

The neural oscillations of speech processing and language comprehension: state of the art and emerging mechanisms

Lars Meyer 

Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1A, 04103 Leipzig, Germany

Keywords: chunking, entrainment, memory, predictive coding

Abstract

Neural oscillations subserve a broad range of functions in speech processing and language comprehension. On the one hand, speech contains—somewhat—repetitive trains of air pressure bursts that occur at three dominant amplitude modulation frequencies, physically marking the linguistically meaningful progressions of phonemes, syllables and intonational phrase boundaries. To these acoustic events, neural oscillations of isomorphous operating frequencies are thought to synchronise, presumably resulting in an implicit temporal alignment of periods of neural excitability to linguistically meaningful spectral information on the three low-level linguistic description levels. On the other hand, speech is a carrier signal that codes for high-level linguistic meaning, such as syntactic structure and semantic information—which cannot be read from stimulus acoustics, but must be acquired during language acquisition and decoded for language comprehension. Neural oscillations subserve the processing of both syntactic structure and semantic information. Here, I synthesise a mapping from each linguistic processing domain to a unique set of subserving oscillatory mechanisms—the mapping is plausible given the role ascribed to different oscillatory mechanisms in different subfunctions of cortical information processing and faithful to the underlying electrophysiology. In sum, the present article provides an accessible and extensive review of the functional mechanisms that neural oscillations subserve in speech processing and language comprehension.

Overview

This review summarises the current research into neural oscillations as subserving both lower-level functions of speech processing and higher-level functions of language comprehension. Throughout the article, the dichotomy of speech processing vs. language comprehension is used to capture an essential difference: speech processing describes the segmentation of speech into linguistically meaningful units, as well as the identification of these units—based on temporal and spectral cues that are present in the physical world and can be recognised by the auditory system. In contrast, language comprehension describes the decoding of the meaning of words and combinations of words, such as phrases and sentences. Meaning is not present in the physical world; rather the meaning of speech sounds

must be acquired first through contextual association during language acquisition, to be recognised and composed in the course of language comprehension.

Accordingly, this review comes in two parts. The first part, on speech processing, illustrates the popular view that neural oscillations subserve the segmentation and identification of more or less discrete phonological units across a range of oscillatory bands. The operation frequency of these bands is thought to be stimulus-bound, corresponding to the occurrence frequency of phonological units in the acoustic spectrum. The second part, on language comprehension, illustrates the major functions that neural oscillations subserve in higher-level linguistic processing. Here, oscillations at the frequency where multiword groups can be decoded from speech have been proposed to functionally support the internal generation of syntactic structures. In addition, oscillations functionally subserve memory-related processes required for, and potentially specific to, the internal computation of sentence-level relational meaning, as well as the cumulative prediction and contextual interpretation of upcoming words.

It is important to note that the proposed links between specific oscillatory frequency bands and specific subdomains of speech processing and language comprehension do not entail domain- or process-specificity of particular frequency bands. The human brain's oscillatory frequency band inventory is well too limited to ascribe

Correspondence: Lars Meyer, as above.

E-mail: lmeyer@cbs.mpg.de

Received 11 July 2017, revised 14 September 2017, accepted 9 October 2017

Edited by Ali Mazaheri

Reviewed by Nicola Molinaro, Basque center on Cognition, Brain and Language, Spain; and Elana Zion-Golumbic, Bar-Ilan University, Israel

The associated peer review process communications can be found in the online version of this article.

specific oscillatory frequency bands to specific linguistic processing domains alone (for review, see Penttonen & Buzsáki, 2003; Buzsáki, 2006). Instead, I share the more parsimonious view that linguistic processing domains instantiate a small general set of basic electrophysiological mechanisms that resurface as oscillatory patterns across cognitive domains (e.g. Friederici & Singer, 2015; Lewis *et al.*, 2015). By implication, the use of neural oscillations as a dependent measure for experimental research may allow for a cognitive neuropsychology of speech and language that is not only faithful to textbook conceptualisations of linguistics, psycholinguistics and neurolinguistics, but also to the systems neuroscientific view that any cognitive function instantiates a circumscribed set of fundamental mechanisms of cortical information processing.

Neural oscillations in speech processing

Speech processing is the set of neural processes enabling the segmentation and identification of more or less discrete phonological units in the acoustic spectrum, which encode to-be-communicated meaning. Speech is built hierarchically from units decreasing in temporal granularity: a series of phonemes constitutes a syllable; a series of syllables constitutes an intonation phrase. To a certain extent, the linguistic units of phonemes, syllables and intonation phrases can be recognised from physical counterparts in speech acoustics—temporal counterparts include repetitive trains of air pressure maxima that mark the on- and offsets of many discrete phonetic units; spectral counterparts distinguish between individual phonetic units. Across a range of operating frequencies, neural oscillations have been proposed to aid speech processing by aligning their phase to acoustic amplitude extrema that occur during the on- or offsets of phonemes, syllables and intonation phrases. In the first part of this review, I summarise these proposals (see Fig. 1 for an overview).

Synchronisation with speech: phonemes, syllables and intonation phrases

During speech processing, neural oscillations have been proposed to track linguistically meaningful acoustic properties of speech across three characteristic frequency bands (for review, see Giraud & Poeppel, 2012; Kösem & Van Wassenhove, 2017). During rest already, oscillatory frequency bands resembling the paces of phonemic units are prevalent in the power spectrum of the auditory cortex (Giraud *et al.*, 2007). During speech processing, these oscillations have been found to synchronise with the pace of both acoustic amplitude modulations and phonemes (Di Liberto *et al.*, 2015), syllables (Peelle *et al.*, 2013) and intonation phrases (Bourguignon *et al.*, 2013). Oscillatory synchronisation facilitates speech processing, given that the magnitude of synchronicity predicts speech intelligibility (Ahissar *et al.*, 2001; Luo & Poeppel, 2007; Nourski *et al.*, 2009; Peelle *et al.*, 2013; Doelling *et al.*, 2014). It is unlikely that the proposed isomorphism between the frequencies of neural oscillations and speech segments of different granularities entails a functional specificity of neural oscillations for speech processing—for instance, phoneme-rate sampling is attested even in rodent models, and deficient sampling in rodent models may associate with decreased rhythmicity of spiking (Che *et al.*, 2014; Centanni *et al.*, 2016). In addition, perceptual sampling is rhythmic not only in the auditory, but also in the visual and tactile modalities (Holcombe, 2009; Giraud & Poeppel, 2012; VanRullen, 2016). It thus appears more plausible to conceive of the rhythmicity of speech at its major temporal granularities as having been shaped evolutionarily by the brain's pre-existing oscillatory frequencies.

Synchronisation of neural oscillations to speech is thought to occur via so-called entrainment, the electrophysiological underpinnings of which are not clearly defined: on the one hand, the phase of the speech amplitude envelope could attract neural phase to synchronise (i.e. phase synchronisation); on the other hand, speech

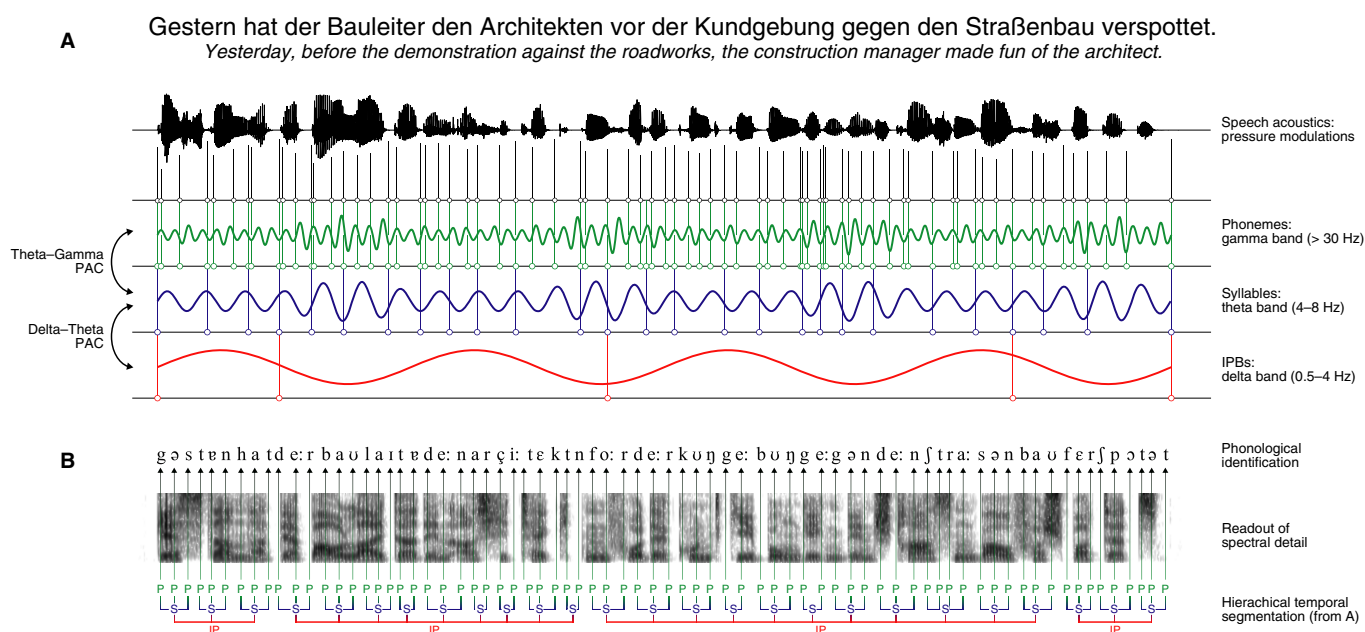


FIG. 1. Neural oscillations in speech processing; (A) gamma- (green), theta- (blue) and delta-band oscillations (red) synchronise with air pressure maxima in the acoustic speech signal that delineates phonemes (green), syllables (blue) and intonational phrase boundaries (IPB; red), respectively; delta–theta and theta–gamma phase–amplitude coupling (PAC) could serve both to (B) bind lower-level phonological units into coherent high-level percepts (i.e. phonemes into syllables, syllables into intonation phrases) and to align neural excitability to linguistically critical spectral features, thereby facilitating phonological identification in spite of sparse amplitude modulations that prohibit stimulus-driven synchronisation.

amplitude itself could attract synchronisation (i.e. amplitude synchronisation; for review, see Hyafil *et al.*, 2015). For phase, it was found that rapid modulations of speech amplitude coincide with phase resets of auditory-cortical neural oscillations across the gamma, theta and delta frequency bands (Gross *et al.*, 2013), and high-amplitude discharges to complex acoustic stimuli were found to reset the phase of local field potentials in rat auditory cortex (Szymanski *et al.*, 2011). Yet, the removal of amplitude envelope information from speech does not necessarily abolish phase synchronisation (Obleser *et al.*, 2012); additionally, at least when measured on the auditory nerve, the phase of spiking activity is only affected by acoustic amplitude modulations at suboptimal response frequencies (Anderson *et al.*, 1971; Rose *et al.*, 1974; Trussell, 2002). Thus, approaches that propose speech amplitude to attract oscillatory synchronisation require an explanation of how speech amplitude modulations are electrophysiologically converted to modulations of neural phase. In addition, while the theta and delta bands have been shown to phase synchronise to speech amplitude modulations, the gamma band has mostly been shown to amplitude synchronise (see below). Thus, two distinct neurophysiological mechanisms of oscillatory synchronisation remain to be clarified.

While there currently is enthusiasm on the isomorphism of electrophysiological sampling frequencies in the auditory system and temporal granularities in the speech stimulus, the interpretation of the available data in terms of oscillatory synchronisation has also received criticism: many, if not most of the studies that observed oscillatory synchronisation to speech used stimuli that contained rhythmic amplitude modulations, which could have resulted in a train of transient evoked electrophysiological responses that could have disguised as an oscillation at amplitude modulation frequency (e.g. Klimesch *et al.*, 2007b; Ding & Simon, 2014). On the other hand, oscillatory synchronisation also occurs in the absence of rhythmic amplitude modulations (Henry & Obleser, 2012; Obleser *et al.*, 2012), rhythmicity of oscillatory synchronisation is to some extent robust to decreased stimulus rhythmicity (cf. Mathewson *et al.*, 2012; Calderone *et al.*, 2014), and auditory processing performance transiently keeps stimulation frequency even after stimulation offset (e.g. Neuling *et al.*, 2012; Hickok *et al.*, 2015).

The gamma band: subsyllabic processing

At subsyllabic timescales, the amplitude of gamma-band oscillations follows the amplitude envelope of speech (Lehongre *et al.*, 2011; Gross *et al.*, 2013; Di Liberto *et al.*, 2015). It is unclear whether this reflects phonemic-categorical processing proper, or rather low-level acoustic segmentation or identification; it is also unclear whether subsyllabic speech processing is subserved by amplitude or phase synchronisation. On the one hand, gamma-band amplitude synchronisation has been linked to phonemic-categorical perception—amplitude decreases of the lower gamma band (i.e. 30 Hz) predict phonemic-categorical deficits in dyslexic subjects (Lehongre *et al.*, 2011). On the other hand, phase synchronisation of the lower gamma band has been linked to acoustic processing (Gross *et al.*, 2013)—decreased phase synchronisation to mere noise bursts has been observed in dyslexic subjects (Lizarazu *et al.*, 2015). It has also been suggested that the lower gamma band synchronises more strongly with the acoustic amplitude envelope than with phonemic-categorical information (Di Liberto *et al.*, 2015). In addition, electrocortical work suggests that phonemic-categorical information is only reflected in the amplitude synchronisation of neural oscillations in the high gamma band (i.e. > 70 Hz; Nourski *et al.*, 2015), likely reflecting spiking activity of auditory-cortical neurons

sensitive to individual phonemes (Mesgarani *et al.*, 2014; Nourski *et al.*, 2015). In sum, there are indications for a relationship between neural oscillations at gamma-band frequency and sound amplitude modulations at subsyllabic frequencies. However, it is left open for future research whether gamma-band oscillations only track acoustic amplitude modulations, or synchronise with the pace of phonemes proper—or whether the lower and higher gamma bands differentially subserve acoustic-perceptual and phonemic-categorical processing, respectively. It is also still unclear whether the prior results reflect oscillatory synchronisation proper or ongoing spiking activity only—disguised as rhythmic by the common stimulation with somewhat rhythmic speech stimuli.

The theta band: syllable processing

At the syllabic timescale, theta-band oscillations (i.e. 4–8 Hz) have been suggested to phase synchronise with syllable onsets (Luo & Poeppel, 2007; Howard & Poeppel, 2012; Peelle *et al.*, 2013; Doelling *et al.*, 2014) and thus to aid the segmentation or identification of syllables. Increased across-trials theta-band phase coherence has been demonstrated in response to speech in general (Luo & Poeppel, 2007; Luo *et al.*, 2010) and to syllable sequences more specifically (Power *et al.*, 2012). These studies, however, did not directly relate oscillatory phase to acoustic stimulus properties (cf. Abrams *et al.*, 2008), and thus leave it unclear whether the observed phase-coherence effects relate directly to amplitude maxima associated with syllable onsets. Further work (Abrams *et al.*, 2008; Nourski *et al.*, 2009) established a direct relationship between amplitude modulations in speech and neural oscillatory phase—yet, their low-pass filter cut-off frequencies (i.e. < 40–50 Hz) were well above syllabic rate (i.e. ~5 Hz; cf. Greenberg *et al.*, 2003; Leong & Goswami, 2014) and thus could not restrict the conclusions to the segmentation or identification of syllables alone. Providing more direct evidence, Gross *et al.* (2013) observed significant mutual information between theta-band phase and the speech amplitude envelope during speech processing; likewise, Vander Ghinst *et al.* (2016) and Molinaro *et al.* (2016) observed significant phase coherence between neural oscillations and speech at theta-band frequency. Additional indirect support for a role of the theta band in syllabic processing comes from work on dyslexia, where an impaired behavioural ability to tap in phase with amplitude modulations in the vicinity of syllabic nuclei has been observed (Goswami, 2011; Goswami & Leong, 2013; Leong & Goswami, 2014). The interpretation that dyslexics' behavioural deficit is directly related to an impaired perception of salient syllable-rate amplitude modulations is also supported by evidence that dyslexic subjects tap more consistently to be stressed as compared to unstressed syllables (Hämäläinen *et al.*, 2012; Leong & Goswami, 2014). In spite of these consistencies across the electrophysiological and clinical data, the electrophysiological mechanism underlying the synchronicity between neural oscillations and the rhythm of speech syllables remains to be clarified—as the statistical evidence includes cross-correlations between the speech amplitude envelope and the electroencephalogram or average evoked potential (e.g. Abrams *et al.*, 2008; Nourski *et al.*, 2009), mutual information between the speech amplitude envelope and oscillatory phase (e.g. Gross *et al.*, 2013), and phase coherence between the speech amplitude envelope and the magnetoencephalogram (Molinaro *et al.*, 2016; Vander Ghinst *et al.*, 2016). The question behind this question is whether syllabic segmentation and identification in the auditory cortex operate on a neural representation of speech amplitude, phase or both, and which of these representations the auditory pathway forwards to start with.

The delta band: processing of intonational phrase boundaries

At the timescale of intonational phrase boundaries, delta-band oscillations (i.e. ~ 0.5 Hz) were found to increase their phase coherence with the fundamental-frequency envelope (i.e. pitch contour) of speech (Bourguignon *et al.*, 2013; Mai *et al.*, 2016; Molinaro *et al.*, 2016). Because amplitude extrema of the fundamental-frequency envelope mark intonational phrase boundaries (Frazier *et al.*, 2006), delta-band synchronisation could help the segmentation or identification of intonation phrases (Giraud & Poeppel, 2012; Bourguignon *et al.*, 2013; Mai *et al.*, 2016). As the wavelength of delta-band oscillations does also capture the pace of syntactic phrases (i.e. multiword information chunks; Wingfield *et al.*, 1984; Frazier *et al.*, 2006; Farrell & Lelievre, 2012) that are encoded in speech, delta-band oscillations might orthogonally help the generation of syntactic phrases (Ding *et al.*, 2015; Ding & He, 2016; Meyer *et al.*, 2016; see below; Bonhage *et al.*, 2017). Critically, because syntactic phrases do not have a physical counterpart in speech, they must be projected in the course of speech decoding by an internal cognitive process that requires the generative application of syntactic knowledge, rather than the tracking of information present in the speech stimulus; for this reason, the delta band's role in syntactic phrase generation will be discussed in the part on language comprehension (see below). It is also worth pointing out here that delta-band oscillations also have an internal role in the self-organisation of the cortical speech and language system, providing causal top-down modulation of auditory-cortical responsiveness to speech (Park *et al.*, 2015), likely via regulating auditory-cortical excitability (cf. Lakatos *et al.*, 2005; see below; Kayser *et al.*, 2015).

Cross-frequency coupling: temporal alignment and binding

In addition to the bottom-up stimulus responsiveness of neural oscillations, these also exhibit a stimulus-independent hierarchical structure, where lower-frequency neural oscillations top-down modulate the amplitude of higher-frequency neural oscillations through phase–amplitude coupling (Giraud & Poeppel, 2012; Gross *et al.*, 2013; Kayser *et al.*, 2015; Riecke *et al.*, 2015). Top-down coupling during speech processing has been described both between the theta and gamma bands (Morillon *et al.*, 2012) and between the delta and theta bands (Lakatos *et al.*, 2005).

As a first putative purpose, top-down coupling could ensure the temporal alignment of neuronal excitability with critical spectral information on the phonemic and syllabic levels (cf. Schroeder *et al.*, 2008; Panzeri *et al.*, 2010; Lehongre *et al.*, 2011), in spite of the aperiodicity of amplitude cues in speech (cf. Kayser *et al.*, 2009; Chang *et al.*, 2010) that hinders bottom-up oscillatory synchronisation (Kelso *et al.*, 1986; Cummins, 2012; Goswami & Leong, 2013). Three arguments speak in favour of this hypothesis: first, slow-frequency synchronisation is robust in relatively more situations than fast synchronisation, as slow speech amplitude modulations suffer little from environmental noise (e.g. Obleser *et al.*, 2008; Peelle *et al.*, 2013). Second, neural rhythmicity during oscillatory synchronisation is robust to decreased stimulus rhythmicity (cf. Mathewson *et al.*, 2012; Calderone *et al.*, 2014). Third, oscillatory phase does reflect neuronal excitability (Bishop, 1932; Lakatos *et al.*, 2005, 2008; Mathewson *et al.*, 2009; Schroeder & Lakatos, 2009; for review, see VanRullen *et al.*, 2011; Henry & Obleser, 2012; Neuling *et al.*, 2012; Kösem *et al.*, 2016)—top-down temporal alignment of excitability to speech would facilitate spectral perception, which is required for speech identification: amplitude cues may be sufficient for the identification of temporally salient, yet

spectrally non-distinctive speech sounds (e.g. vowels), but degradation of spectrally distinctive speech sounds (e.g. consonants) decreases identification performance (Furui, 1986; Shannon *et al.*, 1995; Holt *et al.*, 2000; Lotto & Holt, 2015). Because vowel spaces are limited (i.e. across languages, consonant-to-vowel ratio is above 1, with a mean of 4.25; Haspelmath, 2005), any amplitude envelope alone could, in principle, reflect an infinite number of speech signals.

A second putative function of top-down oscillatory coupling is the neural binding of discrete phonological units at different granularity levels, facilitating the establishment of a coherent percept: a single intonation phrase is made of multiple syllables, each in turn built of multiple phonemes (cf. Nespor & Vogel, 1986; Gussenhoven & Jacobs, 2013). To arrive at a temporally unambiguous speech segmentation, in which each phoneme belongs to a single syllable and each syllable belongs to a single intonation phrase, high-granularity segments (i.e. phonemes and syllables) might be bound inside low-granularity segments (i.e. syllables and intonation phrases, respectively) through neural coupling (cf. Giraud & Poeppel, 2012; Morillon *et al.*, 2012). A role of neural oscillatory top-down coupling in representational binding has been described in research on verbal working memory. Here, auditory events were found to correspond to gamma cycles, bound into event sequences via occurrence inside a joint theta cycle, every gamma cycle occurring at its characteristic theta phase angle (for review, see Lisman & Idiart, 1995; Sauseng *et al.*, 2010; Freunberger *et al.*, 2011; Kaminski *et al.*, 2011; Lisman & Jensen, 2013; Hyafil *et al.*, 2015; Vosskuhl *et al.*, 2015). Nevertheless, behavioural or neuropsychological evidence for a role of top-down coupling in representational binding is still lacking for speech.

Theta–gamma coupling: syllabification of phonemes

Top-down coupling has been described between the phase of theta-band oscillations and the amplitude of gamma-band oscillations within the left hemisphere, in the vicinity of the auditory cortex (Canolty *et al.*, 2006; Morillon *et al.*, 2012). When assuming that theta–gamma phase–amplitude coupling subserves the binding of phonemic representations inside syllabic representations (Giraud & Poeppel, 2012), such results conflict with a body of studies that describe theta-band phase synchronisation to syllables relatively stronger in the right as compared to the left hemisphere (Luo & Poeppel, 2007; Abrams *et al.*, 2008; Hämäläinen *et al.*, 2012; Gross *et al.*, 2013; but see Howard & Poeppel, 2012; Peelle *et al.*, 2013), and conversely, gamma-band amplitude synchronisation to subsyllabic aspects of speech relatively stronger in the left as compared to the right hemisphere (Lehongre *et al.*, 2011; Morillon *et al.*, 2012; Gross *et al.*, 2013; but see Nourski *et al.*, 2015). It is conceivable that syllabification of subsyllabic aspects of speech operates indirectly by relaying right-hemispheric theta via transcallosal phase–phase coupling to left-hemispheric theta, in turn phase–amplitude coupling locally with left-auditory-cortical lower-gamma-band oscillations. This is speculation at present.

Delta–theta coupling: grouping of syllables into intonation phrases

Delta-band oscillations (i.e. 0.5–4 Hz) have been proposed to aid the concatenation of syllables into intonation phrases by employing their phase to top-down modulate the amplitude of theta-band oscillations (Giraud & Poeppel, 2012). This is consistent with the top-down regulation of higher-frequency oscillations by delta-band

oscillatory phase during speech processing (Fontolan *et al.*, 2014) and, in particular, with evidence for a causal top-down regulation of speech-brain coupling by frontal delta-band oscillations (Park *et al.*, 2015). In the macaque, delta-band phase has been observed to regulate theta-band oscillatory amplitude while hearing tones (Lakatos *et al.*, 2005); in the rat, delta-band phase was found to regulate stimulus-dependent spiking rate under acoustic stimulation (Kayser *et al.*, 2015). A further source of evidence for the top-down regulation of the theta band during speech processing comes, again, from the dyslexic population: at rest already, dyslexic subjects exhibit increased power and coherence of frontal delta-band oscillations relative to controls (Arns *et al.*, 2007; Pagnotta *et al.*, 2015), predicting their behavioural deficits in speech processing (Arns *et al.*, 2007). In concert, during speech perception proper, dyslexic subjects exhibit reduced bottom-up synchronisation of gamma- (Lehongre *et al.*, 2011, 2013), theta- (Lehongre *et al.*, 2013) and delta-band oscillations (Hämäläinen *et al.*, 2012; Molinaro *et al.*, 2016). The dualism of decreased auditory-cortical bottom-up speech synchronisation and increased frontal top-down delta-band activity could reflect a potential compensatory top-down mechanism for dyslexics' underlying deficits in bottom-up auditory perception (Goswami, 2011; Leong & Goswami, 2014) caused by a genetically predisposed lack of neuronal migration into those layers of the auditory cortices that subserve bottom-up auditory perception (Humphreys *et al.*, 1990; Raschle *et al.*, 2011; Männel *et al.*, 2015).

Neural oscillations in language comprehension

Once the auditory system is temporally aligned with meaningful speech segments and speech segments are identified and bound into hierarchical phonological percepts, the encoded meaning must be decoded to achieve the goal of language comprehension. There is some consensus in psycho- and neurolinguistics that two parallel processing streams underlie language comprehension: on the one hand, a syntactic processing stream is thought to involve the chunking of multiple words into so-called syntactic phrases to compose complex meaning; multiple phrases form a hierarchy that codes for the relationships within the scenario that the sentence as a whole encodes. Apart from boundaries of sentences proper, syntactic phrases and their relationships do not have physical counterparts in speech, but must be imposed upon speech, based on syntactic knowledge. On the other hand, a predictive processing stream is thought to anticipate upcoming words of a sentence from their frequency of occurrence after the prior word sequence—words are stored in long-term memory in probabilistic association with one another; again, the identity of upcoming words cannot be anticipated from acoustic cues, but from lexical-semantic knowledge. In the second part, I discuss evidence that oscillations support both streams (see Fig. 2 for an overview).

Syntactic structure formation: chunking, storage and retrieval

To decode compositional meaning, single words are chunked into syntactic phrases (Chomsky, 1957; Baddeley *et al.*, 2009; Cowan, 2012; Meyer *et al.*, 2016; Bonhage *et al.*, 2017). To decode relational meaning, phrases early in a sentence must be stored in working memory and retrieved later in the sentence (King & Just, 1991; Nicol *et al.*, 1994; Lewis, 1996; Gibson, 2000; Lewis *et al.*, 2006; Meyer *et al.*, 2012, 2013, 2015; Futrell *et al.*, 2015). Also, the meaning of all words of a sentence must be retrieved from long-term memory for comprehension (Mormann *et al.*, 2005; Bastiaansen *et al.*, 2008; MacGregor *et al.*, 2012; Meyer *et al.*, 2015). In

this subsection, I review a body of literature that points to chunking, storage and retrieval operations being subserved by an interplay of delta-, alpha- and theta-band oscillations (i.e. 0.5–4, 9–13 and 4–8 Hz, respectively; e.g. Meyer *et al.*, 2013, 2015, 2016).

The delta band: chunking of words into syntactic phrases

Recent work suggests a role of delta-band neural oscillations in the chunking of words into syntactic phrases (Ding *et al.*, 2015; Ding & He, 2016; Meyer *et al.*, 2016; Bonhage *et al.*, 2017). Ding *et al.* (2015) presented continuous sequences of monosyllabic Chinese words at a fixed rate (4 Hz; i.e. at theta-band frequency). A word pair could always be grouped into a phrase, allowing for phase formation at half of the syllabic rate (2 Hz; i.e. at delta-band frequency). Critically, because the stimuli contained acoustic amplitude modulations at syllabic rate only, but not at the rate of phrases, the formation of phrases required prior linguistic knowledge of Chinese grammar. Indeed, the response spectra showed delta-band oscillations to emerge only in a group of Chinese-speaking participants, but not in participants incapable of Chinese. As corroborated by further results, this points to a role of delta-band oscillations in the internal generation of phrases, rather than in stimulus-driven bottom-up processing: Meyer *et al.* (2016) presented their participants with ambiguous German sentences, the interpretation of which was indicated by acoustic cues that marked either the ending or the continuation of a phrase. Participants are known to frequently ignore these acoustic cues and base their phrase generation on an internal chunking bias instead (Hemforth *et al.*, 1998; Swets *et al.*, 2007; Wiedmann & Winkler, 2015). Delta-band phase significantly differed between biased and unbiased sentence interpretations, that is, delta-band phase was reset during the phrase generation irrespective of acoustic cues (cf. Fodor & Bever, 1965; Garrett *et al.*, 1966; Buxó-Lugo & Watson, 2016). In line with these results, Bonhage *et al.* (2017) compared delta-band power between the encoding of word lists that could not be grouped into phrases and the encoding of sentence fragments—reporting a delta-band power increase for the encoding of sentence fragments only, potentially reflecting an increased phase consistency across trials.

The role of delta-band oscillations in phrase generation does not necessarily contradict their role in the processing of intonation phrases (Bourguignon *et al.*, 2013; Mai *et al.*, 2016; Molinaro *et al.*, 2016): Delta-band synchronisation with intonational phrase boundaries may underlie the bottom-up segmentation of speech based on acoustic cues (Ghitza, 2017), while delta-band oscillations at the syntactic level could underlie the top-down generation of syntactic phrases that obey internal capacity restrictions. In support, participants' tendency to ignore intonational phrase boundaries when generating syntactic phrases depends on their working memory capacity (Swets *et al.*, 2007) and goes along with a decrease in speech-brain coupling (Meyer *et al.*, 2016). The dissociation between the processing of intonational phrase boundaries and the generation of syntactic phrases is also in line with developmental data, showing an early auditory sensitivity to intonational phrase boundaries in pre-linguistic infants (Männel & Friederici, 2009), a primacy of these boundaries in the generation of syntactic phrase in linguistic infants (Isobe, 2007; Wiedmann & Winkler, 2015), and a solid ignorance of these boundaries in adults (Hemforth *et al.*, 1998; Swets *et al.*, 2007; Meyer *et al.*, 2016)—that is, an emerging primacy of internal syntactic preferences in phrase formation.

Concerning the question whether the delta band's role in syntactic phrase formation is specific to language comprehension, it is

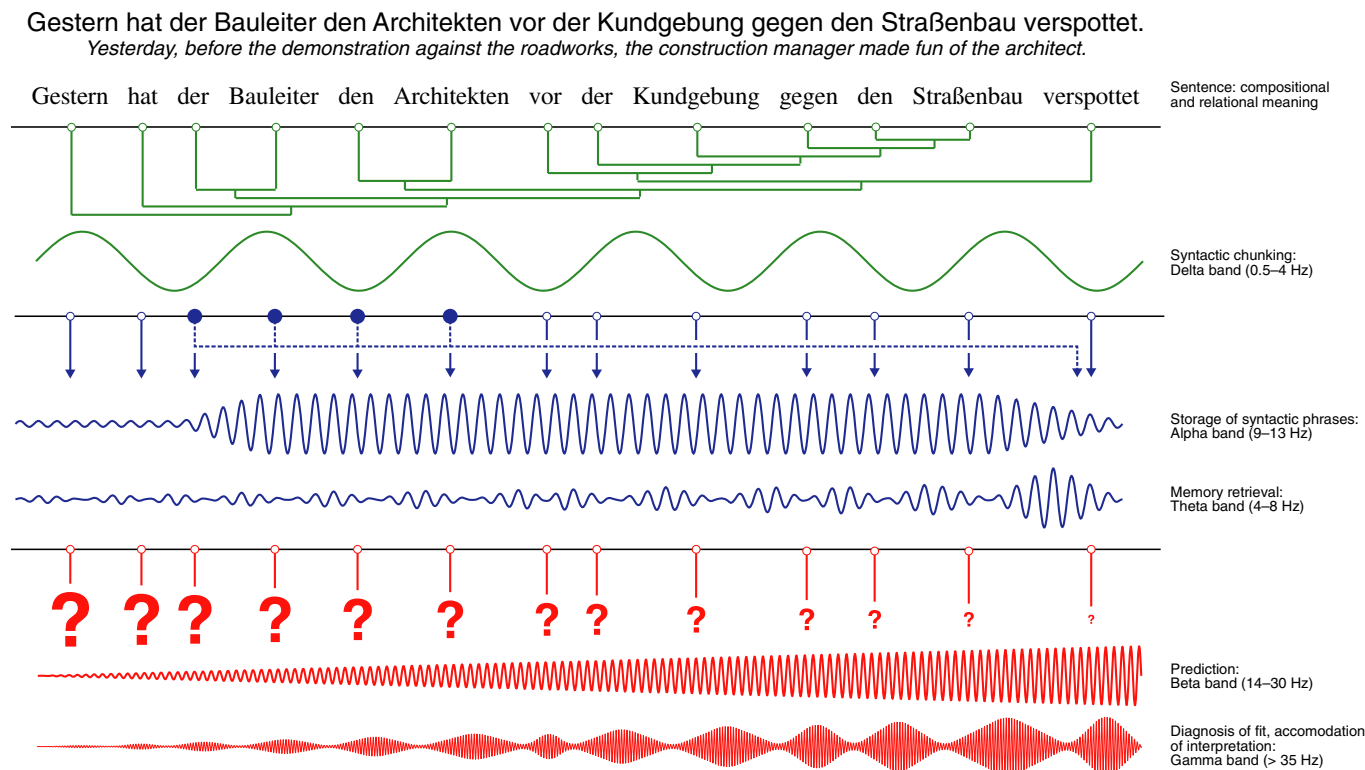


FIG. 2. Neural oscillations in language comprehension; green: chunking of words into syntactic phrases is subserved by delta-band cycles; blue: phrases are stored in working memory (solid circles) with the help of alpha-band oscillations; alpha-band amplitude increases during the storage of the subject (i.e. *der Bauleiter/the construction manager*) and object (i.e. *den Architekten/the architect*), until these can be linked to the main verb (i.e. *verspottet/made fun of*); stored information is retrieved from working memory and long-term memory for integration into the ongoing sentence-level working memory representation, with the support of theta-band oscillations; theta-band power transiently increases during the retrieval of individual words from long-term memory; burst amplitude increases along the sentence, potentially indicating facilitated integration of retrieved words into the sentence-level working memory representation is strongest during working memory retrieval of the subject and object at the sentence-final verb; red: aided by beta-band oscillations, and upcoming words are predicted from the prior cumulative semantic interpretation, based on probabilistic lexical-semantic knowledge; the stronger the predictions (end of the sentence), the higher the beta power on prediction fulfilment; gamma-band oscillations assist diagnosis of lexical-semantic contextual fit of incoming words and the accommodation of the cumulative interpretation; the better the fit of incoming words, the higher the gamma power on prediction fulfilment.

noteworthy that slow cortical potentials (i.e. < 0.5 Hz; Northoff, 2016) have previously been ascribed a domain-general function in the perception of simultaneity (cf. Stefanics *et al.*, 2010; Northoff, 2016). This allows to speculate that the delta band's pre-existing general role in cortical information chunking offered itself as a mechanism for syntactic phrase formation and, potentially, informational fusion of complex meaning by simulating perceptual simultaneity of a phrase's words (Meyer *et al.*, 2016). Hence, rather than thinking that delta-band oscillations specifically fit the necessities of language comprehension, syntactic phrases as a linguistic phenomenon should rather be viewed as an ideal means of exploiting the brain's pre-existing chunking abilities. In line with this speculation, event-related brain potentials indexing the chunking of words into syntactic phrases occur with a regular period (2.6–2.7 s; Roll *et al.*, 2012; Schremm *et al.*, 2015) that matches the canonical duration of syntactic phrases observed in linguistic corpus analyses (Vollrath *et al.*, 1992) and falls into the frequency range of either the lower delta band or slow cortical potentials. Such slow frequencies might just suffice electrophysiologically to integrate information on the time and network scales needed for the composition of complex information—the brain employs long cycles when integrating complex information across large networks, given the variance in conduction delays of large neuronal networks (Buzsaki, 2006). In line with this, slow oscillatory frequencies relate to long-lasting excitatory postsynaptic potentials in

supragranular and granular cortical layers, which exhibit a high degree of cortico-cortical connectivity (Steriade *et al.*, 1993; Lakatos *et al.*, 2008; Northoff, 2016).

The alpha band: storage of syntactic phrases in verbal working memory

The storage of syntactic phrases in verbal working memory for the downstream establishment of dependencies with other phrases associates with increased alpha-band activity (Haarmann & Cameron, 2005; Weiss *et al.*, 2005; Meyer *et al.*, 2013; Bonhage *et al.*, 2017). As an example, an experiment by Meyer *et al.* (2013) manipulated the storage interval for a sentence-initial subject noun phrase that needed to be linked to a sentence-final verb (e.g. Fodor, 1978; Wanner & Maratsos, 1979; Frazier *et al.*, 1983; Kluender & Kutas, 1993; Matzke *et al.*, 2002). First, alpha-band power was observed to increase with storage demands; second, the effect was source-localised to inferior parietal cortex, which is classically related to verbal working memory (for review, see Wager & Smith, 2003; Owen *et al.*, 2005; Leff *et al.*, 2009); and third, source power correlated with verbal working memory capacity.

In general, these results extend prior evidence for a role of alpha-band oscillations in verbal working memory to the sentence comprehension domain (Krause *et al.*, 1996; Maltseva *et al.*, 2000; Jensen *et al.*, 2002; Schack *et al.*, 2005; Leiberg *et al.*, 2006; Van Dijk

et al., 2010), suggesting that the cortical mechanism subserved by alpha-band oscillations is general to the storage of verbal information. This is also suggested by the modulation of alpha-band power by storage demands across verbal domains, such as phonetics and phonology (Krause *et al.*, 1996; Van Dijk *et al.*, 2010), syntax (Bonhage *et al.*, 2017) and semantics (Haarmann & Cameron, 2005). Furthermore, alpha-band oscillations have been attributed the general function of cortical inhibition (for review, see Klimesch *et al.*, 2007a; Jensen & Mazaheri, 2010; Weisz *et al.*, 2011; Klimesch, 2012)—allowing for the speculation that the processing of syntactic dependencies during language comprehension recycles a pre-existing brain mechanism that eventually is functionally identical across cognitive domains; conversely, syntactic dependencies in language may exist because the human brain has a pre-existing functional mechanism for the temporary inhibition of relevant cortices to keep the represented information from premature release. While the physiological basis of the inhibitory function of alpha-band oscillations is a matter of ongoing research, there is evidence that they are generated on the level of cortico-cortical networks, potentially by interneuron systems that can inhibit activity of principal cells across cortical layers (Bollimunta *et al.*, 2008; Haegens *et al.*, 2011; Klimesch, 2012).

The theta band: memory retrieval

When verbal information is retrieved from a sentence in working memory, or when verbal information needs to be retrieved from long-term memory for the comprehension of an unfolding sentence, power and coherence of theta-band oscillations were found to increase. Theta-band power increases after the presentation of each word in a sentence, indicating a possible role in long-term memory retrieval (Bastiaansen *et al.*, 2002, 2008; Bastiaansen & Hagoort, 2006). This was supported by reports of increased theta-band coherence under increased semantic processing demands (Weiss *et al.*, 2000; Mellem *et al.*, 2013) and increased power for semantically rich as compared to semantically lean words (Bastiaansen *et al.*, 2005). However, the initial study by Bastiaansen *et al.* (2002) also reported theta power to be modulated by the position of a word within a sentence, suggesting that retrieval operations subserved by theta-band oscillations link more specifically to the processing of the syntactic structure formed by the words of a sentence. This interpretation has been confirmed by work showing an increase in theta-band power and coherence when retrieval is constrained by the position of the to-be-retrieved information within the hierarchical syntactic structure of a sentence (Nicol & Swinney, 1989; Brysbaert, 1996; Dillon *et al.*, 2014; Meyer *et al.*, 2015), in line with earlier reports of increasing theta-band power for syntactic as compared to semantic tasks (Röhm *et al.*, 2001), sentence processing as compared to word list processing (Bastiaansen *et al.*, 2002, 2010), and language comprehension under increased working memory demands (Weiss *et al.*, 2000, 2005). The proposed role of the theta band in memory retrieval could also account for theta power increases for words that are unexpected from the prior sentence context, and thus hard to retrieve from long-term memory (Rommers *et al.*, 2017).

The extension of the known role of theta-band oscillations in verbal retrieval (i.e. letters, digits and words; Krause *et al.*, 2000; Klimesch *et al.*, 2001; Krause *et al.*, 2001; Jensen & Tesche, 2002; Karrasch *et al.*, 2004; Mormann *et al.*, 2005) to language comprehension suggests that the ability of the theta band to subserve retrieval operations is general to cortical information processing. At first glance, the modulation of theta-band responses by syntactic structure suggests specificity to language comprehension. Yet, this specific function could be

compatible with the emerging role of theta-band oscillations in cortical information sequencing and retrieval from sequences (for review, see Wang, 2010; Hsieh & Ranganath, 2014; Roux & Uhlhaas, 2014), which was first documented for spatial sequencing in rodents (Jensen & Lisman, 2000, 2005) and replicated for working memory in human neocortex (e.g. Kahana *et al.*, 1999). Theta-band oscillations may aid sequencing via their phase, where individual items are encoded and replayed at characteristic phase angles (Lisman & Idiart, 1995; Sauseng *et al.*, 2010; Freunberger *et al.*, 2011; Lisman & Jensen, 2013; Hyafil *et al.*, 2015). Nevertheless, it is an open question whether phase-dependent sequencing is powerful enough to represent the hierarchical memory representations of sentences and the according structure-constrained retrieval operations.

Cumulative prediction and accommodation

The second processing stream of language comprehension employs probabilistic knowledge stored in long-term memory to predict upcoming individual words—based on their memorised frequency of occurrence after the prior word sequence (Marslen-Wilson, 1973; Kutas & Hillyard, 1980; Ehrlich & Rayner, 1981; Van Petten, 1993; Hagoort *et al.*, 2004; Kutas & Federmeier, 2011). Here, I will review evidence suggesting an interplay between beta- and gamma-band oscillations (13–30 and > 35 Hz, respectively) to support the cumulative prediction of upcoming individual words and the accommodation of the current semantic interpretation induced by incoming unpredicted words, respectively (Lewis & Bastiaansen, 2015; Lewis *et al.*, 2016).

The beta band: top-down lexical-semantic predictions

The more certain the meaning of an unfolding sentence gets, the stronger get semantic predictions for words that might occur in the remainder of the sentence—and the stronger beta-band power has been found to decrease when upcoming words do not match the predicted word (Lewis & Bastiaansen, 2015; Lewis *et al.*, 2016). Initially, Weiss & Rappelsberger (1996), von Stein *et al.* (1999) and Weiss & Mueller (2003) observed differences in scalp-level beta-band coherence between the presentation of semantically rich and semantically lean words, suggesting that the beta band is involved in the processing of semantics (cf. Weiss & Mueller, 2003). A study by Haarmann *et al.* (2002) on word processing in sentence context supported this, reporting that semantic interference between words stored in working memory and incoming words modulates scalp-level beta-band coherence. Likewise, Bastiaansen *et al.* (2005) observed decreased beta-band power for semantically rich as compared to semantically lean words in sentence context. Wang *et al.* (2012a) compared incongruent and congruent sentence endings, established through a cloze test (Taylor, 1953; Van Den Brink *et al.*, 2001), reporting decreased beta-band power for semantically incongruent endings. Because cloze probability is a non-statistical approximation to cumulative word probability (Levy, 2008; Roark *et al.*, 2009; Frank *et al.*, 2015), this finding is a strong indication that beta-band oscillations support the semantic prediction of individual words from a prior sequence. The findings of Wang *et al.* (2012a) were replicated in the domain of discourse comprehension: Lewis *et al.* (2017) compared short stories of sentences that either formed a semantically coherent discourse or not. Sentences that were incongruent with the discourse were accompanied by decreased beta-band power.

Instead of a specific role of beta-band oscillations in the contextual semantic prediction of individual words based on the prior

word sequence, it has been proposed that beta-band oscillations subserve top-down predictive functions across processing levels, reaching from low-level auditory processing to syntax and semantics (Lewis & Bastiaansen, 2015; Lewis *et al.*, 2016, 2017). In the domain of auditory processing, predictions have been found to modulate beta-band responses in both an auditory oddball study (cf. Kim & Chung, 2008; Weiss & Mueller, 2012) and in work on audio-visual speech processing (Arnal *et al.*, 2011; Arnal & Giraud, 2012), clearly indicating that beta-band oscillations play a role in prediction formation beyond higher-level language comprehension. In the specific domain of higher-level language comprehension, however, the literature is more consistent with the specific claim that beta-band oscillations reflect only the lexical-semantic prediction of an upcoming individual word, but not its syntactic category. As a first argument, beta-band power during the contextual prediction of upcoming individual words correlates with the amplitude of the N400, which mirrors the lexical-semantic predictability of individual words (Kutas & Federmeier, 2011; Wang *et al.*, 2012a; Hale, 2016; Lewis *et al.*, 2017), but not the contextual probability of their syntactic category (Levy, 2008; Frank *et al.*, 2015). Conversely, lexical-semantic predictability of individual words does not correlate with the amplitude of ERP components previously related to syntactic processing (i.e. the left anterior negativity and late positivities; Osterhout & Holcomb, 1992; Molinaro *et al.*, 2011; Frank *et al.*, 2015). As a second argument, while beta-band oscillations are apparently modulated by syntactic factors, these effects were elicited by syntactic violations (i.e. the syntactic category of an incoming word did not match the appropriate syntactic category; Bastiaansen *et al.*, 2010; Pérez *et al.*, 2012; see Kiehl *et al.*, 2014 for broadband data; for review, see Lewis & Bastiaansen, 2015). It has been argued that such syntactic violations can block semantic processing (e.g. Friederici *et al.*, 1999; for discussion, see Steinhauer & Drury, 2012). Blocked semantic processing could, in turn, result in a beta power decrease—that would, however, not reflect an unfulfilled syntactic prediction, but rather a disrupted semantic prediction.

The gamma band: diagnosis of fit, accommodation of interpretation

In concert with beta-band oscillations, the checking of incoming bottom-up lexical-semantic representations against the top-down contextual predictions generated by beta-band oscillations is reflected by gamma-band oscillations (for review, see Lewis & Bastiaansen, 2015; Lewis *et al.*, 2016). When the semantics of an incoming word do not match its semantics as predicted by the preceding context, gamma cannot synchronise. In line with this proposal, semantic violations are accompanied by decreases in gamma-band power (Hald *et al.*, 2006; Penolazzi *et al.*, 2009; Rommers *et al.*, 2013). Conversely, fulfilled lexical-semantic predictions were found to be accompanied by higher coherence in the lower gamma band (Weiss & Mueller, 2003). In line with this, gamma-band power was observed to increase for words with high cloze probabilities, that is, words that were highly probable to occur after a given preceding word sequence (Taylor, 1953; Wang *et al.*, 2012b; Molinaro *et al.*, 2013; Monsalve *et al.*, 2014). In addition, gamma-band power increases over the course of semantically coherent as compared to semantically incoherent sentences (Bastiaansen *et al.*, 2010). In general, these results support the idea that gamma-band oscillations subserve the checking of incoming bottom-up semantic information against cumulative semantic top-down predictions subserved by beta-band oscillations.

The beta–gamma interplay: predictive coding

The proposed function of the beta–gamma interplay during language comprehension is, of course, an instance of the current all-purpose theory of cognition, the predictive coding framework (e.g. Friston, 2005), as well as an adaptation of the role of beta- and gamma-band oscillations played therein (e.g. Roopun *et al.*, 2008; Engel & Fries, 2010). In this framework, brains are considered to aim for the optimal prediction of upcoming experiences to minimise survival risks for an organism. Predictions are based on prior experience—experiences that mismatch predictions are used for the adaptation of the current cognitive state and the refinement of predictive abilities. As reviewed by Lewis & Bastiaansen (2015), this framework might be consistent with the physiology of beta- and gamma-band oscillations within the columnar hierarchies of cortical information transmission: Beta-band oscillations are strongest in superficial cortical layers, whereas gamma-band oscillations are strongest in deep layers of the cortex (Bastos *et al.*, 2012). A disconnection of superficial and deep cortical layers in rodents leaves both beta- and gamma-band oscillations intact, while their cross-talk is hindered (Roopun *et al.*, 2008). The beta–gamma interplay has been viewed as interaction of motor systems and sensory systems—where top-down information is provided by motor systems and bottom-up information is provided by sensory systems. In line with this, beta-band oscillations are frequently reported in the motor domain (for review, see Engel & Fries, 2010), and it has been discussed that beta-band oscillations during language comprehension reflect the engagement of language production systems (Pickering & Garrod, 2007; Weiss & Mueller, 2012; cf. Lewis & Bastiaansen, 2015). Top-down predictions would thus result from the inner pre-play of speech (cf. Perrone-Bertolotti *et al.*, 2014)—that is, the listener would anticipate the speaker's upcoming words based on their own speech production experiences or habits (Molinaro *et al.*, 2015). In line with this view, a body of studies has observed beta-band power during language production to be modulated by the degree of lexical-semantic association between the prior word sequences and to-be-produced words (Findlay *et al.*, 2012; Piai *et al.*, 2014, 2017). In general, the predictive coding framework is compatible with the data on beta- and gamma-band oscillations on semantics and auditory processing, suggesting that language comprehension partially builds on the pre-existing ability of the cortex to generate and accommodate predictions about upcoming stimuli. Yet, in spite of the widespread optimism towards predictive coding, the major issue with the adaptation of the framework to language comprehension is the gross lack of empirical reports of beta–gamma coupling during language comprehension, as well as the even grosser lack of intracranial evidence for the within-column or network-level interplay of beta and gamma during language comprehension.

Summary

This review has summarised the available literature suggesting that neural oscillations support both speech processing and language comprehension. Neural oscillations subserve speech processing, that is, the segmentation and identification of linguistically meaningful units, on three timescales, such that gamma-band oscillations synchronise with phonemes, theta-band oscillations synchronise with syllables, and delta-band oscillations synchronise with intonational phrase boundaries. The three bands form a hierarchical relationship, such that slow-frequency oscillations can top-down align higher-frequency oscillations, amplifying bottom-up information extraction and establishing a coherent percept. Temporal alignment might serve to

implicitly align neural excitability to linguistically distinctive spectral information, but further evidence is needed to substantiate this claim. When speech processing has succeeded, meaning must be decoded from the speech percept; language comprehension can proceed along two processing streams: The first stream is syntactic in nature, employing delta-band cycles to group words into syntactic phrases, alpha-band power modulations to store syntactic phrases in verbal working memory and theta-band power modulations to retrieve information from sentences' hierarchical working memory representations, as well as from long-term memory. The second processing stream is predictive in nature, employing beta-band oscillations to top-down predict the semantics of upcoming words that fit the cumulative meaning of the prior word sequence, and gamma-band oscillations to bottom-up assess the contextual semantic fit of incoming words.

Acknowledgements

The author is grateful to Angela D. Friederici, Caroline Beese, Benedict Vasileiou and two anonymous reviewers for their very constructive and helpful comments on the manuscript. For invaluable intellectual input, I am also very thankful to the speakers and attendees of the International Symposium on Neural Oscillations in Speech and Language Processing, which took place in May 2017 in the Harnack Haus of the Max Planck Society in Berlin, Germany – and especially to my co-organisers Angela D. Friederici, Cordula Ullah, Alessandro Tavano and David Poeppel.

Conflict of interest

The author declares no competing financial interests.

Author contributions

LM wrote manuscript.

References

- Abrams, D.A., Nicol, T., Zecker, S. & Kraus, N. (2008) Right-hemisphere auditory cortex is dominant for coding syllable patterns in speech. *J. Neurosci.*, **28**, 3958–3965.
- Ahissar, E., Nagarajan, S., Ahissar, M., Protopapas, A., Mahncke, H. & Merzenich, M.M. (2001) Speech comprehension is correlated with temporal response patterns recorded from auditory cortex. *Proc. Natl. Acad. Sci. USA*, **98**, 13367–13372.
- Anderson, D.J., Rose, J.E., Hind, J.E. & Brugge, J.F. (1971) Temporal position of discharges in single auditory nerve fibers within the cycle of a sine-wave stimulus: frequency and intensity effects. *J. Acoust. Soc. Am.*, **49**, 1131–1139.
- Arnal, L.H. & Giraud, A.L. (2012) Cortical oscillations and sensory predictions. *Trends Cogn. Sci.*, **16**, 390–398.
- Arnal, L.H., Wyart, V. & Giraud, A.-L. (2011) Transitions in neural oscillations reflect prediction errors generated in audiovisual speech. *Nat. Neurosci.*, **14**, 797–801.
- Arns, M., Peters, S., Breteler, R. & Verhoeven, L. (2007) Different brain activation patterns in dyslexic children: evidence from EEG power and coherence patterns for the double-deficit theory of dyslexia. *J. Integr. Neurosci.*, **6**, 175–190.
- Baddeley, A., Hitch, G. & Allen, R. (2009) Working memory and binding in sentence recall. *J. Mem. Lang.*, **61**, 438–456.
- Bastiaansen, M.C. & Hagoort, P. (2006) Oscillatory neuronal dynamics during language comprehension. *Prog. Brain Res.*, **159**, 179–196.
- Bastiaansen, M., Van Berkum, J.J. & Hagoort, P. (2002) Event-related theta power increases in the human EEG during online sentence processing. *Neurosci. Lett.*, **323**, 13–16.
- Bastiaansen, M.C., Van Der Linden, M., Ter Keurs, M., Dijkstra, T. & Hagoort, P. (2005) Theta responses are involved in lexical–Semantic retrieval during language processing. *J. Cognitive Neurosci.*, **17**, 530–541.
- Bastiaansen, M.C., Oostenveld, R., Jensen, O. & Hagoort, P. (2008) I see what you mean: theta power increases are involved in the retrieval of lexical semantic information. *Brain Lang.*, **106**, 15–28.
- Bastiaansen, M.C., Magyari, L. & Hagoort, P. (2010) Syntactic unification operations are reflected in oscillatory dynamics during on-line sentence comprehension. *J. Cognitive Neurosci.*, **22**, 1333–1347.
- Bastos, A.M., Usrey, W.M., Adams, R.A., Mangun, G.R., Fries, P. & Friston, K.J. (2012) Canonical microcircuits for predictive coding. *Neuron*, **76**, 695–711.
- Bishop, G.H. (1932) Cyclic changes in excitability of the optic pathway of the rabbit. *Am. J. Physiol.*, **103**, 213–224.
- Bollimunta, A., Chen, Y., Schroeder, C.E. & Ding, M. (2008) Neuronal mechanisms of cortical alpha oscillations in awake-behaving macaques. *J. Neurosci.*, **28**, 9976–9988.
- Bonhage, C.E., Meyer, L., Gruber, T., Friederici, A.D. & Mueller, J.L. (2017) Oscillatory EEG dynamics underlying automatic chunking during sentence processing. *Neuroimage*, **152**, 647–657.
- Bourguignon, M., De Tiege, X., de Beeck, M.O., Ligo, N., Paquier, P., Van Bogaert, P., Goldman, S., Hari, R. *et al.* (2013) The pace of prosodic phrasing couples the listener's cortex to the reader's voice. *Hum. Brain Mapp.*, **34**, 314–326.
- Brysbaert, M. (1996) Modifier attachment in sentence parsing: evidence from Dutch. *Q. J. Exp. Psychol.*, **49**, 664–695.
- Buxó-Lugo, A. & Watson, D.G. (2016) Evidence for the influence of syntax on prosodic parsing. *J. Mem. Lang.*, **90**, 1–13.
- Buzsáki, G. (2006) *Rhythms of the Brain*. Oxford University Press, New York, NY.
- Calderone, D.J., Lakatos, P., Butler, P.D. & Castellanos, F.X. (2014) Entrainment of neural oscillations as a modifiable substrate of attention. *Trends Cogn. Sci.*, **18**, 300–309.
- Canolty, R.T., Edwards, E., Dalal, S.S., Soltani, M., Nagarajan, S.S., Kirsch, H.E., Berger, M.S., Barbaro, N.M. *et al.* (2006) High gamma power is phase-locked to theta oscillations in human neocortex. *Science*, **313**, 1626–1628.
- Centanni, T.M., Booker, A.B., Chen, F., Sloan, A.M., Carraway, R.S., Renaker, R.L., LoTurco, J.J. & Kilgard, M.P. (2016) Knockdown of dyslexia-gene *Dcdc2* interferes with speech sound discrimination in continuous streams. *J. Neurosci.*, **36**, 4895–4906.
- Chang, E.F., Rieger, J.W., Johnson, K., Berger, M.S., Barbaro, N.M. & Knight, R.T. (2010) Categorical speech representation in human superior temporal gyrus. *Nat. Neurosci.*, **13**, 1428–1432.
- Che, A., Girgenti, M.J. & LoTurco, J. (2014) The dyslexia-associated gene *Dcdc2* is required for spike-timing precision in mouse neocortex. *Biol. Psychiat.*, **76**, 387–396.
- Chomsky, N. (1957) *Syntactic Structures*. De Gruyter, Berlin.
- Cowan, N. (2012) *Working Memory Capacity*. Psychology press, Hove.
- Cummins, F. (2012) Oscillators and syllables: a cautionary note. *Front. Psychol.*, **3**, 364.
- Di Liberto, G.M., O'Sullivan, J.A. & Lalor, E.C. (2015) Low-frequency cortical entrainment to speech reflects phoneme-level processing. *Curr. Biol.*, **25**, 2457–2465.
- Dillon, B.W., Chow, W.Y., Wagers, M., Guo, T., Liu, F. & Phillips, C. (2014) The structure-sensitivity of memory access: evidence from Mandarin Chinese. *Front. Psychol.*, **5**, 1025.
- Ding, N. & He, H. (2016) Rhythm of silence. *Trends Cogn. Sci.*, **20**, 82–84.
- Ding, N. & Simon, J.Z. (2014) Cortical entrainment to continuous speech: functional roles and interpretations. *Front. Hum. Neurosci.*, **8**, 311.
- Ding, N., Melloni, L., Zhang, H., Tian, X. & Poeppel, D. (2015) Cortical tracking of hierarchical linguistic structures in connected speech. *Nat. Neurosci.*, **19**, 158–164.
- Doelling, K.B., Arnal, L.H., Ghitza, O. & Poeppel, D. (2014) Acoustic landmarks drive delta-theta oscillations to enable speech comprehension by facilitating perceptual parsing. *Neuroimage*, **85**, 761–768.
- Ehrlich, S.F. & Rayner, K. (1981) Contextual effects on word perception and eye movements during reading. *J. Verb. Learn. Verb. Be.*, **20**, 641–655.
- Engel, A.K. & Fries, P. (2010) Beta-band oscillations—signalling the status quo? *Curr. Opin. Neurobiol.*, **20**, 156–165.
- Farrell, S. & Lelievre, A. (2012) The dynamics of access to groups in working memory. *J. Exp. Psychol. Learn.*, **38**, 1659–1674.
- Findlay, A.M., Ambrose, J.B., Cahn-Weiner, D.A., Houde, J.F., Honma, S., Hinkley, L.B., Berger, M.S., Nagarajan, S.S. *et al.* (2012) Dynamics of hemispheric dominance for language assessed by magnetoencephalographic imaging. *Ann. Neurol.*, **71**, 668–686.
- Fodor, J. (1978) Parsing strategies and constraints on transformations. *Linguist. Inq.*, **9**, 427–473.
- Fodor, J.A. & Bever, T.G. (1965) The psychological reality of linguistic segments. *J. Verb. Learn. Verb. Be.*, **4**, 414–420.

- Fontolan, L., Morillon, B., Liegeois-Chauvel, C. & Giraud, A.L. (2014) The contribution of frequency-specific activity to hierarchical information processing in the human auditory cortex. *Nat. Commun.*, **5**, 4694.
- Frank, S.L., Otten, L.J., Galli, G. & Vigliocco, G. (2015) The ERP response to the amount of information conveyed by words in sentences. *Brain Lang.*, **140**, 1–11.
- Frazier, L., Clifton, C. & Randall, J. (1983) Filling gaps: decision principles and structure in sentence comprehension. *Cognition*, **13**, 187–222.
- Frazier, L., Carlson, K. & Clifton, C. Jr (2006) Prosodic phrasing is central to language comprehension. *Trends Cogn. Sci.*, **10**, 244–249.
- Freunberger, R., Winkle-Bergner, M., Griesmayr, B., Lindenberger, U. & Klimesch, W. (2011) Brain oscillatory correlates of working memory constraints. *Brain Res.*, **1375**, 93–102.
- Friederici, A.D. & Singer, W. (2015) Grounding language processing on basic neurophysiological principles. *Trends Cogn. Sci.*, **6**, 329–338.
- Friederici, A.D., Steinhauer, K. & Frisch, S. (1999) Lexical integration: sequential effects of syntactic and semantic information. *Mem. Cognition*, **27**, 438–453.
- Friston, K. (2005) A theory of cortical responses. *Philos. T. R. Soc. B*, **360**, 815–836.
- Furui, S. (1986) On the role of spectral transition for speech perception. *J. Acoust. Soc. Am.*, **80**, 1016–1025.
- Futrell, R., Mahowald, K. & Gibson, E. (2015) Large-scale evidence of dependency length minimization in 37 languages. *Proc. Natl. Acad. Sci. USA*, **112**, 10336–10341.
- Garrett, M., Bever, T. & Fodor, J. (1966) The active use of grammar in speech perception. *Percept. Psychophys.*, **1**, 30–32.
- Ghitza, O. (2017) Acoustic-driven delta rhythms as prosodic markers. *Lang. Cogn. Neurosci.*, **32**, 545–561.
- Gibson, E. (2000) The dependency locality theory: a distance-based theory of linguistic complexity. In Miyashita, Y., Marantz, A. & O'Neil, W. (Eds), *Image, Language, Brain*. MIT Press, Cambridge, MA, pp. 95–126.
- Giraud, A.L. & Poeppel, D. (2012) Cortical oscillations and speech processing: emerging computational principles and operations. *Nat. Neurosci.*, **15**, 511–517.
- Giraud, A.-L., Kleinschmidt, A., Poeppel, D., Lund, T.E., Frackowiak, R.S. & Laufs, H. (2007) Endogenous cortical rhythms determine cerebral specialization for speech perception and production. *Neuron*, **56**, 1127–1134.
- Goswami, U. (2011) A temporal sampling framework for developmental dyslexia. *Trends Cogn. Sci.*, **15**, 3–10.
- Goswami, U. & Leong, V. (2013) Speech rhythm and temporal structure: converging perspectives? *Lab. Phonol.*, **4**, 67–92.
- Greenberg, S., Carvey, H., Hitchcock, L. & Chang, S. (2003) Temporal properties of spontaneous speech—a syllable-centric perspective. *J. Phonetics*, **31**, 465–485.
- Gross, J., Hoogenboom, N., Thut, G., Schyns, P., Panzeri, S., Belin, P. & Garrod, S. (2013) Speech rhythms and multiplexed oscillatory sensory coding in the human brain. *PLoS Biol.*, **11**, e1001752.
- Gussenhoven, C. & Jacobs, H. (2013) *Understanding Phonology*. Hodder Arnold, London.
- Haarmann, H. & Cameron, K. (2005) Active maintenance of sentence meaning in working memory: evidence from EEG coherences. *Int. J. Psychophysiol.*, **57**, 115–128.
- Haarmann, H., Cameron, K. & Ruchkin, D. (2002) Neural synchronization mediates on-line sentence processing: EEG coherence evidence from filler-gap constructions. *Psychophysiology*, **39**, 820–825.
- Haegens, S., Nácher, V., Luna, R., Romo, R. & Jensen, O. (2011) α -Oscillations in the monkey sensorimotor network influence discrimination performance by rhythmical inhibition of neuronal spiking. *Proc. Natl. Acad. Sci. USA*, **108**, 19377–19382.
- Hagoort, P., Hald, L., Bastiaansen, M. & Petersson, K. (2004) Integration of word meaning and world knowledge in language comprehension. *Science*, **304**, 438–441.
- Hald, L.A., Bastiaansen, M.C. & Hagoort, P. (2006) EEG theta and gamma responses to semantic violations in online sentence processing. *Brain Lang.*, **96**, 90–105.
- Hale, J. (2016) Information-theoretical complexity metrics. *Lang. Linguist. Compass*, **10**, 397–412.
- Hämäläinen, J.A., Rupp, A., Soltesz, F., Szucs, D. & Goswami, U. (2012) Reduced phase locking to slow amplitude modulation in adults with dyslexia: an MEG study. *Neuroimage*, **59**, 2952–2961.
- Haspelmath, M. (2005) *The World Atlas of Language Structures*. Oxford University Press, New York, NY.
- Hemforth, B., Konieczny, L., Scheepers, C. & Strube, G. (1998) Syntactic ambiguity resolution in German. In Hillert, D. (Ed), *Sentence Processing: A Crosslinguistic Perspective*. Bingley, Emerald, pp. 293–312.
- Henry, M.J. & Obleser, J. (2012) Frequency modulation entrains slow neural oscillations and optimizes human listening behavior. *Proc. Natl. Acad. Sci. USA*, **109**, 20095–20100.
- Hickok, G., Farahbod, H. & Saberi, K. (2015) The rhythm of perception entrainment to acoustic rhythms induces subsequent perceptual oscillation. *Psychol. Sci.*, **26**, 1006–1013.
- Holcombe, A.O. (2009) Seeing slow and seeing fast: two limits on perception. *Trends Cogn. Sci.*, **13**, 216–221.
- Holt, L.L., Lotto, A.J. & Kluender, K.R. (2000) Neighboring spectral content influences vowel identification. *J. Acoust. Soc. Am.*, **108**, 710–722.
- Howard, M.F. & Poeppel, D. (2012) The neuromagnetic response to spoken sentences: co-modulation of theta band amplitude and phase. *Neuroimage*, **60**, 2118–2127.
- Hsieh, L.T. & Ranganath, C. (2014) Frontal midline theta oscillations during working memory maintenance and episodic encoding and retrieval. *Neuroimage*, **85**, 721–729.
- Humphreys, P., Kaufmann, W.E. & Galaburda, A.M. (1990) Developmental dyslexia in women - Neuropathological findings in 3 patients. *Ann. Neurol.*, **28**, 727–738.
- Hyafil, A., Giraud, A.L., Fontolan, L. & Gutkin, B. (2015) Neural cross-frequency coupling: connecting architectures, mechanisms, and functions. *Trends Neurosci.*, **38**, 725–740.
- Isobe, M. (2007) The Acquisition of Nominal Compounding in Japanese: A Parametric Approach. Proceedings of the 2nd Conference on Generative Approaches to Language Acquisition North America.
- Jensen, O. & Lisman, J.E. (2000) Position reconstruction from an ensemble of hippocampal place cells: contribution of theta phase coding. *J. Neurophysiol.*, **83**, 2602–2609.
- Jensen, O. & Lisman, J.E. (2005) Hippocampal sequence-encoding driven by a cortical multi-item working memory buffer. *Trends Neurosci.*, **28**, 67–72.
- Jensen, O. & Mazaheri, A. (2010) Shaping functional architecture by oscillatory alpha activity: gating by inhibition. *Front. Hum. Neurosci.*, **4**, 186.
- Jensen, O. & Tesche, C.D. (2002) Frontal theta activity in humans increases with memory load in a working memory task. *Eur. J. Neurosci.*, **15**, 1395–1399.
- Jensen, O., Gelfand, J., Kounios, J. & Lisman, J. (2002) Oscillations in the alpha band (9–12 Hz) increase with memory load during retention in a short-term memory task. *Cereb. Cortex*, **12**, 877–882.
- Kahana, M.J., Sekuler, R., Caplan, J.B., Kirschen, M. & Madsen, J.R. (1999) Human theta oscillations exhibit task dependence during virtual maze navigation. *Nature*, **399**, 781–784.
- Kaminski, J., Brzezicka, A. & Wrobel, A. (2011) Short-term memory capacity (7 ± 2) predicted by theta to gamma cycle length ratio. *Neurobiol. Learn. Mem.*, **95**, 19–23.
- Karrasch, M., Laine, M., Rapinaja, P. & Krause, C.M. (2004) Effects of normal aging on event-related desynchronization/synchronization during a memory task in humans. *Neurosci. Lett.*, **366**, 18–23.
- Kayser, C., Montemurro, M.A., Logothetis, N.K. & Panzeri, S. (2009) Spike-phase coding boosts and stabilizes information carried by spatial and temporal spike patterns. *Neuron*, **61**, 597–608.
- Kayser, C., Wilson, C., Safaai, H., Sakata, S. & Panzeri, S. (2015) Rhythmic auditory cortex activity at multiple timescales shapes stimulus-response gain and background firing. *J. Neurosci.*, **35**, 7750–7762.
- Kelso, J.A., Saltzman, E.L. & Tuller, B. (1986) The dynamical perspective on speech production: data and theory. *J. Phonetics*, **14**, 29–59.
- Kielar, A., Meltzer, J.A., Moreno, S., Alain, C. & Bialystok, E. (2014) Oscillatory responses to semantic and syntactic violations. *J. Cognitive Neurosci.*, **16**, 2840–2862.
- Kim, J.S. & Chung, C.K. (2008) Language lateralization using MEG beta frequency desynchronization during auditory oddball stimulation with one-syllable words. *Neuroimage*, **42**, 1499–1507.
- King, J. & Just, M.A. (1991) Individual differences in syntactic processing: the role of working memory. *J. Mem. Lang.*, **30**, 580–602.
- Klimesch, W. (2012) Alpha-band oscillations, attention, and controlled access to stored information. *Trends Cogn. Sci.*, **16**, 606–617.
- Klimesch, W., Doppelmayr, M., Yonelinas, A., Kroll, N., Lazzara, M., Röhm, D. & Gruber, W. (2001) Theta synchronization during episodic retrieval: neural correlates of conscious awareness. *Cognitive Brain Res.*, **12**, 33–38.
- Klimesch, W., Sauseng, P. & Hanslmayr, S. (2007a) EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Res. Rev.*, **53**, 63–88.

- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W. & Freunberger, R. (2007b) Event-related phase reorganization may explain evoked neural dynamics. *Neurosci. Biobehav. Rev.*, **31**, 1003–1016.
- Kluender, R. & Kutas, M. (1993) Bridging the gap: evidence from ERPs on the processing of unbounded dependencies. *J. Cognitive Neurosci.*, **5**, 196–214.
- Kösem, A. & Van Wassenhove, V. (2017) Distinct contributions of low-and high-frequency neural oscillations to speech comprehension. *Lang. Cogn. Neurosci.*, **32**, 536–544.
- Kösem, A., Basirat, A., Azizi, L. & van Wassenhove, V. (2016) High-frequency neural activity predicts word parsing in ambiguous speech streams. *J. Neurophysiol.*, **116**, 2497–2512.
- Krause, C., Heikki Lang, A., Laine, M., Kuusisto, M. & Pörm, B. (1996) Event-related. EEG desynchronization and synchronization during an auditory memory task. *Electroen. Clin. Neuro.*, **98**, 319–326.
- Krause, C.M., Sillanmäki, L., Koivisto, M., Saarela, C., Häggqvist, A., Laine, M. & Hämäläinen, H. (2000) The effects of memory load on event-related EEG desynchronization and synchronization. *Clin. Neurophysiol.*, **111**, 2071–2078.
- Krause, C.M., Sillanmäki, L., Häggqvist, A. & Heino, R. (2001) Test-retest consistency of the event-related desynchronization/event-related synchronization of the 4–6, 6–8, 8–10 and 10–12 Hz frequency bands during a memory task. *Clin. Neurophysiol.*, **112**, 750–757.
- Kutas, M. & Federmeier, K.D. (2011) Thirty years and counting: finding meaning in the N400 component of the event-related brain potential (ERP). *Annu. Rev. Psychol.*, **62**, 621–647.
- Kutas, M. & Hillyard, S.A. (1980) Reading senseless sentences: brain potentials reflect semantic incongruity. *Science*, **207**, 203–205.
- Lakatos, P., Shah, A.S., Knuth, K.H., Ulbert, I., Karmos, G. & Schroeder, C.E. (2005) An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex. *J. Neurophysiol.*, **94**, 1904–1911.
- Lakatos, P., Karmos, G., Mehta, A.D., Ulbert, I. & Schroeder, C.E. (2008) Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, **320**, 110–113.
- Leff, A.P., Schofield, T.M., Crinion, J.T., Seghier, M.L., Grogan, A., Green, D.W. & Price, C.J. (2009) The left superior temporal gyrus is a shared substrate for auditory short-term memory and speech comprehension: evidence from 210 patients with stroke. *Brain*, **132**, 3401–3410.
- Lehongre, K., Ramus, F., Villiermet, N., Schwartz, D. & Giraud, A.L. (2011) Altered low-gamma sampling in auditory cortex accounts for the three main facets of dyslexia. *Neuron*, **72**, 1080–1090.
- Lehongre, K., Morillon, B., Giraud, A.L. & Ramus, F. (2013) Impaired auditory sampling in dyslexia: further evidence from combined fMRI and EEG. *Front. Hum. Neurosci.*, **7**, 454.
- Leiberg, S., Lutzenberger, W. & Kaiser, J. (2006) Effects of memory load on cortical oscillatory activity during auditory pattern working memory. *Brain Res.*, **1120**, 131–140.
- Leong, V. & Goswami, U. (2014) Assessment of rhythmic entrainment at multiple timescales in dyslexia: evidence for disruption to syllable timing. *Hearing Res.*, **308**, 141–161.
- Levy, R. (2008) Expectation-based syntactic comprehension. *Cognition*, **106**, 1126–1177.
- Lewis, R. (1996) Interference in short-term memory: the magical number two (or three) in sentence processing. *J. Psycholinguist. Res.*, **25**, 93–115.
- Lewis, A.G. & Bastiaansen, M. (2015) A predictive coding framework for rapid neural dynamics during sentence-level language comprehension. *Cortex*, **68**, 155–168.
- Lewis, R., Vasishth, S. & Van Dyke, J. (2006) Computational principles of working memory in sentence comprehension. *Trends Cogn. Sci.*, **10**, 447–454.
- Lewis, A.G., Wang, L. & Bastiaansen, M. (2015) Fast oscillatory dynamics during language comprehension: unification versus maintenance and prediction? *Brain Lang.*, **148**, 51–63.
- Lewis, A.G., Schoffelen, J.-M., Hoffmann, C., Bastiaansen, M. & Schriefers, H. (2017) Discourse-level semantic coherence influences beta oscillatory dynamics and the N400 during sentence comprehension. *Lang. Cogn. Neurosci.*, **32**, 601–617.
- Lewis, A.G., Schoffelen, J.-M., Schriefers, H. & Bastiaansen, M. (2016) A predictive coding perspective on beta oscillations during sentence-level language comprehension. *Front. Hum. Neurosci.*, **10**, 85.
- Lisman, J. & Idiart, M. (1995) Storage of 7 + 1/2 short-term memories in oscillatory subcycles. *Science*, **267**, 1512–1515.
- Lisman, J.E. & Jensen, O. (2013) The theta-gamma neural code. *Neuron*, **77**, 1002–1016.
- Lizarazu, M., Lallier, M., Molinaro, N., Bourguignon, M., Paz-Alonso, P.M., Lerma-Usabiaga, G. & Carreiras, M. (2015) Developmental evaluation of atypical auditory sampling in dyslexia: functional and structural evidence. *Hum. Brain Mapp.*, **36**, 4986–5002.
- Lotto, A.J. & Holt, L.L. (2015) Speech perception. The view from the auditory system. In Hickok, G. & Small, S.L. (Eds), *Neurobiology of Language*. Elsevier, Amsterdam, pp. 185–194.
- Luo, H. & Poeppel, D. (2007) Phase patterns of neuronal responses reliably discriminate speech in human auditory cortex. *Neuron*, **54**, 1001–1010.
- Luo, H., Liu, Z. & Poeppel, D. (2010) Auditory cortex tracks both auditory and visual stimulus dynamics using low-frequency neuronal phase modulation. *PLoS Biol.*, **8**, e1000445.
- MacGregor, L.J., Pulvermüller, F., van Casteren, M. & Shtyrov, Y. (2012) Ultra-rapid access to words in the brain. *Nat. Commun.*, **3**, 711.
- Mai, G., Minett, J.W. & Wang, W.S. (2016) Delta, theta, beta, and gamma brain oscillations index levels of auditory sentence processing. *Neuroimage*, **133**, 516–528.
- Maltseva, I., Geissler, H. & Basar, E. (2000) Alpha oscillations as an indicator of dynamic memory operations—anticipation of omitted stimuli. *Int. J. Psychophysiol.*, **36**, 185–197.
- Männel, C. & Friederici, A.D. (2009) Pauses and intonational phrasing: ERP studies in 5-month-old German infants and adults. *J. Cognitive Neurosci.*, **21**, 1988–2006.
- Männel, C., Meyer, L., Wilcke, A., Boltze, J., Kirsten, H. & Friederici, A.D. (2015) Working-memory endophenotype and dyslexia-associated genetic variant predict dyslexia phenotype. *Cortex*, **71**, 291–305.
- Marslen-Wilson, W. (1973) Linguistic structure and speech shadowing at very short latencies. *Nature*, **244**, 522–523.
- Mathewson, K.E., Gratton, G., Fabiani, M., Beck, D.M. & Ro, T. (2009) To see or not to see: prestimulus α phase predicts visual awareness. *J. Neurosci.*, **29**, 2725–2732.
- Mathewson, K.E., Prudhomme, C., Fabiani, M., Beck, D.M., Lleras, A. & Gratton, G. (2012) Making waves in the stream of consciousness: entraining oscillations in EEG alpha and fluctuations in visual awareness with rhythmic visual stimulation. *J. Cognitive Neurosci.*, **24**, 2321–2333.
- Matzke, M., Mai, H., Nager, W., Rüsseler, J. & Münte, T. (2002) The costs of freedom: an ERP study of non-canonical sentences. *Clin. Neurophysiol.*, **113**, 844–852.
- Mellem, M.S., Friedman, R.B. & Medvedev, A.V. (2013) Gamma- and theta-band synchronization during semantic priming reflect local and long-range lexical-semantic networks. *Brain Lang.*, **127**, 440–451.
- Mesgarani, N., Cheung, C., Johnson, K. & Chang, E.F. (2014) Phonetic feature encoding in human superior temporal gyrus. *Science*, **343**, 1006–1010.
- Meyer, L., Obleser, J., Kiesel, S. & Friederici, A. (2012) Spatiotemporal dynamics of argument retrieval and reordering: an fMRI and EEG study on sentence processing. *Front. Psychol.*, **3**, 523.
- Meyer, L., Obleser, J. & Friederici, A. (2013) Left parietal alpha enhancement during working memory-intensive sentence processing. *Cortex*, **49**, 711–721.
- Meyer, L., Grigutsch, M., Schmuck, N., Gaston, P. & Friederici, A. (2015) Frontal-posterior theta oscillations reflect memory retrieval during sentence comprehension. *Cortex*, **71**, 205–218.
- Meyer, L., Henry, M.L., Schmuck, N. & Gaston, P. (2016) Linguistic bias modulates interpretation of speech via neural delta-band oscillations. *Cereb. Cortex*, **27**, 4293–4302.
- Molinaro, N., Barber, H.A. & Carreiras, M. (2011) Grammatical agreement processing in reading: ERP findings and future directions. *Cortex*, **47**, 908–930.
- Molinaro, N., Barraza, P. & Carreiras, M. (2013) Long-range neural synchronization supports fast and efficient reading: EEG correlates of processing expected words in sentences. *Neuroimage*, **72**, 120–132.
- Molinaro, N., Monsalve, I.F. & Lizarazu, M. (2015) Is there a common oscillatory brain mechanism for producing and predicting language? *Lang. Cogn. Neurosci.*, **31**, 145–158.
- Molinaro, N., Lizarazu, M., Lallier, M., Bourguignon, M. & Carreiras, M. (2016) Out-of-synchrony speech entrainment in developmental dyslexia. *Hum. Brain Mapp.*, **37**, 2767–2783.
- Monsalve, I.F., Pérez, A. & Molinaro, N. (2014) Item parameters dissociate between expectation formats: a regression analysis of time-frequency decomposed EEG data. *Front. Psychol.*, **5**, 847.
- Morillon, B., Liégeois-Chauvel, C., Arnal, L.H., Benar, C.G. & Giraud, A.L. (2012) Asymmetric function of the theta and gamma activity in syllable processing: an intra-cortical study. *Front. Psychol.*, **3**, 248.

- Mormann, F., Fell, J., Axmacher, N., Weber, B., Lehnertz, K., Elger, C.E. & Fernández, G. (2005) Phase/amplitude reset and theta-gamma interaction in the human medial temporal lobe during a continuous word recognition memory task. *Hippocampus*, **15**, 890–900.
- Nespor, M. & Vogel, I. (1986) *Prosodic Phonology*. Foris, Dordrecht.
- Neuling, T., Rach, S., Wagner, S., Wolters, C.H. & Herrmann, C.S. (2012) Good vibrations: oscillatory phase shapes perception. *Neuroimage*, **63**, 771–778.
- Nicol, J. & Swinney, D. (1989) The role of structure in coreference assignment during sentence comprehension. *J. Psycholinguist. Res.*, **18**, 5–19.
- Nicol, J., Fodor, J. & Swinney, D. (1994) Using cross-modal lexical decision tasks to investigate sentence processing. *J. Exp. Psychol. Learn.*, **20**, 1229–1238.
- Northoff, G. (2016) Slow cortical potentials and “inner time consciousness” – A neuro-phenomenal hypothesis about the “width of present”. *Int. J. Psychophysiol.*, **103**, 174–184.
- Nourski, K.V., Reale, R.A., Oya, H., Kawasaki, H., Kovach, C.K., Chen, H., Howard, M.A. & Brugge, J.F. (2009) Temporal envelope of time-compressed speech represented in the human auditory cortex. *J. Neurosci.*, **29**, 15564–15574.
- Nourski, K.V., Steinschneider, M., Rhone, A.E., Oya, H., Kawasaki, H., Howard, M.A. 3rd & McMurray, B. (2015) Sound identification in human auditory cortex: differential contribution of local field potentials and high gamma power as revealed by direct intracranial recordings. *Brain Lang.*, **148**, 37–50.
- Obleser, J., Eisner, F. & Kotz, S. (2008) Bilateral speech comprehension reflects differential sensitivity to spectral and temporal features. *J. Neurosci.*, **28**, 8116–8123.
- Obleser, J., Herrmann, B. & Henry, M.J. (2012) Neural oscillations in speech: don't be enslaved by the envelope. *Front. Hum. Neurosci.*, **6**, 250.
- Osterhout, L. & Holcomb, P. (1992) Event-related brain potentials elicited by syntactic anomaly. *J. Mem. Lang.*, **31**, 785–806.
- Owen, A.M., McMillan, K.M., Laird, A.R. & Bullmore, E. (2005) N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum. Brain Mapp.*, **25**, 46–59.
- Pagnotta, M.F., Zouridakis, G., Li, L., Lizarazu, M., Lallier, M., Molinaro, N. & Carreiras, M. (2015) Low frequency overactivation in dyslexia: Evidence from resting state Magnetoencephalography. Proceedings of the 37th Annual International Conference of the IEEE Engineering in Medicine and Biology Society.
- Panzeri, S., Brunel, N., Logothetis, N.K. & Kayser, C. (2010) Sensory neural codes using multiplexed temporal scales. *Trends Neurosci.*, **33**, 111–120.
- Park, H., Ince, R.A., Schyns, P.G., Thut, G. & Gross, J. (2015) Frontal top-down signals increase coupling of auditory low-frequency oscillations to continuous speech in human listeners. *Curr. Biol.*, **25**, 1649–1653.
- Peelle, J.E., Gross, J. & Davis, M.H. (2013) Phase-locked responses to speech in human auditory cortex are enhanced during comprehension. *Cereb. Cortex*, **23**, 1378–1387.
- Penolazzi, B., Angrilli, A. & Job, R. (2009) Gamma EEG activity induced by semantic violation during sentence reading. *Neurosci. Lett.*, **465**, 74–78.
- Penttonen, M. & Buzsáki, G. (2003) Natural logarithmic relationship between brain oscillators. *Thalamus Relat. Syst.*, **2**, 145–152.
- Pérez, A., Molinaro, N., Mancini, S., Barraza, P. & Carreiras, M. (2012) Oscillatory dynamics related to the Unagreement pattern in Spanish. *Neuropsychologia*, **50**, 2584–2597.
- Perrone-Bertolotti, M., Rapin, L., Lachaux, J.P., Baciú, M. & Loevenbruck, H. (2014) What is that little voice inside my head? Inner speech phenomenology, its role in cognitive performance, and its relation to self-monitoring. *Behav. Brain Res.*, **261**, 220–239.
- Piai, V., Roelofs, A. & Maris, E. (2014) Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint. *Neuropsychologia*, **53**, 146–156.
- Piai, V., Meyer, L., Dronkers, N.F. & Knight, R.T. (2017) Neuroplasticity of language in left-hemisphere stroke: evidence linking subsecond electrophysiology and structural connections. *Hum. Brain Mapp.*, **38**, 3151–3162.
- Pickering, M.J. & Garrod, S. (2007) Do people use language production to make predictions during comprehension? *Trends Cogn. Sci.*, **11**, 105–110.
- Power, A.J., Mead, N., Barnes, L. & Goswami, U. (2012) Neural entrainment to rhythmically presented auditory, visual, and audio-visual speech in children. *Front. Psychol.*, **3**, 216.
- Raschle, N.M., Chang, M. & Gaab, N. (2011) Structural brain alterations associated with dyslexia predate reading onset. *Neuroimage*, **57**, 742–749.
- Riecke, L., Sack, A.T. & Schroeder, C.E. (2015) Endogenous delta/theta sound-brain phase entrainment accelerates the buildup of auditory streaming. *Curr. Biol.*, **25**, 3196–3201.
- Roark, B., Bachrach, A., Cardenas, C. & Pallier, C. (2009) Deriving lexical and syntactic expectation-based measures for psycholinguistic modeling via incremental top-down parsing. Proceedings of the 2009 Conference on Empirical Methods in Natural Language Processing.
- Röhm, D., Klimesch, W., Haider, H. & Doppelmayr, M. (2001) The role of theta and alpha oscillations for language comprehension in the human electroencephalogram. *Neurosci. Lett.*, **310**, 137–140.
- Roll, M., Lindgren, M., Alter, K. & Horne, M. (2012) Time-driven effects on parsing during reading. *Brain Lang.*, **121**, 267–272.
- Rommers, J., Dijkstra, T. & Bastiaansen, M. (2013) Context-dependent semantic processing in the human brain: evidence from idiom comprehension. *J. Cognitive Neurosci.*, **25**, 762–776.
- Rommers, J., Dickson, D.S., Norton, J.J.S., Wlotko, E.W. & Federmeier, K.D. (2017) Alpha and theta band dynamics related to sentential constraint and word expectancy. *Lang. Cogn. Neurosci.*, **32**, 576–589.
- Roopun, A.K., Kramer, M.A., Carracedo, L.M., Kaiser, M., Davies, C.H., Traub, R.D., Kopell, N.J. & Whittington, M.A. (2008) Period concatenation underlies interactions between gamma and beta rhythms in neocortex. *Front. Cell Neurosci.*, **2**, 1.
- Rose, J.E., Kitzes, L.M., Gibson, M.M. & Hind, J.E. (1974) Observations on phase-sensitive neurons of anteroventral cochlear nucleus of the cat: non-linearity of cochlear output. *J. Neurophysiol.*, **37**, 218–253.
- Roux, F. & Uhlhaas, P.J. (2014) Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information? *Trends Cogn. Sci.*, **18**, 16–25.
- Sauseng, P., Griesmayr, B., Freunberger, R. & Klimesch, W. (2010) Control mechanisms in working memory: a possible function of EEG theta oscillations. *Neurosci. Biobehav. Rev.*, **34**, 1015–1022.
- Schack, B., Klimesch, W. & Sauseng, P. (2005) Phase synchronization between theta and upper alpha oscillations in a working memory task. *Int. J. Psychophysiol.*, **57**, 105–114.
- Schremm, A., Horne, M. & Roll, M. (2015) Brain responses to syntax constrained by time-driven implicit prosodic phrases. *J. Neurolinguist.*, **35**, 68–84.
- Schroeder, C.E. & Lakatos, P. (2009) Low-frequency neuronal oscillations as instruments of sensory selection. *Trends Neurosci.*, **32**, 9–18.
- Schroeder, C.E., Lakatos, P., Kajikawa, Y., Partan, S. & Puce, A. (2008) Neuronal oscillations and visual amplification of speech. *Trends Cogn. Sci.*, **12**, 106–113.
- Shannon, R.V., Zeng, F.-G., Kamath, V., Wygonski, J. & Ekelid, M. (1995) Speech recognition with primarily temporal cues. *Science*, **270**, 303.
- Stefanics, G., Hangya, B., Hernadi, I., Winkler, I., Lakatos, P. & Ulbert, I. (2010) Phase entrainment of human delta oscillations can mediate the effects of expectation on reaction speed. *J. Neurosci.*, **30**, 13578–13585.
- von Stein, A., Rappelsberger, P., Sarnthein, J. & Petsche, H. (1999) Synchronization between temporal and parietal cortex during multimodal object processing in man. *Cereb. Cortex*, **9**, 137–150.
- Steinhauer, K. & Drury, J.E. (2012) On the early left-anterior negativity (ELAN) in syntax studies. *Brain Lang.*, **120**, 135–162.
- Steriade, M., Nunez, A. & Amzica, F. (1993) A novel slow (< 1 Hz) oscillation of neocortical neurons *in vivo*: depolarizing and hyperpolarizing components. *J. Neurosci.*, **13**, 3252–3265.
- Swets, B., Desmet, T., Hambrick, D.Z. & Ferreira, F. (2007) The role of working memory in syntactic ambiguity resolution: a psychometric approach. *J. Exp. Psychol. Gen.*, **136**, 64–81.
- Szymanski, F.D., Rabinowitz, N.C., Magri, C., Panzeri, S. & Schnupp, J.W. (2011) The laminar and temporal structure of stimulus information in the phase of field potentials of auditory cortex. *J. Neurosci.*, **31**, 15787–15801.
- Taylor, W.L. (1953) “Cloze procedure”: a new tool for measuring readability. *Journalism Quart.*, **30**, 415–433.
- Trussell, L.O. (2002) Cellular mechanisms for information coding in auditory brainstem nuclei. In Oertel, D. & Fay, R.R. (Eds), *Integrative Functions in the Mammalian Auditory Pathway*. Springer, Berlin, pp. 72–98.
- Van Den Brink, D., Brown, C.M. & Hagoort, P. (2001) Electrophysiological evidence for early contextual influences during spoken-word recognition: N200 versus N400 effects. *J. Cognitive Neurosci.*, **13**, 967–985.
- Van Dijk, H., Nieuwenhuis, I. & Jensen, O. (2010) Left temporal alpha band activity increases during working memory retention of pitches. *Eur. J. Neurosci.*, **31**, 1701–1707.
- Van Petten, C. (1993) A comparison of lexical and sentence-level context effects in event-related potentials. *Lang. Cognitive Proc.*, **8**, 485–531.

- Vander Ghinst, M., Bourguignon, M., Op de Beeck, M., Wens, V., Marty, B., Hassid, S., Choufani, G., Jousmaki, V. *et al.* (2016) Left superior temporal gyrus is coupled to attended speech in a cocktail-party auditory scene. *J. Neurosci.*, **36**, 1596–1606.
- VanRullen, R. (2016) Perceptual cycles. *Trends Cogn. Sci.*, **20**, 723–735.
- VanRullen, R., Busch, N., Drewes, J. & Dubois, J. (2011) Ongoing EEG phase as a trial-by-trial predictor of perceptual and attentional variability. *Front. Psychol.*, **2**, 60.
- Vollrath, M., Kazenwadel, J. & Krüger, H.-P. (1992) A universal constant in temporal segmentation of human speech. *Naturwissenschaften*, **79**, 479–480.
- Voskuhl, J., Huster, R.J. & Herrmann, C.S. (2015) Increase in short-term memory capacity induced by down-regulating individual theta frequency via transcranial alternating current stimulation. *Front. Hum. Neurosci.*, **9**, 257.
- Wager, T. & Smith, E. (2003) Neuroimaging studies of working memory: a meta-analysis. *Cogn. Affect. Behav. Ne.*, **3**, 255–274.
- Wang, X. (2010) Neurophysiological and computational principles of cortical rhythms in cognition. *Physiol. Rev.*, **90**, 1195–1268.
- Wang, L., Jensen, O., van den Brink, D., Weder, N., Schoffelen, J., Magyari, L., Hagoort, P. & Bastiaansen, M. (2012a) Beta oscillations relate to the N400 m during language comprehension. *Hum. Brain Mapp.*, **33**, 2898–2912.
- Wang, L., Zhu, Z. & Bastiaansen, M. (2012b) Integration or predictability? A further specification of the functional role of gamma oscillations in language comprehension. *Front. Psychol.*, **3**, 187.
- Wanner, E. & Maratsos, M. (1979) An ATN approach to comprehension. In Halle, M., Bresnan, J. & Miller, G.A. (Eds), *Linguistic Theory and Psychological Reality*. MIT Press, Cambridge, pp. 119–161.
- Weiss, S. & Mueller, H. (2003) The contribution of EEG coherence to the investigation of language. *Brain Lang.*, **85**, 325–343.
- Weiss, S. & Mueller, H.M. (2012) “Too many betas do not spoil the broth”: the role of beta brain oscillations in language processing. *Front. Psychol.*, **3**, 201.
- Weiss, S. & Rappelsberger, P. (1996) EEG coherence within the 13–18 Hz band as a correlate of a distinct lexical organisation of concrete and abstract nouns in humans. *Neurosci. Lett.*, **209**, 17–20.
- Weiss, S., Müller, H. & Rappelsberger, P. (2000) Theta synchronization predicts efficient memory encoding of concrete and abstract nouns. *Neuroreport*, **11**, 2357–2361.
- Weiss, S., Mueller, H.M., Schack, B., King, J.W., Kutas, M. & Rappelsberger, P. (2005) Increased neuronal communication accompanying sentence comprehension. *Int. J. Psychophysiol.*, **57**, 129–141.
- Weisz, N., Hartmann, T., Müller, N., Lorenz, I. & Obleser, J. (2011) Alpha rhythms in audition: cognitive and clinical perspectives. *Front. Psychol.*, **2**, 73.
- Wiedmann, N. & Winkler, S. (2015) The influence of prosody on children’s processing of ambiguous sentences. In Winkler, S. (Ed), *Ambiguity: Language and Communication*. De Gruyter, Berlin, pp. 185–197.
- Wingfield, A., Lombardi, L. & Sokol, S. (1984) Prosodic features and the intelligibility of accelerated speech: syntactic versus periodic segmentation. *J. Speech Lang. Hear. R.*, **27**, 128–134.