Brain & Language 148 (2015) 51–63

Contents lists available at ScienceDirect

Brain & Language

journal homepage: www.elsevier.com/locate/b&l

Fast oscillatory dynamics during language comprehension: Unification versus maintenance and prediction?

Ashley Glen Lewis [a,b], Lin Wang [c], Marcel Bastiaansen [a,d,*]

[a] Neurobiology of Language Department, Max Planck Institute for Psycholinguistics, Nijmegen, The Netherlands
[b] Radboud University, Donders Institute for Brain, Cognition and Behaviour, Center for Cognitive Neuroimaging, Nijmegen, The Netherlands
[c] Key Laboratory of Behavioral Science, Institute of Psychology, Chinese Academy of Sciences, Beijing, China
[d] Academy for Leisure, NHTV University of Applied Sciences, Breda, The Netherlands

ARTICLE INFO

Article history:
Accepted 3 January 2015
Available online 7 February 2015

Keywords:
EEG
MEG
Language comprehension
Unification
Prediction
Oscillatory dynamics
Beta
Gamma

ABSTRACT

The role of neuronal oscillations during language comprehension is not yet well understood. In this paper we review and reinterpret the functional roles of beta- and gamma-band oscillatory activity during language comprehension at the sentence and discourse level. We discuss the evidence in favor of a role for beta and gamma in unification (the unification hypothesis), and in light of mounting evidence that cannot be accounted for under this hypothesis, we explore an alternative proposal linking beta and gamma oscillations to maintenance and prediction (respectively) during language comprehension. Our maintenance/prediction hypothesis is able to account for most of the findings that are currently available relating beta and gamma oscillations to language comprehension, and is in good agreement with other proposals about the roles of beta and gamma in domain-general cognitive processing. In conclusion we discuss proposals for further testing and comparing the prediction and unification hypotheses.

1. Introduction

Ever since it has been established that electrical activity that originates from the brain can be recorded at the surface of the scalp (Caton, 1875), researchers have been intrigued by the omnipresence of rhythmic, oscillatory activity in these recordings (Beck, 1891 – Polish thesis, for English translation: Beck, 1973; Práwdicz-Neminski, 1913). When Hans Berger published his seminal paper on human scalp EEG (Berger, 1929), he carefully described the conditions under which the so-called alpha (a high-amplitude rhythm at around 10 Hz) and beta (a lower-amplitude rhythm at around 20 Hz) rhythms appear in humans. He is most famous for describing the phenomenon of alpha blocking (also known as the Berger effect), not only upon the opening of the eyes, but also upon the execution of a cognitive task (such as performing arithmetic operations). The latter is probably the first cognitive neuroscience report ever, and it established a clear relationship between a cognitive operation and an event-related change in oscillatory EEG dynamics.

After the initial interest in the functional significance of EEG oscillations, the large majority of 20th century EEG research used the Event-Related Potential (ERP) technique (for a detailed description of ERPs, see Luck, 2005) to uncover the neural basis of cognitive processes. While ERPs have proved to be a very successful tool in cognitive neuroscience, the interest in EEG (and MEG) oscillations saw a renaissance in the early 1990s. Indeed, more than 100 years after the initial discovery of EEG oscillations, interest in these phenomena has been revived, mainly as a result of the view that they might provide a window onto the dynamics of the coupling and uncoupling of functional networks involved in cognitive processing (see e.g., Bastiaansen & Hagoort, 2006; Bastiaansen, Mazaheri, & Jensen, 2012; Singer, 1993, 2011; Varela, Lachaux, Rodriguez, & Martinerie, 2001).

1.1. The brain's language comprehension network

During language comprehension, sounds or orthographic patterns initiate massive memory operations that serve to retrieve the lexical building blocks containing the phonological, syntactic and semantic properties of individual words. These building blocks then have to be 'put together' into a meaningful whole, in order to construct a meaningful interpretation of the linguistic input. In keeping with the framework and terminology used by Hagoort and co-workers (Baggio & Hagoort, 2011; Hagoort, 2005; Hagoort, Baggio, & Willems, 2009), we refer to the latter 'putting together' as unification, a form of combinatorial processing

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* Corresponding author at: Academy for Leisure, NHTV Breda University of Applied Sciences, Archimedesstraat 17, 4816 BA Breda, The Netherlands.
E-mail address: bastiaansen4.m@nhtv.nl (M. Bastiaansen).

http://dx.doi.org/10.1016/j.bandl.2015.01.003

specifically related to and constrained by various levels of linguistic representation. Thus, at a very general level, the cognitive architecture of language comprehension involves at least two components, a memory retrieval component, and a unification component. Our main focus in this review is on the unification component. The memory component has been extensively linked to oscillatory activity in the theta and alpha frequency bands (Bastiaansen & Hagoort, 2006; Bastiaansen, Magyari, & Hagoort, 2010; Bastiaansen, Oostenveld, Jensen, & Hagoort, 2008).

When it comes to the neural architecture of language comprehension, an extensive body of hemodynamic neuroimaging data (PET, fMRI) has provided a wealth of information about the brain areas that are involved in language comprehension (for reviews and meta-analyses, see for instance Bookheimer, 2002; Cabeza & Nyberg, 2000; Hagoort & Indefrey, 2014; Indefrey & Cutler, 2005; Price, 2010). As such, much is known about the neural architecture of language comprehension. The question of how this neural architecture maps onto the cognitive architecture of language comprehension has been the topic of a lively debate. In the past 10 years or so, several models have been proposed for such a mapping (Friederici, 2002; Hagoort, 2005, 2013; Jung-Beeman, 2005; Lau, Phillips, & Poeppel, 2008).

Let us consider in more detail one of these models (Hagoort, 2005, 2009, 2013). Following Jackendoff's notion of a parallel unification of phonological, syntactic and semantic information in an abstract 'unification space' (Jackendoff, 2002), this model proposes that the left inferior frontal gyrus (LIFG), in close cooperation with the left temporal cortex, constitutes the neuronal correlate of this unification space. A meta-analysis of fMRI studies during sentence-level language comprehension (Bookheimer, 2002; Hagoort & Indefrey, 2014) further suggests that within LIFG there is an anterior/posterior 'unification gradient', such 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), while 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 (see also Hagoort, 2005, and Fig. 5 therein). 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 a millisecond after word onset) and in spatially overlapping networks?*

Owing to the inherently poor temporal resolution of the hemodynamic measures (that is, on the order of seconds) on which this model (and most of the models that map cognitive onto neural architectures for that matter) is based, the resulting view is a relatively static one, emphasizing mainly the structural aspects of the brain's language network. A static view does not do justice to the dynamic properties that any language comprehension device must have: Typically, a speaker produces on average 160–260 words per minute (e.g., Tauroza & Allison, 1990); reading is even faster, with an average reader easily handling some 250–300 words per minute (e.g., Rayner, Pollatsek, Ashby, & Clifton, 2012). This means that linguistic retrieval and unification operations must be carried out very rapidly and dynamically. When only the structure of the brain's language network is considered, we are obviously missing out on relevant information about the neural basis of language comprehension, namely its dynamics, and hence also on the necessary tools for answering the above question.

What is lacking then is a view on the rapid dynamics of the brain's language network. This is where studying the patterns of neuronal synchronization and desynchronization, which reveals the underlying network dynamics that are at play during online language comprehension, may be of added value in gaining a better understanding of the neural basis of language comprehension. In Section 2 we will review literature that has been aimed at describing the neuronal dynamics during sentence-level language comprehension, and we will try to use the results of this research to address the question formulated in the previous paragraph. In other words, the question that we want to address more specifically becomes: *What are the neuronal dynamics that mediate the functional segregation of semantic and syntactic unification?*

1.2. Oscillatory dynamics, neuronal synchrony and functional networks: a conceptual framework

One thing that has become very clear on the basis of hemodynamic neuroimaging techniques such as fMRI is that there is no one-to-one mapping between a brain area and a specific (component of a) cognitive function. Imaging studies often report activation of one and the same area during different tasks or cognitive functions, indicating that individual cortical areas can be recruited dynamically for more than one cognitive function. Similarly, one and the same cognitive function typically activates multiple areas in the brain, indicating that these functional correlates tend to be distributed over different parts of the brain. As a result of these insights, spatially distributed, yet functionally coherent networks are increasingly being thought of as the most relevant unit of analysis in cognitive neuroscience (see e.g., Fox et al., 2005; Sporns, 2012; Sporns, Chialvo, Kaiser, & Hilgetag, 2004; Varela et al., 2001, and many more). This has in turn raised the question – for any given functional network – of which mechanism(s) are responsible for the dynamic recruitment of the participating cortical and sub-cortical areas.

Over the last two decades or so evidence has accumulated that patterns of synchronization and desynchronization of neuronal activity are related to the coupling and uncoupling of functional networks in the brain (see e.g., Bastiaansen & Hagoort, 2006; Bastiaansen et al., 2012; Pfurtscheller & Lopes da Silva, 1999b; Singer, 1993, 2011; Varela et al., 2001). Conceptually, the idea is that the synchronous, repetitive firing of neurons is instrumental in activating functional networks because it increases the probability that neurons entrain one another in synchronous firing (Konig & Schillen, 1991). In addition, neurons that are part of one and the same functional network are identifiable as such by virtue of the fact that they fire synchronously, at a given frequency. This frequency-specificity allows one and the same neuron (or neuronal pool) to participate at different times in different representations. Hence, synchronous oscillatory firing is considered to play a crucial role in linking areas that are part of one and the same functional network. Importantly, in addition to recruiting all the relevant network elements, oscillatory neuronal synchrony also serves to bind together the information that is represented in the different elements or subcomponents of the network, as was elegantly demonstrated in a seminal paper by Gray and Singer (Gray, Konig, Engel, & Singer, 1989).

It should be noted here that the alpha frequency band (around 10 Hz) and perhaps, to some extent also the beta frequency band (around 20 Hz), may be something of a special case in this framework. It has been extensively established that in the alpha frequency range, desynchronization in a specific brain area goes hand in hand with the engagement/activation of that brain area, especially when related to motor (Bastiaansen & Brunia, 2001; Pfurtscheller & Lopes da Silva, 1999a; Pfurtscheller, Neuper, Andrew, & Edlinger, 1997) and sensory (Bastiaansen & Brunia, 2001; see also the classical alpha blocking, or Berger effect previously mentioned) processes. Similarly, beta-band desynchronization has often been related to motor cortex activation (see e.g., Parkes, Bastiaansen, & Norris, 2006; Pfurtscheller, Stancak, & Neuper, 1996; Pfurtscheller, Zalaudek, & Neuper, 1998). It is unclear yet how this relates to the process of functional network formation, as the relation between neuronal desynchronization and network recruitment (in the sense of Konig & Schillen, 1991) and binding (in the sense of Gray et al., 1989) is not immediately obvious.

1.3. Quantifying oscillatory neuronal dynamics

In order to empirically study the role of oscillatory dynamics in functional neuronal network formation, one needs to address the question of how to quantify the rapidly changing patterns of synchronization and desynchronization of neuronal activity. First, the fast temporal dynamics involved can only be captured by imaging methods with a high temporal resolution such as EEG and MEG. However, the standard analysis techniques used in EEG and MEG research, which involve the computation of ERPs/ERFs, capture only a restricted range of the underlying neuronal activity (i.e., evoked activity that is strongly time- and phase-locked to an event of interest, but not induced activity, which exhibits time-, but not phase-locking; see e.g., Bastiaansen et al., 2012 for a more detailed discussion). Rather, (restricting ourselves to scalp-recorded activity), two related measures are typically used in this context, namely power and coherence changes (Varela et al., 2001). Event-related changes in frequency band-specific power reflect changes in synchronization of local underlying neural tissue (i.e., within the nodes of a distributed network). Such power changes are typically quantified by means of wavelet analysis (e.g., Tallon-Baudry, Bertrand, Peronnet, & Pernier, 1998) or multitaper analysis (Mitra & Pesaran, 1999). In turn, event-related changes in frequency band-specific (phase) coherence reflect changes in synchronization between spatially distant brain areas (i.e., between the nodes of a distributed network; see Bastiaansen & Hagoort, 2006; Bastiaansen et al., 2012).

Power and coherence measures can be seen as complementary to ERPs/ERFs, providing additional information about the underlying neuronal dynamics that may be overlooked when only using these more traditional approaches. For instance, increases in power are thought to reflect increased synchrony, and hence coupling of the nodes of a functional network. This is what we expect to observe under (for example) normal, successful unification conditions. Decreases in power may (at least some of the time) be related to larger processing costs (e.g., alpha power desynchronization is thought to reflect increased attentional demands, cf., Jensen & Mazaheri, 2010). In contrast, larger ERP components are usually related to more effortful processing (for example when unification, or more general processing difficulties arise). This review focuses on the information obtained about functional network dynamics using power and coherence measures.

It should be mentioned that besides power and coherence changes, other event-related changes in oscillatory EEG/MEG activity could be meaningful in studying the neural basis of cognitive functions (see Makeig, Debener, Onton, & Delorme, 2004 for an excellent overview of potentially relevant phenomena). For instance, there have been several reports of event-related phase resetting (the phase realignment, over trials, of oscillatory activity with respect to an experimental event; e.g., Braeutigam, Bailey, & Swithenby, 2001; Rizzuto et al., 2003). In addition, oscillatory entrainment (mainly in the theta and gamma frequency ranges) has been linked to the 'packaging' of information on varying time-scales during speech perception (e.g., Giraud & Poeppel, 2012). We find this line of research very exciting, but it falls outside the scope of the current paper, and so the interested reader is referred to the paper mentioned above for further details.

2. Fast dynamics during online language comprehension

An increasing number of studies have attempted 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., Bastiaansen & Hagoort, 2010; Bastiaansen et al., 2010; Pena & Melloni, 2012; for reviews, see Bastiaansen et al., 2012; Weiss & Mueller, 2012). 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. At this stage we would like to point out that we do not explicitly make a distinction between studies using auditory and visual input modalities. While it seems clear that at early processing stages the modality in which stimuli are presented could make a difference to the observed oscillatory patterns, we are focusing on the unification component (and to some extent the memory component), where processing is expected to involve representations abstracted away from any particular modality. The oscillatory findings related to unification should therefore be comparable for both visual and auditory input modalities.

2.1. Does beta-band synchronization reflect syntactic unification?

A number of different studies have investigated the relationship between oscillatory dynamics in the EEG/MEG and syntactic unification. In an initial study (discussed in Bastiaansen and Hagoort (2006)), we compared TF transforms of MEG data recorded while participants read syntactically complex center-embedded relative clauses (such as 'The mouse that the cat chased ran away') or syntactically more straightforward right-branching relative clauses (such as 'The cat that chased the mouse ran away'). 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 the center-embedded relative clauses, compared to the 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), we extended our window of analysis, and quantified the temporal evolution of MEG power changes across entire sentences, for three different sentence types (presented in Dutch): Syntactically legal sentences (e.g., 'Janneke got the *blessing* at the river'), sentences that contained a syntactic word category violation (a verb at a position where a noun was expected, e.g., 'Janneke got the *to bless* at the river'), and a sentence in which the syntactic structure was disrupted by randomizing word order (e.g., 'The the Janneke *blessing* got river at'). For syntactically legal sentences we observed a gradual (linear) increase in lower beta power (again, in the range of 13–18 Hz). 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). Additional support comes from Davidson and Indefrey (2007) who have also found higher beta power (14–30 Hz) for syntactically legal sentences compared to sentences containing syntactic violations (phrase-structure and number agreement violations). Finally, Meyer, Obleser, and Friederici (2013) compared long- and short-distance agreement dependencies (e.g., for the subject-relative case – subject and verb italicized – 'Nach einer Saison in der Bundesliga hat *der Trainer* den Stürmer *gewürdigt*/After a season in the German soccer league has *the coach* the striker *honored*' for short- compared to '*Der Trainer* hat nach einer Saison in der Bundesliga den Stürmer *gewürdigt*/*The coach* has after a season in the German soccer league the striker *honored*' for long-distance dependencies) between a subject and a verb in subject- and object-relative clauses in German. At the point in the sentences where agreement was resolved (at the verb) they found higher beta power (7–20 Hz) for long- compared to short-distance dependencies. This was interpreted as an index of successful syntactic unification, since syntactic unification should be more difficult for long- compared to short-distance dependencies (there is more working memory load on the syntactic unification system and hence unification is more difficult in the case of long-distance dependencies).

These five studies together clearly suggest a role for neuronal synchronization in the (lower) beta-band in sentence-level syntactic unification.

2.2. Does gamma-band synchronization reflect semantic unification?

A number of studies are relevant with respect to the relationship between oscillatory EEG/MEG dynamics and sentence-level semantic unification operations. 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 (e.g., 'The Dutch trains are *yellow* and blue'). This gamma increase was abolished when, in contrast, the word at the same position in the sentences was semantically anomalous (e.g., 'The Dutch trains are *sour* and blue'). These results were replicated in later studies (Penolazzi, Angrilli, & Job, 2009; Rommers, Dijkstra, & Bastiaansen, 2013). Rommers et al. (2013) additionally revealed that semantically anomalous words that were nevertheless semantically related to the highly expected word (e.g., 'After lunch the electrician screwed the new light bulb into the *candle* yesterday', where *lamp* was the highly expected word) elicited an intermediate increase in gamma power. Additionally, using EEG coherence analysis, one study (reviewed in Weiss and 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. Further, we found gamma-band activity to be closely associated with cloze probability, rather than with semantic acceptability (Wang, Zhu, & Bastiaansen, 2012). Finally, in a recent study (Pena & Melloni, 2012), 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 unrelated language.

What all these findings have in common, is an increase in gamma power or coherence when semantic unification can be routinely performed, and a disruption of this gamma increase when semantic problems are encountered. This pattern of results suggests that gamma-band neuronal synchronization plays an instrumental role in binding (unifying) the semantics of the individual lexical items within a sentence.

2.3. Frequency-based segregation of syntactic and semantic unification?

Together, the studies discussed in the two previous sections provide robust evidence that during sentence-level language comprehension, gamma-band neuronal synchronization is predominantly related to semantic unification operations, while 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 into 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 proposed a frequency-based segregation of syntactic and semantic unification operations (Bastiaansen & Hagoort, 2010). One should of course bear in mind that syntactic and semantic unification are highly interrelated processes that cannot easily be disentangled in an experimental setting. Rather, the suggestion is that to the extent that an experimental manipulation places greater emphasis on semantic or syntactic unification this should be reflected by changes in gamma or beta oscillatory activity respectively.

Table 1
Example materials used in (Bastiaansen & Hagoort, 2010) and their English translation (in italics).

Condition	Example materials
COR	De ijverige medewerker kopieert het document voor de ongeduldige baas *The industrious employee copies the document for the impatient boss*
PROSE	De stoffige gevangenis graveert het geslacht voor de onschuldige keel *The dusty prison engraves the gender for the innocent throat*
RAND	Baas ijverige voor de de document kopieert ongeduldige het medewerker *Boss industrious for the the document copies impatient the employee*

Notes: COR: fully correct condition; PROSE: syntactically correct but semantically meaningless; RAND: no syntactic structure or semantic meaning.

It is important to realize that unification is an ongoing process that should be engaged throughout the entire sentence. However, the reports of a relation between gamma and semantic unification are mostly based on responses to single words that created semantic anomalies in the sentences. We therefore conducted a fully within-subjects replication study in which we manipulated both the semantics and the syntax at the sentence-level (Bastiaansen & Hagoort, 2010). Participants read (amongst others) fully correct sentences, sentences containing syntactic prose (i.e., sentences that were syntactically correct but were made to be semantically meaningless by replacing all nouns, verbs and adjectives of the correct sentences by frequency- and length-matched counterparts), and sentences that were devoid of syntactic structure (created by randomizing the order of the words from the correct sentences). Example materials are given in Table 1.

Based on the 'frequency-segregation of unification' hypothesis, we expected relatively larger beta power for syntactically correct sentences (COR, but also PROSE) than for syntactically incorrect sentences (RAND). Similarly, we expected 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 sentence incomprehensible). The results clearly confirmed our expectations, and we concluded that there is ample empirical support for the notion of a frequency-based segregation of syntactic and semantic unification during sentence-level language comprehension (Bastiaansen & Hagoort, 2010).

3. Problems with the 'frequency-segregation of unification' hypothesis

As we have seen in the previous section, there is a considerable body of evidence to support the frequency segregation of semantic and syntactic unification hypothesis (subsequently termed the 'unification' hypothesis for the sake of readability). However, one concern is that the gamma effects were found to differ in terms of their spectral characteristics. Effects were found in both a low-gamma frequency range (30–50 Hz): around 30 Hz (Weiss & Mueller, 2003; 40–50 Hz (Hald et al., 2006); 30–45 Hz (Penolazzi et al., 2009); and 45–50 Hz (Wang, Zhu, et al., 2012), as well as a high-gamma frequency range (50–100 Hz): 55–70 Hz (Rommers et al., 2013); 55–75 Hz (Pena & Melloni, 2012); 55–75 Hz, and 75–100 Hz (Penolazzi et al., 2009). Moreover, there is a substantial amount of empirical data that does not fit the beta-syntax and gamma-semantics mappings proposed by the unification hypothesis.

3.1. Beta-band synchronization is not always sensitive to manipulations of syntactic unification

We have found that the beta frequency band is in some cases not only responsive to syntactic manipulations, but also to semantic manipulations. In an MEG study (Wang, Jensen, et al., 2012), participants listened to semantically congruent or incongruent sentences (e.g., *The climbers finally reached the top of the mountain/tulip*. Critical words are underlined). In addition to the classical N400m (the magnetic equivalent of the N400) effect, the incongruent words (e.g., *tulip*) elicited a decrease in beta power compared to the congruent words (e.g., *mountain*) over the left hemisphere. A positive linear relationship was found between N400m amplitude and beta power for the incongruent condition. The source of the beta power decrease was localized to the LIFG, a region that has been related to both semantic and syntactic unification (Hagoort, 2005, 2013). With the source localization techniques available for MEG we do not have sufficient spatial resolution to distinguish parts of the LIFG previously related to semantic unification from parts previously related to syntactic unification. However, since we used a semantic manipulation and since the beta decrease correlated with the amplitude of the N400m, it is not unreasonable to suggest that parts of the LIFG primarily responsible for semantic unification were involved in the observed beta-band effects.

The clear relationship between the N400m (an ERF known to be sensitive to semantic unification, see e.g., Baggio & Hagoort, 2011) and the modulation of oscillatory activity in the beta-band is not compatible with the beta-syntax mapping suggested by the unification hypothesis. Furthermore, another study (Luo, Zhang, Feng, & Zhou, 2010) has found a larger beta decrease for semantic violations compared to semantically legal sentences, offering further evidence that not only manipulations of syntactic, but also of semantic aspects of the language input are associated with modulations of beta power.

3.2. Gamma-band synchronization is not always sensitive to successful semantic unification

Studies have shown that successful semantic unification does not necessarily elicit increased gamma-band power. In a recent EEG study (Wang, Zhu, et al., 2012), participants read three types of sentences (e.g., *In order to cure the disease, the doctor invented a new medicine/device/bottle for the patients*) in which a critical word was (1) both semantically congruent and predictable (e.g., *medicine*), (2) semantically congruent but unpredictable (e.g., *device*), or (3) semantically incongruent and unpredictable (e.g., *bottle*). According to the gamma-semantics mapping suggested by the unification hypothesis, the semantically congruent words (conditions (1) and (2)) should elicit increased gamma power relative to the semantically incongruent words (condition (3)) because words in conditions (1) and (2) can be successfully integrated into their preceding sentence contexts. However, we found that only the highly predictable words (e.g., *medicine* in condition (1) of our example) induced a gamma power increase, whereas no gamma power increase was found in the two conditions where the predictability of the critical words was low (e.g., *device* and *bottle* in conditions (2) and (3)). Therefore, the results seem to suggest that gamma power increases are related to the predictability of an upcoming word rather than to semantic unification.

In addition, Hagoort, Hald, Bastiaansen, and Petersson (2004) found an increase in gamma power for a world knowledge violation (e.g., 'The Dutch trains are *white* and blue' – trains are well known by Dutch participants to be yellow and blue in the Netherlands), which was not present for semantically legal sentences (e.g., 'The Dutch trains are yellow and blue'). This is clearly not in line with the idea that gamma power increases are related to successful semantic unification.

3.3. Moving beyond the sentence level

Further evidence that is not compatible with the unification hypothesis comes from two recent experiments that were designed to test this hypothesis at the discourse level (Hoffmann, Bastiaansen, & Schriefers, 2011; Lewis, Schriefers, Bastiaansen, & Hoffmann, 2012). In both experiments we manipulated the level of semantic coherence in short stories consisting of 4 sentences, by shuffling the second, third and fourth sentences from coherent stories (COH) to create stories where the sentences were semantically unrelated (INCOH). Pre-testing with a separate group of participants indicated that readers clearly rated sentences 2, 3, and 4 of the COH condition as following on coherently from the previous sentence, whereas for the INCOH condition they were rated as not related to the preceding sentence (see Table 2 for example stimuli).

Our hypotheses were twofold: (1) if increased gamma power is a reflection of increased semantic unification then we would expect to find relatively larger gamma power starting around the onset of the second sentence for the COH condition compared to the INCOH condition, and this difference should persist over the remainder of the stories; (2) if increased beta power is a reflection of syntactic unification we would expect that for both conditions beta power would increase over the course of each sentence comprising the stories, decrease during the inter-sentence intervals, and then increase again over the course of the next sentence (yielding something resembling a saw tooth pattern for the evolution of beta power over time).

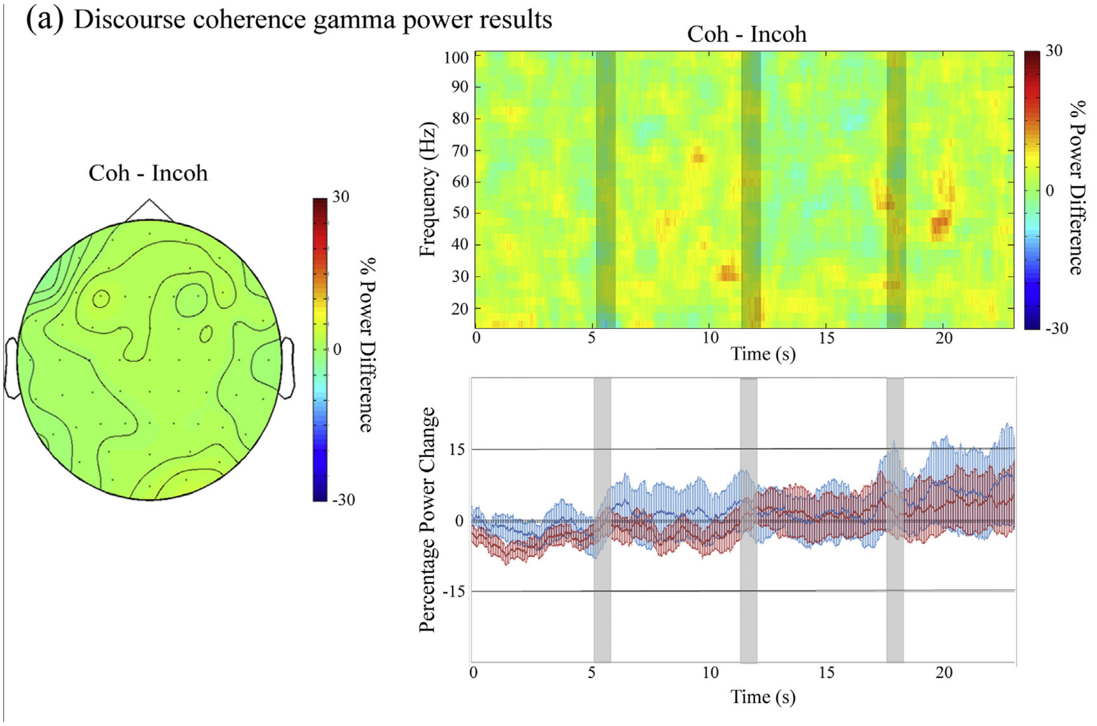
To our knowledge these are the only two studies investigating the effects of a discourse level factor on the evolution of oscillatory power associated with unification beyond the single-sentence. One reason for this may be that analysis (and acquisition) of such data comes along with its own unique set of challenges. For instance, participants were engaged in reading for about 23 s, an unreason-

Table 2
Example materials used in (Lewis et al., 2012) and their English translation (in italics).

Condition	Example materials
COH	Charles verliet zijn vaderland Senegal om in Europa te werken Met een levensgevaarlijk klein bootje werd hij naar Tenerife gesmokkeld Hij moest daar hard werken voor een klein beetje geld Zijn familie had het geld dat hij stuurde hard nodig *Charles left his home country Senegal to work in Europe* *With a dangerously small boat he was smuggled to Tenerife* *There he had to work hard for very little money* *His family desperately needed the money that he was sending*
INCOH	Charles verliet zijn vaderland Senegal om in Europa te werken Een avond hadden ze een taart achtergelaten in de keuken Toevallig kwam een agent de hoek om die hen arresteerde Maar na een jaar moest hij al naar de sloop *Charles left his home country Senegal to work in Europe* *One evening they left a hot pie in the kitchen* *Coincidentally a cop came around the corner that arrested them* *But after just a year it was ready for the dump*

Notes: COH: semantically coherent condition; INCOH: semantically (discourse-level) incoherent condition.

(a) Discourse coherence gamma power results



(b) Discourse coherence beta power results

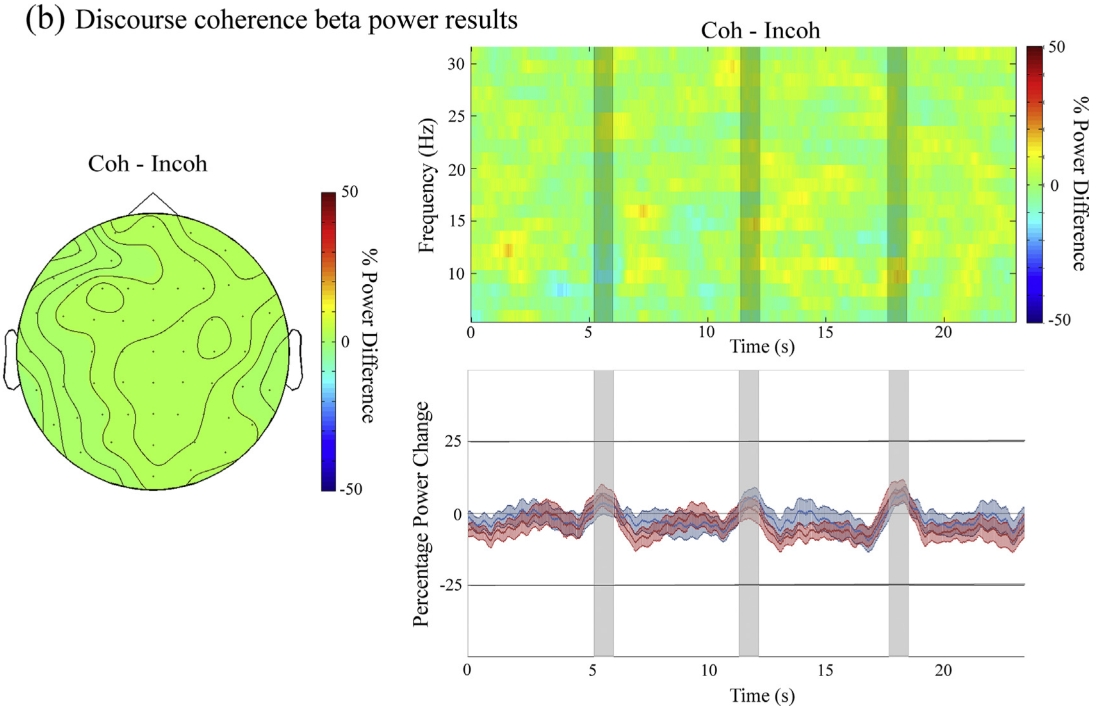


Fig. 1. Results from the time–frequency analysis of power for the discourse coherence data. (a) Time–frequency representation of power in the high frequency range for a representative electrode F3 (right-top), along with the evolution of gamma power (45–55 Hz) over the course of short stories (blue = coherent stories (COH); red = incoherent stories (INCOH)) for the same electrode (right-bottom), and a topographical distribution of the difference between the COH and INCOH conditions averaged over the same gamma frequency range and the entire time course of the stories (left). (b) Time–frequency representation of power in the low frequency range for a representative electrode FCz (right-top), along with the evolution of beta power (13–18 Hz) over the course of short stories (blue = coherent stories (COH); red = incoherent stories (INCOH)) for the same electrode (right-bottom), and a topographical distribution of the difference between COH and INCOH conditions averaged over the same beta frequency range and the entire time course of the stories (left). Error bars indicate standard errors (SE) around the mean. Gray shaded areas indicate inter-sentence intervals lasting 800 ms each.

able amount of time to ask them to avoid blinking for the entire trial. The longer segments also resulted in a larger than normal number of muscle/movement artifacts, potentially contaminating the higher frequencies and certainly reducing the signal-to-noise ratio when investigating power in the high frequency range. Another challenge with these experiments was to find an appropriate baseline with sufficiently artifact-free data to get a good estimate of frequency-specific baseline power. In addition, although we knew that stories became incoherent at the second sentence, exactly where in the second sentence (and in sentences 3 and 4 for that matter) they became incoherent was not clear and probably quite variable across items. This meant that any effects might be differently distributed in time across trials within each sentence.

A selection from the results is presented in Fig. 1. The results presented here are adapted from Lewis et al. (2012), but the results from Hoffmann et al., 2011 are very much the same. As is clear from the figure, there were no consistent differences in gamma power (45–55 Hz) between the COH and INCOH conditions (Fig. 1a). Fig. 1b shows the effects (or lack thereof) in the beta frequency range (13–18 Hz). Again, this figure panel clearly demonstrates that not only are there no differences between the COH and INCOH conditions for beta, but the expected saw tooth pattern for beta power over the course of the stories is also absent. We conclude that neither the gamma-semantics, nor the beta-syntax mapping predicted by the unification hypothesis was confirmed once sentences were embedded within discourse contexts. The reader should bear in mind however the relatively poor signal-to-noise ratio in these data, although this is unlikely to fully account for the lack of any effects, especially for the beta frequency range.

Having reviewed evidence that cannot be easily accounted for by the unification hypothesis, we find ourselves asking the following question: *Is it possible to account for all the evidence linking beta and gamma oscillatory neuronal activity to language comprehension, beyond the level of individual words, under an alternative overarching hypothesis?*.

4. An alternative hypothesis: do beta and gamma relate to maintenance and prediction during language comprehension?

Engel and Fries (2010) have recently proposed a role for beta oscillations in motor and cognitive/perceptual processing. Based on a review of the literature relating beta activity to motor control/processing, they suggest that increased beta promotes maintenance of the current motor set while beta decreases signal a change in motor set. They further suggest that this idea might be extended to the domain of cognitive and perceptual processing so that beta activity might increase when the current cognitive set needs to be actively maintained (under distraction for instance), beta might decrease when the current cognitive set is expected (by the system responsible for that cognitive processing) to change, and beta might remain unchanged when processing of the current cognitive set is ongoing without any expected additional load on the system responsible. In a recent review, Weiss and Mueller (2012) have proposed four possible roles for beta oscillations in language processing. They propose that beta oscillations are related to motor-related cortical activity while processing action semantics, to attention and the violation of expectancies about the current cognitive state, to binding operations during language processing, and to memory-related processing. Their suggested role for beta oscillations in attention and the violation of expectancies about the current cognitive state is very similar to (and in fact is largely based upon) the framework of Engel and Fries (2010) just described. We therefore propose to reinterpret the findings we have discussed thus far on beta-band oscillatory dynamics during language comprehension within that framework, and to only focus on evidence that is directly related to language comprehension beyond the level of individual words (which is the main focus of this review).

As for the gamma frequency range, Herrmann, Munk, and Engel (2004) proposed a role for gamma oscillations in the comparison of bottom-up (stimulus-related) and top-down (memory contents) information while processing a stimulus. Their idea is that an increase in gamma power should be observed whenever information from a stimulus matches the contents of some pre-activated memory representation. No such gamma power increase should be present when the stimulus information does not match the contents of the pre-activated memory representation.

For Engel and Fries (2010) the cognitive system maintains or changes the current mode of processing in preparation for the next processing cycle. In the Herrmann et al. (2004) framework the cognitive system predicts the contents of an incoming stimulus and pre-activates a memory representation for that expected stimulus to be matched with the actual input. Given the above hypotheses on the relationship between beta- and gamma-band oscillations and maintenance/prediction, one should carefully consider whether the high-frequency oscillatory dynamics that have been observed in language comprehension paradigms may be related to maintenance/predictive processes that are at play during language comprehension, rather than to unification operations. As it is becoming increasingly clear that prediction plays an essential role in language comprehension (e.g., DeLong, Urbach, & Kutas, 2005; Federmeier, 2007; Pickering & Garrod, 2007; Staub & Clifton, 2006; Szewczyk & Schriefers, 2013), in the following paragraphs we will evaluate whether the oscillatory dynamics in the beta and gamma frequency ranges that have been discussed so far may be reinterpreted in the context of maintenance and prediction respectively. We will also discuss some additional evidence supporting this idea.

4.1. Does beta-band synchronization reflect active maintenance?

Let us start with the six datasets that we have used to advocate a relationship between beta-band oscillations and syntactic unification (Bastiaansen & Hagoort, 2006, 2010; Bastiaansen et al., 2010; Davidson & Indefrey, 2007; Meyer et al., 2013; Weiss et al., 2005). The relative clause data in Bastiaansen and Hagoort (2006), showed larger beta power during center-embedded relative clauses, which are syntactically more complex (and therefore more difficult to process) than their right-branching counterparts. The increased processing demands might (in the absence of any violations) lead the language comprehension system to actively maintain the current cognitive set at the next processing cycle. This would in turn trigger the larger increase in beta power for center-embedded compared to right-branching relative clauses reported for the MEG study discussed in Bastiaansen and Hagoort (2006). The same argument can be made for object-relative clauses, which showed increased beta-band coherence just after the relative clause, compared to their (easier to process) subject-relative counterparts (Weiss et al., 2005). It may be argued that center-embedded relative clauses deviate from the preferred syntactic structure (i.e., right-branching relative clauses) and that under the current account this could be interpreted by the language comprehension system as a cue that the current cognitive set needs to be changed. If one takes a closer look at the materials used in that experiment however, it is unambiguous that the relative pronoun ‘die’ (Dutch for ‘who’) marks the start of the relative clause. For right-branching relative clauses a verb with two nominal arguments always precedes the relative clause, while for the center-embedded relative clauses only a single noun phrase precedes the relative clause. As far as the language comprehension system is concerned, by the time the relative clause is being processed it is already clear whether the construction will be a right-branching or a center-embedded relative clause. It is therefore unlikely that during the processing of the relative clause (where the beta effects were shown) the language comprehension system interprets the center-embedded constructions as cues for a change in cognitive set. Therefore, in the particular case discussed in Bastiaansen and Hagoort (2006) we do not expect that the language comprehension system interprets the dispreferred center-embedded constructions as a cue that the current cognitive set needs to be changed.

Along similar lines, one might argue that since object-relative clauses (as used by Weiss et al., 2005) are a dispreferred syntactic structure compared to subject-relative clauses, we might expect to see a decrease in beta power for object- compared to subject-relative clauses as an indication that the current cognitive set needs to be changed. Here again a closer look at the materials reveals that because of the inclusion of the relative pronoun 'who', these could never be classical garden-path ambiguous relative clauses (King & Kutas, 1995; Weiss et al., 2005). It is clear from the order of verb and argument (which can be decided already immediately following the relative pronoun) within the relative clause what kind of relative clause is being processed. This makes it unlikely that at the end of the relative clause the language processing system would interpret object-relative clause constructions as unexpected. Instead, the beta power increase just after the end of the relative clause might indicate the active maintenance of the current cognitive set because processing object-relatives is more difficult than processing subject-relatives.

The higher beta power for the comparison of long- and short-distance agreement dependencies (Meyer et al., 2013) can be explained by the fact that near the verb in the sentences containing long-distance dependencies the agreement computation is more difficult than for sentences containing short-distance dependencies. This may act as a cue to the language comprehension system indicating that the current mode of processing needs to be actively maintained (under the additional processing demands due to the more difficult agreement computation), resulting in the observed increase in beta power.

As for the comparison of different levels of syntactic unification (correct sentences compared to syntactic violations and random word lists; Bastiaansen et al., 2010; Davidson & Indefrey, 2007), word category, phrase structure and number agreement violations can be interpreted as a cue to the linguistic comprehension system indicating that the current cognitive set needs to change. According to the Engel and Fries (2010) framework this should result in lower beta power relative to the correct condition, which is exactly what was observed. For the case of random word lists, the current mode of processing for the language comprehension system involves simply reading individual words. This likely becomes clear very early in a 'sentence' without changing over the course of the 'sentence', hence no change in beta power is expected, nor is it observed (Bastiaansen et al., 2010). The same explanation can also account for the findings regarding the evolution of power over the course of a sentence (Bastiaansen et al., 2010). Here the observation was that for syntactically legal sentences beta power increases gradually over the course of each sentence. This gradual increase can be related to the active maintenance of the current processing set of the language comprehension system, which presumably becomes more taxing toward the end of the sentences because the system has more information (has received more input that needs to be integrated into the sentence level representation being constructed) to deal with at later stages of the sentences. In the case of reading random words the mode of processing is maintained but the system does not experience any additional processing demands dependent on the position in the sentence as it does in the syntactically legal condition. This is reflected in the relatively constant level of beta power in the random word list condition. Finally, for the word category violation condition of Bastiaansen et al. (2010), there is a beta decrease after the syntactic violation due to the system being cued for a change in processing set by a violating word.

Notice that in addition to syntactic violations, semantic violations during a sentence can also be interpreted by the language comprehension system as a cue that the current cognitive set needs to change, and this can account for the findings already discussed, of a decrease in beta power following semantic violations (Luo et al., 2010; Wang, Jensen, et al., 2012). Potential further support for this idea comes from Kielar, Meltzer, Moreno, Alain, and Bialystok (2014) who investigated syntactic and semantic violations compared to acceptable control sentences. They found a decrease in power between 8 and 30 Hz for both types of violations compared to semantically and syntactically legal sentences. Unfortunately their method for identifying relevant frequency and time ranges for statistical testing does not allow them to distinguish between the alpha and beta frequency ranges so it is not possible to determine whether the beta-band alone is implicated in these findings.

The lack of findings in the beta-band for the discourse coherence experiments described in Section 3.3 (Hoffmann et al., 2011; Lewis et al., 2012) can be explained if we realize that these experiments are not well suited to investigate the relation between maintenance/change of the current cognitive set and beta-band synchronization. Such maintenance is likely taking place throughout the stories but was not systematically manipulated between conditions.

A recent investigation of oscillatory activity during turn-taking in conversations provides further supporting evidence for a relation between beta oscillations and maintenance/change of the current cognitive set (Magyari, Bastiaansen, de Ruiter, & Levinson, 2014). Participants listened to a recording of natural speech and had to press a button when they predicted an interlocutor would finish his/her turn. There was one condition where the end of the turn was highly predictable and another where it was unpredictable. A large decrease in beta power (11–18.5 Hz) was present just before the key press in the predictable condition, while an increase in beta power was present in the unpredictable condition. These results fit well within the proposed beta-maintenance framework. In the predictable condition the language comprehension system needs to change the current processing set (i.e., a change from comprehension of the current turn to production of one's own turn) and this is reflected in the decrease in beta power. For the unpredictable condition the system needs to actively maintain the current processing set, resulting in the increase in beta power right before the turn-end. Crucially, the authors found no difference in beta power over motor and pre-motor cortex, but rather over mid-frontal and parietal regions, indicating that the differential beta activity was not related to differential motor preparation in the two conditions.

Further support comes from Perez, Molinaro, Mancini, Barraza, and Carreiras (2012), who used so called 'Unagreement' in Spanish where there is a grammatical mismatch between the person feature on the subject and the verb of a sentence, but where this still leaves the sentence perfectly grammatical (see Perez et al., 2012 for details). They contrasted this with syntactically legal sentences and with cases where person mismatch did lead to a grammatical violation. A decrease in beta power at the critical verb was reported for both the person mismatch conditions relative to the no mismatch (syntactically legal) condition, irrespective of whether or not the sentence becomes ungrammatical as a result of that mismatch. This beta decrease cannot be related to syntactic unification since in the Unagreement condition the sentence is perfectly grammatical. It does however fit well with the idea that both morpho-syntactic mismatches serve as cues to the language comprehension system indicating that a change in cognitive set is necessary.

Taken together, the evidence discussed above is largely compatible with a link between beta-band synchronization and the maintenance or change of the current cognitive set by the language comprehension system. This maintenance framework also accommodates a large number of findings that cannot be accounted for by the beta-syntax mapping suggested by the unification hypothesis. It also fits well with a more general role for beta-band oscillations in cognitive neuroscience that has been suggested (Engel & Fries, 2010) on the basis of studies investigating a wide range of cognitive phenomena, such as bi-stable stimulus perception (e.g., Iversen, Repp, & Patel, 2009; Okazaki, Kaneko, Yumoto, & Arima, 2008), attentional control (e.g., Buschman & Miller, 2007, 2009), visual search (e.g., Pesaran, Nelson, & Andersen, 2008), and sensorimotor processing (e.g., Androulidakis, Doyle, Gilbertson, & Brown, 2006; Androulidakis et al., 2007; Gilbertson et al., 2005; Pogosyan, Gaynor, Eusebio, & Brown, 2009).

4.2. Does gamma-band synchronization reflect prediction?

As it seems that the large majority of the findings relating beta to syntactic unification can easily be reinterpreted under the framework put forward by Engel and Fries (2010), let us now turn to the findings that have related gamma-band synchronization to successful semantic unification and see whether they can be captured under the framework of Herrmann et al. (2004).

Three studies have reported an increase in gamma power for semantically congruent compared to incongruent sentences at the violating word (Hald et al., 2006; Penolazzi et al., 2009; Rommers et al., 2013). Since cloze probabilities are zero for the incongruent conditions (indicating that these words are relatively unpredictable) and are relatively high for the congruent conditions in these studies, the gamma power increase in the congruent conditions could be related to the high predictability of the upcoming lexical item. This may lead the language comprehension system to pre-activate the memory representation(s) associated with the highly predictable lexical item, and the gamma power increase in the congruent conditions may reflect the match between the actual input and the pre-activated memory representation. Since the input does not match the prediction in the incongruent conditions there is no gamma power increase. The same explanation would hold for the finding of an increase in gamma-band coherence for congruent (where cloze probability is typically high and thus so is the predictability of the critical word of interest) compared to incongruent (where the critical word of interest is highly unpredictable) sentences (Weiss & Mueller, 2003).

The reported gamma power increase when monolinguals listen to their own language but not when they listen to a phonologically related or unrelated language (Pena & Melloni, 2012) can also be explained by the fact that incoming linguistic information would be highly predictable in one's own language and not at all predictable in a foreign language. In addition, the reported gamma power increase for a referentially successful word (van Berkum et al., 2004) is also in line with the idea that a prediction is made about a potential referent (thus pre-activating a memory representation or set of memory representations related to that referent) and when the linguistic input matches that prediction a gamma power increase is observed. In the cases where the input is referentially ambiguous or non-referential the input does not match the prediction and so no gamma power increase is observed.

Finally, the sentence level findings from Bastiaansen and Hagoort (2010) that gamma power is higher for a syntactically and semantically legal condition compared to both a syntactic prose condition and a random word list can be explained by the fact that for both the syntactic prose and the random word list conditions predictability of the incoming linguistic input would be very low. For the syntactically and semantically legal sentences on the other hand it would be much easier to predict the content of the upcoming linguistic input, and this would lead to consistent increases in gamma power whenever the input matches these predictions throughout the sentence.

Since in a recent study (Wang, Zhu, et al., 2012) a gamma power increase was only observed after highly predictable words, but not after unpredictable yet semantically congruent words, we propose that the gamma findings may be reinterpreted under a prediction framework (Wang, Zhu, et al., 2012; see Penolazzi et al., 2009 for a related proposal). Within this framework, we propose that word-level semantic representations are pre-activated based on contextual information (e.g., sentence/discourse level information). The matching of top-down linguistic predictions and the bottom-up representation of incoming words then translates into gamma-band synchronization. Thus, the gamma power increase is related to a match between the predicted word and the actual incoming word. As discussed above, this hypothesis can account for a wide range of gamma-related findings in language comprehension.

Additional support comes from a recent EEG study using phase-locking values as a measure of the transient phase coupling between two electrodes (conceptually similar to coherence; Molinaro, Barraza, & Carreiras, 2013). They found that the expected words in highly constraining contexts elicited increased frontal-posterior gamma synchronization relative to words in less constraining contexts.

The lack of findings regarding a gamma-band difference between the coherent and incoherent conditions when manipulating discourse coherence in short stories (Hoffmann et al., 2011; Lewis et al., 2012) can be explained if we again realize that these experiments are not well suited to investigate the relation between predictions about the content of upcoming linguistic input and gamma-band oscillations. While it is likely the case that there were points within the incoherent stories where there was a mismatch between predictions about the upcoming linguistic input and the actual input (where at the same time point for the coherent stories the input matched the predictions), the timing of these mismatches was not likely to be consistent across stories. This is not problematic in investigating global semantic unification (as was intended in those studies) but certainly poses a problem in finding consistent (in time) gamma modulations related to matching and mismatching predictions. We therefore think it is the case that those data do not speak to the issue of a possible link between gamma and prediction.

The only study discussed so far that does not easily fit into this framework comes from Hagoort et al. (2004) where a gamma power increase was observed for sentences containing world-knowledge violations, but not for semantically legal sentences. Monsalve, Perez, and Molinaro (2014) have proposed that findings in the gamma band might be affected by the composition of the stimulus set in any particular experimental setting. Since attention can modulate gamma-band activity (Gruber, Müller, Keil, & Elbert, 1999), and the presence of more violations in a stimulus set could lead participants to adopt a strategy where more attention is devoted to bottom-up processing (rather than top-down predictive processing), the presence or number of violations in any particular stimulus set may affect the level at which predictions are made, and therefore also the pattern of gamma results. The results in Hagoort et al. (2004) may therefore be explained as an effect of differential attention between the conditions, which leads to predictions being made at a different level of the processing hierarchy (not at the level of lexical pre-activation). The exact level at which predictions are made, and the content of those predictions is not yet clear, and merits further study.

The prediction framework outlined above fits into a domain-general notion that synchronization in the gamma-band binds together various types of information that originate from the processing of bottom-up input and from top-down control (Herrmann et al., 2004; Tallon-Baudry & Bertrand, 1999). For instance, increased gamma power has been observed when combining different features in visual and auditory modalities to form a coherent percept (Bertrand & Tallon-Baudry, 2000; Rodriguez et al., 1999). Moreover, increased gamma-band synchronization was found when bottom-up input matched with top-down predictions that were triggered by attention (Bauer, Oostenveld, Peeters, & Fries, 2006; Herrmann & Mecklinger, 2001) and memory (Eulitz & Hannemann, 2010; Holz, Glennon, Prendergast, & Sauseng, 2010; Lenz et al., 2008).

4.3. The role of beta and gamma in language comprehension: a tentative new hypothesis

Given the evidence presented against the unification hypothesis (Bastiaansen & Hagoort, 2006, 2010; Bastiaansen et al., 2012) and the fact that almost all the evidence both in favor of, and against that hypothesis can be interpreted in a maintenance or a prediction framework, we propose to answer the question posed at the end of Section 3.3 by introducing a tentative new hypothesis about the role of beta and gamma oscillations during language comprehension. In our opinion there is sufficient evidence to support a link between beta and gamma oscillatory activity and maintenance or prediction in language comprehension.

In making this move, we do not wish to imply that unification is not important for language comprehension. On the contrary, in the literature reviewed above it is clear that the process of unification over the course of an unfolding sentence is essential for the construction of a sentence-level meaning representation, the maintenance or change of which we are proposing is reflected in oscillatory activity in the beta band. We are therefore tentatively suggesting that the current cognitive set can be thought of as the ongoing process of constructing the current sentence-level meaning representation. There are likely many factors external to language comprehension (e.g., current task demands or strategy) which impinge on this cognitive set, but the core cognitive set is sentence-level meaning construction. We believe that the relationship between the exact ways in which the system registers that a particular cognitive set is in operation, how that set changes or needs to change (likely related to monitoring during language comprehension) and the underlying oscillatory neuronal dynamics, is not yet well enough understood for a detailed description to be provided here. These are important outstanding questions and this might prove to be an interesting line of further empirical investigation.

One factor that leads to strong predictions (and hence gamma band oscillations when the input matches those predictions) during language comprehension beyond the level of individual words is the increasingly more constraining sentence-level meaning context, which is a direct result of the process of unification. Since temporally extended increases in theta power have repeatedly been observed in response to semantically anomalous words (Bastiaansen & Hagoort, 2010; Hald et al., 2006; Wang, Zhu, et al., 2012) that cannot be accounted for by the morphology of the ERP (see Wang, Zhu, et al., 2012 and Bastiaansen & Hagoort, 2010), we tentatively propose that this temporally extended theta synchronization might be a potential oscillatory correlate of the compositionality aspect of unification. We think that further discussion and empirical investigation into compositionality (explicitly aiming to tease it apart from prediction) in language comprehension is highly important.

For oscillatory activity in the beta frequency range (the most commonly observed frequency range in language comprehension studies has been 13–18 Hz, i.e., the lower end of the traditional beta range) we believe that the framework of Engel and Fries (2010) can successfully account for the large majority of the results obtained in language comprehension studies. In this framework, an increase in beta activity signals the active maintenance of the current cognitive set (or put in terms of the framework described in Section 1.1, the active maintenance of the current configuration of the underlying functional network), while a decrease in beta activity signals a change in cognitive set (or a change in network configuration). Biophysically inspired computational modeling has shown that beta oscillations have the right characteristics for the maintenance of information over the kinds of time-spans at which short-term and working memory operate (Kopell, Ermentrout, Whittington, & Traub, 2000; Kopell, Whittington, & Kramer, 2011), making them ideal candidates for forming functional networks related to processing information over extended periods of time.

We propose that the language comprehension system uses cues in the linguistic input to maintain (leading to little or no change in beta activity), change (leading to a decrease in beta activity), or actively maintain (leading to increased beta activity) the current cognitive processing set (and hence the underlying functional network configuration). Exactly what kind of cues are most relevant for the comprehension system is currently unclear, but we suggest that syntactic and semantic violations are in most circumstances clear cues to the system that the current processing set needs to change, hence the beta decrease observed for both semantic (e.g., Luo et al., 2010; Wang, Jensen, et al., 2012) and syntactic violations (e.g., Bastiaansen et al., 2010; Davidson & Indefrey, 2007) compared to non-violation words in a sentence context.

We should also point out that we are referring specifically to changes in beta activity relative to some ongoing level of oscillatory activity. Specifically, it is typical in studies investigating the oscillatory dynamics of EEG and MEG to see event-related desynchronization for beta in response to each word presented (e.g., Bastiaansen, van der Linden, ter Keurs, Dijkstra, & Hagoort, 2005; Davidson & Indefrey, 2007). However, what is informative for our hypothesis is how this may be modulated by cues in the input indicating to the language comprehension system whether the current cognitive set needs to be changed or maintained.

Two of the studies already discussed (Magyari et al., 2014 and Wang, Jensen, et al., 2012) used source reconstruction techniques (beamforming with Dynamic Imaging of Coherent Sources; Gross et al., 2001) to localize the differences in beta power between conditions. Wang, Jensen, et al. (2012) localized the source of their beta power difference to left inferior frontal gyrus, while Magyari et al. (2014) reported sources in bilateral frontal, and left inferior parietal and left temporal areas. Since the spatial resolution associated with source estimation in EEG/MEG is relatively poor we do not want to make too much of these results. Furthermore, since the main focus of this paper is the dynamic functional interaction between brain networks, we restrict ourselves to suggesting that these sources may form nodes within the functional network(s) being recruited during sentence-level language comprehension.

Left inferior frontal cortex has been implicated in unification operations (Hagoort, 2005, 2013), and in dynamic interaction with left temporal areas (Hagoort, 2014) may bring about the sentence-level meaning representations which lead to lexical pre-activation in our gamma-prediction hypothesis. We have also suggested that these sentence-level meaning representations constitute the current cognitive set that needs to be maintained or changed during comprehension, and so activation of left inferior frontal cortex and left temporal areas (probably in interaction with other networks responsible for things like attention and monitoring) may reflect parts of the language network that are being engaged or disengaged when the current cognitive set is being maintained or changed respectively. We reiterate that this line of thinking is highly speculative and deserves further investigation with methods that can offer both high spatial and temporal resolution (e.g., combined EEG-fMRI).

For oscillatory activity in the gamma frequency range (most language comprehension studies have observed reactivity in the classical gamma range, i.e., around 40 Hz) we believe that a modified version of the so-called 'match-and-utilization model' from Herrmann et al. (2004) can successfully account for most of the empirical observations of gamma-band reactivity during language comprehension. In brief, in applying this model to language comprehension we assume that the comprehension system makes predictions about various aspects of the content of the upcoming linguistic input based on the preceding linguistic input and other relevant factors (e.g., discourse level or pragmatic information). This leads to the pre-activation of lexical items associated with the prediction (or put in terms of the framework described in Section 1.1, potential new nodes to be incorporated into the existing functional network) before the upcoming linguistic input is read or heard. A match between a predicted lexical item and the new input leads to an increase in gamma power (and an incorporation of the pre-activated node into the functional network), which is absent in the case of a mismatch (none of the pre-activated potential nodes are incorporated into the functional network).

We wish to add two important caveats to the ideas presented above: (1) the ideas about the relation between maintenance of the current cognitive set, predictive processing and oscillatory activity come directly from proposals made in other domains of cognitive neuroscience and have been adapted here to fit the language comprehension literature (for beta see Engel & Fries, 2010 and to some extent Weiss & Mueller, 2012 for a language-related account; for gamma see Herrmann et al., 2004 as well as Pena & Melloni, 2012, and Wang, Zhu, et al., 2012 for the original language-related accounts); (2) the idea of prediction is very popular in cognitive neuroscience at the moment (e.g., Bubic, von Cramon, & Schubotz, 2010; Friston & Kiebel, 2009; Kok, Rahnev, Jehee, Lau, & de Lange, 2012) and we try to avoid more general debates about prediction and its neural implementation by discussing only one very concrete instantiation of prediction during language comprehension.

The common thread that binds these two ideas together is the domain-general role of oscillatory activity in the beta and gamma frequency bands in the language comprehension system. To reiterate how the two proposals differ, we propose that beta indexes the current processing state of the language comprehension system and how that is expected to change (or not) over time. This can be based on any information that must be both available to the language comprehension system and potentially relevant to the state of that system. Gamma on the other hand is an index of how well the actual input matches a lexical item (in long-term memory) that has been pre-activated by some prediction regarding the nature of the upcoming linguistic input. Predictions are based on the preceding sentence context in combination with any other information the language processing system considers relevant to making the prediction (e.g., discourse level/pragmatic information). In brief then, our maintenance/prediction hypothesis tentatively proposes that modulations of beta are related to the processing state of the language comprehension system, while modulations of gamma are related to predictions about specific lexical items the language comprehension system expects to receive.

5. Suggestions for further research

What are needed now are experiments designed to directly test the proposed maintenance/prediction framework, and to directly compare the maintenance/prediction and the unification hypotheses. We now offer a few suggestions in this regard.

The maintenance/prediction hypothesis claims that any time a strong prediction is made about upcoming linguistic input, a memory representation (or set of memory representations) for the predicted lexical item is pre-activated. Since a match between the pre-activated memory representation and the input is purported to produce the gamma power increase, we might explore different ways of pre-activating lexical representations through prediction (other than by manipulating cloze probability). One idea would be to use a masked priming paradigm in sentences containing critical words with low cloze probability. The prime might pre-activate lexical representations and produce a gamma power increase upon reading/hearing the matching linguistic input. The gamma power increase would not be expected without the prime since the critical words in this case are not highly predictable and so no pre-activation would occur.

Another prediction of the maintenance/prediction hypothesis is that the language comprehension system uses cues (from the linguistic input but also non-linguistic cues) as an indication that the current processing set needs to be actively maintained (beta power increase) or changed (beta power decrease). We could test what different types of information the language comprehension system deems relevant in making such 'decisions'. We already know that semantic and syntactic violations seem to be one such cue, but it may for instance be the case that a switch from reading to listening within a sentence might be a similar cue, or a sudden interruption of the linguistic input by say a disfluency ('er' or 'uhm' for instance) or a picture stimulus. We can think of many similar experiments to test the parameters within which the language comprehension system maintains/changes its current mode of processing.

Finally, the maintenance/prediction hypothesis and the unification hypothesis make different predictions regarding the expected changes in beta power while reading or listening to sentences containing violations of expectations (that do not necessarily constitute grammatical violations). If some incoming linguistic input is in violation of a strong expectation (say about the type of syntactic construction that is expected for instance), but is still grammatical, the unification hypothesis predicts that unification should take place as normal and we should observe an associated increase in beta power. The maintenance/prediction hypothesis on the other hand predicts that this should act as a cue to the language comprehension system that something unexpected has occurred and that the current processing set needs to be changed. We have already seen some support for this dissociation in the study of Spanish 'Unagreement' patterns (Perez et al., 2012), but we believe this idea should be explored further as one way of directly comparing the two proposed hypotheses.

6. Conclusions

We have provided a variety of evidence both in favor of and against the unification hypothesis. The idea that there is a strong mapping between gamma-band oscillations and semantic unification on the one hand, and between beta-band oscillations and syntactic unification on the other receives substantial empirical support. There are however a number of empirical findings that are not straightforwardly incorporated into this account, and we suggest instead that a framework linking beta and gamma oscillations to maintenance of the current cognitive set and predictive processing within the language comprehension system might provide a better explanation for the available evidence. On this account beta-band oscillatory neuronal activity is related to whether or not the current mode of processing will be maintained. Gamma-band oscillatory neuronal activity on the other hand is related to predictions the language comprehension system makes about the lexical content of upcoming linguistic input. We argue that this framework can account for the large majority of the evidence on beta- and gamma-band oscillations during language comprehension that are presently available.

Acknowledgments

We would like to thank the three anonymous reviewers for their very helpful comments on an earlier version of this manuscript. This work is partly supported by an IMPRS PhD fellowship from the Max Planck Society to A.G.L., and a grant from the National Science Foundation of China (No. 31200849) to L.W.

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