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Task modulates ERP effects of orthographic neighborhood for pseudowords but not words

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Abstract

Words and pseudowords from high-density orthographic neighborhoods elicit larger amplitude N400s than similar items from low-density orthographic neighborhoods in the lexical decision task. This pattern could be interpreted as an increase in the amount of lexico-semantic information to be processed or as an increase in difficulty identifying a word (or rejecting a pseudoword) amongst many co-activated alternatives. In order to dissociate between these mechanisms, we compared neighborhood effects between a lexical decision task (LDT) and a letter search task (LST). Behaviorally, we found the standard neighborhood and lexicality effects in the LDT, but no significant effects in the LST. Thus, behavioral responses were sensitive to the decisions required by the respective tasks. Electrophysiologically, we found similar N400 neighborhood effects between tasks for words, but the N400 neighborhood effect for pseudowords was only present in the LDT. Moreover, the effect of neighborhood in the LDT occurred earlier for words than for pseudowords. These nuanced differences in the time course and automaticity of word and pseudoword neighborhood effects lend insight into the processes that underlie N400 effects of orthographic neighborhood and how they unfold over time. We propose that the early neighborhood effects for words across tasks were driven by highly automatized word identification processes that are sensitive to the lateral inhibition generated by orthographic neighbors. In contrast, the later neighborhood effects for pseudowords in the LDT could have been driven by task-specific processes tied to how global lexical activity is used to make a lexical decision.

Keywords

orthographic neighborhood; task effects; lexical status; ERPs; N400

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1. Introduction

Readers are able to rapidly recognize individual words from among tens of thousands of alternatives. In theory, efficient word recognition depends in part on the organization of the lexicon and structural connections among form-similar words, or so-called “neighbors”. This perspective is supported by studies showing that words (e.g., *cake*) that have many neighbors (e.g., *care*, *lake*, *coke*) produce different behavioral and electrophysiological patterns than words (e.g. *Jazz*) that have fewer neighbors (e.g., Andrews, 1997; Carreiras, Perea, & Grainger, 1997; Grainger & Jacobs, 1996; Holcomb, Grainger, & O’Rourke, 2002; Laszlo & Federmeier, 2011; Sears, Hino, & Lupker, 1995; van Heuven, Dijkstra, & Grainger, 1998). However, neighborhood effects have almost exclusively been measured in tasks that require explicit lexico-semantic processing (e.g., lexical decision, semantic categorization), with little consideration for how the demands of these tasks might contribute to the effects. Surprisingly few studies have addressed the degree to which co-activation of neighbors occurs automatically, where automaticity is defined as stimulus-driven and contrasted with task-dependent (e.g., Chwilla, Brown, & Hagoort, 1995; Fiebach, Ricker, Friederici, & Jacobs, 2007; Ziegler, Besson, Jacobs, Nazir, & Carr, 1997). Here, we investigated the extent to which neighbor co-activation is automatic versus task-dependent by comparing behavioral and electrophysiological effects of neighborhood in a lexical decision task (LDT) and a letter search task (LST). Investigating the influence of task demands on behavioral and electrophysiological effects of neighborhood lends insight into the processes that underlie them; if neighbor co-activation is automatic and reflective of the underlying lexical structure, then the effects should be similar irrespective of the task.

1.1. Task Demands Modulate Lexicality Effects

Although the automaticity of neighbor co-activation has received little empirical attention, there is a precedent for investigating how differences in the processing of words and pseudowords (i.e., lexicality effects) are influenced by task (e.g., Chwilla et al., 1995; Ziegler et al., 1997). In the LDT, words typically elicit faster responses than pseudowords (i.e., orthotactically and phonotactically legal nonwords; e.g., Braun et al., 2006; Chwilla et al., 1995; Holcomb et al., 2002). The Multiple Read-Out Model (MROM) proposed by Grainger and Jacobs (1996) posits that LDT responses can be based on one of three criteria. ‘Word’ responses are triggered either by a specific lexical representation reaching a threshold level of activation or when the level of global lexical activity (i.e., summed activity across co-activated representations) reaches criterion (see also, e.g., Balota & Chumbley, 1984). When a set time limit is reached and neither of these criteria is met, a ‘not a word’ response is triggered (see also, e.g., Coltheart, Rastle, Perry, Langdon, & Ziegler, 2001). This extended matching process could explain why ‘not a word’ responses are slower than ‘word’ responses (but see Dufau, Grainger, & Ziegler, 2012, for an alternative account of responses to pseudowords in the LDT).

In the ERP waveform, the standard lexicality effect is that pseudowords elicit larger amplitude N400s than words (e.g., Braun et al., 2006; Chwilla et al., 1995; Holcomb et al., 2002). The N400 is a negative peak associated with lexico-semantic processing that appears to be sensitive to both automatic and strategic aspects of word processing (e.g., Holcomb,

1988; Kiefer & Brendel, 2006; Kutas & Hillyard, 1989). At a very general level of explanation, N400 amplitude seems to be driven by the amount of neural activity generated during the processing of a given stimulus in a given task. We further suggest that the amount of neural activity can be related to two primary factors: 1) difficulty in processing - more neural activity and larger N400 amplitude when processing is more difficult (e.g., low frequency words or words in unpredictable contexts; e.g., Kutas & Hillyard, 1980; Rugg, 1990), and 2) the global amount of information to be processed - more neural activity and larger N400 amplitude when more information is activated (e.g., concrete words that activate rich semantic representations; e.g., Kounios & Holcomb, 1994). Both factors could potentially contribute to the larger N400 amplitude seen for pseudowords compared to words. In terms of processing difficulty, pseudowords might elicit larger amplitude N400s than words because of the extra effort involved in finding a lexical representation that matches the input; by definition, no such representation exists for pseudowords. In terms of the global amount of information to be processed, pseudowords might elicit larger amplitude N400s than words due to sustained co-activation of orthographic neighbors. When a word is presented, the corresponding lexical representation can be identified, and activation of the neighbors is suppressed through lateral inhibition. When a pseudoword is presented, activation of the neighbors can continue to resonate.¹ The global level of lexico-semantic activity is therefore higher for pseudowords, leading to a larger amplitude N400 (see Meade, Midgley, Dijkstra, & Holcomb, 2018, for a more direct test of this hypothesis).

The extent to which these lexicality effects persist in form-level tasks that do not require lexico-semantic processing could inform our understanding of the underlying mechanisms. Evidence of lexicality effects in tasks that only require superficial processing would suggest that lexical representations are activated automatically and play some role, even though this information is not required by the task. However, results have been inconsistent across the few studies that have addressed this issue. In an LST, Ziegler and colleagues (1997, Experiment 1) found faster reaction times (RTs) for words compared to pseudowords, but no significant differences in N400 amplitude between the two types of stimuli.² In contrast, Chwilla and colleagues (1995) found that pseudowords elicited larger amplitude N400s in both an LDT and a superficial case discrimination task but the behavioral effect (i.e., faster responses for words compared to pseudowords) was only significant in the LDT. The latter pattern is consistent with a larger literature investigating semantic priming effects in form-level tasks; N400 amplitude tends to be a more sensitive and reliable measure of semantic priming than behavioral measures in tasks that do not require lexico-semantic processing (e.g., Heil, Rolke, & Pecchinenda, 2004; Küper & Heil, 2009). Here, we aim to clarify and extend this literature by making similar comparisons for orthographic neighborhood effects across tasks that require different amounts of lexico-semantic processing.

¹Important for both of the factors that might be driving the N400 lexicality effect, the pseudowords must appear similar to real words in order to elicit larger amplitude N400s (see, e.g., Bentin, Mouchetant-Rostaing, Giard, Echallier, & Pernier, 1999; Coch, 2015; Holcomb & Neville, 1990). Illegal nonwords elicit smaller amplitude N400s than real words or pseudowords, either because they can be more easily categorized as not being a word or because they have fewer orthographic neighbors on average and thus global lexico-semantic activity is lower.

²Note that there have also been reports of words and pseudowords eliciting similar amplitude N400s in tasks that require lexico-semantic processing, especially early in the epoch (e.g., Bentin et al., 1999; Coch, 2015).

1.2. Co-activation of Neighbors in Lexico-semantic Tasks

As mentioned, there is considerable evidence to suggest that the number of orthographic neighbors a word has influences behavioral responses, at least in tasks that encourage explicit lexico-semantic processing. For example, in the LDT, increasing the number of neighbors leads to faster and more accurate ‘word’ responses, but slower and less accurate ‘not a word’ responses (e.g., Carreiras et al., 1997; Grainger & Jacobs, 1996; Holcomb et al., 2002; Sears et al., 1995; van Heuven et al., 1998). According to the interactive-activation model (McClelland & Rumelhart, 1981), the neighbors of a target word should interfere with identification of that word via lateral inhibition and slow decisions. However, the MROM provides an extension of the interactive-activation framework to account for the facilitatory effects of orthographic neighborhood observed at the behavioral level. More specifically, the MROM posits that words from high-density (HD) orthographic neighborhoods produce high levels of global lexico-semantic activity that can trigger a ‘word’ response on some trials. In contrast, words from low-density (LD) orthographic neighborhoods (i.e., that have lower levels of global lexico-semantic activity) elicit slower responses because they rely more on identification of the specific word. If this identification process is too slow and is not completed before the time criterion is reached, then an incorrect ‘not a word’ response is given. HD pseudowords also produce high levels of global lexico-semantic activity, which leads them to be incorrectly identified as words more often than LD pseudowords. Thus, global lexico-semantic activity modulates the difficulty of lexical decision and drives opposite behavioral effects of neighborhood for words versus pseudowords in the LDT.

Given that behavioral responses do not readily lend themselves to distinguishing between the contributions of the different possible mechanisms driving neighborhood effects, it is important to examine the impact of this variable on ERPs. In a seminal study, Holcomb et al. (2002) reported that HD words and pseudowords elicited larger amplitude N400s than LD words and pseudowords in both a lexical decision task and a semantic categorization task. This effect has since been replicated and extended to a number of other tasks that require some degree of lexico-semantic processing, including language decision and reading sentences for grammaticality (e.g., Dufau, Grainger, Midgley, & Holcomb, 2015; Laszlo & Federmeier, 2011; Meade, Grainger, Midgley, Emmorey, & Holcomb, 2018; Meade, Midgley, et al., 2018; Molinaro, Conrad, Barber, & Carreiras, 2010; Müller, Duñabeitia, & Carreiras, 2010; Payne, Lee, & Federmeier, 2015; Vergara-Martínez & Swaab, 2012). The greater amplitude observed for HD words and pseudowords is typically explained in terms of the amount of co-activated information (see, e.g., Holcomb et al., 2002; Meade, Midgley, et al., 2018). More specifically, the N400 neighborhood effect for both words and pseudowords is attributed to an increase in global lexico-semantic processing due to the many co-activated neighbors. The fact that N400 neighborhood effects have been observed in tasks that do not require explicit lexical decisions appears to be in line with this account and the automatic, task-independent activation of orthographic neighbors. Finding the effects in a superficial letter search task that does not require any level of lexico-semantic processing would be further evidence of this.

It is nevertheless possible that difficulty in processing is also partially responsible for the N400 neighborhood effect. In interactive-activation models, an increase in the number of co-activated neighbors leads to stronger lateral inhibition on HD words (compared to LD words), which should make them more difficult to identify. Pseudowords do not have a lexical representation that can be directly influenced by lateral inhibition, but high levels of global lexico-semantic activity might make it more difficult to reject HD pseudowords compared to LD pseudowords in the LDT. In other words, the difficulty of processing account predicts larger N400 amplitudes for HD words and pseudowords compared to their LD counterparts, but also makes it possible for the neighborhood effect for pseudowords to show a different pattern from the effects seen for words. In line with this reasoning, there is preliminary ERP evidence to suggest that the time course of neighbor co-activation may differ for words versus pseudowords. Braun and colleagues (2006) used global lexical activity (based on MROM simulations) instead of neighborhood density as the independent variable in their LDT. They found an early lexicality effect (300-390 ms), which they associate with word identification processes and the time point at which 'word' decisions are made. In the later N400 window (450-550 ms), they found an effect of global lexical activity for pseudowords, such that pseudowords with higher levels of global lexical activity produced larger amplitude N400s. The authors suggest that this later peak is related to the temporal deadline for 'not a word' decisions and that such decisions are more difficult when global lexical activity is high. In contrast, there was no effect of global lexical activity for words within this window, perhaps because 'word' decisions had already been made on the basis of word identification. Consistent with these results, we recently reported N400 orthographic neighborhood effects for both word and pseudoword targets in a masked priming LDT, but found that the effect onset earlier for words than for pseudowords (Meade, Grainger, et al., 2018). Together, the results across these two studies suggest that the mechanisms driving N400 neighborhood effects may differ for words and pseudowords in lexical tasks, consistent with the difficulty of processing account of N400 amplitude. The extent to which neighbors are co-activated in the form-level letter search task may also differ as a function of how the decisions are made for these two types of stimuli.

1.3. The Present Study

The present study builds on the results presented by Braun et al. (2006) and Meade, Grainger et al. (2018) to examine differences in neighborhood effects for words versus pseudowords, this time exploring these differences using two tasks that require different amounts of lexico-semantic processing. We used both behavioral and ERP measures to compare the effects of orthographic neighborhood on processing of the same words and pseudowords in a lexical decision task and a letter search task. We expect our task manipulation to provide additional leverage with respect to revealing the mechanisms that drive N400 effects of neighborhood with words and pseudowords, as well as the automatic versus task-dependent nature of neighbor co-activation. More precisely, if neighborhood effects seen in the modulation of N400 amplitude are driven by differences in the amount of neural activity caused by neighbor co-activation (i.e., global lexico-semantic activity), and this co-activation is automatic and task-independent, then we should observe similar patterns of N400 neighborhood effects for words and pseudowords across both tasks. On the other hand, if the N400 neighborhood effect seen with word targets is partly driven by differences

in word identification difficulty caused by lateral inhibition, then we should see differences in N400 neighborhood effects for words compared to pseudowords in both tasks. This could be reflected in a difference in the time course and/or automaticity of the two neighborhood effects. Furthermore, the N400 neighborhood effect seen with pseudoword targets could either be driven by automatic co-activation of neighbors (i.e., global lexico-semantic activity) or by differences in task-specific processing difficulty. The first possibility predicts that N400 neighborhood effects for pseudowords should be similar across tasks. The second possibility predicts that the effects for pseudowords should be greatest in the LDT, where an increase in global lexical activity makes it harder to reject pseudoword targets. Overall, comparing the effects of lexical status and orthographic neighborhood between the two tasks will lend insight into the extent to which lexical access and co-activation of neighbors, respectively, differ as a function of task demands.

2. Method

2.1. Participants

Participants in the LDT group included 28 native English speakers (25 female; average age 21.6 years, *SD* 2.9 years). A separate group of 28 native English speakers (24 female; average age 21.6 years, *SD* 3.0 years) participated in the LST. None of the participants were fluent in any other language nor were they exposed to another language before the age of six. By self report, all participants were right-handed, had normal or corrected-to-normal vision, and had no history of neurological dysfunction or language or reading disorders. They were volunteers who received course credit or monetary compensation for their time. Six additional participants were excluded from the LDT group due to high artifact rejection rates ($> 15\%$ of trials; $N=4$) or low accuracy in the task ($< 50\%$ accuracy in any of the conditions; $N=2$). Four participants were excluded from the LST group due to high artifact rejection rates. Informed consent was obtained from all participants in accordance with the local institutional review board.

2.2. Stimuli

The stimuli consisted of 80 English nouns and 80 pseudowords from the ARC Nonword Database (Rastle, Harrington, & Coltheart, 2002). These same items were used in the learning study reported by Meade, Midgley, et al. (2018). Half of the stimuli belonged to a LD neighborhood and the other half belonged to a HD neighborhood. Neighborhood was defined using OLD20 (Yarkoni, Balota, & Yap, 2008), the average Levenshtein distance between the target word and the 20 words that it most closely resembled from among all words between three and eight letters in length in the English Lexicon Project (Balota et al., 2007). LD pseudowords had a significantly larger OLD20 than HD pseudowords, $t(78) = 11.22$, $p < .001$. Similarly, LD words had a significantly larger OLD20 than HD words, $t(78) = 10.51$, $p < .001$. Critically, however, there were no significant differences in neighborhood density between the two LD conditions, $t(78) = 1.38$, $p = .17$, the two HD conditions, $t(78) = .20$, $p = .84$, or the word and pseudoword lists overall, $t(158) = .85$, $p = .40$. A similar pattern emerged using Coltheart's *N* as the measure of neighborhood density (see Table 1). Other nuisance variables known to affect N400 amplitude, including constrained and unconstrained unigram and bigram frequencies, were controlled between lists of HD and LD

words and pseudowords using metrics extracted from the MCWord database (Medler & Binder, 2005), all $ps > .14$ (see Table 1). CELEX frequency (Medler & Binder, 2005) and concreteness (Brysbaert, Warriner, & Kuperman, 2014) were also controlled between lists of HD and LD words, both $ps > .20$. Half of the stimuli in each condition were 4 letters long and half of them were 5 letters long. None of the stimuli were neighbors with other items included in the paradigm.

2.3. Procedure

Stimuli were presented in lowercase Arial font such that the widest stimulus subtended a horizontal visual angle of 2 degrees. Each trial began with a 1500 ms purple fixation cross during which participants were asked to blink, followed by a 900 ms white fixation and a 500 ms blank screen. The word or pseudoword then appeared on the screen for 300 ms. After stimulus offset, the screen was blank again until the subsequent trial began 700 ms after the response. Stimuli were presented in one of two possible pseudorandom orders; half of the participants in each group saw each list. No more than three consecutive trials came from the same lexical category or the same neighborhood condition. Orthographic overlap between consecutive words was minimized and words that were semantically related (e.g., *crown* and *king*) were separated by at least 10 trials. The session began with a practice list containing 12 stimuli, six of which were real words. None of the items used in the practice were included in the experimental lists.

Participants in the LDT group were asked to indicate whether the stimulus was a real English word or a made-up word as quickly and accurately as possible. Participants in the LST group were informed that they would be seeing words and made-up words and asked to press one button if the designated target letter was in the stimulus and another button if it was not, as quickly and accurately as possible. The target letter for this group changed throughout the experiment such that there were a total of 18 different target letters, which applied to blocks ranging from 5 to 14 trials in length (average 8.9, SD 3.0). At the beginning of each block, the new letter was displayed on the screen (e.g., new letter: t) until participants pressed a button to advance and begin that letter block. The target letter was present in half of the words and half of the pseudowords. In both tasks, a response was required on every trial and response hand was counterbalanced across participants.

2.4. EEG Recording and Analysis

Participants were fitted with an elastic cap (Electro-Cap) with 29 electrodes. An electrode placed on the left mastoid was used as a reference during recording and for subsequent analyses. Recordings from an electrode located below the left eye was used in conjunction with electrodes on the forehead to identify blink artifacts and an electrode on the outer canthus of the right eye was used to identify artifacts due to horizontal eye movements. Using saline gel (Electro-Gel), mastoid and scalp electrode impedances were maintained below 2.5 k Ω and eye electrode impedances below 5 k Ω . EEG was amplified with SynAmpsRT amplifiers (Neuroscan-Compumedics) with a bandpass of DC to 100 Hz and was sampled continuously at 500 Hz.

ERPs were time-locked to the onset of each stimulus. Offline, separate ERPs for each condition were averaged for each subject at each electrode site over a 1,100 ms epoch, using a 100 ms pre-stimulus-onset baseline, and low-pass filtered at 15 Hz. Trials contaminated by eye movements or drift were excluded (average 6 trials, or 4%, per group), as were trials with incorrect responses. Analyses focused on the 15 representative electrode sites indicated in Figure 1. Based on visual inspection of the grand average waveforms, mean amplitude was calculated between 250 and 450 ms and between 450 and 650 ms. For each time window, repeated-measures ANOVAs with between-subject factor Group (LDT, LST) and within-subject factors Lexicality (Word, Pseudoword), Neighborhood (HD, LD), Laterality (Left, Midline, Right), and Anterior/Posterior (Prefrontal, Frontal, Central, Parietal, Occipital) were used. In planned followups, we used ANOVAs with the same within-subject factors for each group separately. Greenhouse-Geisser correction was applied for all within-subject measures with more than one numerator degrees of freedom. Partial eta squared (η_p^2) is reported as a measure of effect size.

3. Results

Behavioral and ERP results are summarized in Tables 2 and 3, respectively.

3.1. RTs

Correct RTs between 200 and 2000 ms were analyzed using by participant (*FI*) and by item (*F2*) ANOVAs. The LST group was faster than the LDT group overall, but the effect was only significant in the by item analysis, Group, $FI(1,54) = .87, p = .356, \eta_p^2 = .02$, $F2(1,156) = 32.42, p < .001, \eta_p^2 = .17$. Both the Lexicality and Neighborhood RT effects were significantly bigger for the LDT group than the LST group, Group $\times$ Lexicality, $FI(1,54) = 116.10, p < .001, \eta_p^2 = .68$, $F2(1,156) = 114.26, p < .001, \eta_p^2 = .42$, Group $\times$ Neighborhood, $FI(1,54) = 28.04, p < .001, \eta_p^2 = .34$, $F2(1,156) = 6.92, p = .001, \eta_p^2 = .04$. Moreover, the difference between groups in the size of the RT neighborhood effect was larger for pseudowords than for words, Group $\times$ Lexicality $\times$ Neighborhood, $FI(1,54) = 66.51, p < .001, \eta_p^2 = .55$, $F2(1,156) = 33.80, p < .001, \eta_p^2 = .18$.

Planned follow-up ANOVAs were conducted separately for each group. In the LDT group, a main effect of Lexicality indicated that words elicited faster responses than pseudowords, $FI(1,27) = 126.7, p < .001, \eta_p^2 = .82$, $F2(1,156) = 160.39, p < .001, \eta_p^2 = .51$. A main effect of Neighborhood indicated that LD items elicited faster responses than HD responses overall, $FI(1,27) = 40.73, p < .001, \eta_p^2 = .60$, $F2(1,156) = 6.16, p = .014, \eta_p^2 = .04$. However, the effect of Neighborhood differed for words versus pseudowords, Lexicality $\times$ Neighborhood, $FI(1,27) = 113.86, p < .001, \eta_p^2 = .81$, $F2(1,156) = 50.71, p < .001, \eta_p^2 = .24$, prompting follow-up analyses by Lexicality. Consistent with our predictions, the Neighborhood effect in the LDT group went in opposite directions for words versus pseudowords. Responses were faster for HD words than for LD words, Neighborhood, $FI(1,27) = 53.86, p < .001, \eta_p^2 = .67$, $F2(1,78) = 13.70, p < .001, \eta_p^2 = .15$, but slower for HD pseudowords than for LD pseudowords, Neighborhood, $FI(1,27) = 105.28, p < .001, \eta_p^2 = .80$, $F2(1,78) = 37.96, p < .001, \eta_p^2 = .33$. In the LST group, neither of the main effects nor the interaction thereof were significant, all $ps > .12$.

3.2. Accuracy

Accuracy analyses were identical to the RT analyses and yielded a very similar pattern of results. The LDT group was slightly less accurate overall than the LST group, Group, $F(1,54) = 6.40, p = .014, \eta_p^2 = .10, F(2,156) = 8.52, p = .004, \eta_p^2 = .05$. Both the Lexicality and Neighborhood effects were bigger for the LDT group than for the LST group, Group $\times$ Lexicality, $F(1,54) = 12.89, p = .001, \eta_p^2 = .19, F(2,156) = 13.01, p < .001, \eta_p^2 = .08$, Group $\times$ Neighborhood, $F(1,54) = 10.3, p = .002, \eta_p^2 = .16, F(2,156) = 6.64, p = .011, \eta_p^2 = .04$. Finally, a three-way Group $\times$ Lexicality $\times$ Neighborhood interaction indicated that the difference between the groups in the size of the neighborhood effect was larger for pseudowords than for words, $F(1,54) = 45.80, p < .001, \eta_p^2 = .46, F(2,156) = 32.12, p < .001, \eta_p^2 = .17$.

In planned follow-ups, there was a main effect of Lexicality for the LDT group indicating that their accuracy was higher for words than for pseudowords, $F(1,27) = 14.83, p = .001, \eta_p^2 = .35, F(2,156) = 16.79, p < .001, \eta_p^2 = .10$. A main effect of Neighborhood in this group also indicated that their accuracy was higher for LD items than for HD items, $F(1,27) = 15.84, p < .001, \eta_p^2 = .37, F(2,156) = 11.04, p = .001, \eta_p^2 = .07$. However, the effect of Neighborhood density went in opposite directions for words versus pseudowords, Lexicality $\times$ Neighborhood, $F(1,27) = 48.45, p < .001, \eta_p^2 = .64, F(2,156) = 37.18, p < .001, \eta_p^2 = .19$. In follow-up analyses by Lexicality, accuracy was higher for HD words than for LD words, but only significantly so in the by participant analyses, Neighborhood, $F(1,27) = 28.32, p < .001, \eta_p^2 = .51, F(2,178) = 3.54, p = .064, \eta_p^2 = .04$. Accuracy was significantly lower for HD pseudowords compared to LD pseudowords in both types of analyses, Neighborhood, $F(1,27) = 33.23, p < .001, \eta_p^2 = .55, F(2,178) = 48.70, p < .001, \eta_p^2 = .38$. In the LST group, there were no main effects of Neighborhood or Lexicality or interactions between the variables, all $ps > .25$.

3.3. ERPs

3.3.1. 250–450 ms.—Mean amplitude in this window was more negative for the LDT group (mean $-0.16 \mu\text{V}$) than the LST group (mean $3.35 \mu\text{V}$), especially over frontal and central sites, Group, $F(1,54) = 21.69, p < .001, \eta_p^2 = .29$, Group $\times$ Anterior/Posterior, $F(4,216) = 6.29, p < .001, \eta_p^2 = .10$. However, there were no interactions including Group and either Neighborhood or Lexicality within this window, all $ps > .16$.

In planned analyses including only the LDT group, pseudowords (mean $-0.84 \mu\text{V}$) elicited larger negativities than words (mean $.53 \mu\text{V}$), especially across frontal sites, Lexicality, $F(1,27) = 25.48, p < .001, \eta_p^2 = .48$, Lexicality $\times$ Anterior/Posterior, $F(4,108) = 3.71, p = .05, \eta_p^2 = .12$ (see Figure 2). The effect of Neighborhood, such that HD items (mean $-.51 \mu\text{V}$) elicited larger negativities than LD items (mean $0.20 \mu\text{V}$), was also strongest across frontal sites in this group, Neighborhood, $F(1,27) = 5.48, p = .027, \eta_p^2 = .17$, Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 4.2, p = .026, \eta_p^2 = .13$. However, the distribution of the Neighborhood effect differed for words and pseudowords, Lexicality $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 7.46, p = .002, \eta_p^2 = .22$. Follow-up analyses including only words indicated that the Neighborhood effect was strongest over anterior sites and reversed over posterior sites, Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 8.90, p < .001, \eta_p^2 = .25$.

(see Figures 3A and 4). In contrast, in follow-up analyses including only pseudowords, the effect of Neighborhood was only marginally significant within this window, $F(1,27) = 3.22$, $p = .083$, $\eta_p^2 = .11$ (see Figures 3B and 4).

In planned analyses including only the LST group, a main effect of Lexicality indicated that pseudowords (mean 2.91 μV) elicited larger negativities than words (mean 3.79 μV), $F(1,27) = 16.70$, $p < .001$, $\eta_p^2 = .38$ (see Figure 5). A main effect of Neighborhood indicated that HD items (mean 3.07 μV) elicited larger amplitude negativities than LD items (mean 3.63 μV) overall for this group, $F(1,27) = 5.78$, $p = .023$, $\eta_p^2 = .18$. However, a significant interaction between Lexicality and Neighborhood suggested that the neighborhood effect differed for words and pseudowords, $F(1,27) = 5.51$, $p > .026$, $\eta_p^2 = .17$, prompting follow-up analyses. HD words (mean 3.27 μV) elicited larger amplitude negativities than LD words (mean 4.31 μV), Neighborhood, $F(1,27) = 12.73$, $p = .001$, $\eta_p^2 = .32$ (see Figures 6A and 7). This effect of Neighborhood for words was strongest at anterior sites, Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 4.00$, $p = .037$, $\eta_p^2 = .13$. In contrast, there was no significant effect of Neighborhood for pseudowords for the LST group, all $ps > .72$ (see Figures 6B and 7).

3.3.2. 450–650 ms.—Mean amplitude continued to be more negative (i.e., less positive) for the LDT group (mean 2.69 μV) compared to the LST group (mean 5.28 μV) overall in this window, Group, $F(1,54) = 1.95$, $p = .007$, $\eta_p^2 = .13$. The amplitude difference between the groups was strongest at frontal and central sites, Group $\times$ Anterior/Posterior, $F(1,54) = 7.67$, $p = .001$, $\eta_p^2 = .12$. The Lexicality effect was larger in the LDT group than in the LST group, especially over left hemisphere sites, Group $\times$ Lexicality, $F(1,54) = 5.03$, $p = .029$, $\eta_p^2 = .08$, Group $\times$ Lexicality $\times$ Laterality, $F(1,54) = 7.11$, $p = .006$, $\eta_p^2 = .12$. The Neighborhood effect was also larger overall in the LDT group than in the LST group, Group $\times$ Neighborhood, $F(1,54) = 7.34$, $p = .009$, $\eta_p^2 = .12$. Importantly, the differences between groups in the size of the Neighborhood effect differed for words versus pseudowords, Group $\times$ Lexicality $\times$ Neighborhood, $F(1,54) = 5.13$, $p = .028$, $\eta_p^2 = .09$, Group $\times$ Lexicality $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,216) = 4.39$, $p = .021$, $\eta_p^2 = .08$ (see Figures 3 and 6). In follow-up analyses including only words, there were no significant interactions between Group and Neighborhood, all $ps > .16$. In contrast, the Neighborhood effect for pseudowords was clearly larger for the LDT group than for the LST group, especially across central and posterior sites, Group $\times$ Neighborhood, $F(1,54) = 13.02$, $p = .001$, $\eta_p^2 = .19$, Group $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,216) = 5.01$, $p = .013$, $\eta_p^2 = .08$. In sum, the lexicality effect and the neighborhood effect for pseudowords (but not words) were larger in the LDT group than in the LST group in this window.

In planned analyses including only the LDT group, pseudowords (mean 2.12 μV) elicited larger negativities than words (mean 3.25 μV) within this window (see Figure 2). The effect of Lexicality was strongest over left centro-posterior sites for this group, Lexicality $\times$ Anterior/Posterior, $F(4,108) = 5.86$, $p = .006$, $\eta_p^2 = .18$, Lexicality $\times$ Laterality, $F(2,54) = 13.28$, $p = .001$, $\eta_p^2 = .33$, Lexicality $\times$ Laterality $\times$ Anterior/Posterior, $F(8,216) = 3.07$, $p = .042$, $\eta_p^2 = .10$. HD items (mean 1.95 μV) also elicited larger negativities than LD items (mean 3.43 μV) in this group, Neighborhood, $F(1,27) = 25.4$, $p < .001$, $\eta_p^2 = .48$. However, the Neighborhood effect was stronger and had a different scalp distribution for pseudowords

as compared to words, Lexicality $\times$ Neighborhood, $F(1,27) = 9.13$, $p = .005$, $\eta_p^2 = .25$, Lexicality $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 9.41$, $p = .001$, $\eta_p^2 = .26$. In follow-up analyses, the Neighborhood effect for words just failed to reach significance, all $ps > .09$ (see Figures 3A and 4). However, there was a significant effect of Neighborhood for pseudowords in the LDT group, such that HD pseudowords (mean .90 μV) elicited larger amplitude negativities than LD pseudowords (mean 3.34 μV), $F(1,27) = 46.92$, $p < .001$, $\eta_p^2 = .63$ (see Figures 3B and 4).³ The effect of Neighborhood on pseudoword processing was strongest over centro-posterior sites, Neighborhood $\times$ Anterior/Posterior, $F(4,108) = 9.95$, $p = .001$, $\eta_p^2 = .27$.

In contrast, in planned analyses including only the LST group neither the main effect of Lexicality, $F(1,27) = 0.03$, $p = .870$, $\eta_p^2 = 0.001$ (see Figure 5), nor the main effect of Neighborhood, $F(1,27) = 1.89$, $p = .180$, $\eta_p^2 = .07$ (see Figures 6 and 7), reached significance. There were also no significant interactions involving these two variables of interest for this group, all $ps > .12$.

4. Discussion

In order to better characterize N400 effects of neighborhood and evaluate whether coactivation of orthographic neighbors proceeds automatically or is modulated by task demands, we compared the effects of neighborhood and lexicality in an LDT and an LST. The predicted behavioral effects of lexicality and neighborhood were present in the LDT, but not in the LST. Task demands also affected ERP neighborhood effects, but only for pseudowords. Whereas the effect of neighborhood for words was largely constrained to the earlier N400 window and was similar across tasks, the N400 effect of neighborhood for pseudowords occurred later and was only observed in the LDT group. Similarly, the lexicality effect was automatic and comparable across groups within the earlier N400 window, but it only continued into the later N400 window for the LDT group. A comprehensive interpretation of these data must account for differences in the timing (i.e., earlier for words than for pseudowords in the LDT) and automaticity (i.e., more automatic for words than for pseudowords) of the N400 effects of neighborhood. In what follows, we outline how the difficulty of processing account of N400 amplitude lends itself to these nuanced differences.

Starting with the behavioral results, we found the standard lexicality and neighborhood effects on RTs and accuracy in the LDT, but no significant differences in the LST. This pattern is consistent with the notion that behavioral effects are particularly sensitive to task demands. More specifically, these results support the MROM in suggesting that behavioral effects of neighborhood in the LDT are intimately tied to the demands of that particular task (Grainger & Jacobs, 1996, p. 557) and mirror previous findings in suggesting that behavioral effects can disappear when the response criteria do not rely on lexico-semantic processing

³This effect could be due to an apparent shift in the latency of the late positivity that follows the N400. The P300, which is associated with decision making, mirrors RTs in this task (see also, e.g., Kutas, McCarthy, & Donchin, 1977) and appears to peak earlier for LD pseudo words than for HD pseudo words. To eliminate this possibility, we conducted the same analysis on a subset of trials such that the RTs for HD (mean 781 ms, SD 157 ms) and LD (mean 780 ms, SD 157 ms) pseudowords were equated for each participant, $F(1,27) = 0.89$, $p = .35$, $\eta_p^2 = .03$. The ERP effect of Neighborhood within this window remained significant, $F(1,27) = 16.46$, $p < .001$, $\eta_p^2 = .38$.

(e.g., Chwilla et al., 1995; Grainger & Jacobs, 1994, 2005). One caveat to interpreting these behavioral results is that responses were slower (in analyses by items) and less accurate overall in the LDT group, potentially reflecting the increased difficulty of that task. Another caveat is that the responses were not identical across tasks. Both tasks required a binary decision - participants were making a choice between two responses on every trial. However, there was a one-to-one correspondence between lexical status and response hand in the LDT that did not hold in the LST (i.e., the 'letter present' and 'letter absent' buttons were each used for half of the words and half of the pseudowords). Note that this potential confound is inherent to all binary tasks other than lexical decision and also applies to previous studies addressing similar questions (e.g., Chwilla et al., 1995). Moreover, although this difference in the mapping between lexical status and response might have contributed to the disappearance of the lexicality effect in the LST, the same reasoning cannot be used to explain the disappearance of the neighborhood effect.

Crucially, despite the absence of behavioral effects in the LST group, we found evidence in the ERPs to suggest that lexical status and neighborhood both influenced processing in that group. In fact, the sizes of the neighborhood effect for words and the lexicality effect within the early N400 window were statistically indistinguishable between the two tasks. We associate these task-independent effects in the early N400 window with lexical (i.e., word form) identification. Interference from orthographic neighbors makes the process of lexical identification more difficult for HD words compared to LD words (e.g., Grainger & Jacobs, 1996). Theoretically, the strength of the interference should vary as a function of the relative frequency of the word and its neighbors (see, e.g., Chen & Mirman, 2012; Grainger & Segui, 1990; McClelland & Rumelhart, 1981). We did not test this directly, but Vergara-Martínez and Swaab (2012) have reported stronger N400 neighborhood effects for low frequency words compared to high frequency words within a window (260-500 ms) that loosely corresponds to our early N400 window. An effect of neighbor frequency was also reported by Molinaro and colleagues (2010) toward the tail end of this window, but only in low constraint sentences (i.e., not when the word had strong contextual support). The present findings of similar N400 effects of neighborhood density for words across tasks further suggests that neighbors of words are co-activated and exert lateral inhibition automatically (i.e., independent of task demands). This result complements eye-tracking studies in which neighborhood density and frequency effects were found in more natural reading settings (e.g., Dirix, Cop, Drieghe, & Duyck, 2017; Perea & Pollatsek, 1998; Pollatsek, Perea, & Binder, 1999). Together, the patterns across these studies converge to suggest that this early N400 window encompasses automatic word identification and that the increase in N400 amplitude for HD words compared to LD words results from an increased number of co-activated neighbors inhibiting the target word and making it difficult to identify.

By definition, lexical identification cannot be completed for pseudowords because they do not correspond to any single lexical representation. As a result, attempting lexical identification for the pseudowords necessarily requires more effort than the analogous process for words, which contributes to the lexicality effect that we found within the early N400 window in both tasks. The absence of a lexical representation for the pseudowords also implies that lateral inhibition from neighbors cannot impede processing of pseudowords in the same way as it does for words, hence the absence of a neighborhood effect for the

pseudoword stimuli within this early window in both tasks. Note that this does not preclude co-activation of the neighbors of pseudowords. It simply asserts that if neighbors of pseudowords were co-activated, they did not strongly modulate the process of isolating a unique word for identification that characterized this early N400 window.

The early, automatic effects of lexicality and neighborhood for words during lexical identification were followed by a set of highly task-dependent processes. For one, the lexicality effect was prolonged in the LDT, but not in the LST. For another, the size of the neighborhood effect for pseudowords within this window was highly modulated by task, such that it was even stronger than the effect for words within the later N400 window in the LDT group, but virtually nonexistent in the LST group. The absence of a neighborhood effect for pseudowords in the LST is difficult to explain in terms of a lack of power given that the effect was observed in the LDT with the exact same stimuli and number of participants, and for the words in the early N400 window in both tasks. Rather, it seems to suggest that the post-lexical processes that dominated the later N400 window and were driving the pseudoword effect of neighborhood in the LDT were highly dependent on task demands. In the LST, neither lexical status nor global lexico-semantic activity (determined in large part by neighborhood density) were relevant for the task at hand, which limited their influence on processing during this later window. In contrast, following the assumption of the MROM that global lexical activity can be used to make a lexical decision, both lexical status and global lexico-semantic activity were directly relevant for the LDT group. Pseudowords continued to be effortfully processed by the LDT group within this window, which led to increased processing difficulty (i.e., a larger amplitude N400) for pseudowords relative to words. The decision to reject a pseudoword is slower and especially difficult in the presence of co-activated neighbors and high levels of global lexico-semantic activity, which led to larger amplitude N400s for HD pseudowords compared to LD pseudowords. That is, the sustained activation of pseudoword neighbors in the LDT group contributed to the late neighborhood effect for pseudowords and to the late lexicality effect, both of which had similar posterior distributions (see Figures 2 and 3B). In contrast, a lexical decision would have already been made by this point for most of the word stimuli (see also Braun et al., 2006), which should lead to suppression of stimulus-related activity.⁴ If this is true, then neighbors of word stimuli should no longer modulate task difficulty, explaining why they did not have a reliable effect on N400 amplitude in this window for the LDT group. In sum, words have already been identified, but the late neighborhood effect for pseudowords arises via sustained partial activation of lexical representations when this activity is useful for the task at hand.

It is less clear how the amount of global neural processing account of N400 amplitude could accommodate this full pattern of results. This account assumes that the mechanisms underlying neighborhood effects for words and pseudowords are identical, that both effects

⁴Note that the duration of the N400 neighborhood effect for words varies across studies. Although the effect persists into this later window and beyond in some studies (e.g., Holcomb et al., 2002), it does not in others (e.g., Braun et al., 2006; Vergara-Martínez & Swaab, 2012). One of the explanations provided by Vergara-Martínez and Swaab for the shorter duration of their neighborhood effect was the use of OLD20 instead of Coltheart's N as a measure of neighborhood density. Our manipulation of neighborhood was still significant using Coltheart's N (see Table 1), but the difference in N between conditions was considerably smaller than in the study reported by Holcomb et al. The same appears to be true of the stimuli used by Vergara-Martínez and Swaab. Thus, one possibility is that the use of OLD20 led to a weaker neighborhood manipulation and therefore a briefer influence of neighbors on processing.

are due to an increase in global lexico-semantic processing as more neighbors become co-activated. Such a framework is perhaps exemplified by the Parallel Distributed Processing (PDP) model proposed by Laszlo and Plaut (2012), where N400 is calculated as the global semantic activation and is assumed to behave similarly irrespective of lexical status. Characteristic of PDP models, this model does not include lexical representations. Without lexical representations, it is difficult to account for the clear differences in timing and automaticity that we observed between the neighborhood effects for words and pseudowords. Thus, the present results seem to provide evidence against the assumption that the language system “performs what appear to be indistinguishable computations on different input types, regardless of factors like lexicality...” (Laszlo & Plaut, 2012, p. 272). They highlight important differences in the nature of N400 effects of neighborhood for words and pseudowords that potentially challenge these types of models.

We cannot exclude the possibility that amount of global lexico-semantic processing also influences N400 amplitude. One motivation for including such a mechanism might be to explain why N400 effects of neighborhood have been observed with pseudoword stimuli in a semantic categorization task (e.g., Holcomb et al., 2002; Laszlo & Federmeier, 2011). Our difficulty of processing account could only explain this pattern if the number of task-related words (e.g., animal words) was correlated with the number of neighbors the pseudowords had in these studies. Pseudowords with many task-related words as neighbors might be more difficult to reject than those with fewer task-related neighbors and task-related words are more likely to be in the neighborhoods of HD pseudowords, which would contribute to the increase in N400 amplitude relative to LD pseudowords. That said, it seems unlikely that this factor alone would have a strong enough influence to drive the pseudoword neighborhood effects across previous semantic categorization tasks. A full explanation of the effect of neighborhood for pseudowords in the semantic categorization task deserves further empirical attention and may require appealing to an account of N400 amplitude that involves global lexico-semantic activity in some way. Our claim here is simply that the amount of global lexico-semantic activity cannot be the only factor that determines N400 amplitude; there appears to some contribution of task-related difficulty.

Finally, in addition to task-related difficulty, decision-related processes also likely influenced amplitude in the late N400 window. Indeed, this is reflected in the morphology of the waveforms, such that the tail end of the N400 overlaps with a late positivity that is characteristic of forced-choice paradigms. Visually, the peak latency of the P300 mirrors behavioral responses (Kutas et al., 1977; Polich, 2007), as it shifts in the LDT (e.g., earlier for LD pseudowords compared to HD pseudowords), but not the LST. As mentioned, the scalp distributions of both the lexicality effect and the neighborhood effects also seem to change across the two windows in the LDT group, with a more posterior locus in the later window that fits well within the P300 literature (see, e.g., Polich, 2007, for a review). It is therefore possible that we found a significant neighborhood effect for pseudowords in the LDT group, but not in the LST group, because of this shift in the peak latency of the P300. To evaluate this possibility, we conducted analyses on a subset of HD and LD pseudoword trials in the LDT that were equated for RTs (see Footnote 3). This comparison is more analogous to the LST analyses since that group did not show any differences in RTs between HD and LD pseudowords. The effect of neighborhood for pseudowords remained reliable in

the LDT group, but the interactions with Anterior/Posterior were no longer significant. Thus, although the shift in P300 latency that we observed in the LDT group might have modified the distribution of the pseudoword neighborhood effect in that group, it is unlikely that it was the sole contributor to that effect.

In conclusion, our comparison of N400 neighborhood effects in tasks that require different levels of lexico-semantic processing has informed our understanding of these effects. Whereas the early lexicality effect and neighborhood effect for words were automatic and impervious to the task manipulation, evidence of a later N400 lexicality effect and a neighborhood effect for pseudowords was only found in the LDT. These patterns highlight the complexity of the N400, which clearly reflects a multitude of processes that are partially superimposed in time. To account for these results, we have proposed that the early N400 window reflects more automatic lexical identification, which is made more difficult by lateral inhibition from co-activated neighbors. The later N400 window appears to be more characterized by task-related processing difficulty and decision processes. This dissociation highlights important differences in the mechanisms driving word and pseudoword neighborhood effects and fits best within a framework in which N400 neighborhood effects are predominantly determined by the difficulty of neural processing rather than the amount of neural activity. Future research involving a similar task manipulation but with other variables known to affect N400 amplitude will determine the extent to which this characterization of N400 amplitude can be generalized.

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References

- Andrews S (1997). The effect of orthographic similarity on lexical retrieval: Resolving neighborhood conflicts. *Psychonomic Bulletin & Review*, 4(4), 439–461. doi:10.3758/BF03214334
- Balota DA, & Chumbley JI (1984). Are lexical decisions a good measure of lexical access? The role of word frequency in the neglected decision stage. *Journal of Experimental Psychology: Human Perception and Performance*, 10(3), 340–357. doi:10.1037//0096-1523.10.3.340 [PubMed: 6242411]
- Balota DA, Yap MJ, Cortese MJ, Hutchinson KA, Kessler B, Loftis B, ... Treiman R (2007). The English Lexicon Project. *Behavior Research Methods*, 39(3), 445–459. doi:10.3758/BF03193014 [PubMed: 17958156]
- Bentin S, Mouchetant-Rostaing Y, Giard M-H, Echallier JF, & Pernier J (1999). ERP manifestations of processing printed words at different psycholinguistic levels: Time course and scalp distribution. *Journal of Cognitive Neuroscience*, 11(3), 235–260. doi:10.1162/089892999563373 [PubMed: 10402254]
- Braun M, Jacobs AM, Hahne A, Ricker B, Hofmann M, & Hutzler F (2006). Modelgenerated lexical activity predicts graded ERP amplitudes in lexical decision. *Brain Research*, 1073–1074, 431–439. doi:10.1016/j.brainres.2005.12.078
- Brysbaert M, Warriner AB, & Kuperman V (2014). Concreteness rating for 40 thousand generally known English word lemmas. *Behavior Research Methods*, 46(3), 904–911. doi:10.3758/s13428-013-0403-5 [PubMed: 24142837]

- Carreiras M, Perea M, & Grainger J (1997). Effects of orthographic neighborhood in visual word recognition: Cross-task comparisons. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23(4), 857–871. doi:10.1037/0278-7393.23.4.857
- Chen Q, & Mirman D (2012). Competition and cooperation among similar representations: Toward a unified account of facilitative and inhibitory effects of lexical neighbors. *Psychological Review*, 119(2), 417–430. doi:10.1037/a0027175 [PubMed: 22352357]
- Chwilla DJ, Brown CM, & Hagoort P (1995). The N400 as a function of the level of processing. *Psychophysiology*, 32(3), 274–285. doi: 10.1111/j.1469-8986.1995.tb02956.x [PubMed: 7784536]
- Coch D (2015). The N400 and the fourth grade shift. *Developmental Science*, 18(2), 254–269. doi: 10.1111/desc.12212 [PubMed: 25041502]
- Coltheart M, Rastle K, Perry C, Langdon R, & Ziegler J (2001). DRC: A dual route cascaded model of visual word recognition and reading aloud. *Psychological Review*, 108(1), 204–256. doi: 10.1037/0033-295X.108.1.204 [PubMed: 11212628]
- Dirix N, Cop U, Drieghe D, & Duyck W (2017). Cross-lingual neighborhood effects in lexical decision and natural reading. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 43(6), 887–915. doi:10.1037/xlm0000352
- Dufau S, Grainger J, Midgley K, & Holcomb PJ (2015). A thousand words are worth a picture: Snapshots of printed-word processing in an event-related potential megastudy. *Psychological Science*, 26(12), 1887–1897. doi:10.1177/0956797615603934 [PubMed: 26525074]
- Dufau S, Grainger J, & Ziegler J (2012). How to say “no” to a nonword: A leaky competing accumulator model of lexical decision. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 35(4), 1117–1128. doi:10.1037/a0026948
- Fiebach CJ, Ricker B, Friederici AD, & Jacobs AM (2007). Inhibition and facilitation in visual word recognition: Prefrontal contribution to the orthographic neighborhood size effect. *Neuroimage*, 36(3), 901–911. doi: 10.1016/j.neuroimage.2007.04.004 [PubMed: 17498973]
- Grainger J, & Jacobs AM (1994). A dual read-out model of word context effects in letter perception: Further investigations of the word superiority effect. *Journal of Experimental Psychology: Human Perception and Performance*, 20(6), 1158–1176.
- Grainger J, & Jacobs AM (1996). Orthographic processing in visual word recognition: A multiple read-out model. *Psychological Review*, 103(3), 518–565. doi:10.1037/0033-295X.103.3.518 [PubMed: 8759046]
- Grainger J, & Jacobs AM (2005). Pseudoword context effects on letter perception: The role of word misperception. *European Journal of Cognitive Psychology*, 17(3), 289–318. doi: 10.1080/9541440440000131
- Grainger J, & Segui J (1990). Neighborhood frequency effects in visual word recognition: A comparison of lexical decision and masked identification latencies. *Perception & Psychophysics*, 47(2), 191–198. doi:10.3758/BF03205983 [PubMed: 2304817]
- Heil M, Rolke B, & Pecchinenda A (2004). Automatic semantic activation is no myth: Semantic context effects on the N400 in the letter-search task in the absence of response time effects. *Psychological Science*, 15(12), 852–857. doi: 10.1111/j.0956-7976.2004.00766.x
- Holcomb PJ (1988). Automatic and attentional processing: An event-related brain potential analysis of semantic priming. *Brain and Language*, 35(1), 66–85. doi: 10.1016/0093-934x(88)90101-0 [PubMed: 3179703]
- Holcomb PJ, Grainger J, & O’Rourke T (2002). An electrophysiological study of the effects of orthographic neighborhood size on printed word perception. *Journal of Cognitive Neuroscience*, 14(6), 938–950. doi: 10.1162/089892902760191153 [PubMed: 12191460]
- Holcomb PJ, & Neville HJ (1990). Auditory and visual semantic priming in lexical decision: A comparison using event-related brain potentials. *Language and Cognitive Processes*, 5(4), 281–312. doi: 10.1080/01690969008407065
- Kiefer M, & Brendel D (2006). Attentional modulation of unconscious “automatic” processes: Evidence from event-related potentials in a masked priming paradigm. *Journal of Cognitive Neuroscience*, 18(2), 184–198. doi: 10.1162/089892906775783688

- Kounios J, & Holcomb PJ (1994). Concreteness effects in semantic processing: ERP evidence supporting dual-coding theory. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 20(4), 804–823. doi:10.1037/0278-7393.20.4.804
- Küper K, & Heil M (2009). Electrophysiology reveals semantic priming at a short SOA irrespective of depth of prime processing. *Neuroscience Letters*, 453(2), 107–111. doi:10.1016/j.neulet.2009.02.013 [PubMed: 19356603]
- Kutas M, & Hillyard SA (1980). Reading senseless sentences: Brain potentials reflect semantic incongruity. *Science*, 207, 203–205. doi: 10.1126/science.7350657 [PubMed: 7350657]
- Kutas M, & Hillyard SA (1989). An electrophysiological probe of incidental semantic association. *Journal of Cognitive Neuroscience*, 7(1), 38–49. doi:10.1162/jocn.1989.1.1.38
- Kutas M, McCarthy G, & Donchin E (1977). Augmenting mental chronometry: The P300 as a measure of stimulus evaluation time. *Science*, 197(4305), 792–795. doi: 10.1126/science.887923
- Laszlo S, & Federmeier KD (2011). The N400 as a snapshot of interactive processing: Evidence from regression analyses of orthographic neighbor and lexical associate effects. *Psychophysiology*, 48(2), 176–186. doi:10.1111/j.1469-8986.2010.01058.x [PubMed: 20624252]
- Laszlo S, & Plaut DC (2012). A neurally plausible Parallel Distributed Processing model of event-related potential word reading data. *Brain and Language*, 120(3), 271–281. doi:10.1016/j.bandl.2011.09.001 [PubMed: 21945392]
- McClelland JL, & Rumelhart DE (1981). An interactive activation model of context effects in letter perception: I. An account of basic findings. *Psychological Review*, 55(5), 375–407. doi: 10.1037/0033-295X.88.5.375
- Meade G, Grainger J, Midgley KJ, Emmorey K, & Holcomb PJ (2018). From sublexical facilitation to lexical competition: ERP effects of masked neighbor priming. *Brain Research*, 1685, 29–41. doi:10.1016/j.brainres.2018.01.029 [PubMed: 29407530]
- Meade G, Midgley KJ, Dijkstra T, & Holcomb PJ (2018). Cross-language neighborhood effects in learners indicative of an integrated lexicon. *Journal of Cognitive Neuroscience*, 30(1), 70–85. doi: 10.1162/jocn_a_01184 [PubMed: 28880767]
- Medler DA, & Binder JR (2005). MCWord: An on-line orthographic database of the English language. Retrieved from <http://www.neuro.mcgill.edu/mcword>
- Molinero N, Conrad M, Barber HA, & Carreiras M (2010). On the functional nature of the N400: Contrasting effects related to visual word recognition and contextual semantic integration. *Cognitive Neuroscience*, 7(1), 1–7. doi:10.1080/17588920903373952
- Müller O, Duñabeitia JA, & Carreiras M (2010). Orthographic and associative neighborhood density effects: What is shared, what is different? *Psychophysiology*, 47(3), 455–466. doi: 10.1111/j.1469-8986.2009.00960.X [PubMed: 20102534]
- Payne BR, Lee C-L, & Federmeier KD (2015). Revisiting the incremental effects of context on word processing: Evidence from single-word event-related brain potentials. *Psychophysiology*, 52, 1456–1469. doi: 10.1111/psyp.12515 [PubMed: 26311477]
- Perea M, & Pollatsek A (1998). The effects of neighborhood frequency in reading and lexical decision. *Journal of Experimental Psychology: Human Perception and Performance*, 24(3), 767–779. doi: 10.1037/0096-1523.24.3.767 [PubMed: 9627415]
- Polich J (2007). Updating P300: An integrative theory of P3a and P3b. *Clinical Neurophysiology*, 118(10), 2128–2148. doi:10.1016/j.clinph.2007.04.019
- Pollatsek A, Perea M, & Binder K (1999). The effects of “neighborhood size” in reading and lexical decision. *Journal of Experimental Psychology: Human Perception and Performance*, 25(4), 1142–1158. [PubMed: 10464947]
- Rastle K, Harrington J, & Coltheart M (2002). 358,534 nonwords: The ARC Nonword Database. *The Quarterly Journal of Experimental Psychology Section A: Human Experimental Psychology*, 55(4), 1339–1362. doi: 10.1080/02724980244000099 [PubMed: 12420998]
- Rugg MD (1990). Event-related brain potentials dissociate repetition effects of high- and low-frequency words. *Memory & Cognition*, 18(4), 367–379. doi: 10.3758/BF03197126
- Sears CR, Hino Y, & Lupker SJ (1995). Neighborhood size and neighborhood frequency effects in word recognition. *Journal of Experimental Psychology: Human Perception and Performance*, 21(4), 876–900. doi:10.1037/0096-1523.21.4.876

- van Heuven WJB, Dijkstra T, & Grainger J (1998). Orthographic neighborhood effects in bilingual word recognition. *Journal of Memory and Language*, 59(3), 458–483. doi: 10.1006/jmla.1998.2584
- Vergara-Martínez M, & Swaab T (2012). Orthographic neighborhood effects as a function of word frequency: An event-related potential study. *Psychophysiology*, 49(9), 1277–1289. doi: 10.1111/j.1469-8986.2012.01410.x [PubMed: 22803612]
- Yarkoni T, Balota DA, & Yap MJ (2008). Moving beyond Coltheart's *N*: A new measure of orthographic similarity. *Psychonomic Bulletin & Review*, 75(5), 971–979. doi:10.3758/PBR.15.5.971
- Ziegler J, Besson M, Jacobs AM, Nazir TA, & Carr TH (1997). Word, pseudoword, and nonword processing: A multitask comparison using event-related brain potentials. *Journal of Cognitive Neuroscience*, 9(6), 758–775. [PubMed: 23964598]

Highlights:

- Compared N400 effects of neighborhood and lexicality across two tasks
- N400 neighborhood effect for pseudowords in lexical decision but not letter search
- N400 neighborhood effect earlier for words than for pseudowords in lexical decision
- Early N400 reflects automatic word form identification
- Later N400 reflects task-dependent influence of co-activated (pseudoword) neighbors

Figure 1. Electrode Montage.
Sites highlighted in grey were included in analyses.

Figure 2. LDT Group: Lexicality Effect.

Grand average ERP waveforms elicited by words (red) and pseudowords (black) in the LDT group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V. The scalp voltage maps show the distribution of the lexicality effect (pseudowords-words) in each of the time windows that were analyzed.

Figure 3. LDT Group: Neighborhood Effects.

Grand average ERP waveforms showing the effect of neighborhood density for words (A) and pseudowords (B) in the LDT group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V. Scalp voltage maps show the distributions of the two neighborhood effects (high-low) in the time windows that were analyzed.

Figure 4. LDT Group: Neighborhood Difference Waves.

Difference waves showing the time course of the effects of neighborhood density (high-low) for words (red) and pseudowords (black) in the LDT group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V.

Figure 5. LST Group: Lexicality Effect.

Grand average ERP waveforms elicited by words (red) and pseudowords (black) in the LST group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μV . The scalp voltage maps show the distribution of the lexicality effect (pseudowords-words) in each of the time windows that were analyzed.

Figure 6. LST Group: Neighborhood Effects.

Grand average ERP waveforms showing the effect of neighborhood density for words (A) and pseudowords (B) in the LST group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μV . Scalp voltage maps show the distributions of the two neighborhood effects (high-low) in the time windows that were analyzed.

Figure 7. LST Group: Neighborhood Difference Waves.

Difference waves showing the time course of the effects of neighborhood density (high-low) for words (red) and pseudowords (black) in the LST group. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V.

Table 1.

Stimulus Characteristics [mean (SD)]

	OLD 20	N	Constrained Unigram Frequency	Unconstrained Unigram Frequency	Constrained Bigram Frequency	Unconstrained Bigram Frequency	Frequency	Concreteness
HD Words	1.57 (.12)	7.40 (2.54)	9,297 (2,822)	227,330 (54,827)	839 (476)	15,241 (8,999)	38.45 (54.74)	4.57 (.47)
LD Words	2.09 (.29)	0.75 (.90)	8,489 (3,919)	235,093 (62,262)	756 (1,002)	15,768 (11,691)	36.56 (71.08)	4.40 (.73)
HD PWs	1.57 (.15)	8.05 (3.27)	10,171 (4,270)	235,410 (59,714)	1,036 (658)	17,640 (12,760)	----	----
LD PWs	2.18 (.30)	0.65 (.89)	9,166 (3,129)	219,063 (51,789)	864 (829)	14,017 (9,042)	----	----

HD = High-density orthographic neighborhood; LD = Low-density orthographic neighborhood; PWs = Pseudowords

Table 2.

Summary of behavioral results [Mean (SD)]

		Lexical Decision Group		Letter Search Group	
		RT (ms)	Accuracy (%)	RT (ms)	Accuracy (%)
Word	HD	624 (96)	98.3 (1.7)	677 (123)	95.4 (4.0)
	LD	665 (114)	94.5 (4.0)	686 (145)	96.3 (2.6)
Pseudoword	HD	827 (172)	84.1 (13.6)	675 (134)	95.7 (3.2)
	LD	733 (138)	97.3 (2.8)	682 (131)	95.9 (3.0)

Table 3.

Summary of ERP results.

		250-450 ms			450-650 ms		
		LDT	LST	Group	LDT	LST	Group
Lexicality		< .001	< .001		.015		.029
	× Anterior/Posterior	.050			.006		
	× Laterality				.001		.006
	× A/P × Laterality				.042		
Neighborhood		.027	.023		< .001		.009
	× Anterior/Posterior	.026					
	× Laterality						
	× A/P × Laterality						
Lexicality × Neighborhood			.026		.005		.028
	× Anterior/Posterior	.002			.001		.021
	× Laterality						
	× A/P × Laterality						

Significant tests are indicated by *p*-values. Non-significant tests with *p*-values greater than .05 are indicated by grey shading.