

Neural correlates of priming effects in children during spoken word processing with orthographic demands

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ABSTRACT

Priming effects were examined in 40 children (9–15 years old) using functional magnetic resonance imaging (fMRI). An orthographic judgment task required participants to determine if two sequentially presented spoken words had the same spelling for the rime. Four lexical conditions were designed: similar orthography and phonology (O⁺P⁺), similar orthography but different phonology (O⁺P⁻), similar phonology but different orthography (O⁻P⁺), and different orthography and phonology (O⁻P⁻). In left superior temporal gyrus, there was lower activation for targets in O⁺P⁺ and higher accuracy was correlated with stronger activation across all lexical conditions. These results provide evidence for phonological priming in children and greater elaboration of phonological representations in higher skill children, respectively. In left fusiform gyrus, there was lower activation for targets in O⁺P⁺ and O⁺P⁻ than for those in O⁻P⁻, suggesting that visual similarity resulted in orthographic priming even with only auditory input. In left middle temporal gyrus, there was lower activation for targets in O⁺P⁺ than all other lexical conditions, suggesting that converging orthographic and phonological information resulted in a weaker influence on semantic representations. In addition, higher reading skill was correlated with weaker activation in left middle temporal gyrus across all lexical conditions, suggesting that higher skill children rely to a lesser degree on semantics as a compensatory mechanism. Finally, conflict effects but not priming effects were observed in left inferior frontal gyrus, suggesting that this region is involved in resolving conflicting orthographic and phonological information but not in perceptual priming.

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1. Introduction

Priming is thought to reflect a basic neural mechanism of cortical function in which a previous stimulus influences processing of later stimuli due to the fact that they share some characteristics (Tulving & Schacter, 1990). Single neuron recording has revealed that the firing rate of neurons in inferior temporal cortex decreases as a result of repeated exposure to a familiar visual stimulus (Ringo, 1996; Sobotka & Ringo, 1994). Neuroimaging studies have also found repetition-related reductions in ventral temporal cortex when reading words and other word like stimuli (Dehaene et al., 2001, 2004). The purpose of the current study was, to examine, for the first time, cortical priming effects in the auditory modality in children. Moreover, we examined whether priming effects occur not only in superior temporal cortex, related to the auditory modality of the stimuli,

but also in visual association areas related to the orthographic demands of the task.

Several experiments have examined priming by having participants study words presented in the auditory modality and subsequently have them perform stem completion to either novel or previously studied words in the auditory modality. Although one neuroimaging study with adults reported no priming effects (Carlesimo et al., 2004), other studies have reported reduced activation for studied words in left extrastriate cortex, bilateral precuneus, medial prefrontal cortex and right angular gyrus for words presented in the same (Badgaiyan, Schacter, & Alpert, 1999, 2001) and different voice (Badgaiyan et al., 2001). More relevant to the current study are experiments that have sequentially present primes and targets in the auditory modality. These priming studies have reported reduction of activation in left (Bergerbest, Ghahremani, & Gabrieli, 2004) and right insula for primed compared to un-primed targets (Orfanidou, Marslen-Wilson, & Davis, 2006). The most consistent finding of these experiments is a reduction of activation for related targets in bilateral inferior frontal gyrus, bilateral superior

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temporal gyrus/sulcus and medial prefrontal cortex. This has been shown for animal judgments of animal sounds (Bergerbest et al., 2004), for lexical decision to words and pseudowords (Orfanidou et al., 2006), and for size judgments to words (Marinkovic et al., 2003). A recent study examining long-term auditory priming is consistent with these studies in reporting priming effects for both words and pseudowords in bilateral superior temporal gyrus (Gagnepain et al., 2008). Interestingly, they only reported priming effects for words, but not pseudowords, in left posterior middle temporal gyrus, suggesting that the priming related reductions may be due to lexical semantic information of the stimuli. This is consistent with previous studies that have implicated left middle temporal gyrus in semantic processing (Chou, Booth, Bitan, et al., 2006; Chou, Booth, Burman, et al., 2006; Liu et al., in press).

Studies have also examined cross-modality priming effects by having participants study words presented in the auditory modality and subsequently have them perform stem completion to either novel or previously studied words in the visual modality. As with the within-modality experiments, the studies have reported reduced activation for studied words compared to novel words in left superior temporal gyrus (Badgaiyan et al., 2001; Schacter, Badgaiyan, & Alpert, 1999). These cross-modality studies have additionally demonstrated reduced activation in left fusiform/inferior temporal cortex, and these priming effects were larger for cross-modality priming compared to within-modality auditory priming. Furthermore, a larger decrease in left fusiform/inferior temporal cortex was correlated with a larger behavioral priming effect (i.e. greater number of primed words that were recalled) (Carlesimo et al., 2004). These effects for inferior temporal cortex are consistent with an event-related potential (ERP) study in which participants studied words presented in the auditory modality and then completed a lexical decision task in the visual modality (Joyce, Paller, Schwartz, & Kutas, 1999). Repeated words resulted in an increased positivity from 200 to 500 ms stimulus onset as compared to new words, and this was significantly greater over occipito-temporal sites than frontal sites in the left hemisphere. These cross-modality studies suggest that phonologically encoded stimuli influence orthographic processing in inferior temporal cortex.

Several experiments have also examined the correlation between behavior and the neural priming effect in the auditory modality. One study found higher accuracy on animal judgments was correlated with greater decreases for related targets in bilateral superior temporal gyrus and right inferior frontal gyrus (Bergerbest et al., 2004). Another study reported that faster lexical decision times were correlated with greater decreases for related targets in left inferior frontal gyrus and medial prefrontal cortex (Orfanidou et al., 2006). Another study found that increased accuracy in memory (old/new) judgments of studied words was associated with greater decreases in right superior temporal sulcus (Gagnepain et al., 2008). These studies suggest higher skill is associated with greater priming and that both inferior frontal gyrus and superior temporal cortex are critically involved in the auditory priming effect. Indeed, a transcranial magnetic stimulation (TMS) study showed that stimulation over left inferior frontal gyrus, and not right inferior frontal gyrus, eliminated the priming effect (reduction of naming latency) in a verb generation task to repeated auditory words, but did not affect processing of novel words (Thiel et al., 2005).

Behavioral studies have generally shown priming effects in children, but these studies have inconsistently demonstrated developmental differences. In one study, children studied words presented in the visual or auditory modality, and then performed a stem completion task in the same modality (Carlesimo, Vicari, Albertoni, Turriziani, & Caltagirone, 2000). There was no difference between first, third and fifth graders on the auditory stem completion, but there was a developmental increase in priming effects for the visual stem completion. The lack of developmental differences in auditory

priming effects is supported by a study that found no developmental differences in accuracy or reaction time between rhyming versus non-rhyming words in 7-year-olds to adults during an auditory rhyming task (Coch, Grossi, Coffey-Corina, Holcomb, & Neville, 2002); however, a subsequent study by the same group found developmental decreases in the difference in accuracy between rhyming and non-rhyming non-words (Coch, Grossi, Skendzel, & Neville, 2005). Another study in the auditory modality also reported developmental decreases in the negative influence of alliteration primes on target identification as compared to unrelated primes (Bonte & Blomert, 2004).

Only three event-related potentials (ERPs) studies have examined developmental differences in cortical priming effects in the auditory modality, and they have produced inconsistent results. Two studies reported no developmental differences (7-year-olds to adults) for word and non-word priming in the auditory modality during a rhyming task (Coch et al., 2002, 2005). Children and adults showed similar size, distribution and latency of priming effects. Another study examined priming effects for words that shared initial sounds (i.e. alliteration) (Bonte & Blomert, 2004). Although no direct comparisons were made between age groups, 5–6-year-olds did not show a reliable priming effect at about 100–200 ms post stimulus onset, whereas 7–8-year-olds and adults showed reliable effects at fronto-central sites. Only 7–8-year-olds showed a later priming effect at about 600–800 ms post stimulus onset and this effect occurred at all recording sites. Together, the behavioral and neuroimaging studies have revealed auditory priming effects in children, but have reported inconsistent developmental differences. However, all neuroimaging studies of development employed ERPs, so that lack of spatial resolution may have prevented the detection of developmental effects.

The purpose of the present study is to investigate priming effects in children induced by orthographic judgments made about spoken word pairs and to determine whether these priming effects are correlated with age and/or skill differences. The present study used an experimental paradigm where children (9–15 years) were asked to determine if word pairs presented in the auditory modality had the same spelling after the first consonant or consonant cluster. Overlapping participants and the same task was used in the current study and a previous study by the same group (Booth, Cho, Burman, & Bitan, 2007). However the current study is novel because we examined brain responses only to target words to investigate the brain's sensitivity to the similarity of orthography and phonology between the prime and target word, whereas the previous study examined the overall effect of the lexical trials including the response interval, so it did not directly assess priming. Because cortical regions involved in orthographic processing are distinct from cortical regions involved in auditory processing, this auditory spelling paradigm is powerful for differentiating (auditory) perceptual priming effects, from priming effects related to (orthographic) task requirements. We expected priming effects to be larger for pairs that had overlapping orthographic and phonological information (O^+P^+ : gate-hate) compared to those that shared neither (O^-P^- : press-list). Phonological priming effects should occur in left superior temporal gyrus (Bergerbest et al., 2004; Gagnepain et al., 2008; Marinkovic et al., 2003; Orfanidou et al., 2006), orthographic priming effects should occur in left fusiform gyrus (Dehaene et al., 2001) and semantic involvement should be reflected in left middle temporal gyrus activation (Chou, Booth, Bitan, et al., 2006; Chou, Booth, Burman, et al., 2006). Based on behavioral literature examining skill differences in adults, we expected phonological and orthographic priming effects to increase with skill suggesting greater elaboration of these representations. In contrast, we expected semantic involvement to decrease with skill suggesting reduced reliance on semantics as a compensatory mechanism. Indeed, experimental and computational work

suggests that the more effective the mapping between orthographic and phonological representations, the less likely semantics influences rapid word identification (Booth, Perfetti, & MacWhinney, 1999; Plaut & Booth, 2000).

Previous studies have also implicated bilateral inferior frontal gyrus in auditory priming (Bergerbest et al., 2004; Orfanidou et al., 2006; Thiel et al., 2005). However, studies examining spelling and rhyming judgments to auditory words have also found greater activation in inferior frontal gyrus for word pairs with conflicting orthographic and phonological information (O^+P^- : pint-mint; O^-P^+ : jazz-has) than for word pairs with consistent orthographic and phonological information (O^+P^+ : gate-hate; O^-P^- : press-list) (Booth et al., 2007; Cone, Burman, Bitan, Bolger, & Booth, 2008). If priming effects are larger in inferior frontal gyrus for pairs that have overlapping orthographic and phonological information (O^+P^+ : gate-hate) compared to those that do not (O^-P^- : press-list), this implicates this region in perceptual priming. If, however, there is no difference between O^+P^+ and O^-P^- in inferior frontal gyrus, but activation in this region is larger for words with conflicting information (O^+P^- , O^-P^+) than for words with consistent information (O^+P^+ , O^-P^-), this suggests that inferior frontal gyrus is involved in higher-level lexical selection and cognitive control.

2. Methods

2.1. Participants

Forty children (ages 9–15, mean = 12.2), 18 males and 22 females, participated in the study. There were eight 9-year-olds, nine 11-year-olds, twelve 13-year-olds and eleven 15-year-olds. Children were all right handed, (mean = 80, range 45–90) according to the 9-item Likert scale questionnaire (Oldfield, 1971) (–90 to 90, positive scores indicate right hand dominance). All children were native English speakers, with normal hearing and normal or corrected-to-normal vision. All children were free of neurological diseases or psychiatric disorders and were not taking medication affecting the central nervous system. The children were recruited from the Chicago metropolitan area, and the parents of the children were interviewed to ensure that their children did not have a history of reading, attention or oral-language deficits. Children were given a standardized intelligence test wechsler abbreviated scale of intelligence (WASI) (Wechsler, 1999), that showed an average full scale IQ = 112, (range = 85–140, $SD = 14.3$); verbal IQ = 113 (range = 79–142, $SD = 13.6$); and performance IQ = 109 (range = 79–144, $SD = 15.0$). The Institutional Review Board at Northwestern University and Evanston Northwestern Healthcare Research Institute approved the informed consent procedures.

2.2. Tasks

Participants were asked to determine if two spoken words had the same spelling for all letters from the first vowel onwards. The two spoken words, the prime word and then the target word, were presented in sequential order and a black fixation-cross appeared throughout the trial. The duration of each word was between 500 ms and 800 ms followed by a brief period of silence, with the second word beginning 1000 ms after the onset of the first. A 2600-ms interval in which a response was supposed to be made followed the target word. The start of the response interval was signified by a red fixation-cross that appeared on the screen after the target word. If the two words had the same spelling for all letters from the first vowel onwards, the participant was asked to press a button with the index finger; if the two words did not have the same spelling for all letters from the first vowel onwards, the

participant was asked to press a different button with the middle finger.

Twenty-four word pairs of each condition were presented. Each of the word pairs was categorized under one of four lexical conditions, each of which had different constraints on the orthographic and phonological relation between the prime and the target words. In the two non-conflicting conditions, the two words were either similar in both orthography and phonology (O^+P^+ , e.g. gate-hate), or different in both orthography and phonology (O^-P^- , e.g. press-list). In the two conflicting conditions, the two words had either similar orthography but different phonology (O^+P^- , e.g. pint-mint), or different orthography but similar phonology (O^-P^+ , e.g. jazz-has). Table 1 summarizes these lexical conditions. All words were monosyllabic words, 4–7 letters long, and were matched across conditions for written word frequency in adults and children (Zeno, 1996) and for written and spoken word frequency in adults (Baayen & Gulikers, 1995).

There were three kinds of control tasks. The simple perceptual control had 24 pairs of single pure tones, ranging from 325 Hz to 875 Hz. The complex perceptual control had 24 pairs of three-tone stimuli, where all the component tones were within the aforementioned frequency range. For both the simple and complex perceptual controls, participants determined whether the stimuli were identical or not by pressing a yes or no button. The third control task involved 72 null events. The participant was instructed to press a button when a black fixation-cross at the center of the visual field turned red. Procedures for presenting the tones and fixation-cross were the same as the word judgment task. The task was administered in two 108 trial runs, in which the order of lexical, perceptual, and null trials was optimized for event-related design using OptSeq (<http://www.surfer.nmr.mgh.harvard.edu/optseq/>). We present data for target words compared to null, because we were only interested in the effect of the prime word on processing the target word, and not the priming effect compared to a perceptual control.

2.3. Experimental procedure

After the standardized tests were administered, participants were given a practice session in a scanner simulator. Different stimuli were used in the practice and scanning sessions. Scanning took place within 1 week from the practice session.

2.4. MRI data acquisition

Images were acquired using a 1.5 Tesla General Electric (GE) scanner with a standard head coil. Head movement was minimized using vacuum pillow (Bionix, Toledo, OH). The stimuli were projected onto a screen, and viewed through a mirror attached to the inside of the head coil. Participants' responses were recorded using an optical response box (Current Designs, Philadelphia, PA). The blood-oxygen level dependent (BOLD) functional images were acquired using the echo planar imaging (EPI) method. The following parameters were used for scanning: time of echo (TE) = 35 ms, flip angle = 90°, matrix size = 64 × 64, field of view = 24 cm, slice thickness = 5 mm, number of slices = 24; time of repetition (TR) = 2000 ms. Two runs, with 240 repetitions each, were administered for the functional images. In addition, structural T1 weighted 3D images were acquired (TR = 21 ms, TE = 8 ms, flip angle = 20°, matrix size = 256 × 256, field

Table 1
Prime-target pairs varying in their degree of phonological and orthographic similarity.

	Similar orthography	Dissimilar orthography
Similar phonology	O^+P^+ gate-hate	O^-P^+ jazz-has
Dissimilar phonology	O^+P^- pint-mint	O^-P^- press-list

of view = 22 cm, slice thickness = 1 mm, number of slices = 124), using an identical orientation as the functional images.

2.5. Image analysis

Data analysis was performed using Statistical Parametric Mapping (SPM2, <http://www.fil.ion.ucl.ac.uk/spm>). The images were spatially realigned to the first volume to correct for head movements. No individual runs had more than 4 mm maximum displacement. Since interpolation was used to minimize timing-errors between slices. The functional images were co-registered with the anatomical image, and normalized to the standard T1 Montreal Neurological Institute (MNI) template volume. The data was then smoothed with a 10 mm isotropic Gaussian kernel. A high pass filter with a cutoff period of 128 s was applied. Only the target words of each pair were treated as individual events for analysis and modeled using a canonical hemodynamic response function (HRF) with the assumption that any differences between conditions for the target words reflect priming effects due to the first word. Perceptual controls and null trials were also treated as individual events in the model, and null trials served as baseline in all contrasts. Group results were obtained using random-effects analyses by combining subject-specific summary statistics across the group.

Although we attempted to match the lexical conditions for word consistency, the limited number of available words and the specific structure of the conditions precluded this possibility. Two measures of word consistency were calculated: phonological and orthographic (Bolger, Minas, Burman, & Booth, 2008). Consistency was computed as the ratio of friends to the sum of friends and enemies (i.e. friends/(friends + enemies) based on the 2998 mono-syllable words (Plaut, McClelland, Seidenberg, & Patterson, 1996). Phonological enemies were defined as the number of words with similar spelling but different pronunciation of the rhyme, and orthographic enemies were defined as the number of words with similar pronunciation but different spelling of the rime. Friends were defined as words with the same rime spelling and same rhyme pronunciation. Analysis of variance (ANOVAs) with lexical condition (O^+P^+ , O^+P^- , O^-P^+ , O^-P^-) as a factor and phonological or orthographic inconsistency as dependent variables showed a significant effect of condition for phonological and orthographic inconsistency ($F(3, 186) = 86.820$, $p = .000$; $F(3, 186) = 23.067$, $p = .000$, respectively). The highest phonological inconsistency was found in the O^+P^- condition and the highest orthographic inconsistency was found in the O^-P^+ condition. Because of this, we entered phonological inconsistency as a covariate in comparisons involving O^+P^- (e.g. O^+P^- versus O^+P^+) and orthographic inconsistency as a covariate in comparisons involving O^-P^+ (e.g. O^-P^+ versus O^+P^+). We entered no covariates in comparisons involving O^-P^- (i.e. O^-P^- versus O^+P^+), because there was no difference of phonological inconsistency or orthographic inconsistency between O^-P^- and O^+P^+ ($t(94) = 1.326$, $p = .188$; $t(94) = 1.324$, $p = .189$, respectively). In order to determine priming effects in a whole brain analysis, we compared O^-P^- , O^+P^- or O^-P^+ versus O^+P^+ for the contrast of target – null. All whole brain results are reported at $p < .001$ uncorrected and contain 10 or greater voxels.

We conducted subsequent analyses on regions that have shown a priori priming effects to auditorily and visually presented word stimuli. We chose a peak in left superior temporal gyrus because it is implicated in phonological processing (Booth et al., 2002a), a peak in left middle temporal gyrus because it is implicated in semantic processing (Liu et al., in press) and a peak in left fusiform gyrus because it is implicated in orthographic processing (Booth et al., 2002a). Because comparing O^-P^- to O^+P^+ is likely to be most sensitive to priming effects, we extracted beta values (6 mm radius sphere) for each individual for each lexical condition from three regions of interest (ROIs) based on peak voxels shown in the group

contrast of O^-P^- versus O^+P^+ and then compared conditions using analysis of variance (ANOVA) and t -tests, corrected for multiple comparisons ($p < .05/6 = p < .008$; six comparisons among four conditions). In order to determine conflict effects in a whole brain analysis, we combined the two conflicting conditions (i.e. O^+P^- and O^-P^+) and compared it to O^+P^+ for the contrast of target – null. Because studies have shown the importance of left inferior frontal gyrus in processing conflicting orthographic and phonological representations, we extracted beta values (6 mm radius sphere) for each individual for each lexical condition from two ROIs in left inferior frontal gyrus (dorsal and ventral) based on the conflicting contrast and then compared conditions using analysis of variance (ANOVA) and t -tests, corrected for multiple comparisons ($p < .05/6 = p < .008$; six comparisons among four conditions).

In order to determine if there were developmental or skill-related differences in a whole brain analysis, we correlated age, accuracy on the spelling task, or standard scores on a non-word reading test (Woodcock, McGrew, & Mather, 2001) with brain activation in O^-P^- , O^+P^- or O^-P^+ versus O^+P^+ for the contrast of target – null. We also correlated age, accuracy, and standard scores with beta values extracted for each condition from five ROIs described above. We employed analysis of covariance (ANCOVA) for each ROI with age, accuracy or standard scores as the covariate and with lexical condition as the within-subject factor. A main effect of the covariate indicates that age or skill is associated with brain activation regardless of condition. An interaction of the covariate and condition indicates that skill operates differently in the conditions, and therefore, may reflect a priming effect. In order to visualize the relationship between age or skill and activation, we correlated these individual difference measures with activation for each condition.

3. Results

3.1. Behavioral results

Table 2 presents accuracy and reaction time on the four lexical conditions. We calculated repeated measure ANOVAs of lexical conditions (O^+P^+ , O^+P^- , O^-P^+ , and O^-P^-) separately for accuracy and reaction time on correct trials. There were significant main effects of lexical condition for accuracy $F(3, 117) = 75.923$, $p = .000$, and reaction time, $F(3, 117) = 32.020$, $p = .000$. A set of paired t -tests among conditions ($p < .05/6 = p < .008$, corrected for multiple comparisons) showed that the accuracy on O^-P^- was greater than that on O^+P^+ , O^-P^+ , and O^+P^- , ($t(39) = 3.672$, $p = .001$; $t(39) = 11.643$, $p = .000$; $t(39) = 11.180$, $p = .000$, respectively). The accuracy on O^+P^+ was greater than that on O^-P^+ and O^+P^- ($t(39) = 8.128$, $p = .000$; $t(39) = 9.748$, $p = .000$, respectively). The accuracy on O^+P^- and O^-P^+ was not significantly different ($t(39) = 1.510$, $p = .139$). The reaction time on O^-P^- was faster than that on O^+P^+ , O^-P^+ , and O^+P^- ($t(39) = -4.027$, $p = .000$; $t(39) = -9.371$, $p = .000$; $t(39) = -7.411$, $p = .000$, respectively). The reaction time on O^+P^+ was faster than that on O^-P^+ and O^+P^- ($t(39) = -5.932$, $p = .000$; $t(39) = -3.886$, $p = .000$, respectively). The reaction time on O^+P^- and O^-P^+ was not significantly different ($t(39) = -1.150$, $p = .276$).

3.2. fMRI results

Table 3 presents direct comparisons between conditions. We focus the reporting of results in five brain areas in the left hemisphere

Table 2

Means (and standard deviations) for accuracy in % (Acc) and reaction time in ms (RT) on each of the four lexical conditions.

	O^+P^+	O^-P^+	O^+P^-	O^-P^-
Acc	87.9(8.0)	62.2(21.2)	66.9(14.5)	94.4(8.7)
RT	1627(373)	1803(418)	1758(425)	1523(335)

Table 3Greater activations for targets in O⁻P⁻, O⁺P⁻, and O⁻P⁺ compared to O⁺P⁺.

Contrast	Region	H	BA	z-test	Voxels	x	y	z
O ⁻ P ⁻ > O ⁺ P ⁺	Superior temporal gyrus	L	42,22	3.92	32	-51	-51	12
	Postcentral gyrus/superior temporal gyrus	L	3,22	5.70	667	-42	-27	57
	Middle temporal gyrus	L	21	4.43	*	-66	-33	3
	Fusiform/lingual gyrus	L	37,19	3.56	10	-27	-69	-9
	Middle/superior temporal gyrus	R	21,22	3.45	15	63	-27	-3
O ⁻ P ⁺ > O ⁺ P ⁺	Dorsal inferior frontal gyrus	L	9	4.98	835	-51	3	42
	Ventral inferior frontal gyrus	L	45,47	4.52	*	-42	33	6
	Medial frontal gyrus	B	8	5.52	257	-3	27	45
	Middle/superior temporal gyrus	L	21,22	4.12	82	-66	-33	3
	Inferior parietal lobule	L	40	4.08	69	-33	-54	42
	Ventral inferior frontal gyrus	R	47	4.17	61	36	24	0
O ⁺ P ⁻ > O ⁺ P ⁺	Dorsal inferior frontal gyrus	L	9	3.85	55	-45	12	30
	Ventral inferior frontal gyrus	L	47	4.03	112	-45	18	0
	Medial frontal gyrus	B	8	6.00	279	-3	21	48
	Precentral gyrus	L	6,4	4.40	138	-33	-15	66
(O ⁻ P ⁺ , O ⁺ P ⁻) > O ⁺ P ⁺	Dorsal inferior frontal gyrus	L	9	5.02	710	-42	9	30
	Ventral inferior frontal gyrus	L	47	4.46	*	-42	18	0
	Medial frontal gyrus	B	8	6.25	305	-3	27	45
	Ventral inferior frontal gyrus	R	47	4.43	73	36	24	0
	Postcentral gyrus	L	2	3.33	12	-51	-24	54

Note: H, hemisphere; L, left; R, right; B, bilateral; BA, Brodmann's area. Bold italics indicate that this peak was used in the region of interest (ROI) analysis.

*Indicates a second peak in the above cluster.

(superior temporal, middle temporal and fusiform gyri; dorsal and ventral inferior frontal gyri). In a whole brain analysis, there were weaker activations in superior temporal, middle temporal, and fusiform gyrus for O⁺P⁺ compared to O⁻P⁻ (see Fig. 1A–C). In an ROI analysis comparing the four lexical conditions, the main effect of condition was significant for superior temporal gyrus ($F(3, 117) = 5.206, p = .002$); for middle temporal gyrus ($F(3, 117) = 7.400, p = .000$) and for fusiform gyrus ($F(3, 117) = 5.174, p = .002$). A set of paired t -tests showed that O⁺P⁺ had weaker activation compared to O⁻P⁻ in superior temporal gyrus ($t(39) = 3.457, p = .001$) (see Fig. 1D). There were a few participants who showed deactivation in superior temporal gyrus, suggesting that there may be deactivation in auditory cortex during successive presentations of spoken words. In middle temporal gyrus, O⁺P⁺ had weaker activation compared to O⁻P⁻, O⁺P⁻, and O⁻P⁺ ($t(39) = 5.035, p = .000$; $t(39) = 2.823, p = .007$; $t(39) = 3.076, p = .004$, respectively) (see Fig. 1E). In fusiform gyrus, O⁺P⁺ and O⁺P⁻ had weaker activation compared to O⁻P⁻ ($t(39) = 3.101, p = .004$; $t(39) = 3.253, p = .002$, respectively) (see Fig. 1F). In summary, these analyses show priming effects in left superior temporal, middle temporal and fusiform gyrus.

In a whole brain analysis, when comparing O⁺P⁺ to each of the conflicting conditions (i.e. O⁺P⁻ and O⁻P⁺), there was weaker activation in left dorsal (BA 9) and ventral (BA 47) inferior frontal gyrus (see Table 3). Because each conflicting condition showed similar results, we compared O⁺P⁺ to the combination of these two conditions and again showed weaker activation in O⁺P⁺ in dorsal and ventral inferior frontal gyrus (see Table 3 and Fig. 2). In an ROI analysis comparing the four lexical conditions, the main effect of condition was significant for dorsal inferior frontal gyrus ($F(3, 117) = 15.303, p = .000$) and for ventral inferior frontal gyrus ($F(3, 117) = 14.348, p = .000$). A set of paired t -tests showed that, in dorsal inferior frontal gyrus, O⁺P⁻ had greater activation than O⁺P⁺ and O⁻P⁻ ($t(39) = 4.854, p = .000$; $t(39) = 4.257, p = .000$, respectively), and O⁻P⁺ had greater activation than O⁺P⁺ and O⁻P⁻ ($t(39) = 5.067, p = .000$; $t(39) = 4.230, p = .000$, respectively) (see Fig. 2C). In ventral inferior frontal gyrus, O⁺P⁻ had greater activation than O⁺P⁺ and O⁻P⁻ ($t(39) = 4.268, p = .000$; $t(39) = 4.131, p = .000$, respectively), and O⁻P⁺ had greater activation than O⁺P⁺ and O⁻P⁻ ($t(39) = 4.242, p = .000$; $t(39) = 4.192, p = .000$, respectively) (see Fig. 2D). In summary, these analyses show that target

words in pairs with conflicting orthographic and phonological information produced greater activation in dorsal and ventral inferior frontal gyrus than those with non-conflicting orthographic and phonological information.

In a whole brain analysis, correlations of age, accuracy on the spelling task or standard scores on non-word reading with brain activation in O⁻P⁻, O⁺P⁻ or O⁻P⁺ versus O⁺P⁺ were not significant. In an ROI analysis comparing the four lexical conditions, we found that higher accuracy was associated with greater activation in superior temporal gyrus with age partialled out ($F(1, 151) = 5.615, p = .019$), but accuracy did not interact with condition ($F(3, 151) = 0.118, p = .950$) (see Table 3A). We also found that higher standard scores on non-word reading was associated with weaker activation in middle temporal gyrus ($F(1, 152) = 18.774, p = .000$), but non-word reading did not interact with condition ($F(3, 152) = 0.098, p = .961$) (see Fig. 3B). Finally, we found that older age was associated with greater activation in dorsal inferior frontal gyrus with accuracy partialled out ($F(1, 151) = 18.054, p = .000$), but age did not interact with condition ($F(3, 151) = 0.228, p = .877$) (see Fig. 3C). The ROI analysis did not reveal any correlations with age or skill correlations in regions not mentioned above. In summary, although there were skill-related increases of activation in superior temporal gyrus and dorsal inferior frontal gyrus and skill-related decreases in activation in middle temporal gyrus, these effects did not interact with condition thus providing no evidence for skill differences in priming effects.

Priming related increases were found in left inferior parietal lobule ($-27, -66, 42, z = 4.43$, cluster = 58) and left inferior temporal gyrus ($-51, -54, -18, z = 3.81$, cluster = 13) in the contrast of O⁺P⁺ versus O⁻P⁻. Right superior temporal gyrus ($66, -15, 6, z = 4.02$, cluster = 117) showed greater activation for O⁺P⁺ than for O⁺P⁻.

In order to limit the possibility that accuracy level was a confounding factor in our results, additional analyses were calculated based on a subgroup of 24 participants whose accuracy on the two hard conditions (O⁺P⁻, O⁻P⁺) was above 60%. In a whole brain analysis, similar brain activation patterns were observed for the high performer group as in the whole group for the contrasts of O⁻P⁻ minus O⁺P⁺, O⁺P⁻ minus O⁺P⁺, O⁻P⁺ minus O⁺P⁺, and conflicting (O⁻P⁺, O⁺P⁻) minus O⁺P⁺. In addition, we calculated ROI analyses including group (high versus low performers) and condition

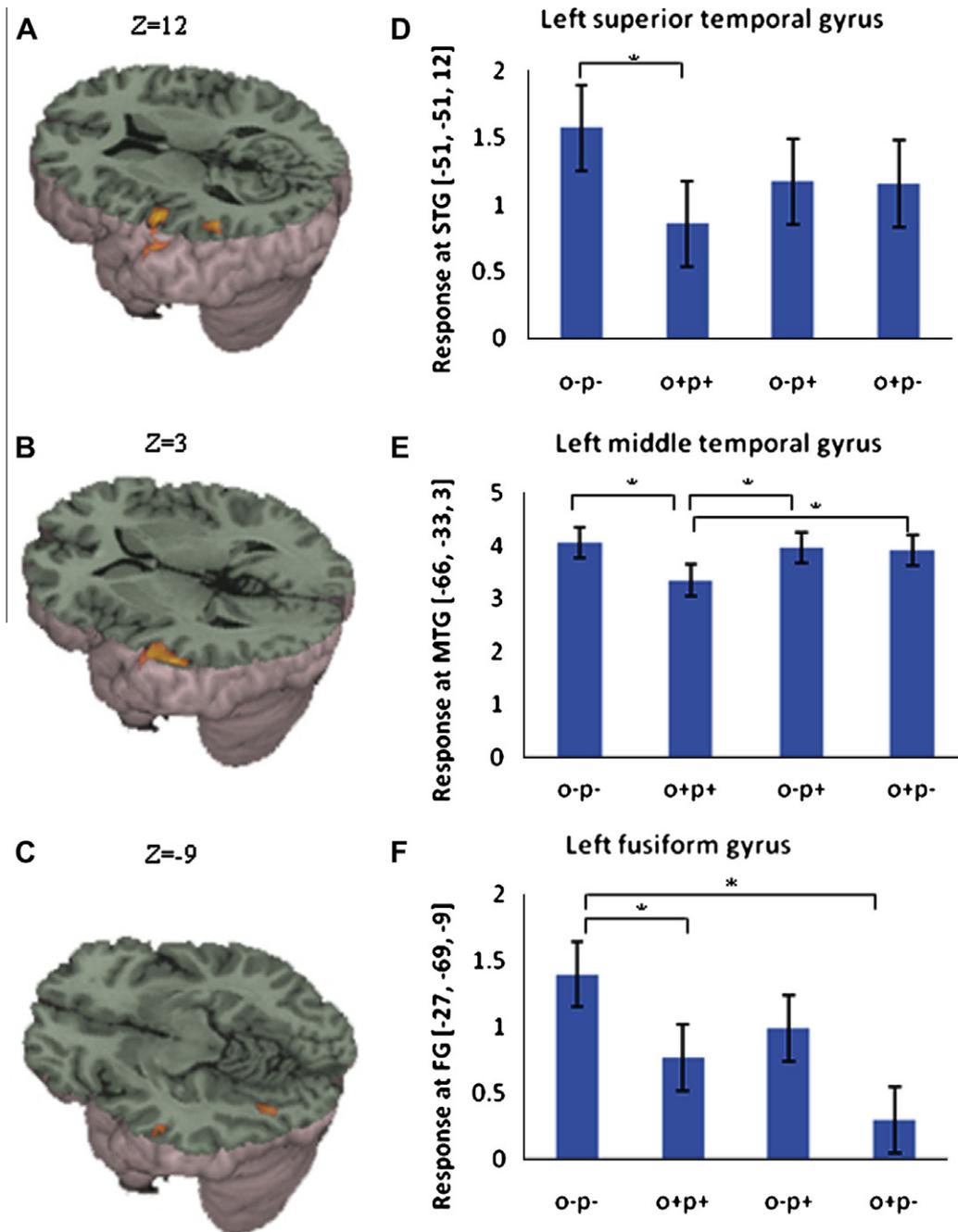


Fig. 1. Priming effects. Brain activations are weaker for targets in O⁺P⁺ than in O⁻P⁻ in left superior temporal gyrus (A), left middle temporal gyrus (B), and left fusiform gyrus (C). Bar graphs (D–F) present brain responses (beta values) at the peak voxel in these three regions for each lexical condition. Asterisks indicate significant differences between conditions at $p < .008$, corrected for multi-comparisons ($p < .05/6 = p < .008$).

(O⁺P⁺, O⁺P⁻, O⁻P⁺, O⁻P⁻) as independent variables. These analyses revealed no main effect of group or an interaction between group and condition for superior temporal gyrus, fusiform gyrus or middle temporal gyrus. Therefore, accuracy may not be a confounding factor for our results. Our data analysis was based on all participants on all trials including incorrect ones, because even when incorrect responses are made, we argue that similar responses to target words should be obtained in brain regions involved in processing phonological, orthographic and semantic representations. Incorrect responses are more likely to produce differential responses in decision making processing in regions such as the anterior cingulate (Holroyd et al., 2004; Kiehl, Liddle, & Hopfinger, 2000).

4. Discussion

The goal of this study was to examine priming effects in children. Our spelling task in the auditory modality required children to map from phonological to orthographic representations. Our results provide evidence for phonological priming effects in left superior temporal gyrus, orthographic priming effects in left fusiform gyrus and semantic involvement of left middle temporal gyrus. The latter two effects emerged despite the fact that our task did not involve visually presented information and did not require access to semantic representations for correct performance. Although our brain-behavior analyses did not provide evidence for skill-based differences in priming, they did show that higher

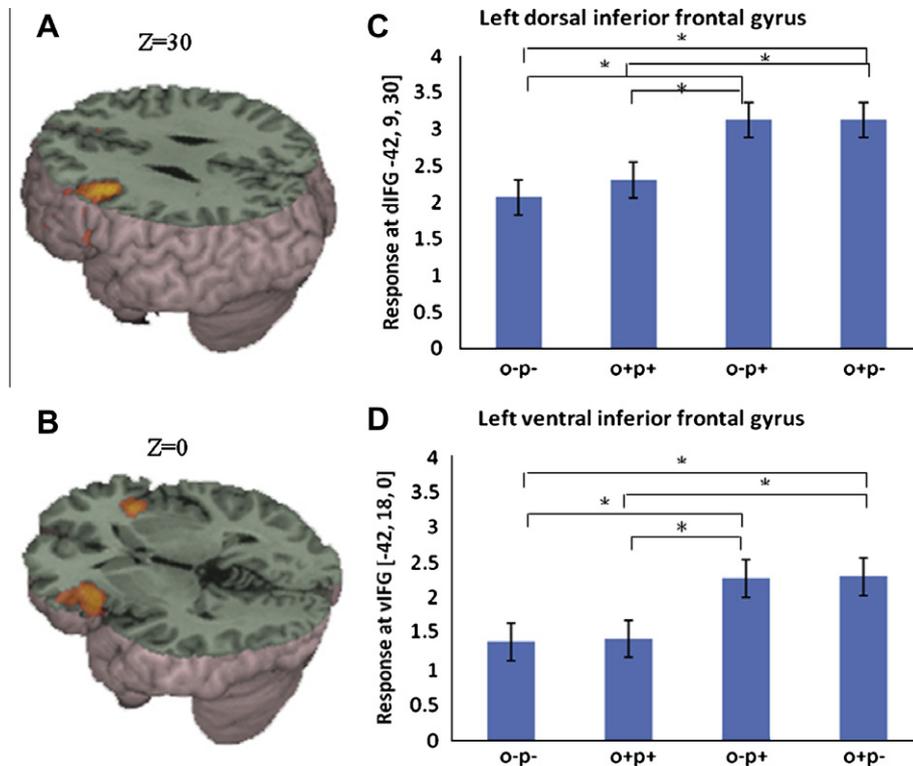


Fig. 2. Conflict effects. Brain activations are weaker for targets in O⁺P⁺ than in conflicting conditions (O⁺P⁻ and O⁻P⁺ combined) in left dorsal inferior frontal gyrus (A), and in left ventral inferior frontal gyrus (B). Bar graphs (C, D) present brain responses (beta values) at the peak voxel in these two regions for each lexical condition. Asterisks indicate significant differences between conditions at $p < .008$, corrected for multi-comparisons ($p < .05/6 = p < .008$).

accuracy was correlated with stronger activation across lexical conditions in left superior temporal gyrus and higher non-word reading skill was correlated with weaker activation across lexical conditions in left middle temporal gyrus. This suggests that higher skill is associated with increasing elaboration of phonological representations and less involvement of semantic representations as a compensatory mechanism. We also replicated conflict effects in left inferior frontal gyrus and found skill-related increases in activity in this region, indicating higher skill is associated with increasing involvement of this region in processing inconsistent orthographic and phonological information.

Consistent with previous studies in the auditory modality (Bergerbest et al., 2004; Marinkovic et al., 2003), we revealed priming effects in left posterior superior temporal gyrus during our auditory spelling task, suggesting facilitation of phonological perception when parts of auditory words are repeated. The left superior temporal gyrus has been found to be associated with phonological processing in many studies (Fiez & Petersen, 1998; Pugh et al., 1996; Rumsey et al., 1997). Even though the current study did not find skill or age differences in the priming effect in left superior temporal gyrus, we demonstrated that children with higher accuracy on the spelling task produced greater activation in this region, possibly indicating greater elaboration of phonological representations. Even though some studies have found developmental decreases in phonological regions in visual word processing (Bitan et al., 2007; Church, Coalson, Lugar, Petersen, & Schlaggar, 2008; Pugh et al., 2000) and auditory word processing (Church et al., 2008), our finding is consistent with studies that have found age-related and skill-related increases in activation of left superior temporal gyrus during rhyming and spelling judgment tasks to orally presented words (Booth, Burman, Meyer, Gitelman et al., 2003; Booth, Burman, Meyer, Zhang et al., 2003). Previous studies have also found that children with reading

disability show reduced activation in left posterior superior temporal gyrus as compared to normal children, indicating the deficient phonological processing (Shaywitz et al., 2002; Simos, Breier, Fletcher, Bergman, & Papanicolaou, 2000).

We also found a priming effect in left fusiform gyrus when word pairs had similar orthography as compared to when they did not, suggesting that orthographic overlap increases priming (reduces activation) in left fusiform gyrus even without visual input. This is consistent with a previous study that found priming effects in this region for both words and non-words in an auditory lexical decision task (Orfanidou et al., 2006). Previous studies of cross-modality priming effects have also reported priming effects in left fusiform gyrus and these effects are greater than within-modality auditory priming (Badgaiyan et al., 2001; Carlesimo et al., 2004; Schacter et al., 1999). The left fusiform gyrus has been implicated in orthographic processing during visual word processing (Binder et al., 2003; Dehaene et al., 2004), but has also been shown to be activated when processing spoken words (Booth et al., 2007; Cone et al., 2008). Our finding suggests that orthography is activated when a child hears a word, and there is orthographic facilitation if the word follows another word that has similar orthography.

We also found weaker activation in left middle temporal gyrus for word pairs with similar spelling that rhymed (O⁺P⁺: gate-hate) compared to all other conditions. A previous study (Gagnepain et al., 2008) found priming in this region only for repeated words but not for repeated non-words, suggesting its role in semantic processing. Indeed, left middle temporal gyrus has been implicated in lexical semantic processing in many studies (Bookheimer 2002; Booth et al., 2002b; Chou, Booth, Bitan, et al., 2006; Liu et al., in press; Price, Moore, Humphreys, & Wise, 1997). Our result supports the idea of spreading activation proposed by connectionist models of lexical processing (Rumelhart & McClelland, 1982). According to the connectionist approach, auditorily presented

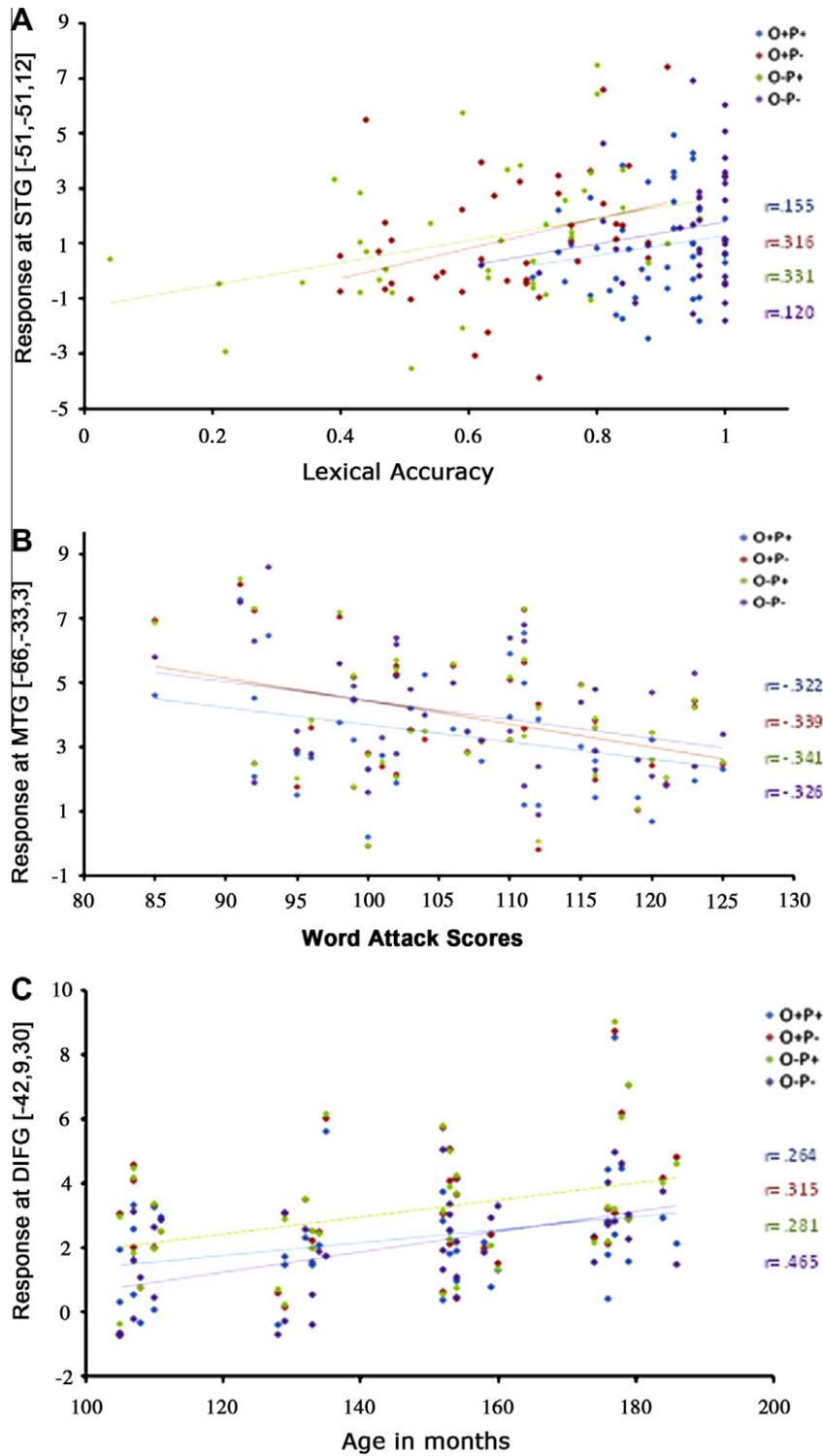


Fig. 3. Brain-behavior correlations. (A) Correlation of accuracy on spelling task and beta values at the peak of left superior temporal gyrus for each condition with age partialled out (from Fig. 1A). (B) Correlation of standard scores on Word Attack and beta values at the peak of left middle temporal gyrus for each lexical condition (from Fig. 1B). (C) Correlation of age on the spelling task and beta values at the peak of left dorsal inferior frontal gyrus for each lexical condition with accuracy partialled out (from Fig. 2A). *R*-values in partial correlation analyses are presented in each scatter-plot for each of the lexical conditions.

words should spread activation to semantic representations regardless of task demands. When the target has a similar spelling and rhymes with the prime, the activation of phonological and orthographic representations of the target are reduced. Therefore the spreading activation to the semantic representation of the target is also reduced. We additionally found that children with lower

non-word reading skill produced greater activation in left middle temporal gyrus for across all lexical conditions, suggesting greater semantic involvement when the mapping between phonology to orthography is inaccurate and slow. This is consistent with a previous neuroimaging study which found that children showed greater activation than adults in left middle temporal gyrus during a rhym-

ing and a spelling judgment task in the visual and auditory modalities (Booth & Burman, 2005). Behavioral and computational modeling studies have suggested that there is a decrease in semantic involvement with increased reading skill in tasks that demand mapping between orthography and phonology (Booth et al., 1999; Plaut & Booth, 2000). One possibility is that low skill children compensate for their deficient knowledge of spelling-sound correspondences by bringing to bear semantic knowledge about the world (Nation & Snowling, 1999). As children learn the statistical regularities between phonology and orthography, they rely less on semantics and more on interactions between orthographic and phonological representations for rapid word processing.

We found greater activation in left dorsal and ventral inferior frontal gyrus in the conflicting conditions (i.e. O⁻P⁺: jazz-has; O⁺P⁻: pint-mint) than in the non-conflicting conditions (i.e. O⁺P⁺: gate-hate; O⁻P⁻: press-list). Previous studies have shown greater activation in this left inferior frontal region for trials with conflicting orthographic and phonological information than for those with non-conflicting information in auditory tasks (Booth et al., 2007; Cone et al., 2008). The current study suggests that the greater involvement of left inferior frontal gyrus for conflicting trials might be associated with decision making because our analysis was on the targets only. When the target contains conflicting information to the prime, decision making may require greater involvement of a selection mechanism to inhibit irrelevant information and/or facilitate relevant information. Because the inferior frontal gyrus did not show a reduction in activation for targets that followed orthographic and phonologically similar primes, we conclude that it did not show perceptual priming effects. Previous studies have found priming effects in this region (Bergerbest et al., 2004; Orfanidou et al., 2006; Thiel et al., 2005), however, these studies have not required explicit judgments between the prime and target as in the present study.

We also found that older children produced greater activation in left dorsal inferior frontal gyrus for all four conditions, suggesting greater involvement of the selection mechanism with age. This is consistent with a previous study that has found a significant positive correlation of age with activation in left inferior frontal gyrus in children during a visual rhyming task (Bitan et al., 2007). Previous studies have generally found developmental increases (Holland et al., 2001; Simos et al., 2001) (Schlaggar et al., 2002; Turkeltaub, Garreau, Flowers, Zefirro, & Eden, 2003) in left inferior frontal gyrus during a variety of lexical tasks, suggesting greater lexical control with age. The current study found an accuracy related increase in left superior temporal gyrus and a skill-related decrease in left middle temporal gyrus, but an age-related increase in left dorsal inferior frontal gyrus. This suggests that posterior regions involved in representing lexical information are more sensitive to experience, whereas the anterior region involved in lexical control is more sensitive to age.

Although the current study found skill- and age-related differences in activation across lexical conditions, we did not find developmental or skill-related differences in priming effects (i.e. age and skill was not related to differences between conditions). This is consistent with studies that have shown priming effects in children, but no developmental differences in priming effects in 7-year-olds to adults during an auditory rhyming task (Coch et al., 2002, 2005) and no developmental changes in first, third and fifth graders in an auditory stem completion task (Carlesimo et al., 2000). Some previous studies have found developmental or skill-related decreases in priming effects in auditory tasks (Bonte & Blomert, 2004; Burden, 1989), whereas others have reported developmental or skill-related increases in priming effects in auditory tasks (Bonte & Blomert, 2004; Holyk & Pexman, 2004). Taken together, findings are not consistent about the skill-related and developmental differences in the auditory priming effect. However,

phonological and orthographic effects are present in children showing that priming represents a fundamental principle of brain organization.

Prime enhancement may reflect the formation of new cell assemblies (Fiebach, Gruber, & Supp, 2005; Henson, Rylands, Ross, Vuilleumier, & Rugg, 2004). Increases in left inferior parietal lobule in O⁺P⁺ may be due to the formation of new cell assemblies involved in the conversion from phonology to orthography. Previous studies have suggested that left inferior parietal lobule is involved in mapping from phonology to orthography (Booth et al., 2004). The conversion is similar for the target and for the prime in O⁺P⁺, therefore, it may facilitate the formation of new cell assemblies for this condition. Increases in right superior temporal gyrus in O⁺P⁺ might be due to the greater similarity of the spectro-temporal profile of the prime and target, as right superior temporal gyrus seems to be involved in processing stimuli with greater spectral correlation over time (Overath, Kumar, von Kriegstein, & Griffiths, 2008; Scott, Rosen, Beaman, Davis, & Wise, 2009). Increases in left inferior temporal gyrus in O⁺P⁺ might be due to the greater integration of phonology and orthography for this condition. This region has been implicated in multi-modal integration as compared to the more medial and posterior fusiform gyrus which is involved in unimodal orthographic processing (Cohen, Jobert, Le Bihan, & Dehaene, 2004). In O⁺P⁺, the two words have both similar orthography and phonology, therefore, there may be more integration of phonology and orthography in this condition.

Acknowledgments

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