RAND.

COR-PROSE Contrast

In the lower-frequency range, we observed no significant effects for this contrast. In the higher-frequency range, there was significantly ($p = .034$) more gamma power

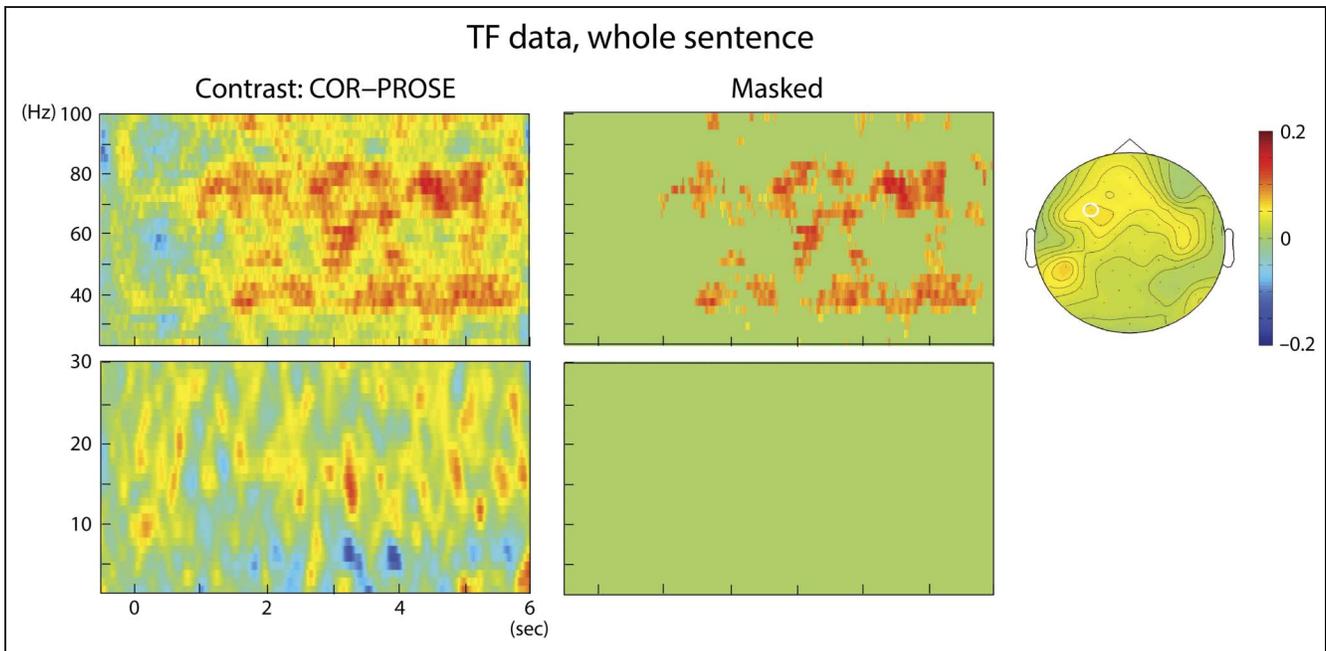


Figure 3. Results of the TF analysis on the entire sentence for the COR-PROSE contrast. See legend to Figure 2 for further details.

for COR than for PROSE from approximately 1–1.5 sec after sentence onset (roughly coinciding with the onset of the third word) for COR than for PROSE. The power increase for COR was most consistently observed in two frequency bands, one around 40 Hz and the other around 70–80 Hz. The scalp topography of the gamma effect showed a left posterior temporal and left frontal maximum.

COR-RAND Contrast

Larger power ($p < .001$) was observed in a frequency band from 10 to 20 Hz for COR than for RAND, starting from 1 to 1.5 sec after sentence onset and lasting throughout the sentence (Figure 4, bottom row). The scalp topography of this beta-band effect shows a maximum at around the vertex.

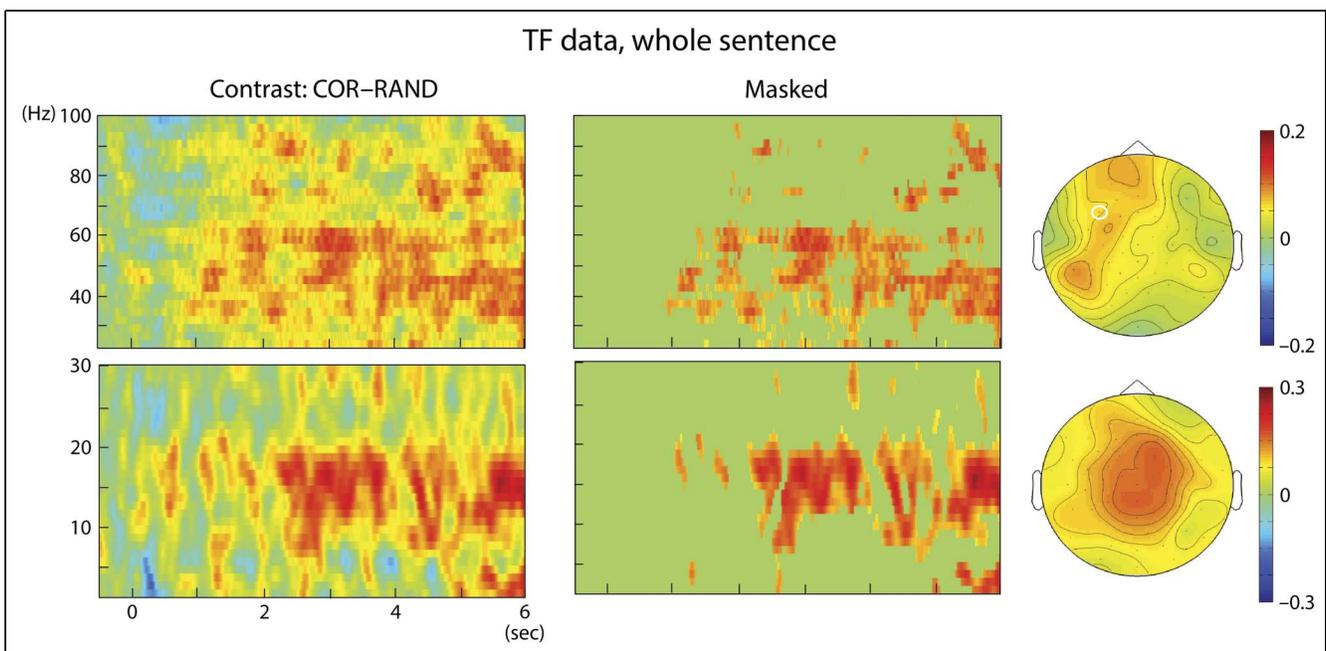


Figure 4. Results of the TF analysis on the entire sentence for the COR-RAND contrast. See legend to Figure 2 for further details.

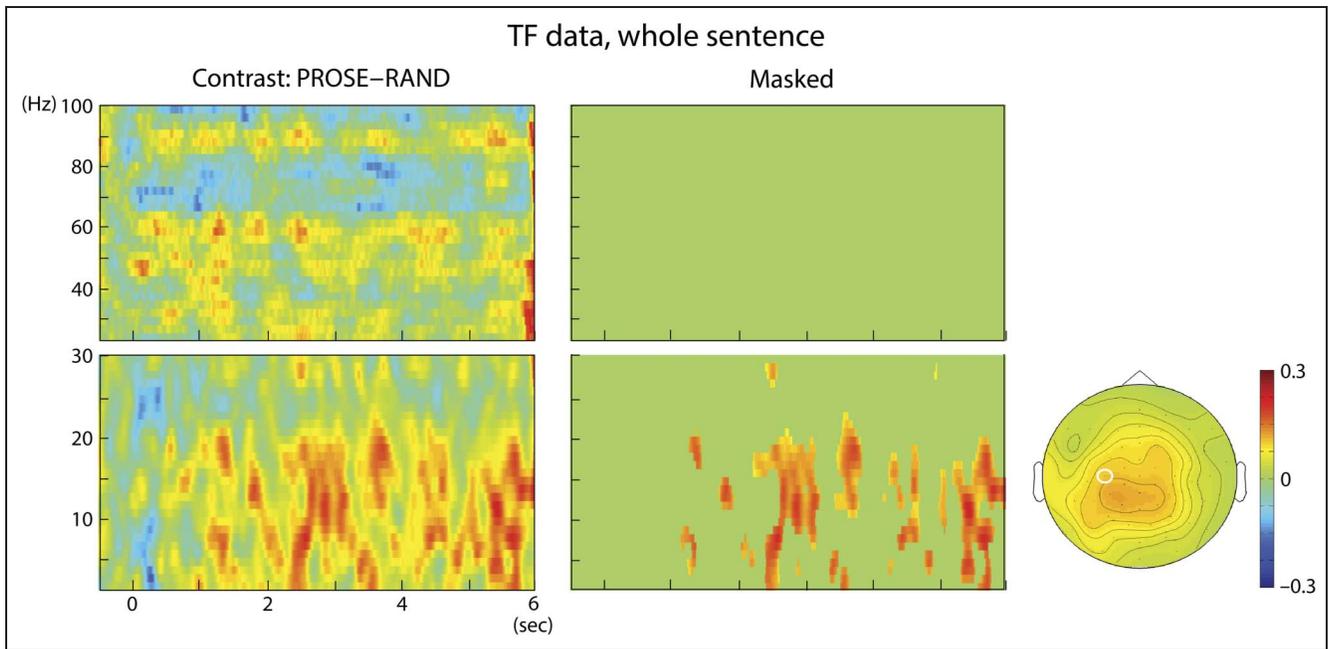


Figure 5. Results of the TF analysis on the entire sentence for the PROSE–RAND contrast. See legend to Figure 2 for further details.

In the higher-frequency range, larger power ($p = .01$) is observed for COR than for RAND in the same time range. This effect is mostly centered in a frequency window from 40 to 60 Hz. The gamma effect has left posterior temporal and left frontal maxima.

PROSE–RAND Contrast

In the lower frequencies, larger power ($p < .001$) was observed for PROSE than for RAND in the 10–20 Hz frequency window (Figure 5), although the cluster has some temporal discontinuities. The beta cluster has a maximum at around the vertex. No significant effects were observed in the higher-frequency range.

Regression Analysis

Regression analyses were performed for the beta and gamma frequency bands separately. For the gamma frequency range, the t tests did not reveal any significant linear regression slopes on any of the channels in any of the conditions. Therefore, we only present the results of the regression analysis in the beta frequency range (Figure 6). Taking the full 6000-msec epoch that covers all words but the sentence-final one, no positive trends are observed in the individual conditions (Figure 6A), but a clear negative trend can be observed for the RAND condition. Testing for differences between the slopes at each channel (Figure 6B), we observe relatively more positive (or less negative) slopes for the COR and PROSE conditions than for the RAND condition.

Note that we did not perform a multiple-comparison correction for the regression analyses. Therefore, we were careful not to interpret the COR–PROSE contrast

as indicating differences in regression slopes between the conditions, as only 5 of 63 channels passed the uncorrected significance threshold. For the other two contrasts (COR–RAND and PROSE–RAND), the uncorrected threshold was passed for at least 57 of the 63 channels, which is highly unlikely to be the result of Type I errors.

DISCUSSION

Semantic and syntactic unification of an incoming word into its preceding sentence context are functionally distinct operations. Nevertheless, both roughly take place at the same place (in spatially overlapping, left frontotemporal networks) and at the same time (in the first few hundred milliseconds after onset of the incoming word). Primed by earlier results from studies addressing either semantic or syntactic unification operations, we tested the hypothesis that semantic and syntactic unification are segregated by means of neuronal synchronization of the functionally relevant networks in different frequency ranges: gamma (40 Hz and up) for semantic unification and lower beta (10–20 Hz) for syntactic unification. In the analysis of power changes across the entire sentence, larger EEG gamma-band power was observed for semantically coherent (and therefore unifiable) sentences (COR condition) than for semantically anomalous sentences (PROSE and RAND conditions) throughout the entire sentence. Similarly, lower beta-band power was larger for syntactically correct sentences (COR and PROSE) than for incorrect ones (RAND), and this effect increased over the first half of the sentence. All observed beta- and gamma-band effects started after 1–1.5 sec after sentence onset, that is, around the onset of the third word of the sentence, and lasted throughout the entire sentence. As

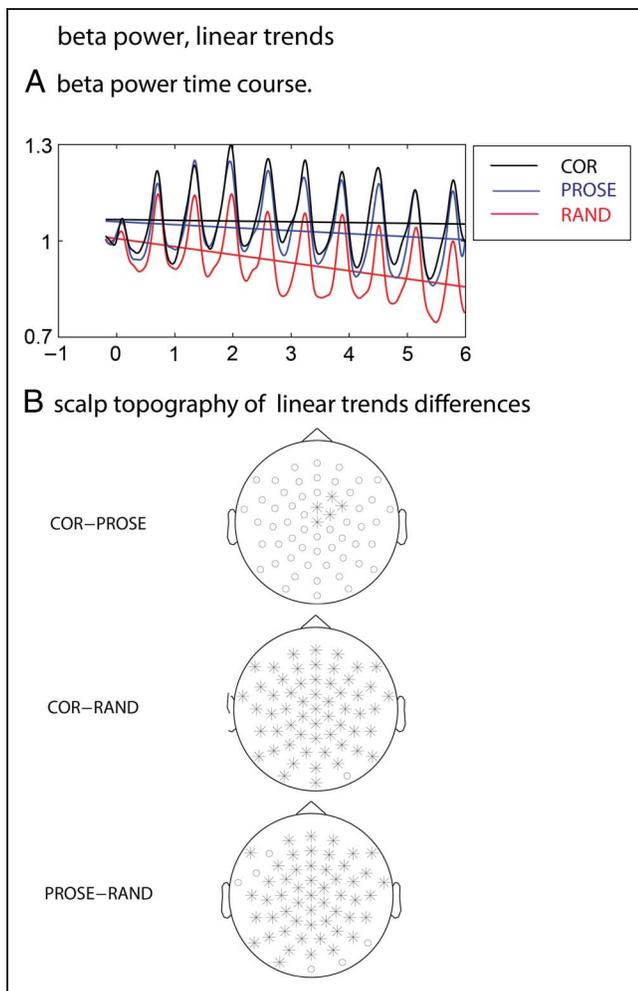


Figure 6. Results of the linear regression analysis on the temporal evolution of beta power (10–20 Hz). (A) Line plot of beta power across the first 6000 msec of each sentence (corresponding to all but the sentence-final word) and the corresponding regression lines for each condition separately. (B) Topographic representation of the significant differences in regression slope between conditions for each of the statistical contrasts. Asterisks indicate electrodes with a significant difference; open circles indicate channels with no significant difference.

the sentences unfolded, beta power gradually decreased for the RAND condition and remained stable for the COR and PROSE conditions.

For the conditions in which syntax or semantics were violated locally, that is, on a single CW (SEM and SYN, respectively), in the CW-locked analyses, we did not observe any effects in the beta and/or gamma frequency ranges. Instead, larger theta power was found for semantically anomalous critical words compared to their correct counterparts. We return to this later.

Beta Power Increases Are Related to Syntactic Structure Building

The observed effects in the beta frequency range essentially replicate previously reported results (Bastiaansen

et al., 2010) and are in line with the hypothesis that beta-band neuronal synchronization is related to syntactic unification operations. The beta-band results further extend these previous findings, in that they indicate that, even in the absence of interpretable semantics, the mere presence of a syntactically correct sequence of words (the syntactic prose in the PROSE condition) is sufficient for eliciting a beta-band power increase compared to equally meaningless but syntactically incorrect word sequences.

In addition, we observe clear differences in the slope of beta power across the entire sentence for the different conditions. In the RAND condition, a negative slope was present, whereas in the two syntactically correct conditions (COR and PROSE), no such negative slope was present. This suggests that when the language comprehension system cannot compute syntactic relations between the words in a sentence (RAND condition), EEG beta power decreases, whereas beta remains stable when syntactic relations can be established (COR and PROSE conditions). Taking the contrast between the conditions as our prime marker for syntactic unification, we interpret this pattern as a relatively more positive-going slope for the syntactically correct conditions (COR and PROSE) compared to the syntactically incorrect condition (RAND). This pattern is similar to the pattern observed in the MEG study reported in Bastiaansen et al. (2010), where we found a positive slope for beta power in the correct sentence conditions and an absence of such a positive slope in the random word order sentences. It should be noted, however, that in terms of “absolute” slopes, the effects differ in the two experiments (positive for the MEG study and zero for the current study in the correct sentence condition vs. zero for the MEG study and negative for the current study in the random word order sentence condition). We have no ready explanation for this difference in absolute slopes. However, as said, in terms of condition contrast, both studies show the same pattern of effects, namely a relatively more positive-going slope for the correct sentence condition than for the syntactically incorrect sentences.

This pattern is exactly what one would expect for an effect that is related to the incremental building of a syntactic structure that represents the incoming sentence (see Jackendoff, 2007; Vosse & Kempen, 2000, for corresponding theoretical positions) and clearly contrasts with the pattern observed for the gamma frequency range (see below), where we did not expect and did not observe such a linear increase in power across the sentence.

Thus, in our view, our data strengthen the notion that beta-band power is related to syntactic structure building at the sentence level. Further evidence for this notion stems from observations of increases in beta power (Bastiaansen & Hagoort, 2006) and beta coherence (Weiss & Mueller, 2003) during the comprehension of syntactically complex/dispreferred sentence structures. Finally, it is remarkable that all of the studies mentioned

here reported effects in almost the same subfrequency range of the beta band, namely 10–20 Hz. It is unclear to us at present why this should be the case.

It is important to note that beta power and/or coherence changes have been observed in a wider range of language comprehension tasks and have been interpreted to relate to different components of language comprehension, from word category discrimination to the retrieval of action semantics (for an excellent review, see Weiss & Mueller, 2012). In the latter review paper, the authors make a commendable effort to integrate all the different research findings into an overall hypothesis of the role of beta oscillations during language comprehension and conclude that beta is related to at least four different aspects of language comprehension (for details, see Weiss & Mueller, 2012). However, in our opinion both the experimental paradigms employed and the research findings observed are so diverse that overarching functional hypotheses are necessarily of a too general nature and that more experimental work is needed to delineate more precisely and more robustly the beta effects obtained in the different experimental paradigms, both at a functional level and (when possible) at a neurophysiological level. We feel that our present study contributes to such a research agenda by narrowing down the functional significance of sentence level beta power increases to syntactic rather than to semantic operations.

Gamma Power Increases Are Related to Semantic Unification

In line with our hypothesis, gamma band power was larger for semantically correct sentences than for incorrect ones, and this effect was present throughout the entire sentence. The observed gamma power effects were present in slightly different frequency ranges for the two relevant contrasts. For the COR–PROSE contrast effects were obtained in two different frequency ranges, around 40 Hz and from 70 to 80 Hz, whereas in the COR–RAND contrast effects were found in the 40–60 Hz range. In addition, the gamma power increases show up in a relatively “patchy” way, especially after thresholding for statistical significance (Figures 3 and 4). However, the frequency range in which the effects occur is clearly distinct from the one in which we observe the effects related to syntactic unification. Our data extend previous reports of a gamma power increase in response to a semantically correct critical word (relative to its semantically anomalous counterpart; Rommers et al., 2013; Hald et al., 2006) to the level of the entire sentence, and as such they are in line with the notion that gamma-band neuronal synchronization is involved in sentence level semantic unification operations.

Note that in some cases gamma-band power increases have been related to microsaccadic activity (Yuval-Greenberg, Tomer, Keren, Nelken, & Deouell, 2008). However, typically the gamma associated with microsaccades is very broadband (typically from 20 to 100 Hz) and

short-lived in nature (for extensive discussion, see Fries, Scheeringa, & Oostenveld, 2008), whereas the gamma that we observe is more narrow-band and longer-lived, making it unlikely that the observed effects in the gamma range are related to microsaccades.

It should be noted however that, in the present data, we failed to replicate the previously observed “local” gamma effect (Rommers et al., 2013; Hald et al., 2006) in the CW-locked analysis, in that we did not observe a CW-locked gamma power difference in the COR–SEM contrast. It is plausible that this is related to the differences in cloze probability of the critical words. These were substantially higher in Hald et al. (2006) and Rommers et al. (2013; 49% and 87%, respectively) than in this study (31%). Recent data confirm that, indeed, transient gamma power responses to semantic violations are highly sensitive to cloze probability (Wang, Zhu, et al., 2012).

Frequency-based Segregation of Syntactic and Semantic Unification?

Apart from the details, the overall picture that emerges from our results is that, in a within-subject, within-imaging modality design, we have replicated and extended the results from previous, isolated studies, in that we show evidence that gamma-band neuronal synchronization is related to sentence level semantic unification, whereas beta-band synchronization is related to syntactic unification. Furthermore, as we hypothesized in the introduction, we observed the (theoretically motivated) pattern of a steady increase in beta throughout the sentences, reflecting increased syntactic unification load. We did not observe such a linear increase across the sentence for gamma power.

Oscillations at beta and gamma frequencies are claimed to be especially effective to engage discrete neuronal populations in supporting transfer of packets of specific information among relevant neuronal assemblies (Lopes da Silva, 2014). In this case there might be overlapping neuronal assemblies in frontal and temporal cortex. As such, our present data and most of the published data (but not all; see e.g., Wang, Jensen, et al., 2012) are clearly compatible with the hypothesis of a frequency-based segregation of semantic and syntactic unification within the frontotemporal language network and thus provide support for the view that, during language comprehension, syntactic and semantic information is processed by groups of neurons that synchronize at different frequencies to transiently couple into functionally distinct networks. Note however that, in the MEG study by Wang and colleagues (Wang, Jensen, et al., 2012), a beta power decrease has been observed following semantically incongruous words in a standard N400 paradigm, where a gamma power decrease would have been expected under the hypothesis of a frequency-based segregation of semantic and syntactic unification. It is unclear to us as yet why the results from this particular study

did not conform to the overall pattern dissociation between beta and gamma observed in other published data.

In the Introduction, we have argued that the necessity for such a frequency-based segregation stems in part from the observation that networks for semantic and syntactic unification are largely spatially overlapping (Bookheimer, 2002; for a discussion, see also Hagoort, 2005, 2013). However, the presently observed gamma and beta effects have clearly distinct scalp topographies (see the topographical maps in Figures 3–5). The gamma-band effects have maxima over the left posterior temporal and the left frontal scalp, which is well compatible with the notion that semantic unification is a result of a dynamic interplay between left posterior superior/medial temporal gyrus and IFG (cf. Baggio & Hagoort, 2011). The beta-band effects, instead, have a maximum around the vertex. The different scalp topographies seem to suggest different underlying neural generators. However, it is difficult to relate scalp topographies to underlying source locations, as it is well established that electrical potentials from different sources mix at the level of scalp EEG recordings and that small changes in source orientation can have a large impact on scalp topographies. As such, it would be desirable to have better view on the neuronal generators of the presently observed power changes to verify whether both the beta and gamma power increases originate from the left IFG. However, EEG, with its spatial imprecision, is not the method of choice for getting at the sources of the observed effects. Replication of the present findings with methods that are well suited for source reconstruction, such as MEG, or simultaneous EEG/fMRI recordings (for the latter, see, e.g., Scheeringa et al., 2011) would therefore be valuable in determining the sources underlying the observed beta and gamma power increases. This would enable a better connection between studies on the dynamics in functional networks, such as the present one, and the large body of hemodynamic literature on the subject (see, e.g., Hagoort & Indefrey, 2014 for a recent and comprehensive meta-analysis).

Note in addition that our present data (and most of the data reported in the literature) are based on analyzing power changes, not coherence changes (e.g., Weiss & Mueller, 2003). Therefore, the current data only speak on local synchronization changes, not on long-range synchronization, that is, between areas in frontal and temporal cortex (see Bastiaansen et al., 2012; Bastiaansen & Hagoort, 2006, for a detailed discussion of the difference between power and coherence changes). For a full view of both local and long-range changes in synchronization and a clear relationship to the underlying neuronal tissue, we advocate the use of MEG power and coherence estimates at the source level (Gross et al., 2001).

Theta Power Changes at the Critical Word

The ERP analysis time-locked to CW onset revealed the classical ERP effects: an N400 effect for the semantic

violations and a P600 effect for the syntactic violations. For the TF analysis of the CW-locked data, an increase in theta power was observed in response to the semantic violations, which replicates previous findings (Hald et al., 2006). This theta power increase is not merely attributable to the fact that the larger N400 in the SEM condition translates into the TF domain as a larger theta wave, as is evidenced by the fact that the TF representation of the ERP (Figure 2B) is different from the TF representation of the (single-trial-based) power changes (Figure 2A). The latter show a longer-lasting theta power increase and a scalp topography that extends to left temporal areas. The observation that the (non-phase-locked) theta power in Figure 2A is more extended in time could potentially be attributed to the fact that as one moves farther away in time from the stimulus, phase-locking may decrease. However, the fact that scalp topographies differ strongly suggests that the observed theta power increase is at least partly a truly non-phase-locked, oscillatory phenomenon. In previous studies, we have related theta power increases during language comprehension to the retrieval of lexical semantic information (Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008; Bastiaansen, Van der Linden, ter Keurs, Dijkstra, & Hagoort, 2005). The current theta effects fit well within such a framework, because the retrieval of a semantically anomalous lexical item can be considered to be more difficult (or rather, less facilitated through its context) than its semantically congruent counterpart.

Conclusion

Our data clearly demonstrate the existence of a functional dissociation in the oscillatory dynamics of the EEG during sentence level language comprehension: Power increases in the gamma frequency range are observed only during semantically congruent sentences, whereas power increases in the lower beta frequency band are observed only during syntactically correct sentences. This functional dissociation is compatible with the notion of a frequency-based segregation of syntactic and semantic unification: During language comprehension, syntactic and semantic unification is represented by groups of neurons that synchronize at different frequencies to transiently couple into functionally distinct networks.

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