



HAL
open science

Frequency-tagged visual evoked responses track syllable effects in visual word recognition

Veronica Montani, Valérie C Chanoine, Jonathan Grainger, Johannes C Ziegler

► **To cite this version:**

Veronica Montani, Valérie C Chanoine, Jonathan Grainger, Johannes C Ziegler. Frequency-tagged visual evoked responses track syllable effects in visual word recognition. *Cortex*, 2019, 121, pp.60-77. 10.1016/j.cortex.2019.08.014 . hal-02281144

HAL Id: hal-02281144

<https://amu.hal.science/hal-02281144v1>

Submitted on 24 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Title: Frequency-tagged visual evoked responses track syllable effects in visual word recognition

Authors:

Veronica Montani
Aix-Marseille University and CNRS, Brain and Language Research Institute
3 place Victor Hugo
13331 Marseille Cedex 3, France
phone: +39 333 8714750
corresponding author : veronica.montani@live.com

Valerie Chanoine
Aix-Marseille University, Institute of Language, Communication and the Brain, Brain and Language Research Institute
13100 Aix-en-Provence
France

Jonathan Grainger
Aix-Marseille University and CNRS, LPC
3 place Victor Hugo
13331 Marseille Cedex 3, France

Johannes C. Ziegler
Aix-Marseille University and CNRS, LPC
3 place Victor Hugo
13331 Marseille Cedex 3, France

Abstract

The processing of syllables in visual word recognition was investigated using a novel paradigm based on steady-state visual evoked potentials (SSVEPs). French words were presented to proficient readers in a delayed naming task. Words were split into two segments, the first of which was flickered at 18.75 Hz and the second at 25 Hz. The first segment either matched (congruent condition) or did not match (incongruent condition) the first syllable. The SSVEP responses in the congruent condition showed increased power compared to the responses in the incongruent condition, providing new evidence that syllables are important sublexical units in visual word recognition and reading aloud. With respect to the neural correlates of the effect, syllables elicited an early activation of a right hemisphere network. This network is typically associated with the programming of complex motor sequences, cognitive control and timing. Subsequently, responses were obtained in left hemisphere areas related to phonological processing.

Keywords: syllable, visual word recognition, SSVEP, frequency tagging, neuroimaging

Frequency-tagged visual evoked responses track syllable effects in visual word recognition

1. Introduction

There is increasing consensus that fast and automatic visual word recognition is made possible through the automatic and parallel decomposition of written words into letters and graphemes but also larger units, such as morphemes and syllables (Carreiras, Armstrong, Perea, & Frost, 2014; Dehaene, Cohen, Sigman & Vinckier, 2005; Grainger, Dufau, & Ziegler, 2016). Indeed, it is well established that syllables are important units in spoken language (Levelt, Roelofs, & Meyer, 1999; MacNeilage, 1998; Mehler, Dommergues, Frauenfelder, & Segui, 1981; Ramus, Nespor, & Mehler, 1999), but they also play a role in visual word recognition, at least in languages with clear syllabic boundaries, such as Spanish or French. However, it is not clear at what stage of processing syllables affect written word recognition. While some evidence points to a late effect, located at the output level, i.e. speech production (e.g., Ferrand, Segui, & Grainger, 1996), syllables have also shown to produce effects at earlier processing stages (e.g. Barber, Vergara, & Carreiras, 2004; Carreiras, Vergara, & Barber, 2005; Hutzler, Bergmann, Conrad, Kronbichler, Stenneken & Jaconbs, 2004; Perry, Ziegler, & Zorzi, 2013).

Studies using masked priming showed that naming latencies are faster when words or nonwords are preceded by primes that correspond to the first syllable compared to primes that contained one letter more or less than the first syllable (Alvarez, Carreiras, & Perea, 2004;

Carreiras & Perea, 2002; Carreiras, Ferrand, Grainger, & Perea, 2005; Ferrand et al., 1996). These syllable priming effects were observed in picture, word, and nonword naming but not in lexical decision. This dissociation led Ferrand and colleagues (1996) to suggest that the effect must be located at the level of output phonology (articulatory encoding). Similarly, later studies that compared phonologically defined syllables to orthographically defined syllables demonstrated that the syllable effect reflects processing of the phonological syllable (Alvarez et al., 2004; Conrad, Grainger, & Jacobs, 2007) and occurs independently of orthographic redundancy (Conrad, Carreiras, Tamm, & Jacobs, 2009). In a word-spotting paradigm, Spanish children were faster in detecting monosyllabic words embedded in a pseudoword, when the boundary between the word and the remaining letters matched the syllabic boundary (Alvarez, Garcia-Saavedra, Luque, & Taft, 2016). The magnitude of the effect was the same regardless of reading ability, supporting the idea that syllable effects are located at the production level.

It is particularly intriguing that the frequency of the first syllable produces an inhibitory effect (i.e., high frequency syllables are associated with longer response times) in lexical decision and progressive demasking (Alvarez, Carreiras, & De Vega, 2000; Alvarez, Carreiras, & Taft, 2001; Carreiras, Alvarez, & De Vega, 1993; Carreiras & Perea, 2002; Conrad & Jacobs, 2004; Mathey & Zagar, 2002; Perea & Carreiras, 1998), while it has a facilitatory effect in reading aloud (Carreiras & Perea, 2004; Perea & Carreiras, 1998). ERP studies comparing syllable and word frequency effects showed that the onset of the syllable frequency effect occurred at an early stage of processing, around 150 msec, and before that of word frequency, which occurred around 350-400 msec (Barber et al., 2004; Hutzler et al., 2004). It has been proposed that high-frequency syllables tend to have more neighbors than low-frequency syllables and the competition between them might produce the inhibitory effect in lexical decision

(Carreiras et al., 1993). In contrast, the reversed effect for speech production tasks can be attributed to facilitation at the articulatory processing level (Levelt et al., 1999). In support of these explanations, words with high-frequency syllables showed increased activation in the left anterior inferior temporal region and the left anterior insula, the first has been previously associated with lexico-semantic processing in lexical decision, while the second has been associated with articulatory planning in reading aloud (Carreiras, Mechelli, & Price, 2006).

In another line of research, the processing of syllable sub-units has been investigated by splitting words in some way and then contrasting the responses to the compatible versus the incompatible segments. The logic is that if reading makes use of syllabically structured representations, processing of a word should be facilitated when the word is split at the orthographic equivalent of the syllabic break (Perry, 2013). For example, the idea that readers break words down into orthographic syllables (i.e. Basic Orthographic Syllable Structure) has been extensively investigated but the results are mixed (see e.g., Taft, 2001, for review).

Carreiras, Vergara, and Barber (2005) used the color congruency paradigm, in which the color either matched or mismatched the syllable boundary, thus creating congruent and incongruent segments. Using EEG, they found that syllable congruency effects occurred as early as 180 msec and had a frontal distribution. In a subsequent fMRI study, the syllable congruency effect involved the precuneus/paracentral gyrus region, the thalamus bilaterally and the superior frontal gyrus, in which incongruent words showed deactivation compared to congruent words (Carreiras, Riba, Vergara, Heldmann, & Münte, 2009). The deactivation in the precuneus was interpreted as reflecting either the differential engagement of semantic processing or the differential allocation of attentional resources while the involvement of the thalamus and frontal regions was attributed to differences in the inhibition or selection of lexical candidates.

However, a recent study provided evidence supporting a different role of the precuneus. Takashima, Wagensveld, van Turenout, Zwitserlood, Hagoort, & Verhoeven (2014) trained Dutch participants to articulate a set of novel disyllabic strings written in an unfamiliar orthography (Greek). After one month of training, articulation became faster and more accurate for the trained pseudowords. Novel pseudowords that were obtained by recombining syllables of the training set (i.e., recombined condition) were named faster and more accurately than completely novel stimuli, suggesting the emergence of syllabic units. Crucially, at the neural level, the efficient conversion of print to sound was associated with an increased activity bilaterally in the angular gyrus and the precuneus extending to the middle cingulate cortex and the middle temporal gyrus (Takashima et al., 2014). Because their pseudowords were meaningless, the activation increase in the angular gyrus and in the precuneus could not be related to semantic access. Rather, the authors interpreted the finding as evidence that those areas code for orthography-phonology associations at multiple levels of units, from small grapheme-phoneme conversion to larger units entailing syllables (Ziegler & Goswami, 2005).

To summarize, syllables are relevant units of processing in reading and syllable processing seems to affect word recognition at multiple stages. The syllable congruency effect has been associated with the early process of syllabic parsing (Carreiras et al., 2009; Perry, 2013). Subsequently, frequent syllables may slow down word recognition because they activate many competing lexical entries, producing the inhibitory effect observed in lexical decision. At the same time, frequent syllables may facilitate reading aloud by speeding up articulation. However, the precise nature of these mechanisms that operate at different times scales is still not clear.

In the present study, we investigated the processing of syllable units during visual word

recognition in French, using a novel paradigm based on steady state visual evoked potentials (SSVEPs). The SSVEPs are the electrophysiological response of the cortex to flickering visual stimuli (Regan, 1989) and have been successfully applied to study a variety of cognitive functions (for recent reviews, see Norcia, Appelbaum, Ales, Cottureau, & Rossion, 2015; Vialatte, Maurice, Dauwels, & Cichocki, 2010). Recently, SSVEPs have also been applied to study written language processing (Lochy, Van Belle, & Rossion, 2015; Lochy, Van Reybroeck, & Rossion, 2016; Montani, Chanoine, Stoianov, Grainger, & Ziegler, 2019; Yeatman & Norcia, 2016). In particular, in a previous study, we demonstrated that the SSVEPs generated by flickering written words and pseudowords are sensitive to fundamental effects of reading aloud and that the paradigm is well suited to investigate the cortical generators of word processing (Montani et al., 2019). SSVEPs are a unique tool for investigating the role of different reading units by virtue of tagging specific subunits using different stimulation frequencies simultaneously (i.e. frequency tagging). Analyzing the frequency bins corresponding to each of the stimulation frequencies allows one to extract the evoked responses from the population of cells that are selectively entrained by each stimulus (Norcia et al., 2015).

We adopted the same paradigm as in Montani and colleagues (2019), a delayed naming task, but crucially, the target words were split into two segments, each of which flickering at a distinct frequency. The use of different stimulation frequencies allowed us to extract and selectively analyze the EEG signal associated with the brain response to the first segment. The segment could either match the first syllable of the word (i.e. congruent condition) or correspond to the first bi/trigram, containing one letter more or less than the first syllable (i.e. incongruent condition). Because the signal coming from the congruent segment reflects the activation of the population of neurons selectively entrained by the syllables, we could directly examine the

neural response associated with the processing of syllables. We compared the SSVEP responses of the congruent and incongruent segments, i.e. syllables vs. bi/trigrams, and we analyzed the time course of the syllable processing. Further, we localized the neural generators of the SSVEP responses associated with the syllable congruency effect, thus providing new evidence with respect to the time course and neural substrate of syllable processing in visual word recognition.

2. Materials and Methods

2.1 Participants

Seventeen proficient readers, naive to the purpose of the experiment, participated in the experiment as paid volunteers (age 17 - 24 years, mean = 20). We used the same number of participants as in Montani et al. (2019), who found robust frequency and lexicality effects using the same SSVEP paradigm and the same task. All participants were native French speakers, they had normal or corrected-to-normal vision and they had no history of developmental disorders. Before the experiment, participants gave informed written consent. The study was approved by the Institutional Review Board of Aix-Marseille University.

2.2 Apparatus and stimuli

Participants were seated 56 cm from the monitor in a dimly lit, electrically isolated room.

Stimuli were generated using OpenSesame 3.0 (Mathôt, Schreij, & Theeuwes, 2012) and PsychoPy (Peirce, 2007) and they were presented on a 17-in. cathode ray tube monitor (resolution 800 x 600 pixels, refresh rate 75 Hz). Strings were presented in black against a white background at the center of the screen, using Selectric font. The first part of the string flickered on and off at a frequency of 18.75 Hz (4 monitor refresh cycles per period: 1 on- and 3 off-cycles). The remaining part of the string flickered on and off at 25 Hz (3 monitor refresh cycles per period: 1 on- and 2 off-cycles). We choose a relatively high flicker frequency (18.75 Hz) because it permits a short stimulus exposure time and it is more suited to capture the fast processes involved in word reading. In addition, a recent study identified the 12–18 Hz as the optimal range for SSVEP stimulation (Kus, Duszyk, Milanowski et al., 2013).

Forty-six pairs of French words sharing the same initial three phonemes (CVC) were selected from the Lexique database (New, Pallier, Brysbaert, & Ferrand, 2004). We selected word pairs that shared the same three phonemes, such as *bal.con* and *ba.lade* (i.e., “bal”), but in one member of the pair the three phonemes coincided with the first syllable (*bal.con*) while in the other pair they did not (*ba.lade*). Eighteen pairs were bisyllabic six letter long words and 31 pairs were three or four syllabic eight letter long words. A full list of stimuli is provided in Appendix A. For each subject, each word appeared in one of two conditions: the congruent condition vs. the incongruent condition. In the congruent condition, the unit flickering at 18.75 Hz matched the first syllable, while in the incongruent condition the unit did not match the first syllable. For instance, if for one subject “*ba.lade*” appeared in the congruent condition, with the first syllable “*ba*” flickering at 18.75 Hz and the second, “*lade*” flickering at 25 Hz, for the subsequent subject, it appeared in the incongruent condition, with the first three letters “*bal*” flickering at 18.75 Hz and the second part of the word, “*ade*”, flickering at 25 Hz. This procedure

guarantees that potential syllable effects cannot be due to differences between congruent and incongruent syllables in terms of bi-or trigram frequency.

2.3 Procedure

Each trial started with a fixation point (black cross on a white screen) displayed at the center of the screen for 500 ms. After an empty screen lasting for 200 ms, the flickering word was presented for 2000 ms. Then, a screen prompted participants to name the word aloud. After 2000 ms, an empty screen replaced the response screen (see Figure 1). The interval from the start of one trial to the start of the next trial was about 7500 ms. Vocal responses were assessed online by the experimenter in order to be sure the participant was engaged in the task. Due to the long presentation time, accuracy was 100%. A session consisted of two blocks of 46 trials each (with each block including both conditions i.e. congruent and incongruent trials), with a brief pause between each block. The block sequence was counterbalanced between participants while the target word sequence in each block was randomized for each subject. The entire experimental session lasted about 20 minutes.

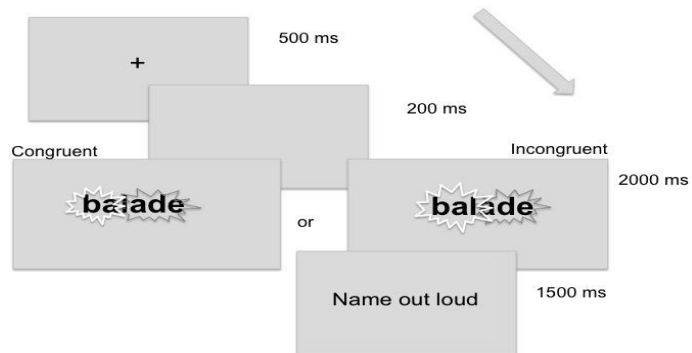


Figure 1. Experimental paradigm: delayed naming task. In the congruent condition, the first part of the word, flickering at 18.75 Hz, matched the first syllable, such as “ba” in “balade”. In the incongruent condition, the first flickering part did not match the syllable, such as “bal” in “balade” (see Procedure for further details).

2.4 EEG recording and analysis

EEG activity was acquired at 512 Hz using a Biosemi Active Two system provided with 64 Ag/AgCl sintered active electrodes. Electrodes were mounted on an elastic cap (Electro-Cap, Inc. Eaton, OH) that was positioned according to the 10-20 International system (American Clinical Neurophysiology Society, 2006). Two additional electrodes (CMS/DRL) were used as on-line reference (see www.biosemi.com). Three extra electrodes were used to monitor eye movements and blinks (two placed at the outer canthi of the eyes, one placed below the left eye). Two additional electrodes were used for an off-line re-referencing (placed behind the ears on the

mastoid bone). For the EEG analysis, we used EEGLAB (Delorme & Makeig, 2004), ERPLab (Lopez-Calderon & Luck, 2014) and Fieldtrip (Oostenveld, Fries, Maris, & Schoffelen 2011) toolboxes for Matlab and Matlab customized functions (Matlab 2014, The Mathworks). Data were re-referenced off-line to the average of left and right mastoid electrodes, bandpass filtered from 5 to 100 Hz (4th order Butterworth filter) and then segmented to include 200 ms before and 2000 ms after stimulus onset. Epoched data were normalized based on a prestimulus period of 200 ms, and then evaluated according to a sample-by-sample procedure to remove noisy sensors that were replaced using spherical splines. Additionally, EEG epochs that contained data samples exceeding threshold (100 μ V) were excluded on a sensor-by-sensor basis, including horizontal and vertical eye channels. On average, 2.85 % of the data were interpolated and 3.07 % of the data rejected. Slow drifts were removed in order to reduce “sawtooth” artifacts in the Fourier spectrum (Bach & Meigen, 1999).

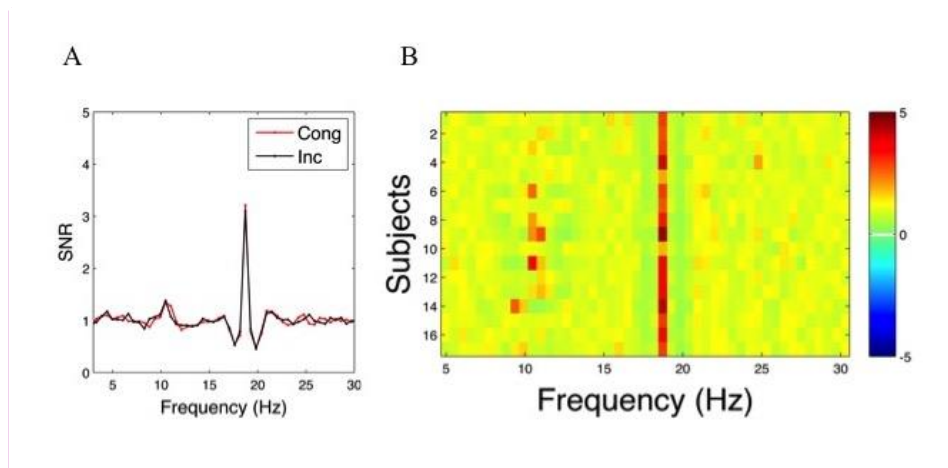


Figure 2. Entrainment to the stimulation frequency. (A) Rhythmic entrainment source separation (RESS) filtered power spectra between 0 and 30 Hz, for the congruent (red) and incongruent

Commenté [VC1]: The title of the colorbar is missing. The axis labels do not have the same size. The image resolution is not optimal. Did you use the `print(...,'-r600')` function to set the resolution? If you send me the matlab matrices of the data, I can work on them again if it suits you.

(black) conditions. The peak in the spectrum at 18.75 Hz corresponds to the entrainment at the stimulation frequency. Cong = Congruent, Inc = Incongruent. SNR = signal-to-noise ratio. (B) Power spectra between 0 and 30 Hz for each participant (rows). The vertical red line corresponds to the response at 18.75 Hz.

2.4.1 SSVEPs analysis. For the purpose of showing the entrainment to the stimulation frequency (e.g., 18.75 Hz), we followed the procedure described in Cohen and Gulbinat (2016), i.e. rhythmic entrainment source separation (RESS). The procedure consists of applying a spatial filter based on denoising source separation that increases the spectral specificity and maximizes the signal-to-noise ratio (SNR) of the steady-state response. The resulting RESS component is a weighted combination of all electrodes. Figure 2A shows the RESS filtered spectral density in which is clearly visible a peak in the spectral response at the stimulation frequency. The same peak is visible in the response of each participant (Figure 2B).

From visual inspection of the spectral response shown in Figure 2, it is also possible to recognize a peak of activity around the alpha band. Alpha band activity at approximately 10 Hz is the dominant frequency in the awake brain (for review, see e.g. Klimesch, 2012). In the present case, the alpha activity was likely related to the relaxed state of the participants and low-task demands.

We performed two different analyses on the SSVEP data for the fundamental frequency: static SSVEP, which provides a good frequency resolution and an overall view of the effect, and dynamic SSVEP, which provides good temporal precision and the possibility to detect time-varying changes in the SSVEP amplitude. We focused on the fundamental frequency rather than higher harmonics (e.g. an integer multiple of a fundamental frequency F like $2F=37.5$ Hz)

because the response was clearly stronger at 18.75 Hz. In addition, the scope of the study was to investigate the effect of the first syllable, which is why we focused the analysis on the response at 18.75 Hz. However, for the sake of completeness, we also analyzed the static SSVEP for the second segment, the remaining portion of the word, which flickered at 25 Hz.

For the static analysis, the Fourier transform was computed over the time window of interest [533-1760 msec]. To this end, EEG data were segmented again, discarding the first 533 ms from stimulus onset in order to remove the initial transient response, and the last 240 ms to have epochs containing an integer number of flicker periods. The resulting epoch, which lasted for 1227 ms, corresponds to 23 complete cycles of stimulation. To extract SSVEP activity synchronized to the stimulus flicker, EEG signals of each epoch were decomposed using Fast-Fourier Transform (FFT, frequency resolution 0.81 Hz).

For the dynamic SSVEP, i.e. a time-frequency power analysis, EEG data were segmented to include 200 ms before and 1934 ms after stimulus presentation. The resulting epoch, which lasted for 2133 ms, corresponds to 40 complete cycles. To extract the time courses of the SSVEP activity synchronized to the stimulus flicker, EEG signals of each epoch were decomposed using a moving window fast Fourier transformation analysis (frequency resolution of 0.47 Hz, temporal resolution of 20 ms). The statistical significance of the syllable congruency effect was assessed by means of cluster-based permutation tests (Maris & Oostenveld, 2007) as implemented in the Fieldtrip toolbox (MonteCarlo method, 2000 iterations, cluster alpha $p < 0.05$, 'weighted cluster mass' criterion). Identified clusters were considered significant at $p < 0.05$ (two tailed, alpha level = 0.025).

2.4.2 Source localization analysis. EEG cortical source analysis was performed using the source reconstruction method eLORETA (exact Low-Resolution Electromagnetic Tomography), which models 3D distributions of EEG cortical sources (Pascual-Marqui, 2007, for a review, see Grech, Cassar, Muscat, Camilleri, Fabri, et al., 2008) in the frequency domain. Power spectral analyses were first performed using a single-taper hanning method implemented in the Fieldtrip toolbox (<http://www.ru.nl/donders/fieldtrip>). Sources are modeled as equivalent current dipoles (ECDs, i.e. point sources or dipoles with a location and orientation) which are restricted to the volume conduction model of the head. We used a standard Boundary Element Method volume conduction model in which the head geometry is realistic and based on the ‘Colin27’ template (see Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002 for method). The standard BEM model is expressed in the Montreal Neurological Institute coordinate system (in mm) and it can be associated with a standard file of electrode positions defined in the same coordinate system. The template file of the 10-20 system for electrode placement was adapted (64 among 97 electrodes were selected) to model the position of the electrodes compatible with the current EEG acquisition system. A three-dimensional grid with 5 mm spacing dipoles was defined in the inner skull volume, resulting in 54180 dipoles. To assess the presence of a syllable congruency effect on the EEG cortical source data, we conducted a time windows analysis contrasting the congruent condition vs. the incongruent condition. In order to select relevant time windows, we inspected the variations in the mean global power, measured averaging the signals of all electrodes over all participants and conditions (Strijkers, Bertrand, & Grainger, 2015). In that manner, we identified four time windows: [50-250 msec], [350-550 msec], [650-850 msec], and [1050-1250 msec]. Notably, the first two windows correspond to relevant timing in syllable processing as reported in previous EEG studies (e.g. Carreiras, et al., 2005). The statistical

significance of the syllable effect was assessed by means of cluster-based permutation tests (Maris & Oostenveld, 2007) as implemented in the Fieldtrip toolbox (MonteCarlo method, 2000 iterations, cluster alpha $p < 0.05$, 'weighted cluster mass' criterion). Identified clusters were considered significant at $p < 0.05$ (two tailed, alpha level = 0.025).

3. Results

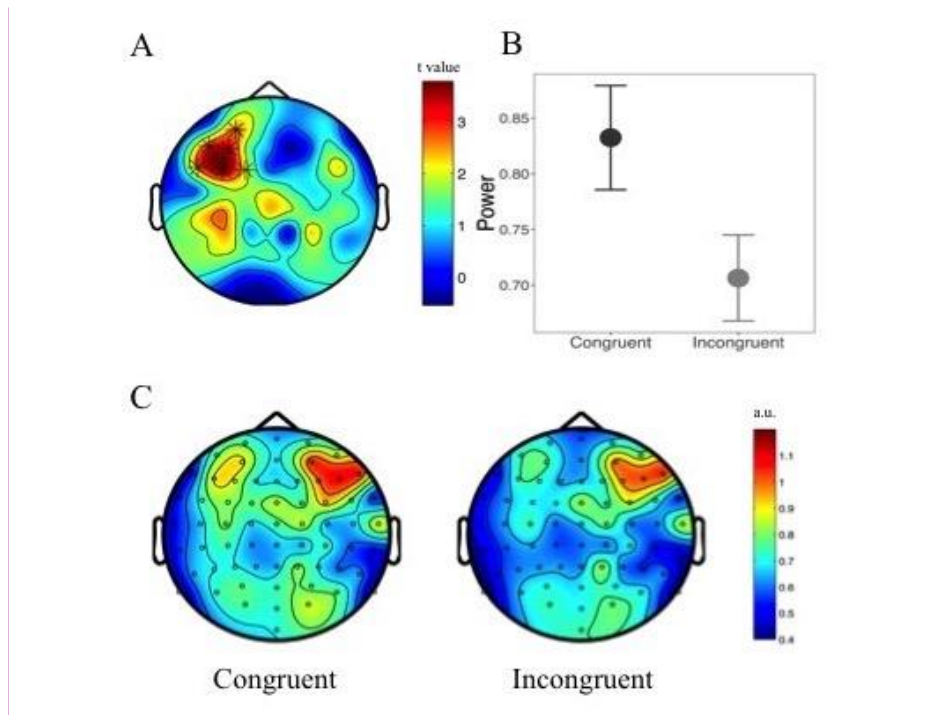


Figure 3. Syllable congruency effect. (A) Topographic distribution of the syllable congruency

Commenté [VC2]:

Commenté [VC3R2]: Could we improve the resolution?

effect. The cluster (locations that are highlighted with the asterisks, see Text) shows the difference in the power at 18.75 Hz between the congruent and incongruent conditions, plotted on top of the T-statistic of the difference. (B) Syllable modulation of the steady state evoked potentials (SSVEPs) elicited by written words. Congruent: when the first flickering unit matched the first syllable. Incongruent: when the first flickering unit did not match the first syllable. Power is collapsed across the significant electrode cluster (see text). Error bars represent standard error of the means (SEMs) adjusted to correctly reflect the variance in the within-subject design (Morey, 2008). (C) Topographic distribution of the response at 18.75 Hz for the congruent condition (left) and the incongruent condition (right).

3.1 SSVEP power. Testing for the syllable effect at 18.75 Hz, the cluster-based permutation test revealed a significant difference between the congruent and the incongruent condition ($p < .05$). Figure 3A shows the topographic distribution of the difference between the SSVEPs elicited by the congruent and the incongruent condition along with the electrode locations (asterisks): AF3, F3, F5, FC5, FC3, FC1. Figure 3B shows the mean SSVEP power for the congruent and incongruent condition, calculated by averaging across the significant electrodes in the cluster.

Testing for the effects of syllable congruency over time, in the latency range from 40 to 1200 ms post-stimulus onset, the cluster-based permutation test revealed a significant difference between the congruent and the incongruent condition ($p < .05$). Figure 4A shows the cluster of significant electrodes between 1000 and 1200 ms along with the electrode locations (asterisks): AF3, F3, F5, FC5, FC3, FC1, CP5, CP3, P3, P5, P7, PO7, PO3. Averaged SSVEP power over time, for congruent and incongruent conditions, is shown in Figure 4B. For the sake of clarity, in

the top panel, mean power is calculated averaging across the electrodes that were also included in the cluster emerged from the static analysis (left frontal cluster shown in Figure 3A). In the bottom panel, mean power is calculated averaging across the remaining electrodes, located in the left occipito-parietal area: CP5, CP3, P3, P5, P7, PO7, PO3.

Testing for the syllable effect of the second syllable that was flickered at a stimulation frequency of 25 Hz, the cluster-based permutation test did not reveal any significant difference between the congruent and the incongruent condition ($p > .05$).

Commenté [JZ4]: OK to add this?

Commenté [VM5]: No, because stimuli were either bisyllabic or three/ four syllabic words. Then, the second segment corresponded to the second syllable just for the bisyllabic words, otherwise it was more than one syllable.

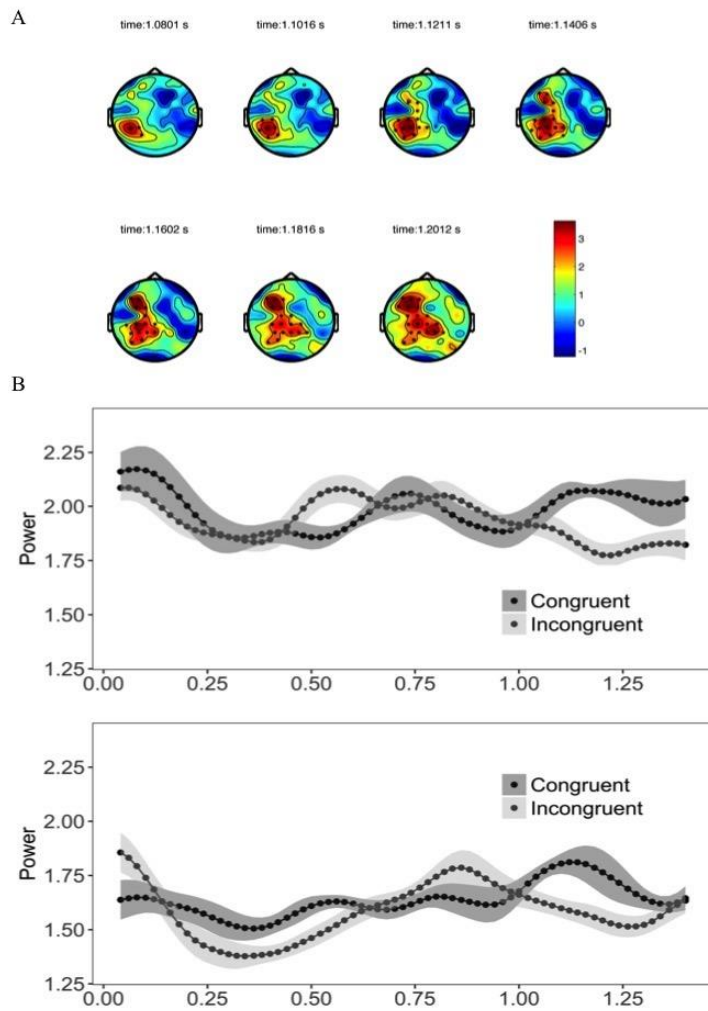


Figure 4. Temporal evolution of the syllable congruency effect. (A) Topographic distribution of the syllable congruency effect. The cluster (locations that are highlighted with the asterisks) shows the difference in the power at 18.75 Hz, from 1000 to 1200 ms after stimulus onset, between the congruent and incongruent conditions. The power is plotted on top of the T-statistic

Commenté [VC6]: Could we improve the figure resolution. The title of colorbar is missing...

of the difference. (B) Temporal evolution of the syllable modulation of the steady state evoked potentials (SSVEPs) elicited by written words. For clarity, the cluster is split into two distinct clusters. Top panel: left frontal cluster (see Figure 3A). Bottom panel: left occipito-parieto-central cluster. Congruent: when the first flickering unit matched the first syllable. Incongruent: when the first flickering unit did not match the first syllable. Power is collapsed across the significant electrode cluster. Shadows represent standard error of the means (SEMs) adjusted to correctly reflect the variance in the within-subject design (Morey, 2008).

3.2 SSVEP in source space. Testing for the syllable congruency effect in the four time windows, [50-250 msec], [350-550 msec], [650-850 msec], and [1050-1250 msec], the cluster-based permutation test revealed a significant difference between the congruent and the incongruent conditions in the [50-250 msec] and [350-550 msec] time windows.

Figure 5A shows the activation map for the syllable congruency effect in the [50-250 msec] window. The congruency effect emerged from medial areas centered around the right middle cingulum [0 -25 35], in which there was greater activation for the congruent syllable condition compared to the incongruent condition ($t(17) = 5.17, p < .05$). The cluster included also the posterior cingulum, the supplementary motor area (SMA), the paracentral lobule bilaterally, and, exclusively on the right, the precentral gyrus, the frontal superior and middle gyri, the thalamus, the caudate nucleus, the post central gyrus, the anterior cingulum, the precuneus and the hippocampus. Figure 5B shows the individual plots of the source estimates for the syllable congruency effect in the [50 250] window.

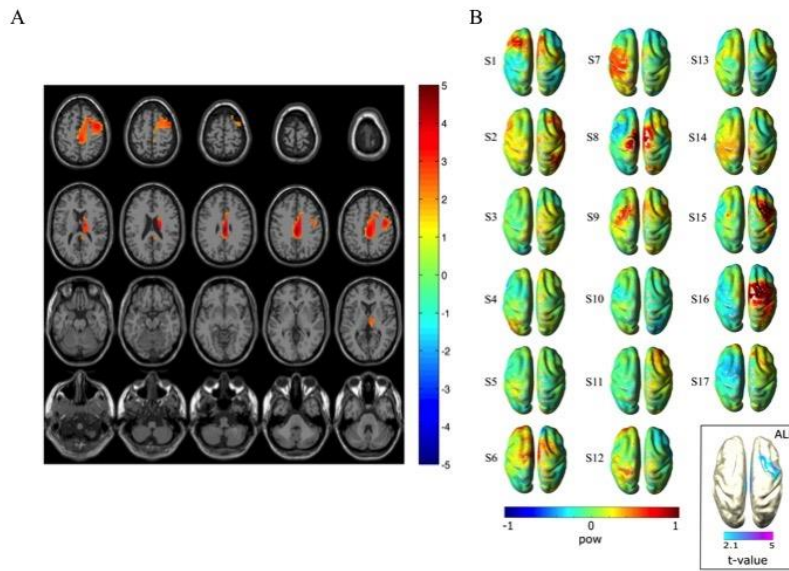


Figure 5. Cortical sources of the syllable congruency effect at the [50 250] window. (A) Statistical maps (masked at cluster-corrected $P < 0.05$) comparing the source reconstructed SSVEPs between the congruent and incongruent conditions localized the congruency effect to medial areas centered around the right middle cingulum [0 -25 35]. (B) The individual brains show the difference in source spectral power (pow) between the Congruent and Incongruent conditions. The box on the bottom right represents the statistical map between the two conditions across all subjects (masked at cluster-corrected $p < .05$).

Figure 6A shows the activation map for the syllable congruency effect in the [350-550 msec] window. The congruency effect emerged from a left top area centered around the precentral and frontal middle gyri [-35 00 55], in which there was greater activation for the congruent syllable condition compared to the incongruent condition ($t(17) = 3.80$, $p < .05$). This

Commenté [VC7]: Same remarks !

cluster included also the precentral and postcentral gyri, the parietal superior and inferior lobule, the frontal superior gyrus, the insula, the rolandic operculum, the supramarginal and angular gyri. Figure 6B shows the individual plots of the source estimates for the syllable congruency effect in the [350 550] window.

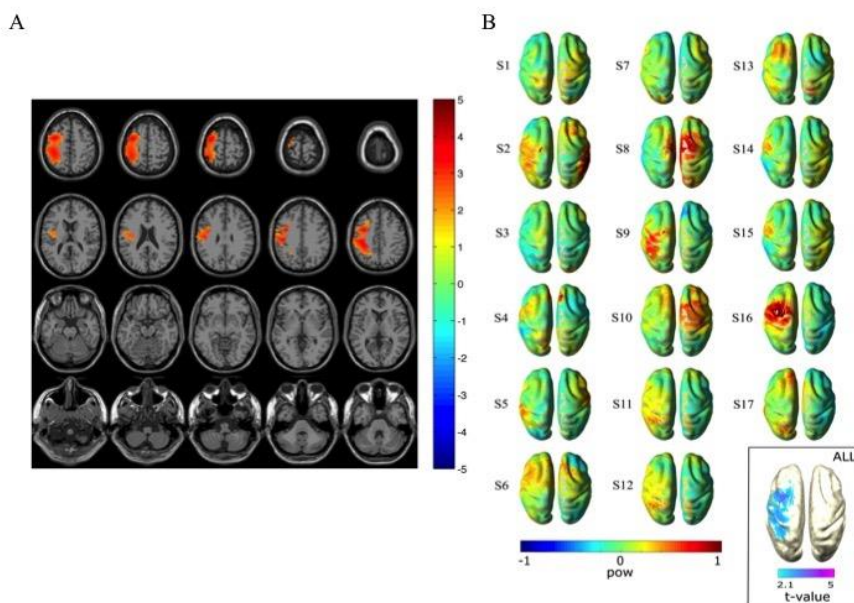


Figure 6. Cortical sources of the syllable congruency effect at the [350 550] window. (A) Statistical maps (masked at cluster-corrected $P < 0.05$) comparing the source reconstructed SSVEPs between the congruent and incongruent conditions localized the syllable congruency effect to left top areas centered around the precentral and frontal middle gyri [-35 00 55]. (B) The individual brains show the difference in source spectral power (pow) between the Congruent and Incongruent conditions. The box on the bottom right represents the statistical map between the two conditions across all subjects (masked at cluster-corrected $p < .05$).

Commenté [VC8]: Same remarks

4. Discussion

In the present study, we directly assessed the spatio-temporal dynamics of syllable processing by tagging the brain responses (SSVEPs) associated with different word segments using distinct stimulation frequencies simultaneously. The flickering segment could either match (i.e., congruent condition) or not match the first syllable (i.e., incongruent condition). The largest SSVEPs were observed in the congruent condition (see Figure 3), which supports the idea that syllables are more relevant units than simple bi/trigrams in processing written words.

The rich literature concerning the role of the syllable in reading has shown that it affects visual word recognition at different and multiple stages, sometimes in contrasting ways. Early facilitatory effects of syllable congruency seem to correspond to the structural parsing of the written word, i.e. syllabification (Álvarez, Carreiras, & Perea, 2004; Carreiras et al., 2005; Conrad, Tamm, Carreiras, & Jacobs, 2010). Syllable frequency, on the other hand, has an inhibitory effect on lexical access (Alvarez, et al., 2000; 2001; Carreiras, et al., 1993; Carreiras & Perea, 2002; Conrad & Jacobs, 2004; Mathey & Zagar, 2002; Perea & Carreiras, 1998), which stands in contrast to the facilitatory effects obtained for other frequently occurring sublexical units, such as bigrams or trigrams (see Dehaene, et al., 2005; Hannagan, Ziegler, Dufau, Fagot, & Grainger, 2014). The facilitatory syllabic parsing and the inhibitory syllable frequency effect have been successfully simulated with a computational model that includes an additional layer containing syllable representations (Conrad et al., 2010). However, the nature of this representation is still elusive. On the one hand, the comparison between orthographically and

phonologically defined syllables showed that the inhibitory effect is attributable to the phonological syllable, which suggests that competition takes place within the phonological lexicon (Conrad et al., 2007). On the other hand, facilitatory syllable priming and syllable frequency effects observed in reading aloud seem to originate at the level of phonetic encoding (Cholin, & Levelt, 2009; Laganaro, & Alario, 2006). Finally, syllables are hypothesized to be stored as packages of abstract motor programs at a postlexical level (Crompton, 1981; Levelt, & Wheeldon, 1994; MacNeilage, 1998).

The major strength of our approach is that we could directly measure the neural response associated with the processing of syllables and potentially shed light on its various roles in reading (but see section 4.6 Limitations). In the following sections, we will suggest a possible interpretation of our findings that may provide a unified framework for the seemingly disparate effects summarized above. However, we will start the discussion by giving a hypothetical mechanistic account of the increased SSVEP for syllables.

4.1 Neural mechanisms of SSVEP

The exact mechanism behind the generation of SSVEPs is still debated (e.g. Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011; Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007; Srinivasan, Bibi, & Nunez, 2006). Here, we propose a possible explanation for the increased power in the congruent syllable condition on the basis of what is known about SSVEP, neural oscillations, and the role of syllables in language processing.

Neural activity follows spontaneously a changing stimulus producing steady-state

potentials. In the auditory domain, entrained cortical activity, which is tuned to the syllabic rhythm of speech (see e.g., Giraud & Poeppel, 2012), can be measured when subjects listen to sentences or spoken passages (for review, see Ding & Simon, 2014). The SSVEP seems to derive from the entrainment of an internal oscillator by the external rhythmic driving force (Notbohm, Kurths, & Herrmann, 2016), possibly by the way of phase alignment (e.g., Kashiwase, Matsumiya, Kuriki, & Shioiri, 2012; Moratti Clementz, Gao, Ortiz, & Keil, 2007).

In general, the amplitude changes in oscillatory activity are thought to arise from the synchronization of neural activity in distributed networks (Pfurtscheller & da Silva, 1999). According to a very influential model of neural oscillations, the temporal synchrony between neurons is crucial for perceptual processing (for reviews, see Buzsáki, 2010, 2004; Fries, 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001). In that view, representational information, such as for example object identity or word meaning, is stored in flexible cell assemblies, transiently synchronized by dynamic connections. Put in other words, the representation of familiar, significant or meaningful items is based on assemblies of strongly connected sets of neurons that behave in a functionally coherent manner (Garagnani Lucchese, Tomasello, Wennekers, & Pulvermuller 2017; Pulvermüller, Garagnani, & Wennekers, 2014). Consequently, because syllables are important functional units in language processing (Geiser, Zaehle, Jancke, & Meyer, 2008; Levelt et al., 1999; MacNeilage, 1998; Ordin, Polyanskaya, Laka, & Nespors, 2017; Ramus et al., 1999), their neural representation should be characterized by more coherent neural dynamics and larger networks (including stronger connections with sensorimotor areas and associations with higher-order regions) compared to simple bi- or trigrams of letters.

Moreover, it is generally assumed that larger SSVEP responses are caused by more

efficient network dynamics (Zhang, Guo, Cheng, Yao, & Xu, 2015). That is, the flickering stimulus causes cortical entrainment and the resulting wave-like activity could “travel” more easily through a preconfigured assembly rather than a relatively “disorganized” set of neurons. Indeed, in a previous study, we have shown that written words showed larger SSVEPs than pseudowords and high-frequency words showed larger SSVEPs than low-frequency words (Montani et al., 2019). In the same vein, we suggest that the processing of syllables is characterized by larger SSVEP responses because the wave-like activity generated by the periodic stimulation might “travel” more easily through a selectively synchronized neural network in the case of existing syllables as compared to sequences of letters that do not match syllables. The fact that cortical entrainment was more efficient for syllables than for non-syllabic bi- or trigrams is in line with the idea that syllables are important functional units in reading (e.g. Carreiras et al, 2009, Conrad & Jacobs, 2004) and explains the facilitatory effects previously observed in masked priming (e.g., Alvarez et al., 2004; Carreiras & Perea, 2002; Carreiras, et al., 2005; Ferrand et al., 1996), in the color-congruency paradigm (Carreiras et al, 2005; 2009), or in the word-spotting paradigm (Alvarez et al., 2016).

It is interesting to note that we did not find any evident intermodulation (IM) terms, i.e. responses at frequencies not present in the stimulus but related to the input frequencies as sums (e.g. $F1+F2 = 43.75$) or differences (e.g. $F2-F1 = 6.25$) of the different harmonics of the stimulus frequencies (Norcia et al., 2015). IM response components reflect convergence processes and the integration of the constituent parts of the object in a unified representation, such as, for example, perceptual binding in binocular rivalry (Sutoyo & Srinivasan, 2009), integration of flickering horizontal and vertical bars to a moving square (Aisssani, Cottureau, Dumas, Paradis, & Lorenceau, 2011), perception of illusory contours (Gundlach & Muller, 2013), ‘holistic’

responses to faces (Boremanse, Norcia, & Rossion, 2014). Manipulations that breaks the ‘whole’ percept into its constituent parts, such as spatial separation by a gap of the two halves of a face (Boremanse et al., 2014) or introducing a discontinuity in figure/background interactions (Appelbaum, Wade, Pettet, Vildavski, & Norcia, 2008) have shown to considerably reduce or even abolish most of the IM responses. In the present paradigm, a hypothetical IM component would have reflected the convergence of the visual processing of the first and second segment, flickering at 18.75 Hz and 25 Hz respectively. Therefore, the absence of IM components suggests that the constituent parts of the written word (letters) are processed as distinct units rather than fused into a single unified percept. On the other hand, the information related to the word converges into a ‘word as a whole’ at a different and more advanced level of processing that it is likely not captured by the IM components.

Commenté [JZ9]: Highly speculative and the IM concept hasn't been introduced before, neither in the hypotheses nor in the results. I would take it out.

4.2 Time course of syllable congruency effects

The syllable congruency effect emerged rather late in time, around 1000 msec, in the left posterior hemisphere (Fig 4B bottom panel), and progressively extended to the left anterior hemisphere (Fig 4B top panel), and to the center, slightly later (Fig. 4A). The left anterior scalp location of the effect is consistent with the left frontal distribution of the ERP syllable–color congruency effect found by Carreiras et al. (2005). However, the syllable–color congruency effect shows to affect the processing of written words much earlier, in the P200 window, and importantly, before the effect of lexical frequency. Consequently, it has been suggested that the syllable–color congruency effect taps early syllabic segmentation processes (Carreiras et al.,

2009). In contrast, the present late effect of the SSVEP modulation seems to suggest that the syllable ‘advantage’ for the congruent condition (in the sense proposed in the previous section, 4.1 Neural mechanisms of SSVEP) emerges from some late process, such as the planning of the articulatory output, in line with the hypothesis that facilitatory effects of syllables operate at the level of output phonology (e.g., Alvarez, et al., 2016; Carreiras, & Perea, 2004; Cholin, & Levelt, 2009; Ferrand et al., 1996; Laganaro, & Alario, 2006). ~~To explain the facilitatory effect of the syllable frequency in tasks that require a spoken response, it has been proposed that accessing a high frequency syllable in the mental syllabary is faster than accessing a low frequency syllable (Levelt & Wheeldon, 1994). (Here, we hypothesize that the network tagged by the flickering stimulation in the congruent condition, i.e. the syllable representation, had privileged access to the mental syllabary compared to simple bi- or trigrams of letters.)~~ However, there was also an early initial advantage starting around 200 msec for the congruent condition in the left-occipito-parietal area, which was no longer significant after correction. This temporal pattern therefore, partially resembles the syllable-color congruency effect suggesting the existence of some sort of connection between the two phenomena.

4.3 Neural generators of the syllable congruency effect in the [50 250] window

The source localization of the syllable congruency effect showed a significant effect in the [50 250] window, which reflected greater activation for syllables compared to simple bi/trigrams. We found a large cluster extending from a mesial area to the right hemisphere (Figures 5). The peak of activation was located in the left and right middle cingulum. The cluster

Commenté [JZ10]: Not sure I fully understand the basis of this argument

Commenté [VM11]: my logic is:

1. the ‘congruent’ flickering stimulation tagged the neural network supporting syllable processing, i.e. the syllable representation
2. representation of syllable includes the mental syllabary, i.e. “consists of highly over-learned and complete gestural patterns associated to high-frequency syllables”
3. Therefore, the network tagged in the congruent condition included the syllabary, while the network tagged in the incongruent condition, i.e. bi.trigram did not get such a direct and fast access to the syllabary (or frequent articulatory patterns)

In other words, this late effect (syllable advantage) is produced by the motor planning because the motor planning is associated to the syllable (not to bigram)

When we articulate a word, we articulate sequences of syllables not sequences of bigrams
Make sense?

Jo: OK, I just don’t see what this adds, especially the term “privileged”. It seems to be speculative. I think you don’t lose anything by stopping after output phonology and start again with “However”. But up to you, I am being picky. Also, I guess I don’t understand why we need to explain the facilitatory syllable frequency effect in naming. We haven’t manipulated syllable frequency and there is no disagreement in naming that facilitatory effects are likely to result from output phonology.

Commenté [JZ12]: Not clear what two phenomena you are talking about. May be stop after “syllable-color congruency effect”.

included also the thalamus, the precuneus, the hippocampus, the caudate nucleus, the supplementary motor area (SMA), the dorsolateral prefrontal cortex (dlPFC), and sensorimotor areas. Overall, these areas are structurally and functionally connected establishing the fronto-striatal circuits that mediate motor control and executive functions (e.g., Miller & Cohen, 2001; Jahanshahi, Obeso, Rothwell, & Obeso, 2015; Morris Kundu, Dowell, Mechelmans, Favre et al., 2016; and Bohland & Guenther, 2006; Ghosh, Tourville, & Guenther, 2008, Riecker, Mathiak, Wildgruber, Erb, Hertrich et al., 2005a for speech motor control). These areas are involved in response selection when there are multiple competing responses (Arsalidou, Duerden, & Taylor, 2013; Bush, Luu, & Posner, 2000; Grahn, Parkinson, & Owen, 2008; Hazy, Frank, & O'Reilly, 2006; Munakata, Herd, Chatham, Depue, Banich, & O'Reilly, 2011; Ullman, 2004; Wenderoth, Debaere, Sunaert, & Swinnen, 2005). It is tempting to speculate that activation of these areas is due to competition between words that share the same syllables (inhibitory syllable frequency effect). Indeed, it has been hypothesized that high-frequency syllables activate a larger number of word candidates compared to low frequency syllables (Carreiras et al., 1993, 2009) and the subsequent competition among different lexical entries requires the involvement of areas devoted to response selection (Carreiras et al., 2009).

The pattern of activation we found at [50 250] was partially right lateralized and encompassed regions associated with motor control. This is in line with the idea that visual word recognition implicates the fast activation of the motor plans associated with syllable articulation. The syllable is as a key unit for speech motor output (MacNeilage, 1998) and the basic motor execution processes of speech control are organized bilaterally (Riecker et al., 2005b; Riecker, Brendel, Ziegler, Erb, & Ackermann, 2008). According to Levelt et al. (1999), most of the articulatory work is done by a small set of syllables that are stored as units in a mental

'syllabary' (Levelt et al., 1999). The syllabary consists of highly over-learned and complete gestural patterns associated to high-frequency syllables and which need not be recomputed each time. Therefore, the pattern of activation at [50 250] could specifically represent the neural correlate of a direct route that links the subcortical structures (i.e. cingulate cortex) implicated in visual perception to the motor routines representing the articulatory programs of syllables (Amiez, Hadj-Bouziane, & Petrides, 2012).

Critically, the key structures for the generation of the syllabic frames (i.e. each cycle generated by the rhythmic alternation between an open and closed mouth) in the frame/content theory of speech production are the anterior cingulate and the SMA (MacNeilage, 1998). Syllables are fundamental units in determining speech rhythm (Geiser et al., 2008) and speech intelligibility depends strongly on syllabic structure (Ramus et al., 1999) and syllable rhythm (Ghitza & Greenberg, 2009). A large number of studies on interval timing, duration perception, rhythm cognition supports the critical role of the same cortico-basal ganglia-thalamic circuits that we found associated with the 'syllable' condition (e.g., Alm, 2004; Gu, van Rijn, & Meck, 2015; Matell & Meck, 2004; Schirmer, 2004; Teki & Griffiths, 2016; Trost, Fruhholz, Schon, Labbe, Pichon, Grandjean, & Vuilleumier, 2014; Wiener, Turkeltaub, & Coslett, 2010). While the left hemisphere is sensitive to fast events (20-50 ms), the right hemisphere is more sensitive to events at the time scale of syllables (150-250 ms; Boemio, Fromm, Braun, & Poeppel, 2005; Poeppel, 2003). The perception of suprasegmentally modulated speech rhythm in the time range of syllables (150-200 ms) recruited specifically the SMA bilaterally, the cingulate gyrus and the insulae, and exclusively on the right, the striatum and the frontal inferior gyrus (Geiser et al., 2008). To conclude, overall the different aspects of the scenario depicted so far indicate a remarkable consistency between our findings and the neural network that is hypothesized to be

responsible for the control of syllables production/perception in speech.

The present cluster of activation includes the regions associated with the syllable-color congruency effect as reported in an fMRI study, i.e. precuneus/paracentral gyrus, superior frontal gyrus and thalamus (Carreiras et al., 2009). In addition, the ERP timing of the syllable-color congruency effect (i.e., P200) corresponds to the present time window (Carreiras et al., 2005). Therefore, as noted earlier, there seems to be a clear connection between the SSVEP syllable ‘advantage’ and the syllable-color congruency effect. Early syllabic effects have been associated with a syllabic parsing mechanism, or ‘syllabic route’, where some sort of syllable representations mediate between the low-level visual processing stage and the word (lexical) level (Álvarez, et al., 2004; Carreiras et al., 2005; Conrad, et al., 2010). Because of the relevance of the motor aspects in defining the brain network that instantiates the syllable representation (e.g., MacNeilage, 1998), it is possible that the ‘syllabic route’ directly connects the sublexical orthographic representations to the representations of syllable in the form of articulatory gestures (Ferrand et al, 1996). Therefore, the pre-activation of the network that might be responsible for the facilitatory effect at the production stage would also, in some way, mediate the syllabic segmentation at the first stages of the recognition process.

However, the present paradigm required participants to name aloud, while the findings associated with the syllable-color congruency effect were obtained with the lexical decision task. Because our participants were required to name aloud, the activation of regions associated with motor control could be exclusively attributed to motor planning. More research is needed to explore the role of motor plans in the decoding process in a task that does not require a spoken response.

4.4 Neural generators of the syllable congruency effect in the [350-550] window

The pattern of activation that we found in the [350-550 msec] window was entirely left lateralized (Fig. 6) and basically included most of the left hemisphere areas historically considered as the neural substrate of language processing (Price, 2012). Specifically, the peak of activation was located in the precentral gyrus and in the middle frontal gyrus. The cluster included also the frontal inferior operculum, the frontal superior gyrus, the rolandic operculum, the insula, the post central gyrus, the parietal superior lobule (SPL), the supramarginal gyrus (SG) and the angular gyrus (AG).

As suggested for the earlier time window, sensorimotor regions are often argued to be a part of cell assemblies that represent written or spoken words (Pulvermüller & Fadiga, 2010; Strijkers & Costa, 2016). However, in contrast to the previous cluster, the areas of the left cluster have been specifically associated with phonological processing (Price, 2012) and the sequencing of subsyllabic information in overt speech production (e.g. Riecker et al. 2008). In the context of the frame/content theory (MacNeilage, 1998), one could argue that this cluster of activation reflects the neural correlate of the segmental (phonological) content, i.e. the modulation of the basic cycle (frame) in the form of different consonants and vowels (MacNeilage, 1998; Bohland Bullock, & Guenther, 2010).

The left ventrolateral prefrontal cortex (VLPFC) has been identified as playing a critical role in resolving conflict among multiple competing representations (e.g., Badre, Poldrack, Pare-Blagoev, Insler, & Wagner, 2005; Han, O'Connor, Eslick, & Dobbins, 2011; Rodriguez-Fornells van der Lugt, Rotte, Britti, Heinze, & Munte, 2005; Thompson-Schill, D'Esposito, Aguirre, & Farah, 1997). The left inferior frontal gyrus (IFG) has been specifically associated with the

resolution of lexical competition (Schnur, Schwartz, Kimberg, Hirshorn, Coslett, & Thompson-Schill, 2009) and verbal suppression in a semantic task (De Zubicaray, Zelaya, Andrew, Williams, & Bullmore, 2000). Therefore, even the involvement of the left frontal regions could be explained in terms of selection of the correct candidate and inhibition of competing candidates (Levelt et al., 1999).

With respect to the recruitment of the parietal lobe, the superior parietal lobule (SPL) seems to be involved in a variety of cognitive processes, such as visually guided visuomotor functions, visual perception, spatial cognition, reasoning, working memory, and attention (Wang, Yang, Fan, Xu, Li, et al., 2015). The inferior parietal lobe is an important constituent of the cortical language network (Binder, Desai, Graves, & Conant, 2009; Graves, Desai, Humphries, Seidenberg, & Binder, 2010; Price, 2012), and its specific contribution to visual word recognition has been documented (Sliwinska, James, & Devlin, 2015; Stoeckel, Gough, Watkins, & Devlin, 2009). There is substantial evidence connecting the supramarginal gyrus to phonological processing (e.g., Graves et al., 2010; Sliwinska, James, & Devlin, 2015; Vigneau et al., 2006), while the angular gyrus seems to be involved in semantic processes or complex high-level integration of information (e.g. Seghier, 2013, for review). However, Takashima et al. demonstrated that the learning of novel syllables was associated with increased activity primarily in the angular gyrus and the precuneus (Takashima et al., 2014). Because their syllables were meaningless, the authors interpreted the finding as evidence that those areas code for orthography-phonology associations from small grapheme-phoneme conversion to larger units entailing syllables.

4.5 Cross-language differences

The importance of phonological syllables as functional units in reading has been confirmed not only in French and Spanish but also in other languages, such as German (e.g. Conrad, Stenneken, & Jacobs, 2006; Conrad & Jacobs, 2004; Hutzler et al., 2004), Greek (Protopapas & Kapnoula, 2016), and Finnish (Häikiö, Hyönä, & Bertram, 2015). In contrast, investigations in English have produced mixed results (see e.g., Taft, 2001). English is characterized by inconsistent spelling-to-sound correspondence (Ziegler, Stone & Jacobs, 1997) as well as poorly marked syllable boundaries. Thus, the syllable may be less functional in English than in other languages. In a corpus-based analysis of lexical decision and naming in English, Macizo and Van Petten (2006) found a facilitatory effect of frequent syllables in naming, and importantly, in lexical decision as well. The finding in lexical decision is in contrast with the inhibitory effects reported for languages in which syllables are more salient units, such as Spanish or German. They concluded that phonological codes in English are accessed more slowly and do not lead to the activation of similar-sounding competitors quickly enough to interfere with visual lexical decision. On the other hand, there is ERPs evidence for an early activation of phonological representations of syllables even in English (Ashby, 2010; Ashby & Martin, 2008). In future work, SSVEPs might give further insights into the effects of syllables and syllable frequency in English. If it is the case that the longer processing times of English syllables prevent the spread of activation to competing entries, we would predict a different pattern of neuronal activity with no or minimal involvement of the fronto-striatal circuits in English.

4.6 Limitations

The location of the generators that gave rise to the scalp potential map can be estimated with reasonable precision (Michel & Murray, 2012, Michel et al., 2004) and the high signal-to-noise ratio of the SSVEP provides an advantage over standard ERP approaches (Norcia et al., 2015). However, the results from the source reconstruction need to be interpreted with caution because the relatively low-density electrical recording adopted in the present study implies a certain degree of uncertainty and approximation in the localization of the neural sources (Sohrabpour, Lu, Kankirawatana, Blount, et al., 2015; Song, Davey, Poulsen, et al., 2015). Also, the steady-state responses in different frequency bands showed different sensitivities to physical stimulus parameters (Regan, 1989). Therefore, the specific stimulation frequency adopted to elicit the SSVEPs (18.75 Hz in the present study) could entrain the specific functional networks in which natural frequencies might match the flicker frequency (Ding, Sperling, & Srinivasan 2005; Srinivasan, Bibi, & Nunez, 2006). Future investigations are needed to systematically explore the use of different frequencies.

4.7 Conclusion

In the present study, we found a clear-syllable congruency effect in SSVEP power at the stimulation frequency of 18.75Hz. Thus, frequency tagging in a SSVEP paradigm provided direct evidence that the brain processes the syllable as a functional unit in reading aloud. At the sensor level, the syllable congruency effect occurred rather late, which suggests that it takes some time for rhythmic entrainment to the stimulation frequency to reach a measurable level of intensity at the sensor level.

However, at the source level, we found significant syllable congruency effects in the two time windows that have been previously reported in ERP studies, around 150 and 450 ms. Source reconstruction suggested the early involvement of a right-hemisphere network associated with overt speech production in favor of the idea that the motor system is part of the neural representation of syllables, as suggested by speech production theories (Bohland & Guenther, 2006; Levelt et al., 1999; MacNeilage, 1998). In the subsequent time window [350 550] ms, the syllable congruency effect showed up in the left phonological processing areas, a finding that can be taken to suggest that the print-to-sound mapping might operate at the level of syllable-sized frames (e.g., MacNeilage, 1998).

The involvement of the frontal areas was interpreted to reflect response selection and inhibition of competing responses (Carreiras et al., 2009). The activation of the right executive function network could suggest the recruitment of a domain-general control process. Overall, and in line with the most recent views on word perception and production (Strijkers, Costa & Pulermüller, 2017; Ziegler Montant, Briesemeister, et al., 2018), our findings argue against a strictly serial architecture of written word processing, and rather support the existence of a highly interactive framework characterized by a system-wide integration of re-entrant activity (Carreiras, et al., 2014; Whaley, Kadipasaoglu, Cox, & Tandon, 2016).

Acknowledgments

This research, carried out within the Labex BLRI (ANR-11-LABX-0036) and the Institute of Convergence ILCB (ANR-16-CONV-0002), has benefited from support from the French government, managed by the French National Agency for Research (ANR) and the Excellence Initiative of Aix-Marseille University A*MIDEX (ANR-11-IDEX-0001-02).

5. References

- Aissani, C., Cottureau, B., Dumas, G., Paradis, A. L., & Lorenceau, J. (2011). Magnetoencephalographic signatures of visual form and motion binding. *Brain research, 1408*, 27-40.
- Alm, P. A. (2004). Stuttering and the basal ganglia circuits: A critical review of possible relations *Journal of communication disorders, 37*(4), 325-369. doi:10.1016/j.jcomdis.2004.03.001
- Alvarez, C., Garcia-Saavedra, G., Luque, J. L., & Taft, M. (2016). Syllabic parsing in children: A developmental study using visual word-spotting in Spanish. *Journal of Child Language, 44*(2), 380-401 doi: 10.1017/S0305000916000040
- Alvarez, C. J., Carreiras, M., & De Vega, M. (2000). Syllable-frequency effect in visual word recognition: Evidence of sequential-type processing. *Psicologica, 21* , 341–374.
- Alvarez, C. J., Carreiras, M., & Perea, M. (2004). Are syllables phonological units in visual word recognition? *Language and Cognitive processes, 19*(3), 427-452. doi:10.1080/01690960344000242
- Alvarez, C. J., Carreiras, M., & Taft, M. (2001). Syllables and morphemes: contrasting frequency effects in Spanish. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 27*(2), 545. doi: 10.1037/0278-7393.27.2.545
- Amiez, C., Hadj-Bouziane, F., & Petrides, M. (2012). Response selection versus feedback analysis in conditional visuo-motor learning. *NeuroImage , 59* (4), 3723–3735. doi: 10.1016/j.neuroimage.2011.10.058
- Appelbaum, L. G., Wade, A. R., Pettet, M. W., Vildavski, V. Y., & Norcia, A. M. (2008). Figure-ground interaction in the human visual cortex. *Journal of Vision, 8*(9), 8-8.
- Arsalidou, M., Duerden, E. G., & Taylor, M. J. (2013). The centre of the brain: Topographical model of motor, cognitive, affective, and somatosensory functions of the basal ganglia. *Human Brain Mapping, 34* (11), 3031–3054. doi: 10.1002/hbm.22124
- Ashby, J. (2010). Phonology is fundamental in skilled reading: Evidence from ERPs. *Psychonomic Bulletin & Review, 17*(1), 95-100.
- Ashby, J., & Martin, A. E. (2008). Prosodic phonological representations early in visual word recognition. *Journal of Experimental Psychology: Human perception and performance, 34*(1), 224.
- Bach, M., & Meigen, T. (1999). Do's and don'ts in Fourier analysis of steady-state potentials. *Documenta Ophthalmologica, 99* (1), 69–82. doi:10.1023/A:1002648202420
- Badre, D., Poldrack, R. A., Par´e-Blagoev, E. J., Insler, R. Z., & Wagner, A. D. (2005). Dissociable controlled retrieval and generalized selection mechanisms in ventrolateral prefrontal cortex. *Neuron, 47* (6), 907–918 doi:10.1016/j.neuron.2005.07.023
- Barber, H., Vergara, M., & Carreiras, M. (2004). Syllable-frequency effects in visual word recognition: evidence from ERPs. *Neuroreport, 15* (3), 545–548. doi: 00001756-200403010-00032
- 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 December, 19* , 2767–2796. doi: 10.1093/cercor/bhp055

- Boemio, A., Fromm, S., Braun, A., & Poeppel, D. (2005). Hierarchical and asymmetric temporal sensitivity in human auditory cortices. *Nature neuroscience*, *8*(3), 389.
- Bohland, J. W., Bullock, D., & Guenther, F. H. (2010). Neural representations and mechanisms for the performance of simple speech sequences. *Journal of cognitive neuroscience*, *22* (7), 1504–1529. doi:10.1162/jocn.2009.21306
- Bohland, J. W., & Guenther, F. H. (2006). An fMRI investigation of syllable sequence production. *NeuroImage*, *32* (2), 821–841. doi:10.1016/j.neuroimage.2006.04.173
- Bush, G., Luu, P., & Posner, M. I. (2000). Cognitive and emotional influences in anterior cingulate cortex. *Trends in cognitive sciences*, *4*(6), 215-222. doi:10.1016/S1364-6613(00)01483-2
- Buzsáki, G. (2004). Large-scale recording of neuronal ensembles. *Nature Neuroscience*, *7* (5), 446–451.
- Buzsáki, G. (2010). Neural Syntax: Cell Assemblies, Synapsembles, and Readers. *Neuron*, *68* (3), 362–385.
- Capilla, A., Pazo-Alvarez, P., Darriba, A., Campo, P., & Gross, J. (2011). Steady-State Visual Evoked Potentials Can Be Explained by Temporal Superposition of Transient Event-Related Responses. *PLoS ONE*, *6* (1), e14543
- Carreiras, M., Alvarez, C., & Devega, M. (1993). Syllable Frequency and Visual Word Recognition in Spanish. *Journal of memory and language*, *32*(6), 766-780. doi:10.1006/jmla.1993.1038
- Carreiras, M., Armstrong, B. C., Perea, M., & Frost, R. (2014). The what, when, where, and how of visual word recognition. *Trends in Cognitive Sciences*, *18* (2), 90–98. doi: 10.1016/j.tics.2013.11.005
- Carreiras, M., Ferrand, L., Grainger, J., & Perea, M. (2005). Sequential effects of phonological priming in visual word recognition. *Psychological Science*, *16* (8), 585–589. doi:10.1111/j.1467-9280.2005.01579.x
- Carreiras, M., Mechelli, A., & Price, C. J. (2006). Effect of word and syllable frequency on activation during lexical decision and reading aloud. *Human Brain Mapping*, *27* (12), 963–972. doi: 10.1002/hbm.20236
- Carreiras, M., & Perea, M. (2002). Masked priming effects with syllabic neighbors in a lexical decision task. *Journal of experimental psychology. Human perception and performance*, *28* (5), 1228–1242. doi:10.1037/0096-1523.28.5.1228
- Carreiras, M., & Perea, M. (2004). Naming pseudowords in Spanish: Effects of syllable frequency. In *Brain and language*, *90*, 393–400. doi: 10.1016/j.bandl.2003.12.003
- Carreiras, M., Riba, J., Vergara, M., Heldmann, M., & Munte, T. F. (2009). Syllable congruency and word frequency effects on brain activation. *Human Brain Mapping*, *30* (9), 3079–3088 doi:10.1002/hbm.20730
- Carreiras, M., Vergara, M., & Barber, H. (2005). Early Event-related Potential Effects of Syllabic Processing during Visual Word Recognition. *Journal of Cognitive Neuroscience*, *17* (11), 1803–1817. doi:10.1162/089892905774589217
- Cholin, J., & Levelt, W. J. (2009). Effects of syllable preparation and syllable frequency in speech production: Further evidence for syllabic units at a post-lexical level. *Language and cognitive processes*, *24*(5), 662-684.
- Cohen, M. X., & Gulbinaite, R. (2017). Rhythmic entrainment source separation: Optimizing analyses of neural responses to rhythmic sensory stimulation. *Neuroimage*, *147*, 43-56.
- Conrad, M., Carreiras, M., Tamm, S., & Jacobs, A. M. (2009). Syllables and bigrams:

- Orthographic redundancy and syllabic units affect visual word recognition at different processing levels. *Journal of Experimental Psychology: Human Perception and Performance*, 35(2), 461.
- Conrad, M., Grainger, J., & Jacobs, A. (2007). Phonology as the source of syllable frequency effects in visual word recognition: Evidence from French. *Memory & Cognition*, 35 (5), 974–983. doi: 10.3758/bf03193470
- Conrad, M., & Jacobs, A. (2004). Replicating syllable frequency effects in Spanish in German: One more challenge to computational models of visual word recognition. *Language and Cognitive Processes*, 19 (3), 369–390 doi:10.1080/01690960344000224
- Conrad, M., Stenneken, P., & Jacobs, A. M. (2006). Associated or dissociated effects of syllable frequency in lexical decision and naming. *Psychonomic Bulletin & Review*, 13(2), 339–345.
- Conrad, M., Tamm, S., Carreiras, M., & Jacobs, A. M. (2010). Simulating syllable frequency effects within an interactive activation framework. *European Journal of Cognitive Psychology*, 22(5), 861–893.
- Crompton, A. (1981). Syllables and segments in speech production. *Linguistics*, 19(7-8), 663–716.
- De Zubicaray, G. I., Zelaya, F. O., Andrew, C., Williams, S. C. R., & Bullmore, E. T. (2000). Cerebral regions associated with verbal response initiation, suppression and strategy use. *Neuropsychologia*, 38 (9), 1292–1304. doi:10.1016/S0028-3932(00)00026-9
- Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: a proposal. *Trends in cognitive sciences*, 9(7), 335–341.
- Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134 (1), 9–21. doi: 10.1016/j.jneumeth.2003.10.009
- Ding, N., & Simon, J. Z. (2014). Cortical entrainment to continuous speech: functional roles and interpretations. *Frontiers in human neuroscience*, 8, 311.
- Ding, J., Sperling, G., & Srinivasan, R. (2005). Attentional Modulation of SSVEP Power Depends on the Network Tagged by the Flicker Frequency. *Cerebral Cortex*, 16 (7), 1016–1029.
- Ferrand, L., Segui, J., & Grainger, J. (1996). Masked priming of word and picture naming: The role of syllabic units. *Journal of Memory and Language*, 723 (35), 708–72 doi:10.1006/jmla.1996.0037
- Fries, P. (2005). A mechanism for cognitive dynamics: neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, 9 (10), 474–480.
- Fuchs, M., Kastner, J., Wagner, M., Hawes, S., & Ebersole, J. S. (2002). A standardized boundary element method volume conductor model. *Clinical Neurophysiology*, 113 (5), 702–712. doi: 10.1016/S1388-2457(02)00030-5
- Garagnani, M., Lucchese, G., Tomasello, R., Wennekers, T., & Pulvermuller, F. (2017). A spiking neurocomputational model of high-frequency oscillatory brain responses to words and pseudowords. *Frontiers in Computational Neuroscience*, 10, 145
- Geiser, E., Zaehle, T., Jancke, L., & Meyer, M. (2008). The Neural Correlate of Speech Rhythm as Evidenced by Metrical Speech Processing. *Journal of Cognitive Neuroscience*, 20 (3), 541–552 doi:10.1162/jocn.2008.20029
- Ghitza, O., & Greenberg, S. (2009). On the possible role of brain rhythms in speech perception: Intelligibility of time-compressed speech with periodic and aperiodic insertions of

- silence. *Phonetica*, 66 (1-2), 113–126. doi: 10.1159/000208934
- Ghosh, S. S., Tourville, J. A., & Guenther, F. H. (2008). A Neuroimaging Study of Premotor Lateralization and Cerebellar Involvement in the Production of Phonemes and Syllables. *Journal of Speech Language and Hearing Research*, 51 (5), 1183. doi: 10.1044/1092-4388(2008/07-0119)
- Giraud, A. L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature neuroscience*, 15(4), 511.
- Grahn, J. A., Parkinson, J. A., & Owen, A. M. (2008). The cognitive functions of the caudate nucleus. *Progress in Neurobiology*, 86 (3), 141–155. doi: 10.1016/j.pneurobio.2008.09.004
- Grainger, J., Dufau, S., & Ziegler, J. C. (2016). A Vision of Reading. *Trends in Cognitive Sciences*, 20(3), 171-179. doi:10.1016/j.tics.2015.12.008
- Graves, W. W., Desai, R., Humphries, C., Seidenberg, M. S., & Binder, J. R. (2010). Neural Systems for Reading Aloud: A Multiparametric Approach. *Cerebral Cortex*, 20, 1799–1815. doi: 10.1093/cercor/bhp245
- Grech, R., Cassar, T., Muscat, J., Camilleri, K.P., Fabri, S.G., Zervakis, M., Xanthopoulos, P., Sakkalis, V., & Vanrumste, B. (2008). Review on solving the inverse problem in EEG source analysis. *J Neuroeng Rehabil*, 7, 5:25.
- Gu, B. M., van Rijn, H., & Meck, W. H. (2015). Oscillatory multiplexing of neural population codes for interval timing and working memory. *Neuroscience & Biobehavioral Reviews*, 48, 160-185. doi: 10.1016/j.neubiorev.2014.10.008
- Gundlach, C., & Müller, M. M. (2013). Perception of illusory contours forms intermodulation responses of steady state visual evoked potentials as a neural signature of spatial integration. *Biological psychology*, 94(1), 55-60.
- Häikiö, T., Hyönä, J., & Bertram, R. (2015). The role of syllables in word recognition among beginning Finnish readers: Evidence from eye movements during reading. *Journal of Cognitive Psychology*, 27(5), 562-577.
- Han, S., O'Connor, A. R., Eslick, A. N., & Dobbins, I. G. (2012). The role of left ventrolateral prefrontal cortex during episodic decisions: semantic elaboration or resolution of episodic interference?. *Journal of cognitive neuroscience*, 24(1), 223-234.
- Hannagan, T., Ziegler, J. C., Dufau, S., Fagot, J., & Grainger, J. (2014). Deep learning of orthographic representations in baboons. *PLoS One*, 9(1), e84843.
- Hazy, T. E., Frank, M. J., & O'Reilly, R. C. (2006). Banishing the homunculus: Making working memory work. *Neuroscience*, 139 (1), 105–118 doi:10.1016/j.neuroscience.2005.04.067
- Hutzler, F., Bergmann, J., Conrad, M., Kronbichler, M., Stenneken, P., & Jacobs, A. M. (2004). Inhibitory effects of first syllable-frequency in lexical decision: An event-related potential study. *Neuroscience Letters*, 372 (3), 179–184. doi: 10.1016/j.neulet.2004.07.050
- Jahanshahi, M., Obeso, I., Rothwell, J. C., & Obeso, J. A. (2015). A fronto-striato-subthalamic-pallidal network for goal-directed and habitual inhibition. *Nature Reviews Neuroscience*, 16 (12), 719–732. doi: 10.1038/nrn4038
- Kashiwase, Y., Matsumiya, K., Kuriki, I., & Shioiri, S. (2012). Time courses of attentional modulation in neural amplification and synchronization measured with steady-state visual-evoked potentials. *Journal of cognitive neuroscience*, 24 (8), 1779–1793.
- Klimesch, W. (2012). Alpha-band oscillations, attention, and controlled access to stored information. *Trends in cognitive sciences*, 16(12), 606-617.

- Klimesch, W., Sauseng, P., Hanslmayr, S., Gruber, W., & Freunberger, R. (2007). Event-related phase reorganization may explain evoked neural dynamics. *Neuroscience & Biobehavioral Reviews*, *31* (7), 1003–1016.
- Kuś, R., Duszyk, A., Milanowski, P., Łabęcki, M., Bierzyńska, M., Radzikowska, Z., ... & Durka, P. J. (2013). On the quantification of SSVEP frequency responses in human EEG in realistic BCI conditions. *PLoS one*, *8*(10), e77536.
- Laganaro, M., & Alario, F. X. (2006). On the locus of the syllable frequency effect in speech production. *Journal of Memory and Language*, *55*(2), 178-196.
- Levelt, W. J., Roelofs, A., & Meyer, A. S. (1999). A theory of lexical access in speech production. *The Behavioral and brain sciences*, *22* (1), 1–38.
- Levelt, W. J., & Wheeldon, L. (1994). Do speakers have access to a mental syllabary?. *Cognition*, *50*(1-3), 239-269.
- Lochy, A., Van Belle, G., & Rossion, B. (2015). A robust index of lexical representation in the left occipito-temporal cortex as evidenced by EEG responses to fast periodic visual stimulation. *Neuropsychologia*, *66*, 18-31. doi: 10.1016/j.neuropsychologia.2014.11.007
- Lochy, A., Van Reybroeck, M., & Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in preschoolers. *Proceedings of the National Academy of Sciences*, *113* (30), 8544–8549. doi: 10.1073/pnas.1520366113
- Lopez-Calderon, J., & Luck, S. J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, *8*, 213. doi: 10.3389/fnhum.2014.00213
- MacNeilage, P. F. (1998). The frame/content theory of evolution of speech production. *The Behavioral and brain sciences*, *21* (4), 499–511. doi: 10.1017/S0140525X98001265
- Macizo, P., & Van Petten, C. (2007). Syllable frequency in lexical decision and naming of English words. *Reading and Writing*, *20*(4), 295.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, *164* (1), 177–190. doi: 10.1016/j.jneumeth.2007.03.024
- Matell, M. S., & Meck, W. H. (2004). Cortico-striatal circuits and interval timing: Coincidence detection of oscillatory processes. *Cognitive brain research*, *21*(2), 139-170. doi: 10.1016/j.cogbrainres.2004.06.012
- Mathey, S., & Zagar, D. (2002). Lexical similarity in visual word recognition: The effect of syllabic neighborhood in french. *Current Psychology Letters: Behaviour, Brain & Cognition*, (2002/2, 8).
- Mathot, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: an open-source, graphical experiment builder for the social sciences. *Behavior research methods*, *44* (2), 314–24. doi: 10.3758/s13428-011-0168-7
- Mehler, J., Dommergues, J. Y., Frauenfelder, U., & Segui, J. (1981). The syllable's role in speech segmentation. *Journal of Verbal Learning and Verbal Behavior*, *20* (3), 298–305. doi:10.1016/S0022-5371(81)90450-3
- Michel, C. M., & Murray, M. M. (2012). Towards the utilization of EEG as a brain imaging tool. *Neuroimage*, *61*(2), 371-385.
- Michel, C. M., Murray, M. M., Lantz, G., Gonzalez, S., Spinelli, L., & de Peralta, R. G. (2004). EEG source imaging. *Clinical neurophysiology*, *115*(10), 2195-2222.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual*

review of neuroscience, 24 , 167–202.

- Montani, V., Chanoine, V., Stoianov, I., Grainger, J., & Ziegler, J.C. (2019). Steady state visual evoked potentials in reading aloud: Effects of lexicality, frequency and orthographic familiarity. *Brian & Language*, (in press).
- Moratti, S., Clementz, B. A., Gao, Y., Ortiz, T., & Keil, A. (2007). Neural mechanisms of evoked oscillations: stability and interaction with transient events. *Human brain mapping*, 28(12), 1318-1333.
- Morey, R. D. (2008). Confidence Intervals from Normalized Data: A correction to Cousineau (2005). *Tutorial in Quantitative Methods for Psychology*, 4 (2), 61–64.
- Morris, L. S., Kundu, P., Dowell, N., Mechelmans, D. J., Favre, P., Irvine, M. A., . . . Voon, V. (2016). Fronto-striatal organization: Defining functional and microstructural substrates of behavioural flexibility. *Cortex*, 74, 118–133 doi:10.1016/j.cortex.2015.11.004
- Munakata, Y., Herd, S. A., Chatham, C. H., Depue, B. E., Banich, M. T., & O'Reilly, R. C. (2011). A unified framework for inhibitory control. *Trends in Cognitive Science*, 15(10), 453-459 doi:10.1016/j.tics.2011.07.011
- New, B., Pallier, C., Brysbaert, M., & Ferrand, L. (2004). Lexique 2 : A new French lexical database. *Behavior Research Methods, Instruments, & Computers*, 36 (3), 516–524. doi:10.3758/BF03195598
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottureau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of vision*, 15(6), 4-4.
- Notbohm, A., Kurths, J., & Herrmann, C. S. (2016). Modification of brain oscillations via rhythmic light stimulation provides evidence for entrainment but not for superposition of event-related responses. *Frontiers in human neuroscience*, 10, 10.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M. (2011). FieldTrip: open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational intelligence and neuroscience*, 2011, 1. doi: 10.1155/2011/156869
- Ordin, M., Polyanskaya, L., Laka, I., & Nespors, M. (2017). Cross-linguistic differences in the use of durational cues for the segmentation of a novel language. *Memory & Cognition*, 45 (5), 863–876. doi:10.3758/s13421-017-0700-9
- Pascual-Marqui, R. D. (2007). Discrete, 3d distributed, linear imaging methods of electric neuronal activity. part 1: exact, zero error localization. *arXiv preprint arXiv:0710.3341* .
- Peirce, J. W. (2007). PsychoPy- Psychophysics software in Python. *Journal of Neuroscience Methods*, 162 (1), 8–13. doi: 10.1016/j.jneumeth.2006.11.017
- Perea, M., & Carreiras, M. (1998). Effects of syllable frequency and syllable neighborhood frequency in visual word recognition. *Journal of Experimental Psychology: Human Perception and Performance*, 24 (1), 134–144. doi:10.1037/0096-1523.24.1.134
- Perry, C. (2013). Graphemic parsing and the basic orthographic syllable structure. *Language and Cognitive Processes*, 28 (3), 355–376. doi:10.1080/01690965.2011.641386
- Perry, C., Ziegler, J. C., & Zorzi, M. (2013). A computational and empirical investigation of graphemes in reading. *Cognitive Science*, 37 (5), 800–828. doi: 10.1111/cogs.12030
- Pfurtscheller G., & da Silva, F.H.L. (1999). "Event-related EEG/MEG synchronization and desynchronization: basic principles". *Clin Neurophysiol.* **110** (11): 1842, 1857. doi:10.1016/S1388-2457(99)00141-8. PMID 10576479
- Price, C. J. (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImag* , 62 (2), 816–84

doi:10.1016/j.neuroimage.2012.04.062

- Poeppel, D. (2003). The analysis of speech in different temporal integration windows: cerebral lateralization as 'asymmetric sampling in time'. *Speech communication, 41*(1), 245-255.
- Protopapas, A., & Kapnoula, E. C. (2016). Short-term and long-term effects on visual word recognition. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 42*(4), 542.
- Pulvermuller, F., & Fadiga, L. (2010). Active perception: sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience, 11* (5), 351–360. doi: 10.1038/nrn2811
- Pulvermüller, F., Garagnani, M., & Wennekers, T. (2014). Thinking in circuits: toward neurobiological explanation in cognitive neuroscience. *Biological cybernetics, 108*(5), 573-593.
- Ramus, F., Nespors, M., & Mehler, J. (1999). Correlates of linguistic rhythm in the speech signal. *Cognition, 73*(3), 265-292. doi:10.1016/S0010-0277(99)00058-X
- Regan, D. (1989). Human brain electrophysiology: evoked potentials and evoked magnetic fields in science and medicine.
- Riecker, A., Brendel, B., Ziegler, W., Erb, M., & Ackermann, H. (2008). The influence of syllable onset complexity and syllable frequency on speech motor control. *Brain and Language, 107* (2), 102–113. doi:10.1016/j.bandl.2008.01.008
- Riecker, A., Mathiak, K., Wildgruber, D., Erb, M., Hertrich, I., Grodd, W., & Ackermann, H. (2005a). fMRI reveals two distinct cerebral networks subserving speech motor control. *Neurology, 64* (4), 700–706. doi: 10.1212/01.WNL.0000152156.90779.89
- Riecker, A., Mathiak, K., Wildgruber, D., Erb, M., Hertrich, I., Grodd, W., & Ackermann, H. (2005b). fMRI reveals two distinct cerebral networks subserving speech motor control. *Neurology, 64* (4), 700–706. doi: 10.1212/01.WNL.0000152156.90779.89
- Rodriguez-Fornells, A., van der Lugt, A., Rotte, M., Britti, B., Heinze, H.-J., & Münte, T. F. (2005). Second language interferes with word production in fluent bilinguals: brain potential and functional imaging evidence. *Journal of cognitive neuroscience, 17* (3), 422–433. doi: 10.1162/0898929053279559
- Schirmer, A. (2004). Timing speech: A review of lesion and neuroimaging findings. *Cognitive Brain Research, 21*(2), 269-287. doi:10.1016/j.cogbrainres.2004.04.003
- 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, 106* (1), 322–327. doi: 10.1073/pnas.0805874106
- Seghier, M. L. (2013). The Angular Gyrus: Multiple Functions and Multiple Subdivisions. *The Neuroscientist, 19* (1), 43–61. doi:10.1177/1073858412440596
- Sliwinska, M. W., James, A., & Devlin, J. T. (2015). Inferior parietal lobule contributions to visual word recognition. *Journal of cognitive neuroscience.*
- Sohrabpour, A., Lu, Y., Kankirawatana, P., Blount, J., Kim, H., & He, B. (2015). Effect of EEG electrode number on epileptic source localization in pediatric patients. *Clinical Neurophysiology, 126*(3), 472-480.
- Song, J., Davey, C., Poulsen, C., Luu, P., Turovets, S., Anderson, E., ... & Tucker, D. (2015). EEG source localization: sensor density and head surface coverage. *Journal of neuroscience methods, 256*, 9-21.
- Srinivasan, R., Bibi, F. A., & Nunez, P. L. (2006). Steady-State Visual Evoked Potentials: Distributed Local Sources and Wave-Like Dynamics Are Sensitive to Flicker Frequency.

Brain Topography, 18 (3), 167–187.

- Stoeckel, C., Gough, P. M., Watkins, K. E., & Devlin, J. T. (2009). Supramarginal gyrus involvement in visual word recognition. *Cortex*, 45 (9), 1091–1096 doi: 10.1016/j.cortex.2008.12.004
- Strijkers, K., Bertrand, D., & Grainger, J. (2015). Seeing the same words differently: The time course of automaticity and top-down intention in reading. *Journal of cognitive neuroscience*, 27(8), 1542-1551
- Strijkers, K., & Costa, A. (2016). The cortical dynamics of speaking: present shortcomings and future avenues. *Language, Cognition and Neuroscience*, 31(4), 484-503. doi: 10.1080/23273798.2015.1120878
- Strijkers, K., Costa, A., & Pulvermüller, F. (2017). The cortical dynamics of speaking: Lexical and phonological knowledge simultaneously recruit the frontal and temporal cortex within 200 ms. *Neuroimage*, 163, 206-219.
- Sutoyo, D., & Srinivasan, R. (2009). Nonlinear SSVEP responses are sensitive to the perceptual binding of visual hemifields during conventional ‘eye’ rivalry and interocular ‘percept’ rivalry. *Brain research*, 1251, 245-255.
- Taft, M. (2001). Processing of orthographic structure by adults of different reading ability. *Language and speech*, 44 (3), 351–376. doi:10.1177/00238309010440030301
- Takashima, A., Wagensveld, B., van Turennout, M., Zwitserlood, P., Hagoort, P., & Verhoeven, L. (2014). Training-induced neural plasticity in visual-word decoding and the role of syllables. *Neuropsychologia*, 61 (1), 299–314. doi: 10.1016/j.neuropsychologia.2014.06.017
- Teki, S., & Griffiths, T. D. (2016). Brain bases of working memory for time intervals in rhythmic sequences. *Frontiers in Neuroscience*, 10, 239. doi: 10.3389/fnins.2016.00239
- Thompson-Schill, S. L., D’Esposito, M., Aguirre, G. K., & Farah, M. J. (1997). Role of left inferior prefrontal cortex in retrieval of semantic knowledge: a reevaluation. *Proceedings of the National Academy of Sciences of the United States of America*, 94 (26), 14792–14797. doi:10.1073/pnas.94.26.14792
- Trost, W., Fruhholz, S., Schon, D., Labbe, C., Pichon, S., Grandjean, D., & Vuilleumier, P. (2014). Getting the beat: Entrainment of brain activity by musical rhythm and pleasantness. *NeuroImage*, 103, 55–64. doi: 10.1016/j.neuroimage.2014.09.009
- Ullman, M. T. (2004). Contributions of memory circuits to language: the declarative/procedural model. *Cognition*, 92 (1-2), 231–270 doi: 10.1016/j.cognition.2003.10.008
- Varela, F., Lachaux, J.-P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, 2 (4), 229–239.
- Vialatte, F.-B., Maurice, M., Dauwels, J., & Cichocki, A. (2010). Steady-state visually evoked potentials: focus on essential paradigms and future perspectives. *Progress in neurobiology*, 90 (4), 418–38. doi:10.1016/j.pneurobio.2009.11.005
- Vigneau, M., Beaucousin, V., Herve, P. Y., Duffau, H., Crivello, F., Houde, O., . . . Tzourio-Mazoyer, N. (2006). Meta-analyzing left hemisphere language areas: Phonology, semantics, and sentence processing *Neuroimage*, 30(4), 1414-143
- Wang, J., Yang, Y., Fan, L., Xu, J., Li, C., Liu, Y., . . . Jiang, T. (2015). Convergent functional architecture of the superior parietal lobule unraveled with multimodal neuroimaging approaches. *Human Brain Mapping*, 36 (1), 238–257. doi: 10.1002/hbm.22626
- Wenderoth, N., Debaere, F., Sunaert, S., & Swinnen, S. P. (2005). The role of anterior cingulate

- cortex and precuneus in the coordination of motor behaviour. *European Journal of Neuroscience*, 22 (1), 235–246. doi:10.1111/j.1460-9568.2005.04176.x
- Whaley, M. L., Kadipasaoglu, C. M., Cox, S. J., & Tandon, N. (2016). Modulation of Orthographic Decoding by Frontal Cortex. *Journal of Neuroscience*, 36 (4), 1173–1184. doi:10.1523/JNEUROSCI.2985-15.2016
- Wiener, M., Turkeltaub, P., & Coslett, H. B. (2010). The image of time: A voxel-wise meta-analysis. *NeuroImage*, 49 (2), 1728–1740 doi: 10.1016/j.neuroimage.2009.09.064
- Yeatman, J. D., & Norcia, A. M. (2016). Temporal tuning of word-and face-selective cortex. *Journal of Cognitive Neuroscience*, 28(11), 1820-1827.
- Zhang, Y., Guo, D., Cheng, K., Yao, D., & Xu, P. (2015). The graph theoretical analysis of the SSVEP harmonic response networks. *Cognitive Neurodynamics*, 9 (3),305–315. doi: 10.1007/s11571-015-9327-3
- Ziegler, J. C., Montant, M., Briesemeister, B. B., Brink, T. T., Wicker, B., Ponz, A., . . . Braun, M. (2018). Do Words Stink? Neural Reuse as a Principle for Understanding Emotions in Reading. *J Cogn Neurosci*, 30(7), 1023-1032.
- Ziegler, J. C., & Goswami, U. (2005). Reading Acquisition, Developmental Dyslexia, and Skilled Reading Across Languages: A Psycholinguistic Grain Size Theory. *Psychological Bulletin*, 131 (1), 3–29. doi: 10.1037/0033-2909.131.1.3
- Ziegler, J. C., Stone, G. O., & Jacobs, A. M. (1997). What is the pronunciation for -ough and the spelling for u/? A database for computing feedforward and feedback consistency in English. *Behavior Research Methods, Instruments & Computers*, 29(4), 600-618.

Appendix A

CVC_6	CV_6	CVC_8	CV_8
pardon	parade	barbelés	baraques
parfum	parent	carcasse	carabine
garçon	garage	cartable	carapace
furtif	fureur	cardinal	caravane
marcha	mariée	carnaval	caresser
marché	marine	cascales	cassette
carton	carafe	constant	conforme
marqué	marier	cultures	culottes
malgré	malade	destinée	descente
partie	pareil	discuter	disciple
partir	parois	disputer	dissiper
balcon	balade	fonction	fontaine
parler	parole	virginie	garantie
destin	dessin	marchand	maréchal
parvis	paraît	marquise	marraine
rejeté	reflet	masculin	massacre
palper	palace	murmurer	muraille
farcir	farine	partager	paradoxe
		pardonne	paraître
		parcours	paralysé
		parvient	pareille
		parcelle	parisien
		parfaite	paroisse
		parterre	parurent
		sections	sécurité
		suspendu	susciter
		terminus	terrible
		virginie	virilité