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From sublexical facilitation to lexical competition: ERP effects of masked neighbor priming

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Abstract

Interactive-activation models posit that visual word recognition involves co-activation of orthographic neighbors (e.g., *note*, *node*) and competition among them via lateral inhibitory connections. Behavioral evidence of this lexical competition comes from masked priming paradigms, in which target words elicit slower responses when preceded by a neighbor (e.g., *note-NODE*) than when preceded by an unrelated word (e.g., *kiss-NODE*). In the present study, we used ERPs to investigate how masked high frequency word primes influence processing of low frequency word and pseudoword targets. Word targets preceded by a neighbor prime elicited larger negativities within the N400 window than those preceded by an unrelated prime (i.e., reversed priming) across bilateral anterior sites, which we call a reversed N400 priming effect. Consistent with the behavioral literature, the size of the reversed N400 priming effect was larger for targets from high-density orthographic neighborhoods and for participants who scored higher on a behavioral measure of spelling recognition. Indeed, the opposite effect (i.e., smaller negativities within the N400 window for word targets preceded by a neighbor) was observed for words from low-density orthographic neighborhoods and for less-skilled spellers. Traditional priming was also observed within the N250 window for word targets and within both the N250 or N400 windows for pseudoword targets. The specificity of the reversed N400 priming effect to situations in which both words have precise lexical representations suggests that this reversed N400 effect, like the behavioral interference effect, indexes lexical competition during visual word recognition.

Keywords

interactive-activation models; lexical competition; orthographic neighbors; N400; masked priming

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1. Introduction

Interactive-activation (IA) models of visual word recognition posit co-activation of, and lateral inhibition among, neighboring word forms (e.g., *note*, *node*, *nose*; e.g., Davis, 2003; Grainger & Holcomb, 2009; Jacobs & Grainger, 1992; McClelland & Rumelhart, 1981). In these models, activation initially spreads from sublexical units to a number of candidate lexical representations, which inhibit one another. Empirical evidence for this lexical inhibition comes from behavioral investigations of masked neighbor priming. Target words preceded by neighbor word primes elicit slower lexical decision responses than those preceded by unrelated word primes (e.g., Andrews & Hersch, 2010; Davis & Lupker, 2006; Jacobs & Grainger, 1992; Segui & Grainger, 1990). Because this neighbor interference effect is specific to pairs of real words (i.e., is not observed when either the prime or target is a pseudoword; e.g., Davis & Lupker, 2006; Forster & Davis, 1991; Forster & Veres, 1998; van Heuven, Dijkstra, Grainger, & Schriefers, 2001), the difference is commonly interpreted as an index of competition between the lexical representations of the prime and target. Further, the size of the interference effect is sensitive to the relative frequency of the two words (e.g., Davis & Lupker, 2006; Segui & Grainger, 1990), their neighborhood structure (e.g., Andrews & Hersch, 2010; Davis & Lupker, 2006; Forster, Davis, Schoknecht, & Carter, 1987; Jacobs & Grainger, 1992; van Heuven et al., 2001), and participants' spelling ability (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012), strengthening the argument that the neighbor interference effect reflects lexical level dynamics. In the present study, we used event-related potentials (ERPs) to further investigate how neighborhood structure and participants' spelling and reading comprehension abilities influence lexical competition among neighbors in a masked priming paradigm.

One of the first variables found to modulate the size of the interference effect in behavioral investigations of masked neighbor priming was the relative frequency of the primes and targets (e.g., Davis & Lupker, 2006; Segui & Grainger, 1990). Segui and Grainger (1990) observed that when the frequency of the target was lower than that of the prime, responses to neighboring pairs of French words were slower than responses to unrelated word pairs. In contrast, when the frequency of the target was higher than that of the prime, there was a non-significant facilitation effect for neighboring word pairs compared to unrelated word pairs. Consistent with these results, relative prime-target frequency is the most important predictor of the size of interference effects in IA model simulations (Davis, 2003; Jacobs & Grainger, 1992). In these models, frequency modulates the resting level of activation of a lexical item; the combination of a high level of baseline activation and recent presentation makes high frequency primes particularly strong competitors during processing of neighboring targets. Thus, relative frequency plays a key role in determining the size of the behavioral interference effect, consistent with the lexical competition posited in IA models.

Using ERPs, Massol and colleagues (2010) aimed to capture how this interference between high frequency primes and lower frequency targets develops over time. The bimodal interactive-activation model (e.g., Grainger & Holcomb, 2009) associates the N250 component of the ERP waveform with the stabilization of activity in sublexical units and their mapping onto whole-word orthographic form representations, and the N400 component

with a similar transition from the level of whole-word orthographic form representations to word-level semantics. Thus, Massol and colleagues reasoned that lexical competition between neighboring word pairs should onset between the N250 and the N400 and result in a larger amplitude N400 (i.e., more effortful processing) for targets in neighbor pairs relative to those in unrelated pairs. They found that targets preceded by neighbor primes elicited smaller amplitude N250s than those preceded by unrelated primes, but did not find any significant differences as a function of prime within the N400 window. The N250 effect was interpreted as reflecting facilitated sublexical processing resulting from the large number of overlapping letters between neighbors (see Massol, Midgley, Holcomb, & Grainger, 2011, for a similar result with pseudoword targets). The absence of an N400 effect was explained by assuming that lexical competition had counteracted the early sublexical facilitation, but was not strong enough to produce the expected effect in the opposite direction. However, null effects are generally difficult to interpret, and the lack of sensitivity to neighbor primes in the N400 window does not provide clear ERP evidence of lexical competition between neighbors.

Recent behavioral work that further characterizes the interference effect and the factors to which it is sensitive could potentially be used to explain why Massol et al. (2010) failed to find a strong N400 competition effect. In particular, Andrews and Hersch (2010) have reported that neighborhood density (N) and the participants' spelling ability modulate the presence and size of behavioral interference effects. They found an interference effect (i.e., slower RTs for neighboring word pairs than for unrelated word pairs) that was specific to skilled spellers and, in their first experiment, to high-N word pairs (cf. Davis & Lupker, 2006). Regression analyses demonstrated that spelling scores were significant predictors of the size of the behavioral interference effect, and that the variance explained by spelling ability could not be accounted for any of the other measures of individual differences that were included in the study (e.g., reading comprehension, reading speed, vocabulary size). Importantly, this relationship between spelling ability and the interference effect was only observed when the target was a high-N word (i.e., under maximal competition conditions). Using a principle components analysis, Andrews and Lo (2012) extended these results to show that the size of the interference effect for targets preceded by transposed-letter primes (e.g., *calm-CLAM*) is also modulated by spelling ability. Indeed, skilled spellers showed even larger interference effects for transposed-letter pairs than they did for neighbor pairs (relative to the respective unrelated conditions). The contribution of spelling ability went above and beyond a separate principle component that captured general written language proficiency (see also, Veldre & Andrews, 2015). The authors interpreted these patterns as support for the lexical quality hypothesis (Perfetti, 1992, 2007), which states that having precise whole-word representations increases the efficiency of visual word processing. Skilled spellers are thought to have precise lexical representations, which enables them to quickly select the prime word and inhibit its neighbors, thereby increasing the interference incurred by neighboring and transposed-letter targets. In contrast, lower levels of spelling skill are associated with less complete lexical representations and less efficient selection of the prime. Indeed, less-skilled spellers showed facilitation rather than interference, suggesting that neighbor and transposed-letter targets had been pre-activated by the prime, but not effectively inhibited. Overall, these patterns suggest that both neighborhood and

spelling ability modulate the direction and size of the behavioral interference effect. Here, we asked whether these same variables affect the size or direction of N400 neighbor priming in this paradigm.

Thus, despite converging evidence for behavioral interference effects when high frequency prime words precede neighboring targets in a masked priming paradigm (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012; Davis & Lupker, 2006; Segui & Grainger, 1990), there is little ERP evidence to support lexical competition as the underlying mechanism (cf. Massol et al., 2010). The present study adopts a more systematic approach to investigating the N400 as a neural correlate of neighbor interference by considering the potential influences of neighborhood density and spelling ability. Specifically, we presented masked high frequency word primes followed by lower frequency word and pseudoword targets that were orthographically related (i.e., neighbors) or unrelated in a lexical decision task with a 70 ms stimulus onset asynchrony (SOA; a 50 ms target followed by a 20 ms backward mask). Prime-target pairs were either from high- or low-density orthographic neighborhoods, and participants were recruited to have a range of spelling and reading comprehension abilities.

We predicted that word targets preceded by related neighbor primes would elicit slower responses than those preceded by unrelated primes, reflecting lexical activation of the prime word and the subsequent lateral inhibition that hinders processing of neighboring targets (e.g., Davis & Lupker, 2006). Following the results of Andrews and Hersch (2010), we further predicted that such inhibitory priming effects would be larger for word targets from high-density neighborhoods compared to word targets from low-density neighborhoods and larger for skilled spellers compared to less-skilled spellers. The critical question we address here is whether N400 amplitude follows a similar pattern. If so, target words preceded by related primes should elicit larger amplitude N400s (reflective of more effortful processing) than those preceded by unrelated primes. Paralleling behavioral findings, this “reversed” N400 priming effect should also be strongest for words from high-density neighborhoods and for skilled spellers, but it should not be correlated with scores on the reading comprehension subtest of the Peabody Individual Achievement Test Revised (PIAT-R; Markwardt, 1989). Indeed, it would not be surprising if the reversed N400 priming effect was *only* present under optimal conditions and did not reach significance in general analyses that include all stimuli and all participants (cf. Massol et al., 2010).

If the reversed N400 priming effect is related to lexical competition, there should be no evidence of it prior to the onset of lexical processing (e.g., Grainger & Holcomb, 2009; Massol et al., 2010), and it should be specific to word-word pairs. To verify that the effect reflects processing at a lexical level, we analyzed an earlier window that corresponds to the N250. We predicted that the sublexical overlap between related word pairs would reduce N250 amplitude relative to the unrelated condition (Massol et al., 2010), opposite the effect predicted for the N400 window, and that there would be no correlations with spelling ability or reading comprehension. To verify that the reversed N400 priming effect is specific to word-word pairs, we conducted similar analyses with pseudoword targets. Here, we expected that targets in related pairs would elicit smaller amplitude N250s relative to targets in unrelated pairs, as in word-word pairs, but that the attenuated negativity would continue

through the N400 window for pseudowords in the absence of lexical competition (Massol et al., 2011). The N400 priming effect for pseudoword targets was not expected to be sensitive to neighborhood density, spelling ability, or reading comprehension scores. Finally, we predicted that the form-relatedness of the prime words would have no effect on the behavioral responses to pseudoword targets (e.g., Andrews & Hersch, 2010; Forster & Davis, 1984). In sum, finding a reversed N400 priming effect that is specific to neighboring word-word pairs and is sensitive to the same lexical variables as the behavioral masked priming interference effect would provide evidence that the N400 is an index of the impact on word recognition of the lexical-level competition that is posited in IA models.

2. Results

2.1. Word Targets

2.1.1. RTs—Mean RTs and accuracy rates are presented in Table 1. Neither the main effect of Neighborhood nor the main effect of Prime was significant, but the two variables interacted, prompting follow-up analyses by Neighborhood, Prime $\times$ Neighborhood, $F(1,23) = 5.86$, $p = .024$, $\eta_p^2 = .20$. The effect of Prime was significant for high-N words, such that high-N word targets elicited slower responses following a related prime (mean 686 ms) compared to an unrelated prime (mean 664 ms), $F(1,23) = 5.71$, $p = .026$, $\eta_p^2 = .20$. In contrast, there was no significant effect of Prime for low-N words, $F(1,23) = 0.03$, $p = .863$, $\eta_p^2 = .00$.

2.1.2. Accuracy—There was a marginally significant effect of Prime such that word targets in unrelated pairs (mean 88%) elicited more accurate responses than those in related pairs (mean 85%), $F(1,23) = 4.17$, $p = .053$, $\eta_p^2 = .15$.

2.1.3. N250 (175–300 ms)—A main effect of Prime in the predicted direction indicated that word targets preceded by related primes (mean 2.15 μV) elicited smaller amplitude N250s than those preceded by unrelated primes (mean 1.56 μV ; i.e., priming), $F(1,23) = 4.26$, $p = .050$, $\eta_p^2 = .16$ (see Figures 1 and 2A). In contrast, there were no significant effects of neighborhood density or interactions between prime relatedness and neighborhood density, all p s $> .15$.

2.1.4. N400 (350–550 ms)—There was a main effect of Neighborhood in this window, indicating that low-N word targets (mean 3.81 μV) elicited smaller N400s than high-N word targets (mean 3.12 μV), $F(1,23) = 13.73$, $p = .001$, $\eta_p^2 = .37$ (see Figure 3). The effect was strongest over anterior midline and right hemisphere sites, Neighborhood $\times$ Laterality, $F(2,46) = 5.23$, $p = .017$, $\eta_p^2 = .18$, Neighborhood $\times$ Laterality $\times$ Anterior/Posterior, $F(8,184) = 2.69$, $p = .050$, $\eta_p^2 = .10$. The direction and scalp distribution of the priming effects differed between high and low neighborhood targets (see Figure 4), Prime $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,92) = 4.24$, $p = .026$, $\eta_p^2 = .16$. Close examination of Figure 4 further reveals that this interaction is also driven by differences in the priming effects for high and low neighborhood pairs across the full N400 window. In order to better characterize the time course of these priming effects, we divided the N400 window into an

earlier portion (350–450 ms) and a later portion (450–550 ms) and conducted similar analyses.

2.1.4.1. Early N400 (350–450 ms): Word targets preceded by related primes elicited larger amplitude negativities than word targets preceded by unrelated primes (i.e., reversed priming) over anterior sites, Prime $\times$ Anterior/Posterior, $F(4,92) = 4.51$, $p = .030$, $\eta_p^2 = .16$ (see Figures 1 and 2A). A significant main effect of Neighborhood also indicated that low-N word targets elicited less early N400 activity than high-N word targets, $F(1,23) = 7.06$, $p = .014$, $\eta_p^2 = .23$. The effects of Prime and Neighborhood did not interact, all $ps > .08$.

2.1.4.2. Late N400 (450–550 ms): Word targets preceded by related primes continued to elicit larger amplitude negativities than those preceded by unrelated primes (i.e., reversed priming) in this later N400 window, especially over left hemisphere sites, Prime $\times$ Laterality, $F(2,46) = 4.52$, $p = .033$, $\eta_p^2 = .16$ (see Figures 1 and 2A). A main effect of Neighborhood further indicated that low-N word targets continued to elicit smaller negativities than high-N word targets, Neighborhood, $F(1,23) = 15.75$, $p < .001$, $\eta_p^2 = .41$. The Neighborhood effect was especially strong over anterior right hemisphere sites, Neighborhood $\times$ Laterality, $F(2, 46) = 8.33$, $p = .003$, $\eta_p^2 = .27$, Neighborhood $\times$ Laterality $\times$ Anterior/Posterior, $F(8, 184) = 2.82$, $p = .047$, $\eta_p^2 = .11$.

However, the effect of Prime differed for high- versus low-N words in this later N400 window (see Figure 4), prompting follow-up analyses by Neighborhood, Prime $\times$ Neighborhood $\times$ Anterior/Posterior, $F(4,92) = 7.55$, $p = .003$, $\eta_p^2 = .25$. High-N targets preceded by related primes elicited larger amplitude negativities than those preceded by unrelated primes (i.e., reversed priming), especially over posterior sites, Prime $\times$ Anterior/Posterior, $F(4,92) = 4.94$, $p = .023$, $\eta_p^2 = .18$. In contrast, low-N word targets preceded by related primes elicited a smaller amplitude negativity than those in unrelated pairs (i.e., priming) over midline and right hemisphere sites, Prime $\times$ Laterality, $F(2,46) = 4.92$, $p = .024$, $\eta_p^2 = .18$.

2.2. Pseudoword Targets

2.2.1. RTs—The only significant RT effect was a main effect of Neighborhood, which indicated that low-N pseudoword targets (mean 721 ms) elicited faster RTs than high-N pseudoword targets (mean 742 ms), $F(1,23) = 17.71$, $p < .001$, $\eta_p^2 = .44$.

2.2.2. Accuracy—As in the RT analyses, the only significant effect on accuracy was a main effect of Neighborhood, such that low-N pseudoword targets (mean 93%) elicited more accurate responses than high-N pseudoword targets (mean 88%), $F(1,23) = 18.52$, $p < .001$, $\eta_p^2 = .45$.

2.2.3. N250 (175–300 ms)—As with word targets, a main effect of Prime indicated that pseudoword targets preceded by related primes (mean 1.99 μ V) elicited smaller amplitude N250s than those preceded by unrelated primes (mean 1.19 μ V), $F(1,23) = 23.05$, $p < .001$, $\eta_p^2 = .50$ (see Figures 2B and 5). However, there were no significant effects of Neighborhood or interactions between Prime and Neighborhood within this window, all $ps > .07$.

2.2.4. N400 (350–550 ms)—A simple main effect of Prime indicated that targets preceded by related primes (mean 2.28 μV) elicited smaller N400s than targets preceded by unrelated primes (mean 1.82 μV), $F(1,23) = 5.02$, $p = .035$, $\eta_p^2 = .18$. The simple main effect of Neighborhood approached significance, indicating that high-N pseudoword targets (1.80 μV) elicited larger amplitude N400s than low-N pseudoword targets, $F(1,23) = 3.71$, $p = .067$, $\eta_p^2 = .14$. There were no significant interactions between these two variables, all $ps > .16$. However, to keep the analysis approach for words and pseudowords parallel, we also followed-up the full N400 window analyses with separate smaller windows.

2.2.4.1. Early N400 (350–450 ms): Although targets preceded by related primes elicited smaller negativities, the main effect of Prime just failed to reach significance within this window, $F(1,23) = 3.71$, $p = .067$, $\eta_p^2 = .14$. There were no significant effects of Neighborhood, all $ps > .13$.

2.2.4.2. Late N400 (450–550 ms): Significant main effects of both Prime and Neighborhood characterized this later N400 window. As predicted, the effect of Prime indicated that pseudoword targets preceded by related primes elicited smaller negativities than those preceded by unrelated primes, $F(1,23) = 4.3$, $p = .049$, $\eta_p^2 = .16$ (see Figures 2B and 5). The main effect of Neighborhood also went in the expected direction (see Figure 3); low-N pseudoword targets elicited smaller negativities than high-N pseudoword targets, $F(1,23) = 11.23$, $p = .003$, $\eta_p^2 = .33$. However, the size of the effect of Prime was not modulated by neighborhood density, all $ps > .29$.

2.3. Correlations

2.3.1. Reading measures and RT effects—The size of the RT effect did not correlate with scores on either the spelling recognition measure or the PIAT-R for either word or pseudoword targets, all $ps > .39$. However, because the interference effect was only significant for high-N words, we tested that correlation separately. The correlation between the size of the RT interference effect for high-N words and spelling scores approached significance, such that skilled spellers had a stronger RT interference effect, $r = -.350$, $p = .094$.

2.3.2. Reading measures and ERP effects—The size of the N250 priming effect for word targets did not correlate with either spelling ability or PIAT-R scores, all $ps > .23$. However, the size of the reversed priming effect for word targets in the overall N400 window (350–550 ms) did correlate with scores on the spelling recognition measure at anterior sites (FP1, F3, FPz, Fz, FP2, F4), such that skilled spellers showed a larger reversed N400 priming effect, all $rs > .41$, all $ps < .05$. Because the N400 reversed priming effect differed for high-N and low-N words in the later N400 window (450–550 ms), we also conducted separate correlations for the two types of words in that window. The correlation held for high-N word targets (at sites FP1, F3, C3, FPz, Fz, F4; see Figure 6A), all $rs > .51$, all $ps < .04$, but not for low-N word targets, all $ps > .19$. In contrast, there were no significant correlations between PIAT-R scores and the size of the N400 reversed priming effect for word targets, all $ps > .18$. There were also no significant correlations between scores on the

spelling test or PIAT-R and the size of the N400 priming effect for pseudoword targets, all $ps > .18$.

2.3.3. N400 and RT effects—There were no significant correlations between the sizes of the RT effect and the N400 priming effect (350–550 ms) for word targets, all $ps > .15$.

3. Discussion

Interactive-activation models are among the most successful theoretical accounts of the mechanisms involved in visual word recognition. One key feature of these models is lateral inhibition among co-activated orthographic neighbors (e.g., Davis, 2003; Grainger & Holcomb, 2009; Jacobs & Grainger, 1992; McClelland & Rumelhart, 1981). Thus far, empirical support for lexical competition among neighbors comes from reports of behavioral interference in masked priming paradigms (slower RTs when the target is preceded by a neighbor). This interference has been shown to be specific to pairs of real words and sensitive to lexical level variables such as frequency, orthographic neighborhood density, and spelling ability (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012; Davis & Lupker, 2006; Segui & Grainger, 1990). The present study investigated the N400 as a possible neural correlate of the influence of lexical competition on word recognition. We presented masked high frequency word primes followed by lower frequency word and pseudoword targets that were orthographically related (i.e., neighbors) or unrelated, and manipulated both neighborhood density and participants' spelling and reading comprehension abilities. We found that N400 amplitude followed remarkably similar patterns as the behavioral interference effect. Word targets in neighbor pairs elicited larger amplitude N400s than those in unrelated pairs (indicative of more effortful processing), and that reversed priming was larger for words from dense neighborhoods. The reversed priming effect was also larger for better spellers, but it did not correlate with our measure of reading comprehension. Finally, the precise temporal resolution of ERPs allowed us to dissociate lexical competition within the N400 window from earlier sublexical facilitation (i.e., priming) within the N250 window. These results converge to suggest that N400 amplitude indexes the influence of lexical competition on word recognition.

It is important to distinguish the reversed N400 priming effect observed here, which we suggest indexes the impact of lexical competition on word recognition, from evidence of neighbor co-activation (i.e., the precursor to lexical competition). Outside of the priming context, evidence of neighbor co-activation has come from the finding that high-N items elicit larger amplitude N400s (i.e., more lexicosemantic processing) than low-N items (e.g., Holcomb, Grainger, & O'Rourke, 2002; Laszlo & Federmeier, 2011; Meade, Midgley, Dijkstra, & Holcomb, 2018). We replicated that N400 effect of neighborhood for both word and pseudoword targets here (see Figure 3), suggesting that neighbors were co-activated irrespective of the lexical status of the target. Additional evidence of neighbor co-activation comes from priming studies in which targets preceded by form-related primes elicit *smaller* amplitude N400s than those preceded by unrelated primes (e.g., Grossi, Coch, Coffey-Corina, Holcomb, & Neville, 2001). For example, Laszlo and Federmeier (2009) compared responses to words at the end of high-constraint sentences that were either orthographic neighbors of the expected target words (which were never explicitly presented) or unrelated.

They found that orthographic neighbors of the expected word elicited smaller amplitude N400s than words in the unrelated condition, and suggested that orthographic neighbors “become active in concert” (p. 335), but do not inhibit one another.

The novelty of the present results comes from the evidence for lateral inhibition reflected in the *reversed* N400 priming effect, which differs from the neighbor co-activation patterns described above in several key ways. For one, contrary to the results reported by Laszlo and Federmeier (2009), the *increase* in N400 amplitude for word targets preceded by neighbor primes indicates that they were *more* effortful to process than targets in the unrelated condition. This pattern is difficult to explain in terms of neighbor co-activation alone, but could be indicative of strong inhibitory lexical connections among neighbors. A second key piece of evidence to suggest that the reversed priming effect indexes competition is that, as with the behavioral interference effect (see, e.g., Andrews & Hersch, 2010; Forster & Davis, 1984, Experiment 2; Forster et al., 1987) but in contrast to neighbor co-activation effects, reversed priming was specific to pairs of real words. The competition posited in IA models is dependent on lexical-level nodes and should only occur when both the prime and target have lexical representations. The opposite effect was observed for pseudoword targets, such that pseudowords preceded by orthographically similar primes elicited smaller amplitude N400s than those preceded by unrelated primes. In this case, neighbor word primes facilitated sublexical processing (as reflected in the attenuation of N250 amplitude), which presumably carried over into the N400 window in the absence of lexical competition. Finally, the bilateral anterior distribution of the reversed priming effect was clearly distinct from the typical distribution of N400 priming effects, which tend to be strongest over right hemisphere centro-posterior sites in visual paradigms (e.g., Grossi et al., 2001; Kutas & Federmeier, 2011), and from that of the main effects of neighborhood in these same participants (see Figure 3). The anterior distribution of the effect may raise questions about whether or not this should be classified as an N400 effect. Indeed, it is plausible that the processes that we are indexing here differ from (or are only a subset of) the typical processes associated with the N400, but they take place within the same time window.¹ Overall, several characteristics of the reversed N400 priming effect are consistent with the interpretation that it indexes lexical competition.

Why were we able to measure this influence of lateral inhibition on word recognition when neighbors apparently remained activated and facilitated processing in previous studies of form priming (e.g., Laszlo & Federmeier, 2009)? Two of the most obvious factors that set the design of this study apart from the large majority of priming studies are the short SOA and the masking of the prime. Indeed, there is behavioral evidence to suggest that a short SOA and masking are critical for obtaining interference between the high frequency primes and lower frequency targets used in the present study (Segui & Grainger, 1990). In one of the few previous ERP studies to meet these two conditions, Massol and colleagues (2010)

¹Although it is impossible to isolate the brain regions that were responsible for the anterior scalp distribution of this effect, another possible interpretation is that the effect originates in the frontal regions that have been identified in fMRI studies of orthographic neighborhood effects (e.g., Binder et al., 2003; Braun et al., 2015; Fiebach, Ricker, Friederici, & Jacobs, 2007). Note however, that the BOLD signal in these regions follows a different pattern from the typical N400 patterns, and the frontal activation in fMRI has been associated with top-down, extra-lexical control rather than lateral inhibition among lexical representations. More research is needed to tease apart the roles of these different control processes.

failed to find a significant effect of prime on the N400s elicited by target words, but nevertheless interpreted the null effect as evidence of lexical competition. These authors suggested that facilitation of sublexical processing, reflected in the attenuated N250 for targets in neighbor pairs, was cancelled out by the lexical competition that onset before the N400. As in that study, the overall effect of prime relatedness on N400 amplitude here was weak. However, by investigating modulations of this effect as a function of spelling ability and neighborhood density, we provide stronger evidence that the N400 is an index of the impact of lexical competition on target recognition in masked neighbor priming paradigms with a short SOA.

Correlations with a behavioral measure of spelling ability suggested that the reversed N400 priming effect was larger for skilled spellers than for less-skilled spellers. In contrast, there were no correlations between the ERP or behavioral effects and scores on the PIAT-R, our measure of reading comprehension. Together with previous behavioral research (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012; Veldre & Andrews, 2015), this pattern of results reinforces that spelling ability plays a special role in determining the size of the interference effect (i.e., above and beyond that of general written language proficiency). However, it was curious that the correlations were especially strong in the later N400 window across anterior sites (see Figure 6A), where the overall reversed priming effect of interest appeared to be weakest (see Figure 2A). To better understand the relationship between spelling skill and this reversed N400 priming effect for high-N words, we followed a strategy used in previous studies where individual differences were proposed to produce different patterns of ERP effects (e.g., Osterhout, 1997). In these supplemental analyses, we divided participants into quartiles based on their spelling scores and examined the effect of priming on processing of high-N word targets separately for the six strongest (see Figure 6B) and six weakest (see Figure 6C) spellers. These plots illustrate that the apparent absence of any priming effect over anterior sites in the whole group analyses can be explained by the fact that skilled spellers showed a reversed N400 priming effect across the anterior sites, whereas less skilled spellers showed the opposite effect. Furthermore, the apparent changes in the distribution of the effect from the early N400 window to the later N400 window (see Figure 2A) are due to the superimposition of this reversed priming effect across bilateral anterior sites with a more typical priming effect in the less-skilled spellers.

Andrews and Hersch (2010) have suggested that skilled spellers have more precise lexical representations, which “facilitates activation of the lexical representation corresponding to the sensory input and minimizes activation of competing alternatives” (p. 312). Lexical precision is characterized by stable representations of the positions of individual letters within words (e.g., Perfetti, 1992), which requires use of a fine-grained orthographic code (Grainger & Ziegler, 2011). Thus, skilled spellers might be better at extracting letter position information from the input and efficiently identifying the appropriate lexical representation. This precision allows them to quickly suppress the neighbors of the prime, making neighbor targets especially difficult to process.² In the present study, such increased difficulty is reflected in the larger amplitude N400s for neighbor targets among skilled spellers. Andrews

²Davis and Lupker (2006) have suggested that it is the number of neighbors that are shared between the prime and target, rather than the total number of target neighbors, that modulates the magnitude of the interference (see also van Heuven et al., 2001). We were

and Lo's (2012) finding that skilled spellers have even stronger behavioral interference effects for targets preceded by transposed-letter primes, which share all letters and are even more orthographically similar than neighbor pairs, provides further evidence that spelling ability is affecting the lexical competition process. If this interpretation is correct, and interference from transposed-letter word primes in skilled spellers is also caused lexical competition, we would expect that transposed-letter word primes yield an even stronger reversed N400 priming effect than the one we observed here for neighbor word primes. This hypothesis awaits further testing.

In comparison, less-skilled spellers presumably have noisier lexical representations and a less refined identification process. The fact that we nevertheless observed positive ERP priming effects (both N250 and N400) and replicated previous reports of behavioral facilitation (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012) suggests that less-skilled spellers are co-activating neighbors but not efficiently inhibiting them. When the target is among the neighbors that remain active, it becomes easier for less-skilled spellers to process, resulting in a decrease in N400 amplitude relative to targets that are unrelated to, and therefore not activated by, their primes.

Two findings reinforce the hypothesis that spelling ability affects the lexical competition process specifically. First, scores on the spelling recognition test did not correlate with the size of N250 priming for the word targets, which we associate with sublexical facilitation (see Andrews & Hersch, 2010, Experiment 2 for further evidence from partial primes to suggest that spelling ability does not determine the degree of sublexical facilitation). Second, the fact that the correlations between the size of the reversed N400 priming effect and spelling ability only held for high-N words indicates that spelling ability affects lexical competition. In high-N pairs, a large number of prime neighbors are co-activated, and those that are shared with the target become stronger competitors for neighbor targets (while having little effect on unrelated targets). The larger reversed N400 priming for high-N words among skilled spellers complements behavioral results, both in the present study and elsewhere (e.g., Andrews & Hersch, 2010), in suggesting that high-N words are particularly susceptible to interference. In contrast, there was little effect of spelling ability on the size of the priming effect for low-N words, and the overall effect was such that targets in neighbor pairs elicited smaller N400s than those in unrelated pairs. Low-N words incur competition from fewer neighbors, and it is possible that this diminishes the need for active inhibition, which in turn eliminates the relationship with spelling ability. Together the specificity of the role of spelling ability to the N400 window and to high-N words suggests that orthographic precision (indexed by spelling skill) modulates lexical competition rather than sublexical facilitation.

An interesting question is whether spelling ability fundamentally changes the role of lexical competition in visual word recognition or whether the processes remain similar, but follow a slower time course in less-skilled spellers. If the latter is true, there should be evidence of interference and reversed N400 priming in the less-skilled spellers when a longer SOA

unable to isolate the effects of the shared neighbors here because the number of shared neighbors was highly correlated with the total number of neighbors across our neighbor word pairs, $r = .80$, $p < .001$.

separates the prime from the target. This extra time would allow the system to identify the prime and inhibit its neighbors before the target is presented. If less-skilled spellers still show typical priming effects at longer SOAs, then this would suggest that they are recognizing the words in a fundamentally different way (i.e., without relying on lexical competition). For example, in the lexical decision task, less-skilled spellers might be using different response criteria and basing their decisions more on global levels of lexical activity than on identification of a single word (see Grainger & Jacobs, 1996). In more typical reading situations where identification of the word is required, less-skilled spellers could compensate for the absence or weakening of lexical competition by relying more on other cues, including context (see Andrews & Bond, 2009).

Taken together, these data converge to suggest that N400 amplitude indexes the influence of lexical competition on visual word recognition. Similarities in the reversed N400 priming patterns we observed here and previous investigations of behavioral interference effects (e.g., Andrews & Hersch, 2010; Andrews & Lo, 2012; Davis & Lupker, 2006) suggest that these measures are indexing a similar underlying process. Both behavioral and ERP effects were larger for skilled spellers and for high-N word targets, whereas facilitatory effects were observed for less-skilled spellers and for low-N word targets. Moreover, we extend the previous behavioral literature by delineating the time course of the competition and dissociating it from facilitated sublexical processing within the N250 window. From behavioral data alone, it would be virtually impossible to discern that what starts out as enhanced processing (N250 priming) in all readers eventually gives way to competitive processing (reversed N400 priming) in skilled spellers only. Together, these patterns suggest that young adult readers process single words in a variety of ways, but that lexical competition is an important component of processing among skilled spellers.

4. Experimental Procedure

4.1. Participants

Participants included 24 young adults (19 female; mean 22.1 years, *SD* 3.0 years) who were right-handed, had normal or corrected-to-normal vision, and had no history of any language, reading, or neurological disorders. They were volunteers who received course credit and/or monetary compensation in return for participation. Informed consent was obtained from all participants in accordance with the Institutional Review Board at San Diego State University. An additional two participants took part in the experiment, but were excluded from analyses; one had a score on the spelling recognition task that was lower than the range of the participants in the study by Andrews and Hersh (2010), and one was excluded because of experimenter error.

4.2. Stimuli

Each trial consisted of a prime and a target that had the same length (4 or 5 letters) and a similar orthographic neighborhood density (high-N or low-N).³ Within each neighborhood

³We thank Sally Andrews for generously providing the stimuli from the study reported by Andrews and Hersch (2010), which were originally adapted from Davis and Lupker (2006). Many of those items were included in the four-letter conditions here.

condition, there were 90 word targets and 88 pseudoword targets, yielding a total of 356 targets. Each word target was paired with a neighbor word prime, a neighbor pseudoword prime, and an unrelated word prime; each pseudoword target was paired with a neighbor word prime and an unrelated word prime. Examples of these conditions are found in Table 2.⁴ The master list of all possible 892 pairs was then subdivided into three lists such that each of the targets was presented only once per list and all of the possible prime-target pairs occurred in at least one of the lists. Presentation of these lists was counterbalanced across participants.

Consistent with Andrews and Hersch (2010), we extracted frequency and orthographic neighborhood metrics from the CELEX database using N-Watch (Davis, 2005; see Tables 4 and 5). Word targets (mean 6.46, *SD* 4.61) and pseudoword targets (mean 5.78, *SD* 4.46) had a similar *N* overall, $t(354) = 1.40$, $p = 0.164$. We expected that including high-*N* pseudoword targets would increase the global lexical activity associated with pseudoword targets and make that an unreliable cue in the lexical decision task (Grainger & Jacobs, 1996). In previous studies, including high-*N* pseudoword targets has been found to increase the size of the behavioral lexical interference effect (e.g., Davis & Lupker, 2006) and potentially the N400 effect of interest (Massol, 2012). High-*N* word targets (mean 10.39, *SD* 2.99) had significantly more neighbors than low-*N* word targets (mean 2.52, *SD* 1.57), $t(178) = 22.09$, $p < .001$, and the same was true for high-*N* (mean 9.40, *SD* 3.54) and low-*N* (mean 2.17, *SD* 1.06) pseudoword targets, $t(174) = 18.34$, $p < .001$. However, high-*N* (mean 20.56, *SD* 33.89) and low-*N* word targets (mean 17.62, *SD* 52.31) had comparable frequencies, $t(178) = .45$, $p = .829$.

Primes preceding high-*N* targets (mean 9.26, *SD* 3.42) also had more neighbors than those preceding low-*N* targets (mean 2.59, *SD* 2.05), reflecting the fact that primes had a similar *N* as their targets, $t(710) = 31.47$, $p < .001$. As with targets, the frequency of high-*N* (mean 139.79, *SD* 338.59) and low-*N* (mean 144.82, *SD* 427.11) word primes did not significantly differ, $t(710) = 0.17$, $p = .862$. However, the primes in word-word pairs (mean 206.54, *SD* 520.09) were of a higher frequency than the targets in those pairs (mean 19.09, *SD* 43.97), $t(538) = 4.82$, $p < .001$. For each condition (e.g., high-*N* word targets), neighbor and unrelated primes had comparable *N*s and frequencies, p s $> .10$. The only exception was that neighbor primes that preceded low-*N* word targets had slightly more neighbors (mean 2.80, *SD* 2.31) than the unrelated primes in the same condition (mean 1.92, *SD* 1.42), $t(178) = 3.08$, $p = .002$.

4.3. Procedure

Stimuli were presented in Courier font such that they subtended at a horizontal visual angle of 1.85 degrees or less. Each trial consisted of a forward mask (#####) presented for 300 ms, a lowercase prime for 50 ms, a backward mask (#####) for 20 ms, and an uppercase target for 300 ms, all of which were presented in white in the center of a black screen. At the end of a trial, after a 700 ms blank screen, purple and white fixation crosses were presented consecutively at the center of the screen for 1100 ms and 900 ms, respectively. Participants

⁴The pseudoword prime condition was not included in analyses because there was no appropriate unrelated condition (i.e., unrelated pseudoword primes and word targets). This condition will not be discussed further and is therefore not included in Table 2.

were asked to try to blink during the purple fixation cross and during longer blink breaks that occurred approximately every 10 trials. Finally, participants were told that they would be seeing real words and made-up words on the screen (i.e., no mention was made of the primes) and were asked to make a lexical decision as quickly as possible while being sure of their response. A left button press indicated a real word response, whereas a right button indicated a made-up word. A practice set with 10 trials (5 word targets) that were not included in the real experiment was administered at the beginning of the session.

In addition to taking part in the ERP experiment, all participants completed a spelling recognition task (Andrews & Hersch, 2010) and the reading comprehension subtest of the PIAT-R. Spelling scores (mean 74.5 out of 88; range 62–85) were within a similar range as the group reported by Andrews and Hersch (2010). PIAT-R scores (mean 89.0 out of 100; range 64–100) indicated that these participants were good comprehenders overall, but that there was a reasonable range of proficiencies. Additional behavioral measures were also collected as part of a larger study comparing reading skills in deaf and hearing adults.

4.4. EEG Recording

Participants wore an elastic cap (Electro-Cap) with 29 active electrodes (see Figure 7). 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 and FP1 were used to identify blinks and an electrode on the outer canthus of the right eye was used to identify 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.

4.5. Data Analysis

Only correct trials with a response between 200 ms and 2000 ms after target onset were included in RT analyses, which involved separate 2×2 repeated-measures ANOVAs with factors Prime (Related, Unrelated) and Neighborhood (High, Low) for word and pseudoword targets. ERPs were time-locked to the onset of each target. Offline, separate ERPs for each condition were averaged for each subject at each electrode site over a 800 ms epoch, including a 100 ms pre-stimulus-onset baseline, and low-pass filtered at 15 Hz. Trials with ocular artifacts (2% on average) and incorrect responses (11% on average) were excluded from analyses, which focused on the 15 representative electrode sites indicated in Figure 7. Based on previous masked priming studies (e.g., Ktori, Midgley, Holcomb, & Grainger, 2015; Massol et al., 2010) and visual inspection of the grand average waveforms in Figures 1 and 5, mean amplitude was calculated between 175 and 300 ms and 350 and 550 ms to capture the N250 and N400, respectively. For both time windows, omnibus ANOVAs with factors Prime (Related, Unrelated), Neighborhood (High, Low), Laterality (Left, Midline, Right), and Anterior/Posterior (Prefrontal, Frontal, Central, Parietal, Occipital) were conducted separately for word and pseudoword targets.

To test the hypothesis that skilled spellers experience greater lexical competition than less-skilled spellers, we used Pearson correlations between each participant's spelling

recognition score and the size of their N400 and RT priming effects (unrelated-related) for word targets. To test whether the correlations were indexing lexical competition specifically, we conducted similar analyses for the pseudoword targets and also tested for correlations within the earlier N250 window for word targets. To test whether the correlations were specific to spelling ability, we conducted a similar set of analyses with PIAT-R reading comprehension scores. Finally, to determine whether the N400 effect and behavioral effect were reflecting the same underlying processes, we calculated the correlation between them for word targets. 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.

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Highlights

- Masked priming with orthographic neighbor and unrelated pairs
- Neighbor word targets elicit larger N400s than unrelated targets (reversed priming)
- Larger reversed priming for targets with many neighbors and for skilled spellers
- N400 amplitude follows similar pattern as behavioral interference in this paradigm
- Reversed N400 priming indexes effects of lexical competition on word recognition

Fig. 1.

Effect of prime on word targets. Grand average ERP waveforms elicited by word targets in unrelated (red dotted line) and related (black solid line) pairs. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks $2\mu\text{V}$. The N250 is indicated at site Pz and the N400 is indicated at site Fz.

Fig. 2.

Voltage maps showing priming effects. Scalp voltage maps showing the effect of prime (unrelated - related) in each of the analyzed time windows for word targets (A) and pseudoword targets (B). The reverse N400 priming effect is indicated in these plots by warm colors.

Fig. 3.

Effect of neighborhood density on word and pseudoword targets. (A) Grand average ERP waveforms to show the effect of neighborhood density for word and pseudoword targets across anterior midline sites FPz, Fz, and Cz. The neighborhood effect had an earlier onset for words (black vs. red lines) than for pseudowords (blue vs. green lines). Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V. (B) Scalp voltage maps show the distribution of the effect (high-N – low-N) over the entire N400 window (350–550 ms) for words and pseudowords, respectively.

Fig. 4.

N400 priming effects for high- and low-density neighborhood word targets. Difference waves (unrelated-related) to show the time course of priming effects for high-density neighborhood word targets (black solid line) and low-density neighborhood word targets (red solid line). Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V. Note that reversed priming is indicated by a positive difference (i.e., plotted below the horizontal line).

Fig. 5.

Priming effects for pseudoword targets. Grand average ERP waveforms elicited by pseudoword targets in unrelated (red dotted line) and related (black solid line) pairs. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V. The N250 is indicated at site O2 and the N400 is indicated at site C4.

Fig. 6.

Correlation between reverse N400 priming effect and spelling skill. (A) A map of the Pearson correlation coefficients between spelling skill and the N400 effect of prime (unrelated-related) between 450 and 550 ms for high-N target words. Warmer colors indicate that skilled spellers had a stronger reverse N400 effect. In (B) and (C), unrelated (red dotted line) and related (black solid line) high-N word targets are plotted at midline anterior sites separately for the six most skilled and six least skilled spellers, respectively. Each vertical tick marks 100 ms and negative is plotted up. The calibration bar marks 2 μ V.

Fig. 7.
Electrode montage. Sites indicated in grey were included in analyses.

Table 1

Behavioral results [Mean (SD)]

		TARGET			
		Word		Pseudoword	
		High-N	Low-N	High-N	Low-N
Neighbor	RT (ms)	686 (85)	683 (79)	740 (78)	720 (70)
Prime	% Correct	86 (9)	84 (8)	89 (8)	93 (6)
Unrelated	RT (ms)	664 (81)	684 (89)	745 (78)	723 (80)
Prime	% Correct	88 (6)	89 (10)	88 (8)	93 (5)

Table 2

Example stimuli

		TARGET				Pseudoword	
		Word		Low-N		High-N	Low-N
PRIME	Neighbor	note-NODE, state-STALE	sure-SURE, shrug-SHRUB	poll-POLD, cover-SOVER	blue-BLIE, civil-CIVIT		
	Unrelated	kiss-NODE, clock-STALE	play-SURE, angel-SHRUB	cart-POLD, watch-SOVER	wish-BLIE, gleam-CIVIT		

High-N = high-density orthographic neighborhood; Low-N = low-density orthographic neighborhood

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Table 3

Target characteristics [Mean (SD)]

	High-N Words	Low-N Words	High-N PWs	Low-N PWs
Frequency	20.56 (33.89)	17.62 (52.31)	---	---
N	10.39 (2.99)	2.52 (1.57)	9.40 (3.54)	2.17 (1.06)

N = number of orthographic neighbors; High-N = high-density neighborhood; Low-N = low-density neighborhood; PW = pseudoword

Table 4

Prime characteristics [Mean (SD)]

	Related Pairs				Unrelated Pairs			
	High-N Words	Low-N Words	High-N PWs	Low-N PWs	High-N Words	Low-N Words	High-N PWs	Low-N PWs
Frequency	235.17 (568.13)	287.93 (730.30)	86.04 (118.05)	70.89 (132.51)	156.40 (304.50)	146.64 (358.58)	78.99 (111.63)	70.52 (131.78)
N	10.12 (3.64)	2.80 (2.31)	8.91 (3.32)	2.68 (2.11)	9.30 (3.27)	1.92 (1.42)	8.69 (3.37)	2.97 (2.14)

N = number of orthographic neighbors; High-N = high-density neighborhood; Low-N = low-density neighborhood; PW = pseudoword

Note: All primes in the conditions that we analyzed were real words. Word and PW refer to the lexical status of the target that followed.