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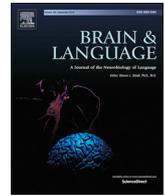
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Steady state visual evoked potentials in reading aloud: Effects of lexicality, frequency and orthographic familiarity

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ABSTRACT

The present study explored the possibility to use Steady-State Visual Evoked Potentials (SSVEPs) as a tool to investigate the core mechanisms in visual word recognition. In particular, we investigated three benchmark effects of reading aloud: lexicality (words vs. pseudowords), frequency (high-frequency vs. low-frequency words), and orthographic familiarity ('familiar' versus 'unfamiliar' pseudowords). We found that words and pseudowords elicited robust SSVEPs. Words showed larger SSVEPs than pseudowords and high-frequency words showed larger SSVEPs than low-frequency words. SSVEPs were not sensitive to orthographic familiarity. We further localized the neural generators of the SSVEP effects. The lexicality effect was located in areas associated with early level of visual processing, i.e. in the right occipital lobe and in the right precuneus. Pseudowords produced more activation than words in left sensorimotor areas, rolandic operculum, insula, supramarginal gyrus and in the right temporal gyrus. These areas are devoted to speech processing and/or spelling-to-sound conversion. The frequency effect involved the left temporal pole and orbitofrontal cortex, areas previously implicated in semantic processing and stimulus-response associations respectively, and the right postcentral and parietal inferior gyri, possibly indicating the involvement of the right attentional network.

1. Introduction

Over the past decades, reading aloud (i.e. naming) has been one of the primary tasks to study the basic processes involved in reading and visual word recognition. In fact, since the seminal triangle model by Seidenberg and McClelland (1989), all major computational models of reading tackled the issue of reading aloud by simulating how a model would read aloud words and pseudowords (Coltheart et al., 1993, 2001; Harm & Seidenberg, 1999; Perry, Ziegler, & Zorzi, 2007, 2010; Plaut, McClelland, Seidenberg, & Patterson, 1996). Coltheart, Rastle, Perry, Langdon, and Ziegler (2001) put forward a list of benchmark effects that any model of reading should be able to address, such as the effects of word frequency, lexicality and orthographic neighbourhood (orthographic familiarity).

It is an interesting paradox that studies on the spatio-temporal dynamics of reading in the brain using EEG have privileged silent reading, lexical decision and semantic categorization rather than reading aloud. An obvious reason for this is that reading aloud involves articulation

and the associated motor artefacts are particularly damaging for EEG measures. Here, we use steady state visual evoked potentials (SSVEPs) in reading aloud words and pseudowords to shed light on the organization of the reading network that is involved in reading aloud words and pseudowords.

SSVEPs are the electrophysiological response of the cortex to flickering visual stimuli (Regan, 1989; for recent reviews, see Norcia, Appelbaum, Ales, Cottareau, & Rossion, 2015, and Vialatte, Maurice, Dauwels, & Cichocki, 2010). That is, stimulus flicker is set to a specific frequency and the brain response is characterized by neuronal entrainment at the flicker frequency and its multiples. Practically speaking, it allows one to test whether different groups of items entrain the network differentially or whether a certain region of interest (either at the surface of source level) is entrained to the specific flicker frequency and is therefore involved in the network. Although the exact mechanisms behind SSVEP generation are still debated (e.g. Capilla, Pazo-Alvarez, Darriba, Campo, & Gross, 2011; Klimesch, Sauseng, Hanslmayr, Gruber, & Freunberger, 2007; Srinivasan, Bibi, & Nunez,

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2006), SSVEPs are generally interpreted as the consequence of the re-organization of spontaneous brain oscillations in response to a stimulus (Vialatte et al., 2010). It is generally assumed that larger SSVEP responses are caused by more efficient network dynamics (Zhang, Guo, Cheng, Yao, & Xu, 2015). SSVEPs have been successfully applied to study a variety of cognitive functions from lower level visual processes (e.g. Norcia, Tyler, Hamer, & Wesemann, 1989; Appelbaum et al., 2012; Garcia, Srinivasan, & Serences, 2013), to higher level functions, such as attention (see e.g. Norcia et al., 2015 for review), working memory (e.g. Perlstein et al., 2003; Peterson et al., 2014), or face processing (see Rossion, 2014 for reviews).

Assuming that information is stored in flexible cell assemblies, transiently synchronized by dynamic connections (see e.g., Buzsáki, 2010, 2004; Fries, 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001 for reviews), two not mutually exclusive mechanisms can explain the emergence of SSVEP. First, a network that is characterized by an internally more coherent activity could be more easily entrained by the external periodic stimulation, possibly by the way of phase alignment (e.g. Kashiwase, Matsumiya, Kuriki, & Shioiri, 2012; Moratti, Clementz, Gao, Ortiz, & Keil, 2007), eventually showing larger steady-state activity. Second, a larger cell assembly showing synchronized activity produce larger SSVEPs (Nikulin et al., 2007). Furthermore, it is well established that attention modulates SSVEP amplitude with attended items systematically exhibiting greater amplitudes compared to unattended (see Norcia et al., 2015, and Vialatte et al., 2010 for reviews). The effects of attention on SSVEP amplitudes probably result from a response gain effect (Di Russo, Spinelli, & Morrone, 2001), possibly mediated by enhanced neural synchronization (Joon Kim, Grabowecy, Paller, Muthu, & Suzuki, 2007).

Only a few studies have applied SSVEP paradigms to written language processing (Lochy, Van Belle, & Rossion, 2015; Lochy, Van Reybroeck, & Rossion, 2016; Yeatman & Norcia, 2016). Lochy et al. (2015) adopted a periodic oddball paradigm in which they presented words interspersed at regular intervals in sequences of either pseudowords, nonwords, or false fonts. They found significant SSVEP activity at the presentation frequency of words in all conditions, demonstrating that words generate a clear SSVEP response in the oddball paradigm. Remarkably, SSVEPs to words were obtained in the absence of an explicit task, which was taken to suggest that SSVEPs can index automatic lexical access. Recently, Lochy et al. (2016) used the same paradigm with preschoolers to demonstrate that SSVEP responses to letter strings correlated with letter knowledge. A different study compared SSVEP responses between images of words and faces (Yeatman & Norcia, 2016). Interestingly, the authors found that temporal acuity, peak response frequency, and delay of the SSVEP differed between words and faces, with temporal acuity for faces being substantially higher than for words.

SSVEP paradigms with flickering words have previously been used to study the processing of emotional content of words. In a study by Trauer, Kotz, Müller, and Vuilleumier (2015) using a lexical decision task, neither emotional content nor lexicality modulated SSVEPs generated by flickering words at 12.14 Hz. In contrast, in a study by Koban et al. (2010), emotional content modulated the SSVEPs but in the opposite direction than the one that was expected, with pleasant words showing reduced power compared to neutral words. To sum up, SSVEP responses associated with lexical processing have been investigated using sequences of stimuli (i.e. the oddball paradigm), whereas flickering stimuli have been used to study emotional content of words. No previous studies used flickering stimuli to investigate some of the main benchmark effects of reading aloud.

In the present study, we focus on the three main benchmark effects: lexicality, frequency and orthographic familiarity. The lexicality effect reflects the fact that readers are typically faster in processing real familiar words than pseudowords. The frequency effect reflects the fact that high-frequency are named more rapidly than low-frequency words. Finally, the orthographic familiarity effect reflects the finding that

pseudowords with familiar letter patterns (high bigram frequency or many orthographic neighbors) are typically read faster than nonwords with unfamiliar letter patterns.

In current computational models of reading aloud (Perry et al., 2007, 2010), reading high-frequency words relies on the fast and efficient lexical route that allows to retrieve the overlearned representation of the word from the orthographic lexicon. By contrast, pseudowords are decoded through the sublexical route that requires the sequential parsing of the string into the constituent orthographic units and then the assembling of the phonology from the sublexical parts (Testolin, Stoianov, Sperduti, & Zorzi, 2016). Similarly, low-frequency word reading, compared to high-frequency word reading, would rely to a greater extent on the less efficient sublexical route. On the other hand, even if familiar and unfamiliar letter patterns are both decoded by the way of the sublexical route, the decoding of the former would be facilitated by the fast retrieval of the familiar orthographic units compared to the most laborious decoding of completely unfamiliar patterns.

Both lexicality and frequency effects have been extensively investigated with standard event-related brain potentials (ERPs) in studies that focused on the time course of visual word recognition (see, e.g. Barber & Kutas, 2007; Grainger & Holcomb, 2009 for reviews). Both of the effects have been reported to emerge quite earlier in the ERP, between 100 and 200 ms from stimulus onset. The frequency effect impacts word processing at multiple time points during visual word recognition, suggesting that several processing stages are sensitive to repeated exposure (Barber & Kutas, 2007). A very stable component across tasks, the N400, has been identified between 300 and 500 ms. The amplitude of the N400 is larger for pseudowords as compared to words, it is an inverse function of the word's frequency, and can be modulated by the semantic context (Kutas & Federmeier, 2000). The N400 has been interpreted as reflecting the interactions between the representational level of whole words and semantics (e.g. Grainger & Holcomb, 2009).

Studies that investigated spectral responses to words and pseudowords consistently showed that words induce stronger responses than pseudowords, mainly for frequencies between 20 and 40 Hz (Mainy et al., 2008; Eulitz et al., 1996; Lutzenberger, Pulvermüller, & Birbaumer, 1994; Pulvermüller, Preißl, Eulitz, Pantev, Lutzenberger, & Feige, 1994). A recent neuroanatomically realistic neural network model was able to simulate those differences on the basis of spontaneous emergence and competitive interactions of cell assembly circuits (Garagnani, Lucchese, Tomasello, Wennekers, & Pulvermüller, 2017). In particular, a closer inspection of the network's dynamic behaviour revealed that weaker responses for pseudowords reflected the partial co-activation of many cell-assembly circuits within which a sub-threshold oscillatory activity occurred. In addition, the simultaneous activation of different circuits led to the reciprocal inhibition among circuits (i.e. competition). By contrast, words induced above-threshold activity within a single cell-assembly, inducing periodic, large-scale and synchronous bursts of activity within the specific assembly.

With respect to the neural basis of reading, there are rather convergent patterns across studies (see e.g. Price, 2012; Wandell, 2011; Taylor, Rastle, Davis, & Holloway, 2013 for reviews). For example, the involvement of the ventral occipito-temporal cortex (vOT) in reading is well established (Dehaene & Cohen, 2011; Testolin, Stoianov, & Zorzi, 2017 for a computational model), even if the specific functional significance of the visual word form area (VWFA) is still debated (e.g., Carreiras, Armstrong, Perea, & Frost, 2014; Cohen et al., 2002; Bruno, Zumbege, Manis, Lu, & Goldman, 2008; Glezer, Jiang, & Riesenhuber, 2009; Kronbichler et al., 2004, 2007). Several loci of the vOT, as well as in other brain areas, showed to be sensitive to the words vs. pseudowords contrast. The meta-analysis of Taylor et al. (2013) identified reliable greater neural responses to words than pseudowords in the left anterior fusiform gyrus, the ventral region of the left middle temporal gyrus, in a cluster encompassing the left middle temporal, middle occipital and angular gyri, a mesial cluster encompassing the left posterior

cingulum and the right precuneus, and few loci in the superior-middle frontal gyri showing the same preference. To explain the anterior fusiform gyrus activation it has been hypothesized that this region corresponds to the orthographic lexicon, while semantic processing should account for the involvement of the frontal, temporal and parietal loci (Taylor et al., 2013).

On the other hand, a cluster encompassing the left posterior fusiform gyrus and part of the occipito-temporal cortex showed greater neural responses to pseudowords than words (Taylor et al., 2013). This greater activation for pseudowords has been hypothesized to reflect the mismatch between forward input and top-down predictions, i.e. greater prediction errors compared to words (Price & Devlin, 2011) and/or the activation of multiple orthographic representations (Kronbichler et al., 2007; Schurz et al., 2014). Greater activation for pseudowords has also been documented in the left inferior parietal cortex, the left inferior frontal gyrus, the insula, and the precentral gyrus, reflecting spelling-to-sound conversion or phonological processing (Taylor et al., 2013).

The most consistent finding across previous studies that compared words of high and low frequency has been greater activation for low relative to high frequency words in the left pre/SMA region, and in the left inferior frontal cortex (Carreiras, Mechelli, & Price, 2006; Carreiras, Riba, Vergara, Heldmann, & Münte, 2009; Chee, Hon, Caplan, Lee, & Goh, 2002; Chee, Westphal, Goh, Graham, & Song, 2003; Fiebach, Friederici, Müller, & von Cramon, 2002; Fiez, Balota, Raichle, & Petersen, 1999; Hauk, Davis, Kherif, & Pulvermüller, 2008; Joubert et al., 2004) and it has been interpreted in terms of differential recruitment of lexico-phonological processes. Although neuropsychological evidence (see Ralph, Jefferies, Patterson, & Rogers, 2016 for review) and performance on semantic tasks and word-association tasks might lead to the expectation of greater involvement of brain areas that support semantic processing for high-frequency words (Graves, Desai, Humphries, Seidenberg, & Binder, 2010), few studies have reported such a pattern (Prabhakaran, Blumstein, Myers, Hutchison, & Britton, 2006; Carreiras et al., 2009; Graves et al., 2010).

The aim of the present study was to investigate the organization of the reading network in a reading aloud task using SSVEPs elicited by a standard visual periodic stimulation (i.e. flickering stimulus). In particular, words and pseudowords were presented in isolation and the SSVEPs were elicited for each item by flickering the stimulus at the selected frequency (i.e. 18.75 Hz). We investigated SSVEP responses to different lexical and nonlexical letter strings. We compared words against pseudowords (i.e., lexicality effect), as well as high-frequency against low-frequency words (i.e., frequency effect). We also compared nonwords with orthographically familiar letter patterns against nonwords with unfamiliar letter patterns (i.e., orthographic familiarity effect). We expected larger SSVEP responses to words than to pseudowords because the visual periodic stimulation should elicit a larger selective synchronization of neuronal populations. Assuming that the representation of familiar items such as words is based on assemblies of strongly connected sets of neurons that behave in a functionally coherent manner (Garagnani et al., 2017; Pulvermüller, Garagnani, & Wennekers, 2014), the wave-like activity elicited by the flickering stimulus should propagate more easily in such “organized” assemblies than in a more “disorganized” set of neurons responding to unfamiliar items. In addition, word representations should be further supported by a more extended network that includes associations with higher-order semantic or sensorimotor areas (Barrós-Loscertales et al., 2012; Boulenger, Hauk, & Pulvermüller, 2009; González et al., 2006; Pulvermüller, 2005). Similarly, larger SSVEP amplitudes were expected for high-frequency words than for low-frequency words (i.e. frequency effect) because neural representations of high-frequency should benefit from stronger connections, more efficient network dynamics, and higher resting levels. Finally, if SSVEP amplitudes reflect processing difficulty, the SSVEP power amplitudes of familiar pseudowords should be higher than those of unfamiliar pseudowords (i.e. orthographic familiarity effect). In contrast, if SSVEP taps lexical processing dynamics,

we expect small or no SSVEP modulations for familiar versus unfamiliar pseudowords. The neural basis of the SSVEP were analyzed both at the surface and the source level.

2. Material and methods

2.1. Participants

Sixteen proficient readers, naive to the purpose of the experiment, participated in the experiment as paid volunteers (age 17–24 years, mean = 20.25). All participants were native French speakers, they had normal or corrected-to-normal vision and they had no history of developmental disorders. Before participating, participants gave informed written consent.

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) with the PsychoPy back-end (Peirce, 2007) and they were presented on a 17-in. cathode ray tube monitor (resolution: 800 × 600 pixels, refresh rate: 75 Hz). Strings were presented in black against a white background, at the center of the screen, using Selectric font, and they flickered at 18.75 Hz (4 monitor refresh cycles per period: 1 on- and 3 off-cycles). The choice of the flicker frequency was based upon different considerations. First of all, there is no consensus with respect to the optimal frequency despite extensive research on this issue. It seems that many studies preferred the alpha or theta bands, but this frequency range requires relatively long period of stimulus exposure, spanning from several seconds to a few minutes (see for example Lochy et al., 2015). For the purpose of our single-trial naming task, we preferred a shorter exposure. In addition, we wanted to avoid the alpha band, which is the natural frequency of the occipital cortex (Rosanova et al., 2009). Finally, a recent study identified the 12–18 Hz as the optimal range for SSVEP stimulation (Kuš et al., 2013).

Two-hundred-forty strings (between five and eight letters long) were used as stimuli. Sixty high frequency words (HFW, mean printed frequency greater than 100 occurrences per million, log-transformed frequency $M = 2.22$, $SD = 0.19$) and 60 low frequency words (LFW, mean printed frequency less than 10 occurrences per million, log-transformed frequency $M = 0.61$, $SD = 0.20$) were selected from a large lexical corpus of written French (*Lexique, New, Pallier, Brysbaert, & Ferrand, 2004*). The number of orthographic neighbors does not differ significantly between HFW and LFW (2.03 vs. 1.44, $p < .16$). Sixty orthographically familiar pseudowords (FPW) and 60 orthographically unfamiliar pseudowords (UPW) were selected from the *French Lexicon Project (FLP, Ferrand et al., 2010)*. The FLP is a set of French words and nonwords that provides lexical decision times collected from several hundreds participants. Corpus analyses using *FLP* confirmed that reaction times (RTs) of FPWs were significantly different from RTs of UPWs ($p < .0001$). In addition, FPWs had on average more orthographic neighbours than UPWs (4.10 vs. 0.35, $p < .0001$) and FPWs contained on average more frequent bigrams than UPWs (type: 146 vs. 100, $p < .0001$; token 1210 vs. 790, $p < .0001$). All types of string were matched for string length. A full list of stimuli is provided in [Appendix A](#).

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 200 ms, the flickering string was presented for 2000 ms. Then, a screen prompted participants to name the string aloud. After 2000 ms, an empty screen replaced the response screen. 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%. The intertrial interval from the start of one trial to the start of the next trial was about 7500 ms. Each session consisted of three blocks of 80 trials each with a brief pause between each block. The block sequence was counterbalanced between participants while the target string sequence in each block was randomized for each subject. The entire experimental session lasted about 40 min.

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). Other two extra electrodes were used for an online re-referencing (placed behind ears on mastoid bone). For the EEG analysis, we used EEGLAB (Delorme & Makeig, 2004), Erplab (Lopez-Calderon & Luck, 2014) and Fieltrip (Oostenvelde et al., 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, 6.54% of the data were interpolated and 4.71% of the data rejected. Slow drifts were removed in order to reduce “sawtooth” artifacts in the Fourier spectrum (Bach & Meigen, 1999). EEG data were then segmented again, discarding the first 533 ms from stimulus onset in order to remove the initial transient response, and the last 400 ms to have epochs containing integer number of flicker periods. The resulting 1092 ms lasting epoch corresponds to 20 complete cycles within stimulation.

2.5. SSVEP statistical analysis

To extract SSVEP activity synchronized to the stimulus flicker, the EEG signal of each epoch was decomposed using Fast-Fourier Transform (FFT, frequency resolution 0.94 Hz). First, in order to verify that words and pseudowords elicited reliable SSVEPs, we calculated a statistic specifically conceived to detect and quantify steady-state responses, T^2_{circ} (Victor & Mast, 1991). T^2_{circ} estimates whether a signal component is present in a set of Fourier components or whether the components can be explained by random fluctuations alone. The statistic is essentially based onto the variability of individual estimates compared to the mean of the response estimates. In contrast to other methods, T^2_{circ} utilizes both amplitude information and the relationship between the real and the imaginary components of Fourier estimates. This method has been shown to be more reliable and efficient compared to the other methods both in practice as well as in numerical simulation (Victor & Mast, 1991).

2.6. Source localization analysis

We further investigated the neural basis of the SSVEPs elicited by words and pseudowords. Due to the spread of the electric field, and to the consequent fact that every electrode picks up signals from different sources (Luck, 2014), discussing potential neural sources of EEG signal on the basis of the topological distribution of the response can lead to wrong interpretation of the data (Michel & Murray, 2012). In

preference, using sophisticated source and head models, 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). In addition, to this end, the high signal-to-noise ratio of the SSVEP provides an advantage over standard ERP approaches (Norcia et al., 2015).

In order to localize the neural sources of the lexicality effect, and mirroring the analysis at the scalp level, we contrasted the activation for words with the activation for pseudowords. To localize the frequency effect, we contrasted the activation for high frequency words vs. the activation for low frequency words. In contrast, the familiar vs. unfamiliar pseudoword contrast was not performed at the source level because the response at the scalp level was not sensitive to the orthographic familiarity effect.

3. Results

3.1. SSVEP power

We calculated T^2_{circ} for each subject and electrode (see Method, Section 2.5). Significant SSVEP responses were obtained for all participants (see Fig. 1 and Fig. 1 in the Supplementary material). Then, following the logic of Chicherov and Herzog (2015), we averaged across subjects and conditions to select the channels with the strongest SSVEP entrainment for further analysis. This resulted in the selection of 7 electrodes (Iz, Oz, O1, O2, PO8, POz, PO4), which showed an overall T^2_{circ} larger than 0.2 (see Fig. 2 in the Supplementary material). Fig. 2 shows the topographic distribution of SSVEP power for the four types of strings along with the selected electrodes.

Because the absolute amplitude of the EEG signal varies widely across participants, we standardized data calculating z-scores of SSVEP power from each electrode, condition and participant based on the participant’s overall average and standard deviation of SSVEP power across all scalp electrodes and across all of the conditions. The effects of lexicality, frequency and orthographic familiarity on SSVEP power were assessed via three different generalized linear mixed-effects regressions (Baayen, Davidson, & Bates, 2008), with a logarithmic link function¹, using lme4 package (Bates, Maechler, Bolker, & Walker, 2014) in the R environment (Core, 2014). The fixed effects were either *lexicality* (two levels: word vs. pseudoword), *frequency* (two levels: high frequency word vs. low frequency word) or *orthographic familiarity* (two levels: familiar pseudoword vs. unfamiliar pseudoword). Models fit was assessed by likelihood ratio test, comparing increasingly complex models. The null model included by-subject and by-electrode random intercepts. The effects of question, by-subject random slopes and by-electrode random slopes were added incrementally.

3.1.1. Lexicality effect

Adding the effect of lexicality on the SSVEP power significantly increased the goodness of fit ($\chi^2(1) = 16.25, p < 0.001$), reflecting the fact that the SSVEP power was higher for words compared to pseudowords ($b = -0.03, SE = 0.008, t = -4.03, p < 0.001$). Adding by-subject random slopes for the lexical effect significantly increased the goodness of fit ($\chi^2(2) = 9.16, p < 0.05$), reflecting high between-subject variability. As a consequence, the lexicality factor became marginally significant ($b = -0.03, SE = 0.018, t = -1.73, p = 0.08$). Adding by-electrode random slopes for the lexicality effect did not significantly increase the goodness of fit ($\chi^2(2) = 2.01, p = 0.37$), indicating low variability among individual slopes for the electrode locations. The SSVEP power for words and pseudowords are shown in the left panel of Fig. 3.

¹ The lognormal distribution resulted to be the best approximate description of the data accordingly to the probability plot.

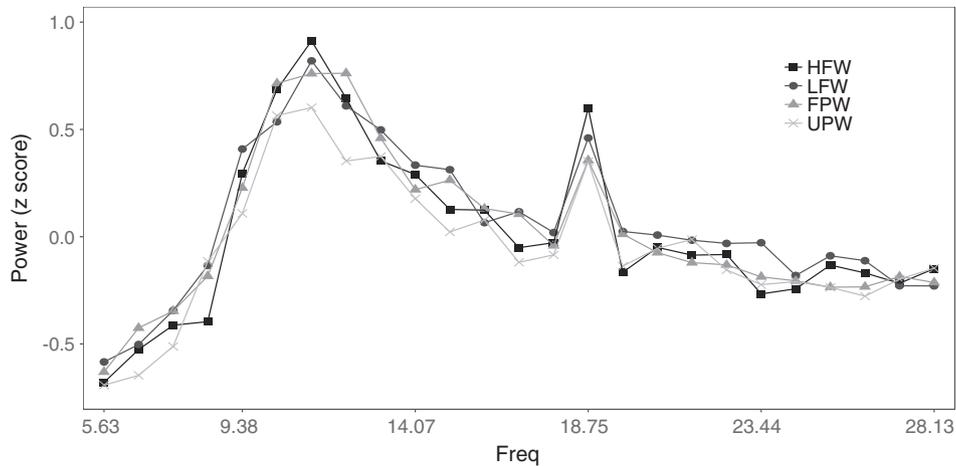


Fig. 1. SSVEP power (z score) averaged across participants and the selected electrodes (see text). The peak in the spectrum at 18.75 Hz corresponds to the strong entrainment at the stimulation frequency. HFW = high frequency word, LFW = low frequency word, FPW = familiar pseudoword, UPW = unfamiliar pseudoword.

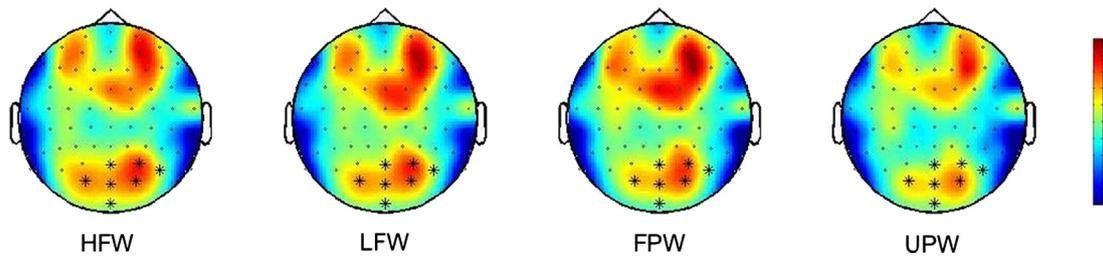


Fig. 2. Topographic distribution of SSVEPs power (z scores) at the stimulation frequency (18.75 Hz) for the four types of string. HFW = high frequency word, LFW = low frequency word, FPW = familiar pseudoword, UPW = unfamiliar pseudoword. “*” symbols indicate electrodes included in the regression models.

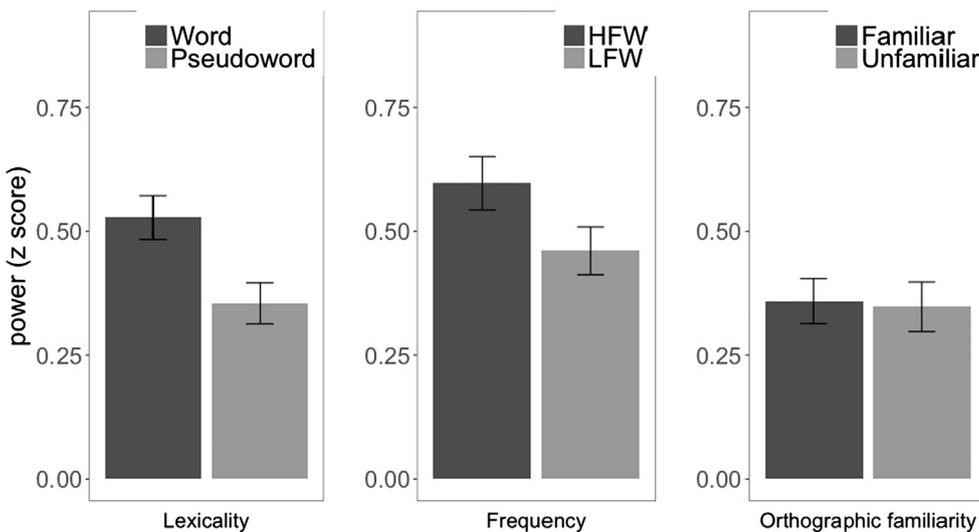


Fig. 3. SSVEP power (z scores) for the three effects: lexicality effect (word vs. pseudoword), frequency effect (high-frequency word vs. low-frequency word), orthographic familiarity effect (orthographically familiar pseudoword vs. orthographically unfamiliar pseudoword). HFW = high frequency word, LFW = low frequency word. Error bars represent standard error of the means (SEMs) adjusted to correctly reflect the variance in the within-subject design (Morey, 2008).

3.1.2. Frequency effect

Adding the effect of frequency on the SSVEP power significantly increased the goodness of fit ($\chi^2(1) = 8.29, p < 0.01$), indicating that the SSVEP power was higher for HFW compared to LFW ($b = -0.03, SE = 0.01, t = -2.88, p < 0.01$). Adding by-subject random slopes or by-electrode random slopes did not significantly increase the goodness of fit ($\chi^2(2) = 1.28, p = 0.53$ and $\chi^2(2) = 0.03, p = 0.98$, respectively), indicating low variability among individual slopes for both effects. SSVEP power for low- and high-frequency words is shown in the middle panel of Fig. 3.

3.1.3. Orthographic familiarity effect

Adding the effect of orthographic familiarity and or by-subject or by-electrode random slopes did not significantly increase the goodness of fit ($\chi^2(1) = 0, p = 0.98, \chi^2(2) = 0, p = 1, \chi^2(2) = 0.36, p = 0.83$, respectively). Right panel of Fig. 3 shows the effect of orthographic familiarity.

3.2. SSVEP in source space

EEG cortical source analysis was performed with 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 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>) using the frequency and time window of interest (frequency: 18.75 Hz; time window between 533 and 1600 ms) as well as a 8 Hz smoothing box. Sources were modelled 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 (BEM) volume conduction model in which the head geometry is realistic and based on the ‘Colin27’ template (see Fuchs, Kastner, Wagner, Hawes, & Ebersole, 2002). 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 54,180 dipoles. Specific contrasts were performed in order to study the effects of interest (with the exclusion of the orthographic familiarity effect that did not significantly modulate the SSVEP power at the scalp level). To identify the neural sources of the lexicality effect, we contrasted the activation for words (collapsing HFW and LFW in one group) with the activation for pseudowords (collapsing FPW and UPW in the other group). To identify neural sources of the frequency effect, we contrasted the activation for HFW with the activation for LFW. Cortical activation was analyzed with nonparametric statistical tests based on Montecarlo permutation (Maris & Oostenveld, 2007). *P*-values were corrected for multiple comparison using False Discovering Rate (e.g. Genovese, Lazar, & Nichols, 2002).

3.2.1. Lexicality effect

Fig. 4 show the activation map for the lexicality effect for corrected contrasts (see Fig. 3 in the Supplementary material for the uncorrected contrasts). Greater activity for words compared to pseudowords occurred in the right middle occipital gyrus, right precuneus, right cerebellum (see upper part of Table 1 for details). Greater activity for pseudowords compared to words occurred in the left postcentral and precentral gyri, rolandic operculum, insula, supramarginal gyrus, inferior parietal lobule, Heschl’s gyrus, and in the right superior and middle temporal gyri (see lower part of Table 1 for details).

3.2.2. Frequency effect

Fig. 5 shows the activation map for the frequency effect for corrected contrasts. Greater activity for high frequency words compared to low frequency words occurred in the right middle and superior temporal pole, orbitofrontal cortex, gyrus rectus, inferior temporal cortex, anterior cingulate (see upper part of Table 2 for details). Greater activity for low frequency words compared to high frequency words occurred in the right postcentral and parietal inferior lobule (see lower part of Table 2 for details).

4. Discussion

In the present study, we used steady-state visual evoked potentials (SSVEPs) as a tool to investigate the organization of the neural network involved in reading aloud with respect to three benchmark effects: lexicality, frequency and orthographic familiarity (Coltheart et al., 2001). We showed that words and pseudowords elicited reliable SSVEPs at the stimulation frequency (Fig. 1) using a paradigm in which the items were presented in isolation and flickered at 18.75 Hz. The results showed a clear modulation of SSVEP power in the expected direction with stronger values for words over pseudowords (i.e., lexicality) and for high- over low-frequency words (i.e., frequency). No modulation of SSVEP power was obtained for the orthographic

familiarity effect (familiar versus unfamiliar pseudowords), which suggests that the SSVEPs elicited in our paradigm tapped lexical rather than sublexical mechanisms (see Fig. 3).

Overall, our results are compatible with the hypothesis that the SSVEP power reflects the underlying network efficiency (Zhang et al., 2015) because words benefit from more efficient lexical network dynamics than pseudowords, which also results in shorter reaction times and higher accuracy in standard naming tasks. Similarly, high-frequency words also benefit from more efficient lexical networks because they tend to have stronger network connections or resting levels, which typically results in faster RTs and higher accuracy for high-frequency over low-frequency words

The result is also in line with the finding that spectral responses induced by words are stronger than those induced by pseudowords in the high beta and gamma bands (Eulitz et al., 1996; Lutzenberger et al., 1994; Mainy et al., 2008; Pulvermüller et al., 1994). Larger amplitudes in the spectral responses are hypothesized to reflect large-scale and synchronous bursts of activity within the specific neuronal assemblies representing familiar items, whereas unfamiliar items induce “out-of-phase” activity within competing circuits resulting in weaker oscillatory responses (Garagnani et al., 2017). Similar dynamics may explain the larger SSVEPs for words compared to PWs, and for HFWs compared to LFWs. For example, the strongly connected set of neurons responding to words could be more easily entrained by the periodic stimulation resulting in larger SSVEPs. The periodic stimulation is supposed to generate a wave-like activity that propagates easily in such functional units, compared to the less coherent neuronal responses associated to pseudowords. However, it is important to note that the relationship between the spontaneous neural rhythm and the narrow-band evoked responses of steady-state responses is not completely clear (Keitel, Quigley, & Ruhnuau, 2014). Indeed, while the frequency effect showed to be quite robust, the lexicality effect showed larger variability among participants. Simulations with a biologically plausible neurocomputational model (Garagnani et al., 2017) revealed that responses to pseudowords exhibit an oscillatory activity peaking in the low beta range (~20 Hz). Therefore, the possibility to detect the lexicality effect could have been reduced by the adoption of a stimulation frequency (18.75 Hz) that matches the characteristic spectral activation fingerprint for this type of stimuli.

Because selective synchronization is also believed to underlie the effects of attention on SSVEPs (e.g. Joon Kim et al., 2007), namely the fact that attended stimuli generate higher SSVEPs than unattended items, it is important to note that lexical processing does not involve more attentional resources than sublexical processing. In contrast, the processing of pseudowords seems to require more attention than the processing of words, as attested by behavioural (e.g. Montani, Facoetti, & Zorzi, 2014, see Besner et al., 2016 for review), neurophysiological (Garagnani, Shtyrov, & Pulvermüller, 2009), and computational evidence (e.g. Perry, Ziegler, & Zorzi, 2007). In addition, in our paradigm, there was no attentional manipulation and we were not explicitly measuring the allocation of attention on the stimulus. Rather, we suggest that SSVEP power reflects the level of coherent activity of the network underlying the processing of the different type of strings. In those paradigms in which attention is manipulated, attended items show higher power because attention selectively increases the synchronization of the population of cells that are involved in the processing of the attended stimulus. Future research may explore the effects of attention on the SSVEP response to words and pseudowords. Considering the explanation depicted above, we would predict that pseudowords should show more attention dependence, with a selective increase of power relative to words in the attended condition.

Two previous studies presenting flickering words reported inconsistent results. Koban et al. (2010) found that SSVEP power for positive emotional words was reduced compared to power for neutral words, contrary to previous results obtained when presenting emotional pictures. However, the unexpected finding could be explained on the basis

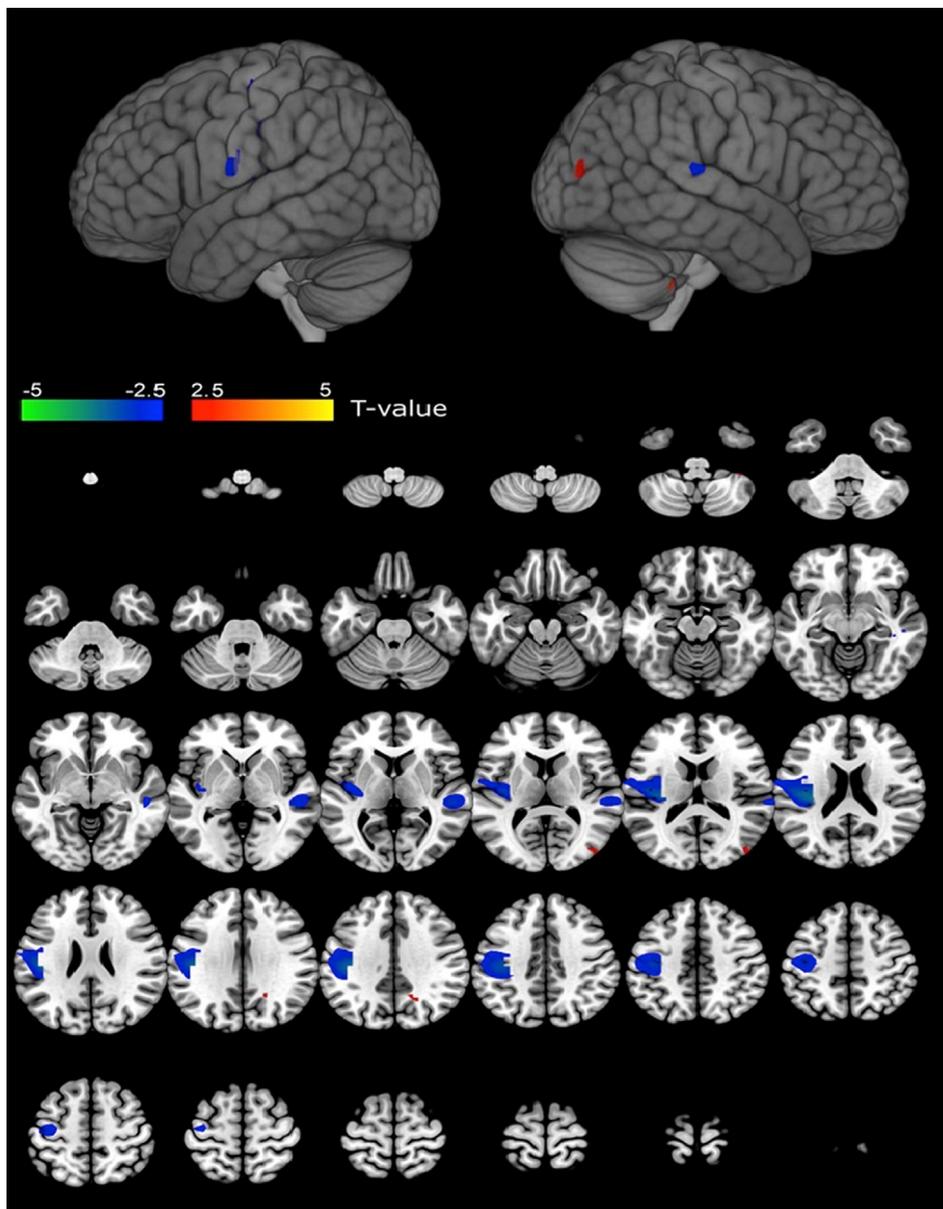


Fig. 4. Regions whose source signal activity differed between words and pseudowords (positive and negative significant activations are shown in red and blue, respectively). Greater activity for words compared to pseudowords occurred in the right middle occipital gyrus, right precuneus, right cerebellum. Greater activity for pseudowords compared to words occurred in the left postcentral and precentral gyri, rolandic operculum, insula, supramarginal gyrus, inferior parietal lobule, Heschl's gyrus, and in the right superior and middle temporal gyri. Statistical threshold = $p < 0.05$, corrected for multiple comparison using FDR (see Table 1 for details).

of some methodological issues, as suggested by the authors. First, words were presented for 8 sec, that is, far longer than the standard time necessary to process written words. During this long time, processes of different nature could have taken place. Then, words were flickered at 7.5 Hz. Steady-state responses in different frequency bands showed different sensitivities to physical stimulus parameters (Regan, 1989) suggesting that at least to some extent, different flicker frequencies can entrain functionally distinct cortical networks (Srinivasan et al., 2006). For example, Kaspar and coll. (Kaspar, Hassler, Martens, Trujillo-Barreto, & Gruber, 2010) found that familiar objects elicited higher SSVEP amplitudes compared to unfamiliar objects at 12 and 15 Hz but the effect reversed at 7.5 Hz. Ding, Sperling, and Srinivasan (2005) found a reversed effect of attention on SSVEP amplitude at frequencies in the lower alpha band. Therefore, adopting a specific stimulation frequency (in our case, 18.75 Hz) could lead to the selection of a specific functional network in which natural frequencies match the flicker frequency (Ding et al., 2005). Future investigations are needed to systematically explore the use of different frequencies.

On the other hand, in a recent study, SSVEP amplitude was completely unaffected by emotional word content, and more importantly for the present discussion, by the lexical status of the string (Trauer

et al., 2015). While the presentation time and stimulation frequency used by Trauer and colleagues were more similar to the parameters used here, they used a lexical decision task, which is known to entail partially different computational processes than reading aloud (e.g. Chen, Davis, Pulvermüller, & Hauk, 2013; Dufau, Grainger, & Ziegler, 2012; Montani, Facoetti, & Zorzi, 2015), which might explain the different findings. In addition, and also with reference to the lack of effect for the emotional content, authors concluded that affective words may not tap early visual processing resources. Yet, both studies reported results relative to few occipital electrodes that reflect activity in early visual cortex only.

At the level of cortical generators of the SSVEP effects, in order to localize the source of the lexicality effect, we contrasted the activation for words with the activation for pseudowords. The generators of the lexicality effect showing higher activation for words than for pseudowords were located in the right hemisphere in the occipital lobe, precuneus, and cerebellum (see Fig. 4 and Table 1). It is noteworthy to report that, before correcting for multiple comparisons the pattern of activation included also portions of the left lingual and fusiform gyri adjacent to the visual word from area (see Fig. 3 in Supplementary material), which is in line with previous studies that reported sensitivity

Table 1

Regions whose source signal activity differed between words and pseudowords (cf. Fig. 3) Size: number of voxels X, Y, Z reflect position in MNI coordinate space T reflects maximum T-value in the region.

Condition		Words > Pseudowords			
Region	Size	X	Y	Z	T
<i>On the right hemisphere</i>					
Occipital_Mid_R	5	46	-77	19	2.88
Precuneus_R	2	14	-52	38	2.71
Cerebellum_6_R	1	33	-31	-36	2.74
Condition		Words < Pseudowords			
Region	Size	X	Y	Z	T
<i>On the left hemisphere</i>					
Postcentral_L	90	-43	-19	30	-3.50
Precentral_L	36	-43	-14	30	-3.23
Rolandic_Oper_L	32	-40	-20	20	-3.56
Insula_L	23	-36	-24	21	-3.61
SupraMarginal_L	14	-43	-22	34	-3.43
Parietal_Inf_L	9	-43	-22	39	-3.22
Heschl_L	4	-41	-16	11	-3.16
<i>On the right hemisphere</i>					
Temporal_Sup_R	31	50	-30	3	-3.70
Temporal_Mid_R	8	51	-25	-11	-2.58

of left vOT to word vs. pseudoword contrasts (Taylor et al., 2013) and hierarchical coding of words in the VWFA (Dehaene & Cohen, 2011; Testolin, Stoianov, & Zorzi, 2017).

The peaks in the posterior right hemisphere overlap with the right cluster identified in the meta-analyses of Taylor et al. (2012) and Binder, Desai, Graves, and Conant (2009) on semantic processing networks. Because we did not match words and pseudowords for bigram frequency, the larger activation for words in the occipital cortex could be explained by reflecting differences in sublexical features. However, the fact that the SSVEPs were not sensitive to the orthographic familiarity (i.e., FPW vs. UPW contrast), suggest that other factors may play a role. The presence of the lexical effect in an area associated with early visual processing, from visual feature extraction to letter processing, suggests feedback effects from higher-order areas and supports an interactive account of word processing (Carreiras et al., 2014; Pattamadilok et al., 2017; Price & Devlin, 2011). The higher activation indicates that the area have been entrained by the flicker to a larger extent by words compared to pseudowords. Hypothetically, the top-down predictions of the familiar orthographic pattern for words as compared to pseudowords fit well the upcoming sensory information resulting in more efficient visual processing, and as a consequence, a larger entrainment to the flickering visual stimulation. The long stimulus presentation in our paradigm could have supported more prolonged and extended feedback effects. Alternatively, the activation in the occipital area could also be explained by assuming that the occipital cortex contains neurons tuned to complex orthographic features such as morphemes or words (Schurz et al., 2014). The fact that the precuneus have been specifically associated to visual imagery and episodic memory (Binder et al., 2009) supports the hypothesis of a greater engagement of the semantic system by words compared to pseudowords, as predicted by all cognitive models of reading (Taylor et al., 2013).

Positive activation was also detected in the posterior lobe of the right cerebellum, at the level of the lobules VI, (see Fig. 4 and Table 1) and, in Crus 1 and 2 (see Fig. 3 in Supplementary material) although these latter effects did not “survive” correction for multiple comparisons. The cerebellar posterior lobe is strongly coupled to the somato-motor cortex, it contains motor maps (Buckner, 2013) and has been also associated with articulation (Ackermann, Vogel, Petersen, & Poremba, 1992; Chen & Desmond, 2005). Therefore, a possible explanation of our finding is that words exhibited a more coordinate articulatory planning

activity compared to pseudowords. However, the involvement of the cerebellum in higher cognition, beyond the motor domain, is widely recognized (Annabel Chen, Ringo Ho, & Desmond, 2012; Buckner, 2013). There is evidence that the cerebellum, in particular the right posterolateral region (Crus 1), is involved in language (Stoodley & Schmahmann, 2008, 2009), and even specific patterns of activations or cerebellum structural properties have been associated to reading disorder (Feng et al., 2016; Laycock et al., 2008; Linkersdörfer et al., 2012; Nicolson, Fawcett, & Dean, 2001). In fact, the cerebellum is connected to the cerebrum mainly by contralateral projections, with the right cerebellum hemisphere connected to the left cerebral cortex (Buckner, 2013). Although its precise role in reading or language processing is not clear, there are attempts to extent this motor theory to the language domain (Ito, 2008; Ramnani, 2006). The cerebellum is thought to have a coordinative role encoding internal models and neural representations of context-specific properties of objects that can be used to predict action consequences. Applied to the domain of language processing, the theory holds that the cerebellum may support predictive language processing (Lesage, Morgan, Olson, Meyer, & Miall, 2012; Moberget, Gullesten, Andersson, Ivry, & Endestad, 2014). Thus, a possible alternative explanation of our finding is that the greater activation for words reflects the activation of the context associated with words, while pseudowords have no such internal models.

Concurrently, we found higher activation for the pseudowords in left sensorimotor areas, in left perisylvian regions classically associated to the language system and in the right temporal superior and middle gyri. Pre- and post-central regions are activated to control orofacial muscles during production of speech sounds, while the right temporal superior gyrus is associated with acoustic and auditory processing (Price, 2012). The involvement of sensorimotor areas as well as areas associated to speech processing likely reflect the articulatory planning activity in preparation of naming (Mahé, Zesiger, & Laganaro, 2015). The involvement of sensorimotor areas is also in line with the growing body of evidence in support of an interactive account of orthographic processing (e.g., Whaley, Kadipasaoglu, Cox, & Tandon, 2016; Bedo, Ribary, & Ward, 2014; Testolin et al., 2016) and the functional link between action and perception (Pulvermüller & Fadiga, 2010). The perisylvian region including the rolandic operculum, the insula and the supramarginal gyrus have been consistently found more activated for reading pseudowords than words (Jobard, Crivello, & Tzourio-Mazoyer, 2003; Price & Mechelli, 2005; Taylor et al., 2013), which suggests that these areas play a specific role in spelling-to sound conversion (e.g. Bitan et al., 2007; Braun et al., 2015; Braun, Hutzler, Ziegler, Dambacher, & Jacobs, 2009). In addition, damage to those areas has been associated to deficits in phonological decoding (Fiez & Petersen, 1998; Roeltgen, Sevush, & Heilman, 1983). Accordingly, the most plausible explanation of our finding is that, while words required less phonological mediation, pseudowords processing relied completely on the sublexical conversion of orthography to phonology, exhibiting therefore a greater recruitment of the areas that subserve sublexical procedures.

With respect to the frequency effect, the contrast between HFW and LFW showed a composite pattern (see Fig. 5 and Table 2). Firstly, we found higher activation for HFW compared to LFW in a left region including the superior and middle parts of the temporal pole, the orbitofrontal cortex, the inferior temporal cortex and the anterior cingulate cortex. The anterior temporal lobe (ATL), of which the temporal pole is the anterior end, is crucial for semantic processing (see Patterson, Nestor, & Rogers, 2007; Ralph et al., 2016, for reviews). In particular, the anterior temporal lobes is hypothesized to allocate the amodal hub in which the sensory-, motor- and language- specific aspects of conceptual knowledge converge from modality-specific regions to achieve higher -order generalizations or unified conceptual representations (Patterson et al., 2007; Peelen & Caramazza, 2012). The left ATL is extensively connected to the left dominant language centers (Friederici, 2009; Friederici et al., 2011) and consistently showed to be more

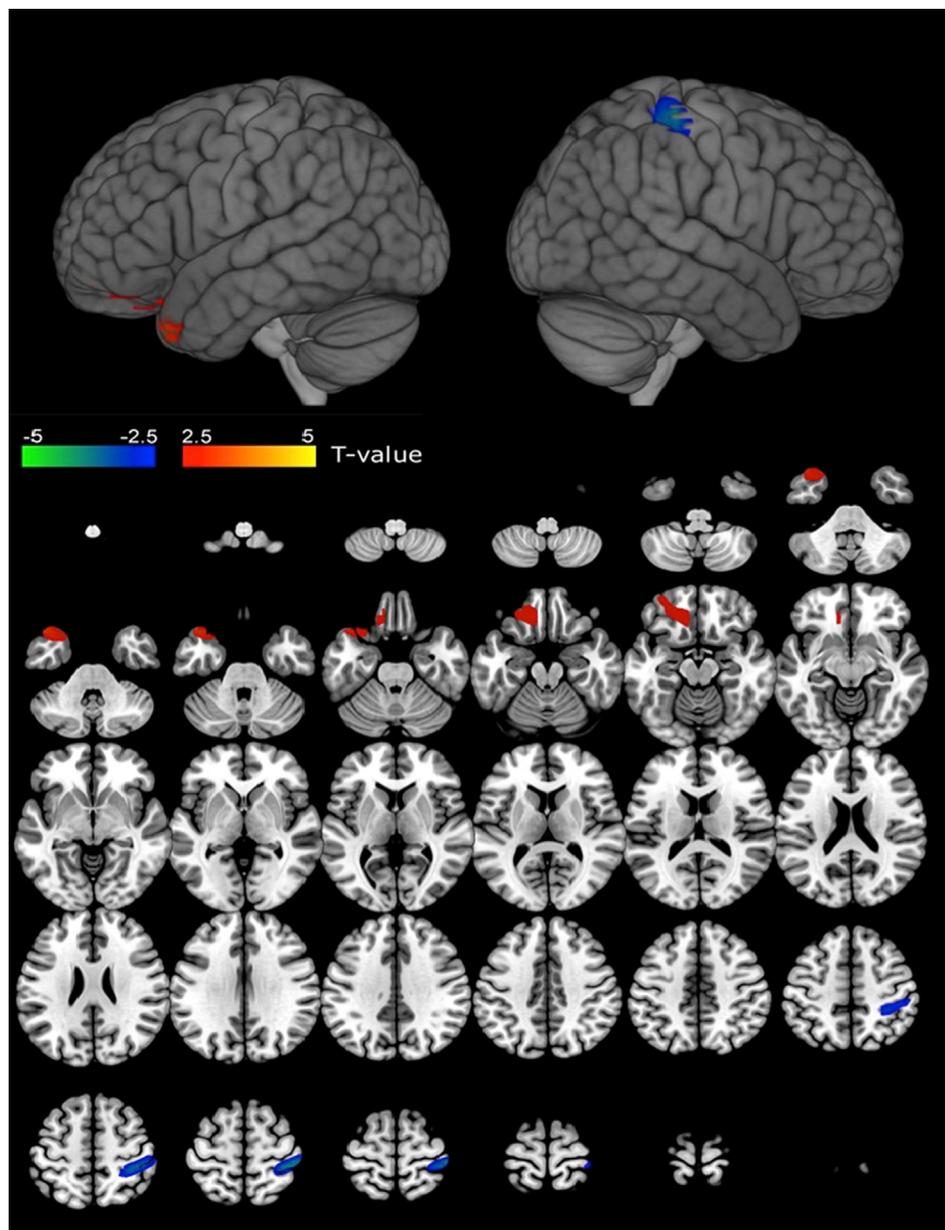


Fig. 5. Regions whose source signal activity differed between HFW and LFW (positive and negative significant activations respectively red and blue). Greater activity for high frequency words compared to low frequency words occurred in the right middle and superior temporal pole, orbitofrontal cortex, gyrus rectus, inferior temporal cortex, anterior cingulate. Greater activity for low frequency words compared to high frequency words occurred in the right postcentral and parietal inferior lobule. Statistical threshold = $p < 0.05$, corrected for multiple comparison using FDR (see Table 2 for details).

engaged in tasks that include a strong verbal component (see Price, 2012; Rice, Lambon Ralph, & Hoffman, 2015; Wong & Gallate, 2012 for reviews). The association between atrophy of anterior temporal regions and surface dyslexia in patients with semantic dementia (Brambati, Ogar, Neuhaus, Miller, & Gorno-Tempini, 2009; Nestor, Fryer, & Hodges, 2006; Patterson & Hodges, 1992; Wilson et al., 2008) also supports the idea that this area plays an important role in representing item-specific knowledge, including pronunciation at the ‘whole-word’ level. Marinkovic and colleagues (Marinkovic et al., 2003) combining high resolution structural MRI with temporally precise whole-head high density MEG and distributed source modelling, showed that spoken and written words were processed by distinct neural substrates during initial processing, but the activation converged onto overlapping areas subsequently during stages of semantic and contextual integration. Crucially, they estimated that the N400m was originated primarily in the left inferior prefrontal and anterior temporal areas. Vigneau et al.

(2006), in their meta-analysis of brain areas related to language processing, concluded that the left temporal pole together with the pars orbitalis of the inferior frontal gyrus, the fusiform gyrus and the angular gyrus constitutes a temporo-frontal semantic network that constructs an overall meaning connecting auditory and visual information to long-term memory.

A possible explanation of our finding, therefore, is the presence of more pronounced semantic associations for high frequency words (Carreiras et al., 2009; Devlin, Matthews, & Rushworth, 2003; Prabhakaran et al., 2006). Accordingly, semantic retrieval for HFW should be facilitated compared to LFW, which would result in greater SSVEPs in areas subserving semantic processing. Multiple lines of evidence suggest the existence of stronger semantic associations for HFW that could involve the left anterior temporal lobe and the inferior frontal cortex. Word frequency facilitates performance on semantic decision tasks and higher-frequency words are more likely to be

Table 2

Regions whose source signal activity differed between high and low frequency words (cf. Fig. 5) Size: number of voxels X, Y, Z reflect position in MNI coordinate space T reflects maximum T-value in the region.

Condition		High > Low Frequency Words			
Region	Size	X	Y	Z	T
<i>On the left hemisphere</i>					
Temporal_Pole_Mid_L	19	−47	21	−33	3.00
Temporal_Pole_Sup_L	17	−47	21	−28	3.04
Frontal_Mid_Orb_L	14	−38	56	−12	2.60
Frontal_Sup_Orb_L	8	−15	37	−22	2.62
Frontal_Inf_Orb_L	6	−37	28	−24	2.68
Rectus_L	6	−10	36	−17	2.62
Frontal_Med_Orb_L	5	−10	36	−12	2.63
Temporal_Inf_L	3	−35	10	−38	2.66
Cingulum_Ant_L	2	−10	36	−8	2.57
Condition		High < Low Frequency Words			
Region	Size	X	Y	Z	T
<i>On the right hemisphere</i>					
Postcentral_R	42	46	−33	62	−3.91
Parietal_Inf_R	14	38	−41	54	−3.06

produced as associates in word-association tasks (see Graves et al., 2010 for review). The high sensitivity of patients with semantic dementia to item familiarity/frequency is considered as evidence that representations of frequently encountered items are more robust in the face of semantic degradation (Jefferies & Lambon Ralph, 2006; Rogers, Patterson, Jefferies, & Ralph, 2015). Baayen (2010) demonstrated that the word frequency effect is largely explained by contextual learning (i.e., co-occurrence in the same linguistic context) and further argued that dual route models are severely limited by assuming that the frequency effect in reading is simply an effect of repeated exposure. Prompted by this evidence, Hofmann and Jacobs (2014) implemented an extended version of the interactive activation and competition model class that includes a semantic layer representing associations in a long-term memory structure. In particular, the architecture of the model includes top-down connections from semantic to orthographic layers that can account for semantic effect in the anterior temporal cortex. Testing the model using a recognition memory task, Stuellein, Radach, Jacobs, and Hofmann (2016) found that when a word is associated with many other words within the stimulus set, responses were facilitated in previously seen words but inhibited in new words, suggesting that semantic associations lead to higher stimulus familiarity. Accordingly, this behavioural effect was associated with smaller N400 amplitudes, reflecting more efficient semantic processing for word with many associates.

The recruitment of the left inferior frontal cortex has been repeatedly associated with the frequency effect (Carreiras et al., 2006, 2009; Chee et al., 2002, 2003; Fiebach et al., 2002; Fiez et al., 1999; Hauk et al., 2008; Joubert et al., 2004). Usually, in fMRI studies, the activation of the left inferior frontal cortex is inversely related to the frequency of the word, and has been interpreted as reflecting either more demanding phonological processing/phonological retrieval (e.g. Carreiras et al., 2009) or more difficult selection of the appropriate semantic representation from multiple competing representations (e.g. Hofmann & Jacobs, 2014) for low frequency words. Coherently, we found that this area has been entrained by the periodic stimulation to a greater extent for high frequency words, suggesting either more efficient phonological retrieval or stronger semantic associations for this type of stimuli.

Interestingly, activation for high-frequency words in the anterior temporal lobes has been difficult to instantiate (see Graves et al., 2010; Patterson et al., 2007 for discussions of the possible causes associated with fMRI). As we have previously mentioned, the long presentation

time of our paradigm together with the high signal-to-noise ratio of SSVEP paradigms could have allowed us to detect more easily the selective recruitment of areas associated with semantic processing. It is also interesting to observe that the analysis of the neural sources repeatedly point to the engagement of the semantic system. Along with the higher entrainment of areas that are hypothesized to constitute the semantic hub for HFW, words showed higher entrainment than pseudowords in the right precuneus, previously identified as a relevant semantic area (Binder et al., 2009), and in the right posterolateral cerebellum, possibly reflecting the activation of the context associated with words (Lesage et al., 2012; Moberget et al., 2014).

Concurrently, we found higher activation for LFW compared to HFW in a right region that extended over the postcentral gyrus, and the inferior parietal lobule. A possible explanation is a greater involvement of the visuo-spatial attentional network in phonological decoding. Visuospatial attention is considered to be primarily controlled by the fronto-parietal attention network (Corbetta & Shulman, 2002), with a prominent role of the right hemisphere (Thiebaut de Schotten et al., 2011). In particular, the role of the inferior parietal lobule (Wang et al., 2016) in attention orientation has been recently confirmed. Consistent behavioral evidence (Auclair & Siéroff, 2002; Givon, Yang, & Gernsbacher, 1990; Montani et al., 2014; Risko, Stolz, & Besner, 2011; Sieroff & Posner, 1988) supports the proposal that phonological decoding is controlled by a top-down mechanism directing the spotlight of attention serially from left to right over the sub-word units (LaBerge & Samuels, 1974). The candidate that most likely subserves this mechanism is the attentional stream located in the parietal lobe (Vidyasagar & Pammer, 2010) and multiple evidence points to a selective involvement of the right parietal lobe when reading is more demanding. Serial reading is required to process unfamiliar format, such as case mixing. Using positron emission tomography (PET), Mayall, Humphreys, Mechelli, Olson, and Price (2001) found that mixed-case words compared to same-case words produced increased activation in the right parietal cortex. Similarly, the disruption produced by transcranial magnetic stimulation (TMS) over the right posterior parietal lobe was more pronounced for mixed-case words (Braet & Humphreys, 2006). Again with an inhibitory TMS protocol, Cazzoli, Müri, Kennard, and Rosenthal (2014), found that TMS application over the right posterior parietal cortex produced an increase in letter migrations errors. Because letter migration is due to an erroneous binding between the letters composing the words and their spatial location, a possible interpretation of that finding is that the transient disruption of the mechanism controlling the precise parsing of the string caused an over reliance on coarse grained orthographic processing (Grainger & Ziegler, 2011). Another example of more demanding reading process from the point of view of visuo-spatial analysis is logographic reading. The square shape of the logograph requires an elaborated analysis of the spatial information and locations of various strokes (Tan et al., 2001). Compared to reading English, a larger involvement of the right hemisphere, including the superior parietal lobule and the supramarginal gyrus, has been demonstrated in Chinese reading (Tan et al., 2001), especially for irregular words (Hai Tan, Ching-Mei Feng, Fox, & Gao, 2001). Finally, visual spatial attention deficits are associated with phonological decoding deficits in developmental dyslexia (Facoetti et al., 2006), and dyslexic readers showed reduced activation in the right superior parietal lobule in tasks requiring visual processing of multiple characters (Lobier, Peyrin, Pichat, Le Bas, & Valdois, 2014). Accordingly, in a treatment protocol with dyslexic children, high frequency repetitive TMS stimulation over the right inferior parietal lobule improved non-word reading accuracy (Costanzo, Menghini, Caltagirone, Oliveri, & Vicari, 2013).

The engagement of the same attentional network would have been expected for pseudowords compared to words, but the effect did not “survive” correction for multiple comparisons (see Fig. 3 in Supplementary material). However, this could be accounted by the fact that the ‘word group’ included both high-frequency words and low-

frequency words, with the processing of the latter partially relying onto the sublexical route. Therefore, it seems reasonable to assume that the possibility to detect the selective engagement of the right attentional network for pseudowords has been weakened by the presence of the low-frequency words in the ‘word group’.

Some potential limitations of this study warrant mention. First, the relatively low-density electrical recording together with the unavailability of individual MRI implies a certain degree of uncertainty and approximation in the localization of the neural sources. Second, we did not take into account other word properties, such as length, that typically has a significant impact on reading aloud. Finally, as discussed earlier, we cannot completely exclude the possibility that some of the effects were blurred or modulated by the characteristic spectral frequency of a specific area. This is especially true for the parietal cortex that has previously shown to exhibit oscillatory activity in the beta range (Rosanova et al., 2009).

In conclusion, using a naming task, we showed that SSVEPs generated by written words and pseudowords are sensitive to fundamental effects of reading aloud. In particular, we found that SSVEPs tapped lexical network dynamics. That is, SSVEP amplitudes were modulated by lexical frequency and lexicality but not by sublexical orthographic familiarity. This finding is in line with the idea that SSVEPs reflect more structured, organized and efficient neural representations, which result in more synchronized network dynamics. The source localization

confirmed that the paradigm is well suited to investigate the cortical generators and neural dynamics of word processing. First, we found a remarkable overlap between the neural generators of the SSVEP effects and findings obtained with other neuroimaging techniques, such as the engagement of the right precuneus for words, the engagement of areas devoted to speech processing and/or speech-to-sound conversion for pseudowords, the involvement of the inferior frontal gyrus in producing the frequency effect. Then, we found effects that although have been predicted by multiple lines of evidence, had been rather difficult to detect previously, such as frequency effects in the left anterior temporal pole and in the right parietal cortex. We believe that the present approach provides a complementary window into studying the organization of the reading network.

Acknowledgements

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Appendix A

HFW	LFW	FPW	UPW
accord	accroc	aciser	acesce
affaire	affront	afrayé	afrilon
argent	argile	arrait	arlore
avenir	averse	avison	aviche
bouche	boudin	bonner	boicun
bureau	buvard	busque	buconq
chaleur	chamois	chevant	chacace
chambre	chanvre	charlon	chogome
chemin	chenal	charpe	chefet
cheval	chenil	chasé	chepit
compte	compas	cousse	cosice
couleur	coupole	couteur	coumour
cuisine	cuisson	culteur	cuvini
droite	dragon	draban	drarce
départ	dédain	déval	dôlunc
escalier	escabeau	estroule	essicore
esprit	escroc	essage	esbyre
exemple	aigreur	excadre	exiscer
famille	fardeau	fautile	fairile
fenêtre	femelle	fentait	fetivec
garçon	gadoue	gadée	gaunos
gauche	gosier	garsil	gatena
jardin	jasmin	jalait	jansir
langue	landau	laçon	laimet
lumière	lucarne	lunique	luchepa
maison	merlan	matice	marect
manière	martyre	manché	mancoua
marche	massue	mamour	masude
mesure	meneur	mendit	mecose
milieu	milice	miable	mirque
moment	mollet	moneur	monhui
mémoire	mélopée	mésion	mésalu
oreille	auréole	orgnant	ortrere
papier	patine	pateur	papuis
partie	patate	parré	paclit
passage	palette	palpier	paucume
personne	perruque	pentrée	pernonde
pierre	pioche	pière	pisove
plaisir	planton	plaiser	plusace
présence	prophète	procuté	pruelque
présent	préface	procher	prinume
question	kermesse	queltire	queltela
raison	raisin	raché	rapota
regard	renard	rebout	renlut

retour	regain	revant	resbas
semaine	semence	septeur	senedece
service	serment	serreur	sermice
silence	circuit	simique	sicason
soleil	saumon	soudre	sosele
sommeil	sottise	soucher	sousied
sourire	soulier	souloir	sosinom
souvenir	soupière	souponne	sousivec
travail	trapèze	trocher	trisire
village	virgule	vicorer	vinonse
visage	vipère	visoir	vinion
voiture	voilier	voyaser	vousace
épaule	éperon	époge	ésins
madame	mazout	mamine	mausin
propos	prieur	proué	propui
travers	tronçon	trouser	trisire

Appendix B. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.bandl.2019.01.004>. The raw data can be found online at <https://doi.org/10.5281/zenodo.2577156>.

References

- Ackermann, H., Vogel, M., Petersen, D., & Poremba, M. (1992). Speech deficits in ischaemic cerebellar lesions. *Journal of Neurology*, *239*(4), 223–227.
- Annabel Chen, S.-H., Ringo Ho, M.-H., & Desmond, J. E. (2012). A meta-analysis of cerebellar contributions to higher cognition from PET and fMRI studies. *Human Brain Mapping*, *35*(2), 593–615.
- Appelbaum, L. G., Ales, J. M., Norcia, A. M., Kastner, S., Weerd, P. D., Ungerleider, L., & Lamme, V. (2012). The time course of segmentation and cue-selectivity in the human visual cortex. *PLoS ONE*, *7*(3), e34205.
- Auclair, L., & Siéroff, E. (2002). Attentional cueing effect in the identification of words and pseudowords of different length. *The Quarterly Journal of Experimental Psychology*, *55*(2), 445–463.
- Baayen, R. H. (2010). Demythologizing the word frequency effect: A discriminative learning perspective. *The Mental Lexicon*, *5*(3), 436–461.
- Baayen, R., Davidson, D., & Bates, D. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language*, *59*(4), 390–412.
- Bach, M., & Meigen, T. (1999). Do's and don'ts in Fourier analysis of steady-state potentials. *Documenta Ophthalmologica*, *99*(1), 69–82.
- Barber, H. A., & Kutas, M. (2007). Interplay between computational models and cognitive electrophysiology in visual word recognition. *Brain Research Reviews*, *53*(1), 98–123.
- Barrós-Loscertales, A., González, J., Pulvermüller, F., Ventura-Campos, N., Bustamante, J. C., Costumero, V., ... Ávila, C. (2012). Reading salt activates gustatory brain regions: fMRI evidence for semantic grounding in a novel sensory modality. *Cerebral Cortex*, *22*(11), 2554–2563.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using eigen and s4 (R package version 1.1-7).
- Bedo, N., Ribary, U., & Ward, L. M. (2014). Fast dynamics of cortical functional and effective connectivity during word reading. *PLoS ONE*, *9*(2).
- Besner, D., Risko, E. F., Stolz, J. A., White, D., Reynolds, M., O'Malley, S., & Robidoux, S. (2016). Varieties of attention: Their roles in visual word identification. *Current Directions in Psychological Science*, *25*(3), 162–168.
- Binder, J. R., Desai, R. H., Graves, W. W., & Conant, L. L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*, 2767–2796.
- Bitan, T., Burman, D. D., Chou, T.-L., Lu, D., Cone, N. E., Cao, F., ... Booth, J. R. (2007). The interaction between orthographic and phonological information in children: An fMRI study. *Human Brain Mapping*, *28*(9), 880–891.
- Boulenger, V., Hauk, O., & Pulvermüller, F. (2009). Grasping ideas with the motor system: Semantic somatotopy in idiom comprehension. *Cereb Cortex*, *19*(8), 1905–1914.
- Braet, W., & Humphreys, G. W. (2006). Case mixing and the right parietal cortex: Evidence from rTMS. *Experimental Brain Research*, *168*(1–2), 265–271.
- Brambati, S. M., Ogar, J., Neuhaus, J., Miller, B. L., & Gorno-Tempini, M. L. (2009). Reading disorders in primary progressive aphasia: A behavioral and neuroimaging study. *Neuropsychologia*, *47*(8–9), 1893–1900.
- Braun, M., Hutzler, F., Ziegler, J. C., Dambacher, M., & Jacobs, A. M. (2009). Pseudohomophone effects provide evidence of early lexico-phonological processing in visual word recognition. *Human Brain Mapping*, *30*(7), 1977–1989.
- Braun, M., Jacobs, A. M., Richlan, F., Hawelka, S., Hutzler, F., & Kronbichler, M. (2015). Many neighbors are not silent. fMRI evidence for global lexical activity in visual word recognition. *Frontiers in Human Neuroscience*, *9*, 423. <https://doi.org/10.3389/fnhum.2015.00423>.
- Bruno, J. L., Zumberge, A., Manis, F. R., Lu, Z.-L., & Goldman, J. G. (2008). Sensitivity to orthographic familiarity in the occipito-temporal region. *NeuroImage*, *39*(4), 1988–2001.
- Buckner, R. (2013). The cerebellum and cognitive function: 25 Years of insight from anatomy and neuroimaging. *Neuron*, *80*(3), 807–815.
- Buzsáki, G. (2004). Large-scale recording of neuronal ensembles. *Nature Neuroscience*, *7*(5), 446–451.
- Buzsáki, G. (2010). Neural syntax: Cell assemblies, synapse assemblies, 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., 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.
- 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.
- Carreiras, M., Riba, J., Vergara, M., Heldmann, M., & Münte, T. F. (2009). Syllable congruency and word frequency effects on brain activation. *Human Brain Mapping*, *30*(9), 3079–3088.
- Cazzoli, D., Müri, R. M., Kennard, C., & Rosenthal, C. R. (2014). The role of the right posterior parietal cortex in letter migration between words. *Journal of Cognitive Neuroscience*, *27*(2), 377–386.
- Chee, M. W., Hon, N. H., Caplan, D., Lee, H. L., & Goh, J. (2002). Frequency of concrete words modulates prefrontal activation during semantic judgments. *NeuroImage*, *16*(1), 259–268.
- Chee, M. W., Westphal, C., Goh, J., Graham, S., & Song, A. W. (2003). Word frequency and subsequent memory effects studied using event-related fMRI. *NeuroImage*, *20*(2), 1042–1051.
- Chen, Y., Davis, M. H., Pulvermüller, F., & Hauk, O. (2013). Task modulation of brain responses in visual word recognition as studied using EEG/MEG and fMRI. *Frontiers in Human Neuroscience*, *7*, 376. <https://doi.org/10.3389/fnhum.2013.00376>.
- Chen, S. A., & Desmond, J. E. (2005). Cerebrocerebellar networks during articulatory rehearsal and verbal working memory tasks. *NeuroImage*, *24*(2), 332–338.
- Chicherov, V., & Herzog, M. H. (2015). Targets but not flankers are suppressed in crowding as revealed by EEG frequency tagging. *NeuroImage*, *119*, 325–331.
- Cohen, L., Lehericy, S., Chochon, F., Lemer, C., Rivaud, S., & Dehaene, S. (2002). Language-specific tuning of visual cortex? Functional properties of the visual word form area. *Brain: A Journal of Neurology*, *125*(5), 1054–1069.
- Coltheart, M., Curtis, B., Atkins, P., & Haller, M. (1993). Models of reading aloud: Dual-route and parallel-distributed-processing approaches. *Psychological Review*, *100*(4), 589.
- Coltheart, M., Rastle, K., Perry, C., Langdon, R., & Ziegler, J. (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, *108*(1), 204.
- Corbetta, M., & Shulman, G. L. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 215–229.
- Costanzo, F., Menghini, D., Caltagirone, C., Oliveri, M., & Vicari, S. (2013). How to improve reading skills in dyslexics: The effect of high frequency rTMS. *Neuropsychologia*, *51*(14), 2953–2959.
- Dehaene, S., & Cohen, L. (2011). The unique role of the visual word form area in reading. *Trends in Cognitive Sciences*, *15*(6), 254–262.
- 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.
- Devlin, J. T., Matthews, P. M., & Rushworth, M. F. S. (2003). Semantic processing in the left inferior prefrontal cortex: A combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *Journal of Cognitive Neuroscience*, *15*(1), 71–84.
- Di Russo, F., Spinelli, D., & Morrone, M. (2001). Automatic gain control contrast mechanisms are modulated by attention in humans: Evidence from visual evoked potentials. *Vision Research*, *41*(19), 2435–2447.
- 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.
- Dufau, S., Grainger, J., & Ziegler, J. C. (2012). How to say “no” to a nonword: A leaky competing accumulator model of lexical decision. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 38(4), 1117–1128.
- Eulitz, C., Maess, B., Pantev, C., Friederici, A. D., Feige, B., & Elbert, T. (1996). Oscillatory neuromagnetic activity induced by language and non-language stimuli. *Cognitive Brain Research*, 4(2), 121–132.
- Facoetti, A., Zorzi, M., Cestnick, L., Lorusso, M. L., Molteni, M., Paganoni, P., ... Mascetti, G. G. (2006). The relationship between visuo-spatial attention and nonword reading in developmental dyslexia. *Cognitive Neuropsychology*, 23(6), 841–855.
- Feng, X., Li, L., Zhang, M., Yang, X., Tian, M., Xie, W., ... Ding, G. (2016). Dyslexic children show atypical cerebellar activation and cerebro-cerebellar functional connectivity in orthographic and phonological processing. *The Cerebellum*, 1–12.
- Ferrand, L., New, B., Brysbaert, M., Keuleers, E., Bonin, P., Méot, A., ... Pallier, C. (2010). The French Lexicon Project: Lexical decision data for 38,840 French words and 38,840 pseudowords. *Behavior Research Methods*, 42(2), 488–496.
- Fiebach, C. J., Friederici, A. D., Müller, K., & von Cramon, D. Y. (2002). fMRI Evidence for dual routes to the mental lexicon in visual word recognition. *Journal of Cognitive Neuroscience*, 14(1), 11–23. <https://doi.org/10.1162/089892902317205285>.
- Fiez, J. A., Balota, D. A., Raichle, M. E., & Petersen, S. E. (1999). Effects of lexicality, frequency, and spelling-to-sound consistency on the functional anatomy of reading. *Neuron*, 24(1), 205–218. [https://doi.org/10.1016/S0896-6273\(00\)80833-8](https://doi.org/10.1016/S0896-6273(00)80833-8).
- Fiez, J. A., & Petersen, S. E. (1998). Neuroimaging studies of word reading. *Proceedings of the National Academy of Sciences*, 95(3), 914–921.
- Friederici, A. D. (2009). Pathways to language: Fiber tracts in the human brain. *Trends in Cognitive Sciences*, 13(4), 175–181.
- Friederici, A. D., Alexander, M., Hiltbrunner, B., Fischer, R., Amedi, A., von Kriegstein, K., ... Zorzi, F. (2011). The brain basis of language processing: From structure to function. *Physiological reviews*, 91(4), 1357–1392.
- 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.
- Garagnani, M., Lucchese, G., Tomasello, R., Wennekers, T., & Pulvermüller, F. (2017). A spiking neurocomputational model of high-frequency oscillatory brain responses to words and pseudowords. *Frontiers in Computational Neuroscience*, 10, 145.
- Garagnani, M., Shtyrov, Y., & Pulvermüller, F. (2009). Effects of attention on what is known and what is not: MEG evidence for functionally discrete memory circuits. *Frontiers in Human Neuroscience*, 3.
- García, J. O., Srinivasan, R., & Serences, J. T. (2013). Near-real-time feature-selective modulations in human cortex. *Current Biology*, 23(6), 515–522.
- Genovesi, C. R., Lazar, N. A., & Nichols, T. (2002). Thresholding of statistical maps in functional neuroimaging using the false discovery rate. *NeuroImage*, 15(4), 870–878.
- Givon, T., Yang, L., & Gernsbacher, M. (1990). The processing of second language vocabulary from attended to automated word recognition. *Variability in Second Language Acquisition*, 1.
- Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the visual word form area. *Neuron*, 62(2), 199–204.
- González, J., Barros-Loscertales, A., Pulvermüller, F., Meseguer, V., Sanjuán, A., Belloch, V., & Ávila, C. (2006). Reading cinnamon activates olfactory brain regions. *NeuroImage*, 32(2), 906–912.
- Grainger, J., & Holcomb, P. J. (2009). Watching the word go by: On the time-course of component processes in visual word recognition. *Language and Linguistics Compass*, 3(1), 128–156.
- Grainger, J., & Ziegler, J. C. (2011). A dual-route approach to orthographic processing. *Frontiers in Psychology*, 2, 54.
- 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.
- Grech, R., Cassar, T., Muscat, J., Camilleri, K. P., Fabri, S. G., Zervakis, M., ... Vanrumste, B. (2008). Review on solving the inverse problem in EEG source analysis. *Journal of NeuroEngineering and Rehabilitation*, 7(5), 25.
- Hai Tan, L., Ching-Mei Feng, C., Fox, P. T., & Gao, J.-H. (2001). An fMRI study with written Chinese. *Neuroreport*, 12(1), 83–88.
- Harm, M. W., & Seidenberg, M. S. (1999). Phonology, reading acquisition, and dyslexia: Insights from connectionist models. *Psychological Review*, 106(3), 491.
- Hauk, O., Davis, M. H., Kherif, F., & Pulvermüller, F. (2008). Imagery or meaning? Evidence for a semantic origin of category-specific brain activity in metabolic imaging. *European Journal of Neuroscience*, 27(7), 1856–1866.
- Hofmann, M. J., & Jacobs, A. M. (2014). Interactive activation and competition models and semantic context: From behavioral to brain data. *Neuroscience & Biobehavioral Reviews*, 46, 85–104.
- Ito, M. (2008). Control of mental activities by internal models in the cerebellum. *Nature Reviews Neuroscience*, 9(4), 304–313.
- Jefferies, E., & Lambon Ralph, M. A. (2006). Semantic impairment in stroke aphasia versus semantic dementia: A case-series comparison. *Brain*, 129(8), 2132–2147.
- Jobard, G., Crivello, F., & Tzourio-Mazoyer, N. (2003). Evaluation of the dual route theory of reading: A meta-analysis of 35 neuroimaging studies. *NeuroImage*, 20(2), 693–712.
- Joon Kim, Y., Grabowecy, M., Paller, K. A., Muthu, K., & Suzuki, S. (2007). Attention induces synchronization-based response gain in steady-state visual evoked potentials. *Nature Neuroscience*, 10(1), 117–125.
- Joubert, S., Beauregard, M., Walter, N., Bourgouin, P., Beaudoin, G., Leroux, J.-M., ... Lecours, A. R. (2004). Neural correlates of lexical and sublexical processes in reading. *Brain and Language*, 89(1), 9–20.
- 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.
- Kaspar, K., Hassler, U., Martens, U., Trujillo-Barreto, N., & Gruber, T. (2010). Steady-state visually evoked potential correlates of object recognition. *Brain Research*, 1343, 112–121.
- Keitel, C., Quigley, C., & Ruhnau, P. (2014). Stimulus-driven brain oscillations in the alpha range: Entrainment of intrinsic rhythms or frequency-following response? *Journal of Neuroscience*, 34(31), 10137–10140.
- 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.
- Koban, L., Ninck, M., Li, J., Gisler, T., Kissler, J., Brosch, T., ... Versace, F. (2010). Processing of emotional words measured simultaneously with steady-state visually evoked potentials and near-infrared diffusing-wave spectroscopy. *BMC Neuroscience*, 11(1), 85.
- Kronbichler, M., Bergmann, J., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., & Wimmer, H. (2007). Taxi vs. Taksi: On orthographic word recognition in the left ventral occipitotemporal cortex. *Journal of Cognitive Neuroscience*, 19(10), 1584–1594.
- Kronbichler, M., Hutzler, F., Wimmer, H., Mair, A., Staffen, W., & Ladurner, G. (2004). The visual word form area and the frequency with which words are encountered: Evidence from a parametric fMRI study. *NeuroImage*, 21, 3.
- Kuś, R., Duszyk, A., Milanowski, P., Łabecki, 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.
- Kutas, M., & Federmeier, K. D. (2000). Electrophysiology reveals semantic memory use in language comprehension. *Trends in Cognitive Sciences*, 4(12), 463–470.
- LaBerge, D., & Samuels, S. J. (1974). Toward a theory of automatic information processing in reading. *Cognitive Psychology*, 6(2), 293–323.
- Laycock, S. K., Wilkinson, I. D., Wallis, L. I., Darwent, G., Wonders, S. H., Fawcett, A. J., & Nicolson, R. I. (2008). Cerebellar volume and cerebellar metabolic characteristics in adults with dyslexia. *Annals of the New York Academy of Sciences*, 1145(1), 222–236.
- Lesage, E., Morgan, B. E., Olson, A. C., Meyer, A. S., & Miall, R. C. (2012). Cerebellar rTMS disrupts predictive language processing. *Current Biology*, 22(18), R794–R795.
- Linkersdörfer, J., Lonnemann, J., Lindberg, S., Hasselhorn, M., Fiebach, C. J., McCandliss, B., ... Nichols, T. (2012). Grey matter alterations co-localize with functional abnormalities in developmental dyslexia: An ALE meta-analysis. *PLoS ONE*, 7(8), e43122.
- Lobier, M. A., Peyrin, C., Pichat, C., Le Bas, J. F., & Valdois, S. (2014). Visual processing of multiple elements in the dyslexic brain: Evidence for a superior parietal dysfunction. *Frontiers in Human Neuroscience*, 8.
- 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.
- Lochy, A., Van Reybroeck, M., & Rossion, B. (2016). Left cortical specialization for visual letter strings predicts rudimentary knowledge of letter-sound association in pre-schoolers. *Proceedings of the National Academy of Sciences*, 113(30), 8544–8549.
- 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.
- Luck, S. J. (2014). *An introduction to the event-related potential technique*. MIT Press.
- Lutzenberger, W., Pulvermüller, F., & Birbaumer, N. (1994). Words and pseudowords elicit distinct patterns of 30-Hz EEG responses in humans. *Neuroscience Letters*, 176(1), 115–118.
- Mahé, G., Zesiger, P., & Laganaro, M. (2015). Beyond the initial 140ms, lexical decision and reading aloud are different tasks: An ERP study with topographic analysis. *NeuroImage*, 122, 65–72.
- Mainy, N., Jung, J., Baci, M., Kahane, P., Schoendorff, B., Minotti, L., ... Lachaux, J. P. (2008). Cortical dynamics of word recognition. *Human Brain Mapping*, 29(11), 1215–1230.
- Marinkovic, K., Dhond, R. P., Dale, A. M., Glessner, M., Carr, V., & Halgren, E. (2003). Spatiotemporal dynamics of modality-specific and supramodal word processing. *Neuron*, 38(3), 487–497.
- Maris, E., & Oostenveld, R. (2007). Nonparametric statistical testing of EEG- and MEG-data. *Journal of Neuroscience Methods*, 164(1), 177–190.
- Mathôt, S., Schrei, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, 44(2), 314–324.
- Mayall, K., Humphreys, G. W., Mechelli, A., Olson, A., & Price, C. J. (2001). The effects of case mixing on word recognition: Evidence from a PET study. *Journal of Cognitive Neuroscience*, 13(6), 844–853.
- 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.
- Moberget, T., Gulleen, E. H., Andersson, S., Ivry, R. B., & Endestad, T. (2014). Generalized role for the cerebellum in encoding internal models: Evidence from semantic processing. *Journal of Neuroscience*, 34(8).
- Montani, V., Facoetti, A., & Zorzi, M. (2014). Spatial attention in written word perception. *Frontiers in Human Neuroscience*, 8, 42.
- Montani, V., Facoetti, A., & Zorzi, M. (2015). The effect of decreased interletter spacing on orthographic processing. *Psychonomic Bulletin & Review*, 22(3), 824–832.
- 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.

- Nestor, P. J., Fryer, T. D., & Hodges, J. R. (2006). Declarative memory impairments in Alzheimer's disease and semantic dementia. *NeuroImage*, *30*(3), 1010–1020.
- 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.
- Nicolson, R. I., Fawcett, A. J., & Dean, P. (2001). Developmental dyslexia: The cerebellar deficit hypothesis. *Trends in Neurosciences*, *24*(9), 508–511.
- Nikulin, V. V., Linkenkaer-Hansen, K., Nolte, G., Lemm, S., Müller, K. R., Ilmoniemi, R. J., & Curio, G. (2007). A novel mechanism for evoked responses in the human brain. *European Journal of Neuroscience*, *25*(10), 3146–3154.
- Norcia, A. M., Appelbaum, L. G., Ales, J. M., Cottoreau, B. R., & Rossion, B. (2015). The steady-state visual evoked potential in vision research: A review. *Journal of Vision*, *15*(6) 4–4.
- Norcia, A. M., Tyler, C. W., Hamer, R. D., & Wesemann, W. (1989). Measurement of spatial contrast sensitivity with the swept contrast VEP. *Vision Research*, *29*(5), 627–637.
- Oostenveld, R., Fries, P., Maris, E., Schoffelen, J.-M., Oostenveld, R., Fries, P., ... Schoffelen, J.-M. (2011). FieldTrip: Open source software for advanced analysis of MEG, EEG, and invasive electrophysiological data. *Computational Intelligence and Neuroscience*, *2011*, 1–9.
- 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.
- Pattamadilok, C., Chanoine, V., Pallier, C., Anton, J. L., Nazarian, B., Belin, P., & Ziegler, J. C. (2017). Automaticity of phonological and semantic processing during visual word recognition. *NeuroImage*, *149*, 244–255.
- Patterson, K., & Hodges, J. R. (1992). Deterioration of word meaning: Implications for reading. *Neuropsychologia*, *30*(12), 1025–1040.
- Patterson, K., Nestor, P. J., & Rogers, T. T. (2007). Where do you know what you know? The representation of semantic knowledge in the human brain. *Nature Reviews Neuroscience*, *8*(12), 976–987.
- Peelen, M. V., & Caramazza, A. (2012). Conceptual object representations in human anterior temporal cortex. *Journal of Neuroscience*, *32*(45), 15728–15736.
- Peirce, J. W. (2007). PsychoPy—psychophysics software in Python. *Journal of Neuroscience Methods*, *162*(1), 8–13.
- Perlstein, W. M., Cole, M. A., Larson, M., Kelly, K., Seignourel, P., & Keil, A. (2003). Steady-state visual evoked potentials reveal frontally-mediated working memory activity in humans. *Neuroscience Letters*, *342*(3), 191–195.
- Perry, C., Ziegler, J. C., & Zorzi, M. (2007). Nested incremental modeling in the development of computational theories: The CDP+ model of reading aloud. *Psychological Review*, *114*(2), 273–315.
- Perry, C., Ziegler, J. C., & Zorzi, M. (2010). Beyond single syllables: Large-scale modeling of reading aloud with the Connectionist Dual Process (CDP++) model. *Cognitive Psychology*, *61*(2), 106–151.
- Peterson, D. J., Gurariy, G., Dimotsantos, G. G., Arciniega, H., Berryhill, M. E., & Caplovitz, G. P. (2014). The steady-state visual evoked potential reveals neural correlates of the items encoded into visual working memory. *Neuropsychologia*, *63*, 145–153.
- Plaut, D. C., McClelland, J. L., Seidenberg, M. S., & Patterson, K. (1996). Understanding normal and impaired word reading: Computational principles in quasi-regular domains. *Psychological Review*, *103*(1), 56.
- Prabhakaran, R., Blumstein, S. E., Myers, E. B., Hutchison, E., & Britton, B. (2006). An event-related fMRI investigation of phonological-lexical competition. *Neuropsychologia*, *44*(12), 2209–2221.
- Price, C. J. (2012). A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. *NeuroImage*, *62*(2), 816–847.
- Price, C. J., & Devlin, J. T. (2011). The interactive account of ventral occipitotemporal contributions to reading. *Trends in Cognitive Sciences*, *15*(6), 246–253.
- Price, C. J., & Mechelli, A. (2005). Reading and reading disturbance. *Current Opinion in Neurobiology*, *15*(2), 231–238.
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Review Neuroscience*, *6*(7), 576–582.
- Pulvermüller, F., Preißl, H., Eulitz, C., Pantev, C., Lutzenberger, W., Feige, B., ... Birbaumer, N. (1994). Gamma-band responses reflect word/pseudoword processing (pp. 243–258).
- Pulvermüller, F., & Fadiga, L. (2010). Active perception: Sensorimotor circuits as a cortical basis for language. *Nature Reviews Neuroscience*, *11*(5), 351–360.
- Pulvermüller, F., Garagnani, M., & Wennekers, T. (2014). Thinking in circuits: Toward neurobiological explanation in cognitive neuroscience. *Biological Cybernetics*, *108*(5), 573–593.
- R Core Team (2014). R: A language and environment for statistical computing.
- Ralph, M. A. L., Jefferies, E., Patterson, K., & Rogers, T. T. (2016). The neural and computational bases of semantic cognition. *Nature Reviews Neuroscience*.
- Ramnani, N. (2006). The primate cortico-cerebellar system: Anatomy and function. *Nature Reviews Neuroscience*, *7*(7), 511–522.
- Regan, D. (1989). *Human brain electrophysiology: Evoked potentials and evoked magnetic fields in science and medicine*. Amsterdam, the Netherlands: Elsevier.
- Rice, G. E., Lambon Ralph, M. A., & Hoffman, P. (2015). The roles of left versus right anterior temporal lobes in conceptual knowledge: An ALE meta-analysis of 97 functional neuroimaging studies. *Cerebral Cortex*, *25*(11), 4374–4391.
- Risko, E. F., Stolz, J. A., & Besner, D. (2011). Basic processes in reading: On the relation between spatial attention and familiarity. *Language and Cognitive Processes*, *26*(1), 47–62.
- Roelting, D. P., Sevush, S., & Heilman, K. M. (1983). Phonological agraphia: Writing by the lexical-semantic route. *Neurology*, *33*(6), 755–765.
- Rogers, T. T., Patterson, K., Jefferies, E., & Ralph, M. A. L. (2015). Disorders of representation and control in semantic cognition: Effects of familiarity, typicality, and specificity. *Neuropsychologia*, *76*, 220–239.
- Rosanova, M., Casali, A., Bellina, V., Resta, F., Mariotti, M., & Massimini, M. (2009). Natural frequencies of human corticothalamic circuits. *Journal of Neuroscience*, *29*(24), 7679–7685.
- Rossion, B. (2014). Understanding individual face discrimination by means of fast periodic visual stimulation. *Experimental Brain Research*, *232*(6), 1599–1621.
- Schurz, M., Kronbichler, M., Crone, J., Richlan, F., Klackl, J., & Wimmer, H. (2014). Top-down and bottom-up influences on the left ventral occipito-temporal cortex during visual word recognition: An analysis of effective connectivity. *Human Brain Mapping*, *35*(4), 1668–1680.
- Seidenberg, M. S., & McClelland, J. L. (1989). A distributed, developmental model of word recognition and naming. *Psychological Review*, *96*(4), 523.
- Sieroff, E., & Posner, M. I. (1988). Cueing spatial attention during processing of words and letter strings in normals. *Cognitive Neuropsychology*, *5*(4), 451–472.
- 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.
- Stoodley, C. J., & Schmahmann, J. D. (2008). Functional topography in the human cerebellum: A meta-analysis of neuroimaging studies. *NeuroImage*, *44*, 489–501.
- Stoodley, C. J., & Schmahmann, J. D. (2009). The cerebellum and language: Evidence from patients with cerebellar degeneration. *Brain and Language*, *110*(3), 149–153.
- Stuellein, N., Radach, R. R., Jacobs, A. M., & Hofmann, M. J. (2016). No one way ticket from orthography to semantics in recognition memory: N400 and P200 effects of associations. *Brain Research*, *1639*, 88–98.
- Tan, L. H., Liu, H.-L., Perfetti, C. A., Spinks, J. A., Fox, P. T., & Gao, J.-H. (2001). The neural system underlying Chinese logograph reading. *NeuroImage*, *13*(5), 836–846.
- Taylor, J. S. H., Rastle, K., Davis, M. H., & Holloway, R. (2013). Can cognitive models explain brain activation during word and pseudoword reading? A meta-analysis of 36 neuroimaging studies. *Psychological Bulletin*, *139*(4), 766.
- Testolin, A., Stoianov, I., Sperduti, A., & Zorzi, M. (2016). Learning Orthographic Structure With Sequential Generative Neural Networks. *Cognitive Science*, *40*(3), 579–606. <https://doi.org/10.1111/cogs.12258>.
- Testolin, A., Stoianov, I., & Zorzi, M. (2017). Letter perception emerges from unsupervised deep learning and recycling of natural image features. *Nature Human Behaviour*, *1*, 657–664. <https://doi.org/10.1038/s41562-017-0186-2>.
- Thiebaut de Schotten, M., Dell'Acqua, F., Forkel, S. J., Simmons, A., Vergani, F., Murphy, D. G. M., & Catani, M. (2011). A lateralized brain network for visuospatial attention. *Nature Neuroscience*, *14*(10), 1245–1246.
- Trauer, S. M., Kotz, S. A., Müller, M. M., Vuilleumier, P., Carretti, L., Aldhafeeri, F., ... Pozo, M. (2015). Emotional words facilitate lexical but not early visual processing. *BMC Neuroscience*, *16*(1), 89.
- 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), 418–438.
- Victor, J. D., & Mast, J. (1991). A new statistic for steady-state evoked potentials. *Electroencephalography and Clinical Neurophysiology*, *78*(5), 378–388.
- Vidyasagar, T. R., & Pammer, K. (2010). Dyslexia: A deficit in visuo-spatial attention, not in phonological processing. *Trends in Cognitive Sciences*, *14*(2), 57–63.
- 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), 1414–1432.
- Wandell, B. A. (2011). The neurobiological basis of seeing words. *Annals of the New York Academy of Sciences*, *1224*(1), 63–80.
- Wang, J., Zhang, J., Rong, M., Wei, X., Zheng, D., Fox, P. T., ... Jiang, T. (2016). Functional topography of the right inferior parietal lobule structured by anatomical connectivity profiles. *Human Brain Mapping*, *37*(12), 4316–4332.
- 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.
- Wilson, S. M., Brambati, S. M., Henry, R. G., Handwerker, D. A., Agosta, F., Miller, B. L., ... Gorno-Tempini, M. L. (2008). The neural basis of surface dyslexia in semantic dementia. *Brain*, *132*(1), 71–86.
- Wong, C., & Gallate, J. (2012). The function of the anterior temporal lobe: A review of the empirical evidence. *Brain Research*, *1449*, 94–116.
- 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.