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The rhythms of language: an overview of linguistic processes and neural oscillations

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Abstract

For the last decades neuroscientists have grown interest in the analysis of the rhythmic activity of the brain synchronized at temporal and spatial level. These neural oscillations, grouped by their frequency, have been proposed to govern all cognitive processes. In the field of the neurobiology of language, considerable research has linked speech processing and language comprehension to neural oscillations. On one hand, neural rhythmic activity is thought to synchronize to relevant spectral information of speech on three-time scales – which physically reflect phoneme, syllable and phrase processing. On the other hand, syntactic and semantic processing is subserved by faster oscillatory patterns not necessarily related to the acoustic properties of speech. For each linguistic process, this article summarizes the neural oscillations involved. Further evidence comes from studies on language-related pathologies.

Keywords: brain rhythms, linguistic operations, speech processing, language comprehension

1. *Introduction*

Neuroscientists using magnetoencephalography (MEG) and electroencephalography (EEG) have greatly relied on event-related potentials (ERPs) and event-related magnetic fields (ERFs) to investigate the major components involved in linguistic processes – a positive or negative deflection of the signal in respect of a baseline – such as P100, N100, P200, P300, N400, P600 (Swaab et al. 2012). Thereby, considerable research has tested the involvement of distinct brain regions and the concomitant electrical/magnetic activity for various linguistic processes, highlighting the spatiotemporal distribution of neural activation. This approach is based on the idea that each stimulus (visual, auditory and so on) a subject is exposed may elicit a time-locked neural response. However, this response cannot be seen in the raw EEG signal, due to the overlapping of ongoing background activity. To determine these systematic responses, a certain experimental paradigm is repeated a number of times: each time a stimulus is presented to the subject, a marker is set into EEG/ERF signal to obtain time-locked epochs to the experimental event of interest: that is, the components previous cited. By averaging all the epochs, only the systematic response should remain (Sauseng and Klimesch 2008).

Recent advancement in neurolinguistic research have seen a shift in paradigm: a central question has become not only which brain region is responsible for which function but also how brain regions interact with each other. In fact, it is necessary to explore “not only what is connected, but how and in what directions regions of the brain are connected” (Kopell et al. 2014, 1319) by adding a functional perspective to understand how the brain’s regions are involved in producing and processing brain signals (Murphy 2015).

Although ERPs/ERFs have proved to be extremely useful, this approach overshadows that the EEG activity of the human brain is not flat and that functions, especially complex ones, involve different areas. In fact, all the electrical activity recorded at the scalp is characterized by rhythms, which are driven by fluctuations in excitability of large-sized populations of neurons, with specific spatiotemporal patterns that differ in amplitude, timing, and frequency (Cohen 2017). Depending on their frequency, such rhythms are grouped in delta (δ: ~0.5–4 Hz), theta (θ: ~4–8 Hz), alpha (α: ~8–12 Hz), beta (β: ~12–30 Hz) and gamma (γ: ~30–120 Hz). Neural oscillations have found wide use in clinical applications, providing useful information about levels of consciousness, psychological states, or presence of neurological disorders.

Recently, researchers have come to realize that these oscillatory rhythms also subserve a wide variety of cognitive processes: it has been argued that the synchronization and de-synchronization of these oscillations in distinct clusters can shape input gain and assist information transfer (Akam and Kullmann 2010; Muller et al. 2018). In fact, strong evidence suggests that the reorganization of ongoing oscillatory patterns might explain some of the features of ERPs/ERFs, due to phase reset (i.e., the reshaping of the signal) once a stimulus is presented to the subject (Başar et al. 2001; Başar 2011). Therefore, event-related oscillations, further than to have the time-locked EEG information, permits the retrieval of non-phase locked EEG information related to the cognitive activity induced by the stimulus

As for language, neural oscillations have been linked to a number of linguistic operations. This article provides an overview of neural oscillations subserving linguistic operations. Following Meyer (2018), a dichotomy between lower-level functions of speech processing and higher-level functions of language comprehension will be assumed: on one hand, linguistically meaningful units must be segmented from speech, based on temporal and spectral cues recognized by the auditory system; on the other hand, two streams of language comprehension are assumed to occur to decode the meaning of words (semantic stream) and the relations between words (syntactic stream).

2. *The delta-(theta-gamma) neural code for speech pro- cessing*

2.1. *Speech processing on three timescales*

By paraphrase of Meyer (2018), the segmentation and identification of discrete phonological units have been found to occur in a particular range of operational frequencies. Phonological units decreasing in granularity hierarchically build speech: the combination of phonemes result into syllables; the combination of syllables result into intonation phrases. Each phonological unit has an acoustics-temporal counterpart (Gussenhoven and Jacobs 2017).

In the last decade, researchers have found that neural oscillations might subserve a set of neural operations that allows the segmentation and identification of discrete phonological units. In fact, during speech processing, three frequency bands, gamma, theta and delta bands, seem to synchronize respectively with the pace of phonemes, syllables and intonational phrases, by tracking linguistically meaningful acoustic properties of speech on three different time scales (Bourguignon et al. 2020; Giraud and Poeppel 2012; Molinaro and Lizarazu 2018). The synchronization of neural oscillations to speech is thought to occur thanks to the so-called neural entrainment which relies on phase synchronization and amplitude synchronization (Obleser and Kayser 2019): on one hand, bottom-up modulations of neural oscillations are stimulus-dependent, relying on acoustic properties of speech; on the other hand, neural oscillations have been found to internally organize, building hierarchical structures, where lower-frequency bands top-down modulate higher-frequency bands, regardless of stimulus properties (Fontolan et al. 2014).

2.2. *Stimulus-bound processing*

Starting with bottom-up modulations, the phonemic time scale falls within the gamma band frequencies (30-120 Hz). As discussed by Meyer (2018), low and high gamma band oscillations may subserve acoustic and categorical processing, respectively: low gamma-band phase synchronization seems to be related to acoustic processing (Gross et al. 2013), while phonemic-categorical perception is subserved by amplitude synchronization of high gamma bands (Lehongre et al. 2011), which reflect the spiking activity of neurons in the auditory cortex sensitive to phonemes (Mesgarani et al. 2014). In addition, it has been argued that low gamma band synchronization occurs more strongly with the acoustic amplitude envelope compared to phonemic-categorical information (Di Liberto, O'Sullivan, and Lalor 2015).

Going up in granularity, theta bands oscillations (4-8 Hz) capture the pace of syllables, thus subserving syllabic processing. In fact, recent works have suggested that theta oscillations phase-synchronize to the onset of syllables, allowing the segmentation of syllables (Luo and Poeppel 2007; Howard and Poeppel 2012; Peelle, Gross, and Davis 2013; Doelling et al. 2014; references from Meyer 2018). Moreover, further evidence suggests a relation- ship between the amplitude modulations of speech and the phase of neural oscillations (Gross et al. 2013; Vander Ghinst et al. 2016; Molinaro, Monsalve, and Lizarazu 2016).

Lastly, delta bands (0.5-4 Hz) have shown increased phase coherence to the fundamental frequency envelope of speech: delta oscillations have been proposed to aid the segmentation of intonational phrases (Giraud and Poeppel 2012), due to the amplitude extrema of the pitch contour marking the boundaries of intonational phrases. Interestingly, delta bands also capture the pace of syntactic phrases (Ding et al. 2016; Molinaro and Lizarazu 2018), which do not have a direct physical counterpart, in the case prosodic cues were explicitly removed (Ding et al. 2017). However, the role of delta oscillations in speech processing is still under debate (see for example Boucher, Gilbert, and Jemel 2019).

2.3. *Top-down modulations*

While strong evidence suggests bottom-up modulations of neural oscillations, it has been argued that these oscillations hierarchically self-organize, regardless of acoustic properties of speech: particularly, the phase of lower-frequency bands top-down modulates the amplitude of higher-frequency bands (Giraud and Poeppel 2012; Fontolan et al. 2014), opening a new window on brain dynamics of speech processing. In fact, theta-gamma cross frequency coupling in the left hemisphere have been proposed to subserve the concatenation of phonemes into syllables (Canolty et al. 2006), although this hypothesis contrasts with a number of studies that show a theta-gamma coupling in the right auditory cortex (Luo and Poeppel 2007; Abrams et al. 2008; Hämäläinen et al. 2012; Gross et al. 2013; Howard and Poeppel 2012; Peelle, Gross, and Davis 2013; references from Meyer 2018). Interestingly, it has been shown that phase-amplitude coupling between theta and gamma oscillations adapts to speech rate (Lizarazu, Lallier, and Molinaro 2019). The combination of syllables into intonational phrases is then subserved by delta-theta cross-frequency coupling (Giraud and Poeppel 2012; Ding et al. 2016). It is worth noticing that the neural underpinnings of prosody are still not clear and need future research (for a discussion see Myers, Lense, and Gordon 2019), given that, at least in some cases, prosody conveys crucial information on the syntactic structure which suggests a tight relation with top-down information.

3. *Language comprehension along two streams*

3.1 *Syntactic processing*

Once all phonological units are segmented from speech and the auditory system is tempo- rarily aligned, the brain must decode the rela- tions between words which are recursively combined into syntactic phrases (Chomsky 1957). Recent evidence suggests that the group- ing of words into phrases might be subserved by delta band cycles through phase resetting. In fact, Ding and colleagues (2016) have found an increase in delta-power associated with internal syntactic phrase generation. These findings were later confirmed by Bonhage et al. (2017): subjects involved in this study showed an in- crease in delta band power while exposed to a list of words that could be combined into syn- tactic phrases, while a decrease in delta band power was found for a list of words that could not be grouped into phrases. As mentioned above, delta band oscillations also play a role in the segmentation of intonational phrases. Interestingly, these results may not contradict each other: in fact, Ghitza (2017) argued that the relation between delta bands and intonational phrases would reflect a stimulus-bound bottom-up segmentation, while delta oscillations subserving syntactic chunking would reflect top-down generation based on a priori syntactic knowledge. However, the role of delta bands in syntactic phrase generation is still under debate. While a sentence unfolds word by word, phrases have to be stored in verbal working memory and retrieved later on to assess their dependencies with other phrases and generate syntactic hierarchies. A number of studies have linked the storage of phrases in verbal working memory with an increase in alpha band activity (Haarmann and Cameron 2005; Weiss et al. 2005; Meyer, Obleser, and Friederici 2013; Bonhage et al. 2017; references from Meyer 2018). Particularly, alpha band power increases with storage demands, local- ized in the inferior parietal cortex.

Interesting findings come from violation studies that examined time-locked neural oscillations related to syntactic anomalies. Many of these studies have found a consistent pattern in response to syntactic violations, such as gender and number agreement violation (Bastiaansen, van Berkum, and Hagoort 2002; Davidson and Indefrey 2007; Schneider et al. 2016), mostly confirming the aforementioned findings.

A groundbreaking result concerns the possible role of gamma band in structure-building operations, what generative linguists call *Merge*: (Nelson and colleagues (2017) found a specific gamma band pattern that they claim as evidence for Merge, the binding. Particularly, gamma power increases every time a new word is added to an unfolding sentence, while it sharply decreases when words can be compressed into a syntactic node. In addition, a recent study has shown a difference in high gamma response for the syntactic disambiguation of homophones phrases (Artoni et al. 2020). However, these results may be in contrast with aforementioned studies linking delta activity to syntactic processing.

3.2. Semantic processing

Along the syntactic parsing, language comprehension also implies a semantic processing which has been linked primarily with beta and gamma oscillations. Evidence of beta-bands involvement in semantic processing have come from a number of violation studies, focused on semantic anomalies (Kielar et al. 2014; 2015; Wang et al. 2012a; Luo et al. 2010). Particularly, these studies have found a decrease both in alpha and beta oscillations related to semantic anomalies. Willems, Oostenveld, and Hagoort (2008) have linked both alpha and beta decrease to audio-visual semantic anomalies. However, they found that alpha activity decreases where both a visual and linguistic context mismatch occurs.

Interestingly, other research on semantic anomalies has also found an increase in theta power (Hagoort et al. 2004; Hald, Bastiaansen, and Hagoort 2006; Davidson and Indefrey 2007; M. Bastiaansen and Hagoort 2015; Wang, Zhu, and Bastiaansen 2012; references from Prystauka and Lewis 2019). Bastiaansen, Mazaheri, and Jensen (2012) proposed that theta power increase due to semantic anomalies might reflect the integration of the anomalous word into the sentence. Another interesting proposal comes from Prystauka and Lewis (2019): given that theta increase has also been found in syntactic violation studies and has been proposed to aid lexical-semantic retrieval (Bastiaansen, Mazaheri, and Jensen 2012; Marko, Cimrová, and Riečanský 2019), an increase in theta power may reflect a general error detection mechanism. This idea is also supported by other studies on incorrect solutions to mathematical equations (Tzur and Berger 2007) or motor error in reaching a task (Arrighi et al. 2016).

However, violation studies do not give the full picture: semantic processing also relies on predictions of upcoming words. Each word is stored in the long-term memory with a certain probability of occurring in a given context, prior and after other words (Hagoort et al. 2004; Kutas and Federmeier 2010). Top-down predictions, independent of stimuli, have also been linked with beta bands power which increases when expectations of upcoming words are confirmed and decreases when such predictions do not match the sequence of incoming words (Lewis and Bastiaansen 2015; Lewis et al. 2016). For example, Wang et al. (2012) performed a cloze test, finding a beta power decrease in sentence ending that did not matched expectations. These findings were further confirmed by Lewis et al. (2017) that compared short stories of sentences, observing an increase in beta power in semantically coherent stories and a decrease in beta power for semantically incongruent stories. An interesting proposal about the role of beta bands and prediction comes from Lewis et al. (2016), yielding that they might subserve predictions across different linguistic levels, from the auditory domain to the syntactic level (Kim and Chung 2008; Sabine Weiss and Mueller 2012; Arnal, Wyart, and Giraud 2011; Arnal and Giraud 2012). However, Meyer

(2018) argues that beta bands only subserve lexical-semantic predictions for two reasons: beta bands power increase during contextual prediction of upcoming words correlates with the amplitude of N400, indicating the lexical-semantic predictability of a word (Kutas and Federmeier 2010; Wang et al. 2012; Hale 2016; Lewis et al. 2016) but not its syntactic category (Levy 2008; Frank et al. 2015); beta-bands have been shown to be modulated by syntactic factors only in syntactic violation studies (e.g.: the syntactic category of the upcoming words do not match expectations), possibly yielding that semantic processing does not occur when syntactic parsing is not accomplished (Steinhauer and Drury 2012).

Alongside top-down predictions based on the occurrence frequency of each word in context stored in long-term memory, lexical-semantic representations of incoming words must be checked. When lexical-semantic predictions are fulfilled, gamma power has been found to increase (Wang, Zhu, and Bastiaansen 2012; Molinaro, Barraza, and Carreiras 2013; Monsalve, Pérez, and Molinaro 2014). Conversely, gamma power decreases when the incoming word does not match expectations (Hald, Bastiaansen, and Hagoort 2006; Penolazzi, Angrilli, and Job 2009; Rommers, Dijkstra, and Bastiaansen 2012; references from Meyer 2018).

The interplay between beta and gamma bands has been included in the predictive coding framework (e.g. Friston 2005). In fact, data collected on beta and gamma bands are compatible with the predictive coding framework (Lewis and Bastiaansen 2015; for a discussion see Meyer 2018; Prystauka and Lewis 2019).

4. *Language-related disorders and neural oscillations*

Further evidence of the implications of neural oscillations into linguistic operations comes from research on language-related pathologies and disorders. In fact, a number of studies has confirmed the aforementioned findings on linguistic operations and neural oscillations.

Current models of aphasia classifications still rely on the Wernicke-Lichtheim model which links damages in a brain area with a specific function. This model has the advantage of being simple: for example, a damage in the motor area of language, Broca's area, will be linked to a non-fluent aphasic syndrome, while damage in the sensory area of language, Wernicke's ar- ea, will be linked to fluent aphasia syndrome (Lichteim 1885; Wernicke 1974).

A number of studies have observed an alteration of neural oscillations both at resting state and while performing a linguistic task. Spironelli and Angrilli (2009), for example, demonstrated that an increase in delta amplitude in the perilesional area is a marker of brain damage in chronic non-fluent aphasic patients. In fact, delta band might be an index of neural inhibition. Other research has shown that focal lesions in the left hemispheric language regions may lead to a change in brain physiology. For example, Meinzer et al. (2004) found an increase in spontaneous delta activity in the perilesional area in a group of stroke patients suffering from different aphasia types, while also reporting a decrease in spontaneous perilesional delta activity after an intense speech and language therapy. Dubovik et al. (2012) also found a shift from fast to slow spontaneous neural oscillations, particularly in delta and theta frequency range. Interestingly, Nicolo et al. (2015) reported that more coherent beta oscillations in lesioned Broca's area in early post stroke recovery patients predicts future language improvement during recovery.

Functional restoration of the brain in post-stroke patients seems to be related to an increase in spontaneous alpha-band synchronization (Westlake et al. 2012; Dubovik et al. 2012). Moreover, Kielar et al. (2016) investigated the functional reorganization of language networks: particularly, in a group of subjects suffering from different types of aphasia, they found a decrease in alpha and beta power in the left hemisphere, where the lesion occurred, in response to semantic anomalies during sentence comprehension.

A previous study also reported a possible role of beta activity as an index of the reorganization of language networks in aphasic patients: Spironelli, Manfredi, and Angrilli (2013) reported that non-fluent aphasic subjects, after linguistic recovery, showed a reduced beta activation in the core damaged area during a phonological and semantic task, while also showing an increased delta activity compared to healthy control subjects. They also found an increased high beta-activity in the left anterior sites during the phonological and orthographic task. The authors of the study have interpreted these findings as an index of the reorganization of language in recovered non-fluent aphasic subjects at the left prefrontal sites.

In addition, many studies on dyslexic subjects have confirmed the role of neural oscillation into linguistic operations. For example, Lehongre et al. (2011) linked a decreased entrainment of the lower gamma band to phonological deficits, while Leong and Goswami (2014) suggested that rhythmic entrainment at the syllabic timescale is disrupted in dyslexic subjects. These results were recently confirmed by Lizarazu et al. (2021), proving an impairment of cortical entrainment in the delta and theta range to speech in dyslexic subjects.

7. *Conclusions*

Although this article is far from offering an exhaustive overview, it is clear that neural oscillations provide a new window on brain dynamics related to linguistic operations. The number of studies following the oscillation-based framework has been growing in the last decade, yielding an increasing interest in brain's oscillatory nature. On one hand, speech processing seems to be subserved by delta, theta and gamma bands, respectively at phrase, syllable and phoneme timescales. On the other hand, language comprehension is subserved by a variety of frequency bands involved in syntactic and semantic processing, including more general cognitive functions such as the implication of short- and long-term memory.

Bottom-up and top-down modulations of neural oscillations may provide a neural code for linguistic operations: the cyclicity of oscillatory rhythms' synchronization and desynchronization may represent a neural coding (and decoding) that matches linguistic computations, shortening the gap between broader neuroscientific investigations and more fine-grained linguistic investigations (Granularity Mismatch Problem, (Embick and Poeppel 2015). Accordingly, formal proposals of hierarchical organization of neural oscillations have emerged (Murphy 2019; Grimaldi 2019).

8. *References*

- Abrams, D. A., T. Nicol, S. Zecker, and N. Kraus. (2008). "Right-Hemisphere Auditory Cortex Is Dominant for Coding Syllable Patterns in Speech." *Journal of Neuroscience* 28 (15): 3958–65. https://doi.org/10.1523/JNEUROSCI.0187-08.2008.
- Akam, Thomas, and Dimitri M. Kullmann. (2010). "Oscillations and Filtering Networks Support Flexible Routing of Information." *Neuron* 67 (2): 308–20. https://doi.org/10.1016/j.neuron.2010.06.019.
- Arnal, Luc H., and Anne-Lise Giraud. (2012). "Cortical Oscillations and Sensory Predictions." *Trends in Cognitive Sciences* 16 (7): 390–98. https://doi.org/10.1016/j.tics.2012.05.003.
- Arnal, Luc H, Valentin Wyart, and Anne-Lise Giraud. (2011). "Transitions in Neural Oscillations Reflect Prediction Errors Generated in Audiovisual Speech." *Nature Neuroscience* 14 (6): 797–801. https://doi.org/10.1038/nn.2810.
- Arrighi, Pieranna, Luca Bonfiglio, Fabrizio Minichilli, Nicoletta Cantore, Maria Chiara Carboncini, Emily Piccotti, Bruno Rossi, and Paolo Andre. (2016). "EEG Theta Dynamics within Frontal and Parietal Cortices for Error Processing during Reaching Movements in a Prism Adaptation Study Altering Visuo-Motor Predictive Planning." Edited by Luigi Cattaneo. *PLOS ONE* 11 (3): e0150265. https://doi.org/10.1371/journal.pone.0150265.
- Artoni, Fiorenzo, Piergiorgio d'Orio, Eleonora Catricalà, Francesca Conca, Franco Bottoni, Veronica Pelliccia, Ivana Sartori, et al. (2020). "High Gamma Response Tracks Different Syntactic Structures in Homophonous Phrases." *Scientific Reports* 10 (1): 7537. https://doi.org/10.1038/s41598-020-64375-9.
- Başar, Erol. (2011). *Brain-Body-Mind in the Nebu- lous Cartesian System: A Holistic Approach by Oscil- lations*. New York, NY: Springer New York. https://doi.org/10.1007/978-1-4419-6136-5.
- Başar, Erol, Canan Başar-Eroglu, Sirel Karakaş, and Martin Schürmann. (2001). "Gamma, Alpha, Delta, and Theta Oscillations Govern Cognitive Processes." *International Journal of Psychophysiology* 39 (2–3): 241–48. https://doi.org/10.1016/S0167-8760(00)00145-8.
- Bastiaansen, Marcel, Jos J.A. van Berkum, and Peter Hagoort. (2002). "Event-Related Theta Power Increases in the Human EEG during Online Sentence Processing." *Neuroscience Let- ters* 323 (1): 13–16.

https://doi.org/10.1016/S0304-3940(01)02535-6.

- Bastiaansen, Marcel, and Peter Hagoort. (2015). "Frequency-Based Segregation of Syn- tactic and Semantic Unification during Online Sentence Level Language Comprehension." *Journal of Cognitive Neuroscience* 27 (11): 2095– 2107. https://doi.org/10.1162/jocn_a_00829.
- Bastiaansen, Marcel, Ali Mazaheri, and Ole Jensen. (2012). "Beyond ERP's: Oscillatory Neuronal Dynamics." In *Oxford Handbook of Event-Related Potential Components*, 40.
- Bonhage, Corinna E., Lars Meyer, Thomas Gruber, Angela D. Friederici, and Jutta L. Mueller. (2017). "Oscillatory EEG Dynamics Underlying Automatic Chunking during Sentence Processing." *NeuroImage* 152 (May): 647– 57. https://doi.org/10.1016/j.neuroimage.2017.03.018.
- Boucher, Victor J., Annie C. Gilbert, and Boutheina Jemel. (2019). "The Role of Low-Frequency Neural Oscillations in Speech Processing: Revisiting Delta Entrainment." *Journal of Cognitive Neuroscience* 31 (8): 1205–15. https://doi.org/10.1162/jocn_a_01410.
- Bourguignon, Mathieu, Nicola Molinaro, Mikel Lizarazu, Samu Taulu, Veikko Jousmäki, Marie Lallier, Manuel Carreiras, and Xavier De Tiège. (2020). "Neocortical Activity Tracks the Hierarchical Linguistic Structures of Self-Produced Speech during Reading Aloud." *NeuroImage* 216: 116788. https://doi.org/10.1016/j.neuroimage.2020.116788.
- Canolty, R. T., E. Edwards, S. S. Dalal, M. Soltani, S. S. Nagarajan, H. E. Kirsch, M. S. Berger, N. M. Barbaro, and R. T. Knight. (2006). "High Gamma Power Is Phase-Locked to Theta Oscillations in Human Neocortex." *Science* 313 (5793): 1626–28. https://doi.org/10.1126/science.1128115.
- Chomsky, Noam. (1957). *Syntactic Structures*. Berlin: De Gruyter.
- Cohen, Michael X. (2017). "Where Does EEG Come From and What Does It Mean?" *Trends in Neurosciences* 40 (4): 208–18. https://doi.org/10.1016/j.tins.2017.02.004.
- Davidson, D.J., and P. Indefrey. (2007). "An Inverse Relation between Event-Related and Time–Frequency Violation Responses in Sentence Processing." *Brain Research* 1158 (July): 81–92. https://doi.org/10.1016/j.brainres.2007.04.082.
- Di Liberto, Giovanni M., James A. O'Sullivan, and Edmund C. Lalor. (2015). "Low-Frequency Cortical Entrainment to Speech Reflects Phoneme-Level Processing." *Current Biol- ogy* 25 (19): 2457–65. https://doi.org/10.1016/j.cub.2015.08.030.
- Ding, Nai, Lucia Melloni, Aotian Yang, Yu Wang, Wen Zhang, and David Poeppel. (2017). "Characterizing Neural Entrainment to Hierarchical Linguistic Units Using Electroencephalography (EEG)." *Frontiers in Human Neuroscience* 11 (September): 481. https://doi.org/10.3389/fnhum.2017.00481.
- Ding, Nai, Lucia Melloni, Hang Zhang, Xing Tian, and David Poeppel. (2016). "Cortical Tracking of Hierarchical Linguistic Structures in Connected Speech." *Nature Neuroscience* 19 (1): 158–64. https://doi.org/10.1038/nn.4186.
- Doelling, Keith B., Luc H. Arnal, Oded Ghitza, and David Poeppel. (2014). "Acoustic Landmarks Drive Delta–Theta Oscillations to Enable Speech Comprehension by Facilitating Perceptual Parsing." *NeuroImage* 85 (January): 761–68. https://doi.org/10.1016/j.neuroimage.2013.06.035.
- Dubovik, Sviatlana, Jean-Michel Pignat, Radek Ptak, Tatiana Aboulafia, Lara Allet, Nicole Gillabert, Cécile Magnin (2012). "The Behavioral Significance of Coherent Resting-State Oscillations after Stroke." *NeuroImage* 61 (1): 249–57. https://doi.org/10.1016/j.neuroimage.2012.03.024.
- Embick, David, and David Poeppel. (2015). "Towards a Computational(Ist) Neurobiology of Language: Correlational, Integrated and Explanatory Neurolinguistics." *Language, Cognition and Neuroscience* 30 (4): 357–66. https://doi.org/10.1080/23273798.2014.980750.
- Fontolan, L., B. Morillon, C. Liegeois-Chauvel, and Anne-Lise Giraud. (2014). "The Contribution of Frequency-Specific Activity to Hierarchical Information Processing in the Human Auditory Cortex." *Nature Communications* 5 (1): 4694. https://doi.org/10.1038/ncomms5694.
- Frank, Stefan L., Leun J. Otten, Giulia Galli, and Gabriella Vigliocco. (2015). "The ERP Response to the Amount of Information Conveyed by Words in Sentences." *Brain and Language* 140 (January): 1–11. https://doi.org/10.1016/j.bandl.2014.10.006.
- Friston, Karl. (2005). "A Theory of Cortical Responses." *Philosophical Transactions of the Royal*

Society B: Biological Sciences 360 (1456): 815–36. https://doi.org/10.1098/rstb.2005.1622.

- Ghitza, Oded. (2017). "Acoustic-Driven Delta Rhythms as Prosodic Markers." *Language, Cognition and Neuroscience* 32 (5): 545–61. https://doi.org/10.1080/23273798.2016.1232419.
- Giraud, Anne-Lise, and David Poeppel. (2012). "Cortical Oscillations and Speech Processing: Emerging Computational Principles and Operations." *Nature Neuroscience* 15 (4): 511–17. https://doi.org/10.1038/nn.3063.
- Grimaldi, Mirko. (2019). "From Brain Noise to Syntactic Structures: A Formal Proposal within the Oscillatory Rhythms Perspective." In *Linguistic Variation: Structure and Interpretation* edited by Ludovico Franco and Paolo Lorusso, 293–316. De Gruyter Mouton. https://doi.org/10.1515/9781501505201-017.
- Gross, Joachim, Nienke Hoogenboom, Gregor Thut, Philippe Schyns, Stefano Panzeri, Pascal Belin, and Simon Garrod. (2013). "Speech Rhythms and Multiplexed Oscillatory Sensory Coding in the Human Brain." Edited by David Poeppel. *PLoS Biology* 11 (12): e1001752. https://doi.org/10.1371/journal.pbio.1001752.
- Gussenhoven, Carlos, and Haike Jacobs. (2017). *Understanding Phonology*. Fourth edition. Understanding Language Series. London; New York: Routledge, Taylor & Francis Group.
- Haarmann, H, and K Cameron. (2005). "Active Maintenance of Sentence Meaning in Working Memory: Evidence from EEG Coherences." *International Journal of Psychophysiology* 57 (2): 115–28. https://doi.org/10.1016/j.ijpsycho.2005.03.017.
- Hagoort, Peter, Lea Hald, Marcel Bastiaansen, and Karl Magnus Petersson. (2004). "Integration of Word Meaning and World Knowledge in Language Comprehension." *Science* 304 (5669): 438. https://doi.org/10.1126/science.1095455.
- Hald, Lea A., Marcel C.M. Bastiaansen, and Peter Hagoort. (2006). "EEG Theta and Gamma Responses to Semantic Violations in Online Sentence Processing." *Brain and Language* 96 (1): 90–105. https://doi.org/10.1016/j.bandl.2005.06.007.
- Hale, John. (2016). "Information-Theoretical Complexity Metrics." *Language and Linguistics Compass* 10 (9): 397–412. https://doi.org/10.1111/lnc3.12196.
- Hämäläinen, Jarmo A., André Rupp, Fruzsina Soltész, Denes Szücs, and Usha Goswami. 2012. "Reduced Phase Locking to Slow Amplitude Modulation in Adults with Dyslexia: An MEG Study." *NeuroImage* 59 (3): 2952–61. https://doi.org/10.1016/j.neuroimage.2011.09.075.
- Howard, Mary F., and David Poeppel. (2012). "The Neuromagnetic Response to Spoken Sentences: Co-Modulation of Theta Band Amplitude and Phase." *NeuroImage* 60 (4): 2118– 27. https://doi.org/10.1016/j.neuroimage.2012.02.028.
- Kielar, Aneta, Tiffany Deschamps, Regina Jokel, and Jed A. Meltzer. (2016). "Functional Reorganization of Language Networks for Semantics and Syntax in Chronic Stroke: Evidence from MEG." *Human Brain Mapping* 37 (8): 2869–93. https://doi.org/10.1002/hbm.23212.
- Kielar, Aneta, Jed A. Meltzer, Sylvain Moreno, Claude Alain, and Ellen Bialystok. (2014). "Oscillatory Responses to Semantic and Syntactic Violations." *Journal of Cognitive Neuroscience* 26 (12): 2840–62. https://doi.org/10.1162/jocn_a_00670.
- Kielar, Aneta, Lilia Panamsky, Kira A. Links, and Jed A. Meltzer. (2015). "Localization of Electrophysiological Responses to Semantic and Syntactic Anomalies in Language Comprehension with MEG." *NeuroImage* 105 (January): 507–24. https://doi.org/10.1016/j.neuroimage.2014.11.016.
- Kim, June Sic, and Chun Kee Chung. (2008). "Language Lateralization Using MEG Beta Frequency Desynchronization during Auditory Oddball Stimulation with One-Syllable Words." *NeuroImage* 42 (4): 1499–1507. https://doi.org/10.1016/j.neuroimage.2008.06.001.
- Kopell, Nancy J., Howard J. Gritton, Miles A. Whittington, and Mark A. Kramer. (2014). "Beyond the Connectome: The Dynome." *Neuron* 83 (6): 1319–28. https://doi.org/10.1016/j.neuron.2014.08.016.
- Kutas, Marta, and Kara D. Federmeier. (2010). "Thirty Years and Counting: Finding Meaning in the N400 Component of the Event-Related Brain Potential (ERP)." *Annual Review of Psychology* 62 (1): 621–47. https://doi.org/10.1146/annurev.psych.093008.131123.

- Lehongre, Katia, Franck Ramus, Nadège Villiermet, Denis Schwartz, and Anne-Lise Giraud. (2011). "Altered Low-Gamma Sampling in Auditory Cortex Accounts for the Three Main Facets of Dyslexia." *Neuron* 72 (6): 1080– 90. https://doi.org/10.1016/j.neuron.2011.11.002.
- Leong, Victoria, and Usha Goswami. (2014). "Assessment of Rhythmic Entrainment at Multiple Timescales in Dyslexia: Evidence for Disruption to Syllable Timing." *Music: A Window into the Hearing Brain* 308 (February): 141–61. https://doi.org/10.1016/j.heares.2013.07.015.
- Levy, Roger. (2008). "Expectation-Based Syntactic Comprehension." *Cognition* 106 (3): 1126–77. https://doi.org/10.1016/j.cognition.2007.05.006.
- Lewis, Ashley G., and Marcel Bastiaansen. (2015). "A Predictive Coding Framework for Rapid Neural Dynamics during Sentence-Level Language Comprehension." *Cortex* 68 (July): 155–68. https://doi.org/10.1016/j.cortex.2015.02.014.
- Lewis, Ashley G., Jan-Mathijs Schoffelen, Herbert Schriefers, and Marcel Bastiaansen. (2016). "A Predictive Coding Perspective on Beta Oscillations during Sentence-Level Language Comprehension." *Frontiers in Human Neurosci- ence* 10 (March). https://doi.org/10.3389/fnhum.2016.00085.
- Lewis, Ashley G., Jan-Mathijs Schoffelen, Christian Hoffmann, Marcel Bastiaansen, and Herbert Schriefers. (2017). "Discourse-Level Semantic Coherence Influences Beta Oscillato- ry Dynamics and the N400 during Sentence Comprehension." *Language, Cognition and Neuro- science* 32 (5): 601–17. https://doi.org/10.1080/23273798.2016.1211300.
- Lichteim, L. (1885). "On Aphasia1." *Brain* 7 (4): 433–84. https://doi.org/10.1093/brain/7.4.433.
- Lizarazu, Mikel, Marie Lallier, Mathieu Bourguignon, Manuel Carreiras, and Nicola Molinaro. 2021. "Impaired Neural Response to Speech Edges in Dyslexia." *Cortex* 135 (Febru- ary): 207–18. https://doi.org/10.1016/j.cortex.2020.09.033..
- Lizarazu, Mikel, Marie Lallier, and Nicola Molinaro. (2019). "Phase−amplitude Coupling between Theta and Gamma Oscillations Adapts to Speech Rate." *Annals of the New York Acade- my of Sciences* 1453 (1): 140–52. https://doi.org/10.1111/nyas.14099.
- Luo, Huan, and David Poeppel. (2007). "Phase Patterns of Neuronal Responses Reliably Discriminate Speech in Human Auditory Cortex," *Neuron* 54 (6): 1001–10. https://doi.org/10.1016/j.neuron.2007.06.004.
- Luo, Y., Y. Zhang, X. Feng, and X. Zhou. 2010. "Electroencephalogram Oscillations Differentiate Semantic and Prosodic Processes during Sentence Reading." *Neuroscience* 169 (2): 654–64. https://doi.org/10.1016/j.neuroscience.2010.05.032.
- Marko, Martin, Barbora Cimrová, and Igor Riečanský. 2019. "Neural Theta Oscillations Support Semantic Memory Retrieval." *Scientific Reports* 9 (1): 17667. https://doi.org/10.1038/s41598-019-53813-y.
- Meinzer, Marcus, Thomas Elbert, Christian Wienbruch, Daniela Djundja, Gabriela Barthel, and Brigitte Rockstroh. 2004. "Intensive Language Training Enhances Brain Plasticity in Chronic Aphasia." *BMC Biology* 2 (1): 20. https://doi.org/10.1186/1741-7007-2-20.
- Mesgarani, N., C. Cheung, K. Johnson, and E. F. Chang. 2014. "Phonetic Feature Encoding in Human Superior Temporal Gyrus." *Science* 343 (6174): 1006–10. https://doi.org/10.1126/science.1245994.
- Meyer, Lars. 2018. "The Neural Oscillations of Speech Processing and Language Comprehension: State of the Art and Emerging Mechanisms." *European Journal of Neuroscience* 48 (7): 2609–21. https://doi.org/10.1111/ejn.13748.
- Meyer, Lars, Jonas Obleser, and Angela D. Friederici. 2013. "Left Parietal Alpha Enhancement during Working Memory-Intensive Sentence Processing." *Cortex* 49 (3): 711–21. https://doi.org/10.1016/j.cortex.2012.03.006.
- Molinaro, Nicola, Paulo Barraza, and Manuel Carreiras. 2013. "Long-Range Neural Synchronization Supports Fast and Efficient Reading: EEG Correlates of Processing Expected Words in Sentences." *NeuroImage* 72 (May): 120–32. https://doi.org/10.1016/j.neuroimage.2013.01.031.
- Molinaro, Nicola, and Mikel Lizarazu. 2018. "Delta(but Not Theta)-Band Cortical Entrainment Involves Speech-Specific Processing." *European Journal of Neuroscience* 48 (7): 2642–50. https://doi.org/10.1111/ejn.13811.
- Molinaro, Nicola, Irene F. Monsalve, and Mikel Lizarazu. (2016). "Is There a Common Oscillatory Brain Mechanism for Producing and Predicting Language?" *Language, Cognition*

and Neuroscience 31 (1): 145–58. https://doi.org/10.1080/23273798.2015.1077978.

- Monsalve, Irene F., Alejandro Pérez, and Nico- la Molinaro. (2014). "Item Parameters Dissoci- ate between Expectation Formats: A Regres- sion Analysis of Time-Frequency Decomposed EEG Data." *Frontiers in Psychology* 5 (August). https://doi.org/10.3389/fpsyg.2014.00847.
- Muller, Lyle, Frédéric Chavane, John Reynolds, and Terrence J. Sejnowski. (2018). "Cortical Travelling Waves: Mechanisms and Computational Principles." *Nature Reviews Neuroscience* 19 (5): 255–68. https://doi.org/10.1038/nrn.2018.20.
- Murphy, Elliot. (2015). "The Brain Dynamics of Linguistic Computation." *Frontiers in Psychol- ogy* 6 (October). https://doi.org/10.3389/fpsyg.2015.01515.
- ———. 2019. "Interfaces (Traveling Oscillations) + Recursion (Delta-Theta Code) = Language." In , 251–69.
- Myers, Brett, Miriam Lense, and Reyna Gordon. (2019). "Pushing the Envelope: Developments in Neural Entrainment to Speech and the Biological Underpinnings of Prosody Perception." *Brain Sciences* 9 (3): 70. https://doi.org/10.3390/brainsci9030070.
- Nelson, Matthew J., Imen El Karoui, Kristof Giber, Xiaofang Yang, Laurent Cohen, Hilda Koopman, Sydney S. Cash, et al. (2017). "Neurophysiological Dynamics of Phrase-Structure Building during Sentence Processing." *Proceed- ings of the National Academy of Sciences* 114 (18): E3669–78. https://doi.org/10.1073/pnas.1701590114.
- Nicolo, Pierre, Sviatlana Rizk, Cécile Magnin, Marie Di Pietro, Armin Schnider, and Adrian G. Guggisberg. (2015). "Coherent Neural Oscillations Predict Future Motor and Language Improvement after Stroke." *Brain* 138 (10): 3048–60. https://doi.org/10.1093/brain/awv200.
- Obleser, Jonas, and Christoph Kayser. (2019). "Neural Entrainment and Attentional Selection in the Listening Brain." *Trends in Cognitive Scienc- es* 23 (11): 913–26. https://doi.org/10.1016/j.tics.2019.08.004.
- Peelle, J. E., J. Gross, and M. H. Davis. (2013). "Phase-Locked Responses to Speech in Human Auditory Cortex Are Enhanced During Comprehension." *Cerebral Cortex* 23 (6): 1378–87. https://doi.org/10.1093/cercor/bhs118.
- Penolazzi, Barbara, Alessandro Angrilli, and Remo Job. (2009). "Gamma EEG Activity Induced by Semantic Violation during Sentence Reading." *Neuroscience Letters* 465 (1): 74–78. https://doi.org/10.1016/j.neulet.2009.08.065.
- Prystauka, Yanina, and Ashley Glen Lewis. (2019). "The Power of Neural Oscillations to Inform Sentence Comprehension: A Linguistic Perspective." *Language and Linguistics Compass* 13 (9). https://doi.org/10.1111/lnc3.12347.
- Rommers, Joost, Ton Dijkstra, and Marcel Bastiaansen. (2012). "Context-Dependent Semantic Processing in the Human Brain: Evidence from Idiom Comprehension." *Journal of Cognitive Neuroscience* 25 (December). https://doi.org/10.1162/jocn_a_00337.
- Sauseng, Paul, and Wolfgang Klimesch. (2008). "What Does Phase Information of Oscillatory Brain Activity Tell Us about Cognitive Processes?" *Neuroscience & Biobehavioral Reviews* 32 (5): 1001–13. https://doi.org/10.1016/j.neubiorev.2008.03.014.
- Schneider, Julie M., Alyson D. Abel, Diane A. Ogiela, Anna E. Middleton, and Mandy J. Maguire. (2016). "Developmental Differences in Beta and Theta Power during Sentence Processing." *Developmental Cognitive Neuroscience* 19 (June): 19–30. https://doi.org/10.1016/j.dcn.2016.01.001.
- Spironelli, Chiara, and Alessandro Angrilli. (2009). "EEG Delta Band as a Marker of Brain Damage in Aphasic Patients after Recovery of Language." *Neuropsychologia* 47 (4): 988–94. https://doi.org/10.1016/j.neuropsychologia.2008.10.019.
- Spironelli, Chiara, Mirella Manfredi, and Alessandro Angrilli. (2013). "Beta EEG Band: A Measure of Functional Brain Damage and Language Reorganization in Aphasic Patients after Recovery." *Cortex* 49 (10): 2650–60. https://doi.org/10.1016/j.cortex.2013.05.003.
- Steinhauer, Karsten, and John E. Drury. (2012). "On the Early Left-Anterior Negativity (ELAN) in Syntax Studies." *Brain and Language* 120 (2): 135–62. https://doi.org/10.1016/j.bandl.2011.07.001.
- Swaab, Tamara Y., Kerry Ledoux, C.C. Camblin, and Megan Boudewyn. (2012). "Language-Related ERP Components." *Oxford Handbook of Event-Related Potential Components*, January, 397–440. https://doi.org/10.1093/oxfordhb/9780195374148.013.0197.
- Tzur, Gabriel, and Andrea Berger. (2007). "When Things Look Wrong: Theta Activity in Rule Violation." *Neuropsychologia* 45 (13): 3122–

26. https://doi.org/10.1016/j.neuropsychologia.2007.05.004.

- Vander Ghinst, Marc, Mathieu Bourguignon, Marc Op de Beeck, Vincent Wens, Brice Marty, Sergio Hassid, Georges Choufani, et al. (2016). "Left Superior Temporal Gyrus Is Coupled to Attended Speech in a Cocktail- Party Auditory Scene." *The Journal of Neurosci- ence* 36 (5): 1596–1606. https://doi.org/10.1523/JNEUROSCI.1730-15.2016.
- Wang, Lin, Ole Jensen, Danielle van den Brink, Nienke Weder, Jan-Mathijs Schoffelen, Lilla Magyari, Peter Hagoort, and Marcel Bastiaansen. (2012). "Beta Oscillations Relate to the N400m during Language Comprehension." *Human Brain Mapping* 33 (12): 2898–2912. https://doi.org/10.1002/hbm.21410.
- Wang, Lin, Zude Zhu, and Marcel Bastiaansen. (2012). "Integration or Predictability? A Further Specification of the Functional Role of Gamma Oscillations in Language Comprehension." *Frontiers in Psychology* 3. https://doi.org/10.3389/fpsyg.2012.00187.
- Weiss, S, H Mueller, B Schack, J King, M Kutas, and P Rappelsberger. (2005). "Increased Neuronal Communication Accompanying Sentence Comprehension." *International Journal of Psychophysiology* 57 (2): 129–41. https://doi.org/10.1016/j.ijpsycho.2005.03.013.
- Weiss, Sabine, and Horst M. Mueller. (2012). "'Too Many Betas Do Not Spoil the Broth': The Role of Beta Brain Oscillations in Language Processing." *Frontiers in Psychology* 3. https://doi.org/10.3389/fpsyg.2012.00201.
- Wernicke, Carl. (1974). "Der Aphasische Symptomenkomplex." In *Der Aphasische Symptomencomplex*, 1–70. Springer.
- Westlake, Kelly P., Leighton B. Hinkley, Mon- ica Bucci, Adrian G. Guggisberg, Anne M. Findlay, Roland G. Henry, Srikantan S. Naga- rajan, and Nancy Byl. (2012). "Resting State Alpha-Band Functional Connectivity and Re- covery after Stroke." *Experimental Neurology* 237 (1): 160–69. https://doi.org/10.1016/j.expneurol.2012.06.020.
- Willems, Roel M., Robert Oostenveld, and Peter Hagoort. (2008). "Early Decreases in Alpha and Gamma Band Power Distinguish Linguistic from Visual Information during Spoken Sentence Comprehension." *Brain Research* 1219 (July): 78–90. https://doi.org/10.1016/j.brainres.2008.04.065.