

Oscillatory neuronal dynamics during language comprehension

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Abstract: Language comprehension involves two basic operations: the retrieval of lexical information (such as phonologic, syntactic, and semantic information) from long-term memory, and the unification of this information into a coherent representation of the overall utterance. Neuroimaging studies using hemodynamic measures such as PET and fMRI have provided detailed information on which areas of the brain are involved in these language-related memory and unification operations. However, much less is known about the *dynamics* of the brain's language network. This chapter presents a literature review of the oscillatory neuronal dynamics of EEG and MEG data that can be observed during language comprehension tasks. From a detailed review of this (rapidly growing) literature the following picture emerges: memory retrieval operations are mostly accompanied by increased neuronal synchronization in the theta frequency range (4–7 Hz). Unification operations, in contrast, induce high-frequency neuronal synchronization in the beta (12–30 Hz) and gamma (above 30 Hz) frequency bands. A desynchronization in the (upper) alpha frequency band is found for those studies that use secondary tasks, and seems to correspond with attentional processes, and with the behavioral consequences of the language comprehension process. We conclude that it is possible to capture the dynamics of the brain's language network by a careful analysis of the event-related changes in power and coherence of EEG and MEG data in a wide range of frequencies, in combination with subtle experimental manipulations in a range of language comprehension tasks. It appears then that neuronal synchrony is a mechanism by which the brain integrates the different types of information about language (such as phonological, orthographic, semantic, and syntactic information) represented in different brain areas.

Keywords: language comprehension; unification; syntax; semantics; neuronal synchronization; oscillatory dynamics; EEG power; EEG coherence

Introduction

Understanding natural language or, roughly stated, the mapping of sound or orthography onto meaning, is a deceptively simple task for most of us. The fact that language comprehension is a hard-to-suppress “reflex” is nicely illustrated, for

instance, by the word interference effect in a standard color–word Stroop task (e.g., MacLeod, 1991). Yet, understanding how language comprehension is achieved is by all means a much more difficult enterprise. Indeed, studying language comprehension (and other aspects of language processing, such as language production, language acquisition, and more generally the relation between language, thought, and culture) has evolved into a large and active research field, that of psycholinguistics.

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Traditionally, psycholinguistic research has made use of empirical methods such as behavioral experiments, computational modeling, the analysis of cross-linguistic differences, and many more. However, a seminal paper by Kutas and Hillyard (1980) showed that some aspects of semantic processing induce reliable responses in the EEG recordings of normal, healthy subjects. Since then, cognitive neuroscientific methods have become increasingly popular in psycholinguistic research (see, e.g., Brown and Hagoort, 1999). The success, or popularity of the cognitive neuroscience of language (although being stimulated by the emergence of new brain imaging techniques like PET, fMRI, and MEG), is for a large part based on the insight that the human brain is the only known system that is able to fluently produce and understand natural language. Therefore, it seems reasonable to assume that a better understanding of the neuronal processes underlying language comprehension will be helpful in shaping the existing functional models of language comprehension (this is sometimes referred to as *upward adequacy*). Vice versa, the same functional models may be helpful in guiding our understanding of the neuronal processes that are observed during language comprehension (downward adequacy).

In this chapter we concentrate on the rapid dynamics of the neural processes underlying language comprehension. However, before turning to this, let us first briefly delineate at a very general level what is thought to be the cognitive architecture of language comprehension.

It is generally agreed that during language comprehension, incoming sounds or orthographic patterns trigger a cascade of memory retrieval operations that make available the phonologic, syntactic, and semantic properties of individual words. Once available, these different ingredients have to be integrated (unified) at the sentence and/or discourse levels into a meaningful whole, in order to yield a coherent interpretation of the linguistic input (see Hagoort, 2005 for a more detailed elaboration of this framework). Thus, two different cognitive processes, namely memory retrieval operations and unification operations, play a crucial role during language comprehension.

Note that in this formulation it is a very general framework that does not address most of the more detailed — and often hotly debated — issues in language comprehension research (e.g., whether or not syntactic analysis precedes semantic analysis, compare, e.g., Marslen-Wilson and Tyler, 1980 and Friederici, 2002). However, exactly by avoiding such details it provides a common ground for most psycholinguistic researchers — and a good starting point for entering the available neural data into the debate.

The brain's language network: structure

Ever since Paul Broca and Carl Wernicke identified separate areas in the brain that are specialized for certain aspects of language processing, it has been evident that there must be a distributed network in the brain that is responsible for language processing. Hemodynamic neuroimaging techniques such as PET and fMRI, with their excellent spatial resolution, are particularly suited for identifying the different brain areas that participate in this distributed network, or stated differently, to unveil the structure of the brain's language network.

Although language is a very well-delineated cognitive function, the neural structures involved in the memory operations involved in retrieving stored linguistic knowledge are likely to have evolved from, and therefore at least show a good deal of overlap with, the structures involved in retrieving domain-general knowledge. A large number of hemodynamic studies have linked the (domain-general) retrieval of declarative (i.e., factual and episodic) information from long-term memory to increased blood oxygenation level dependent (BOLD) activity in a large number of areas including prefrontal, temporal, anterior cingulate, and cerebellar areas (see Cabeza and Nyberg, 2000 for a review). The medial temporal lobe (MTL) system is assumed to play a central role in memory operations, in that it establishes cortico-hippocampal loops that serve the purpose of coactivating distributed cortical areas in which the relevant information is stored (e.g., Miller, 1991; Murre et al., 2001). Among the cortical areas that have been specifically associated with retrieval

of lexical information in the context of language comprehension are the central and posterior parts of the left middle and superior temporal gyri, and the posterior inferior frontal gyrus (see Wise, 2003; Indefrey, 2004; Indefrey and Cutler, 2005 for reviews and meta-analyses).

Linguistic unification operations pertaining to the domains of phonology, syntax, and semantics are thought to be carried out in a set of brain regions including the left inferior frontal gyrus (Broca's area and surrounding tissue, roughly BAs 44, 45, 47, and ventral BA 6, see Hagoort, 2005 for details), and possibly the left posterior superior temporal gyrus (Indefrey and Cutler, 2005). In the left inferior frontal gyrus, there appears to be regional specificity for phonology, syntax, and semantics (see the review by Bookheimer, 2002).

The brain's language network: what about the dynamics?

The brief literature overview presented above shows that the network of brain structures that contributes to the process of language comprehension is becoming increasingly well understood. However, due to the inherently poor temporal resolution of hemodynamic measures (i.e., in the order of seconds), the resulting picture is a rather static one, emphasizing mainly the structural aspects of the brain's language network. This static view does not do justice to the dynamic properties that any language comprehension device must have. Normal speech has a rate of about three to five words per second, which means that the linguistic retrieval and unification operations must be carried out very rapidly. Therefore, trying to understand the neuronal implementation of language comprehension by relying exclusively on hemodynamic techniques would be analogous to trying to understand a piece of music by making an inventory of the instruments that constitute the orchestra. What is missing in such a static description is each instrument's melody, and the way the different instruments interact. Similarly, in order to capture the fast dynamics of the brain's language network, the information obtained from PET and fMRI studies needs to be complemented with information derived from EEG and MEG, which record neuronal activity on a millisecond time scale.

This chapter aims at providing a literature review of the rapid, oscillatory changes that are present in the EEG or MEG signals while subjects perform a variety of language comprehension tasks. In the following section we briefly indicate why these oscillatory changes are considered to provide a window onto the neuronal dynamics of the brain's language comprehension system. In addition, we delineate a general methodological framework for analyzing oscillatory brain dynamics. In the section "Experimental data," we review the available experimental data, and the "Discussion" section contains a discussion of the data and some concluding remarks.

Methodological framework

Neuronal synchronization, functional networks, and the integration of information

One thing that has become very clear on the basis of PET and fMRI studies is that a one-to-one mapping between a brain area and a specific component of a cognitive function is very often far too simplistic. Imaging studies often report activations of one and the same area during different tasks or cognitive functions. This indicates that individual cortical areas can be recruited dynamically in more than one functional network (Mesulam, 1998). This raises the question of how, for a given function (i.e., language comprehension), the dynamic recruitment of the participating cortical and subcortical areas takes place. Another, yet related, question is how different sources of information (e.g., information about phonology, syntax, or semantics), that are stored in different parts of the network, are integrated in order to form a coherent representation of the message that is conveyed by the speaker.

An answer to both these questions may be found in the patterns of synchronization and desynchronization of neuronal activity. Over the last 15 years evidence has accumulated that (de)synchronization is related to the coupling and uncoupling of functional networks in the brain (see, e.g., Pfurtscheller and Berghold, 1989; Singer, 1993, 1999; Pfurtscheller and Neuper, 1997; Pfurtscheller

and Lopes da Silva, 1999b; Varela et al., 2001, and many more). The idea is that synchronous, repetitive firing of neurons facilitates the activation of functional networks because it increases the probability that neurons entrain one another in synchronous firing (e.g., Konig and Schillen, 1991). In addition, elements pertaining to 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 oscillations in a wide range of frequencies are 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 would also serve to bind together the information that is represented in the different elements, as was elegantly demonstrated in a seminal paper by Gray and Singer (Gray et al., 1989). Fries recently proposed a simple, yet powerful, mechanistic account of this so-called binding-by-synchrony hypothesis (Fries, 2005).

Quantification of neuronal synchronization

The question is then, how can we obtain information about the rapidly changing patterns of synchronization and desynchronization of neuronal activity? The fast temporal dynamics of neural activity can be captured by imaging methods with a high temporal resolution such as EEG and MEG. The computation of event-related potentials, or event-related fields (ERPs/ERFs¹) has proved to be particularly fruitful in providing fine-grained information about the time course of subcomponents of language comprehension (e.g., Kutas and Hillyard, 1980; Hagoort et al., 1993). However, in ERP research EEG signals are averaged in order to improve the signal-to-noise ratio. This averaging procedure destroys any temporal structure of the single EEG traces that is not phase locked to

the eliciting experimental event. Hence, oscillatory phenomena that are not precisely phase locked to the eliciting event are severely attenuated, if not completely cancelled, when average ERPs are computed (Pfurtscheller and Lopes da Silva, 1999a).

The canceling of oscillatory activity as it occurs in ERP computation thus hampers our view on the dynamic interactions of neuronal ensembles both within and between brain areas. Therefore, other methods than traditional ERP analysis are needed to optimally capture (de)synchronization phenomena.

Which analysis procedures would be adequate then for studying changes in oscillatory synchrony? Here we must make a distinction between local synchrony, i.e., synchronization *within* a node of a functional network, and long-range synchrony, i.e., synchronization *between* different nodes of a network.

Local synchronous activation of a large number of neurons will, by virtue of the spatial summation of postsynaptic potentials, result in an increase in amplitude of the resulting field potential at the recording site. It follows that an increase in local synchronous oscillatory firing of a neuronal population will lead to an increase in amplitude of the scalp-recorded EEG oscillations. Such amplitude (or power, i.e., squared amplitude) changes should be studied at the single trial level (although the average amplitude, or power change, can subsequently be computed over trials). Different methods for studying event-related power changes have been used in the literature: the most widely used are event-related band power analyses like event-related desynchronization (ERD; Pfurtscheller and Aranibar, 1979; Pfurtscheller and Lopes da Silva, 1999b) or induced band power (IBP; Klimesch et al., 1998), single-trial wavelet analysis (Tallon-Baudry et al., 1998), or the more recently proposed and more sophisticated multitaper analysis (Mitra and Pesaran, 1999).

In contrast, activity in distant neuronal populations is, for the largest part, not picked up by one and the same electrode or gradiometer, but by different electrodes/gradiometers. Therefore, the above-mentioned methods do not apply. Here the relevant information lies in the phase relationship

¹To enhance readability, we will speak about EEG and ERPs in the remainder of the text, but the argumentation applies equally to MEG and ERFs.

between the field potentials recorded from or above different areas. An increase in synchrony will logically lead to an increased stability in the phase difference of two oscillatory field potentials, which is typically termed coherence (see, e.g., Varela et al., 2001). This can be quantified using methods such as event-related coherence analysis (Andrew and Pfurtscheller, 1996; Nunez et al., 1997) or phase-locking statistics (Lachaux et al., 1999). 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 et al., 2004 for an excellent overview of potentially relevant phenomena). For instance, there have been several reports on event-related phase resetting (the phase realignment, over trials, of oscillatory activity with respect to an experimental event, e.g., Braeutigam et al., 2001; Rizzuto et al., 2003).

As we will see in the literature review presented in the next section, a majority of the studies addressing the neuronal dynamics of language comprehension have concentrated on analyzing power changes. Thus, there is a bias toward local synchronization phenomena (i.e., synchrony within a node of a functional network) that the reader should keep in mind while going through the literature. In addition, studies addressing both power and coherence changes during language comprehension are completely lacking. We are convinced that such studies are highly desirable in order to arrive at a full description of the neuronal dynamics of the language comprehension process.

Experimental data

In sum, the above discussion suggests that a topographical analysis of event-related changes of power and coherence in oscillatory EEG or MEG activity recorded during a range of language comprehension tasks might be informative with respect to the neuronal dynamics (i.e., synchronization and desynchronization) that are instrumental in the coupling and uncoupling of synchronous functional networks. This (un)coupling, in turn, serves to recruit the different elements of the brain's

language network, and to integrate the information that is represented in each of the network elements.

Below we present a review of the literature that aims at identifying the neuronal dynamics observed in a wide range of language comprehension tasks, with an emphasis on our own work. Note that this review is not fully exhaustive. However, the large majority of the relevant literature is addressed, and as such the review is representative for the developments in the field. In our opinion, such a comprehensive literature review is very useful at this point in time, as we signal a trend toward an increasing number of papers that address the neuronal dynamics underlying language comprehension in recent years, while no comprehensive review papers are available yet.

Power and coherence changes in oscillatory neuronal responses during language comprehension have been observed in four different frequency bands: theta (4–7 Hz), alpha (8–12 Hz), lower beta (13–18 Hz), and gamma (above 30 Hz). The effects can roughly be subdivided into effects related to memory retrieval operations during language comprehension, and effects related to unification of linguistic information. Where possible, we will try to isolate *time frequency components* (by which we mean robust event-related changes in power or coherence) that can be identified on the basis of their scalp topography, frequency band, temporal evolution, and the extent to which they can be modulated by experimental manipulations.

Oscillatory neuronal dynamics related to the retrieval of lexical information

A number of studies suggest that oscillatory neuronal dynamics in the theta frequency range are involved in the retrieval of lexical-semantic information. In an initial study (Bastiaansen et al., 2005), we examined EEG power changes in a range of frequencies from 1 to 30 Hz while subjects read a short story. Power changes were averaged selectively for open-class (OC) words (e.g., nouns, verbs, and adjectives), which carry most of the semantic information in a sentence, and for closed-class (CC) words (e.g., articles, determiners, and

prepositions), which carry much less semantic information, but rather serve as "syntactic glue" at the sentence level. As Fig. 1 shows, both OC words and CC words elicited a power increase in the theta frequency range, together with decreases in the alpha and beta frequency ranges, roughly in an interval of 100–600 ms after word onset. The OC words generally elicited stronger power changes. Interestingly however, while the scalp topography of the alpha and beta responses was qualitatively similar, in the theta frequency range we observed a qualitative difference between OC and CC words. Whereas both types elicited a theta power increase over left occipital and midfrontal areas, the OC words additionally elicited a power increase over left temporal areas, which was not observed for the CC words (see Fig. 1). A regression analysis showed that this effect was not dependent upon word length or word frequency. This topographical pattern connects well to existing hemodynamic

data. The left occipital power increase may be related to complex visual processing either in Broca's area 18/19 (see, e.g., Petersen et al., 1988; Indefrey et al., 1997) or in the fusiform gyrus (the putative visual word form area, cf. Cohen et al., 2000; McCandliss et al., 2003). Most interestingly however, with respect to the differential (OC-specific) theta response over the left temporal cortex, it has been shown that left temporal areas (more precisely, left posterior superior and/or middle temporal gyrus) are involved in lexical retrieval (see, e.g., Indefrey, 2004; Indefrey and Cutler, 2005). Therefore, the qualitative difference between OC and CC words led us to hypothesize that theta-band synchronization of neuronal activity is related to lexical-semantic retrieval.

A subsequent experiment (Bastiaansen et al., submitted) aimed at further testing this hypothesis. Subjects performed a lexical decision task, in which they had to decide whether or not a visually

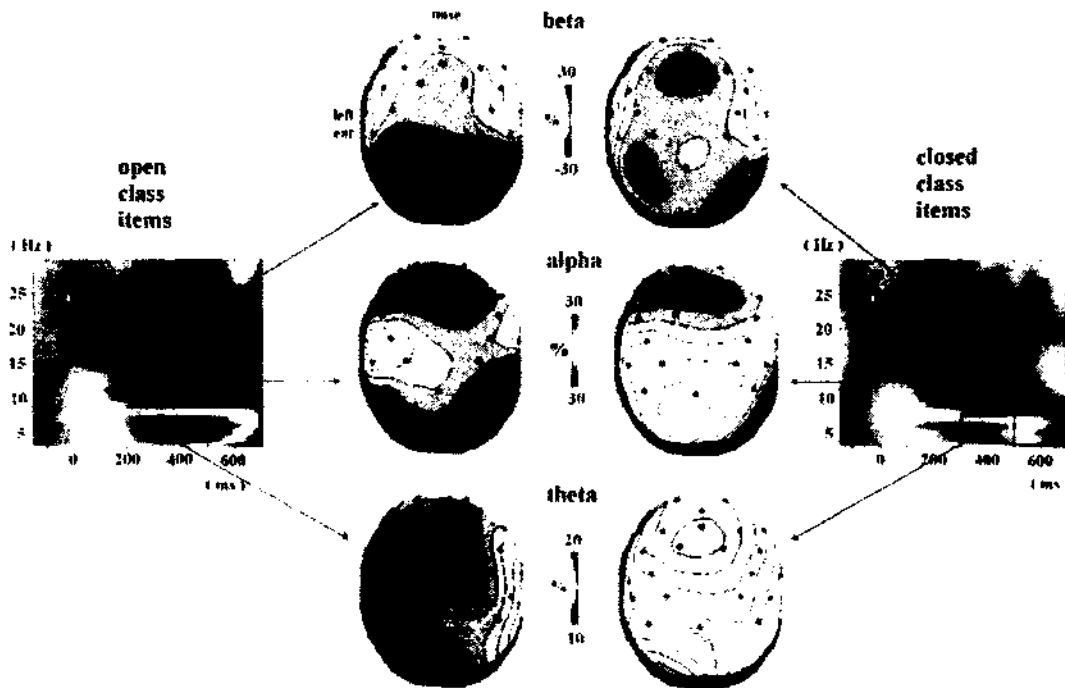


Fig. 1 Results of a time-frequency analysis of power changes, for open-class words and closed-class words separately. Left- and right-hand parts of the figure show a time-frequency representation (TFR) of the percentage power changes at one frontal channel (F7). Words are presented at $t = 0$. Middle part of the figure shows the topographical distributions of power changes in three time-frequency intervals, indicated by the black tiles in the TFRs. Note the qualitative difference in scalp topography of the theta power increase.

presented string of letters constituted a real word. Nonwords could be either pseudowords (phonologically legal, but nonsensical letter strings) or consonant strings. Real words could either be nouns with visual semantic properties (i.e., referring to colors and shapes) and nouns with auditory semantic properties (i.e., referring to sounds).

Again, both sets of words elicited an increase in theta power and decreases in the alpha and beta frequency ranges. And again, qualitatively different responses were found only in the theta band, where the following double dissociation was found (see Fig. 2): words with auditory semantic properties showed larger theta power increases in electrodes overlying the left auditory cortex than in electrodes overlying the left visual cortex, while the opposite pattern was found for words with visual semantic

properties. Note that, as both sets of words were presented visually, and were matched for length and frequency, they only differed in terms of semantic properties. We therefore concluded that the results of this study confirm the hypothesis that neuronal synchronization in the theta frequency range is involved in the retrieval of lexical semantic information. In addition, our data are in agreement with the hypothesis that spatially distributed functional networks form the basis of semantic representations, and that the topographies of these networks reflect the semantic properties of individual items (for similar hypotheses, see Pulvermüller, 1999, 2001; Martin and Chao, 2001).

While the above studies suggest a strong involvement of theta-band synchronization in retrieving lexical-semantic information, the neuronal

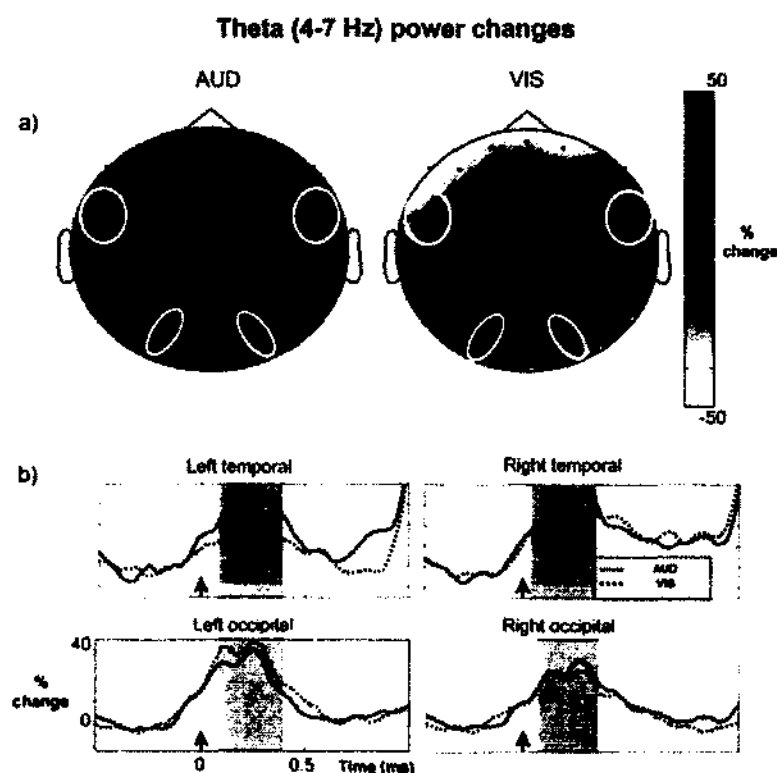


Fig. 2. Topographical distribution (a) and region-of-interest time courses (b) of percentage theta power changes induced by visually presented words with auditory semantic properties (AUD) and visual semantic properties (VIS). The regions of interest are indicated by the white ellipses in (a). Shaded areas in (b) indicate the time interval used for the statistical analyses. In the left hemisphere, there is a double dissociation in the power changes between semantic properties and regions of interest.

dynamics of language comprehension-related retrieval operations are certainly not restricted to the theta frequency band. Other studies have related semantic memory operations to power changes in the alpha frequency band (for review, see Klimesch, 1999). For instance, in a study by Klimesch and colleagues (Klimesch et al., 1997b) subjects were asked to judge whether pairs of words were semantically related, and this was accompanied by power decreases in the (upper) alpha band. In another study from the same group (Rohm et al., 2001), subjects had to find a superordinate concept (i.e., a semantic retrieval task) while reading sentences, and this was accompanied by a stronger alpha power decrease compared to a condition where only reading was required. In yet another study (Klimesch et al., 1997a), subjects judged whether sequentially presented feature-concept pairs were semantically congruent. It was found that only (upper) alpha power discriminated between good and poor performers. The distinction reported in this latter paper between upper and lower alpha frequency bands seems to hold over a range of empirical data showing that different patterns of alpha desynchronization can be observed when the broad alpha frequency range is subdivided into lower and upper alpha bands on the basis of individual alpha peak frequency (see Klimesch, 1999 for review). The lower alpha band has been shown to be more sensitive to general task demands such as attentional processes, while oscillatory neuronal activity in the upper alpha frequency range likely reflects specific task requirements. In strong support of these findings, it has been demonstrated that event-related power changes in the lower and the upper alpha frequency bands increasingly dissociate as task demands increase (Fink et al., 2005).

It should be noted, finally, that in many of the studies by Klimesch et al. (but not the ones cited above), the term semantic memory is often used in the sense of declarative (as opposed to episodic) memory. Although this is perfectly valid terminology, there is a potential confusion with the term "semantic" as it is meant in language comprehension theories. There the term semantic is used in its more narrow sense, referring to the meaning aspect of words (as opposed to syntax, phonology,

etc.). This terminology issue should be kept in mind as one reads through the literature.

A few studies have reported effects of memory retrieval in higher frequency bands (beta/gamma). For instance, Weiss and colleagues (cf. Weiss and Mueller, 2003 for review) found different coherence patterns in the lower beta frequency range (roughly 13–18 Hz) between concrete and abstract nouns, and between concrete nouns and verbs. Pulvermueller et al. (1999) contrasted nouns (which were taken to have predominantly visual semantic properties) with verbs (presumed to have movement-related semantic properties) in a lexical decision task, and found power decreases in the gamma frequency range compared to baseline, which were smaller for verbs than for nouns at central electrodes, but smaller for nouns than for verbs over occipital electrodes. These data were interpreted to reflect different network topographies that followed the semantic properties of the stimuli (much as the above-described difference in theta topography between auditory and visual semantic properties). However, the reported effects consisted of gamma power *decreases* with respect to a prestimulus baseline. This is in contradiction with the general notion that networks emerge through increased synchrony (although the alpha frequency range may constitute an exception, see, e.g., Pfurtscheller, 1992; Pfurtscheller and Neuper, 1994 for relevant data, Bastiaansen et al., 2005 for a brief discussion, and Steriade et al., 1990 and Lopes da Silva, 1991 for a possible underlying physiological mechanism), which, in scalp recordings, should be reflected by power *increases* rather than decreases compared to baseline (cf. Varela et al., 2001; Bastiaansen and Hagoort, 2003).

Oscillatory dynamics related to unification operations in language comprehension

As sentences extend over relatively long time periods, maintaining the working memory (WM) trace of the linguistic input is a prerequisite to performing unification operations. In addition to retrieval operations, theta-band changes in neuronal synchrony also appear to play a role in such WM processes. For example, theta power (Bastiaansen et al., 2002a) and coherence (Weiss and

Mueller, 2003) linearly increase over the course of correct sentences. In addition, theta power is larger over the frontocentral midline following words constituting syntactic (Bastiaansen et al., 2002b) and semantic (Hagoort et al., 2004; Hald et al., 2006) violations in sentences (see, e.g., the right-hand part of Fig. 3). These effects were interpreted to be related to the larger demands that they impose on verbal WM (Hald et al., 2006). Also, theta coherence is larger following WM-demanding

object-relative vs. subject-relative clauses (Weiss et al., 2005). A clear relationship between theta-band oscillations and WM has also been found using intracranial recordings in humans (Raghavachari et al., 2001; Rizzuto et al., 2003).

There is however more to unification than just maintaining the input in WM. Unification requires the active manipulation of phonological, syntactic, semantic, and likely also of pragmatic information, resulting in a message-level understanding of

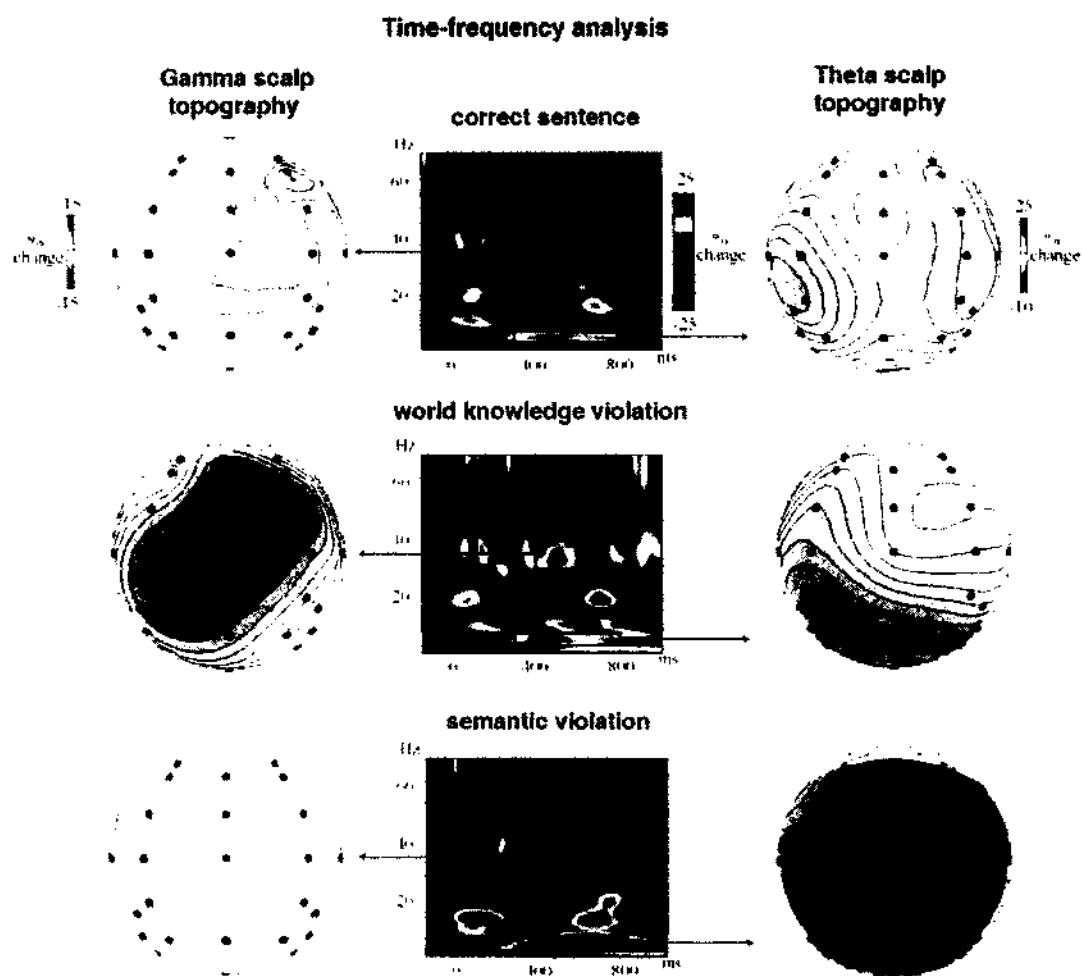


Fig. 3 Time-frequency analysis of the power changes elicited by the critical words in correct sentences, sentences containing violations of world knowledge, and sentences containing semantic violations. The middle part shows the TFRs, the left- and right-hand parts show the topographical distribution of gamma and theta power changes, respectively. Note the small but significant increase in gamma power over lateral frontal areas in the correct condition, the strong gamma power increase following a world knowledge violation, and the absence of gamma power increase after a semantic violation.

the linguistic input. So far, experimental research into the neuronal dynamics of unification operations have concentrated on semantic and syntactic unification only.

Semantic unification

Recently we have addressed the oscillatory correlates of semantic unification in the following way (Hagoort et al., 2004; Hald et al., 2006). Subjects read the following three versions of sentences such as: "The Dutch trains are *yellow/white/sour* and very crowded." In fact, Dutch trains are yellow, and therefore the first version of this sentence is the correct sentence condition. However, the linguistic meaning aspects of the alternative color term *white* apply equally well to trains as the predicate *yellow*. It is world knowledge about trains in Holland that make the second version of this sentence false (the world knowledge violation condition). This is different for the third version. The core meaning of *sour* is related to taste and food. Under standard interpretation conditions a predicate requires an argument whose semantic features overlap with that of its predicate. For vehicles such as trains, this is clearly not the case, since semantic features related to taste and food do not apply to the materials that trains are made of. Thus, for semantic-internal reasons the third sentence is an outright semantic violation condition.

The results are presented in Fig. 3. In the correct sentence condition, where normal semantic unification takes place, we observed a small increase in gamma power relative to baseline in response to the critical word (e.g., yellow). This gamma power increase was much stronger in the world knowledge violation condition, where semantic unification is difficult but not impossible. In the semantic violation condition however, where semantic unification is impossible for the reasons mentioned above, the gamma power increase was absent.

The parametric relation between semantic unification and gamma power described above suggests that gamma oscillations are functionally related to semantic unification operations. Several other studies support this notion. First, gamma coherence is larger for semantically congruous than for incongruous sentence endings (Weiss et al., 2003). In a different approach, van Berkum et al. (2004)

studied the effects of referential success, referential ambiguity, or referential failure in a sentence, and found a drop in gamma power following the ambiguous and failing reference conditions, which render semantic unification problematic.

A final link between gamma-band synchronization and semantic unification operations was reported by Braeutigem et al. (2001). These authors report an increase in *phase-locked* gammaphase-locked gamma power in response to semantic violations in sentences relative to correct control sentences. Thus, the results go in the opposite direction (larger gamma power for violations) compared to the three studies discussed above. However, this may be partially explained by the difference in analysis methodology: only phase-locked power changes were considered in this paper, which suggests that some sort of phase alignment or phase resetting occurred in the gamma band as a result of the semantic violation. Note that phase resetting has also been reported to occur in the theta frequency range during a WM task (Rizzuto et al., 2003); so the phenomenon is likely to have functional significance in a range of cognitive tasks.

Taken together, the above studies lead us to hypothesize that neuronal synchronization in the gamma frequency range is in some way related to the unification of semantic information is implemented in the brain.

Syntactic unification

The neuronal dynamics of syntactic unification have been addressed in a number of different experimental paradigms. For instance, Haarmann et al. (2002) used sentences in which EEG coherence was examined in the interval between the object and the main verb of a sentence (the so-called filler gap interval, cf. Haarmann et al., 2002 for details). Although this filler gap interval places a relatively large demand on verbal WM, the gap filling that the reader has to perform on-line can be seen as a syntactic unification operation. The authors found increased coherence over many scalp areas in the sentences containing a filler gap interval compared to nonfiller sentences, in the lower beta frequency range (roughly 15–18 Hz). This increased coherence is indicative of an

increase in long-range neuronal synchronization during the syntactically more demanding filler sentences. A study by the Weiss et al. (2005) compared EEG coherences during sentences in which the subject of the main clause is also the subject of the relative clause (so-called subject-relative (SR) sentences), with EEG coherences during sentences in which the subject of the main verb is the object of the relative clause (object-relative (OR) sentences). SR sentences are syntactically relatively simple, and have a high frequency of occurrence in everyday language, whereas OR sentences are less frequent, syntactically more demanding, and place a larger load on verbal WM. The authors showed that increased theta and gamma coherences were associated with the higher WM load.

The effects of syntactic complexity (which become most evident in the time period just following the relative clause) however were expressed in the lower beta frequency range (13–18 Hz). In a similar type of experiment with Dutch subjects and stimuli, we are currently investigating power and coherence changes of the MEG between OR and SR sentences, and between sentences with right-branching (RB) relative clauses compared to the syntactically more demanding center-embedded (CE) relative clauses. Preliminary results from this experiment suggest that CE sentences elicit larger MEG power in the (lower) beta frequency range (in this case, 15–25 Hz) compared to RB sentences (see Fig. 4). Analyses of the coherence data, and of the SR-OR comparisons, are still in progress.

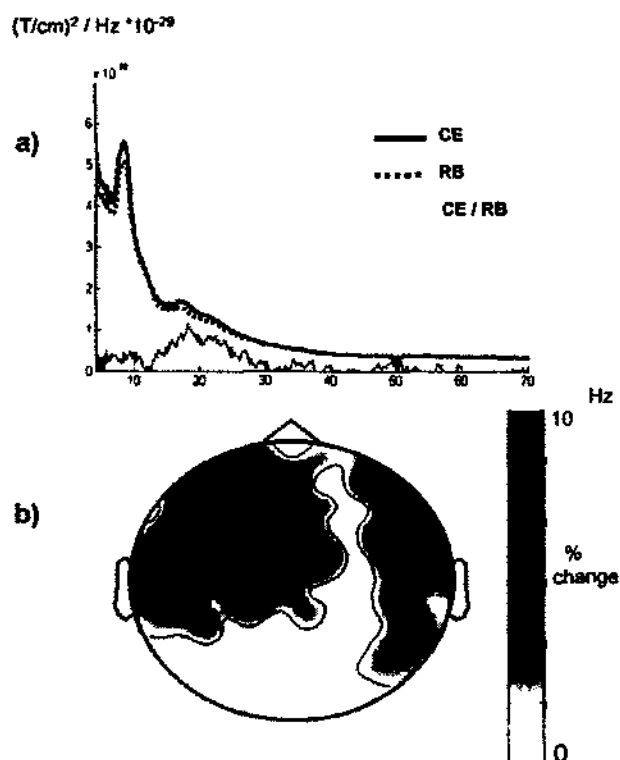


Fig. 4. (a) MEG power spectra computed on the relative clauses (RC) of sentences in which the RC was either right-branching (RB, simple syntactic structure) or center-embedded (CE, complex syntactic structure). The relative change (thin line, CE/RB) has been scaled to fit the graph, and is therefore in arbitrary units. Note that although there are power differences in the theta, alpha, and beta frequency ranges, the relative change is the largest in the beta frequency range (15–25 Hz), and only significant there. (b) Topographical distribution of the relative increase in beta power from RB to CE. Only the significant changes, as obtained from a randomization test, are displayed (i.e., the data are masked with significance).

Discussion

As we have seen in the previous section, the general pattern emerging from the experimental data shows a clear and robust distinction in network dynamics between memory-related processes (synchronization of neuronal activity within and between network nodes in the theta and alpha frequency ranges) and semantic and syntactic unification-related processes (beta-band and gamma-band synchronization). Thus, it appears that there is a well-characterized pattern of *frequency specificity* in the observed time-frequency components. Another aspect of the available experimental data that is well-characterized is the *temporal evolution* of the different oscillatory responses: the large majority of the oscillatory responses that have been observed are concentrated in roughly the first 500 ms after word presentation, whether it be in isolated word studies or in sentence materials. This time interval is known, on the basis of a large body of behavioral and ERP evidence, to be crucial in language comprehension. Also, there seems to be a large consistency over studies in the *direction of the modulation* of power and coherence changes, which is different for the different frequency bands. In general, theta and gamma power and coherence increase relative to baseline. Alpha power generally decreases relative to baseline (alpha coherence has not been studied), whereas the overall pattern for beta-band effects seems to be that beta power decreases, while beta coherence increases relative to baseline (but there are a few exceptions to this latter pattern).

An aspect of the oscillatory dynamics during language comprehension that is less well characterized is the *topographical distribution* of the reported effects. This may be partially due to the fact that in the early days of time-frequency analysis of EEG/MEG, scalp topographies of power/coherence changes were often not reported, perhaps to reduce the relatively high computational load that comes with time-frequency analyses, perhaps also because it was not considered to be of crucial importance. In addition, with coherence analyses it is sometimes difficult to point to a clear topographical distribution in the pattern of interactions between brain areas. However, when studied, the

topographical distribution of oscillatory dynamics is often not very consistent across studies. This makes it difficult to connect and integrate the increasing knowledge about the dynamics with existing knowledge about the structure of the brain's language network as obtained from hemodynamic studies. Possible avenues for improving this situation may be (1) the use of advanced source reconstruction techniques that are developed specifically for the localization of oscillatory activity, such as dynamic imaging of coherent sources (DICS; cf. Gross et al., 2000, 2001; Hoogenboom et al., 2006), or (2) the simultaneous measurement of EEG and fMRI, where recent developments have made it possible to correlate oscillatory activity in distinct frequency bands with fMRI BOLD changes (see, e.g., Goldman et al., 2002; Laufs et al., 2003; Parkes et al., 2006).

Memory

The neuronal dynamics that have been observed in relation to memory retrieval operations in the context of language comprehension are characterized by synchronization of neuronal activity in the theta frequency band, and desynchronization in the alpha band. This pattern of results connects well to the results that have been obtained outside the domain of language. In a large number of experiments that use domain-general memory tasks, theta and alpha power changes have been related systematically to the encoding and retrieval of episodic and declarative information. This has been observed both in scalp EEG recordings (see Klimesch, 1999 for a comprehensive review) and, as far as the theta-band results are concerned, in intracranial recordings in humans (Kahana et al., 1999, 2001; Caplan et al., 2001).

With respect to theta-band activity, there is an even larger body of literature, based for a large part on animal studies, that supports a role for theta in memory operations (for extensive review see, e.g., Miller (1991)). In this literature, theta-band oscillations are considered to establish dynamic links between the neocortex and the MTL memory system. Eichenbaum et al. (Eichenbaum et al., 1994, 1996), amongst others,

have proposed that neocortical association areas maintain short-term memories for specific items prior to MTL processing, and eventually provide the final repositories of long-term memory. The latter idea is consistent with that proposed by Miller (Miller, 1991), that "the hippocampus (...) acts in some ways as an 'index' to memories, the cortex being, as it were, the 'book' to which this index refers" (Miller, 1991, p. 159). Similar, although slightly different, ideas have been put forward by Treves and Rolls (1994). According to Miller (1991), the transfer of information between the MTL system and cortical association areas may well be mediated by rhythmic activity in the theta frequency range (see Bastiaansen and Hagoort, 2003 for a more detailed discussion).

An important implication of Miller's notion of self-organizing, resonant theta-synchronized loops between the MTL system and the neocortex is that studying the reactivity of theta at the "cortical end" of the loop (e.g., with scalp EEG/MEG) might provide us with a window on the MTL contribution to different types of memory processes. It is therefore not unlikely that the theta power responses that have been observed in the context of language comprehension are also an expression of synchronized activity in cortico-hippocampal circuits. This notion is at least indirectly supported by a number of studies that have used intracranial recordings directly from the human MTL during language comprehension tasks. These studies have reported negative deflections in the anterior MTL that show a similar reactivity as the scalp-recorded N400 (such as larger amplitude for semantically unrelated words, larger amplitudes for highly imageable words, etc.; McCarthy et al., 1995; Nobre and McCarthy, 1995; Heckers et al., 2002; Klaver et al., 2005; Meyer et al., 2005).

In sum, we might conclude from the above that the mechanisms involved in the retrieval of lexical information are of a domain-general nature, i.e., the neuronal dynamics by which the brain's language network operates are not specific to language comprehension, but apply more generally for memory retrieval (which has been extensively studied in animals). However, since

this mechanism is apparently also involved in language comprehension it does add to a better comprehension of the dynamics of the brain's language network.

The observed alpha power changes are more difficult to relate to a neuronal circuitry involved in memory. Traditionally, alpha-band oscillations are associated with thalamo-cortical information transfer, and, at the functional level, with the transmission of sensory and motor input to the cortex, and with attentional modulation of this transmission (see, e.g., Skinner and Yingling, 1977; Lopes da Silva, 1991; Brunia, 1999; Bastiaansen and Brunia, 2001). In this context it is interesting to note that alpha power has been sensitive to linguistic manipulations mainly in those situations where a secondary task was used (e.g., finding a superordinate concept, or performing a semantic judgment, etc.; see subsection "Oscillatory neuronal dynamics related to the retrieval of lexical information"). In those studies, differential effects are usually found for the lower and upper alpha bands, where the lower alpha band is generally modulated by general task demands such as attention, and the upper alpha band is sensitive to specific task demands. In addition, the event-related power changes in the lower and the upper alpha frequency bands increasingly dissociate as task demands increase (Fink et al., 2005). This data pattern seems to suggest that both alpha subband ranges are sensitive (though in different ways) to secondary task demands. These findings stand in sharp contrast to our own work, where we typically ask subjects just to read for comprehension. In those studies, we have not observed a systematic modulation of (either upper or lower) alpha power as a function of linguistic manipulations, which might suggest that the alpha band reactivity observed during language comprehension is not necessarily related to the comprehension process per se, but to general attentional levels (lower alpha) and the specific behavioral consequences of the language comprehension process (upper alpha). This explanation is very speculative though, and we doubt that it could account for all the findings described in subsection "Oscillatory neuronal dynamics related to the retrieval of lexical information."

Unification

As said, syntactic and semantic unification operations during language comprehension are accompanied by neuronal synchronization in the higher frequency ranges (beta and gamma). So far, syntactic unification has been associated exclusively with beta-band synchronization, whereas semantic unification has been associated both with beta- and gamma-band synchronization. Although this is suggestive of a qualitative difference in the dynamics of syntactic and semantic unification, no single study has addressed both types of operations within the same sample of subjects. In addition, the neuronal dynamics of syntactic unification have been addressed only in a limited number of studies (three in total). Hence, it is too early to draw any firm conclusions regarding a possible qualitative difference between syntactic and semantic unification dynamics on the basis of the existing database.

The integration, or binding, of information from different brain areas has repeatedly been associated with neuronal synchronization in the gamma frequency range outside the domain of language comprehension. For instance, gamma synchronization has been shown to play a role in feature binding in the visual system (e.g., Gray and Singer, 1989; Roelfsema et al., 1997; Fries et al., 2001a; see, e.g., Singer and Gray, 1995 for a review), and is subject to attentional modulation (Fries et al., 2001b). In addition, gamma-band synchronization has been related to top-down integrative processes in perception (e.g., Rodriguez et al., 1999; Tallon-Baudry and Bertrand, 1999). Therefore, the observed relationship between gamma-band synchronization and semantic unification operations fits well within the larger context of the integrative role that gamma-band neuronal synchronization appears to play in a wider range of cognitive domains.

Such a connection to domain-general processes is less clear for the effects observed in the beta frequency range. Traditionally, beta-band activity has been related to the planning and execution of movements (see, e.g., Pfurtscheller et al., 1996, 1998), where the typical pattern is a desynchronization of beta-band activity before and

during movement execution, and a somatotopically organized beta synchronization after movement offset. However, as we saw in subsection "Oscillatory dynamics related to unification operations in language comprehension," beta reactivity is a robust phenomenon in language comprehension tasks, in the sense that it is observed during a variety of tasks, with different analysis procedures and in different laboratories. It is therefore likely that neuronal synchronization in the beta frequency range is truly instrumental during linguistic unification operations, although its exact role remains unclear at present.

Conclusion

We have provided an overview of the neuronal dynamics that can be observed during a wide range of language comprehension tasks. Overall, the experimental data indicate that the two components of language comprehension, namely, the retrieval of lexical information from the mental lexicon and the subsequent unification of semantic and syntactic information, yield distinct patterns of synchronization in the brain's language network: retrieval operations are associated with neuronal dynamics in the theta and alpha frequency ranges, whereas unification operations are associated with neuronal synchronization in the beta and gamma frequency ranges. As such, the general pattern of results suggests that at the level of the dynamic neuronal mechanisms by which the brain operates during language comprehension, domain-general processes are operative (i.e., the observed mechanisms are not exclusively engaged by linguistic processing, but are also observed in other cognitive domains). This opposes to the representational level, where there is a relative domain-specificity for language comprehension (i.e., there are brain areas that are partly dedicated to the storage and manipulation of linguistic information, as evidenced by hemodynamic studies).

We conclude that it is possible to capture the dynamics of the brain's language network by a careful analysis of the event-related changes in power and coherence of EEG and MEG data in a

wide range of frequencies, in combination with subtle experimental manipulations in a range of language comprehension tasks. It appears then, that neuronal synchrony is a mechanism by which the brain integrates the different types of information about language (such as phonological, orthographic, semantic, and syntactic information) represented in different brain areas.

Finally, we feel that a word of caution with respect to the above conclusions is appropriate. Compared to the more classical ERP approach, analyzing the oscillatory brain responses in relation to language is still in its infancy. Relatively few studies have been done, and the functional characteristics of the oscillatory brain responses reported in language studies are not yet well understood. Nevertheless, we believe that analyzing oscillatory brain dynamics has quite some mileage that motivates further studies. We have here provided a psycholinguistically and neurobiologically plausible framework for studying the neurocognition of language. In this framework, an important distinction is made between memory and unification operations. Based on a review of the literature, our current working hypothesis is that synchronization in the theta frequency and, possibly, desynchronization in the alpha frequency ranges are mechanistically involved in memory retrieval. Unification operations, on the other hand, are thought to be associated with synchronization in the beta and gamma frequency bands. So far, we have not seen any convincing evidence that this generalization would be different for local synchrony (reflected in power changes), or in synchronizing activity in distant areas (changes in coherence). However, we are the first to admit that much more work is needed to get a firm grasp on the functional significance of the different oscillatory responses that are reported in the context of language comprehension.

Abbreviations

BOLD	blood oxygenation level dependent response
DICS	dynamic imaging of coherent sources

EEG	electro-encephalography
ERD/ERS	event-related desynchronization/ event-related synchronization
ERP	event-related potential
fMRI	functional magnetic resonance imaging
MEG	magneto-encephalography
PET	positron emission tomography
WM	working memory

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