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Word-specific repetition effects revealed by MEG and the implications for lexical access

Diogo Almeida^{1,2} and David Poeppel^{1,3}

¹Department of Linguistics, University of Maryland College Park

²Science Division, Psychology, New York University – Abu Dhabi

³Department of Psychology, New York University

Abstract

This magnetoencephalography (MEG) study investigated the early stages of lexical access in reading, with the goal of establishing when initial contact with lexical information takes place. We identified two candidate evoked responses that could reflect this processing stage: the occipitotemporal N170/M170 and the frontocentral P2. Using a repetition priming paradigm in which long and variable lags were used to reduce the predictability of each repetition, we found that (i) repetition of words, but not pseudowords, evoked a differential bilateral frontal response in the 150–250 ms window, (ii) a differential repetition N400m effect was observed between words and pseudowords. We argue that this frontal response, an MEG correlate of the P2 identified in ERP studies, reflects early access to long-term memory representations, which we tentatively characterize as being modality-specific.

Keywords

MEG; lexical access; repetition priming; episodic memory; P2; N400

1 Introduction

The mental lexicon stores different kinds of information necessary for language comprehension, such as perceptual codes that map (visual or auditory or tactile) input onto stored lexical representations, motor codes, and syntactic and semantic information. As such, the lexicon acts as an *interface* between perceptual processes and higher-level linguistic processes. Understanding the mapping from orthographic visual input onto lexical representations is an important step in understanding language comprehension, but there is considerable disagreement about the neurobiological mechanisms and the time course of lexical access from print. We address these questions using magnetoencephalography (MEG), capitalizing on the well-established repetition priming effect.

Research on reading has used a variety of empirical methods, from classic behavioral psycholinguistic paradigms to eye-tracking and electrophysiological approaches (EEG and

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Address for Correspondence: Diogo Almeida, Sama Tower, room 1316, Electra Street, Next to NMC Hospital, P.O. Box 129188, Abu Dhabi, United Arab Emirates, +917 2 628 5040, diogo@nyu.edu.

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MEG). Different time frames have been implicated in the early stages of lexical access, often by different methodologies. Therefore, to derive an increasingly accurate and granular time–course of lexical access, it is necessary to investigate how their results fit together.

1.1 Time course implicated by behavioral and eye–tracking data

Lexical access research has largely focused on behavioral tasks with *single words* (e.g., lexical decision, speeded or delayed naming, and semantic categorization) to probe the variables that affect lexical retrieval. Reaction time (RT) is typically used as a dependent variable. However, the late and highly variable time frame associated with task execution (about 500 – 900 ms), coupled with the decisional nature of such tasks, raises questions about whether RT constitutes an accurate index of lexical *access* (see Balota & Chumbley, 1984, 1990 for review).

Research using *eye–tracking* has implicated a much earlier time–frame. Because the experimental paradigms typically do not require any task beyond reading, fixation latencies are thought to constitute more faithful indices of the underlying cognitive processes involved in reading than button presses or vocal responses (Radach & Kennedy, 2004). The average fixation time during reading is about 250 ms, but eye movement preparation takes about 150 ms. Therefore, in order for fixation time to reflect lexical processing, access to lexical information must already be underway by 100 ms, much earlier than the time frame implicated by experiments using single word reading and self–paced sentence reading (Serenio et al., 1998).

1.2 Time course implicated by electrophysiology

1.2.1 N400—The most commonly studied electrophysiological response in the context of lexical access is the N400 and its MEG counterpart (alternatively called N400m or M400; see Kutas & Federmeier, 2000, 2011; Lau et al., 2008 for review). The N400 displays many of the characteristics of a lexically–induced ERP. First, it is reliably elicited by words or word–like stimuli, either in sentential contexts (Van Petten & Kutas, 1990) or in isolation or pairs (Holcomb & Neville, 1990), but *not* for nonword–like written stimuli, like non–meaningful, orthographically illegal strings (e.g., NPMO, TBUA, LSIA; Rugg & Nagy, 1987, but see Laszlo & Federmeier, 2008). Second, it is found across paradigms – such as passive reading (Van Petten & Kutas, 1990), lexical decision (Holcomb & Neville, 1990), semantic discrimination (Rugg et al., 1995), and repetition judgment (Curran & Dien, 2003) – suggesting a high degree of task–independence. Third, the N400 seems to reflect meaning retrieval (see Kutas & Federmeier, 2000, 2011). Finally, the N400 is found in both the visual and auditory modalities (Holcomb & Neville, 1990) as well as in signed languages (Kutas et al., 1987), suggesting modality independence.

1.2.2 N170—One of the earlier ERP components reliably implicated in reading is the occipitotemporal N170 and its MEG counterpart (alternatively called N170m or M170). ERP and MEG research show this response to be sensitive to orthographic processing (Tarkiainen et al., 1999, 2002; Cornelissen et al., 2003; Maurer et al., 2005; Simon et al., 2004), but the findings are divided on whether it reflects access to *lexical* information. Some studies report lexicality effects at the N170, which distinguishes words versus pseudowords and nonwords (McCandliss et al., 1997; Compton et al., 1991), whereas other studies report no sensitivity of the N/M170 to lexicality (Pylkkänen et al., 2002; Stockall et al., 2004; Cornelissen et al., 2003; Simon et al., 2004; Maurer et al., 2005; Fiorentino & Poeppel, 2007). Similarly, the N170 appears to be sensitive to lexical or morpheme frequency (Serenio et al., 1998; Zweig & Pylkkänen, 2009) – but not always (Embick et al., 2001). Finally, Sekiguchi et al. (2001) report a Japanese MEG repetition priming experiment in which a component peaking around 200 ms was sensitive to the repetition of words but not

pseudowords, speculating that the source of this effect lies in inferior occipitotemporal cortex, the same source implicated in the occipitotemporal N/M170 effects for words (McCandliss et al., 1997, 2003; Tarkiainen et al., 1999, 2003).

1.2.3 P2—Another ERP component occasionally implicated in lexical processing in electrophysiological research is the P2, a response generally showing a frontocentral distribution. To our knowledge, this component has been only identified in ERP work, and lacks a clearly identified MEG counterpart. One of the clearest characterizations of this component was reported by Van Petten et al. (1991), who studied lexical repetitions within naturalistic texts and described an early effect of repetition between 180 to 300 ms, with a more anterior scalp distribution than the subsequent negativity (N400). Early reports for P2 effects for orthographic string repetition (Rugg, 1987; Nagy & Rugg, 1989) were found for immediate repetition only, as opposed to the long lags used by Van Petten et al. (1991; see also Curran & Dien, 2003). There is at least some evidence that the P2 effect for repetition of strings is word specific, suggesting lexical processing is being reflected. For instance, an ERP study by Rugg et al. (1995), found that word repetition elicited early frontal effects starting at around 240 ms, while repetition of pseudowords elicited no such effects. Further evidence comes from masked priming experiments which reported P2 enhancement effects for immediate word repetition (Misra & Holcomb, 2003; Woollams et al., 2008). Moreover, in a sentence processing experiment, Dambacher et al. (2006) reported strong effects of lexical frequency, but not contextual predictability, in the P2 component at frontocentral electrodes, leading the authors to link the P2 to word recognition procedures (see also Curran et al., 1993; Barnea & Breznitz, 1998). The ERP findings of Hauk et al. (2006) are also compatible with a frontocentral P2 that reflects contact with lexical entries. These authors performed a novel multiple regression analysis of single-word reading ERP data and reported a lexicality effect (words vs pseudowords) starting at 160 ms, with a frontocentral scalp distribution (Hauk et al., 2006, Figure 5). Moreover, the early bilateral evoked MEG response found by Sekiguchi et al., (2001) is also compatible with this component, although the authors themselves linked it to the M170. Finally, it is important to note that at least one study (Joyce & Rossion, 2005) has proposed that the N170 response for human faces can also surface as a central positivity (called the Vertex Positive Potential, VPP) depending on the choice of reference electrode sites. Although it should be pointed out that there are anatomical and functional differences between the N170 obtained in response to visually presented words and the N170 obtained in response to human faces, the results of Joyce & Rossion (2005)'s study still raise an important question as to whether the frontocentral P2 reported in several reading studies is a functionally independent evoked response, or simply a different scalp projection of the N170 obtained in response to visually presented words. Incidentally, MEG can help adjudicate this question, as MEG data does not depend on reference sites and is less spatially smeared than ERP data, due to the lack of volume conduction distortion (Hämäläinen et al., 1993; Nunez, 1986).

1.3 Deriving a time course for word recognition

Given that there are robust effects at the N/M170 and the P2 related to lexical processing, it seems that the N400 is too late to reflect (at least) the early stages of lexical access. Some eye-tracking data suggest that lexical access in the context of normal reading is under way even earlier, around 100 ms. However, most eye-tracking studies investigate the natural reading of sentences, which might recruit top-down processes to a larger extent than single word reading, and therefore may not reflect the identical collection of processes. The most plausible remaining candidates for early lexical access are the two early electrophysiological evoked responses, the occipitotemporal N/M170 and the frontocentral P2.

1.4 Distinguishing the processing of words and pseudowords

To test the proposal that lexical access is reflected in physiological responses roughly 200 ms after word-onset, it is important to identify a task that can index lexicality. Two approaches can be pursued. First, one can manipulate well-known properties of lexical items (phonological, morphological, semantic) and seek neurophysiological (or behavioral) correlates that co-vary with the manipulated features (eg., Hauk et al., 2006). Second, one can aim for a signal of ‘global’ lexical access. Here we pursue the latter strategy, using an experimental paradigm seemingly sensitive to overall lexicality independently of local (sublexical) manipulations.

By definition, words have a representation in long-term memory, whereas pseudowords do not. However, distinguishing the processing of pseudowords and existing words is more difficult than this would suggest. For instance, it has long been known that repeated presentation of words in a lexical decision task improves performance (e.g., Scarborough et al., 1977). Such repetition priming effects are generally interpreted as reflecting facilitation in retrieving information from long-term memory (i.e., the lexicon). Repetition effects are also investigated in electrophysiological studies, where an N400 modulation occurs for word repetition (Rugg, 1987; Van Petten et al., 1991; Rugg et al., 1995).

However, it is also known that not only words, but phonologically legal nonwords (pseudowords) and even illegal nonwords (nonwords) can, in some circumstances, elicit behavioral repetition effects (Logan, 1988; Bowers, 1994), particularly in lexical decision experiments (Wagenmakers et al., 2004). The repetition effect of pseudowords has also been observed in ERP research, both in immediate priming paradigms (Deacon et al., 2004) and short-term priming contexts (Fiebach et al., 2005; Rugg et al., 1995), showing very similar neural signatures to the repetition of words. Within immediate priming contexts, repetition of words and pseudowords alike elicit smaller evoked potentials within the N400 time window (300-500ms). Immediate repetition effects of both words and pseudowords have also been replicated in MEG for the same time window (Pykkänen et al., 2000).

Presumably, the repetition effects for pseudowords and nonwords should not have their origin in access to or modification of long-term memory representations (which do not exist). Following this line of reasoning, several models accommodate repetition effects of pseudowords by linking facilitation to retrieval of the episodic memory trace formed in the first encounter with the item (Logan, 1988; Wagenmakers et al., 2004). This raises the possibility that episodic encoding could also be at play in the repetition of words. Indeed, some researchers argue that there is little evidence or theoretical necessity for positing that modification of access conditions for long-term memory representations has anything to do with the repetition effect for words (see Tenpenny, 1995 for review).

Alternatively, even though pseudowords are not stored in long-term memory, it is conceivable that they nonetheless engage the lexical system to some extent, perhaps by facilitating access to similar words (eg., Bowers, 2000). A number of experiments provide evidence compatible with this hypothesis. For example, Deacon et al. (2004) reported a semantic priming experiment in which a prime-target pair of pseudowords (*plynt – tlee*) showed N400 priming effects that could only be explained by positing that the pseudowords accessed the semantic representations of the words they resembled in form (*plant – tree*). In the same vein, Holcomb et al. (2002) reported that words and pseudowords alike can show N400 modulation effects due to the size of their lexical neighborhoods (i.e., lexical entries that resemble the experimental stimuli in form) – another result that is hard to explain without allowing that pseudowords at least partially activate pre-existing lexical representations. Therefore, on the basis of these results, a simple comparison of words

versus pseudowords might not provide the relevant information about whether access to lexical representations happens.

However, other researchers claim that, despite their sometimes similar behavioral and electrophysiological profiles (as reflected by N400 modulations), there are indeed two different mechanisms underlying the repetition effects of words and pseudowords (e.g., Bowers, 1996; Wagenmakers et al., 2004), and that these mechanisms are dissociable experimentally by varying tasks or task demands (eg., Wagenmakers et al., 2004; see Bowers, 2000 for review). Dual-process accounts generally posit that two different and potentially opposing processes underlie the triggering of a lexical decision: a fast-acting familiarity-based process, and a slow-acting, episodic memory-based facilitatory process. Moreover, these processes can interact with strategic processes (for e.g., words being more familiar than pseudowords could produce a word bias in repeated presentations) in tasks such as lexical decision to either produce or eliminate repetition priming of pseudowords (Orfanidou et al., 2011; Wagenmakers et al., 2004). Dual-process models receive some support from the MEG study conducted by Sekiguchi et al. (2001). Using a medium term visual repetition priming paradigm, these authors reported word-specific reduction in the amplitude of the MEG evoked response over left hemisphere sensors in both the 200–300 and 300-500 ms post-stimulus onset window. They concluded that the neural sources of these effects subserve the mental lexicon (i.e. long term memory storage of words), but not general visual episodic memory traces.

1.5 The Present Study

We designed an MEG study to identify the time window in which early contact with the mental lexicon occurs. Our design featured variable lag medium term priming in a simple lexical decision task (eg., Fiebach et al., 2005). The lag between repetition of words and pseudowords was varied to reduce the predictability of repetitions, since predictability has been shown to affect ERP and MEG responses very early in the processing stream, as well as in the N400 time window (Dambacher et al, 2009, Dikker et al, 2010). Given the arguments above that the N400 response does not reflect the earliest stages of lexical access, we expected that either the occipitotemporal M170 or an MEG correlate of the frontocentral P2 (henceforth, P2m) should be more sensitive to the repetition of words than to the repetition of pseudowords, even though we might expect to find behavioral repetition priming effects in both cases, due to the more slow-acting episodic-memory retrieval process that often dominates the triggering of a lexical decision (Wagenmakers et al, 2004).

Therefore, our hypothesis predicts a statistical interaction between Lexicality (word, pseudoword) and Order of Presentation (1st and 2nd) in the temporal window compatible with the M170 or P2m (150-250 ms), in which larger repetition effects should be observed for words compared to pseudowords. In addition, based on prior research, we also expected to observe a simple repetition effect for words and pseudowords alike in the N400 time window (i.e., a simple main effect of Order of Presentation).

However, if a lack of interaction between Lexicality and Order of Presentation in the 150 – 250 ms window were to be followed by a significant interaction in the 300 - 500 ms window, then this would have been interpreted as evidence that, contrary to our expectations, it is the N400, and not the earlier responses, that reflects the earliest stages of lexical retrieval.

2. Methods

2.1 participants

Twenty-two native English speakers (11 women) participated in the experiment (Mean age: 20, age range: 18-24). Fifteen data sets were included in the final analyses. All were right-handed, had normal or corrected-to-normal vision, and reported no history of hearing problems, language disorders or mental illness. All participants gave their written informed consent to take part in the study, which was approved by the University of Maryland Institutional Review Board. Subjects were paid for their participation.

2.2 Stimuli

A list of 108 common (i.e., relatively high-frequency) words (all predominantly nouns in terms of lexical frequency according to CELEX (Baayen et al., 1993); table 1 shows the average log₁₀ frequency based on the SUBTLEX-US database; cf. Brysbaert & New, 2009) and 108 pseudowords was created. The choice of common, relatively high-frequency words was due to a desire to match the lexical contents between this and a related planned experiment in American Sign Language. It is important to note that this choice biases the experiment against our hypothesis, as high-frequency words have a marked tendency to produce weaker repetition effects (see Bowers, 2000 for review) than low frequency words. Pseudowords were all pronounceable, phonotactically legal strings. Each word and pseudoword was presented twice in a standard lexical decision task. The lag between the first and second presentations for each item varied pseudorandomly between 9 and 25 items ($M = 18$). As shown in table 1, words and pseudowords were matched for number of characters (i.e., orthographic length), number of syllables¹ and average log₁₀ mean bigram frequency. The raw mean bigram frequencies were calculated by a custom R script based on the bigram frequency tables provided by James & Mewhort (2004), obtained from a large New York Times corpus. Pseudowords had on average higher raw mean bigram frequency than words. In addition, words and pseudowords were reasonably well controlled (but not perfectly matched) on their lexical neighborhoods using the recently proposed mean orthographic Levenshtein distance of the 20 closest neighbors (OLD20; see Yarkoni et al., 2008 for details), which was shown to be superior to the older Orthographic Neighborhood (ON) metric in predicting a number of behavioral results. OLD20 counts were calculated using the function *old20* from the R package *vwr* (Keulers, 2011), and indicated that words had a slight tendency to come from denser neighborhoods than pseudowords ($OLD20_{\text{words}} = 1.4$; $OLD20_{\text{pseudowords}} = 1.6$; noting that lower OLD20 values indicate denser neighborhoods, which is the opposite of the ON metric). The full list of materials and their lexical and sublexical characteristics is available in appendix 1.

2.3 Procedure

Subjects were in the scanner in supine position, in a dimly lit magnetically shielded room (Yokogawa Corporation, Tokyo, Japan). A scout scan was performed (1 kHz and 250 Hz pure tones) to verify responsivity as well as adequate head positioning inside the scanner. Stimulus presentation was carried out by Presentation® software (Version 10.3, www.neurobs.com). Subjects were instructed to decide whether each stimulus was a real word or not (lexical decision), and to respond as quickly and accurately as possible using a button box placed in their right hand. Each trial began with a fixation cross projected onto the center of a rear-projection screen (pseudorandomly varied between 500 and 600 ms), followed by a blank screen (250 - 350 ms), and subsequently by the stimulus. Items remained on the screen for 3000 ms or until subjects responded, and accuracy and reaction

¹Pseudoword syllable counts were validated by a phonetically-trained native English speaker.

times from the onset of stimulus presentation were recorded. The inter-trial interval (ITI) varied between 300 and 750 ms. Participants were familiarized to the task with 12 practice items (half words and half pseudowords not included in the experiment). The experiment was administered in four blocks, the order of which was counter-balanced across subjects, and lasted approximately 35 minutes.

2.4 MEG data acquisition

MEG data were acquired using a 160-channel axial gradiometer (157 data channels, 3 reference channels²) whole-head system (Kanazawa Institute of Technology, Kanazawa, Japan). Data were sampled at 1000 Hz and acquired continuously (bandwidth DC - 200 Hz). A time-shifted PCA filter removed external noise artifacts recorded by the reference channels (de Cheveigné & Simon, 2007). Furthermore, epochs in which eye-movements, blinks or amplitudes exceeding $\pm 2\text{pT}$ were identified were excluded from both behavioral and MEG analysis. Three participants were excluded due to excessive artifacts; one participant was excluded due to technical problems during data acquisition; three participants were excluded due to an error rate larger than 15%. Incorrect behavioral response trials and no-response trials were excluded from both behavioral and MEG data analysis.

Items for which both stimulus pair presentations survived the exclusion criteria were further analyzed (85% of epochs of the remaining 15 subjects). Following averaging, data were baseline corrected using a 100 ms prestimulus interval. No digital filter was applied to the data submitted to statistical analysis. We did not perform source localization on these data as we had (i) no spatial hypotheses about sources and (ii) no access to subjects' MRI data.

2.5 Temporal windows of analysis

Because we had clear predictions about the time course of the early stages of lexical access, we pre-selected two time windows to be analyzed: 150-250 ms and the 300 – 500 ms post-stimulus onset. The 150 – 250 ms window captures the M170 evoked-field distribution (see figure 1), and also covers the time window in which P2 effects have been reported to occur by previous ERP research. The 300 – 500 ms window captures the N400m evoked-field distribution (see figure 1) and is typically the window of analysis used for studying the N400 in the electrophysiological literature.

2.6 Topographic analyses of the MEG data

Because high-density sensor arrays such as ours ($N = 157$) pose challenges to traditional repeated-measures ANOVA approaches to the analysis of multichannel electrophysiological data, we opted to sidestep these issues by employing non-parametric, permutation-based topographic analyses. Topographic tests provide a summary of the strength of a particular experimental manipulation over the whole sensor space, which, unlike individual sensors, can be meaningfully compared between groups of participants whose head position is not standardized in MEG recordings. Furthermore, there are good reasons to treat the entire sensor space, as opposed to individual channels, as the unit of analysis in multichannel electrophysiological recordings (see Karniski, Blair, & Snider, 1994, and Koenig & Melie-García, 2009 for reviews).

²Reference channels in MEG are only used to record external sources of magnetic noise inside the Magnetically Shielded Room (Hämäläinen et al., 1993). Thus, they do not serve the same purpose of the reference electrodes in EEG. Whereas the EEG is the potential difference between two electrodes, the MEG is a unique property of each point in space, and therefore does not need a reference sensor (Nunez, 1986), much like the scalp laplacian transformation of EEG data (Nunez, 1986; Yao et al., 2005).

The strategy behind topographic analyses is as follows. The first step is to summarize the brain activity recorded throughout the sensor space by means of a test statistic that reveals some interesting aspect of the data. For instance, Karniski et al. (1994) proposed comparing two conditions at a particular time point (or averaged temporal window) by taking a t -test at every sensor, squaring them and then summing them. This statistic, which they named $Tsum2$, has an intuitive interpretation: if the two conditions have different brain states as sources, these brain states will surface as different sensor-space projections, which will be reflected in the individual t -tests, which in turn will be reflected in the overall sum of the (squared) t -tests. Therefore, the larger the $Tsum2$ value, the larger the difference between the brain states underlying the two conditions. Unfortunately, the sampling distribution of test statistics such as $Tsum2$ is not known, which precludes parametric tests of statistical significance. Karniski et al. (1994) proposed that permutation tests can be used in these cases to determine whether any value of an observed test statistic (such as $Tsum2$) could be seen as a trivial (ie, it could have easily been observed by chance), or extreme (ie, it would have been a rare occurrence if it occurred only by chance). The permutation test simply assumes that if the null hypothesis holds, then the observed results for each condition are completely fortuitous, and any random permutation of the whole sensor space data for each condition from each participant would have been an equally likely result. By performing such permutations a large number of times and calculating $Tsum2$ for each permutation, we can obtain a distribution of the test statistic under the null hypothesis of no treatment effect. The test of statistical significance is carried out by observing whether the $Tsum2$ obtained in the actual data is as extreme or more extreme than 5% (or any other predefined threshold) of values in the reference $Tsum2$ distribution.

One of the useful features of the permutation test is that its logic holds regardless of the chosen test statistic. For instance, some researchers have proposed using vector dissimilarity metrics to compare multichannel electrophysiological recordings, either by capitalizing on the correlation coefficient (Srebro, 1986; Greenblatt & Pflieger, 2004) or the cosine similarity metric (Desmedt & Chalklin, 1989; Tian & Huber, 2008), since a sensor-space topography is ultimately simply a multi-dimensional vector (Hauk et al., 2006, Tian & Huber, 2008). A permutation test based on these vector dissimilarity metrics would therefore test for a difference in shape between two topographies, but not a difference in strength between them. Thus, a permutation test based on a vector dissimilarity metric offers an interesting way of refining the results of an *omnibus* test like $Tsum2$. Since the latter is sensitive to *any* differences between two topographies, but the former is only sensitive to differences in shape between two topographies, a significant $Tsum2$ result that is not accompanied by a significant result in the vector dissimilarity permutation test might serve as a *prima facie* evidence that the two conditions share a very similar underlying brain configuration (eg, the same number of sources with similar locations and orientations), which differs only in the strength of its activity. Alternatively, a significant vector dissimilarity permutation test might indicate that two conditions are subserved by somewhat different underlying brain configuration (eg, different number of sources, and/or their locations and/or orientations).

Since our experimental hypothesis predicts that larger repetition effects for words than pseudowords can serve as a potential reflection of the first stages of contact with the mental lexicon, we decided to use the difference between the repetition effects (as quantified by $Tsum2$) of words and pseudowords as our test statistic for the interaction between Lexicality and Order of Presentation (i.e., $Tsum2_{words} - Tsum2_{pseudowords}$). The permutation test for this statistic requires freely permuting the sensor-space topographies of each condition within each subject. This test used 10000 permutations to derive the reference distribution of the interaction test statistic. It should also be noted that this is a directional interaction test statistic, sensitive only to cases where repetition of words yield larger topographic effects

compared to the repetition of pseudowords. Planned comparisons of the effect of repetition for words and pseudowords also employed the permutation test (10000 permutations of data restricted to their Lexicality factor) of *Tsum2* (Karniski et al., 1994) and the *cosine dissimilarity metric* (henceforth *Topographic Dissimilarity*, cf. Tian & Huber, 2008). All the analyses in this study were performed using the R statistical platform (R Development Core Team, 2011). Code is available from the corresponding author upon request.

3 Results

We defined a *repetition effect* as an average difference between first and second presentations that is significantly different from zero. We had a directional prediction for the behavioral results: Second presentations should be faster than first presentations. We also had a directional prediction for the electrophysiological data: Repetition of words, because they involve modifications in the conditions of access to specific items in long term memory, should yield, in the 150 – 250 ms window, larger topographic differences compared to the repetition of pseudowords, which should at best modulate access to specific items in long term memory only very briefly and temporarily.

3.1 Behavioral data

A factorial two-way repeated-measures ANOVA (rmANOVA) was computed for participants' **reaction times**, with Lexicality (Word vs Pseudoword) and Order of Presentation (1st vs 2nd) as factors. The results are presented in Table 2. A main effect of Lexicality was observed ($F(1,14) = 23.295$; $p = .0003$), with Words ($M = 656$ ms) responded to faster than Pseudowords ($M = 708$ ms). A main effect of Order was also observed ($F(1,14) = 17.596$; $p = .001$), with second presentations ($M = 661$ ms) responded to faster than first presentations ($M = 703$ ms). The interaction between Lexicality and Order was not significant ($F(1,14) = 0.4$; $p = .54$).

Two planned comparisons tested whether the **repetition effect** was observed for both Words and Pseudowords. For each item, we subtracted RT_{second} from RT_{first} . Independent one-sample two-sided t-tests were conducted for each Lexicality level. A significant effect of repetition was obtained both for words ($t(14) = 2.104$; $p = 0.001$; $M = 38$ ms) and pseudowords ($t(14) = 3.05$; $p = 0.009$; $M = 47$ ms). Exact permutation tests yield the same conclusion as did post-hoc analyses removing trials in which participants took longer than 2 s to respond.

3.1.1 Can the behavioral repetition effect be simply due to practice with the task?—A decrease in RT for the second presentation could in principle be due to an overall practice effect (e.g., Wagenmakers et al., 2004; Logan, 1988), rather than repetition priming. However, if practice or accommodation was the principal source of the significant decrease in RT, we should see RT trending down over the course of the experiment; only 6 subjects out of 15 showed such a trend (see Figure 2). To assess to what extent the significant repetition effect was potentially attributable to practice effects in these 6 subjects, a mixed effect model with Subjects and Items as crossed random effects, and Lexicality, Order of Presentation and their interaction as fixed effects, was fit to the data of the fifteen subjects, coding the linear order in which each item was presented as a covariate (Baayen et al., 2008). Markov chain Monte Carlo sampling (10000 replications) of the parameters of the fitted model, performed by the function *pvals.fnc* from package *languageR*, revealed that the effects of Lexicality ($t = 5.914$, $p < 0.001$) and Order of Presentation ($t = 4.821$, $p < 0.001$) were significant, but their interaction ($t = 0.694$, $p = 0.5$) was not. Words were responded to on average 55 ms faster than pseudowords, and 2nd presentations were responded to on average 37 ms faster than 1st presentations. Crucially, the effect of linear order of items in the experiment was significant ($t = 3.186$, $p = 0.015$). However, the effect of linear order

was only 0.07 ms (70 microseconds). This means that, on average, subjects were, for every presentation, 0.07 ms faster when compared to the previous one. The maximum lag between repetitions in this experiment was 25 presentations. Therefore, the maximum contamination of the repetition effect by practice effects would be 1.75 ms; this effect can be safely considered too small to be relevant.

Although practice effects can be discounted as an explanation for the observed repetition effects, it is still possible that stimulus-response learning might underlie our behavioral effects. However, this kind of mechanism is maximally influential in cases of effortful processing (Orfanidou et al., 2011), which was not particularly the case in our experiment. Moreover, the fact that the repetition of words and pseudowords produced comparable priming effects could perhaps be explained by the choice of materials (since higher frequency words produce less repetition priming; see Bowers, 2000 for review).

3.2 MEG data

3.2.1 150 – 250 ms window—As shown in Figure 1, the event-related fields are similar across conditions in the 150 – 250 ms window. Nonetheless, the interaction between Lexicality and Order of Presentation was significant ($Tsum2_{words} - Tsum2_{pseudowords} = 337$, $p = .0001$; see Table 3). Planned comparisons further demonstrated that the repetition effect was significant for words ($Tsum2 = 406$, $p = .0043$; *Topographic Dissimilarity* = 0.017, $p = .0032$), but crucially not for pseudowords ($Tsum2 = 69$, $p = .9875$; *Topographic Dissimilarity* = 0.0047, $p = .9895$; see Table 3). Visual inspection of the field distribution of the mean difference between 1st and 2nd presentation shows that the repetition effect for words is found bilaterally, and mostly in frontal sensors (see Figure 3), arguing against an occipital source, and therefore against an interpretation of this effect as being due to an M170 modulation. The results are instead more compatible with the frontocentral P2 effects observed in the ERP literature.

3.2.2 300 – 500 ms window—As shown in Figure 1, the event-related fields are somewhat similar across conditions in the 300 – 500 ms window. Nonetheless, the interaction between Lexicality and Order of Presentation was significant ($Tsum2_{words} - Tsum2_{pseudowords} = 257$, $p = .0001$; see Table 3). Planned comparisons (see Table 3) further demonstrated that the repetition effect was reliable for both words ($Tsum2 = 617$, $p = .0018$; *Topographic Dissimilarity* = 0.07, $p = .0005$), and pseudowords, although the latter only in the $Tsum2$ permutation test ($Tsum2 = 360$, $p = .0257$), with no statistically significant difference being detected in the *Topographic Dissimilarity* permutation test (*Topographic Dissimilarity* = 0.002, $p = .2944$). Visual inspection of the field distribution of the mean difference between 1st and 2nd presentation (see Figure 3) shows that the repetition effect for both words and pseudowords is found in the typical bilateral dipolar pattern of the N400m (eg., Pylkkänen et al, 2002; Lau et al, 2009).

3.2.3 Hemisphere and Quadrant analysis—In order to supplement and refine the interpretations of the main topographic analyses, we also conducted a hemisphere and quadrant analysis, as shown in figure 4. The sensor space was divided into four quadrants, each of which captured the most relevant topographic features of the field distributions in the two temporal windows of analysis (figure 4A-B). The mean RMS of all channels in each quadrant shows a marked difference in amplitude in the 150-250 ms window for the first and second presentations of words, in the anterior quadrants of the left and right hemispheres (figure 4C, left), while little to no difference is observed between the first and second presentations of pseudowords in the same time windows and quadrants (figure 4C, right). These results are largely compatible with the topographic analyses.

However, when we focus on the 300-500 ms window, we can only observe small differences between first and second presentations, in all quadrants, for words and pseudowords alike. This result is perhaps a bit unexpected given the large differences observed in the topographic analyses for the same time window (at least for words). However, it is important to notice that the quadrants' RMS combines the data from a large number of sensors (36 for each anterior quadrant, and 38 for each posterior one). Moreover, the two sets of findings are not necessarily incompatible, as they measure two different aspects of cortical activity: topographic analyses are sensitive to both changes in strength and configuration of the underlying sources, while areal averages such as the quadrant RMSs are less sensitive to small changes in the configurations of underlying sources, and thus capture primarily differences in the magnitude of the activity from these sources. The apparent disparity between the two sets of analyses can therefore be reconciled if we assume that the primary differences in the processing of first and second presentations of words and pseudowords in the 300-500 ms window is a relatively small change in the underlying configurations of the sources, as opposed to a simple change in the magnitude of their activity.

Finally, in order to better articulate the results of the topographic analyses with the quadrant averages, we calculated the mean absolute t-value for the comparison between first and second presentation in each hemisphere (figure 4D, left) and in each quadrant (figure 4D, right). The mean absolute t-value has a similar interpretation to the Tsum2 statistic: larger mean absolute t-values indicate a stronger repetition effect, whereas smaller mean absolute t-values indicate a weaker repetition effect. The primary reason to use the mean absolute t-value as opposed to the Tsum2 statistic is that the anterior and posterior areas are of slightly different sizes (36 vs 38 sensors), which could bias the latter test statistic, but poses less problems for the former. The error bars displayed in figure 4D represent the bootstrap standard errors of the mean absolute t-value statistic for each area, obtained via 10000 bootstrap samples.

The results for the 150-250 ms window are generally in line with the main topographic analysis, as there is a strong visual indication of an interaction between the Lexicality and Order of Presentation, with words displaying larger repetition effects than pseudowords. Moreover, the hemisphere analysis (figure 4D, left) shows that this interaction is observed in both hemispheres, and that there is little lateralization of the repetition effect. The quadrant analysis (figure 4D, right) shows that the locus of the repetition effect in the 150-250 ms window is primarily in the anterior quadrants (see also figure 3).

The results for the hemispheric analysis of the 300-500 ms window also pattern closely with the results of the topographic analyses: overall stronger repetition effects than those observed in the 150-250 ms window, but with a weaker interaction between Lexicality and Order of Presentation, with words showing stronger repetition effects than pseudowords. These results are also equally bilateral, and stronger in the anterior quadrants.

3.2.4 Whole-epoch confirmatory analysis—Although multiple analyses of our pre-selected time windows revealed the predicted interaction pattern (larger repetition effects for words compared to pseudowords in the 150-250 ms window), we decided to perform an extra confirmatory analysis to make sure our results were not due to a serendipitous averaging over a large temporal window. To that end, we calculated the time course of *Tsum2* between 1st and 2nd presentations of both words and pseudowords. These two time series are presented in the top part of Figure 5. Larger topographic differences do occur for words compared to pseudowords throughout the duration of the 150 – 250 ms window. In the 300 – 500 ms window, however, large topographic differences between the repetition of words and pseudowords are mainly observed post 350 ms. We also calculated the *p*-values

for the interaction statistic over the whole epoch via another permutation test (10000 permutations). The results are shown on the bottom part of Figure 5. A clear pattern of temporally clustered, statistically significant time points are observed throughout the duration of the 150 – 250 ms window and the post 350 ms part of the 300 – 500 ms window. It is interesting to note that, unlike what we observe in the 150-250 ms window, the magnitude of the topographic differences between the repetition of words and pseudowords are comparable between around 250 ms to 350 ms, when they start diverging again, until around 460 ms. The *p*-values time series also present indications that later time windows (between 600-750 ms) might display the interaction between Lexicality and Order of Presentation. However, since these time windows are much too late to be reflecting the earliest stages of lexical access and they do not have any obvious theoretical interpretation given our research questions, we will not analyze them further.

4 General Discussion

Behavioral repetition effects were found for both words and pseudowords, a result that is sometimes reported in written word lexical decision studies (eg., Fiebach et al., 2005; Pykkänen et al., 2000; Scarborough et al., 1977; Wagenmakers et al., 2004), which might indicate that the lexical decision response in our repeated pseudowords was dominated by facilitatory slow-acting episodic memory retrieval processes.

Contrary to the behavioral findings, however, the MEG results demonstrated clear word-specific priming effects in the 150-250 ms window. The topographic differences between 1st and 2nd presentations of words were much larger than those observed in the pseudowords. Moreover, planned permutation test comparisons showed that only words demonstrated significant repetition effects in this time window, and that these repetition effects involved different underlying brain configurations (as indicated by the Topographic Dissimilarity test). This result is consistent with the view that prior access to long-term lexical representations somehow influences their subsequent retrieval (by potentially modifying the actual long-term representation), but less so with the view that access to words and pseudowords rely on a similar, unified memory mechanism (episodic memory representations).

The second main finding was that the interaction between Lexicality and Order of Presentation was also observed in the 300–500ms window. In this time window, however, both words and pseudowords exhibited significant repetition effects. However, the repetition of words still involved different underlying brain configurations (as in the 150-250 ms window), as opposed to the repetition of pseudowords, which apparently involved a simple modulation of the activity of a common underlying brain configuration. These results are compatible with views of lexical access that posit differential processing mechanisms for lexical decision on words and pseudowords (Bowers, 1996, 2000; Wagenmakers et al., 2004) in spite of their sometimes similar behavioral profiles in simple priming tasks, especially those using the lexical decision task (Wagenmakers et al., 2004).

The asymmetry between the word-specific repetition effects in the 150-250 ms window and the lack of word-specific repetition effects in the behavioral data also deserves discussion. What does it mean to have such an early word-specific effect that is not apparently reflected in behavior? We can think of two reasons for this asymmetry. The first is that, as mentioned before, RT data in lexical decision tasks can be strongly influenced by the more slow-acting process of retrieval and manipulation of episodic memory traces (Orfanidou et al., 2011; Wagenmakers et al., 2004). This could explain why the topographic results in the later time window (300-500 ms) are more similar to the behavioral results. The second reason is that the processes underlying early contact with the lexicon, especially in the contextually

impoverished environment of a simple lexical decision task, might be largely automatic ones (and thus impervious to strategic processing), the results of which could be easily overruled by subsequent more controlled processes. We turn to a more detailed discussion of this topic below.

4.1 Lexical repetition effects in the 150-250 ms window

In our view, the early (150-250 ms window) repetition effect found is the MEG analogue of the P2 (i.e., P2m) response described by Van Petten et al. (1991) reflecting facilitatory processing effects of word repetition: It responds to the same experimental manipulation (repetition), occurs in the same time window (150- 250), and has a similar sensor-space distribution. Convergent evidence for this interpretation comes from two MEG experiments that investigated word processing in source space (Dhond et al., 2001; Marinkovic et al., 2003). Both studies used a similar variable-lag paradigm between written word presentations (in stem completion and semantic judgment tasks, respectively), and found an increase of activity for repeated relative to novel words in left ventrolateral areas in the 200-250 ms time window (cf. Fujimaki et al., 2009, for further results from MEG source analyses linking lexical access to this time window and source locations).

Finally, our MEG results are also in line with the ERP findings of Hauk et al. (2006). This study demonstrated that the distributed sources for their observed lexicality effect progressively shifted from 160 to 240 ms, involving at its onset a broad network of regions including the left perisylvian cortex, left anterior temporal and inferior frontal areas as well as right inferior temporal and a centro-occipital area. The effect of lexicality signaled by this broad network was observable at the scalp, with its maxima at frontocentral sites.

Having established that the early effect we found is compatible with previous findings in the ERP and MEG literatures, what can be concluded? The selective response in the 150 – 250 time window to word repetition suggests that it underpins *some* sort of lexical processing. However, P2 repetition effects seem to only be found for the simultaneous repetition of both orthographic and phonologic information. For instance, Rugg et al. (1995) reported no P2 effect for cross modal repetition (auditory – visual), only for within visual modality repetition (visual – visual). Sekiguchi et al. (2004) found that presentation of homophone pairs with completely different orthographic representation (different Kanji characters in Japanese) did not elicit the apparent P2m effect found in their previous study (Sekiguchi et al., 2001), and Sereno et al., (1998) reported a P2 effect for regular versus irregular spellings (orthography-to-spelling consistency). Moreover, Liu et al. (2003) reported an experiment wherein Chinese participants had to judge whether graphically similar pairs of words had the same meaning or the same pronunciation. A P2 mismatch effect was found in the pronunciation task, but not in the semantic task. Similarly, Lee et al. (2006) reported that the presentation of Chinese pseudocharacters paired to unpredictable pronunciations elicited P2 effects compared to when they were paired to predictable pronunciations. Also suggestive of orthography—phonology involvement is a series of studies that reported consistent P2 differences in word recognition tasks between normal and dyslexic readers, who are diagnosed by their lower reading accuracy and slower reading pace (e.g., Breznitz & Misra, 2003; Meyler & Breznitz, 2005). These studies conclude that dyslexic readers have temporal differences in processing visual and phonological information, which hinders the process of combining orthographic and phonological information in reading. P2 word repetition effects are also observed in masked priming experiments (Misra & Holcomb, 2003; Woollams et al., 2008), suggesting that this response can index automatic processes. This is compatible with the results from Barnea and Breznitz (1998), who reported that task instruction (orthographic vs phonological matching) modulated only the N400, not the P2 mismatch effect. In a sentence processing experiment, strong effects of lexical frequency were found

for the P2, with contextual predictability affecting only the N400 (Dambacher et al., 2006, but see Dambacher et al., 2009 for earlier effects of predictability), which is compatible with the idea that this early frontocentral component reflects the initial stages of lexical access.

The current and previous experiments advance an interesting hypothesis: *The computations indexed by this early component (P2 and its MEG counterpart, the P2m) are related to (perhaps automatically) retrieving or manipulating modality-specific lexical information in long term memory - as opposed to episodic information in short term memory.* This would explain the lexical selectivity found in our experiment and in Sekiguchi et al. (2001) and Rugg et al. (1995), and also the lack of effects in experiments using cross-modal or phonological repetition alone. Moreover, the sensitivity to frequency effects, imperviousness to task instructions and contextual support in sentences, and automaticity of processing are all compatible with relatively automatic processes of retrieval/selection of long term memory representations, most likely based on bottom up evidence. This hypothesis is also compatible with the interpretation given by Marinkovic et al. (2003) for the functional role of the areas showing the early (peak ~ 225 ms), modality-specific (found for visual, but not auditory presentation) left-lateralized word-repetition effect observed in their study. Finally, these results argue for a functionally distinct role for this frontocentral component in the processing of visual words, unlike what has been reported for human faces (Joyce & Rossion, 2005), as most studies with data compatible with our hypothesis that have conducted source analysis have found a distributed network involving ventrolateral frontal areas as well as posterolateral temporal regions (Dhond et al., 2001; Fujimaki et al., 2009; Hauk et al., 2006; Marinkovic et al., 2003).

4.2 Interpreting the N400 repetition effects

While it is encouraging that we have found an early anterior bilateral effect that can be linked to access to specific long-term memory representations, the presence of repetition effects in the 300–500 ms time window also requires an interpretation. These repetition effects were not lexically specific, but the planned comparisons provide some evidence that there might be a difference between the repetition effect of words and pseudowords in this time window. Not only were the repetition effects of words significantly larger than those observed for pseudowords, they also involved a qualitative change in the brain states underlying the processing of 1st and 2nd presentations, whereas the repetition effects of pseudowords seems to have involved only a quantitative change in the activity of a common brain state underlying the processing of 1st and 2nd presentations. A provocative way to interpret this finding is that the N400 repetition effect can be broken down into two different processes according to the lexicality of the stimuli: for words, the manipulation of lexical level information from the long-term representations; for pseudowords, the manipulation of episodic level information from short-term memory representations. This is in line with the dual process models of the lexical decision task, but further research is necessary to explore this particular hypothesis.

4.3 Conclusion

In summary, the behavioral and MEG results discussed here are compatible with existing findings on word and pseudoword repetition in the MEG and ERP literatures, and suggest that (i) bottom-up, automatic contact with putative modality-specific (orthographic) representations of lexical items in long term memory happens around 200 ms post-stimulus onset in reading, and (ii) the N400 repetition effect can be related to post-lexical processing of words and the attempt to retrieve pseudowords from short-term (episodic) memory representations.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Highlights

- The time course of visual word recognition remains poorly understood.
- Prediction: Access to stored lexical representations should occur at around 200 ms.
- We combined MEG and psycholinguistics to test this hypothesis.
- Topographical analyses reveal that P2(m), not the N/M170 or the N400(m), reflects first contact with mental lexicon.
- N400(m) reflects both the manipulation of long-term memory traces and short-term episodic memory traces.

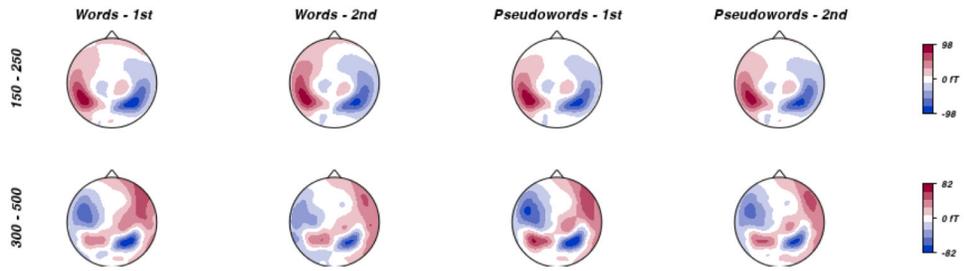


Figure 1. Topographic maps of the grand-average Event-Related Fields in the 150-250 ms window (top row) and 300-500 ms window (bottom row) for each Lexicality and Order of Presentation condition.

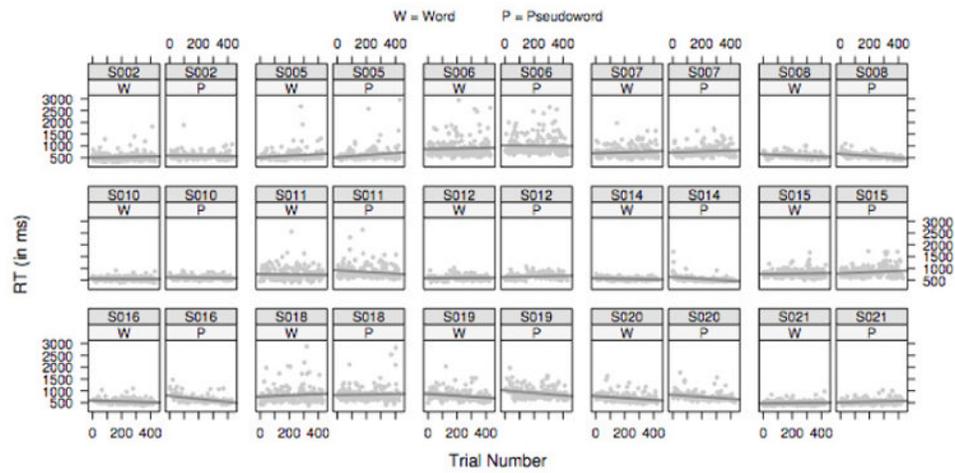


Figure 2. RT over the course of the experiment for individual subjects. Lines represent best-fit linear trend.

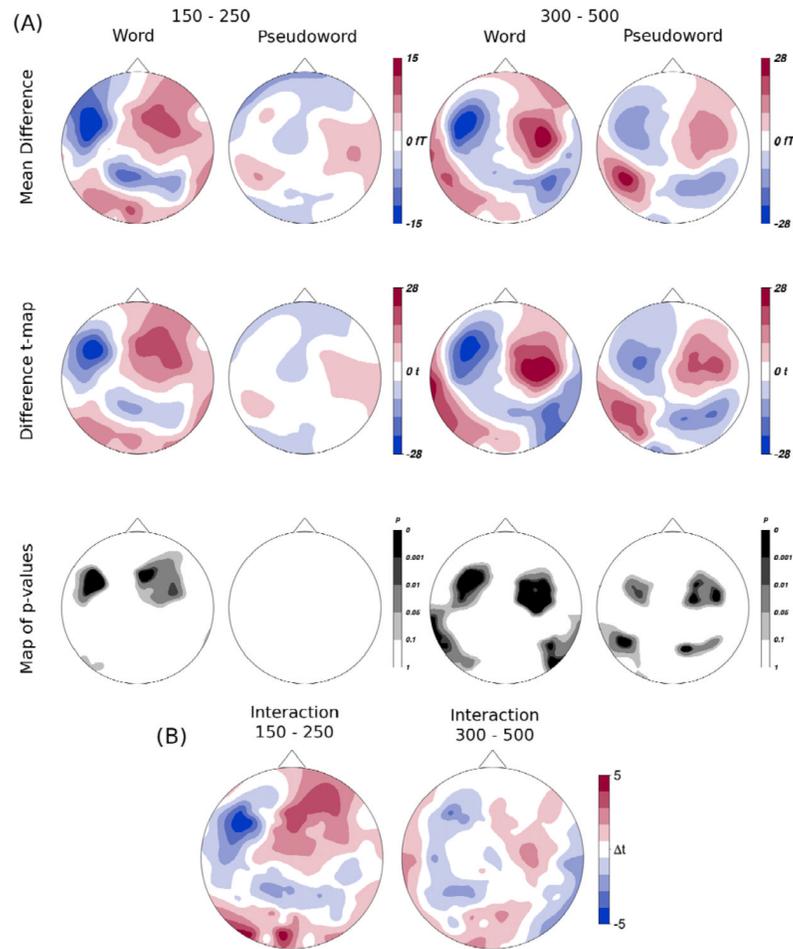
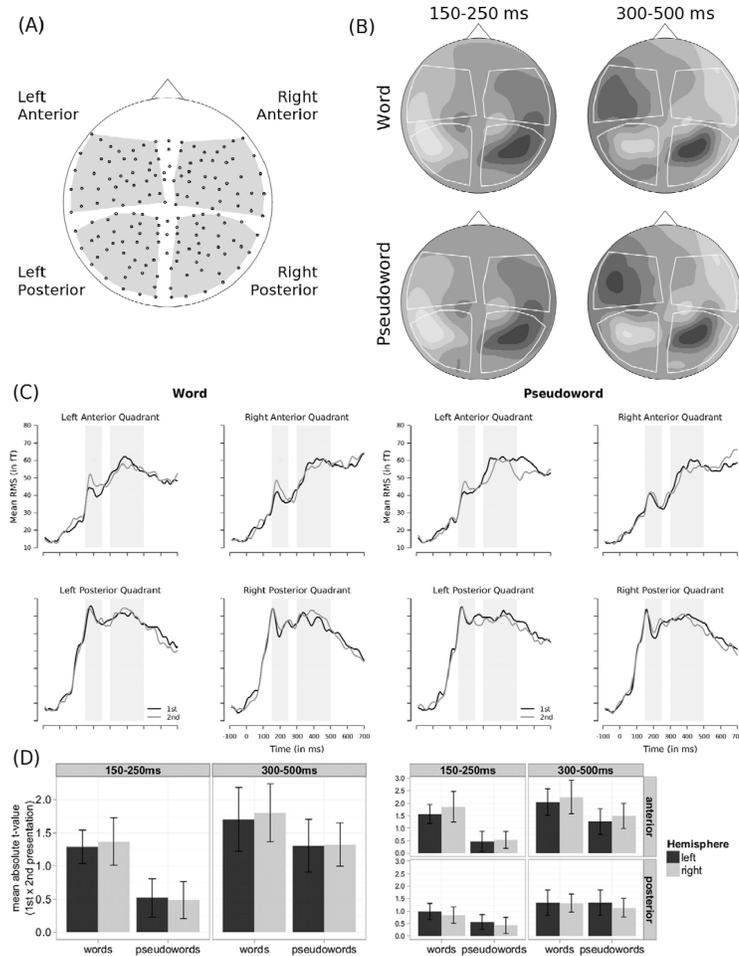


Figure 3.

(A) Topography of the grand average difference (top), the difference t-map (middle), and uncorrected p-value map (bottom) between first and second presentations in the 150 – 250 ms and 300 – 500 ms post-stimulus onset windows, for words (left) and pseudowords (right). (B) Topographic map of the interaction between Lexicality and Order of Presentation, for the 150 – 250 ms (left) and 300 – 500 ms (right) post-stimulus onset windows.

**Figure 4.**

(A) distribution of sensors and the quadrant selection. (B) quadrants displayed over the grand average field patterns of the two time windows for the words and pseudowords. (C) left: Mean RMS of each quadrant for first (black line) and second (grey line) presentation of words; right: Mean RMS of each quadrant for first and second presentation of pseudowords. (D) left: hemispheric analysis of the strength of the repetition effect in the two time windows of interest; right: quadrant analysis of the strength of the repetition effect in the two time windows of interest. Error bars in (D) are bootstrap standard errors, obtained via 10000 bootstrap samples.

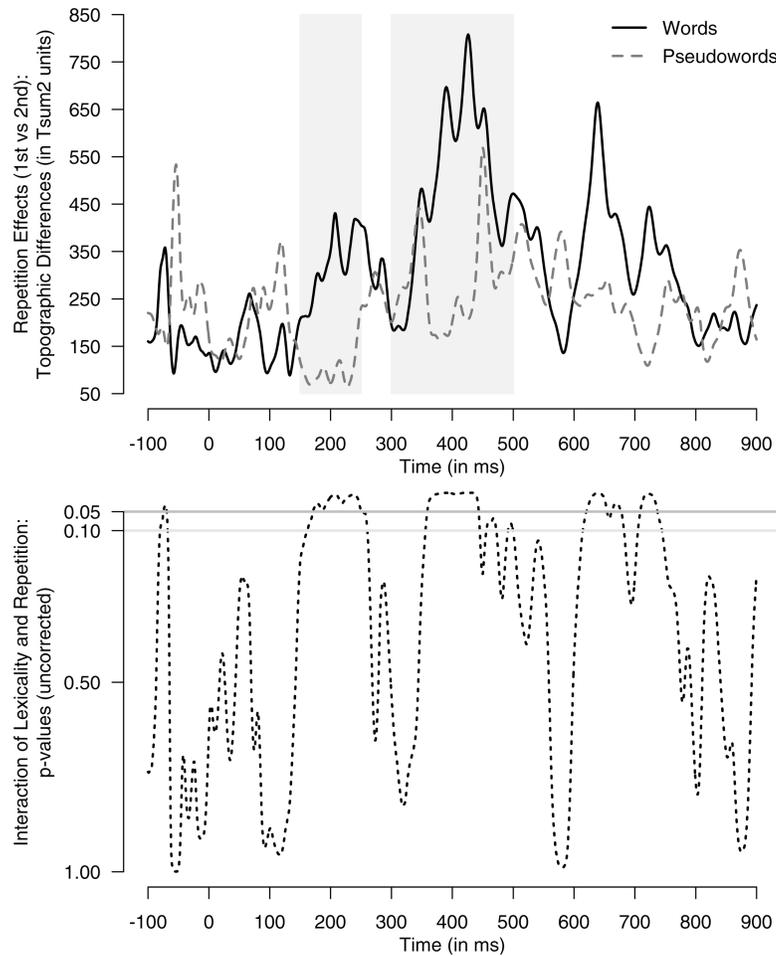


Figure 5.

Top: Time courses of topographic differences (in Tsum2 units) between 1st and 2nd presentation, for words (black line) and pseudowords (dashed gray line). The two windows preselected for planned comparisons (150 – 250 ms and 300 – 500 ms) are in light gray. Bottom: Uncorrected p-values for the interaction statistic between Lexicality and Order of Presentation ($Tsum2_{words} - Tsum2_{pseudowords}$), calculated via a permutation test (dotted black line). The darker gray line shows the 0.05 threshold and the lighter gray line shows the 0.1 threshold. Both graphs are based on filtered data (bandpass between 0.03 and 40 Hz), to increase the clarity of the presentation (by providing smoother time-series).

Table 1

Lexical and sublexical characteristics of stimuli. Frequency = Mean Log10 frequency from the SUBTLEX-US database. Length = Number of letters. Syllables = Number of syllables. OLD20 = Orthographic Levenshtein Distance 20. Log10 Mean Bigram = Average Log10 of mean bigram frequency. Raw Mean Bigram = Average raw mean bigram frequency. Standard deviations are in parentheses.

	LogFrequency	Length	Syllables	OLD20	Log10 Mean Bigram	Raw Mean Bigram
Words	3.5 (.6)	4.2 (.84)	1 (.35)	1.4 (.3)	5.4 (.3)	287,752
Pseudowords		4.2 (.88)	1 (.21)	1.6 (.4)	5.4 (.3)	295,213

Table 2

Behavioral results from the lexical decision task. Reaction times are in milliseconds, and standard errors are in parentheses. MOP = magnitude of priming (in ms).

	1st Presentation	2nd Presentation	MOP	Lexicality influence in MOP
Word	675 (33.6)	637 (32.5)	38	-9
Pseudoword	731 (44.1)	684 (32.1)	47	

Table 3

Results of the permutation topographic tests in the pre-selected 150-250 and 300-500 ms time windows. The interaction between Lexicality (word, pseudoword) and Order of Presentation (1st, 2nd) was quantified by the difference between the two Tsum2 statistics within the Lexicality factor ($Tsum2_{\text{words}} - Tsum2_{\text{pseudowords}}$). A large value of this test statistic indicates that the magnitude of the topographic differences between the 1st and 2nd presentation varies as a function of Lexicality. Planned comparisons relative to the repetition effect, conducted within the Lexicality factor used the Tsum2 and Topographic Dissimilarity permutation tests. Tsum2 is sensitive both to changes in amplitude and underlying source configuration, while the Topographic Dissimilarity is only sensitive to the latter. The p-values of all permutation tests are between parentheses, with statistically significant results in bold.

	150-250 ms window	300-500 ms window
<i>Interaction of Lexicality and Order of Presentation</i>		
Tsum2 _{words} – Tsum2 _{pseudowords}	337 (0.0001)	257 (0.0001)
<i>Repetition effect for Words</i>		
Tsum2	406 (0.0043)	617 (0.0018)
Topographic Dissimilarity	0.017 (0.0032)	0.07 (0.0005)
<i>Repetition effect for Nonwords</i>		
Tsum2	69 (0.9875)	360 (0.0257)
Topographic Dissimilarity	0.0047 (0.9895)	0.02 (0.2944)