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Orthographic and phonological processing in developing readers revealed by ERPs

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Abstract

The development of neurocognitive mechanisms in single word reading was studied in children ages 8–10 years using ERPs combined with priming manipulations aimed at dissociating orthographic and phonological processes. Transposed-letter (TL) priming (barin–BRAIN vs. bosin–BRAIN) was used to assess orthographic processing, and pseudohomophone (PH) priming (brane–BRAIN vs. brant–BRAIN) was used to assess phonological processing. Children showed TL and PH priming effects on both the N250 and N400 ERP components, and the magnitude of TL priming correlated positively with reading ability, with better readers showing larger TL priming effects. Phonological priming, on the other hand, did not correlate with reading ability. The positive correlations between TL priming and reading ability in children points to a key role for flexible sublexical orthographic representations in reading development, in line with their hypothesized role in the efficient mapping of orthographic information onto semantic information in skilled readers.

Descriptors: Masked priming, Reading development, N250, N400, Event-related potentials, Orthographic and phonological processing

Normal-hearing children's first exposure to language is with the auditory modality through which spoken language is naturally acquired, and when children learn to read they are typically taught how to map unfamiliar visual forms of written words onto the corresponding familiar sounds of spoken words. For most beginning readers, this process of phonological recoding provides the primary pathway from print to meaning (Ehri, 1992; Share, 1995). Reading research has asked how the mapping of orthographic information onto semantics develops during reading acquisition, and how the nature of phonological processing adapts in order to accompany this development (Castles & Nation, 2006; Grainger, Lété, Bertrand, Dufau, & Ziegler, 2012; Grainger & Ziegler, 2011). In the current study, we used masked pseudohomophone (PH) priming and transposed-letter priming (TL) combined with the recording of ERPs to dissociate phonological and orthographic contributions to single word reading in children spanning the age range when reading skills are typically mastered (8 to 10 years of age).

Previous behavioral and ERP studies have established masked priming as a useful tool for examining orthographic and phonological contributions to reading. A series of masked priming effects have been found in ERP studies with adults, and have been linked to different neurocognitive stages in visual word recognition (see Grainger & Holcomb, 2009, for a review). Two of these ERP effects are of particular interest here: (1) priming effects seen in a midlatency component, the N250, thought to reflect the neural system that maps sublexical orthographic and phonological representations onto whole-word representations (Grainger, Kiyonaga, & Holcomb, 2006); and (2) priming effects seen on a later component, the N400, thought to reflect the neural system that maps whole-word orthographic and phonological representations onto meaning (Holcomb & Grainger, 2006, 2007). The N250 component is sensitive to both orthographic and phonological processing as assessed, respectively, by orthographic and phonological priming manipulations (Grainger et al., 2006). Orthographic processes were isolated by TL priming (e.g., barin–BRAIN) and phonological processes were isolated by PH priming (e.g., brane–BRAIN). TL priming is thought to tap orthographic processing since TL priming effects are not observed for pseudohomophones of the TL primes (e.g., relobución–REVOLUCIÓN; note that B and V are pronounced as/b/in Spanish; Perea & Carreiras, 2006). PH priming taps phonological processing because the effects of PH primes are measured against carefully matched orthographic control primes (e.g., brant–BRAIN). Grainger et al. (2006) found a TL priming effect on the N250 component with a posterior scalp distribution

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(consistent with a locus in the ventral visual system). The pseudohomophone condition, on the other hand, produced an N250 priming effect with a more anterior distribution (consistent with a locus in auditory brain areas) that onset slightly later than the TL priming effect.

In single word reading, the N400 is thought to reflect the mapping of whole word orthographic and phonological representations onto meaning (Grainger & Holcomb, 2009). The N400 has been studied extensively in the context of reading development and has been suggested to index "integrative automaticity for word processing" (Coch, 2015). This component is also sensitive to lexicality, as differences between words, pseudowords, nonwords, and false fonts have been observed in both adults and children (Coch, 2015). In addition, word relatedness in priming paradigms has been found to modulate the N400 (e.g., Holcomb, Reder, Misra, & Grainger, 2005).

While the N400 has been well characterized in adults and children, N250 ERP priming effects, sensitive to orthographic and phonological processing, have been observed in typical reading adults, but how these are related to reading development and reading skills is yet to be investigated. Evidence for different developmental trajectories for orthographic and phonological processes has been reported in previous behavioral masked priming studies with children (e.g., Acha & Perea, 2008; Castles, Davis, Cavalot, & Forster, 2007; Davis, Castles, & Lakovidis, 1998; Pratarelli & Perry, 1994). The results of these studies suggest that there is both a relatively rapid shift to increasingly automatized orthographic processing that is accompanied by a decline in the use of slow and effortful process of phonological recoding during reading acquisition (Ehri, 2005; Grainger et al., 2012; Share, 1995; Wolf, 1991). Clear behavioral evidence for different developmental trajectories for orthographic and phonological processes was provided by Ziegler, Bertrand, Lété, and Grainger (2014) in a masked priming experiment testing children in Grades 1 (average age 6 years, 9 months) to Grade 5 (average age 10 years, 11 months) of elementary school with TL priming and PH priming. TL priming increased with grade, but PH priming did not. The stable PH priming may reflect the development of more automatized mechanisms for translating print to sound that would compensate for the decreased use of phonological recoding. The increase in TL effects with age, on the other hand, suggests that the development of flexible orthographic processing is an essential part of becoming a fluent reader (Grainger et al., 2012; Grainger & Ziegler, 2011). It is hypothesized that the flexible representation of sublexical orthographic information provides a more efficient mapping of orthography onto semantics, while being one important source of TL effects (Grainger, Dufau, & Ziegler, 2016; Ktori, Kingma, Hannagan, Holcomb, & Grainger, 2014). In line with this account is the finding that children (Grades 2–4) with larger sight-word vocabularies (measured by the TOWRE, Torgesen, Wagner, & Rashotte, 1999) make more migration errors (e.g., *beard* read as *bread*; Kohnen & Castles, 2013).

In the current experiment, we examined TL and PH priming effects in a group of 8- to 10-year-old children while recording ERPs. Our prior research (Eddy, Grainger, Holcomb, Mitra, & Gabrieli, 2014) has shown robust repetition priming effects on the N250 and N400 ERP components in children of that age. Measuring TL and PH ERP priming effects in the present study allowed us to examine if there are differences in the neural systems underlying phonological and orthographic processing, reflected by N250 priming effects, and the mapping of this information onto semantic representations, reflected by N400 priming effects, in beginning to intermediate readers. More importantly, it allowed us to relate measures of reading ability, as measured by standardized reading tests, to the magnitude of these TL and PH priming effects. We predicted that, if the developmental trajectories of orthographic and phonological reading skills differ, this should be reflected in the relationship between reading ability and the TL and PH priming effects. This approach should allow a better characterization of the relationship between objective measures of the subcomponents of reading skill and neural markers of the hypothesized subprocesses involved in reading.

Table 1. *Means and Standard Deviations of Standard Scores*

Test	Mean	*SD*	*N**
KBIT–Matrices	120	11.5	20
TOWRE–Sight Word Efficiency	110	9.5	20
TOWRE–Phonemic Decoding Efficiency	109	11.1	20
CTOPP–Elision	11	3	20
CTOPP–Blending Words	10	2.2	20
CTOPP–Non-Word Repetition	10	2	19
WRMT–Word ID	112	8.9	20
WRMT–Word Attack	111	11.9	20
WMRT–Passage Comprehension	116	8.5	18
WJIII–Reading Fluency	113	11.7	20
PIAT–Spelling	113	10.8	17
PPVT–Vocabulary	123	12.7	17

*Number of participants with a score for each individual measure.

Method

Participants

Participants were all native English speakers, right-handed, with no history of neurological or psychiatric impairments or medications, or family history of reading disability. This study included data from 20 child participants (11 males) between the ages of 8 and 10 years old (mean: 9.3 ± 0.9 years). All participants scored at or above average on the Performance IQ measure from the Kaufman Brief Intelligence Test (KBIT-2)–Matrices subtest (Kaufman & Kaufman, 2004). To confirm participants' status as typical readers, their performance on standardized reading and phonological measures was assessed (Table 1). A legal guardian gave consent for the child to participate, and the child signed an assent form in accordance with the Massachusetts Institute of Technology (MIT) Committee on Use of Humans as Experimental Subjects (COUHES).

Behavioral Assessment

Standardized measures of cognitive, reading, and reading-related abilities were administered to assess participants' status as typically developing readers. Trained researchers at MIT performed one-on-one assessments of nonverbal intelligence (KBIT-2–Matrices subtest), sentence fluency (Woodcock-Johnson Test of Cognitive Abilities III [WJ-III]–Reading Fluency subtest), timed tests of single word and pseudoword reading (Test of Word Reading Efficiency [TOWRE]–Sight Word Efficiency & Phonemic Decoding subtests), untimed tests of single word and pseudoword reading (Woodcock Reading Mastery Test [WRMT-R/NU]–Word Identification & Word Attack subtests), sentence level comprehension (WRMT-R/NU–Passage Comprehension subtest), phonological processing (Comprehensive Test of Phonological Processing [CTOPP]–Elision, Blending Words & Non-Word Repetition subtests), spelling (Peabody Individual Achievement Test-Revised Normative Update

[PIAT-R/NU]–Spelling subtest), and vocabulary (Peabody Picture Vocabulary Test, Fourth Edition [PPVT-4]), see Table 1.

Stimuli

The critical stimuli for this experiment were created using five-letter words and their respective five-letter PH and TL nonwords. A separate rating study with adults checked for phonological similarity, selecting the most similar pairs for this experiment (average similarity rating for the included stimuli was 6.8 ± 0.5 on a scale of 1 to 7, with 7 = *most similar*). Our stimulus construction followed the same pattern as Grainger et al. (2006) where 200 target words were paired with four types of prime stimuli: a PH prime (e.g., brane–BRAIN), a PH control (PHc) prime (e.g., brant–BRAIN), a TL prime (e.g., barin–BRAIN), and a TL control (TLc) prime (e.g., bosin–BRAIN). TL primes were created by transposing the 2nd and 3rd letters in half of the stimuli and the 3rd and 4th letters in the other half. Control primes for PHs were formed by replacing one or two letters of the PH that did not overlap with the target word (e.g., the *e* in brane became a *t* in brant); the PH primes and PH control primes were therefore matched in terms of the number of letters shared by prime and target and the position of the shared letters. In addition, the PH and PH control primes did not differ in orthographic neighborhood size, $t(199) = .39$, $p = .70$, or bigram frequency, $t(199) = 1.47$, $p = .14$ (nonword statistics from http://www.neuro.mcw.edu/mcword/, Medler & Binder, 2005). Control primes for TL primes had two different letters replacing the transposed letters that maintained the same C-V structure (e.g., the barin becomes bosin). Like the PH condition, the TL primes and control primes did not differ in orthographic neighborhood size, $t(199) = 1.4$, $p = .16$, or bigram frequency, $t(199) = .86$, $p = .39$ (Medler & Binder, 2005). Four counterbalanced lists were created from the stimulus set, where each list contained all four priming conditions, but each target word was presented only once, so that no participant saw the same target word twice, but across all participants the four manipulations for each word were presented. Sixty noncritical trials were intermixed with the 200 critical trials. The 200 target words were relatively high frequency (mean log HAL frequency = 9.52, range 5.8–12.6, English Lexicon Project: Balota et al., 2007) so as to ensure these would be words known by the children. Thirty of the noncritical trials contained an animal name in the prime position and a filler word in the target position (e.g., horse–TABLE), and 30 contained an animal name in the target position and a PH, TL, or corresponding control prime in the prime position (e.g., horce–HORSE, horbe–HORSE, hosre–HORSE, hopde–HORSE). Each of 30 animal names was used once as a prime and once as a target in each list.

Procedure

Participants sat in a sound-attenuated, dimly lit room where words were presented time-locked to the vertical refresh rate of the monitor (75 Hz). Participant responses were collected through a button box. Stimuli were presented in pseudorandom order in white on a black background in Arial font. For each 4-s trial, a forward mask consisting of a series of seven pound signs ####### was presented for 300 ms, immediately followed by the prime stimulus for 100 ms, and then immediately after that, the target word for 500 ms (Figure 1). Prime duration was increased compared to the Grainger et al. (2006) study in order to ensure robust priming effects with the youngest participants. Each trial was then followed by a 700-ms blank screen followed by 2,400-ms prompt to allow for eye blinking. Between trials, there was a randomly jittered intertrial interval. Animal names served as probe items in a go/no-go semantic categorization task (described below). The 260 experimental trials were broken down into five blocks of 52 trials, giving the participant a break approximately every 4 min.

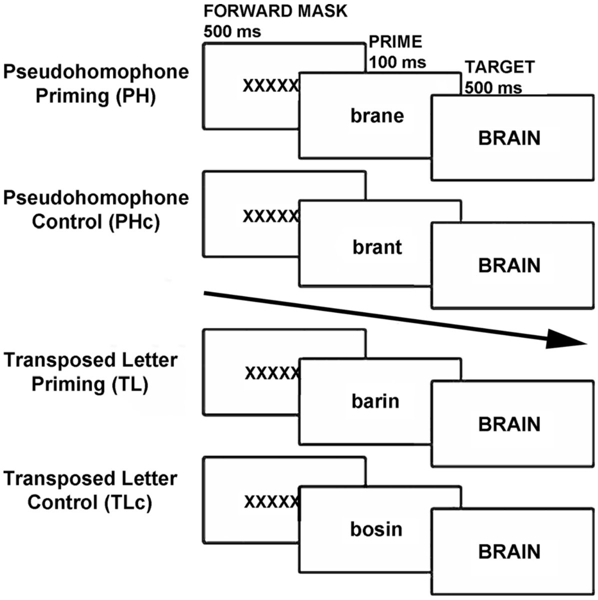

Figure 1. Example trials.

Semantic Categorization Task

Participants saw a series of stimuli in a sequence of trials consisting of pairs of words. They were instructed to monitor each trial for occasional animal-name probe items (30 in the prime position, 30 in the target position) and to press a button as quickly as possible whenever they detected an animal name. Participants were instructed to only press to animal names and that no response was required for other words. Therefore, responses were only to be made to noncritical trials. Probes occurred both as primes and targets, the former providing a check of the effectiveness of masking. Of experimental interest were the critical trials that did not contain animal probe items.

EEG Acquisition

EEG recordings were acquired with the Biosemi ActiveTwo System (Biosemi B.V., Amsterdam, The Netherlands) using active Ag-AgCl electrodes mounted on an elastic cap (Electro-Cap, Inc.). The recordings were made in single-ended mode that amplify the difference between each electrode site and a common mode sensor electrode with referencing taking place offline. Impedance does not need to be lowered with this system due to the combination of preamplifiers at each electrode site, a driven right leg circuit, and high electrical isolation that provide good signal-to-noise ratio (see Kappenman & Luck, 2010, for more details). However, to ensure good signal quality, it was confirmed the offset potentials for each electrodes were under ± 40 mV (a recommendation from Biosemi), and visual inspection of the data was performed prior to and throughout the recording to ensure stability and quality of the EEG signal. EEG was recorded from 61 scalp sites (10-20 system positioning, see Figure 2), a vertical eye channel for detecting blinks, a horizontal eye channel to monitor for saccades, and two additional

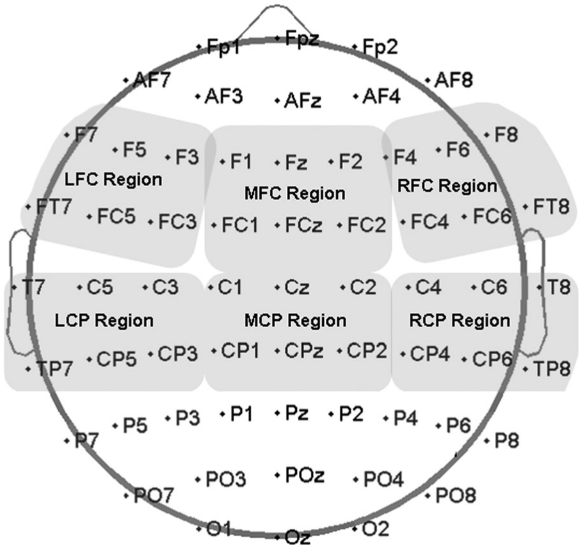

Figure 2. Electrode locations and regions for analysis. LFC = left frontocentral; MFC = midline frontocentral; RFC = right frontocentral; LCP = left centroparietal; MCP = midline centroparietal; RCP = right centroparietal.

electrodes affixed to the mastoid bone. The EEG was recorded with a low-pass hardware filter at 104 Hz and then digitized at 512 Hz with 24 bits of resolution. Signal processing and analysis were performed in MATLAB using EEGLAB toolbox (Delorme & Makeig, 2004) and ERPLAB toolbox (Lopez-Calderon & Luck, 2014). All channels were referenced offline to an average of the mastoids. Offline filtering was applied (band-pass 0.1–30 Hz). Artifact detection was performed using the steplike artifact function available through the ERPLAB toolbox and confirmed with visual inspection. Trials with blinks, eye movements, and muscle artifact were rejected prior to averaging. Overall, 15.9% of trials were rejected due to ocular, movement, or other artifacts. However, there was no difference in the number of trials for each condition, Fs < 1.8, ps $> .2$. The analysis included on average 40.5 trials ($SD = 4.96$) for the PH condition, 40.7 ($SD = 5.5$) for the PHc condition, 41 ($SD = 5.1$) for the TL condition, and 41.7 ($SD = 5.3$) for the TLc condition.

Data Analysis

ERP averages were formed by time-locking to the onset of the target word and averaging across primed trials for each condition and across unprimed trials for each condition from 100 ms prior to target onset until 700 ms after using a -100 to 0 baseline. Mean amplitude measurements were taken between 150–350 ms (N250 epoch) and 350–550 ms (N400 epoch).

Six regions were computed by collapsing across the following electrodes (Figure 2): left frontocentral (LFC) region—F7, F5, F3, FT7, FC5, FC3; midline frontocentral (MFC) region—F1, Fz, F2, FC1, FCz, FC2; right frontocentral (RFC) region—F8, F6, F4, FT8, FC6, FC4; left centroparietal (LCP) region—T7, C5, C3, TP7, CP5, CP3; midline centroparietal (MCP) region—C1, Cz, C2, CP1, CPz, CP2; right centroparietal (RCP) region—T8, C6, C4, TP8, CP6, CP4. These regions were entered in a Type (PH, TL) × Priming (primed, unprimed) × Anterior-Posterior (FC, CP) × Hemisphere (midline, left, central) repeated measures analysis of variance (ANOVA). These overall ANOVAs were then followed up by planned comparisons for each type of priming separately and included all the same factors as the previous ANOVA aside from type. The Geisser and Greenhouse (1959) correction was applied to all repeated measures having more than one degree of freedom, and the corresponding p values are reported.

Correlational analysis. In addition, correlational analyses were performed with the raw reading scores in order to quantify absolute reading skills, rather than reading skill relative to peers. Two measures of overall reading ability were calculated: WRMT Basic Reading Skills (Word Identification & Word Attack) and TOWRE Total (Sight Word Efficiency & Phonemic Decoding). In addition, to explore the relationship between phonological processing and the pseudohomophone priming effects, a raw measure of CTOPP Phonological Awareness (CTOPP Blending & CTOPP Elision subtests) were correlated with priming effects. Correlations were performed for each of the two time epochs analysis (150–350 ms; 350–550 ms) with the mean amplitude of the TL and PH priming effects average across the electrode regions included in the analysis described above. One child was excluded as an outlier from the correlational analysis between ERP measures of priming and WRMT Basic Reading Skills (WRMT Basic Reading Skills was less than 2 standard deviations from the mean score, also confirmed with stem and leaf plot).

Results

Behavioral Performance

Participants detected significantly more animal target words than animal prime words (d' animal prime words = 0.48; d' animal target words = 3.24; $t(17) = 12.38$, $p < .001$).[1] This translated to an average of 11% of prime probes being detected (3.3 out of 30) and 84.8% of target probes being detected (25.4 out of 30).

Electrophysiological Data

The PH and TL priming results are shown in Figure 3. Visual inspection of the waveforms revealed that both PH and TL priming appeared to onset around 150 ms and continued into the N400 epoch. PH priming had an anterior distribution and TL priming had a more central parietal distribution in the N250 epoch.

N250 epoch (150–350 ms). The overall ANOVA with the factors of type, priming, anterior-posterior distribution, and hemisphere revealed a main effect of priming, $F(1,19) = 14.623$, $p = .001$, $\eta_p^2 = .435$, where unprimed targets across both conditions were more negative going than primed targets across the two levels of anterior/posterior distribution analyzed. In addition, there was a significant interaction between type, priming, and anterior-posterior distribution, $F(1,19) = 4.78$, $p = .041$, $\eta_p^2 = .2$. To further explore this three-way interaction, each of the anterior/posterior levels was entered into a repeated measures ANOVA with type and priming as factors. In the frontocentral region, there was a main effect of priming, $F(1,19) = 10.35$, $p = .005$, $\eta_p^2 = .35$, where both PH and TL priming effects were observed. In the centroparietal region, both PH and TL priming effects were observed as well, indicated by a main effect of priming, $F(1,19) = 16.13$, $p = .001$,

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[1] Due to an equipment error, responses were not recorded from two of the children. However, they were observed to be performing the task; therefore, their data was not excluded from the ERP analysis, but was excluded from the analysis of behavioral performance.

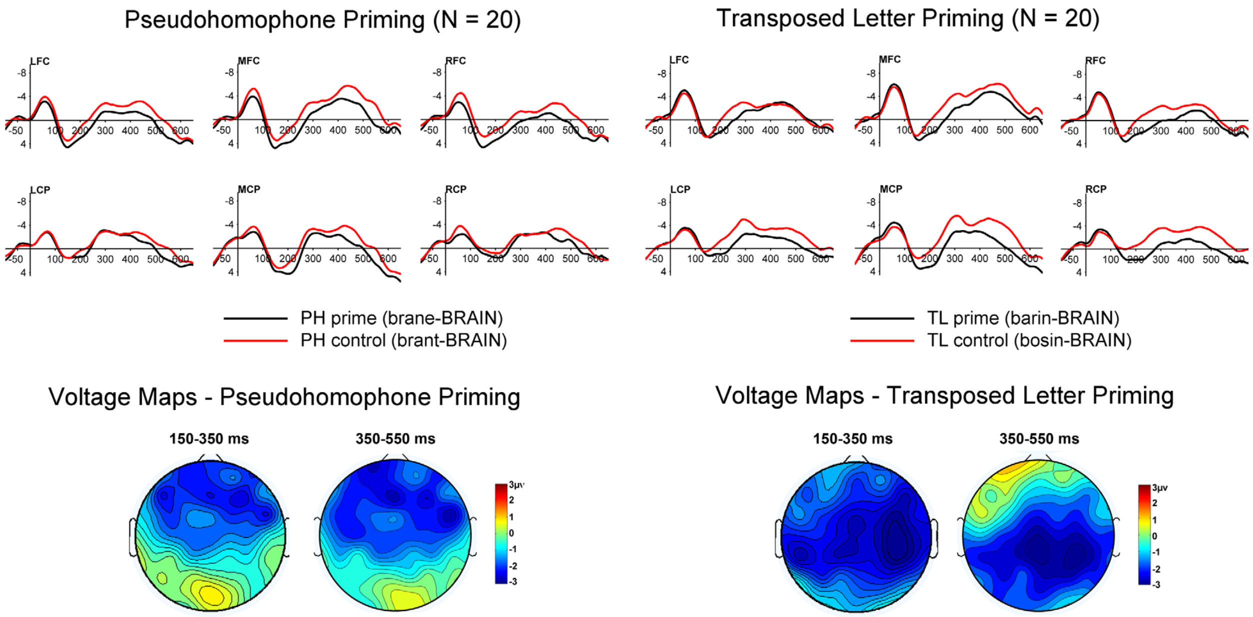

Figure 3. Grand-averaged waveforms and voltage maps for PH priming (left) and TL priming (right) time-locked to target onset. The voltage maps reflect difference wave (i.e., priming effects) mean amplitudes.

$\eta_p^2 = .46$. However, there was also a Type × Priming interaction reflecting larger priming effects for the TL condition compared to the PH condition in this region, $F(1,19) = 4.61$, $p = .045$, $\eta_p^2 = .2$ (PH priming effect $= -.71$ µV; TL priming effect $= -2.42$ µV).

N400 epoch (350–550 ms). The overall ANOVA with the factors of type, priming, anterior-posterior distribution, and hemisphere revealed a main effect of priming, $F(1,19) = 9.57$, $p = .006$, $\eta_p^2 = .34$, where unprimed targets across both conditions were

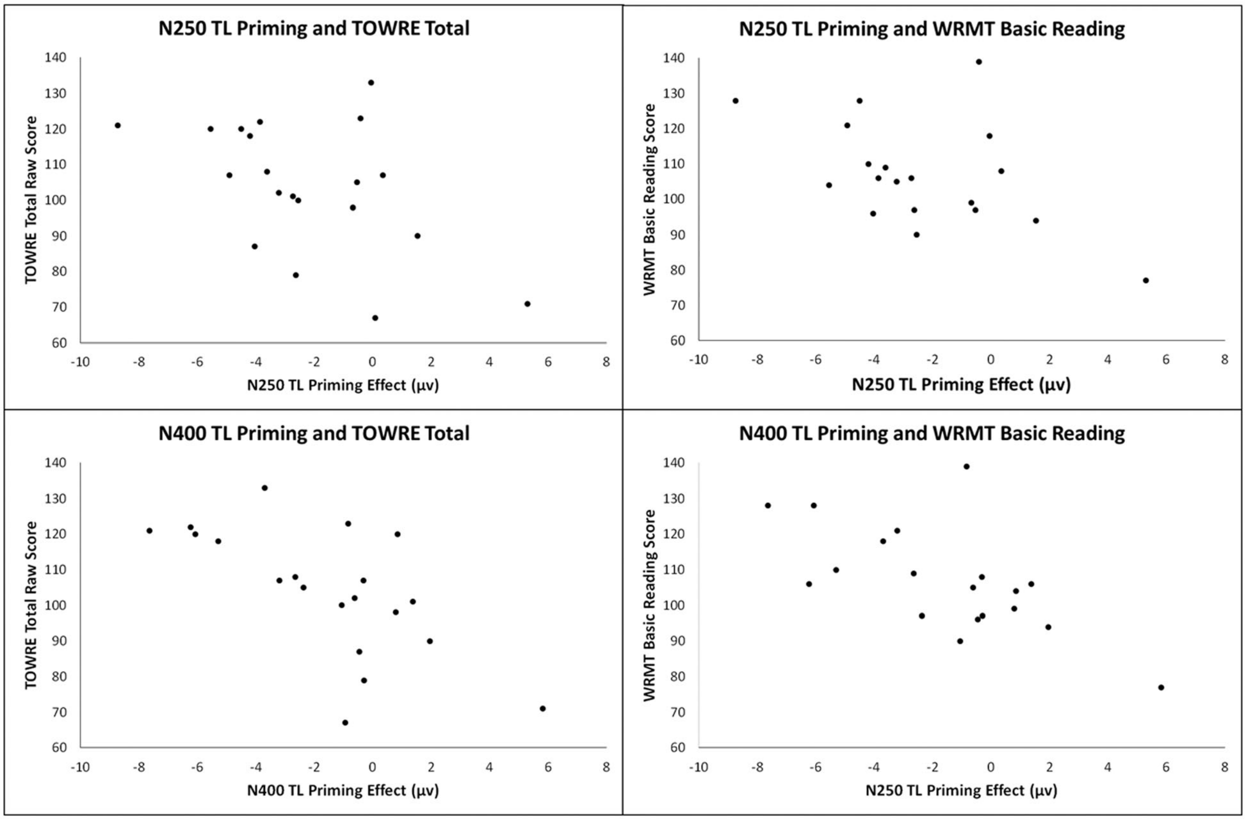

Figure 4. Scatter plots showing the relationship between N250 and N400 TL priming effects and reading ability as measured by the WRMT (Word ID & Word Attack) and the TOWRE (Phonemic Decoding & Sight Word Efficiency). Both the N250 and N400 are negative-going effects; therefore, larger negative values equal larger priming effects.

more negative going than primed targets across the two levels of anterior/posterior distribution analyzed. In addition to this main effect, there was also a Type × Priming × Anterior-Posterior Distribution interaction, $F(1,19) = 13.17$, $p = .002$, $\eta_p^2 = .41$. To further explore this interaction, type and priming were entered into repeated measures ANOVAs for each region (frontocentral and centroparietal) separately. In the frontocentral region, both PH and TL priming showed repetition priming effects as reflected by the overall main effect of priming, $F(1,19) = 4.91$, $p = .039$, $\eta_p^2 = .21$. There was no Priming × Type interaction in this region, $F(1,19) = 1.19$, $p = .289$, $\eta_p^2 = .06$. The same pattern was observed in the centroparietal region where across the PH and TL conditions significant priming effects were observed, $F(1,19) = 14.74$, $p = .001$, $\eta_p^2 = .44$, but no interaction between type and priming, $F(1,19) = 1.33$, $p = .264$, $\eta_p^2 = .07$.

Correlational Results

Correlational analysis (see Figure 4) revealed that higher scores on tests of reading ability were related to larger TL priming effects in the N250 epoch for the WRMT Basic Reading Skills, $r(19) = .495$, $p = .031$, and TOWRE Total, $r(20) = .494$, $p = .027$. There were no significant correlations with PH priming during this epoch: WRMT Basic: $r(19) = .066$, $p = .789$; TOWRE Total: $r(20) = -.186$, $p = .433$. Comparing the TL and PH N250 priming effect correlations with the WRMT Basic using a Fisher r to z transform revealed these correlations did not differ significantly, $z = 1.35$, $p = .18$ (two-tailed). However, the correlations between the priming effects and the TOWRE Total in the N250 epoch did differ significantly, $z = 21.3$, $p = .03$ (two-tailed).

Larger TL priming effects in the N400 epoch were associated with higher scores on the WRMT Basic Reading Skills, $r(19) = .653$, $p = .002$, and TOWRE Total, $r(20) = .656$, $p = .002$. There were no significant correlations with PH priming and the TOWRE Total, $r(20) = -.011$, $p = .962$, or the WRMT Basic Reading Skills, $r(19) = .044$, $p = .857$, during the N400 epoch. The correlations for the TOWRE Total and priming effects significantly differed between the TL and PH conditions, $z = 2.32$, $p = .02$ (two-tailed), and for the WRMT Basic Reading Skills correlations, $z = 2.08$, $p = .038$ (two-tailed). Examining the relationship between the PH priming effect and CTOPP Phonological Awareness, there were no significant correlations between the two in the N250 epoch, $r(20) = -.141$, $p = .554$, or the N400 epoch, $r(20) = -.068$, $p = .774$.

Discussion

In the current experiment, we manipulated phonological and orthographic overlap between masked prime-target pairs while a group of 8- to 10-year-old children performed a semantic categorization task. The neural underpinnings of orthographic priming was measured by comparing the scalp distribution of ERPs effects of TL primes with appropriate controls (e.g., barin–BRAIN vs. bosin–BRAIN), and the neural basis of phonological priming was measured by comparing the scalp distribution of ERP effects of PH primes with appropriate controls (e.g., brane–BRAIN vs. brant–BRAIN). Orthographic and phonological processing were indexed by the N250 while successful mapping onto semantic representations was measured by the N400. TL and PH priming effects with characteristic scalp patterns shown in prior work in adults (Grainger et al., 2006) were observed in this group of 8- to 10-year-olds on both the N250 and N400 components.

The presence of an early N250 effect for the TL priming condition suggests relatively mature orthographic processing is being performed by these developing readers and parallels behavioral (Ziegler et al., 2014) and ERP (Eddy et al., 2014) findings that relatively automatic orthographic processing occurs in children of this age group. The N250 PH priming effects observed parallel those found in studies with adults (Grainger et al., 2006), suggesting, as other research has (Ziegler et al., 2014), that children have relatively stable phonological processing by this age. In addition, presence of N400 priming effects suggests that the processing taking place at earlier stages (reflected by N250 effects) is sufficient for accessing whole-word semantic representations (as reflected by N400 effects) and these children have established “integrative automaticity” (Coch, 2015). Given that previous research has shown that adult-like N400 effects emerge as early as kindergarten (e.g., Coch, Maron, Wolf, & Holcomb, 2002; Friedrich & Friederici, 2004; Hahne, Eckstein, & Friederici, 2004), it is not surprising that we see N400 priming effects in the current study reflecting established semantic processing in these beginning readers. The N400 PH priming effect did appear to have a slightly more frontal distribution than the N400 TL priming effect. However, this more frontal phonological N400 effect is not inconsistent with previous phonological N400 effects (e.g., see Coch, 2015). While these priming effects are informative about the development of orthographic, phonological, and semantic reading skills, relating these priming effects to reading ability allows us to better interpret the observed priming effects.

In the current experiment, we found positive correlations between TL priming (on both the N250 and N400) and reading ability, whereas we did not observe this relationship between PH priming and reading ability. The positive correlation between TL priming and reading ability is an important result that is highly constraining for theories of orthographic development in particular, and orthographic processing in general. There are currently two interpretations of TL effects. The most common interpretation is that they reflect noise in a mechanism for coding letter position information that would otherwise not produce TL effects (Davis, 2012; Gomez, Ratcliff, & Perea, 2008; Norris & Kinoshita, 2012). Another interpretation is that they reflect the inherent flexibility of a mechanism that represents the order of letters in a word via ordered letter combinations (e.g., bigrams) that are not necessarily adjacent—so-called open-bigram coding (Grainger & Hannagan, 2014; Grainger & van Heuven, 2003; Ktori et al., 2014; Whitney, 2001). In terms of orthographic development, one might expect positional noise to decrease as reading proficiency increases, and this should therefore be accompanied by a decrease in TL priming. On the other hand, models of orthographic processing that explain TL effects as reflecting the operation of a mechanism that is used to represent the order of letters in words clearly predict that that TL effects should increase as this mechanism is increasingly used during reading development. In line with the present findings, Grainger and Ziegler’s (2011) account of reading development specifically states that the development of flexible orthographic processing is a key ingredient in the overall process of becoming a skilled reader.

While TL priming effects were related to reading ability, there was no evidence for a correlation between reading level and the size of PH priming. This suggests that, while there is an increased use of direct mapping of orthography to semantics during reading development, the use of phonology is not entirely abandoned, as might be expected simply because adult readers show robust phonological priming effects (see Rastle & Brysbaert, 2006, for a review). These findings are consistent with Ziegler et al.'s (2014) observation that behavioral PH priming effects remain relatively stable across grade level in children, at least when behavioral measures are corrected for the overall increase in performance with age. These null correlations might reflect a tradeoff between the decline of the slow, sequential, and laborious process of phonological recoding accompanied by an increased use of more automatized and more efficient mechanisms for the sublexical conversion of print to sound. Therefore, beginning readers who are still using phonological recoding will show phonological priming effects, and more skilled readers will also show phonological priming effects, but the effects are thought to be driven by different mechanisms. In other words, as developing readers become more skilled, they would indeed assign more weight to direct orthographic access to semantics, and at the same time would continue to use phonological information but with a gradual shift toward more automatized processing of such information.

Further evidence has been obtained from a study measuring parafoveal preview benefits during sentence reading with TL and PH previews (Tiffin-Richards & Schroeder, 2015). In this study, it was found that TL preview benefits were greater in adults than 8-year-old children, whereas PH preview benefits were only present in children. TL effects are also found in the same-different matching task, where participants have to decide whether or not two successive briefly presented stimuli are the same or not. In this task, it is harder to detect a transposition change than a substitution change, and this is particularly difficult with letter stimuli (e.g., PGFMR–PGMFR; Duñabetia, Dimitropoulou, Grainger, Hernandez, & Carreiras, 2012; Massol, Dunabeitia, Carreiras, & Grainger, 2013). Importantly, a longitudinal investigation of beginning readers using the same-different matching task with random consonant strings (Duñabeitia, Lallier, Paz-Alonso, & Carreiras, 2015) revealed robust TL effects only in children who had acquired basic literacy skills, in line with the observation that illiterate adults do not show TL effects in this task (Dunabeitia, Orihuela, & Carreiras, 2014).

Conclusion

The robust correlations we found between neural measures of orthographic processing (TL priming effects) and measures of reading ability in children demonstrate that such priming effects, as revealed in differences in ERP waveforms across priming conditions, provide a valid marker for tracking the time course of neural processes involved in orthographic development. Future research may extend this paradigm to manipulations of specific orthographic properties of the stimuli (orthographic neighborhood size, bigram frequency) to understand precisely how this mapping from visual forms to whole word representations becomes automatic and efficient. Furthermore, testing a wider range of reading ability including a group of beginning readers will provide an important test of the account of reading development supported by the present results. In addition, given the observed correlation of TL priming effects with reading skills in children, this may be an appropriate paradigm to apply to populations with reading difficulties (e.g., dyslexia) to separate the contributions of orthographic and phonological processing to such disorders. This paradigm could be applied in cases of developmental letter position dyslexia, where the main symptom is reading words such as *smile* as *slime* (Kohnen, Nickels, Castles, Friedmann, & McArthur, 2012), in order to dissociate orthographic and phonological contributions to the errors made in silent reading and reading aloud in this population.

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