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ERP correlates of letter identity and letter position are modulated by lexical frequency

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ABSTRACT

The encoding of letter position is a key aspect in all recently proposed models of visual-word recognition. We analyzed the impact of lexical frequency on letter position assignment by examining the temporal dynamics of lexical activation induced by pseudowords extracted from words of different frequencies. For each word (e.g., BRIDGE), we created two pseudowords: A transposed-letter (TL: BRIGDE) and a replaced-letter pseudoword (RL: BRITGE). ERPs were recorded while participants read words and pseudowords in two tasks: Semantic categorization (Experiment 1) and lexical decision (Experiment 2). For high-frequency stimuli, similar ERPs were obtained for words and TL-pseudowords, but the N400 component to words was reduced relative to RL-pseudowords, indicating less lexical/semantic activation. In contrast, TL- and RL-pseudowords created from low-frequency stimuli elicited similar ERPs. Behavioral responses in the lexical decision task paralleled this asymmetry. The present findings impose constraints on computational and neural models of visual-word recognition.

1. Introduction

The process of visual-word recognition in alphabetic languages involves a number of stages, including graphemic feature detection, letter identification, phonological decoding, lexical access, and semantic activation. Over the last decades, all of these stages have been extensively studied. However, the encoding of letter position within a word has only recently begun to receive attention in studies of visual-word recognition (see Frost, 2012; Grainger & Ziegler, 2011, for reviews). And yet, without encoding of the position of letters in a word we would be unable to distinguish between, say, SALT and SLAT. There is empirical evidence from a number of studies showing that switching the positions of two letters in a word (e.g., the transposed-letter pseudoword JUGDE – the base word is JUDGE) affect visual-word recognition in different ways than other orthographic transformations such as changing the identity of one of the letters (e.g., the replacement-letter pseudoword JUDPE) (e.g., O'Connor & Forster, 1981; Perea, Rosa, & Gómez, 2005).

In the present study, we used electrophysiological measures of brain activity (Event Related Potentials or ERPs) to compare letter position coding vs. letter identity coding by analyzing pseudowords created from words which are easy to identify (i.e., high-frequency words) and pseudowords created from words which are difficult to identify (i.e., low-frequency words). More specifically, we compared the time course of lexical activation (as inferred by the ERP waves) of pseudowords created by replacing one letter (e.g., replacement-letter [RL] pseudowords like BRITGE) and by transposing two adjacent letters (e.g., transposed-letter [TL] pseudowords like BRIGDE). This approach is similar to that used in prior behavioral work (see Forster, Davis, Schoknecht, & Carter, 1987; O'Connor & Forster, 1981; Perea et al., 2005, among others) – double-letter replacement pseudowords (e.g., the pseudoword BRITPE) were not employed because they produce little lexical activation compared to the other types of pseudowords (i.e., double-letter replacement pseudowords are merely employed to serve as orthographic controls of TL-pseudowords in priming experiments). In the following paragraphs, we will first discuss empirical evidence that manipulations of letter position affect visual-word recognition differently than manipulations of letter identity. We will then review the ability of several models of visual-word recognition to predict the effects of letter position and letter identity that have been observed in the literature. Finally, we will introduce the experiments of the present study.

1.1. Empirical evidence for transposed-letter effects on visual-word recognition

A number of behavioral experiments have investigated the coding of letter position and of letter identity, typically employing a

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lexical decision task (“is the letter string a word?”). The results of these studies have shown that the responses to transposed-letter (TL) pseudowords (e.g., MOHTER) are slower and less accurate than the responses to replacement-letter (RL) pseudowords (e.g., MOSHER) (e.g., Chambers, 1979; O’Connor & Forster, 1981; Perea & Fraga, 2006; Perea & Lupker, 2004; Perea et al., 2005). This suggests that TL pseudowords are perceptually closer to their base words than RL pseudowords. Furthermore, several masked priming studies have revealed that TL pseudoword primes (e.g., MOHTER) facilitate the processing of their corresponding base words (MOTHER) to a greater extent than replacement-letter pseudowords (e.g., MOSHER), and almost to the same extent as identity primes (e.g., Forster et al., 1987; Lupker, Pera, & Davis, 2008; Perea & Lupker, 2003a, 2004). This suggests that masked TL-pseudowords primes like JUGDE may be initially processed as if they were real words. Indeed, there is empirical evidence that shows that TL pseudowords can produce masked associative priming (e.g., lexical decisions to COURT are faster when preceded by the TL pseudoword jugde than when preceded by the control prime ocaen), whereas the corresponding effect with RL primes (e.g., junge-COURT vs. oceln-COURT) is much less robust (Bourassa & Besner, 1998; Perea & Lupker, 2003b; see also Perea, Palti, & Gómez, 2012, for evidence with unmasked, visible primes).

Letter transposition effects are not restricted to laboratory word identification tasks. Johnson, Perea, and Rayner (2007) found letter transposition effects during sentence reading using the boundary technique with parafoveal previews. Specifically, Johnson et al. found that readers benefited more from TL-pseudoword previews in the parafovea compared to their orthographic controls (two-letter RL-pseudowords) on word reading times (e.g., the parafoveal preview jugde produced shorter fixation times on the target word judge than jupte). Furthermore, White, Johnson, Liversedge, and Rayner (2008) found that the processing cost of reading sentences that contained TL pseudowords was relatively small, and much smaller than that obtained when using RL pseudowords in the sentences (Rayner & Kaiser, 1975). Importantly, the high degree of word-likeness of the transposed-letter pseudowords to their base words is not specific to the Roman alphabet, as these effects have been demonstrated in very different orthographies and languages (e.g., Japanese: Perea, Nakatani, & van Leeuwen, 2011; Hebrew: Velan & Frost, 2011; Arabic: Perea, Abu Mallouh, & Carreiras, 2010; Korean: Lee & Taft, 2009; Thai: Perea, Winskel, & Ratitamkul, 2012; Basque: Perea & Carreiras, 2006b; Maltese: Perea, Gatt, Moret-Tatay, & Fabri, 2012).

The misperceptions that may occur with pseudowords created by adjacent letter transpositions (i.e., JUGDE can be misperceived as JUDGE) suggests that the matching of the actual input with the stored lexical representations during visual-word recognition may be tolerant of positional errors in the letter sequence. Importantly, behavioral evidence suggests that this flexibility varies as a function of the lexical frequency of the base words: In lexical decision experiments, TL-pseudowords derived from high-frequency words tend to produce many more errors (e.g., JUGDE resulting in “word”-responses) than TL-pseudowords derived from low-frequency words (e.g., DIUNRAL [base word: DIURNAL] does not appear to be particularly word-like; see Andrews, 1996; O’Connor & Forster, 1981; Perea et al., 2005; see also Gómez, 2002, with a “signal-to-respond” paradigm). Similarly, in a normal reading setting, high-frequency TL-pseudowords are more effective in activating their word’s base form than low-frequency TL-pseudowords (White et al., 2008). Thus, the representations of high-frequency words may work as powerful attractors for input stimuli that overlap in letter identity with stored word-forms. In contrast, the evidence concerning effects of word-frequency on RL-pseudowords is scarce and less clear (see Gómez, 2002; Perea et al., 2005, for behavioral evidence). As Perea et al. (2005) indicated, the “less robust effect of pseudoword frequency for RL than for TL pseudowords is in line with the view that RL pseudowords (i.e., BUDRET) may not be as perceptually similar to their base words (BUDGET) as TL pseudowords (BUGDET)” (p. 311).

Although behavioral experiments with a lexical decision task (either with single-stimulus presentations or in combination with masked priming) may be particularly informative to examine the intricacies of letter position coding during visual-word recognition, they have an intrinsic limitation: Behavioral experiments only measure discrete responses (i.e., response latency and accuracy). To track in greater detail the time course of lexical access, behavioral tasks can be combined with the recording of event-related potentials, which offer a continuous measure of word-recognition as it unfolds in real-time. ERPs are potentially sensitive to different stages of lexical access and may therefore shed some light on the temporal dynamics of the availability and nature of the representations activated as a function of the orthographic code – note that this is a question that cannot be ignored in the specifications of any model of visual word recognition. An ERP component especially relevant to studies of visual-word recognition is the N400, a negative deflection that is maximal typically 300–500 ms post-stimulus onset, and is elicited by potentially meaningful stimuli. In studies of visual-word recognition, the N400 has been associated with lexical and semantic processing. The modulation of its amplitude may reflect processing costs during the retrieval of properties associated with a visual word-form stored in memory (see Holcomb, Grainger, & O’Rourke, 2002; Kutas & Federmeier, 2000). The amplitude of the N400 component is also an inverse function of lexicality, such that pronounceable pseudowords produce larger N400 amplitudes than words (Bentin, McCarthy, & Wood, 1985; Carreiras, Vergara, & Barber, 2005; Deacon, Dynowska, Ritter, & Grose-Fifer, 2004; Holcomb, 1993; Holcomb & Neville, 1990; Neville, Mills, & Lawson, 1992; see also Barber & Kutas, 2007, for a review).

The aim of the present study is to use ERPs to investigate the role of letter position and letter identity during visual-word recognition by comparing real words, TL-pseudowords and RL-pseudowords as a function of the frequency of their base-words. To do so, we employed a single presentation paradigm rather than the masked priming technique. Although we acknowledge that masked priming is an excellent technique to unveil the effects of prime stimuli on a target word, masked priming experiments focus on the relationship between prime and target, but not on the specific timing of the processing of the critical stimulus itself (Andrews, 1996; see also Perea & Rosa, 2000). To our knowledge, there is only one recent lexical decision experiment on letter position coding that has employed a single stimulus presentation procedure with ERPs (Carreiras, Vergara, & Perea, 2007). ERPs were measured to two types of Spanish pseudowords in a yes/no lexical decision task: TL-pseudowords were obtained by transposing two nonadjacent letters (e.g., RELOVUCION instead of the base word REVOLUCION) and, as a control, Carreiras et al. created double RL-pseudowords by substituting two nonadjacent letters (e.g., RETOSUCION) rather than standard RL pseudowords. An N400 modulation was observed as a function of the type of pseudoword: Larger negativities were obtained for double RL-pseudowords than for TL-pseudowords. These results revealed that TL-pseudowords were treated more like words than the pseudowords created by replacing two letters. However, leaving aside that replacing two letters from a given word produces pseudowords which may not be particularly wordlike, the Carreiras et al. study did not include the base words (e.g., REVOLUCION) and, therefore, there was no direct measure of the differential impact of letter identity and/or letter position overlap between the pseudowords and their corresponding base-words. Furthermore, Carreiras, Vergara, and Perea (2007) did not manipulate word-frequency; the mean frequency of the base words for the pseudowords was relatively high (32 per million).

1.2. How do models of visual-word recognition account for the effects of letter position?

In a number of highly influential computational models of visual-word recognition (e.g., interactive-activation model: McClelland & Rumelhart, 1981; multiple read-out model: Grainger & Jacobs, 1996; dual-route cascaded model: Coltheart, Rastle, Perry, Ziegler, & Langdon, 2001), perceptual similarity is computed by matching, position-by-position, the letters of the stimulus item to the brain's lexical representation, without taking into consideration the identity of the adjacent letters. Thus, these models would predict that MOSHER (an RL-pseudoword) would be perceptually closer to MOTHER than MOHTER (a TL pseudoword), because MOSHER shares five out of six letter positions and MOHTER only four, and this does not fit the empirical findings discussed earlier. This is illustrated in Fig. 1, which graphically displays the activation levels for the most activated units in the interactive-activation model with the stimuli used in the present study. Indeed, RL-pseudowords produce a greater activation level at the lexical level than TL-pseudowords. Furthermore, pseudowords created from high-frequency words generate more lexical activation than the pseudowords created from low-frequency words.

In order to be able to explain transposed-letter confusability effects in visual-word recognition and reading, a number of researchers have proposed more flexible orthographic coding schemes that do take into account the identity of the neighboring letters (e.g., the spatial coding model: Davis, 2010; the Local Combination Detector [LCD] model: Dehaene, Cohen, Sigman, & Vinckier, 2005; the overlap model: Gómez, Ratcliff, & Perea, 2008; the open-bigram model: Grainger & van Heuven, 2003; the noisy Bayesian Reader model: Norris, Kinoshita, & van Casteren, 2010; the SERIOL model: Whitney, 2001). In the overlap model (Gómez et al., 2008), the locations of letters are modeled as distributions along ordinal positions in the string, rather than as precise points. In the open-bigram model (Grainger & van Heuven, 2003), the relative position of a letter is coded within the context of letters that co-occur within the string up to a limit of two intervening letters. In the SERIOL model (Whitney, 2001) the ordinal position of a letter is coded along with the activation of bigram nodes. These types of models can readily explain the finding that TL-pseudowords (e.g., MOHTER–MOTHER) are more similar to their corresponding base words than the RL pseudowords (e.g., MOSHER–MOTHER). Similarly, the spatial coding model (Davis, 2010) assumes that the order of letters in printed words is coded in terms of relative activation of the letter nodes so that TL-pseudowords are more similar to their base words than RL pseudowords.

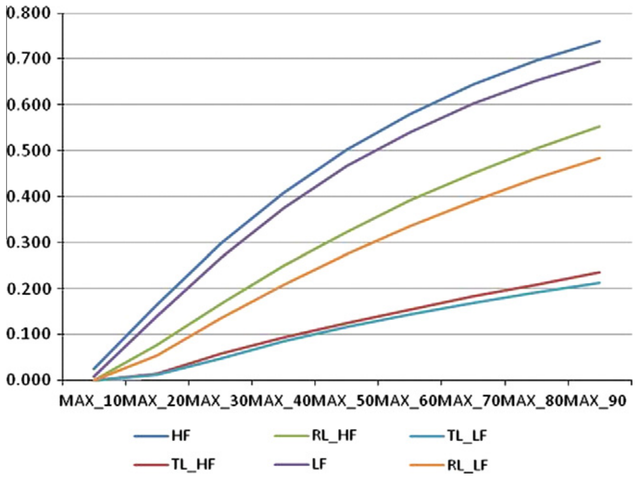

Fig. 1. Activation level of the most activated units in the early stages of processing in an interactive activation model.

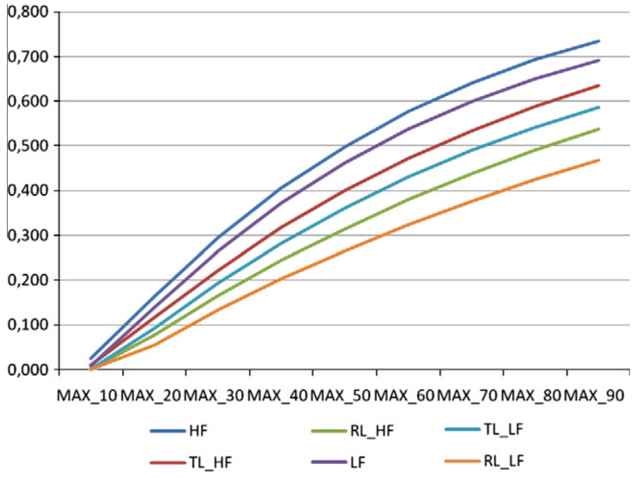

Fig. 2. Activation level of the most activated units in the spatial coding model (Davis, 2010) using the stimuli used in the present study.

As an illustration of these more flexible orthographic encoding models, we display the activation levels for the most activated units in the spatial coding model for the items used in the present experiments (see Fig. 2) – the predictions from the other above-cited models would be quite similar. Using the default parameters from this model, it is clear that TL pseudowords generate more lexical activity (i.e., they are more wordlike) than RL pseudowords. This contrasts with the predictions of models illustrated in Fig. 1. Furthermore, and not surprisingly, high-frequency pseudowords produce more lexical activity than their corresponding low-frequency pseudowords – which is the same as the modeling results for the interactive activation model.

1.3. The present study

In the present study we examined if and when the lexical frequencies of base-words modulate processing of letter identity and letter position during visual-word recognition. To achieve this goal, we compared the amount of activation triggered by words and two types of pseudowords (TL and RL pseudowords) that varied in the frequency of their base words. ERP correlates of visual-word recognition could provide a sensitive measure of the different stages of lexical access. In our study we will examine the way in which the ERP correlates of lexicality vary in amplitude and latency as a function of: (1) the overlap between words and TL-pseudowords or RL pseudowords, and (2) the frequency of the base words (high vs. low). Most studies of ERP lexicality effects have reported systematic differences between words and pseudowords on the N400 amplitude, which, as discussed before, is maximal in the 300–500 ms epoch after onset of the stimulus. However, behavioral and eye-tracking studies have indicated that early lexical access and selection may be possible within the first 200 ms after written word onset (see Sereno & Rayner, 2003), and several pieces of evidence suggest that the electrophysiological correlate of this "identification process" may precede the N400 window (Friedrich, Kotz, Friederici, & Gunter, 2004; Grainger & Holcomb, 2009; Holcomb & Grainger, 2006; Pylkkänen, Stringfellow, & Marantz, 2002; Stockall, Stringfellow, & Marantz, 2004), or at least correspond to a shorter interval within the classic latency of the N400 (300–390 ms; Braun et al., 2006). Along these lines, Pulvermüller (2001) suggested that the initial contact with word representations might modulate ERPs in the early latency range, whereas longer latency ERPs (the N400) may reflect the retrieval of lexical information (memory for words). In line with this proposal, Friedrich et al. (2004) showed that full match of prime and target had an effect on a positive ERP component peaking around 300 ms (P350). As this component was observed in unimodal (visual–visual) and cross-modal (auditory–visual) priming, it was interpreted as an "index of lexical identification in a modality-independent mental lexicon" (Friedrich et al., 2004, p. 548). This component may be similar to the M350 component observed in MEG studies (Pylkkänen et al., 2002; Stockall et al., 2004); note that this component has been interpreted to reflect lexical activation.

In sum, by analyzing the time-course of lexicality effects we may be able to disentangle the way in which letter position and letter identity have an impact on lexical selection and/or lexical-semantic activation during visual-word recognition. In the present study, we recorded ERPs as participants read single words of low- and high-frequency, and their corresponding TL and RL pseudowords. In Experiment 1, we used a go/no-go semantic categorization task ("is this an animal?"), in which the experimental stimuli (words, TL pseudowords, and RL-pseudowords) corresponded to the no-go category. We created three lists of counterbalanced materials in a Latin square design so that each word or pseudoword in the no-go category appeared once in each list but each time in a different condition (e.g., the word MOTHER in list 1, the TL-pseudoword MOHTER in list 2, and the RL pseudoword MOSHER in list 3).This manipulation allowed for the examination of the ERP effects of letter position and identity when the task demands semantic processing but does not require evaluation of the lexical status of the stimulus. Note that semantic categorization demands semantic access without need for evaluating the lexical status of the stimulus and that "the meanings of written words begin to be activated before they are uniquely identified" (see Rodd, 2004, p. 437). Thus, distinguishing "animal names" from other stimuli (non-animal names and pseudowords) does not put large processing demands at the sublexical level. However, correct performance in a yes/no lexical decision task may put a higher processing load at the sublexical level in order to be able to distinguish words from pseudowords (i.e., misspelled words). In Experiment 2, we used a yes/no lexical decision task ("does the letter string form a word?"), as a way of examining the generality of letter position/identity effects across tasks and to further examine whether the specific demands of each task may modulate letter position coding.

Based on previous behavioral studies (e.g., Chambers, 1979; Andrews, 1996; Davis, 1999; Perea & Lupker, 2003a, 2003b; Perea & Fraga, 2006), and according to simulations from recently proposed computational models (e.g., the spatial coding model; Davis, 2010, see Fig. 2), TL-pseudowords were expected to be more likely confusable with words, as they may be more perceptually similar to their base words than RL-pseudowords. What is not yet established is the level at which this behavioral TL confusability effect affects the process of visual-word recognition. If TL confusability impacts early lexical selection processes during visual-word recognition, then this would be evident from modulation of the amplitude of earlier ERP deflections than the N400 latency. That is, if the cognitive system disregards (to some extent) information on letter position during lexical selection, both words and TL pseudowords would be expected to elicit similar ERP amplitudes that would differ from RL pseudowords in early latency ERP responses. However, a difference between words and both types of pseudowords at early latencies would indicate that both types of deviation (letter identity and letter position) have similar consequences on the selection of a single whole-word representation. In contrast, TL confusability effects could also result from greater activation at the lexical-semantic level induced by a larger overlap between letter string and word-form representation, which would result in a modulation of the amplitude of the N400. According to previous findings (e.g., Carreiras et al., 2007) we predict that the N400 amplitude elicited by TL pseudowords would not differ from real words, but would be reduced relative to the N400 elicited by RL pseudowords, at least for high-frequency stimuli.

Even though our main focus is on the latency and amplitude of ERP components that are sensitive to lexical selection and lexical-semantic processing (especially the N400 component), the present manipulation is also likely to elicit an N200 typically found in go/no-go categorization tasks. The N200 is a negative polarity ERP that peaks around 200 ms after stimulus onset and is maximal over fronto-central scalp sites. The amplitude of the N200 may be reduced to no-go stimuli when they are "easy" to discriminate from go-stimuli (Jodo & Kayama, 1992; Maguire et al., 2009; Nieuwenhuis, Yeung, & Cohen, 2004). For instance, previous studies using a go/no-go semantic categorization task (Ziegler, Besson, Jacobs, Nazir, & Carr, 1997, Experiment 3) have obtained a larger task-specific N2 for pseudowords compared to both words and nonwords.[1] This was taken to reflect an early categorization of words and nonwords (even before the semantic categorization is achieved), compared to the processing difficulties encountered with pseudowords: Pseudowords were not as easily categorized as the other two stimulus types due to being orthographically and phonologically similar to words (Ziegler et al., 1997). In our present experiment, differences between words and pseudowords regarding the N2 amplitude may reflect the impact of the TL- and RL-manipulations on an early categorization of the stimuli – in particular in the go/no-go semantic categorization task (Experiment 1).

2. Experiment 1 (semantic categorization)

2.1. Method

2.1.1. Participants

Sixteen undergraduate students from UC Davis (11 women) participated in the experiment in exchange for course credit. All of them were native English speakers with no history of neurological or psychiatric impairment, and with normal or corrected-to-normal vision. Ages ranged from 18 to 23 years (mean: 19.1 years). All participants were right-handed, as assessed with an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971). Participants gave informed consent prior to the experiment.

2.1.2. Materials

A list of 240 words of six and seven letters was selected from the Kučera and Francis (1967) database. The words were selected based on their word frequency and were grouped in one of two categories: Low-frequency words, with 4 to 5 occurrences per million words (mean 4.5; SD = 0.50), and high-frequency words, with more than 50 occurrences per million (mean = 127.5; SD = 88.65). The selected words constituted the base words in this study and for each base word, we created: (i) a transposed-letter pseudoword (TL-pseudoword), created by transposing the fourth and fifth letters, and (ii) a replacement-letter pseudoword (RL-pseudoword), created by randomly replacing the fourth letter of the words (vowels were replaced with other vowels and consonants were replaced with other consonants). TL and RL manipulations were always done for internal letters of the base words, since the effects of letter transposition/substitution are attenuated if the transposed/replaced letters are at the beginning or at the end of the string (e.g., Gómez et al., 2008; Holmes & Ng, 1993; Perea, 1998). The details of the experimental stimuli are presented in

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[1] Although Ziegler et al. interpreted this effect in terms of a P200, we think it is more appropriate to refer to it as an N2, according to the findings in preceding literature.

Table 1
Mean values of Psycholinguistic Characteristics of words across conditions (SDs in brackets). Lexical frequency is provided in Kucera and Francis (1967) database (K–F freq.). Both imageability (range: 100–700) and bigram frequency, shown as the mean log token frequencies of the bigrams in the input stimulus, were taken from Davis' N-Watch database (2005). Concreteness was assessed by 12 external judges (all of them natives of American English) who rated the pool of 240 words in a 1–7 Likert scale ranging from 1 (highly abstract) to 7 (highly concrete). We used the Orthographic Levenshtein Distance as our measure for orthographic neighborhood (OLD20; Yarkoni, Balota, & Yap, 2008), since it provides a richer metric of orthographic similarity than Coltheart's *N* metric (Vergara-Martínez & Swaab, 2012).

	# Letters	K–F freq.	Imageability	Concreteness	Mean log bigram freq.			OLD20		
					Word	TL-ps	RL-ps	Word	TL-ps	RL-ps
HF words	6.4	127.5 (88.6)	418 (110.4)	4.1 (1.6)	2.7	2.2	2.4	2.2 (.3)	2.5 (.3)	2.4 (.3)
LF words	6.4	4.5 (.5)	434 (121.4)	4.3 (1.7)	2.6	2.1	2.3	2.2 (.3)	2.5 (.2)	2.4 (.3)

Table 1. As can be seen in this table, stimuli in the high and low frequency conditions were matched for number of letters, imageability, concreteness, mean Bigram Frequency, and orthographic neighborhood (as measured by the OLD20 index). In addition, a list of 40 animal names (15% of the stimuli), proportionally equated for lexical frequency and length with the experimental word set, served as probe items in the go/no-go semantic categorization task. For the "non-animal" experimental stimuli, three lists of materials were constructed so that each word or pseudoword appeared once in each list but each time in a different condition (e.g., MOTHER would be in list 1, MOHTER would be in list 2, and MOSHER would be in list 3). Across lists the same number of experimental stimuli appeared in each condition. Different participants were assigned randomly to each list, which included 80 experimental words (40 of high frequency and 40 of low frequency) and 160 experimental pseudowords (80 RL-pseudowords, 40 of high frequency and 40 of low frequency, and 80 TL-pseudowords, 40 of high frequency and 40 of low frequency).

2.1.3. Procedure

Participants were seated comfortably in a dimly lit, electrically shielded and sound-attenuated chamber. All stimuli were presented on a high-resolution monitor that was positioned at eye level 1 meter in front of the participant. The stimuli were displayed in white lowercase Courier 24-pt font against a dark-gray background. The animal names served as probe items in the go/no-go semantic categorization task. Participants were instructed to press a single button as soon as they detected an animal name. Importantly, critical stimuli did not require an overt response. The hand used for each type of response was counterbalanced across subjects. The sequence of events in each trial was as follows: A fixation cross ("+") appeared in the center of the screen for 800 ms, this was followed by a 200 ms blank screen which was replaced by a stimulus word or pseudoword that was presented in lowercase letters and remained on the screen for 400 ms. After a 1000-ms blank screen, a picture of a smiley face was presented for 1500 ms. The appearance of the smiley face signaled to the participants that they could move their eyes or blink. In order to minimize subject-generated artifacts in the EEG signal during the presentation of the experimental stimuli, participants were asked to refrain from blinking and eye-movements from the onset of the fixation cross to the onset of the smiley face. Each participant saw the stimuli in a different random order. Twelve warm-up trials (including 3 animal names), which were not further analyzed, were presented at the beginning of the session and were repeated if necessary. Participants were instructed to read the stimuli and to press the button when they saw an animal name.

After the participants had finished the ERP experiment, they were given a list of all the experimental items and were asked to mark those words that were unknown to them. This was done to check if participants knew the meaning of the words. Four words (virile, austere, salient, and pulpit) were unknown by more than 85% of the participants, and these words and their corresponding pseudowords were excluded from further analyses.

2.1.4. EEG recording and analyses

The electroencephalogram (EEG) was recorded from 29 electrodes mounted in an elastic cap, referenced to the right mastoid (except for the electrodes that were used to measure potential blinks and eye-movements: One electrode placed beneath the left eye was referenced to FP1 and two placed at the outer canthi of both eyes were referenced to each other). The EEG recording was re-referenced off-line to an average of the left and right mastoids. Impedances were kept below 5 kΩ. All single-trial waveforms were screened offline for amplifier blocking, drift, muscle artifacts, eye movements, and blinks. This was done for a 700 ms epoch with a 200 ms pre-stimulus baseline. Trials containing artifacts were not included in the average ERPs or in the statistical analyses. This led to an average rejection rate of 10% of all trials with no statistical difference in the number of rejections across conditions (*F*s < 1.33). The EEG signal was band-pass filtered between 0.01 and 30 Hz and sampled at 250 Hz. ERPs were averaged separately for each of the experimental conditions, each of the subjects and each of the electrode sites.

Statistical analyses were performed on the mean ERP values in four contiguous time windows (N2: 180–260 ms, P350: 260–360 ms; early N400 (N4a): 360–470 ms; late N400 (N4b): 470–580 ms). This was done for the six experimental conditions defined by the factorial combination of the factors Frequency (low, high) and Type of similarity (word, TL-pseudoword, RL-pseudowords). The selection of these epochs was motivated by our aim to identify the time-course of potential differences between experimental conditions, and was determined by visual inspection and on the basis of previous studies (Carreiras et al.,

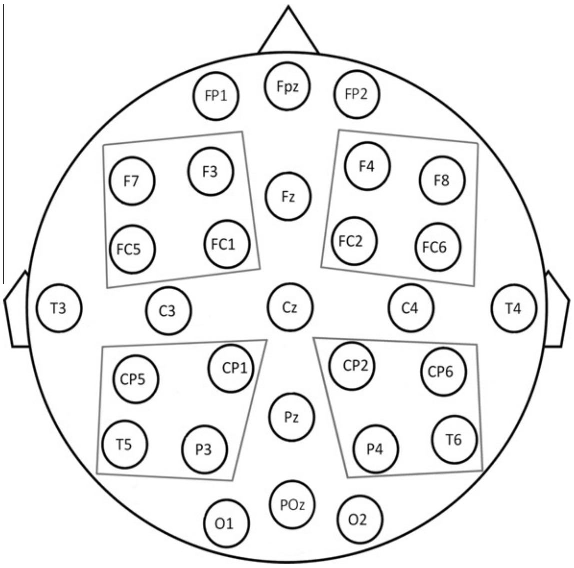

Fig. 3. Schematic distribution of recording sites, indicating each of the 4 areas of interest computed as the average of 4 electrode sites in each of the regions.

2007; Holcomb & Grainger, 2006; Grainger & Holcomb, 2009). Following a similar strategy in related literature (Carreiras et al., 2007), we analyzed the topographical distribution of the ERP results by including the averaged amplitude values across four electrodes of four representative scalp areas that result from the factorial combination of the factors Hemisphere (left, right) and the anterior–posterior (AP) distribution (anterior, posterior): left-anterior (F7, F3, FC5, FC1), left-posterior (CP5, CP1, T5, P3), right-anterior (F4, F8, FC2, FC6), and right-posterior (CP2, CP6, P4, T6) (see Fig. 3). For each time window, a separate repeated-measures analysis of variance (ANOVA) was performed, including the factors Hemisphere, AP distribution, frequency, and type of similarity. List (list 1, list 2, and list 3) was included as a between-subjects factor to separate out the variance due to counterbalancing the lists (Pollatsek & Well, 1995). Main effects of lexical frequency are reported when relevant for the interpretation of the results. Where appropriate, critical values were adjusted using the Greenhouse–Geisser correction. Effects for the AP distribution or for the hemisphere factor are reported when they interact with the experimental manipulations. Interactions between factors were followed up with paired *t*-tests.

2.2. Results

2.2.1. Behavioral results

The behavioral results from the "go" trials showed that participants categorized correctly more than 92% of the animal target words. The rate of false alarms for the "no-go" trials was 0.28%, and no significant differences were observed between conditions (all *F*s < 1).

2.2.2. ERP results

The grand average ERPs, time-locked to the onset of the experimental words and pseudowords for both the high and low frequency stimuli are displayed in Figs. 4 and 5, respectively. As can be seen in each of these Figures, in all conditions, an early negative shift (maximal around 100 ms post stimulus) is followed by a large positive deflection between 200 and 300 ms, and by a negative deflection that extends approximately between 350 ms and 600 ms and is maximal around 400 ms post stimulus (i.e., the N400). The positive deflection peaks earlier (approx. at 250 ms) over most frontal-central areas compared to central-parietal scalp areas (300 ms), and carries a small negativity that is maximal around 200 ms post-stimulus onset (no-go N2) and more prominent over frontal and central electrode sites.

Visual inspection of the waveforms suggests that the ERP differences between words, TL-pseudowords and RL-pseudowords vary as a function of lexical frequency. For the high-frequency stimuli, the N2 amplitude was slightly larger for RL- compared to both TL-pseudowords and words. Around 300 ms post stimulus, larger positivities were observed for words compared to RL- and TL-pseudowords (see central-posterior electrodes in Fig. 1). Importantly, the N400 amplitude appears increased to RL-pseudowords relative to both TL-pseudowords and words. Interestingly

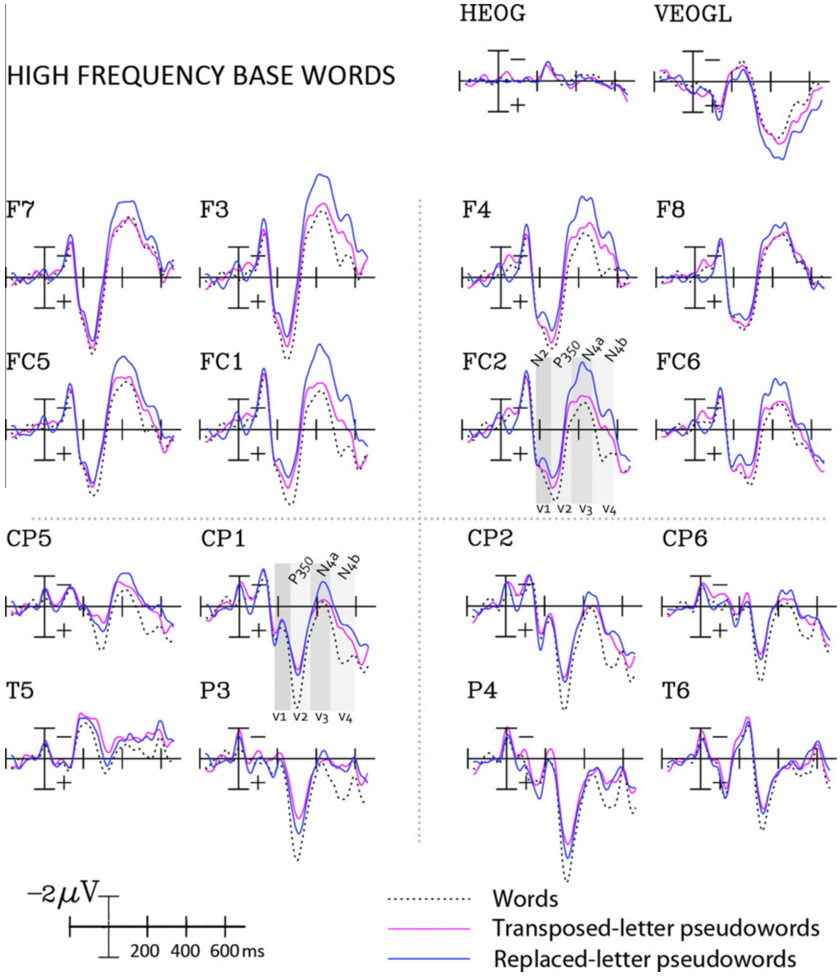

Fig. 4. Grand average ERPs to HIGH FREQUENCY words and the corresponding TL- and RL-pseudowords (Experiment 1). In this and all subsequent figures, the ERP waveforms are plotted for the 16 representative electrodes, and for the horizontal and vertical EOG channels. Different gray columns mark the four epochs under analysis (v1: 180–260 ms, v2: 260–360 ms, v3: 360–470 ms, and v4: 470–580 ms). Negative potentials are plotted upwards and each tick mark on the horizontal axis represents 200 ms.

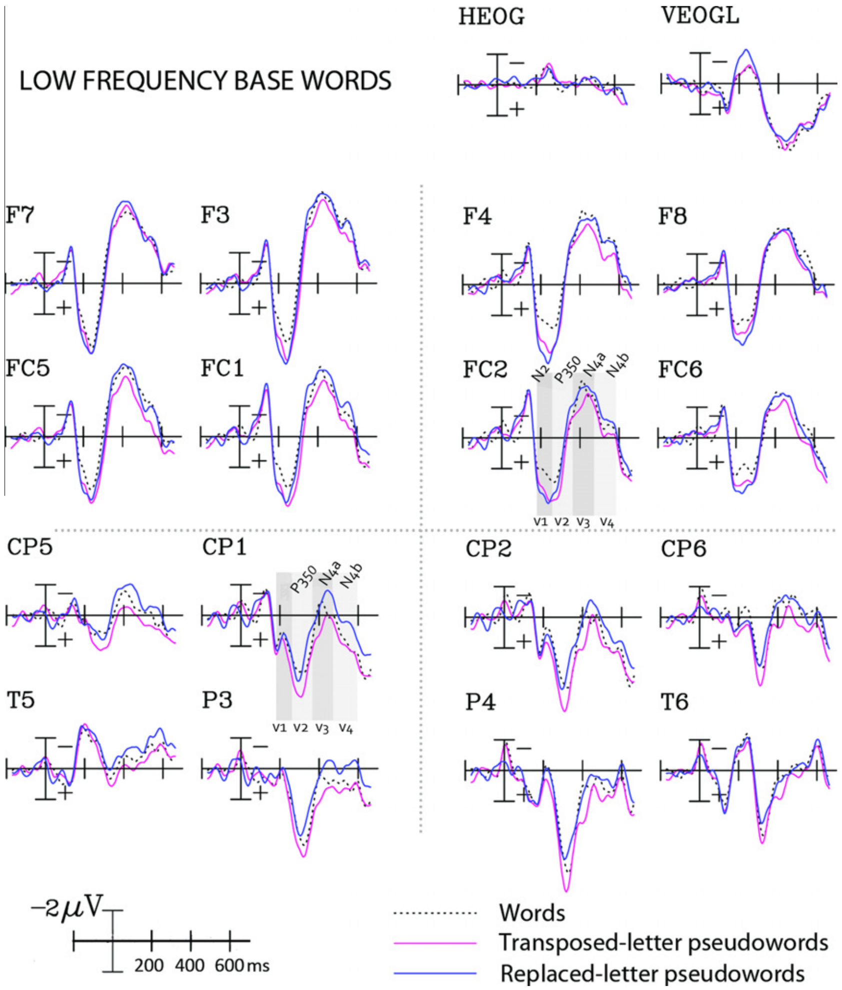

Fig. 5. Grand average ERPs to LOW FREQUENCY words and the corresponding TL- and RL-pseudowords (Experiment 1).

Table 2
Summary of the results of the ANOVAs on the ERP waves in the semantic categorization task. Significant interactions involving frequency and type of similarity were obtained across the 4 epochs. Paired comparisons within the high and low frequency conditions are presented.

Significant effects, *F*				Similarity comparison		
				W-TL	W-RL	TL-RL
180–260	Fr × S × AP = 9.79***	High F	*Frontal*	<1	4.06	3.69
			Posterior	2.06	<1	1.14
		Low F	*Frontal*	10.27**	6.60*	<1
			Posterior	1.58	<1	<1
260–360	Fr × S = 11.9***	High F		15.44***	14.53***	<1
		Low F		3.25	<1	2.69
360–470	Fr × S × AP = 4.39*	High F	*Frontal*	<1	15.45***	4.96*
			Posterior	1.61	2.38	<1
		Low F	*Frontal*	<1	<1	1.02
			Posterior	2.48	<1	5.80*
470–580	Fr × S = 5.91**	High F		6.34*	23.45***	<1
		Low F		<1	<1	3.35

df of Interaction: 2,26; df of simple comparisons: 1,13.
Fr = frequency, S = type of similarity and AP = anterior–posterior distribution.
* $p < .05$.
** $p < .01$.
*** $p < .001$.

TL-pseudowords and words do not differ in the first 100 ms interval of the N400 epoch (N4a; see Fig. 4), but the ERP waves start to diverge for all three conditions in a later time-window (N4b). In contrast, for the low-frequency stimuli, the N2 amplitude was larger for words relative to either of the two types of pseudowords, especially over frontal electrode sites. Most importantly, no clear differences between conditions were observed for the low frequency stimuli after 300 ms. In Table 2, we present a summary of the results of the ANOVAs for the different epochs Fig. 6 shows the ERPs for high vs. low frequency words, which shows the typical

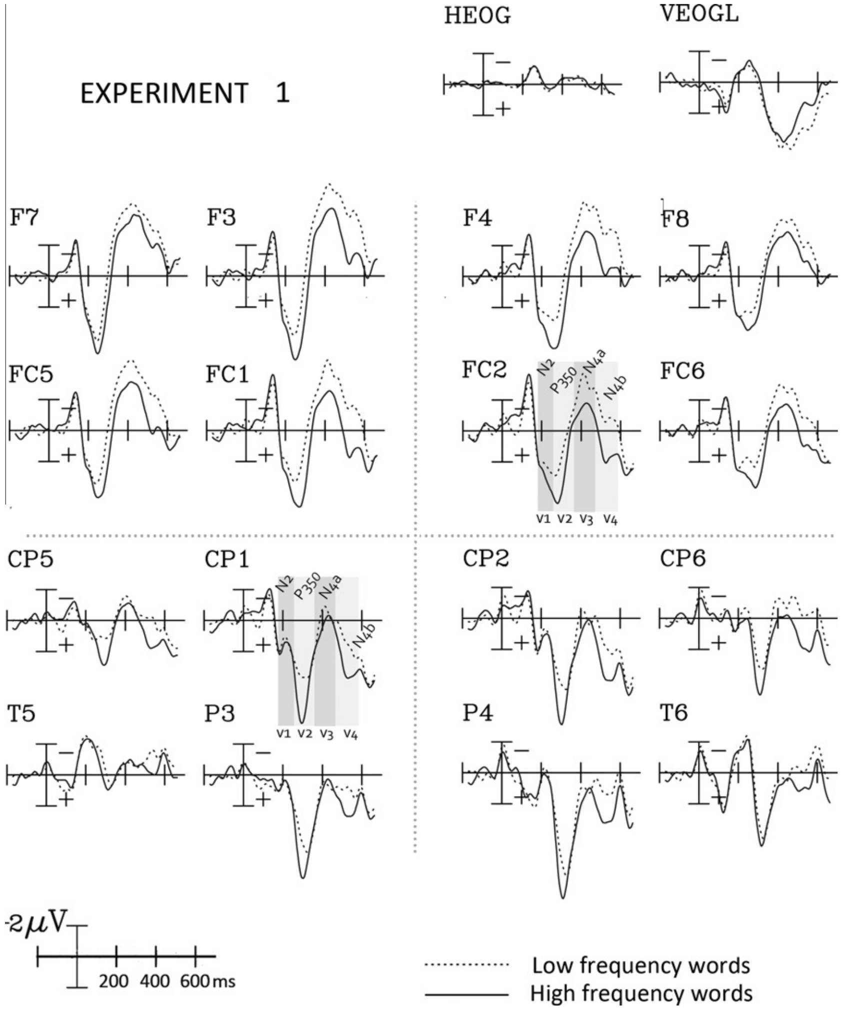

Fig. 6. Grand average ERPs to HIGH and LOW FREQUENCY words (Experiment 1).

word-frequency effect (reduced N400 to high relative to low frequency words: e.g., Vergara-Martínez & Swaab, 2012; Barber, Vergara, & Carreiras, 2004; Smith & Halgren, 1987; Van Petten & Kutas, 1990) –given that the focus of this paper was not on the comparison of low vs. high-frequency, we will not further examine this effect.

As shown in Table 2, significant interactions between Frequency and Type of similarity were observed across the 4 epochs. Significant interactions between Frequency, Type of similarity and AP distribution were observed in the first (180–260 ms) and second (360–470 ms) epochs. For the sake of clarity in presenting the results, we report paired *t*-test results for the type of similarity comparison, separately for the high- and low-frequency stimuli. We also report paired *t*-test results for the AP comparison in those epochs where the triple interaction was statistically significant.

2.3. High-frequency

2.3.1. 180–260 ms Epoch

Marginally significant differences were observed regarding type of similarity, with RL-pseudowords eliciting larger N2 amplitudes than both TL-pseudowords and words.

2.3.2. 260–360 ms Epoch

Significant differences were obtained between words and both TL- and RL-pseudowords: Words elicited larger positive amplitudes, whereas the two types of pseudowords did not differ from each other.

2.3.3. 360–470 ms Epoch

Significant differences between RL-pseudowords and both words and TL-pseudowords were observed over frontal areas (see Table 2; RL-pseudowords elicited larger negativities). Importantly, words and TL-pseudowords did not differ from each other.

2.3.4. 470–580 ms Epoch

Significant differences were obtained between words relative to both TL- and RL-pseudowords (both types of pseudowords elicited larger negativities), whereas the two types of pseudowords did not differ from each other.

2.4. Low-frequency

2.4.1. 180–260 ms Epoch

Significant differences were obtained between words relative to both TL- and RL-pseudowords over frontal regions (see Table 2; words elicited larger negative amplitudes), whereas the two types of pseudowords did not differ from each other.

2.4.2. 260–360 ms Epoch

No significant differences were observed.

2.4.3. 360–470 ms Epoch

Significant differences between RL-pseudowords and TL-pseudowords were observed in posterior areas (RL-pseudowords elicited larger negativities).

2.4.4. 470–580 ms Epoch

No significant differences were obtained.

2.5. Discussion

The results of this experiment support the view that transposed-letter pseudowords generate a large amount of activation of their base words' representations, especially when created from high-frequency words. Given that there were differences in the ERP results for the high- and low-frequency stimuli, we will first discuss the findings for the high-frequency stimuli, and then for the low-frequency stimuli. Finally, we will provide a general framework that can serve to explain the results obtained in this experiment.

2.5.1. High-frequency stimuli

At the earliest time epoch under scrutiny (180–260 ms, see Fig. 4), RL-pseudowords elicited slightly larger negativities compared to both words and TL-pseudowords – note that this difference only approached the classical criterion for statistical significance: words vs. RL-pseudowords: $F(1,13) = 4.06$; $p = .06$; TL-pseudowords vs. RL-pseudowords: $F(1,13) = 3.69$; $p = .07$. No differences were observed between words and TL pseudowords. The pattern of this ERP (frontal–central distribution) matches well with the no-go N2 window, which is an ERP component with larger amplitude for no-go stimuli when difficulties for discriminating between go and no-go stimuli are increased (Jodo & Kayama, 1992; Maguire et al., 2009; Nieuwenhuis et al., 2004). This would reflect greater difficulty in categorizing the RL-pseudowords relative to words and TL-pseudowords, who did not differ from each other (consistent with findings of Ziegler et al., 1997, Experiment 3). That is, whereas both words and highly wordlike pseudowords (i.e., TL-pseudowords) may be included in the same category ("words"), RL-pseudowords may not yet have been mapped onto any stable stored word representation.

In addition, between 260 and 360 ms, high-frequency words elicited larger positivities than their corresponding pseudowords in both TL and RL pseudoword conditions. Thus, at this point, the cognitive system appears to discriminate between words and pseudowords. This positivity peaked at around 300 ms post stimulus and was maximal over posterior and central scalp regions. Previous ERP evidence in the form of early positivities peaking at this latency has been interpreted in terms of lexical selection or lexical identification (Braun et al., 2006; Friedrich et al., 2004; Pylkkänen et al, 2002; see also Holcomb, Grainger, & O'Rourke, 2002). Importantly, a positivity peaking around this latency and with similar scalp distribution has been previously referred to as the P325 in masked priming experiments (Holcomb & Grainger, 2006), a component which is sensitive to full matching between the input and a single whole-word representation (see Holcomb & Grainger, 2006). The P325 component is sensitive to full orthographic overlap between prime and target (with larger amplitudes for the full repetition condition), while it shows no differences to targets that are unrelated to or that partially overlap with the (masked) preceding prime. As different types of prime-target deviations (prime-target partial overlap or prime-target unrelated conditions in masked priming experiments) do not affect the P325 amplitude, this mismatch process has been proposed to operate on an all-or-none basis, when the lexical processor attempts to settle on a single whole-word representation as a unique interpretation of the input (i.e., lexical selection) (see Holcomb & Grainger, 2006). Although differences between experimental paradigms (i.e., single-presentation in the current study vs. masked priming in the previous study) may impose limitations to the extent to which these results can be directly compared, the ERP effects obtained in this specific time window may be interpreted as reflecting lexical selection processes (approximately between 260 and 360 ms post stimulus, see Friedrich et al., 2004; Grainger & Holcomb, 2009; Holcomb & Grainger, 2006; Pylkkänen et al, 2002). Thus, the observed pattern of results in the 260–360 ms time window for high-frequency stimuli do indicate that lexical selection processes were taking place in this time window, since the ERPs to the words differed from those to the pseudowords in both conditions, while the ERPs to TL and RL pseudowords were not different from each other.

Importantly, between 360 and 470 ms, RL pseudowords elicited larger negativities than TL pseudowords and words, which in turn did not differ from each other. This ERP deflection coincides temporally with an N400 subcomponent. Nonetheless, its scalp distribution differs from the typical N400 in that it is maximal at frontal scalp-locations, whereas the typical N400 distribution is central-parietal (as observed in the classic N400 paradigm with words matching or mismatching the semantic expectations established by the preceding context: Kutas & Hillyard, 1983; Kutas & Van Petten, 1988). What we should note here, however, is that the N400 scalp distribution can vary as a function of task demands or stimulus properties (sensory modality of the input); in particular, its distribution is more frontal in single-word tasks (Boddy, 1986; Nobre & McCarthy, 1995; Vergara-Martínez & Swaab, 2012). Given that the N400 component has been related to semantic processing (e.g., Bentin, Kutas, & Hillyard, 1993, 1995; Cristescu & Nobre, 2008; McCarthy & Nobre, 1993), the present results suggest that even though some sort of mismatch for the pseudoword stimuli was detected earlier, the TL pseudowords were able to elicit semantic activation to a similar extent as their base words. This is consistent with masked/unmasked associative priming experiments with transposed-letter stimuli (e.g., jugde-COURT faster than ocean-COURT; see Perea & Lupker, 2003; Perea et al., 2012). Finally, the late N400 (470–580 ms) differentiated both types of pseudowords from the words, presumably because the word units activated by the TL-pseudowords earlier on are finally verified and deactivated (see Bourassa & Besner, 1998).

2.5.2. Low-frequency stimuli

The pattern of data for low-frequency stimuli was different from that of the high-frequency stimuli in several respects. In the early 180–260 ms epoch, the N2 to the words was more negative than to *both* types of pseudowords (see Fig. 5) (recall that, for high-frequency stimuli the N2 component to the RL-pseudowords was slightly larger in amplitude than to the words and the TL-pseudowords). Regarding the larger N2 amplitude elicited by words as compared to pseudowords, it appears that low-frequency words were more difficult to process because of their delayed/weak access to the word's stored representations. That is, lexical entries for low frequency words might not be represented strongly enough to supply any effective feedback during the encoding of the TL and RL pseudowords. Therefore, the pseudowords could also be easily discarded into the no-go category, thus eliciting smaller N2 amplitudes. In addition, unlike high-frequency stimuli, no differences between words and pseudowords were observed in the 260–360 ms time-window. This suggests that the low levels of activation produced by the word units corresponding to low-frequency words lead to minimal feedback from the word-level to the orthographic representations, which in turn results in slower (or even non-existent) matching operations between the input signal and the stored representation of the stimulus.

For the low frequency stimuli, the early N400 (360–470 ms) was larger in amplitude for RL- compared to TL-pseudowords over posterior scalp sites. Finally, in the late N400 epoch (470–580 ms), there was a nonsignificant trend reflecting larger negativities for RL- than for TL-pseudowords. These results may reflect the slower time-course of semantic access in low frequency stimuli, as well as the inaccuracy in distinguishing the (low frequency) pseudowords from the low-frequency words, possibly due to the less stable representation corresponding to the low frequency stimuli stored in memory.

2.6. Summary

We found an interaction between frequency and similarity on the early N2 component: Whereas high frequency stimuli elicited a (slightly) larger N2 amplitude to RL pseudowords than to words and TL pseudowords (which did not differ from each other), the low frequency stimuli showed a larger N2 to words relative to both pseudoword conditions. The N2 has usually been interpreted as reflecting a task-specific categorization process (Jodo & Kayama, 1992; Maguire et al., 2009; Nieuwenhuis et al., 2004). In the present experiment, this categorization was to select what could plausibly be animal names from those that could not. For the high frequency stimuli, we found no differences in the N2 response to words and TL-pseudowords, which suggests that fast access to stored lexical representations is tolerant of positional errors in the letter sequence. On the contrary, low frequency words elicited larger N2 amplitudes (thus reflecting difficulties in early categorization) compared to both types of pseudowords. This suggests that it is easier for the cognitive system to categorize these stimuli as pseudowords since the spread of activation to and from their base-word lexical representations is weak/slow.

The results regarding the P350 component suggest that at this time in processing, deviation on letter identity and letter position have equivalent consequences on the selection of a single whole-word representation. However the N400 findings suggest that, for high-frequency stimuli, the code that is used to trigger semantic activation discards information on letter position during an early stage of processing (360–470 ms), which is in line with previous behavioral findings (see Carreiras et al., 2007; Perea & Carreiras, 2006a; Perea & Lupker, 2004). Note that matching operations between input stimuli and stored representation allowed for the distinction between words and pseudowords in the preceding window of analysis (260–360 ms, the P350), where TL- and RL pseudowords did not differ from each other.

Although for high-frequency stimuli both types of pseudowords differed from word stimuli in the last epoch (N400), this was not the case for low frequency stimuli. This can be interpreted in at least two different ways. First, one could argue that the absence of differences between words and pseudowords may reflect a “floor effect” in lexical access due to the less stable linking between semantic information and word-form representations for low-frequency words. Note that correct execution of the semantic categorization task could be made without a word/nonword discrimination, and the task itself would impose a deadline for executing or inhibiting a response. Second, it could be argued that the absence of differences between pseudowords and words of low-frequency resulted not only from a delayed access to meaning but because participants were unaware of the meaning of a significant proportion of the low-frequency words. Even though we checked after the experiment whether or not the participants knew the meanings of the words in the experiment, it is possible that semantic access to the present (no-go) low-frequency words was not achieved in time under the conditions of the present setup.[2]

In order to examine if the categorization task of Experiment 1 led to fast lexico-semantic matching at the cost of fine-grained orthographic processing, we performed Experiment 2 with the same critical manipulation but this time with a standard, yes/no lexical decision task. Accurate performance on a word/nonword discrimination task requires a more fine-grained analysis of the orthographic input, which in turn could lead to better discrimination of words from pseudowords.

3. Experiment 2 (lexical decision)

3.1. Method

3.1.1. Participants

Eighteen undergraduate students of UC Davis (10 women) participated in the experiment in exchange for course credit. All of them were native English speakers with no history of neurological or psychiatric impairment, and with normal or corrected-to-normal vision. Ages ranged from 18 to 21 years (mean: 18.6 years). All participants were right-handed, as assessed with an abridged version of the Edinburgh Handedness Inventory (Oldfield, 1971). Participants gave informed consent prior to the experiment.

3.1.2. Materials

The materials were the same as in Experiment 1. To equate the number of words and pseudowords in the lexical decision task (i.e., 50% words and 50% pseudowords), a new set of filler words was included: 80 filler words were selected that matched in length (6 and 7 letters) and lexical frequency (40 of high-frequency and 40 of low-frequency) with the experimental words.

3.1.3. Procedure

The procedure was identical to that of Experiment 1, except for the change in task (lexical decision: “is the letter string a real word?”). Participants were instructed to decide as accurately and rapidly as possible whether or not the stimulus was an English word. They pressed one of two response buttons (YES/NO). The hand used for each type of response was counterbalanced across subjects. Reaction Times (RTs) were measured from target onset until the participants’ response.

3.1.4. EEG recording and analyses

The procedures were identical to Experiment 1. Trials containing artifacts and/or trials with incorrect lexical decision responses were not included in the average ERPs or in the statistical analyses. Due to artifacts and/or incorrect responses, approximately 15% of the trials were excluded. There was no statistical difference across conditions in the number of rejections due to artifacts ($p > .1$). An ANOVA on the number of included trials per condition showed significant effects of lexical frequency [$F(1,17) = 9.15$, $p < .01$], reflecting that on average, more correct responses were observed for high- than low-frequency words, and type of similarity [$F(2,34) = 9.80$, $p < .001$], because more correct responses were made to RL-pseudowords than to TL pseudowords [$F(1,17) = 13.30$, $p < .01$] and to words than to TL pseudowords [$F(1,17) = 15.42$, $p < .001$]. There was no difference between the number of trials in the Word and RL pseudoword conditions ($F < 1$). Importantly, at least 30 trials were included for each condition in the average ERP data from each participant.

3.2. Results

3.2.1. Behavioral results

The mean RTs for correct responses and error rates for words and pseudowords are presented in Table 3. Incorrect responses (7.9% of the data) were excluded from the latency analysis. To avoid the influence of outliers, RTs less than 250 ms or greater than 2000 ms (less than 5% of the responses) were excluded from the RT analyses. ANOVAs on the RTs (and error rates) for words and

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[2] However this is not a likely explanation as we matched experimental words and “go” words in frequency, and accuracy measures were over 90% correct. Note that we only gathered behavioral responses for the “go” stimuli.

pseudowords were performed including lexical frequency (low vs. high) and type of similarity (word, TL-pseudoword, RL-pseudoword) as within-subjects factors, and list (1, 2, 3) as a between-subjects factor.

The ANOVA on the latency data revealed a significant interaction between lexical frequency and type of similarity [$F(2,30) = 24.61$, $p < .001$, MSE = 832]. This reflected that, for high-frequency stimuli, there were significant differences between the three conditions: words vs. TL-pseudowords [731 vs. 874 ms, respectively; $F(1,15) = 88.6$, $p < .001$, MSE = 2074), words vs. RL-pseudowords [731 vs. 842 ms, respectively; $F(1,15) = 43.9$, $p < .001$, MSE = 2522], and TL- vs. RL-pseudowords [874 vs. 842 ms; $F(1,15) = 18.1$, $p < .001$, MSE = 509] where the TL-pseudowords showed the slowest RTs. In contrast, for the low-frequency stimuli, significant differences were observed between words and the two types of pseudowords: words vs. TL-pseudowords [809 vs. 864 ms; $F(1,15) = 13.4$, $p < .01$, MSE = 2058) and words vs. RL-pseudowords [809 vs. 842 ms; $F(1,15) = 8.8$, $p < .01$, MSE = 2401], but not between TL- vs. RL-pseudowords ($F < 1$).

The ANOVA on the error data also revealed an interaction of lexical frequency and type of similarity [$F(2,30) = 4.1$, $p < .05$, MSE = 33]. For high-frequency stimuli, participants made fewer errors to words than to TL-pseudowords [$F(1,15) = 32.7$, $p < .001$, MSE = 30) or RL-pseudowords [$F(1,15) = 7.26$, $p < .05$, MSE = 7], and importantly, more errors to TL- pseudowords than to RL-pseudowords [12.1% vs. 3.9% of errors, respectively; $F(1,15) = 23.3$, $p < .001$, MSE = 25]. In contrast, for low-frequency stimuli, the only significant effect was that participants made more errors to TL-pseudowords than to RL-pseudowords [13.3% vs. 7.1%, respectively; $F(1,15) = 10.5$, $p < .01$, MSE = 33.2].

Table 3
Mean lexical decision times (in ms), percentage of errors, and standard deviations (in parentheses) for words and pseudowords in Experiment 2.

	Words	TL-pseudowords	RL-pseudowords
Low-frequency			
RT(SD)	809 (31.8)	864 (37.7)	857 (38)
Errors	9.5 (1.4)	13.3 (1.9)	7.1 (1.3)
High-frequency			
RT(SD)	731 (31.6)	874 (38.4)	842 (35.2)
Errors	1.52 (.46)	12.1 (1.59)	3.88 (.96)

3.3. ERP results

Figs. 7 and 8 show the ERP waves for the words and the pseudowords for both high- and low-frequency stimuli. As can be seen in these figures, ERPs show a negative potential reaching its maximum at around 100 ms post stimulus, which was followed by a large positive deflection peaking at around 200 ms, followed by another positive deflection that was maximal around 300 ms and over posterior regions. This latter positive deflection appears

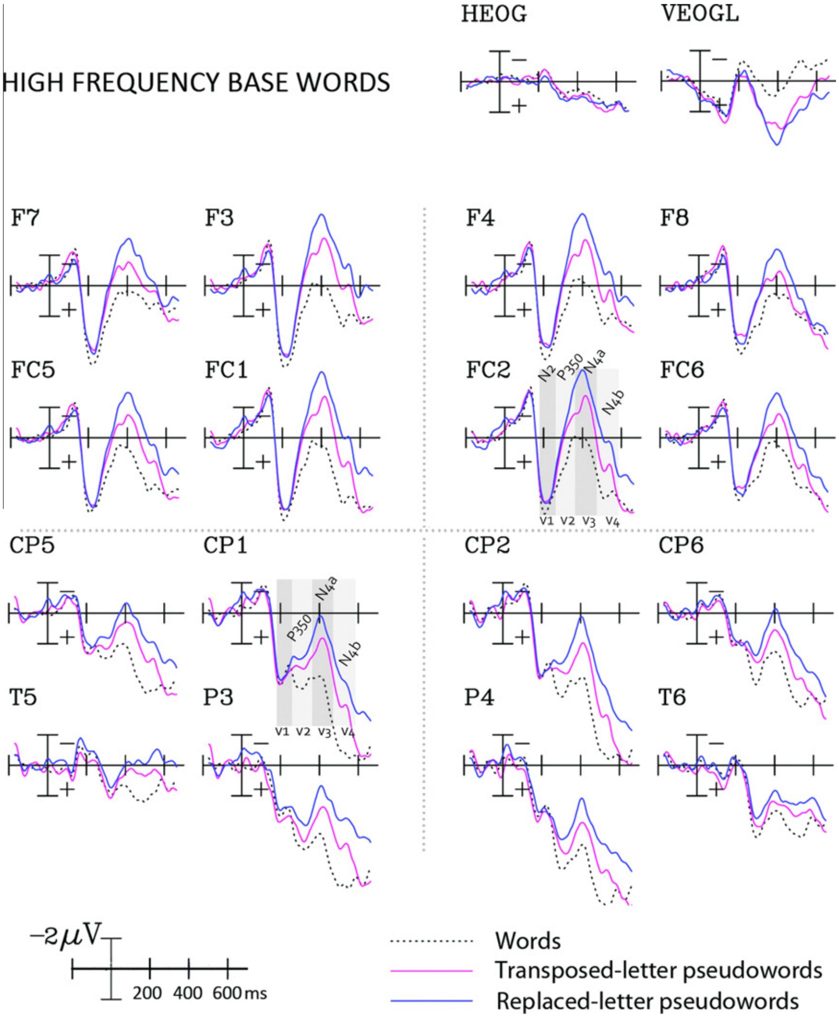

Fig. 7. Grand average ERPs to HIGH FREQUENCY words and the corresponding TL- and RL-pseudowords (Experiment 2).

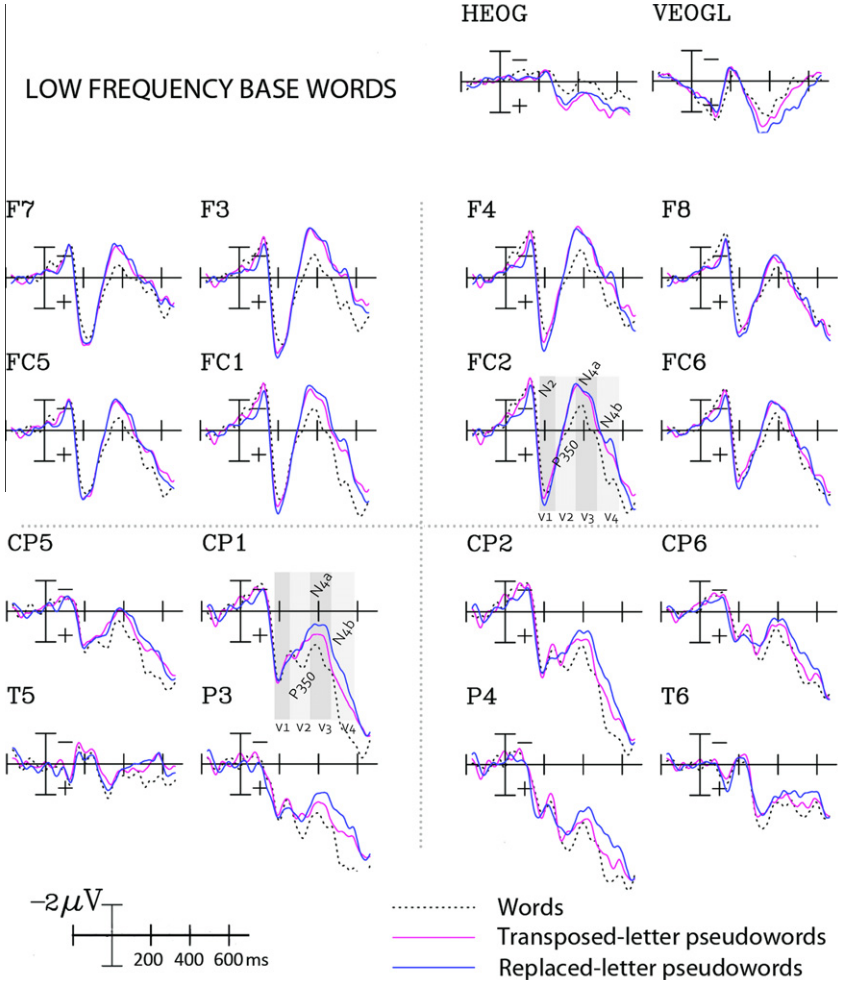

Fig. 8. Grand average ERPs to LOW FREQUENCY words and the corresponding TL- and RL-pseudowords (Experiment 2).

greater in amplitude for word stimuli. Finally there is a negative deflection that peaks around 400 ms (N400).

Visual inspection shows that words differed from the two types of pseudowords around 300 ms post stimulus for both high- and low-frequency stimuli, with words eliciting larger positive amplitudes than both types of pseudowords. However, between 350 ms and 600 ms approx. (N400) different effects can be seen for the high- compared to the low-frequency stimuli. For the high-frequency stimuli, the N400 was larger for RL-pseudowords than for TL-pseudowords, which in turn was larger than that for words. In contrast, for the low-frequency stimuli, both TL- and RL-pseudowords did not differ from each other, and showed larger negative amplitudes than words. In order to compare results between experiments, the statistical analyses were performed in the same time epochs as in Experiment 1. The results of the ANOVAs for each epoch are shown in Table 4. Fig. 9 shows the ERPs for high vs. low frequency words – reflecting the usual pattern of word-frequency effects (e.g., Vergara-Martínez & Swaab, 2012).

Table 4
Summary of the results of the ANOVAs on the ERP waves in the lexical decision task (Experiment 2). Significant interactions involving frequency and type of similarity were obtained across the 3rd and 4th epochs. Paired comparisons within the high and low frequency conditions are presented for those epochs.

			Similarity comparison		
Significant effects, *F*			W-TL	W-RL	TL-RL
180–260	S < 1				
260–360	S = 18.81***		18.74**	25.62***	4.10
360–470	S = 20.1***	High F	12.79**	36***	8.82**
	F × S = 5.43*	Low F	4.94*	7.84*	<1
470–580	S = 39.8***	High F	16.97**	42.81***	29.44***
	F × S = 4.69*	Low F	8.64**	40.62***	2.16

df of S: 2,30; df of interaction: 2,30; df of simple comparisons: 1,15.
Fr = frequency, S = type of similarity.
[*] $p < .05$.
[**] $p < .01$.
[***] $p < .001$.

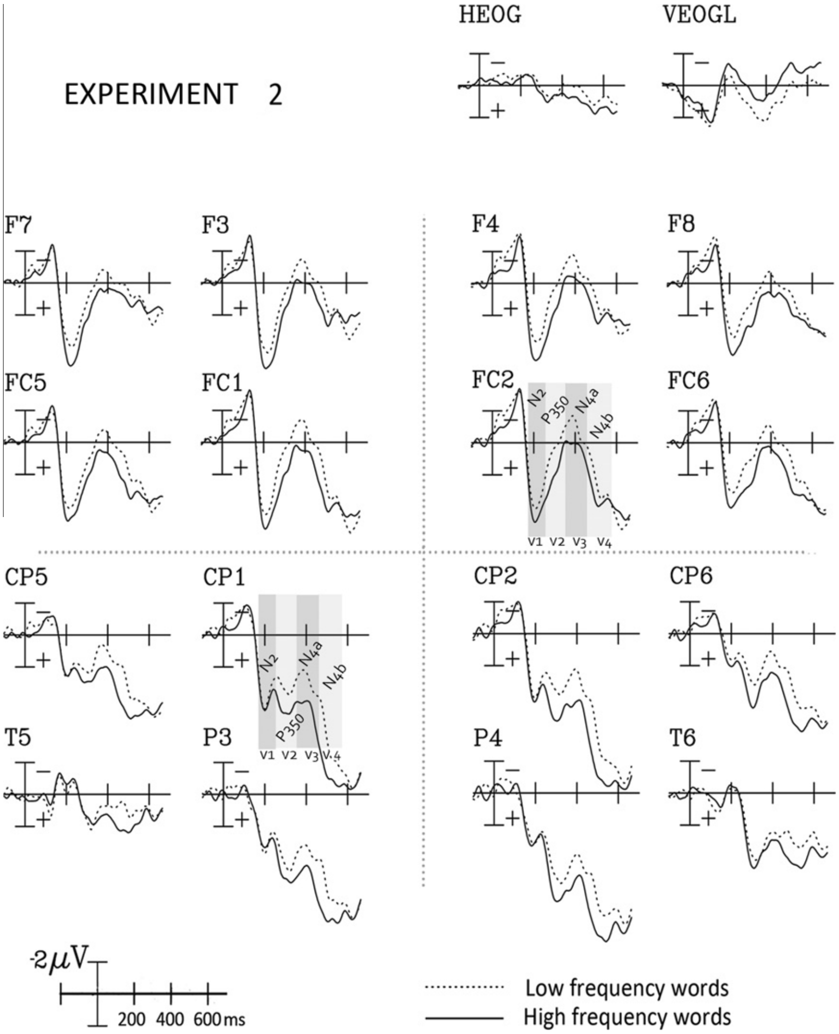

Fig. 9. Grand average ERPs to HIGH and LOW FREQUENCY words (Experiment 2).

3.3.1. 180–260 Epoch

No significant differences were obtained in this time window.

3.3.2. 260–360 Epoch

The ANOVA showed main effects of type of similarity: Words showed larger positive amplitudes compared to both type of pseudowords. No difference was observed between the two types of pseudowords.

Table 4 shows that a significant interaction between frequency and type of similarity was obtained across the next two epochs of analysis (360–470 ms and 470–580 ms). As in Experiment 1, and for the sake of clarity in presenting the results, we will report paired *t*-test results separately for the low and high-frequency stimuli.

3.4. High-frequency stimuli

3.4.1. 360–470 and 470–580 Epochs

Significant differences were obtained between the three conditions: RL-pseudowords showed the largest negativity followed by the TL-pseudowords, which in turn showed larger amplitudes than words (see Table 4).

3.5. Low-frequency stimuli

3.5.1. 360–470 and 470–580 Epochs

Significant differences were obtained between words and both TL- and RL-pseudowords (pseudowords elicited larger negativities), while the two types of pseudowords did not differ from each other.

3.6. Discussion

The use of the word/nonword discrimination task produced clear differences between the high- and low-frequency stimuli with respect to the TL effects. Despite the necessity of fine-grained orthographic processing to make fast and accurate lexical decisions, both the behavioral and electrophysiological results reveal that TL pseudowords are more "wordlike" than RL pseudowords, and that this effect is modulated by word frequency. Specifically, TL-pseudowords derived from high-frequency words (e.g., JUGDE) were responded to slower, produced more "word" errors, and elicited smaller N400 amplitudes than the corresponding RL-pseudowords (e.g., JUDPE). The low frequency stimuli also showed more word errors to TL than to RL pseudowords. But in contrast to the high-frequency stimuli, results show that TL- and RL-pseudowords derived from low-frequency words were rejected at the same speed and elicited similar N400 amplitudes.

The results from the present yes/no lexical decision experiment partially replicate those obtained in Experiment 1 (with a go/no-go semantic categorization task) and also offer complimentary behavioral evidence on the modulatory influence of word frequency on TL effects. On the one hand, no differences were observed regarding the N2 component, thus supporting the interpretation of N2 as a task-specific component in the processing of no-go stimuli during abstract categorization. Whereas a no-go N2 was observed in Experiment 1, this was not found in the present lexical decision experiment; in contrast a positivity peaking around 200 ms post-stimuli over posterior regions appears to show larger amplitudes for Experiment 2 (lexical decision) compared to Experiment 1 (semantic categorization). These differences are presumably related to each task's specific demands. This is further supported by findings of a recent ERP study with a lexical decision task that used similar manipulations of letter replacement and letter position (TL- and RL-pseudowords; Carreiras et al., 2007); in this study no effects were observed in the N200 time window either.

The ERP data revealed that between 260 and 360 ms and for both low- and high-frequency stimuli, words elicited a larger P350 component compared to both types of pseudowords. That is, different types of mismatch between the stored representation and the input stimuli (i.e., TL-pseudowords and RL-pseudowords) did not result in a different ERP response in this time window. This finding seems to reflect lexical selection processes during which an input word form is mapped onto a stored lexical representation. Note that with the semantic categorization task (Experiment 1), P350 differences were only observed in high frequency stimuli while in the present experiment with the lexical decision task, P350 differences were observed both in high and in low frequency stimuli. That is, when the task demands an explicit discrimination between words and pseudowords, the greater involvement of fine-grained processing of the stimuli can indeed override differences in lexical frequency. Different task demands are also evident when we compare the N400 results from Experiments 1 and 2. Computations that operate automatically under the specific goal of a semantic categorization (Experiment 1) may be under control of more attentional resources when the task is to make an explicit distinction between words and pseudowords (Experiment 2). As a result, differences between words and pseudowords were found in the N400 time window in Experiment 2. For high-frequency stimuli there were significant differences between words, TL pseudowords and RL pseudowords from 360 ms until 580 ms. Influence from activation of high frequency word representations on the TL pseudowords was found on the N400 where RL pseudowords elicited larger amplitudes than TL pseudowords (along with slower lexical decision latencies and increased percentage of word errors). Recall that in Experiment 1 words and TL pseudowords elicited similar ERPs in the 360–470 ms and did not start to diverge until the 470–580 ms post stimulus epoch, and this pattern of results was only obtained for the high-frequency stimuli. This suggests that, for high-frequency stimuli, semantic activation does not rely on full coding of letter position, which is in line with previous behavioral findings (see Perea & Carreiras, 2006a,b; Carreiras et al., 2007; Perea & Lupker, 2004; Perea et al., 2012).

In contrast to Experiment 1, there was a reduced N400 to the words relative to the pseudowords for the low frequency stimuli in Experiment 2. Furthermore, even though TL pseudowords elicited more word errors that RL pseudowords, both TL and RL pseudowords were rejected at the same speed. Thus, it seems that even when fine processing at the orthographic level is involved in a word/nonword discrimination task, TL and RL pseudowords are more comparable when created from low-frequency words than when created from high-frequency words.

4. General discussion

The present study was designed to examine the impact of word-frequency on letter position assignment and letter identity by comparing the electrophysiological correlates of the effects of TL vs. RL pseudowords created from high vs. low-frequency words. Specifically, we assessed the effects of base word-frequency on the time course of the processing of words and pseudowords by measuring ERPs during single-word reading in a semantic categorization task (Experiment 1) and in a lexical decision task (Experiment 2). At the behavioral level, high-frequency TL pseudowords produced a large percentage of "word" responses in lexical decision as well as long latencies for correct "nonword" responses, thus replicating earlier research (e.g., Andrews, 1997; Carreiras et al., 2007; Gómez, 2002; O'Connor & Forster, 1981; Perea et al., 2005). At the electrophysiological level, a series of changes in the ERP waveforms (from 260 to 600 ms post-stimuli) permit the distinction between different subprocesses involved in word reading. The use of different tasks (semantic categorization and lexical decision) together with the experimental manipulations on Type of Similarity (TL and RL pseudowords) allows us to differentiate between electrophysiological markers of different psycholinguistic processes: the P350 (260–360 ms) consistently showed larger amplitudes for words compared to both types of pseudowords (whilst TL- and RL-pseudowords elicited similar voltage amplitudes) across experiments, whereas the N400 effects (360–580 ms) were modulated as a function of the task and the type of similarity (larger N400 lexicality effects were obtained in the Lexical Decision compared to the Semantic Categorization task; larger N400 amplitudes were obtained for the RL- compared to the TL-pseudowords). But the most critical finding here is that the ERP results from the two experiments reflected that, for high-frequency stimuli, the N400 to TL-pseudowords (but not RL-pseudowords) resembled that of their base words: (i) in the semantic categorization task, there were no differences between word stimuli and TL-pseudowords in the 360–470 ms epoch, while the RL-pseudowords showed a greater amplitude N400; and (ii) in the lexical decision task, the N400 to RL-pseudowords showed a larger amplitude than to TL-pseudowords, and in contrast with Experiment 1, there was a difference between TL-pseudowords and words. We attribute this apparent discrepancy to different response demands: in the lexical decision task, words and pseudowords required different responses ("yes" for words and "no" for pseudowords), whereas in the go/no-go categorization task, these experimental stimuli corresponded to "no-go" responses (i.e., "non animal").

Importantly, the low-frequency stimuli revealed a very different pattern of results: In the early N400 epoch (360–470 ms), words did not differ from pseudowords. We only found a (small) difference between RL and TL pseudowords in the semantic categorization task (Experiment 1), suggesting that in this time window, RL-pseudowords were more difficult to process. In the lexical decision task (Experiment 2), words were efficiently distinguished from pseudowords (starting around 260 ms until 580 ms), which suggests that processing in the lexical decision task focuses on orthographic features. Despite this change, low frequency RL- and TL-pseudowords did not show any differences regarding the ERP measures or in the reaction time measures (i.e., they were both identified as "no" responses at the same speed). This difference between tasks is probably due to the less stable representations for low frequency stimuli together with the "no-go" response to experimental word and pseudoword stimuli.

In summary, the N400 results of the present study demonstrate that transposed-letter pseudowords created from high frequent words activated lexical-semantic representations to a similar degree as their base words. In contrast, pseudowords created by just replacing one letter from high frequency words generate larger N400 amplitudes than their base words. Importantly, these effects do not occur (or rather occur to a much lesser degree) for the transposition/replacement pseudowords created from infrequent words.

4.1. Letter identity/position in visual-word recognition

The present findings suggest that, at an early stage of processing, the retrieval of lexical information can be triggered by pseudoword letter-strings depending on two factors: (i) How perceptually similar they are to the existing representations of word forms in memory, and (ii) The resting activation level of the word form representations. Thus, if the word-form representation is frequently encountered and the perceptual match is perfect, as is the case for high-frequency words, lexical access is fast and accurate. Importantly, a perfect perceptual match is not always required, and the word recognition system appears flexible under these circumstances: pseudowords that are derived from high frequency words and which share all the letters with the target word, as in the transposed letter condition of this study (e.g., MOHTER), can activate word-form representations to a considerable degree. Indeed, differences between TL-pseudowords and word stimuli did not appear until around 470 ms post-stimulus onset in the semantic categorization task. However, if the perceptual match is less strong, as in the replaced letter pseudowords (e.g., MOSHER), then they are distinguished from words at a much earlier point in time (around 360 ms).

One remarkable finding of this study is that this pattern of results for the high-frequency stimuli follows an epoch during which the word stimuli do seem to be distinguished from both the replaced letter and the transposed letter pseudowords: In the 260–360 ms epoch, a larger positive shift is found to words than to both types of pseudowords. Prior studies have shown that a positive deflection preceding the N400 may be sensitive to lexical selection during visual-word recognition (P325: see Holcomb & Grainger, 2006; P350: see Braun et al., 2006; Friedrich et al., 2004). These apparently conflicting effects of the P350 and N400 components can be accounted for in a cascaded model of visual-word recognition if one assumes that semantic activation starts before the coding of sublexical form representations has been completed. Given that the P350 and the N400 have different scalp distributions and are maximal in different time windows, they may indeed reflect lexical selection and semantic activation processes that occur in parallel.

What are the implications of the present electrophysiological data for models of visual-word recognition? Consistent with recently proposed computational models of letter position coding, TL pseudowords produce quite a large degree of activation on their base words, and substantially more than RL pseudowords. This is mostly found for pseudowords that are created from high-frequency stimuli rather than for the pseudowords created from low-frequency words. As shown in the Introduction, simulations of the spatial coding model (Davis, 2010), using the default parameters, revealed that lexical activation of TL pseudowords is substantially higher than that of RL pseudowords (see Fig. 2), which is consistent with the observed data. Indeed, the data from high-frequency stimuli in the present experiments reflect that the N400 to TL pseudowords is very similar to that of their corresponding base words, especially in the semantic categorization task. With respect to low-frequency stimuli, the simulations on the spatial coding model show that, for the low-frequency stimuli, TL pseudowords should be closer to the activation of word stimuli than the RL pseudowords. Indeed, in the semantic categorization experiment, there was a small (but significant) difference between these two conditions in an early N400 epoch: The N400 to RL-pseudowords was larger than to TL-pseudowords, and furthermore, in the lexical decision experiment, there were more errors for TL pseudowords than for RL pseudowords. However, in the lexical decision experiment, there were no significant ERP differences between TL and RL pseudowords created from low frequency base words, which suggests that the pre-response level of activation induced by these pseudowords did not yet pass the threshold to activate the word-form representations. Thus, Davis' (2010) spatial coding model cannot easily accommodate the interaction between the effects of pseudoword frequency and letter transposition in the N400 amplitude – in fairness to Davis (2010), we should note that the spatial coding model is a computational model intended to simulate word-identification times and error rates rather than electrophysiological data.

As a reviewer indicated, the dual-route model proposed by Grainger and Ziegler (2011) can provide an appropriate account of the interaction between pseudoword frequency and letter transposition in the N400 amplitude (along with the smaller letter transposition effects obtained in the lexical decision task). In the Grainger and Ziegler framework, letter transposition effects reflect fast access to semantics via an orthographic code that uses diagnostic features based on coarse-grained orthographic representations (i.e., using approximate positional information). Specifically, the faster the processing of the stimuli, the more this will reflect the use of such coarse-grained information compared to the slower processing associated with the more fine-grained orthographic information (e.g., grapheme-to-phoneme correspondences). This would explain why high-frequency stimuli show greater letter transposition effects than low-frequency stimuli in the N400 amplitude. Furthermore, this account can also accommodate the observed differences across tasks regarding transposed-letter effects: because of the inclusion of transposed-letter pseudowords in the lexical decision task, accurate lexical decisions require the use of more fine-grained orthographic information than accurate semantic categorizations – note that there were no transposed-letter animal names in Experiment 1. Under those circumstances, the lexical decision task should reveal somewhat smaller transposed-letter effects for the pseudowords than the semantic categorization task, and furthermore the effects with transposed-letter pseudowords should line up with the replacement-letter pseudowords, as was the case in our experiments.

In conclusion, the present study has demonstrated that pseudowords that are perceptually similar to their base words activate word-form representations to such a degree that their semantic representations are activated as well, thus providing electrophysiological evidence of the high degree of flexibility of the brain mechanisms responsible for letter position coding. Furthermore, these effects are modulated by the frequency of the base words. We believe that these findings impose constraints for future implementations of models of visual-word recognition at a neural level (e.g., see Grainger & Ziegler, 2011).

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