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Masked Priming From Orthographic Neighbors: An ERP Investigation

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Two experiments combined masked priming with event-related potential (ERP) recordings to examine effects of primes that are orthographic neighbors of target words. Experiment 1 compared effects of repetition primes with effects of primes that were high-frequency orthographic neighbors of low-frequency targets (e.g., faute-faune [error-wildlife]), and Experiment 2 compared the same word neighbor primes with nonword neighbor primes (e.g., aujel-autel [altar]). Word neighbor primes showed the standard inhibitory priming effect in lexical decision latencies that sharply contrasted with the facilitatory effects of nonword neighbor primes. This contrast was most evident in the ERP signal starting at around 300 ms posttarget onset and continuing through the bulk of the N400 component. In this time window, repetition primes and nonword neighbor primes generated more positive-going waveforms than unrelated primes, whereas word neighbor primes produced null effects. The results are discussed with respect to possible mechanisms of lexical competition during visual word recognition.

Keywords: event-related potential, lexical competition, orthographic priming, visual word recognition

There is a general consensus today that printed words are recognized via their constituent letters (see Grainger, 2008, for a summary of the arguments). One consequence of such letter-based processing within the framework of a generic parallel activation approach to visual word recognition is that orthographic representations of words that share a majority of the target words' letters will receive considerable bottom-up support upon stimulus presentation. Whether or not the simultaneous activation of these orthographically similar words has any influence on target word processing will depend on the specific architecture of the model, particularly in terms of the presence or absence of competitive interactions between lexical representations.

One prominent model of visual word recognition, McClelland and Rumelhart's (1981) interactive-activation model (IAM), implements such competitive interactions in the form of lateral inhibitory connections between whole-word representations. This mechanism ensures that one word will emerge as the winner whereas inhibiting its competitors (a winner-take-all mechanism). Two factors determine the inhibitory influence of competing words during target word recognition: the amount of orthographic overlap with the target, and the frequencies of the competitor and target words. Grainger and colleagues concluded in favor of a winner-take-all mechanism based on experiments where they varied the number and frequency of the orthographic neighbors of stimuli in single word reading paradigms (e.g., Grainger, 1990; Grainger, O'Regan, Jacobs, & Segui, 1989, 1992; Grainger & Segui, 1990). However, the evidence obtained with this paradigm was not considered as conclusive, possibly because of the fact that orthographic neighborhood characteristics correlate highly with other variables such as single letter and bigram frequency as well as the characteristics of the phonological neighborhood (e.g., Andrews, 1997; Grainger, Muneaux, Farioli, & Ziegler, 2005; Yates, Locker, & Simpson, 2004; Ziegler & Perry, 1998).

Segui and Grainger (1990) turned to the masked priming paradigm combined with the lexical decision task (Forster & Davis, 1984) as an alternative means of putting this mechanism to test. In one critical condition of Segui and Grainger's study, low-frequency target words were primed with a high-frequency orthographic neighbor (e.g., blue-blur). In line with the predictions of the IAM, these authors found that briefly presented high-frequency neighbor primes inhibited performance to low-frequency targets relative to unrelated high-frequency primes, causing an increase in reaction times and error rate. In the same study, it was found that there were no significant priming effects when the primes were low-frequency word neighbors of the target, and the targets high-frequency words. Jacobs and Grainger (1992) showed that the IAM correctly simulated this pattern of priming effects. They demonstrated this by testing the model (implemented with a lex-

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icon of French four and five-letter words) with exactly the same set of stimuli as used in the Segui and Grainger study. The IAM not only simulated the inhibitory priming effect with high-frequency primes and low-frequency targets, but also the absence of an effect when primes were low-frequency and targets high-frequency. These basic findings have been replicated and extended in the work of Bijeljac-Babic, Biardeau, and Grainger (1997); Brysbaert, Lange, and Van Wijnendaele (2000); Davis and Lupker (2006); De Moor and Brysbaert (2000); Grainger and Ferrand (1994); and Nakayama, Sears, and Lupker (2008).

According to the IAM's account of these inhibitory priming effects, they have a lexical rather than a prelexical or postlexical locus. The fact that the effect was found to depend on the frequencies of prime and target words is strong evidence against a prelexical origin. Furthermore, there is evidence that nonword primes that are orthographic neighbors of target words can facilitate, not inhibit, performance in the lexical decision task under appropriate conditions (e.g., Forster & Davis, 1991; van Heuven, Dijkstra, Grainger, & Schriefers, 2001). Facilitatory priming is also observed in certain conditions with partial word primes, formed of the target word with one letter substituted by a filler symbol such as a hash mark (Grainger & Jacobs, 1993; Hinton, Liversedge, & Underwood, 1998; Perry, Lupker, & Davis, 2008). Therefore, there is evidence of a graded effect of prime lexicality/frequency, moving from facilitatory priming with nonword primes, no priming with low-frequency word primes, and inhibitory effects with high frequency word primes.

More recent work has shown that the effects of word neighbor primes can be modulated by the number of orthographic neighbors of prime and target words (Davis & Lupker, 2006; Nakayama et al., 2008), and that a combination of a high-frequency prime with a low-frequency target is not always necessary for obtaining the effect (De Moor & Verguts, 2006; Nakayama et al., 2008). Nevertheless, the fact that inhibitory priming has never been reported with masked nonword neighbor primes does strongly suggest a lexical locus of the inhibitory word priming effect. Finally, De Moor, Van der Herten, and Verguts (2007) have shown that the effects of word neighbor primes become more inhibitory with increasing prime durations (from 14–57 ms; see Grainger, 1992, for an earlier report of this finding), whereas at the same time the effects of nonword neighbor primes become more facilitatory. Therefore, all this evidence points to a lexical locus of the inhibitory effects of word neighbor primes. However, given that practically all the above-cited studies used the lexical decision task (only Grainger & Ferrand, 1994, used a different task—perceptual identification), one might wonder to what extent the effect depends on some specificity of this particular task. An analysis of how the lexical decision task might be performed suggests that this is very unlikely. If anything, the lexical decision task would more likely reduce the effects of within-word competition, because successful word–nonword discrimination can be made based on information that is available before a word is actually recognized. This could take the form of summed lexical activation, for example (Grainger & Jacobs, 1996). Such biases, specifically associated with the lexical decision task, might be expected to generate facilitatory effects of word neighbor primes since these neighbors provide converging evidence in favor of a "word" response.

Finding an inhibitory effect of orthographic neighbor primes in the lexical decision task is therefore strong evidence for lexical competition during visual word recognition, as implemented in the IAM (McCelland & Rumelhart, 1981). According to this account, the related prime word preactivates its own lexical representation as well as that of the target word. The subsequent presentation of the related target word continues to provide evidence in support of the prime word representation, hence allowing this representation to reach higher levels of activation during target word processing than an unrelated prime word. It is this specific combination of preactivation from the prime stimulus plus continued support from the target stimulus that generates maximum activation in a competing word representation during target word recognition (see Grainger & Jacobs, 1999, for more detail). In the IAM and its successors (Davis & Lupker, 2006; Grainger & Jacobs, 1996; Perry et al., 2008), a given word representation sends inhibitory input to all other word representations as a function of its activation level. Therefore, the inhibitory influence of orthographic neighbors operates during the build-up in activation of whole-word orthographic representations.

Summing up, there is strong evidence from prior behavioral research that the inhibitory effects of high frequency orthographic neighbors reflect competitive processes operating on whole-word representations. The present study provides a further test of this hypothesis by investigating the timing of priming effects obtained from high-frequency orthographic neighbors using event-related potential (ERP) recordings. Our main prediction is that these lexical competition effects should be reflected in the latest phase of form-level processing, at the point where the lexical processor is homing in on a unique whole-word form representation.

ERPs and Visual Word Recognition

Recent research has combined the masked priming paradigm with electrophysiological recordings to provide complementary data particularly with respect to the relative timing of effects found in behavioral experiments. In one such study, Holcomb and Grainger (2006) compared priming from repetition primes (primes are the same word as targets or a different word) and a partial repetition condition in which primes were nonwords that differed from targets by a single letter (e.g., teble-table). These authors found a series of ERP components that were sensitive to this priming manipulation, two of which are particularly relevant for the present study: the N250 and N400 (peaking at approximately 250 and 400 ms posttarget onset).

Figure 1 illustrates a tentative mapping of ERP components obtained with the masked priming procedure onto the component processes of a generic IAM of word recognition (the bi-modal IAM, Diependaele, Ziegler, & Grainger, 2009; Grainger & Ferrand, 1994; Grainger & Holcomb, 2009; Grainger & Ziegler, 2007; Holcomb & Grainger, 2007). On presentation of a printed word, visual features are mapped onto prelexical orthographic representations (letters and letter clusters: O-units), which are subsequently mapped onto whole-word orthographic representations (O-words) and at the same time onto sublexical phonological representations via the central interface between orthography and phonology (O ⇔ P). Whole-word form representations then send activation onto semantic representations (S-units).

Focusing on the ERP components of interest for the present study, the N250 is hypothesized to reflect the mapping of prelexical orthographic representations onto whole-word orthographic

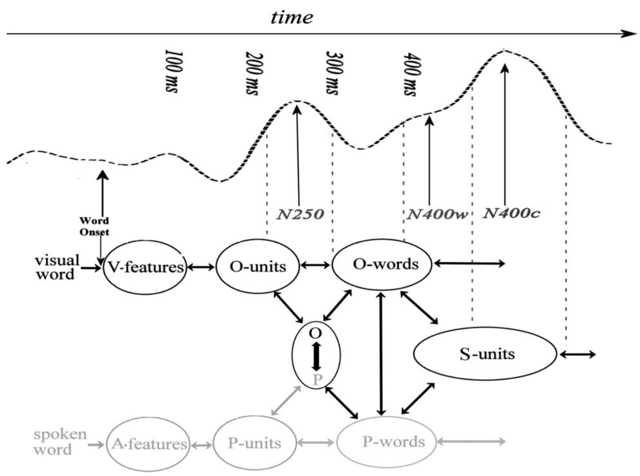

Figure 1. ERP masked repetition priming effects mapped onto the Bimodal IAM, highlighting the two components of interest in the present study–the N250 and N400. The model has been turned on its side to better accommodate the temporal correspondence with ERP effects, and the auditory pathway has been dimmed. See main text for a description of the model, and Grainger and Holcomb (2009) for a more detailed analysis.

representation. Within the general framework of interactive-activation, this mapping process involves the transfer of activation (feedforward and feedback) from letter and letter cluster representations to whole-word representations, and therefore indexes the initial build-up of activation at the lexical level and the stabilization of activation at the sublexical level. The N400 (at least in its early phase, N400w) is hypothesized to reflect the mapping of lexical form onto meaning (later effects could reflect integration across semantic representations, labeled as N400c in Figure 1). Again, translated into the mechanics of interactive-activation, this mapping process reflects the transfer of activation from whole-word representations to semantic representations and therefore indexes the initial phase of activation of semantic representations and the stabilization of activation at the level of whole-word units.

Therefore, at a very general level of analysis, our masked priming studies all point to a shift from a dominance of prelexical form-level processing in the N250 to a dominance of lexical/semantic-level processing in the N400 (see Barber & Kutas, 2007, for a similar time-course analysis). In support of this analysis, Holcomb and Grainger (2007) found that manipulating prime-target SOA had a distinct influence on the size of repetition priming effects on the N250 and N400. The N400 was found to be relatively insensitive to prime-target SOA, whereas the N250 disappeared at longer SOAs (>300 ms) for a fixed (60 ms) prime duration. Furthermore, Kiyonaga, Grainger, Midgley, and Holcomb (2007) reported that the N400, but not the N250, is modulated by masked cross-modal (visual-auditory) priming.

How does the latency and amplitude of these ERP components reflects changes in the underlying processes? Our IAM does not generate ERPs, but our initial attempts at bridging the gap between model and data suggest that the amplitude of the ERP components obtained in the masked priming paradigm at least partly reflect ease of target processing (see Grainger & Holcomb, 2009, for a recent review). For the two negative-going components of interest in the present study (N250 and N400), unrelated prime stimuli have systematically been found to generate more negative-going waveforms than related prime stimuli (Chauncey, Holcomb, & Grainger, 2008; Dufau, Grainger, & Holcomb, 2008; Grainger, Kiyonaga, & Holcomb, 2006; Holcomb & Grainger, 2006, 2007; Kiyonaga et al., 2007). Therefore, we would tentatively associate greater negativity of these components with increased difficulty of target processing.

The tentative mapping of ERP components onto component processes in word recognition, illustrated in Figure 1, would appear to stand in contradiction with reports of early influences of lexical (i.e., word frequency) and semantic variables on ERPs (e.g., Dell'Acqua, Pesciarelli, Jolicoeur, Eimer, & Peressotti, 2007; Hauk, Davis, Ford, Pulvermüller, & Marslen-Wilson, 2006; Hauk & Pulvermüller, 2004). There are two possible reasons for this apparent discrepancy. One is that the masked priming procedure, used in our studies, produces an overall slowing down of target word processing (a general interference from prime and masking stimuli against which prime relatedness effects emerge). Therefore, our timing estimates will be longer compared with studies using unprimed word recognition. The other possible reason is that major ERP components, such as the widely distributed N250 and N400, may reflect the bulk of processing at a given level of representation (or perhaps resonant activity across two adjacent levels, as argued above), but such processing could be evident in the ERP signal at an earlier point in time given sufficient measurement sensitivity.

The Present Study

The present study provides a further combination of masked priming and ERP recordings to examine effects of high-frequency orthographic neighbor primes. These priming effects will be compared with the effects of repetition primes in Experiment 1, and with nonword neighbor primes in Experiment 2. Based on the IAMs account of inhibitory priming effects from orthographic neighbors as reflecting competitive interactions at the level of whole-word orthographic representations, and based on our interpretation of the ERP components found in prior masked priming studies, we expect to see a divergence in the effects of word neighbor primes compared with both repetition primes (Experiment 1) and nonword neighbor primes (Experiment 2) starting at the end of the N250 component (i.e., at around 300 ms posttarget onset), and continuing into the N400.

Experiment 1

In Experiment 1 participants were presented with brief (48 ms) visual primes that were masked by both a forward and backward pattern mask and were rapidly (12 ms later) followed by a target word that was a full repetition of the prime (e.g., fable-FABLE [fable-FABLE]), a target word that was an orthographic neighbor of the prime (e.g., faute-FAUNE [error-WILDLIFE]), or a target word that was unrelated to the prime (e.g., pigne-FABLE [pinecone-FABLE], tueur-FAUNE [killer-WILDLIFE]). Participants were instructed to silently read all stimuli and to press a button to occasional probe words in a particular semantic category (animals). ERPs were time-locked to the onset of the targets and recorded for 1,000 ms after the onset of target words.

Method

Participants. Twenty eight undergraduate students (18–28 years old) at the University of Provence received 15€ for participation in this experiment. All were right-handed native speakers of French with normal or corrected to normal vision. Eight of these participants were excluded from analysis because of excessive movement artifacts during the experiment.

Design and stimuli. The critical stimuli for this experiment were 180 pairs of 4–6 letter French words. The first member of each pair was referred to as the prime and the second as the target. All the targets had a printed frequency lower than 20 occurrences per million (New, Pallier, Ferrand, & Matos, 2001). All targets had at least one high frequency orthographic neighbor (average printed frequency = 213 occurrences per million). Half of the targets were used to test for priming from a high-frequency neighbor, and the remaining targets were used to test for effects of repetition priming.[1] These two sets of 90 targets were separated into two subsets to create two lists of experimental stimuli presented to different participants. Targets paired with a related prime (either repetition or orthographic neighbor) in one list were paired with an unrelated prime in the other list and vice versa. In this way, participants saw each target word once only, but were tested in each experimental condition with different targets. However, across participants each item occurred an equal number of times in both the related and unrelated conditions. Type of Prime (repetition vs. neighbor) was crossed with Priming (related vs. unrelated prime) in a 2 × 2 factorial design. Unrelated prime-target pairs were formed by re-arranging the related prime-target pairs whereas ensuring that there was minimal orthographic overlap and semantic overlap between primes and targets in the re-pairings. Note that this implies that the unrelated primes were high-frequency words in the neighbor prime condition, and low-frequency words in the repetition prime condition. Following Davis and Lupker (2006), one additional constraint in the selection of the primes and targets in the orthographic neighbor condition was that each prime-target pair had at least one shared neighbor (e.g., "fauve" is a neighbor of both the prime "faute" and the target "faune"). The two sets of target stimuli were matched for frequency with an average of five occurrences per million (New et al., 2001) and number of neighbors ($N = 7.9$). An additional set of noncritical stimulus pairs was formed by 15 pairs of animal names. These words were used as probe items in a go/no-go semantic categorization task.

Procedure. All visual stimuli were displayed in the center of a CRT monitor as white letters on a black background in Courier New font (size 18). The background luminance of the screen was ~1 cd/m^2 and stimulus luminance was ~33 cd/m^2. Each trial began with a fixation stimulus for 2,500 ms followed by a forward mask composed of six hash marks (######) for a duration of 500 ms. The forward mask was replaced at the same location on the screen by a lowercase prime item for 48 ms. The prime was replaced by a backward mask (######) that remained on the screen for 12 ms and was replaced by the visual target in uppercase letters for a duration of 500 ms. Each trial ended with a 2,000 ms blank screen. Participants were instructed to rapidly press a response button whenever they detected an animal name in the target position, and were told to read all other words passively (i.e., the critical stimuli did not require an overt response). Figure 2 summarizes the sequence of events on each trial. Participants were

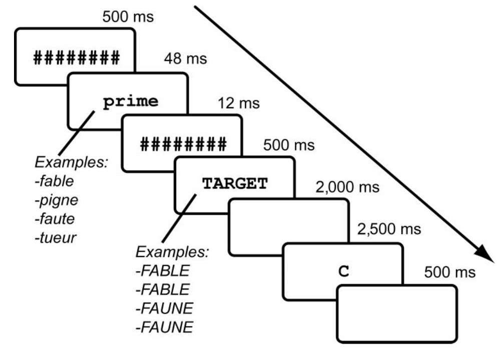

Figure 2. A typical trial with examples of the various types of items in the prime and target positions. Note that no participant was presented with any word on more than one trial, and that unrelated primes were formed by re-arranging the related primes.

asked to refrain from blinking and moving their eyes when the fixation stimulus appeared on the screen to minimize eye blink artifact during the recorded trials. A short practice session was administered before the main experiment to familiarize participants with the procedure and the categorization task.

Electroencephalogram recording procedure. After completing informed consent, participants were seated in a comfortable chair in a sound attenuated darkened room and dimly illuminated room. The electroencephalogram (EEG) was recorded continuously through the Active Two Biosemi system from 64 active Ag-AgCl electrodes mounted on an elastic cap (Electro-Cap Inc.) that was positioned according to the 10-10 International system (American Clinical Neurophysiology Society, 2006). Two additional electrodes (CMS/DRL nearby PZ) were used as an online reference (for a complete description, see Schutter, Leitner, Kenemans, & van Honk, 2006; www.biosemi.com). The montage included 10 midline sites and 27 sites over each hemisphere (see Figure 3). Four additional electrodes were used to monitor eye movements and blinks (two placed at lateral canthi and two below the eyes), and two additional electrodes were used for offline re-referencing (placed behind the ears on mastoid bone). Continuous EEG was digitized at 256 Hz and filtered offline (20 Hz low-pass, 24 dB/octave) using EEGLAB software (Delorme & Makeig, 2004). All electrode sites were re-referenced offline to the average of the right and left mastoids. Epochs with eye movements, blinks, or electrical activities greater than ±50 μV were rejected. To maintain an acceptable signal-to-noise ratio, a lower limit of 35 artifact-free trials per participant per condition was set. On this basis, eight participants were excluded from further analysis.

Data and analysis. ERPs were calculated by averaging the EEG time-locked to a point 100 ms pretarget onset and lasting until 1,000 ms posttarget onset. A 100 ms pretarget period was used as the baseline. Only trials without muscle artifact or eye movement/blink activity were included in the averaging process.

[1] Different target words were tested in the repetition and neighbor prime conditions. This was because of the numbers of items per condition per participant that are necessary to obtain an acceptable signal-to-noise ratio in the ERP recordings.

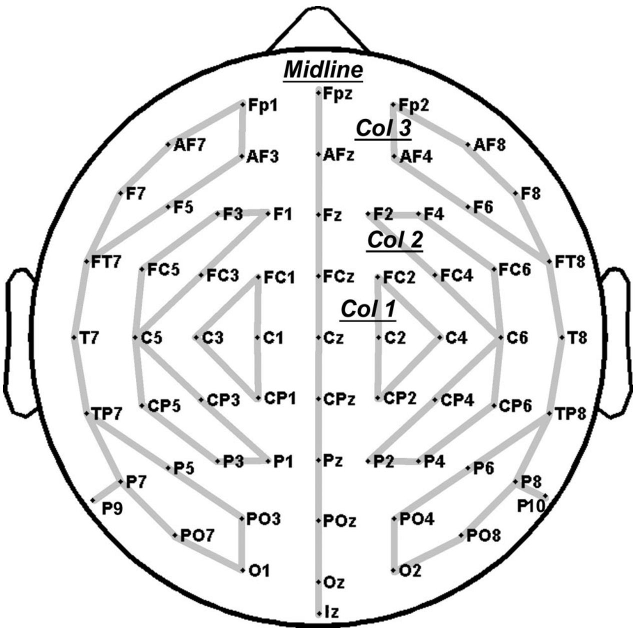

Figure 3. Electrode montage and four analysis columns used for ANOVAs.

Separate ERPs were formed for the four experimental conditions defined by the factorial combination of the factors Priming (related vs. unrelated) and Type of Prime (repetition vs. orthographic neighbor). We employed an approach to data analysis in which the head is divided up into seven separate parasagittal columns along the antero-posterior axis of the head (see Figure 3). The electrodes in each of three pairs of lateral columns and one midline column were analyzed in separate ANOVAs. Three of these analyses (column 1, column 2, and column 3) involved a hemisphere factor (left vs. right). The fourth analysis only involved midline electrode sites (see Figure 3). Finally, a fifth analysis included an anterior/posterior factor dividing all electrode sites, except those lying on the horizontal central line (T7, C5, C3, C1, Cz, C2, C4, C6, and T8), into two regions (anterior vs. posterior). We used the columnar approach to analyzing the spatial component of the ERP data because it provides a thorough analysis of the entire head breaking the scalp up into regions (left and right, front and back), whereas at the same time allowing single or small clusters of sites to influence the analysis (using a single electrode factor and a large number of sites can easily mask small regional effects). We have used this approach successfully in a number of previous studies (e.g., Holcomb & Grainger, 2006). The Geisser and Greenhouse (1959) correction was applied to all repeated measures with more than one degree of freedom (corrected *p* values are reported). Only significant effects are reported, except when nonsignificance is relevant for the hypotheses being tested.

Results

Behavioral data. Participants successfully detected 95% (*SD* = 7.8) of animal probe words.

Electrophysiological data.

Visual inspection of ERPs. Plotted in Figures 4 and 5 are the ERPs contrasting the conditions with related and unrelated primes for repetition priming (Figure 4) and orthographic neighbor priming (Figure 5). As can be seen in these figures, the ERPs in this experiment produced a set of positive and negative deflections consistent with previous masked priming studies (e.g., Holcomb &

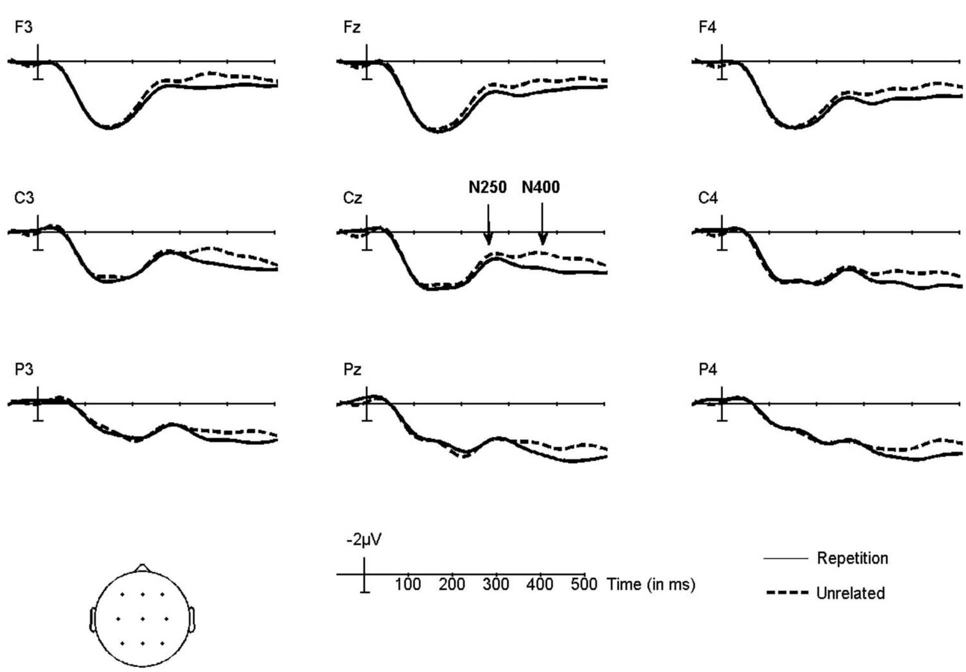

Figure 4. ERPs time locked to target onset in two conditions (solid line: repetition prime, dashed line: unrelated) over nine electrode sites in Experiment 1.

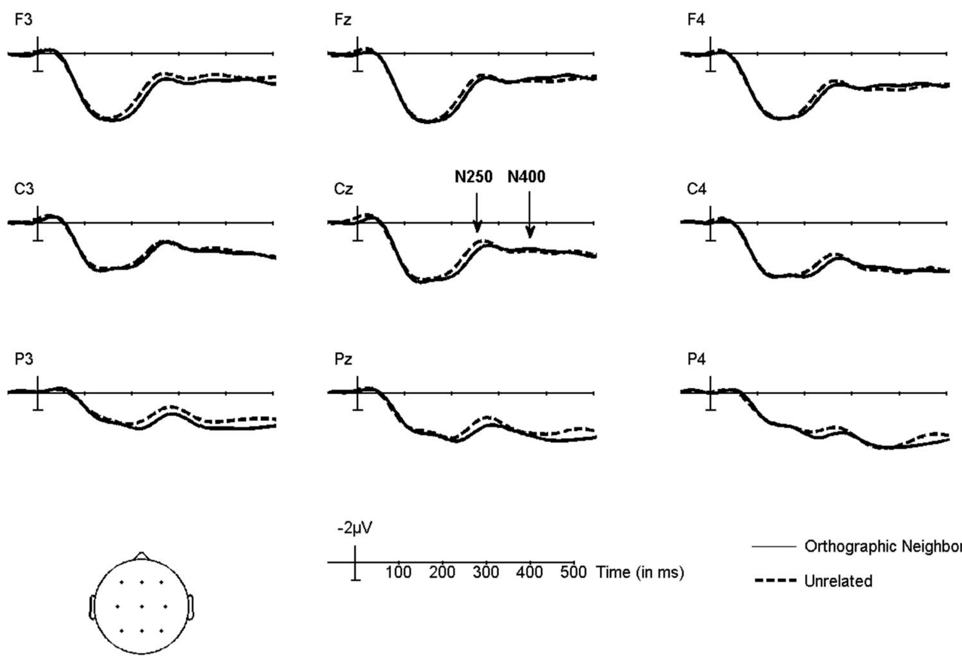

Figure 5. ERPs time locked to target onset in two conditions (solid line: orthographic neighbor prime, dashed line: unrelated) over nine electrode sites in Experiment 1.

Grainger, 2006). In examining the ERPs in these figures (and those of Experiment 2) it is important to keep in mind that the waves to both prime and target words are an amalgamation of overlapping components produced by the rapid succession of mask – prime – mask – target stimuli and therefore the traditional componentry seen in unmasked word processing studies is not apparent here. Holcomb and Grainger (2006) argued that it is more important in interpreting the results for ERP masked priming studies to concentrate on the differences between related and unrelated conditions where all potentially confounding effects of pretarget events have been controlled. Starting at approximately 200 ms and lasting until about 300 ms, target words following unrelated primes produced more negative-going ERPs than targets following repetition primes (Figure 4) or orthographic neighbor primes (Figure 5). This N250 effect can best be seen in Figure 6 that plots the differences waves for the two priming conditions. Following the N250, in the traditional window of the N400 component, the unrelated targets also produce a more negative-going response, especially when contrasted with the repetition prime condition (see Figure 6).

Analysis of ERP data.

175–300 ms target epoch (N250). As can be seen in Figures 4 and 5, between 175 and 300 ms, target words following unrelated primes were associated with a larger negativity than target words following the same prime word (i.e., repetition) or a prime word that differed by a single letter (i.e., orthographic neighbor). This observation was confirmed by the presence of an effect of PRIMING that interacted with ELECTRODE SITE across all electrode sites ($F(63, 1197) = 2.71$, $MSE = 1.12$, $p = .02$, $\eta_p^2 = .12$) and in two columns (column 1: $F(3, 57) = 6.65$, $MSE = 0.55$, $p < .01$, $\eta_p^2 = 0.25$; column 3: $F(13, 247) = 3.13$, $MSE = 1.74$, $p = .04$, $\eta_p^2 = .14$). The PRIMING × ELECTRODE SITE interaction reflects the fact that the effect of PRIMING was only significant at the anterior electrode sites of these columns (column 1 at FC1, FCz, and FC2): $F(1, 19) = 4.40$, $MSE = 11.24$, $p = .04$, $\eta_p^2 = .18$; column 3 at AF8, F6, and F8: $F(1, 19) = 5.16$, $MSE = 6.59$, $p = .03$, $\eta_p^2 = .21$). Although Figure 6 shows that the effects of orthographic neighbor primes appear to be more widespread than the effects of repetition primes in this time window, the critical two-way interaction between PRIMING × TYPE OF PRIME was not significant and did not interact with any of the electrode configurations (all Fs < 1).

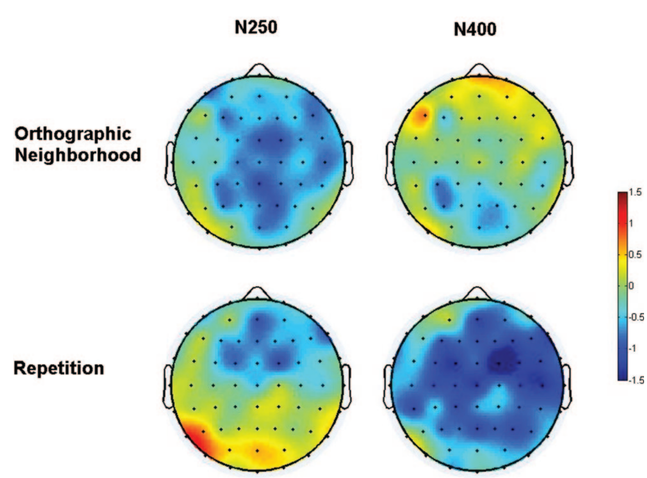

Figure 6. Voltage maps centered on the two epochs used in the statistical analyses. The maps represent voltage differences at each electrode site calculated by subtracting the voltage values in the related prime condition from the voltage values in the corresponding unrelated prime condition in Experiment 1.

300–550 ms target epoch (N400). Examination of Figures 4 and 5 reveals that this interval contains the bulk of the activity resembling the classic N400 component. As can be seen in Figures 4 and 5, targets following unrelated primes produced a more negative-going wave in this epoch than target words following repeated primes, whereas the differences between targets following unrelated and orthographic neighbor primes were quite small. Figure 6 clearly reveals the widespread nature of repetition priming effects in this time window, and the notable absence of priming effects from orthographic neighbor primes. These observations were confirmed by the presence of a PRIMING × TYPE of PRIME interaction in column 1 ($F(1, 19) = 5.07$, $MSE = 12.34$, $p = .03$, $\eta_p^2 = .21$). Follow-up analyses revealed a significant effect of REPETITION PRIMING, $F(1, 19) = 8.08$, $MSE = 15.58$, $p = .01$, $\eta_p^2 = .29$, and no effect of ORTHOGRAPHIC NEIGHBOR PRIMES in this column ($F < 1$).

Discussion

The results of Experiment 1 are in line with the predictions of the lexical inhibition account of priming from orthographic neighbors (Jacobs & Grainger, 1992; Segui & Grainger, 1990) and the functional significance of certain ERP components proposed by Holcomb and Grainger (2006, 2007) and Grainger and Holcomb (2009). Repetition priming and priming from orthographic neighbors showed similar effects on the N250 component, although repetition priming effects were less widely distributed. On the other hand, whereas repetition-priming effects became stronger and more widely distributed on the N400 component, the effects of orthographic neighbor primes were greatly reduced. This provides converging evidence that the bulk of lexical influences on visual word recognition, at least in the conditions of masked priming, are arising after the N250 component. The fact that orthographic neighbor primes did not significantly affect ERP waveforms in the time window of the N400 suggests that the facilitatory effects of orthographic overlap, as seen in the reduced negativity following repetition primes in this time window, were offset by an inhibitory influence of orthographic neighbor primes.

Nevertheless, it could be argued that the differences between repetition priming and priming from orthographic neighbors found in Experiment 1 are not because of the inhibitory influence of neighbor primes, but simply because of the different level of orthographic overlap in the two related prime conditions (full vs. partial). Therefore, Experiment 2 provides a further investigation of this issue by comparing priming effects from orthographic neighbors that are high-frequency words (as in Experiment 1) with the effects of nonword orthographic neighbors matched in terms of their orthographic overlap with targets. As noted in the introduction, orthographically related nonword primes tend to produce facilitatory priming in the lexical decision task (e.g., van Heuven et al., 2001). Furthermore, a number of studies have shown facilitatory priming from nonword primes and inhibitory priming from word primes in the same experiments (Davis & Lupker, 2006; De Moor et al., 2007; Ferrand & Grainger, 1996). Therefore, we expect to observe the same pattern of effects as in Experiment 1, with a dissociation between the two types of priming (word neighbors vs. nonword neighbors) emerging after the N250 component. Experiment 2 also provides a direct comparison of ERP effects and behavioral effects of orthographic neighbor primes by using the lexical decision task,[2] and slightly increasing prime duration to be in line with the prime durations typically used to obtain behavioral effects. Indeed, prior behavioral research has shown that the size of the inhibitory effects of orthographic neighbor primes increases with small increases in prime duration in the lexical decision task (De Moor et al., 2007; Grainger, 1992).

Experiment 2

Experiment 2 provides a replication of the effects of orthographic neighbor primes found in Experiment 1 using a different task–lexical decision. The other main difference with respect to the first experiment is that the repetition condition from Experiment 1 is replaced with a nonword neighbor prime condition. This manipulation of the lexical status of prime stimuli while maintaining degree of orthographic overlap constant will provide a further means to distinguish prelexical and lexical influences of orthographic neighbor primes.

Method

Participants. Thirty one undergraduate students (average age 21.2 years old, 9 men) at the University of Provence received 15€ for participation in this experiment. All were right-handed native speakers of French with normal or corrected to normal vision. Six of these participants were excluded from analysis because of excessive movement artifacts during the experiment.

Design and stimuli. A new set of prime-target pairs were generated with low-frequency target words and nonword primes. None of the target words had orthographic neighbors, and their average printed frequency was six occurrences per million (New et al., 2001). Orthographically related nonword primes were created by changing a single letter in the target word with a different letter to produce an orthographically legal letter string (e.g., hibit – HABIT [CLOTHES]). The target was the only orthographic neighbor of these prime stimuli. The word neighbor prime condition included in this experiment used the same set of low-frequency word targets and high-frequency orthographic neighbor primes as Experiment 1, such that Type of Prime (word vs. nonword) was crossed with Priming (related vs. unrelated) in a 2 × 2 factorial design. Therefore, as in Experiment 1, different sets of low-frequency target word were tested in the two levels of the Type of Prime factor. Unrelated prime – TARGET pairs were formed by re-arranging the related prime–target pairs within each level of the Type of Prime factor, whereas ensuring that there was minimal orthographic and semantic overlap between primes and targets in the re-pairings. Two lists of 180 prime–target pairs were constructed for word targets (90 word prime trials and 90 nonword prime trials), counterbalancing prime–target relatedness across lists such that targets preceded by a related prime in one list were paired with an unrelated prime in the other list, as in Experiment

[2] A change in task was necessary. Although there are very few studies examining this question, it has been shown that responses in a semantic categorization experiment (e.g., animal vs. nonanimal) are affected by whether or not the target's neighbors belong to the same semantic category or not (Pecher, Zeelenberg, & Wagenmakers, 2005). Therefore, this would have necessitated a complete change in stimuli and very likely too few stimuli per condition for an ERP study.

1. An additional set of 180 nonword target trials were constructed for the purposes of the lexical decision task. Half of the nonword targets were primed by word primes that were either orthographically related or unrelated to the target, and half were primed by related or unrelated nonwords (e.g., oncle-ONPLE, glace-ONPLE, lovre-LUVRE, ramio-LUVRE; where "oncle" and "glace" are words in French).

Procedure. This was identical to that of Experiment 1, except for the change in task and the increase in prime duration to 59 ms. Participants were instructed to decide as rapidly and as accurately as possible whether or not the target was a word in French (lexical decision task). They responded yes by pressing one of the two response buttons with the thumb of their preferred hand and no by pressing the other response button with the thumb of the other hand. Reaction times, measured from target onset until participants' response, were accurate to the nearest millisecond. A short practice session (20 trials) was administered before the main experiment to familiarize participants with the procedure of the lexical decision task.

EEG recording procedure and data analysis. These were identical to Experiment 1.

Results

Behavioral data. Means per condition of correct response times (RTs) lying between 100 ms and 2,000 ms (98.7% of the data) to word targets are shown in Figure 7. An ANOVA on these RTs was performed with TYPE of PRIME (word vs. nonword) and PRIMING (orthographic neighbor vs. unrelated) as main factors. There was a significant main effect of TYPE of PRIME (F(1, 24) = 40.34, MSE = 1146, $p < .001$, $\eta_p^2 = .62$). Longer RTs were observed for word targets following a word prime than word targets following a nonword prime. There was no main effect of PRIMING ($p > .1$), but a significant TYPE of PRIME × PRIMING interaction (F(1, 24) = 47.52, MSE = 509, $p < .001$, $\eta_p^2 = .66$). Follow-up analyses revealed significantly longer RTs when target words followed a word neighbor prime than an unrelated prime (F(1, 24) = 18.25, MSE = 428, $p < .001$, $\eta_p^2 = .43$), and shorter RTs following a nonword neighbor prime than an unrelated prime (F(1, 24) = 17.11, MSE = 1012, $p < .001$, $\eta_p^2 = .41$). A direct comparison of RTs in the related word and related nonword conditions revealed a significant difference, F(1, 24) = 72.69, MSE = 944, $p < .001$, $\eta_p^2 = .75$, whereas the two unrelated conditions did not differ significantly, $p > .1$.

An ANOVA on the error data for word targets showed a main effect of TYPE of PRIME (F(1, 24) = 33.39, MSE = 21.29, $p < .001$, $\eta_p^2 = .58$), no effect of PRIMING ($p > .07$), and a significant TYPE of PRIME × PRIMING interaction (F(1, 24) = 4.54, MSE = 21.06, p = .04, $\eta_p^2 = .15$). The inhibitory effect of word neighbor primes was significant, F(1, 24) = 8.32, MSE = 20.93, $p < .01$, $\eta_p^2 = .25$, whereas the facilitatory effect of nonword neighbor primes was not significant ($p > .1$). As with the RT data the two related conditions differed significantly, F(1, 24) = 23.13, MSE = 28.70, $p < .001$, $\eta_p^2 = .49$. However, percent error also differed significantly in the two unrelated conditions, with more errors in the unrelated word prime condition, F(1, 24) = 10.48, MSE = 13.60, $p < .01$, $\eta_p^2 = .30$.

Electrophysiological data.

Visual inspection of ERPs. Plotted in Figures 8 and 9 are the ERPs contrasting the conditions with related and unrelated primes for word targets preceded by word primes (Figure 8) and nonword primes (Figure 9). As can be seen in these figures, the ERPs in this experiment produced a set of positive and negative deflections consistent with the previous experiment.

Analysis of ERP data.

175–300 ms target epoch (N250). As can be seen in Figures 8 and 9, between 175–300 ms, target words following unrelated primes were associated with a larger negativity compared with target words following a word neighbor prime or a nonword neighbor prime. Figure 10 reveals the widespread nature of these priming effects for both word and nonword neighbor primes in this time window. These observations were confirmed by the presence of an effect of PRIMING over all electrode sites (F(1, 24) = 5.20, MSE = 136.05, p = .03, $\eta_p^2 = .17$) and in three columns (Midline: F(1, 24) = 7.14, MSE = 24.94, p = .01, $\eta_p^2 = .22$; column 1: F(1, 24) = 5.21, MSE = 29.39, $p < .001$, $\eta_p^2 = .36$; column 2: F(1,

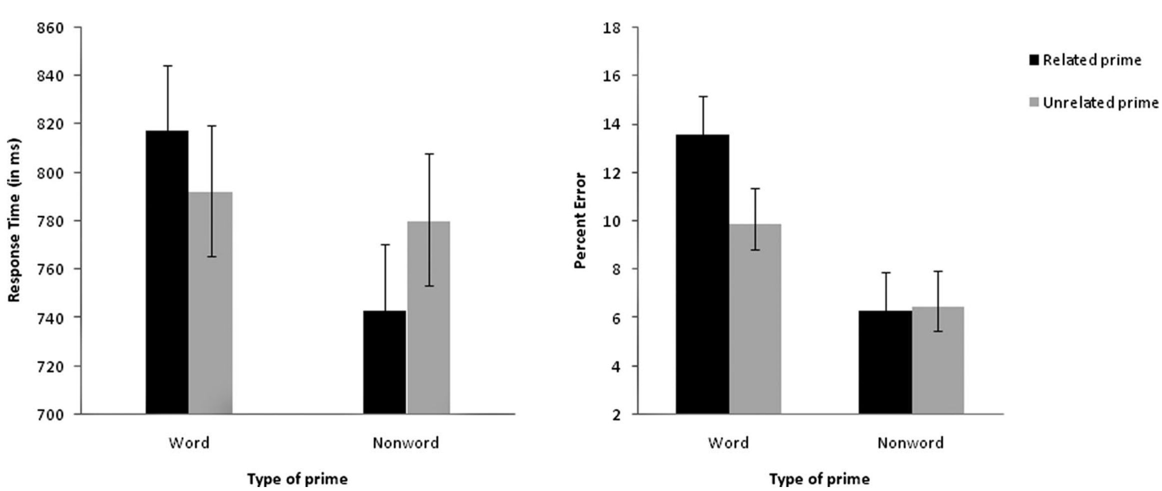

Figure 7. Lexical decision latencies (in milliseconds, left panel) and percent error (right panel) to target words preceded by a word neighbor prime or by a nonword neighbor prime compared with unrelated word and nonword primes in Experiment 2.

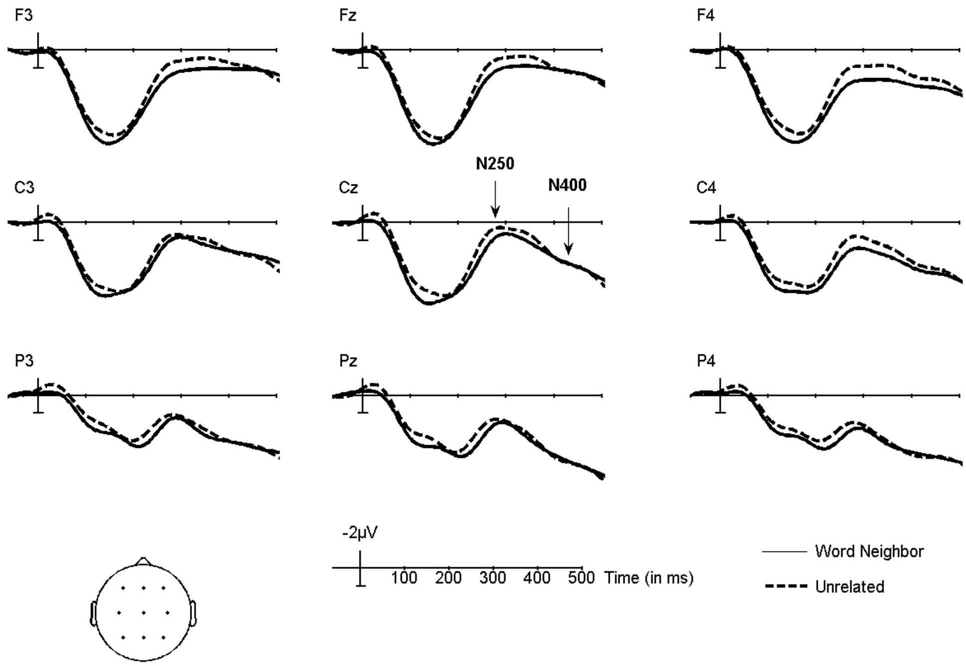

Figure 8. ERPs time locked to target onset in two conditions (solid line: word neighbor prime, dashed line: unrelated) in Experiment 2.

24) = 5.09, *MSE* = 46.35, $p = .03$, $\eta_p^2 = .17$). There was no interaction between PRIMING and TYPE of PRIME in this epoch (all *F*s < 1).

300–550 ms target epoch (N400). Examination of Figures 8 and 9 reveals that this interval contains the bulk of the N400 component. Figure 9 shows that targets following a nonword neighbor prime produced less negativity than the unrelated target words, whereas in Figure 8 it can be seen that the effect of word neighbor primes were very small and highly localized in this time window. Figure 10 clearly reveals the widespread nature of the effect of nonword neighbor primes in this epoch, and the almost total absence of priming effects for word neighbor primes. These observations were confirmed by the presence of a PRIMING × TYPE of PRIME interaction in two analysis columns (Midline: $F(1, 24) = 8.95$, *MSE* = 17.45, $p < .01$, $\eta_p^2 = .27$; column 1: $F(1, 24) = 4.54$, *MSE* = 19.67, $p = .04$, $\eta_p^2 = .15$). Follow-up analyses showed that target words following a nonword neighbor prime were associated with a reduced negativity compared with target words following an unrelated prime ($F(1, 24) = 4.32$, *MSE* = 132.66, $p = .04$, $\eta_p^2 = .15$). The effect of word neighbor primes was not significant at any of the electrode configurations (all *F*s < 1).

Effects of prime lexicality. Since in Experiment 2 the two related conditions and the two unrelated conditions only varied with respect to a single dimension (lexicality), we performed contrasts across these conditions to investigate the effects of prime lexicality independently of prime relatedness.[3] These analyses were performed using the two time windows of the main analysis, and the results are summarized in Figure 11.

In the 175–300 ms time window, the comparison between the related word and related nonword conditions revealed a significant effect of prime lexicality over all electrode sites, $F(1, 24) = 6.02$, *MSE* = 85.74, $p = .02$, $\eta_p^2 = .20$. The related word condition produced a reduced negativity than the related nonword condition in this epoch. However, the two unrelated conditions also differed significantly, over all electrode sites, with a larger negativity in the unrelated nonword condition, $F(1, 24) = 8.55$, *MSE* = 77.74, $p < .01$, $\eta_p^2 = .26$. In the 300–550 ms time window, the comparison between the related word and related nonword conditions revealed a significant difference over all electrode sites, $F(1, 24) = 11.67$, *MSE* = 111.79, $p < .01$, $\eta_p^2 = .32$, whereas the two unrelated conditions did not differ significantly, $p > .1$. The related word condition produced a larger negativity than the related nonword condition in this epoch.

Discussion

The behavioral results of Experiment 2 replicate the standard behavioral finding of inhibitory priming from high-frequency orthographic neighbor primes in the lexical decision task (e.g., Davis & Lupker, 2006; Segui & Grainger, 1990). At the same time our nonword neighbor primes facilitated responses to target words, thus replicating prior research showing such facilitatory priming when the target word is the unique orthographic neighbor of the nonword prime stimulus (e.g., van Heuven et al., 2001). The ERP data are in line with the results of Experiment 1. There was a very similar pattern of effects for word and nonword neighbor primes on the N250 component. In

[3] These comparisons should in general be avoided since they involve different sets of target words that might differ with respect to possible uncontrolled variables. The main statistical comparisons of the present study all involved the exact same set of prime and target words, with only the pairing of primes and targets varying across conditions.

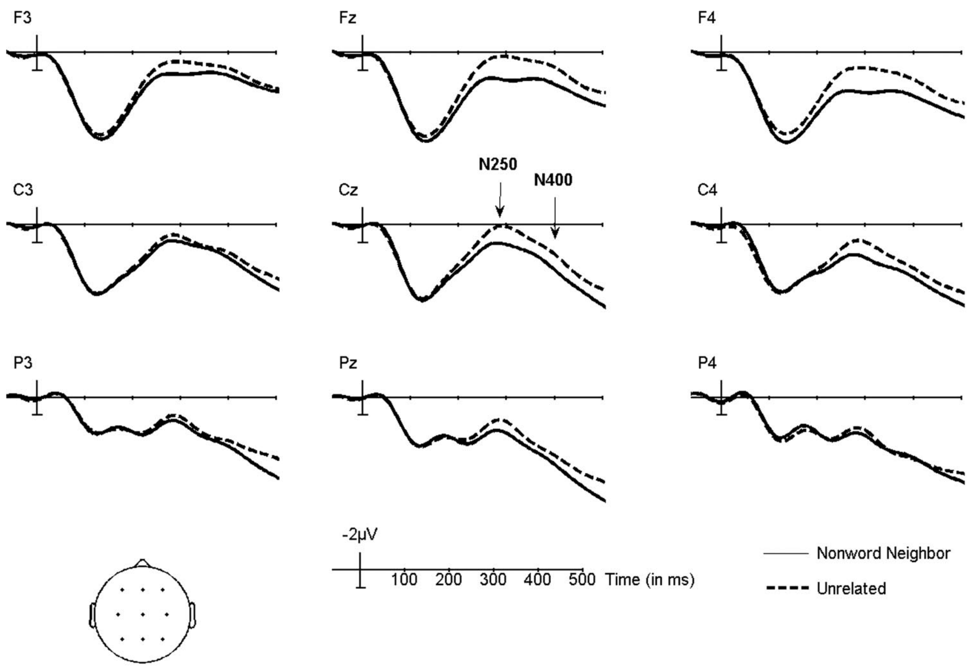

Figure 9. ERPs time locked to target onset in two conditions (solid line: nonword neighbor prime, dashed line: unrelated) in Experiment 2.

the N400 time window, on the other hand, priming from word neighbors differed significantly from the priming effects found with nonword neighbors. As in Experiment 1, word neighbor primes produced little or no priming in this epoch. Nonword neighbor primes, on the other hand, showed the standard effect of priming on the N400 with reduced negativities in the related prime condition.

Finally, a direct comparison of the two related prime conditions and the two unrelated conditions revealed that it is indeed the related conditions that are driving the differences between word and nonword neighbor primes seen in the behavioral results and ERPs in the N400 epoch. This analysis also revealed an effect of prime lexicality in the earlier time window, suggesting that whether the prime is a word or not (independently of its relation to the target) influences ERPs during the early phases of target word processing.

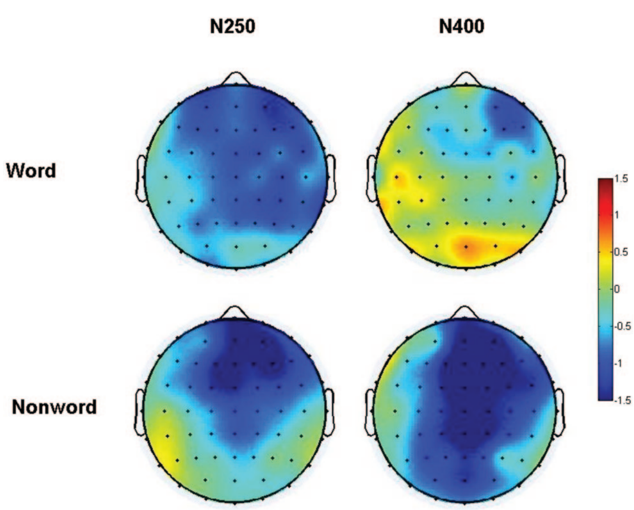

Figure 10. Voltage maps centered on the two epochs used in the statistical analyses. The maps represent voltage differences at each electrode site calculated by subtracting the voltage values in the related prime condition from the voltage values in the corresponding unrelated prime condition in Experiment 2.

General Discussion

The present study combined the masked priming paradigm with electrophysiological recordings to provide a more fine-grained temporal analysis of the effect of primes that are high-frequency orthographic neighbors of target words. According to one prominent account of the inhibitory effects of orthographic neighbor priming found in behavioral studies, it is lateral inhibitory connections between whole-word orthographic representations that are the source of the inhibitory priming effect (Davis & Lupker, 2006; Grainger & Jacobs, 1996; Jacobs & Grainger, 1992). Based on this account and our prior work combining ERPs and masked priming, we predicted a very specific pattern of priming effects from such word neighbor primes compared with the effects of repetition priming (Experiment 1) and nonword neighbor priming (Experiment 2). According to Holcomb and Grainger (2006, 2007; Grainger & Holcomb, 2009), the N250 and N400 components, found to be modulated by masked priming, are thought to reflect the transition from form-level processing (orthographic and phonological) to semantic-level processing during visual word recognition. The N250 component is thought to reflect the mapping of prelexical form representations onto whole-word form representations, whereas the N400 would reflect the mapping of whole-word form representations onto semantics. Furthermore, the N250 is hypothesized to reflect stabilization of activation in prelexical

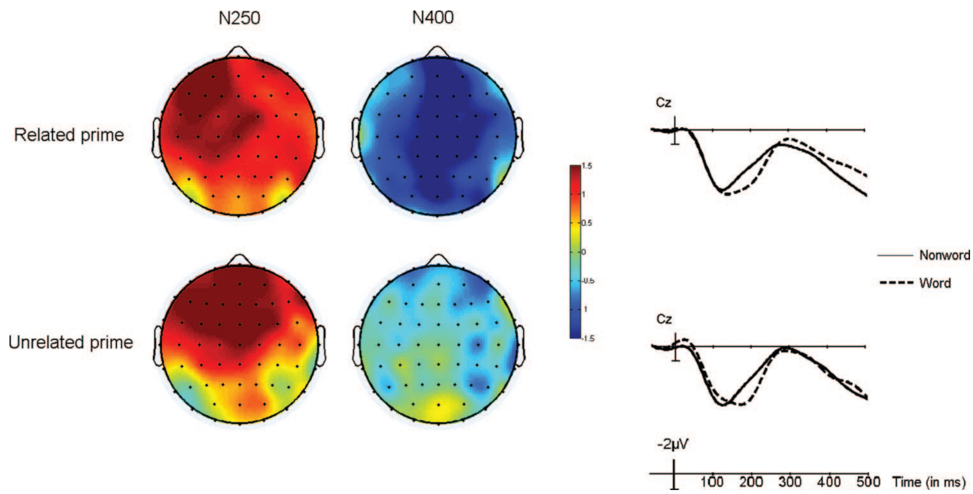

Figure 11. Left: Voltage maps centered on the two epochs used in the statistical analyses. The maps represent voltage differences at each electrode site calculated by subtracting the voltage values in the word prime condition from the voltage values in the corresponding nonword prime condition in Experiment 2, for related primes (upper) and unrelated primes (lower). Right: Blowup of site Cz showing effects of prime lexicality for related primes (upper) and unrelated primes (lower).

representations as well as the initial build-up of activation in whole-word form representations, whereas the N400 would reflect stabilization in activation at the level of whole-word form representations. Therefore, it was argued that if the effects of word neighbor primes reflect competitive interactions between whole-word form representations, then these effects should become evident in the ERP signal somewhere in between the N250 and N400 components, and remains effective throughout the N400.

The effects of word neighbor primes were compared with effects of repetition priming in Experiment 1 and effects of nonword neighbor primes in Experiment 2. As argued above, we expected to see similar patterns of priming effects for repetition primes and nonword neighbor primes in both the N250 and N400 ERP components, and both of these priming effects were expected to line-up with the effects of word neighbor primes in the N250 component but differ in the N400 component. Therefore, we predicted main effects of priming and no interaction with type of prime in the N250 component, and an interaction between priming and type of prime in the N400. The results of the present study are in line with these predictions. All types of prime showed similar priming effects in the N250 component, whereas in the N400 component the word neighbor prime condition produced a distinct pattern of effects in both experiments. This pattern was particularly clear in Experiment 2 where the only difference between the two types of prime was their lexicality.

The results of the present study therefore provide support for the hypothesis that the inhibitory effects of word neighbor primes found in behavioral responses reflect competitive interactions between whole-word representations that influence the final phase of homing in on a unique interpretation of the target word. The results are also supportive of the interpretative framework proposed by Holcomb and Grainger (Grainger & Holcomb, 2009; Holcomb & Grainger, 2006, 2007), according to which the shift from form-level processing to semantic-level processing during visual word recognition is reflected in the transition between the N250 and the N400 ERP components. As noted in the introduction, this analysis may only be applicable to results obtained with masked priming, and some clarification is still in order with respect to how such a framework could accommodate reports of lexical and semantic influences arising earlier in the course of visual word recognition (e.g., Hauk et al., 2006; Hauk & Pulvermüller, 2004).

The priming effects found with word neighbor primes in the present study are in line with the findings of Holcomb, Grainger, and O'Rourke (2002) in a study manipulating the number of orthographic neighbors of word targets (in the absence of priming). Words with many orthographic neighbors were found to generate significantly more negative-going waveforms in the region of the N400 than words with small numbers of orthographic neighbors (see Debruille, 1998, for an earlier report of a similar finding). This increased negativity for words with more orthographic neighbors was found in both a lexical decision and a semantic categorization experiment.

In the present study, word neighbor primes did not generate significantly greater negativity than unrelated primes. Instead, in the N400 time window, these primes did not significantly affect target word processing relative to unrelated word primes. We interpret this null effect as the combined influence of an underlying facilitatory component, as reflected in the reduced negativity found with nonword neighbor primes, plus an inhibitory influence of word neighbor primes via competitive interactions across whole-word representations. This account predicts that a direct comparison of the related word and related nonword prime conditions tested in Experiment 2 should reveal significantly greater negativity in the word prime condition in the N400 time window. This was found to be the case.

Finally, the pattern of priming effects in the N400 component is compatible with the knowledge inhibition account of variations in N400 amplitude proposed by Debruille (2007). Within this theoretical context, orthographic neighbors of a given target word represent activated but inappropriate knowledge that must be inhibited for successful target recognition. Although we interpret the increased N400 amplitude as reflecting increased difficulty in processing the target word as the result of inhibition from its orthographic neighbor(s), the knowledge inhibition hypothesis proposes that it reflects inhibitory processes operating on the nonperceived neighbor(s).

The present study also revealed significant priming effects in the N250 component that did not discriminate between the different types of priming manipulation (repetition, word neighbor, nonword neighbor). This fits with our proposal that the N250 reflects the mapping of prelexical form representations onto whole-word form representations during visual word recognition (Grainger & Holcomb, 2009; Holcomb & Grainger, 2006, 2007; Kiyonaga et al., 2007). Several studies have provided additional support for this, showing modulation of N250 amplitude for various types of prelexical orthographic manipulation, such as transposing letters in prime stimuli (e.g., tarin-train vs. tosin-train: Carreiras, Vergara, & Perea, 2009; Grainger et al., 2006), and delaying the appearance of some of the target's letters (Carreiras, Gillon-Dowens, Vergara, & Perea, 2009). However, N250 amplitude has also been shown to be sensitive to semantic overlap across prime and target stimuli such as with morphologically related items (Morris, Franck, Grainger, & Holcomb, 2007), and with noncognate translation equivalents in bilingual participants (Midgley, Holcomb, & Grainger, 2009). Our preferred interpretation of these early semantic influences is sketched within the framework of a cascaded interactive-activation account of visual word recognition. The idea is that although the bulk of the N250 may reflect the feedforward mapping of prelexical form representations onto whole-word form representations, during this time the fastest feedforward processes have already reached semantic representations and are starting to feedback information to lower levels of processing, hence influencing processing at those levels. Only future research will clarify such important issues, and hopefully, reconcile what still appears to be contradictory evidence from ERP studies concerning the time-course of component processes in visual word recognition.

Summing up, the key results of the present study provide support for the hypothesis that orthographic neighbors interfere in the process of visual word recognition, and that this interference is reflected in an increased negativity in the ERP waveform starting around 300 ms poststimulus onset. This strongly suggests that the inhibitory neighbor priming effects found in behavioral studies cannot simply be the result of task-specific, decision-related processes. Lateral inhibitory connections between whole-word representations, as implemented in the IAM (McClelland & Rumelhart, 1981), therefore remain one viable explanation of this phenomenon (Grainger & Jacobs, 1996; Jacobs & Grainger, 1992).

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