Speaking waves: neuronal oscillations in language production

Vitória Piai[1,2], Xiaochen Zheng[1]

1. Radboud University, Donders Centre for Cognition, Nijmegen, the Netherlands

2. Radboudumc, Donders Centre for Medical Neuroscience, Department of Medical Psychology, Nijmegen, the Netherlands

Corresponding author:

Vitória Piai, PhD

Email: v.piai@donders.ru.nl

To Ardi Roelofs, who planted the seed for our fascination with language production.

Abstract

Language production involves the retrieval of information from memory, the planning of an articulatory programme, and executive control and self-monitoring. These processes can be related to the domains of long-term memory, motor control, and executive control. Here, we argue that studying neuronal oscillations provides an important opportunity to understand how general neuronal computational principles support language production, also helping elucidate relationships between language and other domains of cognition. For each relevant domain, we provide a brief review of the findings in the literature with respect to neuronal oscillations. Then, we show how similar patterns are found in the domain of language production, both through review of previous literature and novel findings. We conclude that neurophysiological mechanisms, as reflected in modulations of neuronal oscillations, may act as a fundamental basis for bringing together and enriching the fields of language and cognition.

1. Introduction

Psycholinguistic models of language production, despite differing from one another in many ways, generally agree that producing words involves the retrieval and selection of a concept to be expressed, retrieval and selection of syntactic and morphophonological properties of an associated word, and post-lexical articulatory planning and self-monitoring processes (Bock, 1982; Dell, 1986; Hickok, 2012; Levelt, Roelofs, & Meyer, 1999; Rapp & Goldrick, 2000). Roughly speaking, these processes can be related to three other (cognitive) domains, namely long-term memory (i.e., access of conceptual, lexical, and phonological information in long-term memory), motor control (i.e., motor preparation and execution of an articulatory programme), and executive control (i.e., regulatory processes involved in selection and monitoring).

Understanding language production in relation to these other domains is important for various reasons. Firstly, partly thanks to studies in animals, much is known about memory functioning (Buzsáki, 2005; Düzel, Penny, & Burgess, 2010; Hasselmo & Stern, 2013; Jacobs, 2014), executive control (Knight, Staines, Swick, & Chao, 1999; Lundqvist et al., 2016; E. K. Miller & Cohen, 2001), and motor control (Cheyne, 2013; K. J. Miller et al., 2012; Murthy & Fetz, 1996; van Wijk, Beek, & Daffertshofer, 2012). If the neurophysiological underpinnings of these processes are shared with language, the existing knowledge can help us achieve a better understanding of language functioning. Conversely, language research can have an impact on knowledge in other cognitive domains, not least thanks to providing more naturalistic means of probing the underlying physiological mechanisms. For example, long-term memory is often studied with episodic memory paradigms that create artificial pairings between stimuli. By contrast, language provides the means for assessing the binding between concepts and words, acquired in a naturalistic manner, and carried in our memories for much longer periods than the short setting of an experiment. Finally, the ultimate aim of the cognitive (neuro)sciences is integrating knowledge to arrive at a unified theory of brain and cognition, and the type of cross-domain fertilisation we just described helps move us in the right direction.

1.1. Electrophysiology and neuronal oscillations

Language production relies on dynamic and rapid cognitive processes, best demonstrated by the fact that an average speaker produces 2 to 5 words every second. Investigating such processes requires techniques that can track brain activity at a high temporal resolution. This is what makes the brain's electrophysiological signal instrumental in our undertaking (see for similar arguments e.g., Cohen, 2011b; Hauk, 2016; Lopes da Silva, 2013).

Most electrophysiological studies done in the language domain have measured the electroencephalogram (EEG) or magnetoencephalogram (MEG) over the scalp. The post-synaptic activity of a large group of synchronised neurones generates an electric field, often called the local field potential. This electric field also generates a magnetic field around it. Both electric and magnetic fields can be measured over a distance from their sources, for example, over the scalp. When recorded over the scalp, an attenuated and distorted version of these fields is measured with the EEG or MEG.

As already mentioned, neurones work in a synchronised fashion. Individual neurones have intrinsic oscillatory properties and, under many circumstances, they will oscillate collectively in different frequencies. These collective oscillations are the most efficient way for a population to achieve synchrony. At the level of neuronal populations, oscillations enable controlling the timing of neuronal firing. They also allow neuronal assemblies (even in more distant regions) to become temporally linked (Buzsáki, 2002; Buzsáki & Draguhn, 2004). Morevoer, oscillations are preserved across species, suggesting that they are relevant for brain function (Buzsáki, Logothetis, & Singer, 2013). Large-scale oscillations manifest in the brain's electrophysiological signal, measured over the scalp with EEG or MEG, or intracranially with depth electrodes or electrocorticography (Buzsáki, Anastassiou, & Koch, 2012; Lopes da Silva, 2013).

In sum, oscillations are thought to enable the dynamic coordination of neuronal networks and we can measure this activity in humans at the scalp level with EEG or MEG, or with intracranial EEG.

1.2. Neuronal oscillations and language production: A thesis

Neuronal oscillations have been argued to provide the link between cognitive and neurophysiological computations (e.g., Friederici & Singer, 2015; Siegel, Donner, & Engel, 2012). Here, we argue that neuronal oscillations provide an important and exciting avenue to understand how general neuronal computational principles support language functioning, enabling us to link language to other domains of cognition. In order to connect the domains, we will draw parallels in the multidimensional space afforded by oscillations, i.e., whether a presupposed process (shared across domains) is reflected in oscillatory activity modulated in the same direction, in the same frequency band, with the same time course, in respectively analogous brain areas.

In humans, neuronal oscillations are typically studied with MEG, and scalp or intracranial EEG. Therefore, most work on oscillations in humans is not at the level of individual neurones, but rather at the scale of large neuronal populations. Thus, neuronal synchronisation and desynchronisation cannot be directly observed and must be inferred from increases and decreases, respectively, in power in a particular frequency band (e.g., Cohen & Gulbinaite, 2014). In keeping with suggestions in the literature, we will use the terms *changes in power*, or *increases/decreases in power* to indicate modulations of neuronal oscillations in the context of cognitive tasks. Moreover, following the literature, we will discuss the classic frequency-bands of theta (typically 4-8 Hz), alpha (typically 8-12 or 8-15 Hz), and beta (typically 15-30 Hz), which are more relevant for language production. Most of the figures in this chapter show time-resolved power spectra (see e.g., Figure 1), which provide a visualisation of how power (the colour scale) changes over time (represented in the x axis) and frequency (represented in the y axis).

For each relevant domain mentioned above (i.e., motor, memory, and executive control), we provide a brief review of the findings in the literature with respect to neuronal oscillations. Then, we show how similar patterns are found in the domain of language production, both through review of previous literature and novel findings. Although writing (and typing) are also forms of language production, in this chapter, we will focus on speaking. When reviewing the literature in relation to the motor domain, we include studies employing a range of production or articulation tasks, ranging from picture naming to the articulation of simple syllables and execution of mouth movements. By contrast, for the memory and executive domains, we focus on so-called conceptually driven production tasks, e.g., picture naming and verb or noun generation, that is, tasks that require the initial access to concepts, followed by subsequent stages of production (Indefrey & Levelt, 2004). Repeating words or reading aloud does not require access to lexical concepts and lemmas, as evidenced by the fact that healthy speakers can repeat or read aloud words that they have never encountered before.

2. Motor domain

The motor domain perhaps forms the most straightforward case for our comparison for two reasons. Firstly, the articulation of speech is a motor activity. Secondly, movement is associated with a well-characterised oscillatory signaure in associated motor regions, namely power decreases (also termed desynchronisation) in the beta band, typically defined as 15-30 Hz (see for reviews Cheyne, 2013; Pfurtscheller & Lopes da Silva, 1999). Beta-power decreases over sensorimotor areas start prior to movement onset and continue throughout execution, increasing again after movement execution, often termed “beta rebound”. Put together, one would expect to find beta-band power decreases in motor regions associated with speaking. For language production, cortical areas associated with motor-related processes are the ventral precentral gyrus (Penfield & Roberts, 1959), and inferior frontal cortex and insula of the language-dominant hemisphere (e.g., Baldo, Wilkins, Ogar, Willock, & Dronkers, 2011; Flinker et al., 2015; Henseler, Regenbrecht, & Obrig, 2014; Indefrey & Levelt, 2004; Krieg et al., 2016).

One of the earliest investigations of brain rhythms related to movements executed with speech organs has been performed by participants being monitored for epilepsy with intracranial EEG before undergoing surgery to remove the epileptic focus (Crone et al., 1998; see for an overview of the procedure and review of early language studies, Flinker, Piai, & Knight, 2018; Llorens, Trébuchon, Liégeois-Chauvel, & Alario, 2011). In the study of Crone et al., participants were asked to execute tongue protrusion. Tongue movements, just like fist-clenching, elicited beta-power decreases and subsequent beta rebound in premotor cortical regions.

Evidence of power decreases in lower frequencies over motor-related areas was also found in other intracranial EEG studies (e.g., Conner, Chen, Pieters, & Tandon, 2014; Flinker et al., 2015; Grappe et al., 2019; Kojima et al., 2013). However, these studies focused on gamma and broadband high gamma signals above 50 Hz, hence the exact frequency range of these power decreases cannot be determined. One study that used the repetition of monosyllabic words found low-frequency power decreases over left ventral premotor cortex and inferior frontal gyrus roughly prior to speech onset and during articulation (Flinker et al., 2015). Two other studies examining picture naming also reported alpha and beta power decreases over the left inferior frontal gyrus starting after picture presentation relative to a prestimulus baseline (Conner et al., 2014; Grappe et al., 2019). Another study employed picture naming and auditory naming tasks, where participants are asked to provide an answer to questions such as "What do you hear with?" (Kojima et al., 2013). This study reported time-resolved spectra time locked to response onset (i.e., time aligned to when people start speaking), enabling a more precise inspection of the time course of power decreases over the ventral precentral gyrus. These results are showin in Figure 1, where the timepoint of 0 ms indicates response onset. Despite the lack of precise information regarding the lower frequency range, power decreases are observed already prior to response onset and during articulation, especially in electrode 6 over ventral precentral/postcentral gyrus.

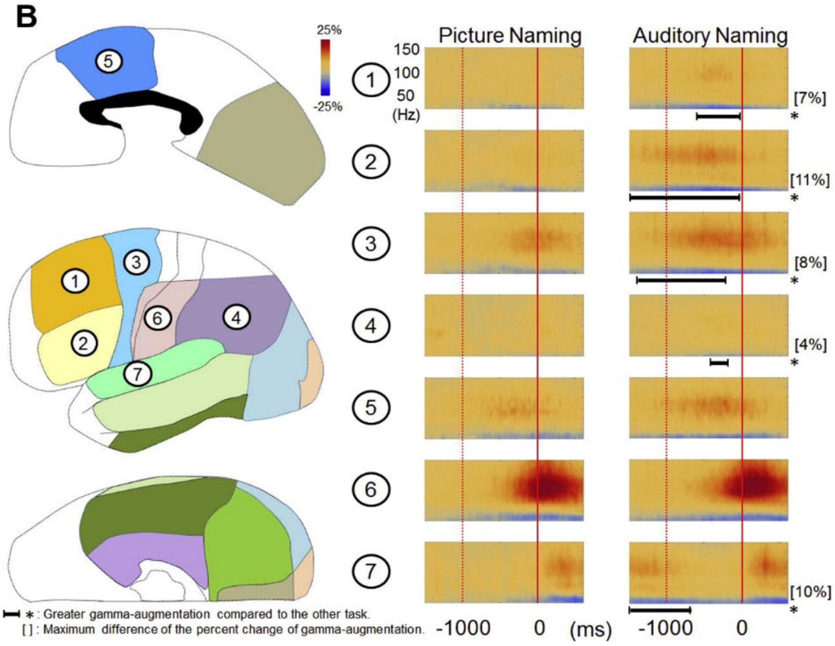

Figure 1. Time-resolved spectra of power changes relative to a rest baseline period for picture naming (left) and auditory naming (right) time locked to response onset (0 ms). The spectra are shown for each of the contacts in the brain model to the left. Reprinted from Clinical Neurophysiology, 124/9, Kojima, K., Brown, E. C., Matsuzaki, N., Rothermel, R., Fuerst, D., Shah, A., Mittal, S., Sood, S., and Asano, E. "Gamma activity modulated by picture and auditory naming tasks: intracranial recording in patients with focal epilepsy", 1737–1744, Copyright (2013), with permission from Elsevier. This figure has been modified relative to its original in that only panel B is presented here.

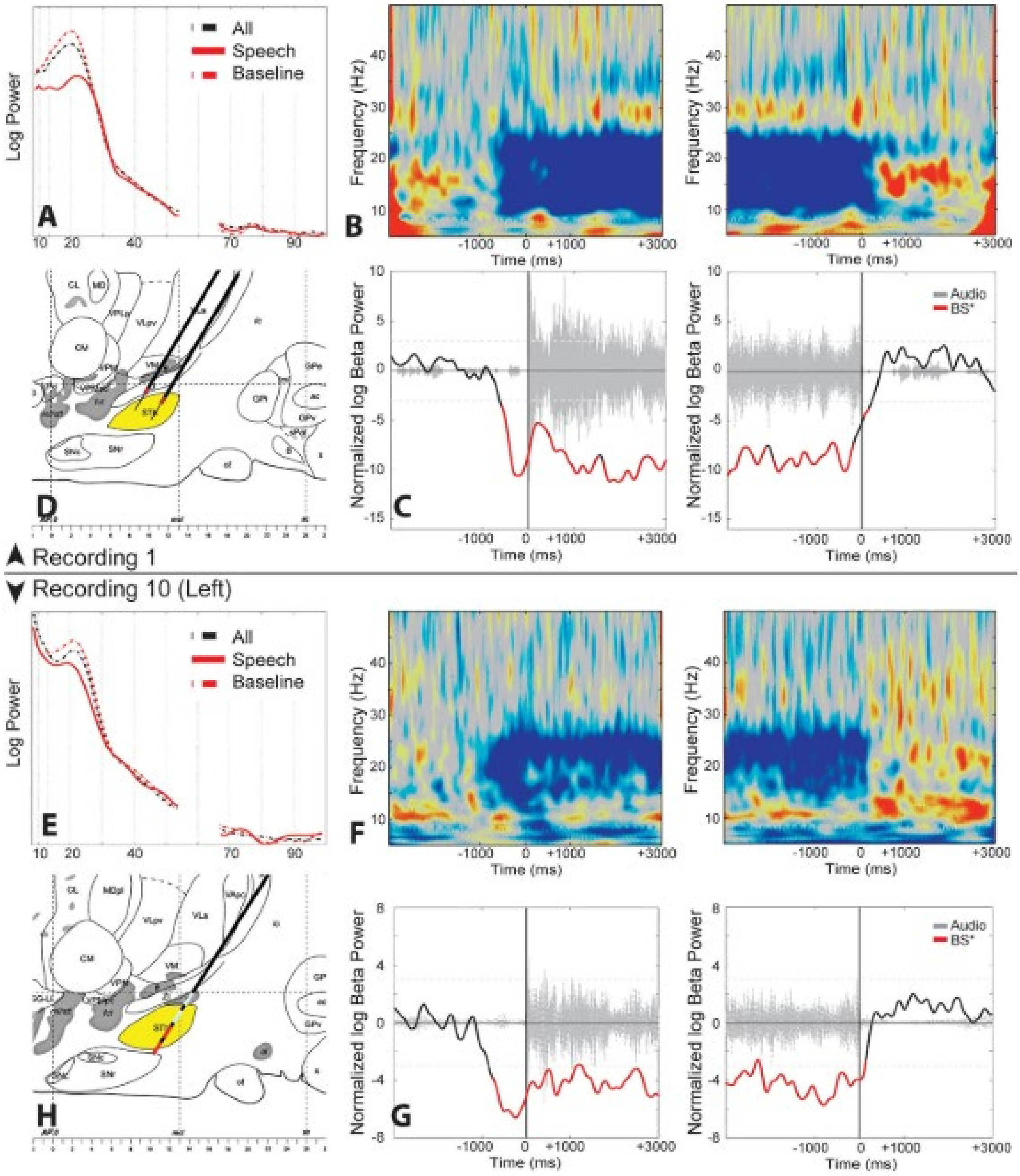

Figure 2. Spectral power changes for naming the months of the year and counting in subthalamic nucleus contacts. **(A, E)** Power spectral density over the entire recording (“All”), over speech production intervals (“Speech”), and over a pre-speech baseline (“Baseline”). **(B, F)** Time-resolved spectra locked to speech onset (left panel, 0-ms time point) and speech offset (right panel, 0-ms time point). **(C, G)** Averaged power in the 13-30 Hz range over speech production intervals (black and red lines), locked to speech onset (left panel, 0-ms time point) and speech offset (right panel, 0-ms time point). Red lines indicate time points differing significantly from baseline. The averaged audio track is shown in grey. **(D, H)** Atlas illustration and electrode placement. Reprinted from Neuroscience, 202, Hebb, A. O., Darvas, F., and Miller, K. J., “Transient and state modulation of beta power in human subthalamic nucleus during speech production and finger movement”, 218-233, Copyright (2012), with permission from Elsevier.

Another study employing intracranial EEG provided further evidence of the similarity in terms of neuronal oscillations between motor aspects of speaking and finger movement (Hebb, Darvas, & Miller, 2012). Participants undergoing surgery for implantation of a deep-brain stimulator in the subthalamic nucleus (STN) named the months of the year and counted from one up. Given that both types of utterances are fairly stereotypical, these tasks are more likely to probe the motor aspects of speaking, rather than the access to conceptual and lexical information. Motor-related beta-power modulations had previously been found in the STN, for example for hand movements (Cassidy et al., 2002). Hebb et al. (2012) showed that beta-power decreased in the STN just before speech onset and remained decreased during speech production, as shown in Figure 2.

MEG recordings in healthy adults have provided further evidence for beta-power decreases, localised to the mouth area along the central sulcus, during speech-related movements and during speech (Salmelin, Hámáaláinen, Kajola, & Hari, 1995; Salmelin, Schnitzler, Schmitz, & Freund, 2000; Salmelin & Sams, 2002). For example, in one study participants performed tongue movements, lip protrusion, articulation of one vowel, utterance of the same word repeatedly, and free generation of words (Salmelin & Sams, 2002). For all tasks, beta-power decreases were observed bilaterally over the face motor area, whereas beta rebound was stronger over the left face area.

It is important to point out that the alpha band has also been implicated in movement, in which case it is also commonly termed the *mu rhythm* in the literature. Studies have identified differences (but also commonalities) between the beta power decreases and mu power decreases (Cheyne, 2013; Crone et al., 1998; Salmelin et al., 1995), but this distinction falls outside the scope of our review.

2.1. Interim summary

To summarise, beta-band power decreases are found prior to movement onset and during movement execution over the cortical and subcortical motor areas responsible for that movement. This pattern holds true for speaking: Beta-band power decreases are observed prior to and during speech and speech-related mouth movements. These power decreases are localised to motor-related areas not only over the cortex (along the central sulcus), but also in subcortical motor-related areas such as the subthalamic nucleus.

3. Memory domain

Episodic memory is perhaps the most relevant subfield of memory to discuss in relation to language production. Language is tightly related to semantic memory and both episodic and semantic memory form the declarative memory system (Squire, 1992). Episodic memory is mainly subserved by medial temporal lobe structures, including the hippocampus (Squire & Wixted, 2011). With respect to language, however, it is debated to what extent these medial structures are critical for producing words and sentences (Hamamé, Alario, Llorens, Liégeois-Chauvel, & Trébuchon-Da Fonseca, 2014; Kurczek & Duff, 2011; MacKay, Burke, & Stewart, 1998; Skotko, Andrews, & Einstein, 2005). The evidence for the involvement of lateral, as opposed to medial, cortical regions in the memory aspects of production (i.e., retrieval of conceptual, lexical, and phonological information), is clearer. These processes have been mainly associated with the temporal and inferior parietal lobes of the language-dominant hemisphere (e.g., Baldo, Arévalo, Patterson, & Dronkers, 2013; Henseler et al., 2014; Indefrey & Levelt, 2004; Krieg et al., 2016; Roelofs, 2008; Schwartz, Faseyitan, Kim, & Coslett, 2012; Walker et al., 2011).

Episodic memory processes are often studied with tasks that require participants to encode information (e.g., pictures, words, or pairs of stimuli) and later retrieve the encoded information via recall or recognition tasks. A well-studied effect in the field of episodic memory is the *subsequent memory effect*: Trials are categorised depending on whether the respective items were successfully recalled or recognised during the retrieval phase. Then a comparison is made for the brain activity originating *from the encoding phase* between the later forgotten versus later remembered trials (Sanquist, Rohrbaugh, Syndulko, & Lindsley, 1980). Thus, the subsequent memory effect has been used to examine what makes the encoding of information successful so that it can later be retrieved.

The subsequent memory effect has been extensively characterised in terms of neuronal oscillations and two patterns of oscillatory activity have clearly emerged: successful encoding is associated with *increases* in theta power and *decreases* in alpha and beta power (see for reviews Hanslmayr, Staudigl, & Fellner, 2012; Nyhus & Curran, 2010).

3.1. Memory-related theta oscillations

Theta oscillations are prominent in the mammalian hippocampus and have been well studied in relation to memory processes (Buzsáki & Moser, 2013; Jacobs, 2014; Kahana, Seelig, & Madsen, 2001). Current views largely converge on theta oscillations functioning as a mechanism enabling binding in memory via the coordination of spike timing of groups of neurones (Buzsáki, 2002; Hasselmo, Bodelón, & Wyble, 2002; Jacobs, Kahana, Ekstrom, & Fried, 2007; Rutishauser, Ross, Mamelak, & Schuman, 2010). Intracranial recordings from electrodes placed in the hippocampus, as well as scalp recordings, have shown assocations between increased theta power and successfull memory encoding (e.g., Klimesch, Doppelmayr, Russegger, & Pachinger, 1996; Lega, Jacobs, & Kahana, 2012; Osipova et al., 2006).

3.1.2. Memory-related theta oscillations in language

To the best of our knowledge, the only evidence for the role of hippocampal theta oscillations in language use comes from a recent study that used depth recordings from medial temporal lobe structures of patients with intractable epilepsy (Piai et al., 2016). Even though in this study the hippocampal theta oscillations were not associated with language *production*, the results are worth discussing as an illustration of how hippocampal theta oscillations are also found in the language domain (for a review of scalp theta oscillations and language comprehension, we refer the reader to Meyer, 2018). To examine binding in memory during sentence comprehension, the authors utilised a context-driven word production paradigm. In this task, participants complete a sentence by naming a picture that appears at the end of the sentence, as shown in Figure 3. The sentences are either semantically constrained (e.g., "She locked the door with the") or neutral (e.g., "She walked in here with the") towards one final ending (e.g., "key"). Theta power increased for contextually constraining sentences relative to neutral sentences in medial temporal lobe structures during sentence comprehension, preceding picture presentation, as shown in Figure 4. These results demonstrated how hippocampal theta oscillations also play a role in language processing. Importantly, the semantic associations given by the sentence are naturalistic, as they also occur in everyday life. Moreover, the theta oscillatory effect was observed without the requirement that the associations be encoded *first* for retrieval at a later time point. The authors interpreted these findings as suggesting that the neuronal computations used by the hippocampus to support memory functioning are also utilised by language processes.

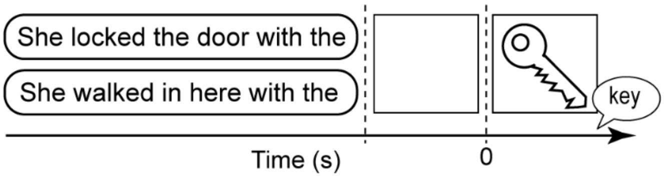

Figure 3. An example of the context-driven picture naming task for a constraining trial (upper) and a neutral trial (lower). Particiapnts name the picture after hearing or reading the incomplete sentence.

3.2. Memory-related alpha-beta oscillations

In episodic memory tasks, it has been noted that memory effects are not only reflected in theta power increases, but also in alpha and beta power *decreases* (e.g., Hanslmayr, Spitzer, & Bäuml, 2009; Khader & Rösler, 2011; Klimesch, Doppelmayr, Schimke, & Ripper, 1997; Lega et al., 2012; see for reviews Fellner & Hanslmayr, 2017; Hanslmayr et al., 2012; Klimesch, 1997). The exact sources of the alpha-beta power decreases are still unclear, however. Whereas some studies suggest cortical sources, especially the left inferior frontal gyrus (Hanslmayr et al., 2011; Hanslmayr, Matuschek, & Fellner, 2014), power decreases in this range have also been found in the hippocampus (e.g., Lega et al., 2012).

A theoretical view has been advanced on the functional meaning of the alpha-beta power decreases in episodic memory and their relation to the hippocampal theta power increases (Hanslmayr, Staresina, & Bowman, 2016; Hanslmayr et al., 2012). According to this view, information is represented by neuronal *desynchronisation*. To demonstrate this, Hanslmayr and collagues (2012) simulated neuronal populations that varied in their degree of synchrony, while keeping the sum of neuronal spikes constant. These simulations are shown in Figure 5A, with the no synchrony condition shown in green, the low synchrony condition in blue, and the high synchrony condition in red. The resulting local field potentials are shown under each panel. Figure 5B shows how power in the local field potential increases with increasing synchrony. Information was then operationalised with Shannon's Entropy over the firing rates of the three synchronisation conditions. The resulting entropy values are shown in Figure 5C.

A state of high neuronal synchrony (in red) is associated with less (specific) information being encoded in the pattern of neuronal spiking. By contrast, a state of low synchrony (in blue) is associated with more (specific) information being encoded. In Figure 5D, results of more simulations with varying degrees of synchrony, reflected in the power of the local field potential, are shown in relation to entropy values. Synchrony of the firing patterns is inversely related to the richness of information encoded in the firing rate (Figure 5D).

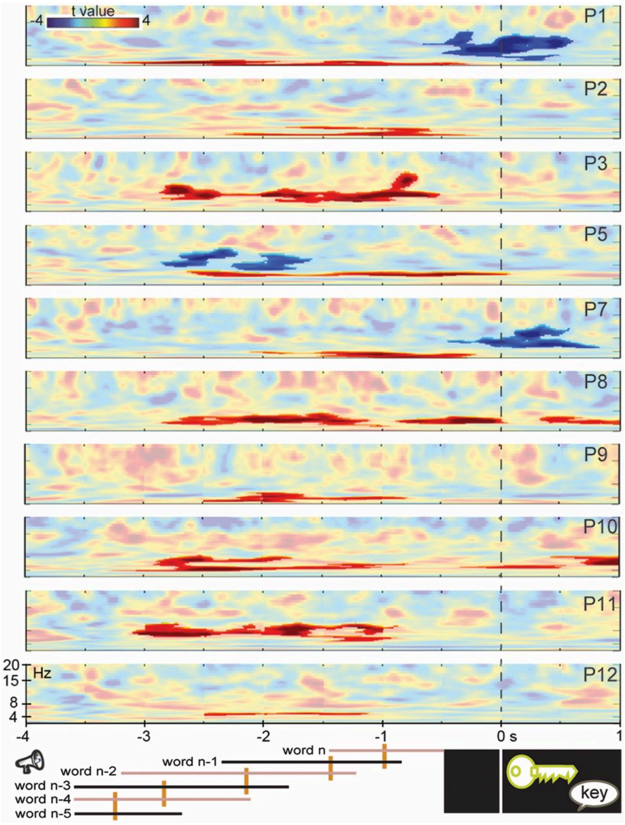

Figure 4. Time-resolved power spectra of the context effect (constrained vs. neutral) time locked to picture presentation for ten individuals with electrode contacts in medial temporal lobe. Significant effects are shown in stronger colors (multiple comparisons corrected). Trial events are shown at the bottom. The timing of each word position is indicated by the continuous lines. The left end of each line indicates the earliest possible word onset. The right end indicates the latest possible word offset (and next word onset). Median word onset (and previous word offset) is indicated by the orange vertical bars. Adapted from Vitória Piai, Kristopher L. Anderson, Jack J. Lin, Callum Dewar, Josef Parvizi, Nina F. Dronkers, and Robert T. Knight, Direct brain recordings reveal hippocampal rhythm underpinnings of language processing, Proceedings of the National Academy of Sciences of the United States of America, 113 (40), pp. 11366–71, Figure 3, doi: 10.1073/ pnas.1603312113 ©2016 Vitória Piai, Kristopher L. Anderson, Jack J. Lin, Callum Dewar, Josef Parvizi, Nina F. Dronkers, and Robert T. Knight. This work is licensed under the Creative Commons.

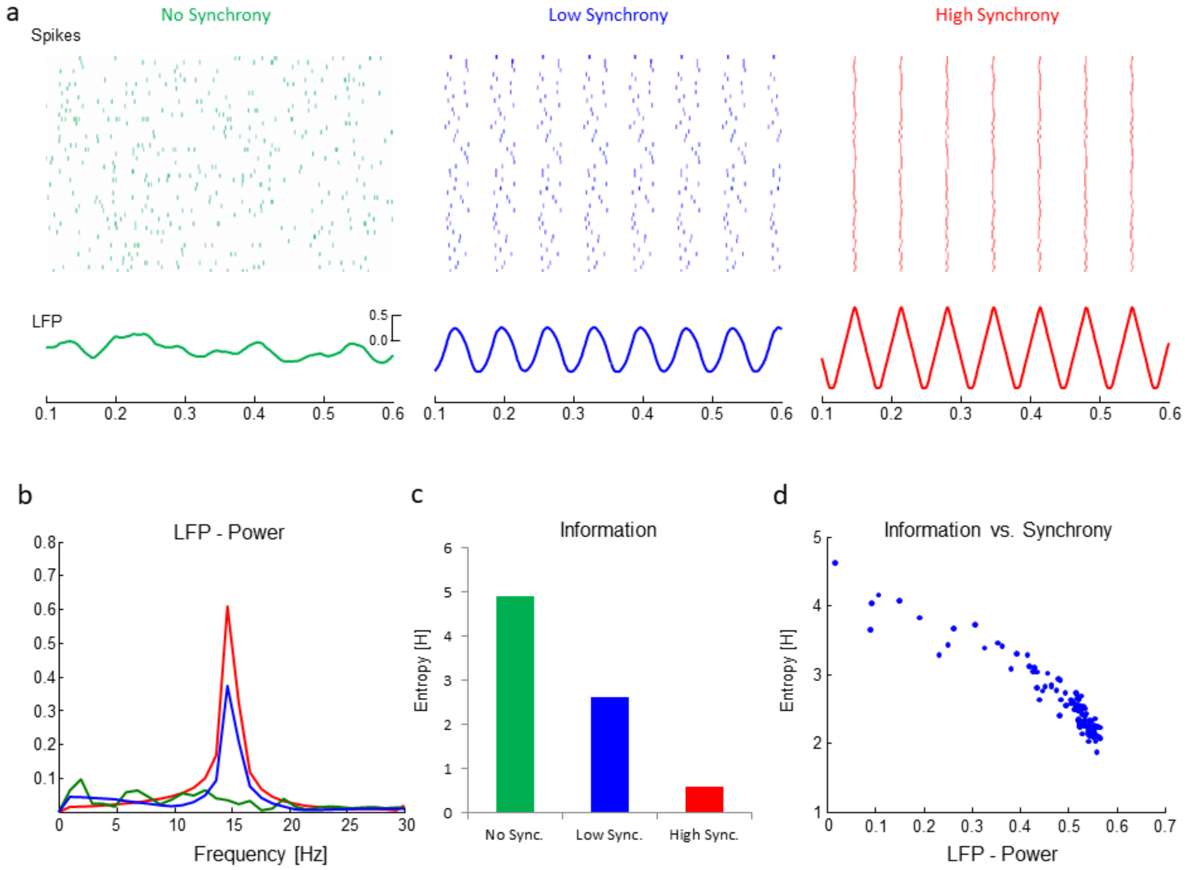

Figure 5. A. Simulated firing rates of neuronal populations vayring in degree of synchrony with a constant number of spikes. A state of no synchrony is shown in green, a state of low synchrony is shown in blue, and a high synchrony state is shown in red. The corresponding local field potentials are shown under each panel. **B**. Power spectra of each state of synchrony shown in panel A. **C.** Information, measured with Shannon's Entropy over the firing rates shown in A for each state of synchrony. **D.** Association between power of the local field potentials for various simulations with varying degrees of synchrony and Shannon's Entropy values. Reprinted with permission from Hanslmayr, S., Staudigl, T., & Fellner, M.-C. (2012). Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. Frontiers in Human Neuroscience, 6, 74.

3.2.2. Memory-related alpha-beta oscillations in language production

Although the hypothesis that information is represented by patterns of alpha-beta desynchronisation was proposed for the domain of episodic memory, it is possible that these same principles apply to the domains of semantic memory and language (e.g., Jafarpour, Piai, Lin, & Knight, 2017; Piai et al., 2016). In the current memory and language literatures, a distinction between alpha and beta frequency bands is not always drawn nor are there clear bases for how and why that distinction should be drawn. Therefore, for the remainder of this section, we will refer to alpha-beta oscillations without drawing a clear distinction between them, except for the cases where the reviewed articles do make a distinction. See also section 6, "Concluding remarks and open questions" for further comments on this issue.

Early evidence for the involvement of alpha-beta power decreases in the memory aspects of language production comes from picture naming studies using electrode grids placed on the cortical surface. For example, in a single-case study (Hart et al., 1998), direct cortical stimulation was used to identify critical sites for language. One site was identified in the left lateral occipitotemporal gyrus that, when stimulated, affected naming, spontaneous speech, and comprehension, while leaving repetition and object recognition intact. Therefore, this site can be considered critical for lexical-level processes. The alpha and beta bands in this site were examined in an overt picture naming task. Power in the alpha-beta band decreased relative to a pre-stimulus baseline starting around 250 ms. Meta-analysis estimations indicate that the reported time window is roughly aligned with the timing when lexical-level processes start (Indefrey & Levelt, 2004). In another study including seven patients with intractable epilepsy, a silent picture naming task was administered (Ojemann, Fried, & Lettich, 1989). Critical sites for language in temporoparietal areas, that is, middle and superior temporal gyri and inferior parietal lobe, in the language-dominant hemisphere were identified by means of direct cortical stimulation. These sites showed power decreases in the alpha range between 200-700 ms and 700-1200 ms after stimulus onset. Moreover, the power decreases were always greater in the critical language sites than in surrounding sites. Power decreases were also greater for naming than for visuo-spatial processes, with the latter measured with a matching task in which participants indicated whether two lines presented in succession on the screen had the same angle. A more recent study using depth electrodes also reported beta power decreases in the fusiform gyrus during picture naming, but before speech onset. This pattern was consistently found across individuals (Grappe et al., 2019).

The context-driven word production paradigm described above (see Figure 3) has been used in various EEG and MEG studies to study conceptual and lexical retrieval in a manner that is not triggered by a picture, but rather more naturalistically (Piai et al., 2016; Piai, Meyer, Dronkers, & Knight, 2017; Piai, Roelofs, Rommers, & Maris, 2015; Piai, Rommers, & Knight, 2018; Piai, Roelofs, & Maris, 2014). In a real conversation, words are typically produced embedded in the context of a speaker's own sentence or that of the interlocutor. Although the context-driven word production paradigm is not perfect in simulating such a naturalistic situation, it is a fair yet controlled approximation thereof (Griffin & Bock, 1998). Attesting to the contextual influence on the ease of word production processes, picture naming times are about 200-300 ms faster following constraining relative to neutral sentences. This strongly suggests that certain, presumably early, processes necessary for picture naming are already initiated prior to picture onset, enabled by the semantic information in the sentence. Besides faster word production latencies, studies have also shown that power in the alpha-beta band decreases consistently for constraining relative to neutral sentences, an effect particularly prominent prior to picture presentation (Piai, Meyer, Dronkers, & Knight, 2017; Piai, Roelofs, & Maris, 2014; Piai, Roelofs, Rommers, & Maris, 2015; Piai, Rommers, & Knight, 2018, see also Piai et al., 2016 and Figure 4 above). An example is given in Figure 6, which shows the relative power differences for constrained relative to neutral sentences, with significant patterns shown in stronger colour (family-wise error corrected for multiple comparisons).

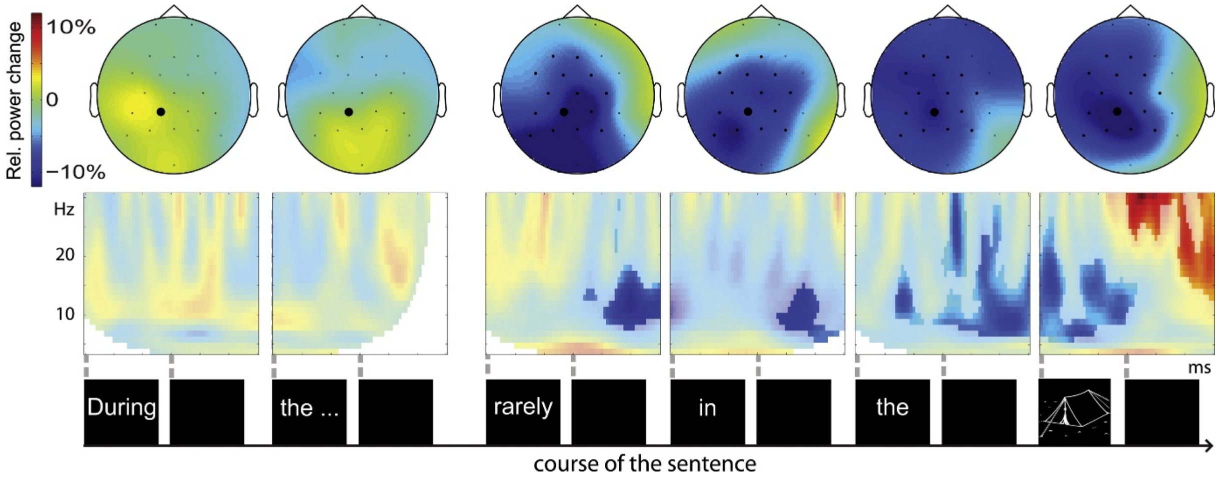

Figure 6. Time-resolved spectra showing the time course of the context effect. The trial events are shown at the bottom. The spectra are shown for the channel marked in black (big dot) in the topographical maps. Rel.=Relative. Reprinted from Neuropsychologia, 53, Piai, V., Roelofs, A., and Maris, E., "Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint", 146-156, Copyright (2014), with permission from Elsevier.

The results shown in Figure 6 were the first to demonstrate the alpha-beta power decreases in a context-driven word production task (Piai, Roelofs, & Maris, 2014). As such, it was somewhat difficult to interpret this effect. Attention is known to modulate power in a similar frequency range (e.g., van Ede, de Lange, Jensen, & Maris, 2011). Moreover, as mentioned in Section 2 above, motor preparation also modulates power in a comparable frequency range. Thus, instead of reflecting conceptual and lexical retrieval, the alpha-beta power decreases prior to picture onset could be the index of attentional effects or motor preparation. To elucidate this issue, a follow-up MEG study examined context-driven picture naming, requiring conceptual and lexical retrieval, versus picture judgement via a button press (with the left hand) and localised the sources of the power decreases during the interval prior to picture presentation (Piai et al., 2015). The neuronal sources where pre-picture beta power decreases are observed for constraining relative to neutral sentences are shown in Figure 7 for picture naming (upper) and picture judgement (lower). For picture judgement, the power decreases were localised to the left inferior parietal lobe and posterior temporal cortex, in addition to right motor cortex, in agreement with the left hand button-press responses. By contrast, for picture naming, the power decreases were localised to the left inferior parietal lobe, the entire temporal lobe, and left inferior frontal gyrus, all areas associated with conceptual processing (Binder, Desai, Graves, & Conant, 2009) and word production processes (Indefrey & Levelt, 2004). An additional study examined the across-session consistency of the alpha-beta power decreases in healthy young adults (Roos & Piai, *in preparation*). Participants were tested twice in the context-driven word production task, with an interval of 2-4 weeks in between. The alpha-beta power decreases for constraining relative to neutral sentences were replicated and showed consistency across the two sessions in the left temporal and inferior parietal lobes. By contrast, the alpha-beta power decreases in the left frontal lobe was more variable across the two sessions, with no consistent across-session patterns being observed anywhere in the frontal cortex.

To further clarify the role of the previously identified brain areas in generating the power decreases, on the one hand, and the link between the power decreases and the behavioural context-facilitation effect, on the other hand, a follow-up EEG study examined individuals with stroke-induced lesions to the areas previously identified (Piai et al., 2018). A group of individuals had lesions overlapping in left frontal areas and another group had lesions in the left temporal lobe, also involving the inferior parietal lobe in some cases. These areas were previously identified in an MEG study, as shown in Figure 7 (Piai et al., 2015). The facilitation effect in picture naming times was absent for individuals with lesions involving the left temporal and inferior parietal cortex. These were also the areas found to show consistent alpha-beta power decreases over the course of weeks (Roos & Piai, *in preparation*). Importantly, for these same individuals, the context alpha-beta power decreases were also absent. These findings demonstrated a causal link between the alpha-beta power decreases and the left temporoparietal cortex, on the one hand, and also between the alpha-beta power decreases in the left posterior cortex and the context facilitation in word production, on the other hand.

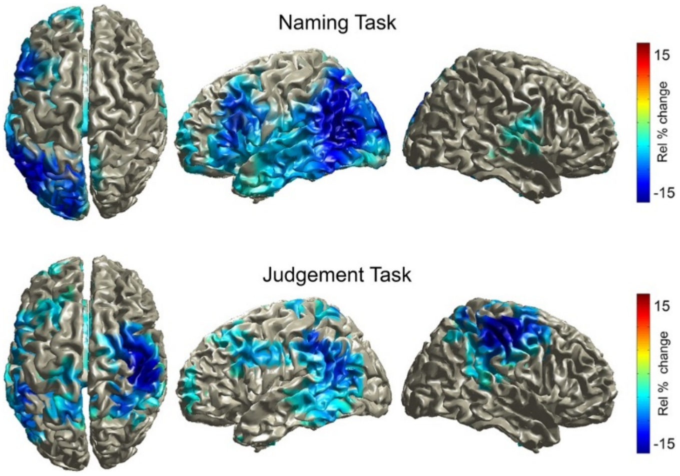

Figure 7. Source localisation of the beta power differences (15-25 Hz) for constraining relative to neutral contexts during the blank pre-picture interval for picture naming (upper) and picture judgement (lower). The color bars show relative power changes, masked by the statistically significant effect corrected for multiple comparisons. Rel = relative.

Another way to study conceptually driven production is through verb generation, which has been extensively used to study brain organisation for language functioning, both in healthy and neurological populations (e.g., Edwards et al., 2010; Pang, Wang, Malone, Kadis, & Donner, 2011; Petersen, Fox, Posner, Mintun, & Raichle, 1988; Thompson-Schill et al., 1998). In a verb generation task, participants are given a noun (e.g., “apple”) and are asked to generate a verb associated with it (e.g., “eat”). Haemodynamic measures, acquired with functional magnetic resonance imaging or positron emission tomography, have shown a relatively good consistency in picking up signal changes in the left prefrontal cortex associated with verb generation (Fiez, Raichle, Balota, Tallal, & Petersen, 2007; McCarthy, Blamire, Rothman, Gruetter, & Shulman, 1993; Petersen et al., 1988; Rutten, Ramsey, Van Rijen, Alpherts, & Van Veelen, 2002).

For MEG in particular, the verb generation task elicits power decreases in the beta band (Findlay et al., 2012; Fisher et al., 2008; Pang et al., 2011; Pavlova et al., 2019; Traut et al., 2019). The hemisphere in which these beta power decreases are found largely agrees with the hemispheric dominance for langauge as determined by the Wada test (Findlay et al., 2012; Pang et al., 2011). The Wada test (Wada, 1949) is (or was) the gold-standard procedure for determining language lateralisation: It consists of injecting sodium amobarbital into the vasculature nourishing one cerebral hemisphere, shutting it down. If language functioning is disrupted – e.g., the patient can no longer name pictures – one can conclude that that particular hemisphere is critical for language. However, this procedure has the disadvantage of being highly invasive, potentially risky in terms of complications, and also unsuitable for certain populations (Meador & Loring, 1999), motivating the use of neuroimaging alternatives (e.g., Benke et al., 2006; Fisher et al., 2008; Watanabe et al., 1998).

The beta power decreases found during verb generation are typically localised to the inferior and middle frontal gyri and regions in the temporal and inferior parietal lobes of the language dominant hemisphere (Findlay et al., 2012; Fisher et al., 2008; Pang et al., 2011; Pavlova et al., 2019; Traut et al., 2019). An example is shown in Figure 8, for verb generation following a picture cue (upper) and a word cue (lower). Additionally, it has recently been found that differences between strongly associated noun-verb pairs (e.g., noun: nightingale, response: "sing") and weakly associated pairs (e.g., noun: paper, responses differ widely across participants) are also reflected in beta-power decreases (Pavlova et al., 2019). These differences were localised to areas in the frontal lobe bilaterally, i.e., anterior and middle portions of the cingulate cortex and superior frontal gyrus, comprising the supplementary and pre-supplementary motor areas, and to the left lateral precentral gyrus and sulcus.

The findings of beta-power decreases during verb generation in temporal and inferior parietal areas agree with the presupposed role of beta oscillations in retrieval from memory for word production. Although in the sections above, we considered the inferior frontal gyrus to be mainly implicated in the motor aspects of speaking, this same region is also involved in top-down control aspects of retrieval in word production (Badre & Wagner, 2002; Riès, Greenhouse, Dronkers, Haaland, & Knight, 2014; Schnur et al., 2009; Thompson-Schill et al., 1998). The beta-power decreases found in the inferior frontal cortex of the language-dominant hemisphere, even when particiapnts generate verbs covertly, without articulation, are presumably more related to the controlled aspects of retrieval, rather than to the motor aspects of speaking.

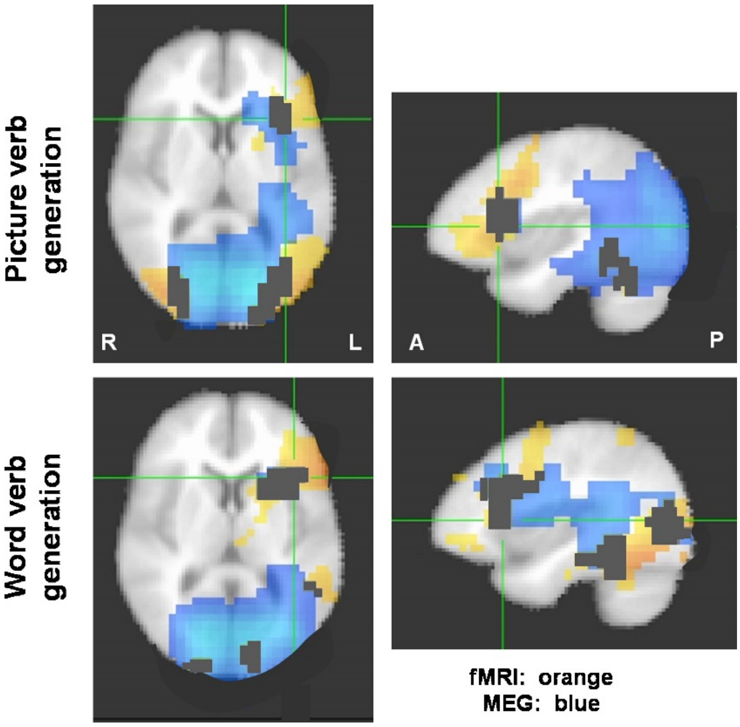

Figure 8. Source localisation of the beta power decreases (in blue) between 600-800 ms post-picture onset for picture-induced verb generation (upper) and between 400-600 ms post-word onset for word-induced verb generation (lower). The areas in dark grey indicate where the beta power decreases from MEG overlap with clusters from the fMRI counterpart (orange) of the experiment. Reprinted from Neuroscience Letters, 490, Pang, E. W., Wang, F., Malone, M., Kadis, D. S., and Donner, E. J., "Localization of Broca's area using verb generation tasks in the MEG: Validation against fMRI", 215-219, Copyright (2011), with permission from Elsevier.

Interim summary

In sum, alpha-beta power decreases are found in temporal and inferior parietal brain areas, and under certain circumstances also in frontal areas, in tasks that require conceptually driven word production, such as context-driven word production, picture naming, and verb generation. Importantly, these brain areas are not implicated in the motor aspects of speaking, but rather in the memory aspects of language production -- in particular, the retrieval of conceptual and lexical information from memory. Despite the lack of abudant evidence, the results in the current literature indicate that, similarly to the episodic-memory domain, retrieving conceptual and lexical information from memory is associated with power decreases in the alpha-beta band.

4. Language production and executive control

Broadly speaking, executive control is an umbrella term to refer to regulatory and monitoring processes that ensure that our actions are in accordance with our goals. Several components are implicated in executive control, including monitoring and updating of working memory representations (e.g., Diamond, 2013; Miyake et al., 2000).

When planning a word or a multi-word utterance, speakers need to engage executive control processes. At a more general level, speakers need to maintain the conversation goals and update the contents of working memory during the planning process, especially in the case of multi-word utterances and sentences (e.g., Levelt et al., 1999; Martin & Slevc, 2014; Piai & Roelofs, 2013; Roelofs, 2003). They also need to prevent interference from semantically related words that get co-activated in their lexicon, or they need to choose between alternative words that refer to a concept they want to express (e.g., Piai et al., 2013; Shao, Roelofs, Martin, & Meyer, 2015). As part of the control process, speakers also constantly monitor what they have just said and what they are about to say, inspecting (potential) speech errors and further recruiting top-down control when necessary (Hartsuiker, 2014). In the case of individuals who speak more than one language, executive control is also engaged to inhibit the nontarget language, and to overcome previous inhibition when switching from one language to another (Green, 1998).

Executive control in language production is commonly investigated using the picture-word interference task (Hermans, Bongaerts, De Bot, & Schreuder, 1998; Lupker, 1979; Piai et al., 2013; Shitova, Roelofs, Schriefers, Bastiaansen, & Schoffelen, 2017) or the switching task (Meuter & Allport, 1999; Sikora, Roelofs, & Hermans, 2016; Zheng, Roelofs, Farquhar, & Lemhöfer, 2018). In a picture-word interference task, participants name pictures while trying to ignore distractor words presented either visually superimposed on the word or auditorily. The distractor words can be, for example, semantically related (e.g., pictured dog, distractor *cat*) or unrelated (e.g., pictured dog, distractor *pin*) to the target picture name, or congruent with the target picture name (e.g., pictured dog, distractor *dog*). In a switching task, speakers are instructed to switch, according to a given cue, between different types of phrases, for example a bare noun (e.g., "dog") versus a complex noun phrase (e.g., "the small dog"), or between languages. In repeat trials, the response type is the same as in the previous trial, whereas in switch trials, the type of response changes. Compared to repeat trials, switching to the alternative language or to the alternative type of noun phrase requires more executive control.

With respect to the anatomy, previous research on control processes in language production has shown the engagement of brain regions involved in (domain-general) executive control, including the anterior cingulate cortex, lateral prefrontal cortex, and (pre-)supplementary motor area (e.g., Alario, Chainay, Lehericy, & Cohen, 2006; de Bruin, Roelofs, Dijkstra, & Fitzpatrick, 2014; Gauvin, De Baene, Brass, & Hartsuiker, 2016; Klaus & Schutter, 2018; Piai et al., 2013; Piai, Roelofs, Jensen, Schoffelen, & Bonnefond, 2014), suggesting a domain-general control mechanism underlying speech production (Nozari & Novick, 2017; Ye & Zhou, 2009).

4.1. Theta-band oscillations and executive control

A hallmark EEG signature of executive control and working-memory manipulation is midline frontal theta oscillations (e.g., Cavanagh, Zambrano-Vazquez, & Allen, 2012; Cohen, 2014; Cohen & Donner, 2013; Cooper et al., 2019; Itthipuripat, Wessel, & Aron, 2013; Sauseng, Griesmayr, Freunberger, & Klimesch, 2010; Sauseng, Hoppe, Klimesch, Gerloff, & Hummel, 2007). Increases in theta-band power have been found for tasks manipulating working-memory load (e.g., Jensen & Tesche, 2002), when items in working memory are successfully manipulated (Itthipuripat et al., 2013), during the monitoring of errors (Cavanagh et al., 2012; Cohen, 2011a; Luu, Tucker, & Makeig, 2004), and when the amount of top-down control is increased due to interfering information. In this latter case, tasks have been used with a conflicting stimulus dimension. For example, in the Stroop task (Stroop, 1935), an ink colour has to be named that is either congruent (*red* written in red) or incongruent (*red* written in blue) with the written word. Theta-band power increases were observed for the incongruent relative to the congruent condition (Hanslmayr et al., 2008). In the Simon task, stimuli are presented in relative locations that are congruent or incongruent to the response, despite stimulus location being irrelevant to the task (Simon, 1969). Again, theta-band power increases were observed for the incongruent relative to the congruent condition (Cohen & Donner, 2013; Nigbur, Ivanova, & Stürmer, 2011). Other tasks manipulating various aspects of congruency, such as a flanker task (Eriksen & Eriksen, 1974) or a go/no-go task, also elicit the same pattern (Cohen, Ridderinkhof, Haupt, Elger, & Fell, 2008; Nigbur et al., 2011). Based on intracranial recordings and source localisation of scalp effects, it is known that midline frontal theta effects reflecting executive control are generated by the anterior cingulate cortex and superior frontal gyrus (Asada, Fukuda, Tsunoda, Yamaguchi, & Tonoike, 1999; Cohen et al., 2008; Hanslmayr et al., 2008; Sauseng et al., 2007).

In conclusion, increases in midline frontal theta power, generated by the anterior cingulate cortex and superior frontal gyrus, provide a neuronal signature of executive-control mechanisms (Cavanagh & Frank, 2014; Cohen, 2014).

4.2. Theta-band oscillations and control in language production

In the language domain, a few electrophysiological studies have utilised interference paradigms to investigate control demands during language production. Piai and colleagues (Piai, Roelofs, Jensen, et al., 2014) employed the picture-word interference task in an MEG study with congruent picture-distractor pairs and two types of incongruent picture-distractor pairs: semantically related and unrelated pairs. Semantically related pairs were constrasted to congruent pairs (i.e., an interference effect due to congruency) and, in addition, to semantically unrelated pairs, a contrast well-known as “semantic interference” in the language production literature (Glaser & Düngelhoff, 1984; Lupker, 1979). Theta-power increases were observed for both types of interference roughly around 350-650 ms post-stimulus onset, as showin in Figure 9 for the congruency interference (upper panel) and semantic interference (lower panel). In line with the literature outside of the language domain, the theta-power increases were localised to the superior frontal gyrus, possibly also including the anterior cingular cortex, as shown in Figure 9. A more recent EEG study has replicated the theta-power increases for semantically related relative to unrelated picture-word pairs in a roughly similar time window (Krott, Medaglia, & Porcaro, 2019).

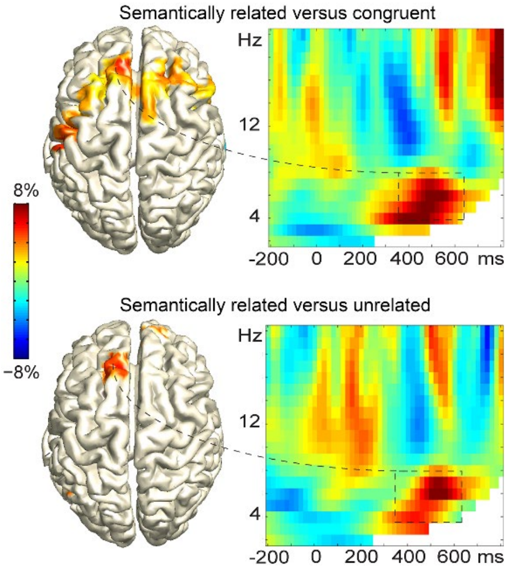

Figure 9. Time-resolved spectra of the contrast semantically related versus congruent (upper) and semantically related versus unrelated (lower) for the source in the superior frontal gyrus. Colour scale indicates the amount of relative power differences between the conditions. Modified from Piai, V., Roelofs, A., Jensen, O., Schoffelen, J.-M., & Bonnefond, M. (2014). Distinct patterns of brain activity characterise lexical activation and competition in spoken word production. PloS One, 9(2), e88674.

In another EEG study, semantically related pairs were also constrasted to congruent pairs (Shitova et al., 2017). Theta-power increases were again observed for the semantically-related pairs relative to congruent pairs. Moreover, in this same study, trial-by-trial adaptations in top-down control given the interference from a previous trial, known as the *Gratton effect* (Gratton, Coles, & Donchin, 1992) also modulated theta power.

4.3. Theta-band oscillations and control: New evidence from bilingual word production

Here we report new evidence on the similarity in terms of neurophysiological signatures between general executive control and language control from a bilingual word production study. To properly speak one language rather than another, bilingual speakers need to constantly control their language in use and monitor for errors, such as selecting the nontarget language for use, generating so-called language selection errors. Previous research in the domain of action monitoring has consistently shown theta power increases in the anterior cingulate cortex and superior frontal gyrus immediately following an error commission, such as pressing the wrong button in a flanker or a Simon task (Cavanagh, Cohen, & Allen, 2009; Cohen, 2011a; Trujillo & Allen, 2007). The theta power increases have been interpreted as reflecting the signal that increased executive control is needed.

To test whether speech monitoring shares the same neural mechanism with other domains of action monitoring, we reanalysed the EEG data from a recent bilingual picture naming study (Zheng et al., 2018). In that study, 24 unbalanced Dutch-English bilinguals were asked to name pictures in either English or Dutch and switch languages according to a color cue.

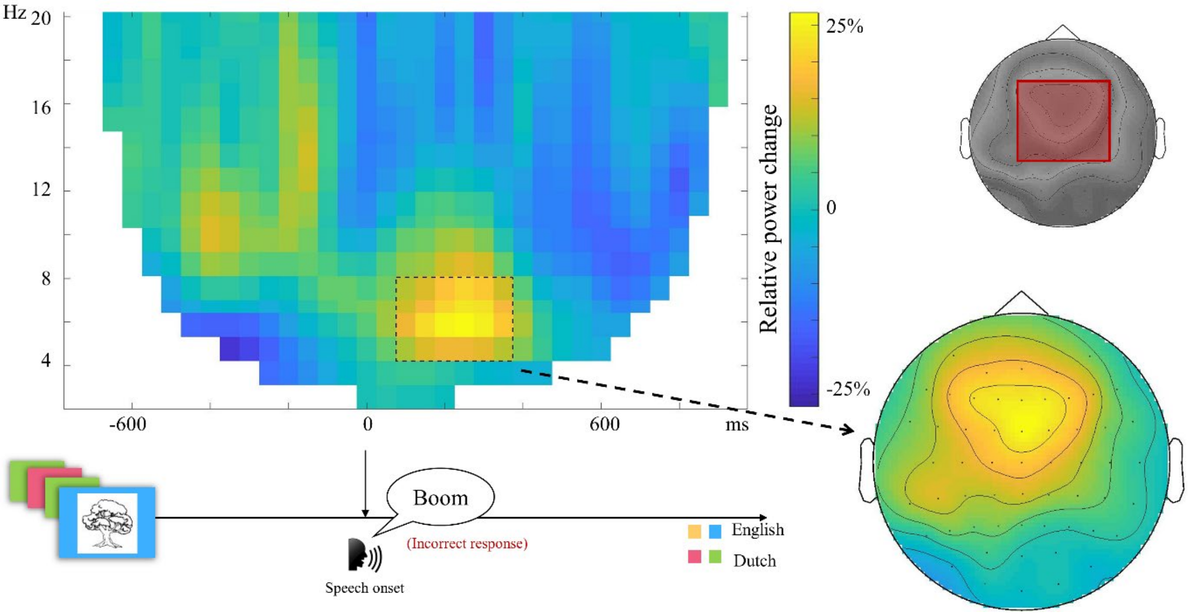

Figure 10. Response-locked time-resolved spectrum of the contrast between language selection errors versus correct responses on switch trials, averaged over a cluster of frontocentral channels highlighted in red on the right upper corner. Dashed lines indicate the cluster for plotting the topographical map shown in the right bottom corner. The target pictures were presented in a coloured frame, indicating the response language (i.e., yellow or blue for English and red or green for Dutch, or vice versa). The bottom left scheme depicts a trial where participants had to switch to English. Language selection errors are defined as the use of the translation equivalent of the target word (e.g., saying the Dutch translation word “boom” instead of the target English word “tree”). Response-locked time-resolved spectra were computed between 750 ms pre-response to 1 s post-response, at frequencies between 2 and 20 Hz. A variable length Hanning-tapered window was applied to estimate the power at each frequency using three oscillation cycles (e.g., the window was 300 ms long at 10 Hz), advanced in steps of 50 ms and of 1 Hz.

Under severe time pressure, the speakers made languge selection errors (e.g., saying the Dutch translation equivalent “boom” instead of the target English word “tree”) on 37.3% of the trials where they were supposed to switch languages. For more details on the methods of that study, we refer the reader to the original article. Here, we contrasted the time-resolved spectra of the trials with language selection errors versus those with correct responses. Time-resolved power was estimated with the same method described previously in other studies (Piai, Roelofs, Jensen, et al., 2014; Shitova et al., 2017) and a cluster-based permutation test (Maris & Oostenveld, 2007) was applied to the spectrotemporal data points of interest (i.e., 4-8Hz, 0-400 ms relative to response onset). A cluster of power increases for trials with language selection errors relative to trials with correct responses was identified by the statistical testing (Monte-Carlo p = .002, family-wise error corrected for multiple comparisons). As can be seen in Figure 10, power increases were prominent in the theta band (4-8 Hz) following language selection errors compared to correct responses, starting after (incorrect) speech onset (the 0-ms time point) and sustained until around 400 ms after response onset. The theta power increases had a frontocentral distribution. Thus, language selection errors in bilingual word production show a neurophysiological response that resembles the one reported in action monitoring in all its respects, i.e., in the temporal, spatial, and spectral dimensions, and in the same direction of relative power increases. We interpret the observed midline frontal theta power increases to reflect domain-general monitoring of speech errors, supporting an account of (partially) shared neural mechanisms between speech monitoring and action monitoring.

4.4. Interim summary

Midline frontal theta oscillations, originating from the anterior cingulate cortex and superior frontal gyrus, are a hallmark electrophysiololgical signature of executive control processes. We reviewed three recent language production studies that reported midline frontal theta power increases for the condition requiring more control due to stimuli interfering with production processes. We also reported novel evidence from bilingual word production showing that, similarly to the domain of action monitoring, midline frontal theta power increases when participants select the wrong language for speaking relative to when the correct language is selected. Thus, the same hallmark signature of executive control is found in language production tasks once the need for control is increased due to task circumstances.

5. Beyond speaking

Humans spend a substantial part of their days speaking, which implies that they also spend a substantial amount of time listening to another speaker. It is widely accepted that conceptual reprensetations are shared between comprehenion and production (Levelt et al., 1999). However, the extent to which other levels of representation are also shared is not fully established.

The electrophysiological signal, and in particular neuronal oscillations, could potentially provide clues for answering this latter question. For the relationship between language comprehension and production, memory-related processes are relevant, so below we focus on a few, relevant studies examining lexical selection for single words. An excellent review of other processes involved in comprehension and their oscillatory underpinnings is provided by Meyer (2018).

Previous word comprehension studies have observed alpha and beta power decreases as a function of manipulations affecting lexical-semantic processes. Bastiaansen and colleagues (Bastiaansen, van der Linden, Ter Keurs, Dijkstra, & Hagoort, 2005; Mellem, Bastiaansen, Pilgrim, Medvedev, & Friedman, 2012) compared the oscillatory signal time locked to open class words (i.e., nouns, verbs, and adjectives) versus closed class words (i.e., determiners, prepositions, and conjunctions). Open class words contain more semantic information than closed class words. Stronger power decreases were observed for open relative to closed class words between 8-12 Hz (Mellem et al., 2012) and 8-21 Hz (Bastiaansen et al., 2005) roughly between 200-600 ms after word presentation. In a different study, participants were asked to perform a semantic identification or a voice identification task on spoken words (Shahin, Picton, & Miller, 2009). Alpha-beta power decreases were found for the semantic identification task relative to the voice identification task for which no access to lexical concepts is needed. Another study manipulated the intelligibility of spoken words parametrically and participants had to indicate how comprehensible the words were (Obleser & Weisz, 2012). Alpha power decreases were correlated with comprehension ratings as well as with speech degradation such that stronger alpha-power decreases were associated with better comprehension on the one hand, and with less degraded speech on the other hand. In a lexical decision study, "lexicality" was manipulated such that not only real words and pseudowords were presented to participants, but also ambiguous words, for which only one vowel of an existing word was changed, forming a lexicality continuum (Strauß et al., 2014). Alpha power decreases were strongest for real words, for which lexical-semantic representations exist, followed by ambiguous words.

The earlier studies followed the state of the field at that point and interpreted the alpha power decreases as reflecting sensory processes or selective attention and inhibition (e.g., Jensen & Mazaheri, 2010; Klimesch, Doppelmayr, Russegger, Pachinger, & Schwaiger, 1998). However, some authors also conjectured the possibility that the alpha-power decreases reflected retrieval of lexical-semantic representations (e.g., Mellem et al., 2012; Strauß et al., 2014). The latter interpretation is in line with the hypothesis (and evidence) reviewed above that alpha-beta power decreases are related to the richness of the information being retrieved.

It is important to note that the hypothesis that information is represented in alpha-beta power decreases was formulated for episodic memory. As such, most of the evidence in its support comes from studies investigating the encoding stage in episodic-memory tasks (see for discussion Hanslmayr et al., 2012). However, for the language domain, *retrieval* from memory is more relevant: It underlies both word production and comprehension. The brief review above illustrates how alpha-beta power decreases are also found in comprehension tasks tapping lexical-level processes (e.g., Bastiaansen et al., 2005; Brennan, Lignos, Embick, & Roberts, 2014; Mellem et al., 2012; Rommers, Dickson, Norton, Wlotko, & Federmeier, 2017; Strauß et al., 2014). It is conceivable that alpha-beta power decreases support the more fundamental computation of retrieving information from memory, regardless of whether that is episodic information, or lexical-semantic information necessary for word production or comprehension. Notably, retrieval, on the one hand, and sensory processes or selective attention, on the other, are not necessarily mutually exclusive. In many cases, retrieval is associated with attentional demands (e.g., Craik, Naveh-Benjamin, Govoni, & Anderson, 1996). Moreover, conceptual (and lexical) retrieval are argued to also include retrieving sensorimotor information stored in sensorimotor areas (e.g., Fernandino, Humphries, Conant, Seidenberg, & Binder, 2016). In future research, it could be fruitful to consider retrieval processes as the explanation of alpha-power effects observed in language tasks, which (due to historical reasons) have been explained in terms of sensory or attentional processes[1] (see also the "Concluding remarks and open questions" section 6 below for further discussion on this issue).

---

[1] We are grateful to Kara Federmeier for this suggestion.

6. Concluding remarks and open questions

In this article, we have argued that studying neuronal oscillations provides an important opportunity to understand how general neuronal computational principles support language functioning, also helping elucidate relationships between language and other domains of cognition. We have reviewed the literature on beta oscillations in relation to the motor aspects of speaking and how it resembles the neurophysiological signature in motor tasks not involving speech or mouth movements. We have also reviewed the literature on the memory aspects of speaking and described the parallels with the domain of episodic memory, both for the theta and alpha-beta bands. Finally, we discussed the literature on executive control and midline frontal theta, and how it parallels the findings on executive aspects of speaking.

Note that we have argued for shared neuronal computations across cognitive domains on the basis of similarity in terms of oscillatory patterns across domains. However, it is known that the "same macroscopic extracellular signal can be generated by diverse cellular events. Thus, a seemingly similar theta oscillation in the hippocampus and neocortex may be brought about by different elementary mechanisms" (Buzsáki et al., 2012, p. 414). The parallels we have drawn between language production and other cognitive domains, however, were between oscillations generated within the same area across two different domains of cognition. Therefore, we believe that the approach we suggest here is less problematic than comparing, for example, theta oscillations between two different areas. It is worth noting that the argumentation we have presented focuses on language production rather than on comprehension. Therefore, our argument may not be directly extendable to comprehension processes.

If the approach we adopted is valid, it opens many exciting avenues for future research. For example, with respect to the memory domain, we have refered to alpha-beta oscillations throughout, without drawing a clear distinction between alpha and beta oscillations. This choice is driven by the fact that currently, evidence is lacking on what basis that distinction should be drawn. It may turn out that memory-related processes in language production (and possibly comprehension) are reflected in a frequency band that is neither the classic alpha (8-12 Hz) or beta (15-30 Hz) bands, as these are more often conceived of as sensorimotor rhythms. Using the labels alpha and beta has been important for advancing our understanding of oscillations, but it does not necessarily mean that neuronal operations always respect the alpha versus beta boundaries researchers have created. We may find that memory-related processes operate in a frequency band that is intermediate to the classic alpha and beta bands[2], explaining why the language and memory literatures often have difficulty in making findings fit in either one or the other, therefore adopting the term alpha-beta band. We hope that future studies will elucidate these questions. Moreover, oscillations aside, it is easier to draw a parallel between motor and executive processes necessary for language production and the motor and executive-control domains as such. For memory-related mechanisms, however, the fields being compared (i.e, episodic memory versus language) are more distinct and have less often been discussed in relation to each other. As such, strong evidence is still lacking in favour of the hypothesis that alpha-beta power decreases represent conceptual and lexical

---

[2] We would like to thank Marina Laganaro for discussing this idea with us.

information that is retrieved by speakers. We hope that future studies will expand this evidence.

In conclusion, neurophysiological mechanisms, as reflected in modulations of neuronal oscillations, may act as a fundamental basis for bringing together and enriching the fields of language and cognition.

References

Alario, F.-X., Chainay, H., Lehericy, S., & Cohen, L. (2006). The role of the supplementary motor area (SMA) in word production. *Brain Research*, *1076*(1), 129–143. https://doi.org/10.1016/j.brainres.2005.11.104

Asada, H., Fukuda, Y., Tsunoda, S., Yamaguchi, M., & Tonoike, M. (1999). Frontal midline theta rhythms reflect alternative activation of prefrontal cortex and anterior cingulate cortex in humans. *Neuroscience Letters*, *274*(1), 29–32. https://doi.org/10.1016/S0304-3940(99)00679-5

Badre, D., & Wagner, A. D. (2002). Semantic retrieval, mnemonic control, and prefrontal cortex. *Behavioral and Cognitive Neuroscience Reviews*, *1*(3), 206–218. Retrieved from http://bcn.sagepub.com/content/1/3/206.short

Baldo, J. V., Arévalo, A., Patterson, J. P., & Dronkers, N. F. (2013). Grey and white matter correlates of picture naming: evidence from a voxel-based lesion analysis of the Boston Naming Test. *Cortex*, *49*(3), 658–667. https://doi.org/10.1016/j.cortex.2012.03.001

Baldo, J. V., Wilkins, D. P., Ogar, J., Willock, S., & Dronkers, N. F. (2011). Role of the precentral gyrus of the insula in complex articulation. *Cortex*, *47*(7), 800–807. https://doi.org/10.1016/j.cortex.2010.07.001

Bastiaansen, M. C. M., van der Linden, M., Ter Keurs, M., Dijkstra, T., & Hagoort, P. (2005). Theta responses are involved in lexical-semantic retrieval during language processing. *Journal of Cognitive Neuroscience*, *17*(3), 530–541. https://doi.org/10.1162/0898929053279469

Benke, T., Köylü, B., Visani, P., Karner, E., Brenneis, C., Bartha, L., … Willmes, K. (2006). Language lateralization in temporal lobe epilepsy: a comparison between fMRI and the Wada Test. *Epilepsia*, *47*(8), 1308–1319. https://doi.org/10.1111/j.1528-1167.2006.00549.x

Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*(12), 2767–2796. https://doi.org/10.1093/cercor/bhp055

Bock, K. J. (1982). Toward a cognitive psychology of syntax: Information processing contributions to sentence formulation. *Psychological Review*, *89*, 1–47. Retrieved from http://psycnet.apa.org/journals/rev/89/1/1/

Brennan, J., Lignos, C., Embick, D., & Roberts, T. P. L. (2014). Spectro-temporal correlates of lexical access during auditory lexical decision. *Brain and Language*, *133*, 39–46. https://doi.org/10.1016/j.bandl.2014.03.006

Buzsáki, G. (2002). Theta oscillations in the hippocampus. *Neuron*, *33*(3), 325–340. https://doi.org/10.1016/S0896-6273(02)00586-X

Buzsáki, G. (2005). Theta rhythm of navigation: Link between path integration and landmark navigation, episodic and semantic memory. *Hippocampus*, *15*(7), 827–840. https://doi.org/10.1002/hipo.20113

Buzsáki, G., Anastassiou, C. A., & Koch, C. (2012). The origin of extracellular fields and currents--EEG, ECoG, LFP and spikes. *Nature Reviews Neuroscience*, *13*(6), 407–420. https://doi.org/10.1038/nrn3241

Buzsáki, G., & Draguhn, A. (2004). Neuronal oscillations in cortical networks. *Science*, *304*, 1926–1929. https://doi.org/10.1126/science.1099745

Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron*, *80*(3), 751–764. https://doi.org/10.1016/j.neuron.2013.10.002

Buzsáki, G., & Moser, E. I. (2013). Memory, navigation and theta rhythm in the hippocampal-entorhinal system. *Nature Neuroscience*, *16*(2), 130–138. https://doi.org/10.1038/nn.3304

Cassidy, M., Mazzone, P., Oliviero, A., Insola, A., Tonali, P., Di Lazzaro, V., & Brown, P. (2002). Movement-related changes in synchronization in the human basal ganglia. *Brain*, *125*, 1235–1246. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/12023312

Cavanagh, J. F., Cohen, M. X., & Allen, J. J. B. (2009). Prelude to and resolution of an error: EEG phase synchrony reveals cognitive control dynamics during action monitoring. *The Journal of Neuroscience : The Official Journal of the Society for Neuroscience*, *29*(1), 98–105. https://doi.org/10.1523/JNEUROSCI.4137-08.2009

Cavanagh, J. F., & Frank, M. J. (2014). Frontal theta as a mechanism for cognitive control. *Trends in Cognitive Sciences*, 1–8. https://doi.org/10.1016/j.tics.2014.04.012

Cavanagh, J. F., Zambrano-Vazquez, L., & Allen, J. J. B. (2012). Theta lingua franca: A common mid-frontal substrate for action monitoring processes. *Psychophysiology*, *49*(2), 220–238. https://doi.org/10.1111/j.1469-8986.2011.01293.x

Cheyne, D. O. (2013). MEG studies of sensorimotor rhythms: A review. *Experimental Neurology*, *245*, 27–39. https://doi.org/10.1016/j.expneurol.2012.08.030

Cohen, M. X. (2011a). Error-related medial frontal theta activity predicts cingulate-related structural connectivity. *NeuroImage*, *55*(3), 1373–1383. https://doi.org/10.1016/j.neuroimage.2010.12.072

Cohen, M. X. (2011b). It's about Time. *Frontiers in Human Neuroscience*, *5*, 2. https://doi.org/10.3389/fnhum.2011.00002

Cohen, M. X. (2014). A neural microcircuit for cognitive conflict detection and signaling. *Trends in Neurosciences*, *37*(9), 480–490. https://doi.org/10.1016/j.tins.2014.06.004

Cohen, M. X., & Donner, T. H. (2013). Midfrontal conflict-related theta-band power reflects neural oscillations that predict behavior. *Journal of Neurophysiology*, *110*(12), 2752–2763. https://doi.org/10.1152/jn.00479.2013

Cohen, M. X., & Gulbinaite, R. (2014). Five methodological challenges in cognitive electrophysiology. *NeuroImage*, *85*, 702–710. https://doi.org/10.1016/j.neuroimage.2013.08.010

Cohen, M. X., Ridderinkhof, K. R., Haupt, S., Elger, C. E., & Fell, J. (2008). Medial frontal cortex and response conflict: Evidence from human intracranial EEG and medial frontal cortex lesion. *Brain Research*, *1238*, 127–142. https://doi.org/10.1016/j.brainres.2008.07.114

Conner, C. R., Chen, G., Pieters, T. a, & Tandon, N. (2014). Category specific spatial dissociations of parallel processes underlying visual naming. *Cerebral Cortex*, (October), 2741–2750. https://doi.org/10.1093/cercor/bht130

Cooper, P. S., Karayanidis, F., McKewen, M., McLellan-Hall, S., Wong, A. S. W., Skippen, P., & Cavanagh, J. F. (2019). Frontal theta predicts specific cognitive control-induced behavioural changes beyond general reaction time slowing. *NeuroImage*, *189*, 130–140. https://doi.org/10.1016/j.neuroimage.2019.01.022

Craik, F. I. M., Naveh-Benjamin, M., Govoni, R., & Anderson, N. D. (1996). The effects of divided attention on encoding and retrieval processes in human memory. *Journal of Experimental Psychology: General*, *125*(2), 159–180.

Crone, N. E., Crone, N. E., Miglioretti, D. L., Miglioretti, D. L., Gordon, B., Gordon, B., … Lesser, R. P. (1998). Functional mapping of human sensorimotor cortex with electrocorticographic spectral analysis. I. Alpha and beta event-related desynchronization. *Brain*, *121*, 2271–2299. https://doi.org/10.1093/brain/121.12.2271

de Bruin, A., Roelofs, A., Dijkstra, T., & Fitzpatrick, I. (2014). Domain-general inhibition areas of the brain are involved in language switching: fMRI evidence from trilingual speakers. *NeuroImage*, *90*, 348–359. https://doi.org/10.1016/j.neuroimage.2013.12.049

Dell, G. S. (1986). A spreading-activation theory of retrieval in sentence production. *Psychological Review*, *93*(3), 283–321. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/3749399

Diamond, A. (2013). Executive Functions. *Annual Review of Psychology*, *64*(1), 135–168. https://doi.org/10.1146/annurev-psych-113011-143750

Düzel, E., Penny, W. D., & Burgess, N. (2010). Brain oscillations and memory. *Current Opinion in Neurobiology*, *20*, 143–149. https://doi.org/10.1016/j.conb.2010.01.004

Edwards, E., Nagarajan, S., Dalal, S. S., Canolty, R. T., Kirsch, H., Barbaro, N. M., & Knight, R. T. (2010). Spatiotemporal imaging of cortical activation during verb generation and picture naming. *NeuroImage*, *50*, 291–301. https://doi.org/10.1016/j.neuroimage.2009.12.035

Eriksen, B. A., & Eriksen, C. W. (1974). Effects of noise letters upon the identification of a target letter in a nonsearch task. *Perception & Psychophysics*, *16*(1), 143–149. https://doi.org/10.3758/BF03203267

Fellner, M.-C., & Hanslmayr, S. (2017). Brain oscillations, semantic processing, and episodic memory. In M. Mody (Ed.), *Neural Mechanisms of Language* (pp. 63–80). Springer. https://doi.org/10.1007/978-1-4939-7325-5_4

Fernandino, L., Humphries, C. J., Conant, L. L., Seidenberg, M. S., & Binder, J. R. (2016). Heteromodal cortical areas encode sensory-motor features of word meaning. *Journal of Neuroscience*, *36*(38), 9763–9769. https://doi.org/10.1523/JNEUROSCI.4095-15.2016

Fiez, J. A., Raichle, M. E., Balota, D. A., Tallal, P., & Petersen, S. E. (2007). PET activation of posterior temporal regions during auditory word presentation and verb generation. *Cerebral Cortex*, *6*(1), 1–10. https://doi.org/10.1093/cercor/6.1.1

Findlay, A. M., Ambrose, J. B., Cahn-Weiner, D. a., Houde, J. F., Honma, S., Hinkley, L. B. N., … Kirsch, H. E. (2012). Dynamics of hemispheric dominance for language assessed by magnetoencephalographic imaging. *Annals of Neurology*, *71*(5), 668–686. https://doi.org/10.1002/ana.23530

Fisher, A. E., Furlong, P. L., Seri, S., Adjamian, P., Witton, C., Baldeweg, T., … Thai, N. J. (2008). Interhemispheric differences of spectral power in expressive language: A MEG study with clinical applications. *International Journal of Psychophysiology*, *68*(2), 111–122. https://doi.org/10.1016/j.ijpsycho.2007.12.005

Flinker, A., Korzeniewska, A., Shestyuk, A. Y., Franaszczuk, P. J., Dronkers, N. F., Knight, R. T., & Crone, N. E. (2015). Redefining the role of Broca's area in speech. *Proceedings of the National Academy of Sciences*, *112*(9), 201414491. https://doi.org/10.1073/pnas.1414491112

Flinker, A., Piai, V., & Knight, R. T. (2018). Intracranial electrophysiology in language research. In S. Rueschemeyer & M. G. Gaskell (Eds.), *The Oxford Handbook of Psycholinguistics*. Oxford, UK: Oxford University Press.

Friederici, A. D., & Singer, W. (2015). Grounding language processing on basic neurophysiological principles. *Trends in Cognitive Sciences*. Elsevier Ltd. https://doi.org/10.1016/j.tics.2015.03.012

Gauvin, H. S., De Baene, W., Brass, M., & Hartsuiker, R. J. (2016). Conflict monitoring in speech processing: An fMRI study of error detection in speech production and perception. *NeuroImage*, *126*, 96–105. https://doi.org/10.1016/j.neuroimage.2015.11.037

Glaser, W. R., & Düngelhoff, F. J. (1984). The time course of picture-word interference. *Journal of Experimental Psychology: Human Perception and Performance*, *10*(5), 640–654. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/6238124

Grappe, A., Sarma, S. V, Sacré, P., González-Martínez, J., Liégeois-Chauvel, C., & Alario, F.-X. (2019). An intracerebral exploration of functional connectivity during word production. *Journal of Computational Neuroscience*, *46*, 125. https://doi.org/10.1007/s10827-018-0699-3

Gratton, G., Coles, M. G., & Donchin, E. (1992). Optimizing the use of information: strategic control of activation of responses. *Journal of Experimental Psychology: General*, *121*, 480–506.

Green, D. W. (1998). Mental control of the bilingual lexico-semantic system. *Bilingualism: Language and Cognition*, *1*(2), 67–81. https://doi.org/10.1017/S1366728998000133

Griffin, Z. M., & Bock, K. J. (1998). Constraint, word frequency, and the relationship between lexical processing levels in spoken word production. *Journal of Memory and Language*, *38*, 313–338. Retrieved from http://www.sciencedirect.com/science/article/pii/S0749596X9792547X

Hamamé, C. M., Alario, F.-X., Llorens, A., Liégeois-Chauvel, C., & Trébuchon-Da Fonseca, A. (2014). High frequency gamma activity in the left hippocampus predicts visual object naming performance. *Brain and Language*, *135*, 104–114. https://doi.org/10.1016/j.bandl.2014.05.007

Hanslmayr, S., Matuschek, J., & Fellner, M. C. (2014). Entrainment of prefrontal beta oscillations induces an endogenous echo and impairs memory formation. *Current Biology*, *24*(8), 904–909. https://doi.org/10.1016/j.cub.2014.03.007

Hanslmayr, S., Pastötter, B., Bäuml, K.-H., Gruber, S., Wimber, M., & Klimesch, W. (2008). The electrophysiological dynamics of interference during the Stroop task. *Journal of Cognitive Neuroscience*, *20*, 215–225. https://doi.org/10.1162/jocn.2008.20020

Hanslmayr, S., Spitzer, B., & Bäuml, K. (2009). Brain oscillations dissociate between semantic and nonsemantic encoding of episodic memories. *Cerebral Cortex*, *19*(July), 1631–1640. https://doi.org/10.1093/cercor/bhn197

Hanslmayr, S., Staresina, B. P., & Bowman, H. (2016). Oscillations and Episodic Memory: Addressing the Synchronization/Desynchronization Conundrum. *Trends in Neurosciences*, *39*(1), 16–25. https://doi.org/10.1016/j.tins.2015.11.004

Hanslmayr, S., Staudigl, T., & Fellner, M.-C. (2012). Oscillatory power decreases and long-term memory: the information via desynchronization hypothesis. *Frontiers in Human Neuroscience*, *6*(April), 74. https://doi.org/10.3389/fnhum.2012.00074

Hanslmayr, S., Volberg, G., Wimber, M., Raabe, M., Greenlee, M. W., & Bäuml, K.-H. T. (2011). The relationship between brain oscillations and BOLD signal during memory formation: a combined EEG-fMRI study. *Journal of Neuroscience*, *31*, 15674–1580. https://doi.org/10.1523/JNEUROSCI.3140-11.2011

Hart, J., Crone, N. E., Lesser, R. P., Sieracki, J., Miglioretti, D. L., Hall, C., … Gordon, B. (1998). Temporal dynamics of verbal object comprehension. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(11), 6498–6503. https://doi.org/10.1073/pnas.95.11.6498

Hartsuiker, R. J. (2014). Monitoring and control of the production system. In M. Goldrick, V. Ferreira, & M. Miozzo (Eds.), *The Oxford handbook of language production* (pp. 417–436). Oxford, England: Oxford University Press.

Hasselmo, M. E., Bodelón, C., & Wyble, B. P. (2002). A proposed function for hippocampal theta rhythm: separate phases of encoding and retrieval enhance reversal of prior learning. *Neural Computation*, *14*(4), 793–817. https://doi.org/10.1162/089976602317318965

Hasselmo, M. E., & Stern, C. E. (2013). Theta rhythm and the encoding and retrieval of space and time. *NeuroImage*. https://doi.org/10.1016/j.neuroimage.2013.06.022

Hauk, O. (2016). Only time will tell – why temporal information is essential for our neuroscientific understanding of semantics. *Psychonomic Bulletin & Review*, *23*(4), 1072–1079. https://doi.org/10.3758/s13423-015-0873-9

Hebb, A. O., Darvas, F., & Miller, K. J. (2012). Transient and state modulation of beta power in human subthalamic nucleus during speech production and finger movement. *Neuroscience*, *202*, 218–233. https://doi.org/10.1016/j.neuroscience.2011.11.072

Henseler, I., Regenbrecht, F., & Obrig, H. (2014). Lesion correlates of patholinguistic profiles in chronic aphasia: comparisons of syndrome-, modality- and symptom-level assessment. *Brain*, *137*(Pt 3), 918–930. https://doi.org/10.1093/brain/awt374

Hermans, D., Bongaerts, T., De Bot, K., & Schreuder, R. (1998). Producing words in a foreign language: Can speakers prevent interference from their first language? *Bilingualism: Language and Cognition*, *1*(3), 213–229. https://doi.org/10.1017/S1366728998000364

Hickok, G. (2012). Computational neuroanatomy of speech production. *Nature Reviews Neuroscience*, *13*, 135–145. Retrieved from http://www.nature.com/nrn/journal/v13/n2/full/nrn3158.html?WT.ec_id=NRN-201202

Indefrey, P., & Levelt, W. J. M. (2004). The spatial and temporal signatures of word production components. *Cognition*, *92*, 101–144. https://doi.org/10.1016/j.cognition.2002.06.001

Itthipuripat, S., Wessel, J. R., & Aron, A. R. (2013). Frontal theta is a signature of successful working memory manipulation. *Experimental Brain Research*, *224*(2), 255–262. https://doi.org/10.1007/s00221-012-3305-3

Jacobs, J. (2014). Hippocampal theta oscillations are slower in humans than in rodents: implications for models of spatial navigation and memory. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *369*(1635), 20130304. https://doi.org/10.1098/rstb.2013.0304

Jacobs, J., Kahana, M. J., Ekstrom, A. D., & Fried, I. (2007). Brain oscillations control timing of single-neuron activity in humans. *Journal of Neuroscience*, *27*(14), 3839–3844.

https://doi.org/10.1523/JNEUROSCI.4636-06.2007

Jafarpour, A., Piai, V., Lin, J. J., & Knight, R. T. (2017). Human hippocampal pre-activation predicts behavior. *Scientific Reports*, *7*(1). https://doi.org/10.1038/s41598-017-06477-5

Jensen, O., & Mazaheri, A. (2010). Shaping Functional Architecture by Oscillatory Alpha Activity: Gating by Inhibition. *Frontiers in Human Neuroscience*, *4*(November), 1–8. https://doi.org/10.3389/fnhum.2010.00186

Jensen, O., & Tesche, C. D. (2002). Frontal theta activity in humans increases with memory load in a working memory task. *European Journal of Neuroscience*, *15*(8), 1395–199. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11994134

Kahana, M. J., Seelig, D., & Madsen, J. R. (2001). Theta returns. *Current Opinion in Neurobiology*, *11*(6), 739–744. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/11741027

Khader, P. H., & Rösler, F. (2011). EEG power changes reflect distinct mechanisms during long-term memory retrieval. *Psychophysiology*, *48*(3), 362–369. https://doi.org/10.1111/j.1469-8986.2010.01063.x

Klaus, J., & Schutter, D. J. L. G. (2018). The role of left dorsolateral prefrontal cortex in language processing. *Neuroscience*, *377*, 197–205. https://doi.org/10.1016/j.neuroscience.2018.03.002

Klimesch, W. (1997). EEG-alpha rhythms and memory processes. *International Journal of Psychophysiology*, *26*, 319–340. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9203012

Klimesch, W., Doppelmayr, M., Russegger, H., & Pachinger, T. (1996). Theta band power in the human scalp EEG and the encoding of new information. *Neuroreport*, *7*(7), 1235–1240.

Klimesch, W., Doppelmayr, M., Russegger, H., Pachinger, T., & Schwaiger, J. (1998). Induced alpha band power changes in the human EEG and attention. *Neuroscience Letters*, *244*(2), 73–76. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/9572588

Klimesch, W., Doppelmayr, M., Schimke, H., & Ripper, B. (1997). Theta synchronization and alpha desynchronization in a memory task. *Psychophysiology*, *34*(2), 169–176. https://doi.org/10.1111/j.1469-8986.1997.tb02128.x

Knight, R. T., Staines, W. R., Swick, D., & Chao, L. L. (1999). Prefrontal cortex regulates inhibition and excitation indistributed neural networks. *Acta Psychological1*, *101*, 159–178.

Kojima, K., Brown, E. C., Matsuzaki, N., Rothermel, R., Fuerst, D., Shah, A., … Asano, E. (2013). Gamma activity modulated by picture and auditory naming tasks: intracranial recording in patients with focal epilepsy. *Clinical Neurophysiology*, *124*(9), 1737–1744. https://doi.org/10.1016/j.clinph.2013.01.030

Krieg, S. M., Sollmann, N., Tanigawa, N., Foerschler, A., Meyer, B., Ringel, F., & Meyer, B. (2016). Cortical distribution of speech and language errors investigated by visual object naming and navigated transcranial magnetic stimulation. *Brain Structure and Function*, 2259–2286. https://doi.org/10.1007/s00429-015-1042-7

Krott, A., Medaglia, M. T., & Porcaro, C. (2019). Early and late effects of semantic distractors on electroencephalographic responses during overt picture naming. *Frontiers in Psychology*, *10*, 696. https://doi.org/10.3389/fpsyg.2019.00696

Kurczek, J., & Duff, M. C. (2011). Cohesion, coherence, and declarative memory: Discourse patterns in individuals with hippocampal amnesia. *Aphasiology*, *25*(6–7), 700–712. https://doi.org/10.1080/02687038.2010.537345

Lega, B. C., Jacobs, J., & Kahana, M. (2012). Human hippocampal theta oscillations and the formation of episodic memories. *Hippocampus*, *22*(4), 748–761. https://doi.org/10.1002/hipo.20937

Levelt, W. J. M., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *Behavioral and Brain Sciences*, *22*, 1–75. https://doi.org/10.1017/S0140525X99001776

Llorens, A., Trébuchon, A., Liégeois-Chauvel, C., & Alario, F.-X. (2011). Intra-cranial recordings of brain activity during language production. *Frontiers in Psychology*, *2*(December), 375. https://doi.org/10.3389/fpsyg.2011.00375

Lopes da Silva, F. (2013). EEG and MEG: relevance to neuroscience. *Neuron*, *80*(5), 1112–1128. https://doi.org/10.1016/j.neuron.2013.10.017

Lundqvist, M., Rose, J., Herman, P., Brincat, S. L., Buschman, T. J., & Miller, E. K. (2016). Gamma and beta bursts underlie working memory. *Neuron*, *90*(1), 152–164. https://doi.org/10.1016/j.neuron.2016.02.028

Lupker, S. J. (1979). The semantic nature of response competition in the picture-word interference task. *Memory and Cognition*, *7*(6), 485–495.

Luu, P., Tucker, D. M., & Makeig, S. (2004). Frontal midline theta and the error-related negativity: neurophysiological mechanisms of action regulation. *Clinical Neurophysiology*, *115*(8), 1821–1835. https://doi.org/10.1016/j.clinph.2004.03.031

MacKay, D. G., Burke, D. M., & Stewart, R. (1998). H.M.'s Language Production Deficits: Implications for Relations between Memory, Semantic Binding, and the Hippocampal System. *Journal of Memory and Language*, *38*(38), 28–69. https://doi.org/10.1006/jmla.1997.2544

Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164*, 177–190. https://doi.org/10.1016/j.jneumeth.2007.03.024

Martin, R. C., & Slevc, L. R. (2014). Language production and working memory. In M. Goldrick, V. Ferreira, & M. Miozzo (Eds.), *The Oxford handbook of language production* (pp. 120–131). Oxford, England: Oxford University Press.

McCarthy, G., Blamire, A. M., Rothman, D. L., Gruetter, R., & Shulman, R. G. (1993). Echo-planar magnetic resonance imaging studies of frontal cortex activation during word generation in humans. *Proceedings of the National Academy of Sciences of the United States of America*, *90*(11), 4952–4956.

Meador, K. J., & Loring, D. W. (1999). The Wada test: Controversies, concerns, and insights. *Neurology*, *52*(8), 1535–1535. https://doi.org/10.1212/WNL.52.8.1535

Mellem, M. S., Bastiaansen, M. C. M., Pilgrim, L. K., Medvedev, A. V., & Friedman, R. B. (2012). Word class and context affect alpha-band oscillatory dynamics in an older population. *Frontiers in Psychology*, *3*, 97. https://doi.org/10.3389/fpsyg.2012.00097

Meuter, R. F. I., & Allport, A. (1999). Bilingual language switching in naming: Asymmetrical costs of language selection. *Journal of Memory and Language*, *40*(1), 25–40. https://doi.org/10.1006/jmla.1998.2602

Meyer, L. (2018). The neural oscillations of speech processing and language comprehension: state of the art and emerging mechanisms. *European Journal of Neuroscience*, *48*(7), 2609–2621. https://doi.org/10.1111/ejn.13748

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202. https://doi.org/10.1146/annurev.neuro.24.1.167

Miller, K. J., Hermes, D., Honey, C. J., Hebb, A. O., Ramsey, N. F., Knight, R. T., … Fetz, E. E. (2012). Human motor cortical activity is selectively phase-entrained on underlying rhythms. *PLoS Computational Biology*, *8*(9), e1002655. https://doi.org/10.1371/journal.pcbi.1002655

Miyake, A., Friedman, N. P., Emerson, M. J., Witzki, a H., Howerter, A., & Wager, T. D. (2000). The unity and diversity of executive functions and their contributions to complex “Frontal Lobe” tasks: a latent variable analysis. *Cognitive Psychology*, *41*(1), 49–100. https://doi.org/10.1006/cogp.1999.0734

Murthy, V. N., & Fetz, E. E. (1996). Synchronization of neurons during local field potential oscillations in sensorimotor cortex of awake monkeys. *Journal of Neurophysiology*, *76*(6), 3968–3982. https://doi.org/10.1152/jn.1996.76.6.3968

Nigbur, R., Ivanova, G., & Stürmer, B. (2011). Theta power as a marker for cognitive interference. *Clinical Neurophysiology*, *122*(11), 2185–2194. https://doi.org/10.1016/j.clinph.2011.03.030

Nozari, N., & Novick, J. (2017). Monitoring and control in language production. *Current Directions in Psychological Science*, *26*(5), 403–410. https://doi.org/10.1177/0963721417702419

Nyhus, E., & Curran, T. (2010). Functional role of gamma and theta oscillations in episodic memory. *Neuroscience and Biobehavioral Reviews*, *34*(7), 1023–1035. https://doi.org/10.1016/j.neubiorev.2009.12.014

Obleser, J., & Weisz, N. (2012). Suppressed alpha oscillations predict intelligibility of speech and its acoustic details. *Cerebral Cortex*, *22*(11), 2466–2477. https://doi.org/10.1093/cercor/bhr325

Ojemann, G. A., Fried, I., & Lettich, E. (1989). Electrocorticographic (ECoG) correlates of language. I. Desynchronization in temporal language cortex during object naming. *Electroencephalography and Clinical Neurophysiology*, *73*(5), 453–463. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/2479524

Osipova, D., Takashima, A., Oostenveld, R., Fernández, G., Maris, E., & Jensen, O. (2006). Theta and gamma oscillations predict encoding and retrieval of declarative memory. *Journal of Neuroscience*, *26*(28), 7523–7531. https://doi.org/10.1523/JNEUROSCI.1948-06.2006

Pang, E. W., Wang, F., Malone, M., Kadis, D. S., & Donner, E. J. (2011). Localization of Broca’s area using verb generation tasks in the MEG: Validation against fMRI. *Neuroscience Letters*, *490*(3), 215–219. https://doi.org/10.1016/j.neulet.2010.12.055

Pavlova, A. A., Butorina, A. V, Nikolaeva, A. Y., Prokofyev, A. O., Ulanov, M. A., Bondarev, D. P., & Stroganova, T. A. (2019). Effortful verb retrieval from semantic memory drives beta suppression in mesial frontal regions involved in action initiation. *Human Brain Mapping*, 1–13. https://doi.org/10.1002/hbm.24624

Penfield, W., & Roberts, L. (1959). *Speech and brain-mechanisms.* Princeton, NJ: Princeton

University Press.

Petersen, S. E., Fox, P., Posner, M. I., Mintun, M., & Raichle, M. (1988). Positron emission tomographic studies of the cortical anatomy of single-word processing. *Nature*, *331*, 585–589. Retrieved from http://psych.stanford.edu/~jlm/pdfs/PetersenEtAl88Nature.pdf

Pfurtscheller, G., & Lopes da Silva, F. H. (1999). Event-related EEG/MEG synchronization and desynchronization: basic principles. *Clinical Neurophysiology*, *110*(11), 1842–1857. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10576479

Piai, V., Anderson, K. L., Lin, J. J., Dewar, C., Parvizi, J., Dronkers, N. F., & Knight, R. T. (2016). Direct brain recordings reveal hippocampal rhythm underpinnings of language processing. *Proceedings of the National Academy of Sciences*, *113*(40), 11366–11371. https://doi.org/10.1073/pnas.1603312113

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. *Human Brain Mapping*, *38*(6), 3151–3162. https://doi.org/10.1002/hbm.23581

Piai, V., & Roelofs, A. (2013). Working memory capacity and dual-task interference in picture naming. *Acta Psychologica*, *142*, 332–342. https://doi.org/10.1016/j.actpsy.2013.01.006

Piai, V., Roelofs, A., Acheson, D. J., & Takashima, A. (2013). Attention for speaking: domain-general control from the anterior cingulate cortex in spoken word production. *Frontiers in Human Neuroscience*, *7*(832), 832. https://doi.org/10.3389/fnhum.2013.00832

Piai, V., Roelofs, A., Jensen, O., Schoffelen, J.-M., & Bonnefond, M. (2014). Distinct patterns of brain activity characterise lexical activation and competition in spoken word production. *PloS One*, *9*(2), e88674. https://doi.org/10.1371/journal.pone.0088674

Piai, V., Roelofs, A., & Maris, E. (2014). Oscillatory brain responses in spoken word production reflect lexical frequency and sentential constraint. *Neuropsychologia*, *53*, 146–156. https://doi.org/10.1016/j.neuropsychologia.2013.11.014

Piai, V., Roelofs, A., Rommers, J., & Maris, E. (2015). Beta oscillations reflect memory and motor aspects of spoken word production. *Human Brain Mapping*, *36*(7), 2767–2780. https://doi.org/10.1002/hbm.22806

Piai, V., Rommers, J., & Knight, R. T. (2018). Lesion evidence for a critical role of left posterior but not frontal areas in alpha-beta power decreases during context-driven word production. *European Journal of Neuroscience*, *48*(7), 2622–2629. https://doi.org/10.1111/ejn.13695

Rapp, B., & Goldrick, M. (2000). Discreteness and interactivity in spoken word production. *Psychological Review*, *107*(3), 460–499. https://doi.org/10.1037//0033-295X.107.3.460

Riès, S. K., Greenhouse, I., Dronkers, N. F., Haaland, K. Y., & Knight, R. T. (2014). Double dissociation of the roles of the left and right prefrontal cortices in anticipatory regulation of action. *Neuropsychologia*, *63*, 215–225. https://doi.org/10.1016/j.neuropsychologia.2014.08.026

Roelofs, A. (2003). Goal-referenced selection of verbal action: modeling attentional control in the Stroop task. *Psychological Review*, *110*(1), 88–125.

Roelofs, A. (2008). Attention to Spoken Word Planning: Chronometric and Neuroimaging

Evidence. *Language and Linguistics Compass*, *2*(3), 389–405. https://doi.org/10.1111/j.1749-818X.2008.00060.x

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. *Language, Cognition and Neuroscience*, *32*(5), 576–589. https://doi.org/10.1080/23273798.2016.1183799

Rutishauser, U., Ross, I. B., Mamelak, A. N., & Schuman, E. M. (2010). Human memory strength is predicted by theta-frequency phase-locking of single neurons. *Nature*, *464*(7290), 903–907. https://doi.org/10.1038/nature08860

Rutten, G. J. M., Ramsey, N. F., Van Rijen, P. C., Alpherts, W. C., & Van Veelen, C. W. M. (2002). fMRI-determined language lateralization in patients with unilateral or mixed language dominance according to the Wada test. *NeuroImage*, *17*(1), 447–460. https://doi.org/10.1006/nimg.2002.1196

Salmelin, R., Hámáaláinen, M., Kajola, M., & Hari, R. (1995). Functional segregation of movement-related rhythmic activity in the human brain. *NeuroImage*, *2*(4), 237–243. https://doi.org/10.1006/nimg.1995.1031

Salmelin, R., & Sams, M. (2002). Motor cortex involvement during verbal versus non-verbal lip and tongue movements. *Human Brain Mapping*, *16*(2), 81–91. https://doi.org/10.1002/hbm.10031

Salmelin, R., Schnitzler, A., Schmitz, F., & Freund, H. J. (2000). Single word reading in developmental stutterers and fluent speakers. *Brain*, *123*, 1184–1202. Retrieved from http://www.ncbi.nlm.nih.gov/pubmed/10825357

Sanquist, T. F., Rohrbaugh, J. W., Syndulko, K., & Lindsley, D. B. (1980). Electrocortical signs of levels of processing: perceptual analysis and recognition memory. *Psychophysiology*, *17*(6), 568–576.

Sauseng, P., Griesmayr, B., Freunberger, R., & Klimesch, W. (2010). Control mechanisms in working memory: a possible function of EEG theta oscillations. *Neuroscience and Biobehavioral Reviews*, *34*, 1015–1022. https://doi.org/10.1016/j.neubiorev.2009.12.006

Sauseng, P., Hoppe, J., Klimesch, W., Gerloff, C., & Hummel, F. C. (2007). Dissociation of sustained attention from central executive functions: local activity and interregional connectivity in the theta range. *European Journal of Neuroscience*, *25*(2), 587–593. https://doi.org/10.1111/j.1460-9568.2006.05286.x

Schnur, T. T., Schwartz, M. F., Kimberg, D. Y., Hirshorn, E., Coslett, H. B., & Thompson-Schill, S. L. (2009). Localizing interference during naming: convergent neuroimaging and neuropsychological evidence for the function of Broca’s area. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(1), 322–327. https://doi.org/10.1073/pnas.0805874106

Schwartz, M. F., Faseyitan, O., Kim, J., & Coslett, H. B. (2012). The dorsal stream contribution to phonological retrieval in object naming. *Brain*, *135*, 3799–3814. https://doi.org/10.1093/brain/aws300

Shahin, A. J., Picton, T. W., & Miller, L. M. (2009). Brain oscillations during semantic evaluation of speech. *Brain and Cognition*, *70*(3), 259–266. https://doi.org/10.1016/j.bandc.2009.02.008

Shao, Z., Roelofs, A., Martin, R. C., & Meyer, A. S. (2015). Selective inhibition and naming performance in semantic blocking, picture-word interference, and color–word Stroop tasks. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *41*(6), 1806–1820. https://doi.org/10.1037/a0039363

Shitova, N., Roelofs, A., Schriefers, H., Bastiaansen, M., & Schoffelen, J. M. (2017). Control adjustments in speaking: Electrophysiology of the Gratton effect in picture naming. *Cortex*, *92*, 289–303. https://doi.org/10.1016/j.cortex.2017.04.017

Siegel, M., Donner, T. H., & Engel, A. K. (2012). Spectral fingerprints of large-scale neuronal interactions. *Nature Reviews Neuroscience*, *13*(2), 121–134. https://doi.org/10.1038/nrn3137

Sikora, K., Roelofs, A., & Hermans, D. (2016). Electrophysiology of executive control in spoken noun-phrase production: Dynamics of updating, inhibiting, and shifting. *Neuropsychologia*, *84*, 44–53. https://doi.org/10.1016/j.neuropsychologia.2016.01.037

Simon, J. R. (1969). Reactions toward the source of stimulation. *Journal of Experimental Psychology*, *81*(1), 174–176. https://doi.org/10.1037/h0027448

Skotko, B. G., Andrews, E., & Einstein, G. (2005). Language and the medial temporal lobe: Evidence from H.M.'s spontaneous discourse. *Journal of Memory and Language*, *53*(3), 397–415. https://doi.org/10.1016/j.jml.2005.05.003

Squire, L. R. (1992). Memory and the hippocampus: a synthesis from findings with rats, monkeys, and humans. *Psychological Review*, *99*(2), 195–231. https://doi.org/10.1037/0033-295X.99.3.582

Squire, L. R., & Wixted, J. T. (2011). The Cognitive Neuroscience of Human Memory Since H.M. *Annual Review of Neuroscience*, *34*(1), 259–288. https://doi.org/10.1146/annurev-neuro-061010-113720

Strauß, A., Kotz, S. a, Scharinger, M., & Obleser, J. (2014). Alpha and theta brain oscillations index dissociable processes in spoken word recognition. *NeuroImage*, *97*, 387–395. https://doi.org/10.1016/j.neuroimage.2014.04.005

Stroop, J. R. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, *18*, 643–662.

Thompson-Schill, S. L., Swick, D., Farah, M. J., D'Esposito, M., Kan, I. P., & Knight, R. T. (1998). Verb generation in patients with focal frontal lesions: a neuropsychological test of neuroimaging findings. *Proceedings of the National Academy of Sciences of the United States of America*, *95*(26), 15855–15860. Retrieved from http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=28134&tool=pmcentrez&rendertype=abstract

Traut, T., Sardesh, N., Bulubas, L., Findlay, A., Honma, S. M., Mizuiri, D., … Tarapore, P. E. (2019). MEG imaging of recurrent gliomas reveals functional plasticity of hemispheric language specialization. *Human Brain Mapping*, *40*(4), 1082–1092. https://doi.org/10.1002/hbm.24430

Trujillo, L. T., & Allen, J. J. B. (2007). Theta EEG dynamics of the error-related negativity. *Clinical Neurophysiology*, *118*(3), 645–668. https://doi.org/10.1016/j.clinph.2006.11.009

van Ede, F., de Lange, F., Jensen, O., & Maris, E. (2011). Orienting attention to an upcoming tactile event involves a spatially and temporally specific modulation of sensorimotor alpha- and beta-band oscillations. *Journal of Neuroscience*, *31*(6), 2016–2024. https://doi.org/10.1523/JNEUROSCI.5630-10.2011

van Wijk, B. C. M., Beek, P. J., & Daffertshofer, A. (2012). Neural synchrony within the motor system: what have we learned so far? *Frontiers in Human Neuroscience*, *6*, 252. https://doi.org/10.3389/fnhum.2012.00252

Wada, J. (1949). A new method for determination of the side of cerebral speech dominance: a preliminary report on the intracarotid injection of sodium amytal in man. *Iqakaa Te Seibutzuqaki*, *14*, 221– 222.

Walker, G. M., Schwartz, M. F., Kimberg, D. Y., Faseyitan, O., Brecher, A., Dell, G. S., & Coslett, H. B. (2011). Support for anterior temporal involvement in semantic error production in aphasia: new evidence from VLSM. *Brain and Language*, *117*(3), 110–122. https://doi.org/10.1016/j.bandl.2010.09.008

Watanabe, E., Maki, A., Kawaguchi, F., Takashiro, K., Yamashita, Y., Koizumi, H., & Mayanagi, Y. (1998). Non-invasive assessment of language dominance with near-infrared spectroscopic mapping. *Neuroscience Letters*, *256*(1), 49–52. https://doi.org/10.1016/S0304-3940(98)00754-X

Ye, Z., & Zhou, X. (2009). Executive control in language processing. *Neuroscience and Biobehavioral Reviews*, *33*(8), 1168–1177. https://doi.org/10.1016/j.neubiorev.2009.03.003

Zheng, X., Roelofs, A., Farquhar, J., & Lemhöfer, K. (2018). Monitoring of language selection errors in switching: Not all about conflict. *PLOS ONE*, *13*(11), e0200397. https://doi.org/10.1371/journal.pone.0200397