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Development of brain networks involved in spoken word processing of Mandarin Chinese

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Abstract

Developmental differences in phonological and orthographic processing of Chinese spoken words were examined in 9-year-olds, 11-year-olds and adults using functional magnetic resonance imaging (fMRI). Rhyming and spelling judgments were made to two-character words presented sequentially in the auditory modality. Developmental comparisons between adults and both groups of children combined showed that age-related changes in activation in visuo-orthographic regions depended on task. There were developmental increases in left inferior temporal gyrus and right inferior occipital gyrus in the spelling task, suggesting more extensive visuo-orthographic processing in a task that required access to these representations. Conversely, there were developmental decreases in activation in left fusiform gyrus and left middle occipital gyrus in the rhyming task, suggesting that the development of reading is marked by reduced involvement of orthography in a spoken language task that does not require access to these orthographic representations. Developmental decreases may arise from the existence of extensive homophony (auditory words that have multiple spellings) in Chinese. In addition, we found that 11-year-olds and adults showed similar activation in left superior temporal gyrus across tasks, with both groups showing greater activation than 9-year-olds. This pattern suggests early development of perceptual representations of phonology. In contrast, 11-year-olds and 9-year-olds showed similar activation in left inferior frontal gyrus across tasks, with both groups showing weaker activation than adults. This pattern suggests late development of controlled retrieval and selection of lexical representations. Altogether, this study suggests differential effects of character acquisition on development of components of the language network in Chinese as compared to previous reports on alphabetic languages.

Keywords

Rhyming; Spelling; Development; Chinese; Orthography; Phonology

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Introduction

Applying neuroscientific methods to areas of cognitive processing that are educationally relevant has become increasingly common. With the advent of noninvasive neuroimaging methods, it is now possible to study the neural basis of academically relevant tasks in typical children. One of the most important early educational achievements in children is learning to read. While some studies have explored the nature of brain organization for reading in Chinese children and how this changes with development (Xue et al., 2005, Cao et al., 2009), little is known about the brain networks involved in spoken word processing in Chinese. The goal of the current study was to examine the effect of acquiring an orthographic system over typical development on spoken language processing in Chinese. "Development" refers to the changes over time rather than making a claim that this change is due to maturation or education.

Chinese is unique in both its phonological structure and the nature of the correspondence between phonological and orthographic representations. In terms of phonological structure, Chinese is a tonal language in which pitch distinguishes the meanings of words that are otherwise the same phonologically, and studies show that tone recognition and tone awareness develop early and reach adults level before school age (Xu, 2004). Moreover, all Chinese characters (the smallest unit of meaning) are mono-syllabic, which makes the syllabic structure of Chinese simpler than alphabetic languages (Bao, 1995). In terms of the mapping from phonology to orthography, the most salient difference between Chinese and alphabetic languages is that there is no phoneme-grapheme (sound to letter) correspondence in Chinese, as this mapping is from a syllable to a whole character. This mapping is one-tomany in that one spoken syllable is often associated with multiple written characters. The existence of extensive homophony (i.e. multiple ways to spell a single syllable) is likely to impact the influence that reading acquisition has on the nature of spoken language processing in Chinese.

The involvement of orthographic representations in spoken language is likely to depend on the nature of processing that the task demands. When the task requires access to orthography, such as spelling judgments to auditorily presented words, there may be developmental or skill-related increases in the involvement of orthography. Studies of reading in Chinese show that higher skill children are more accurate than lower skill children in deciding whether an unfamiliar character or a character with unfamiliar radicals presented in the visual modality is a real character or not (Li et al., 2000, Shu, 2003a). These studies suggest that reading acquisition is marked by greater elaboration of orthographic representations in that the number of orthographic entries and the number of connections between these entries increase (Perfetti et al., 2005). In terms of spoken language processing, neuroimaging studies with Chinese adults have found activation in regions thought to be involved in orthographic processing, such as bilateral inferior temporal gyrus and fusiform gyrus, in imaginary writing to dictation (Nakamura et al., 2000, Lin et al., 2007). Because of the increased elaboration of orthographic representations over development in Chinese, we would expect greater activation in inferior temporal and fusiform cortex in spoken language tasks that require access to these representations. This would be consistent with previous studies of alphabetic languages that have found skillrelated increases in left fusiform gyrus in spoken tasks with orthographic demands, such as spelling judgments to auditorily presented words (Booth et al., 2003a). Together, these results suggest that developmental effects for spoken language tasks with orthographic demands should be relatively similar across writing systems.

There appears to be a cross-linguistic difference in the involvement of orthographic representations in spoken language tasks that do not require access to these representations

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for correct performance. There is strong evidence from neuroimaging studies in alphabetic languages for orthographic involvement in spoken language tasks that show activation in fusiform gyrus during rhyming judgments to auditorily presented words (Booth, Burman et al. 2002; Booth, Burman et al. 2004; Burton, Locasto et al. 2005; Cone, Burman et al. 2008) and in speech listening (Yoncheva et al., 2010). This is consistent with the behavioral literature showing an influence of orthography on spoken language processing in alphabetic languages (Tunmer and Nesdale 1982; Ziegler, Petrova et al. 2008). Because alphabetic languages have a relatively systematic mapping between phonemes and graphemes, orthography may be automatically activated when processing spoken word forms. The robust orthographic effects found in alphabetic languages during spoken tasks are in contrast to those found in Chinese. One study found that there was lack of activation in orthographic regions in an rhyming task to auditorily presented words (Liu et al., 2009). Other studies have shown lack of activation in orthographic processing regions in spoken language tasks in Chinese (Bi et al., 2009). As noted above, there is a one-to-many mapping between phonology and orthography in Chinese in that the same auditory word can be spelled in many ways. The existence of many homophones in Chinese may actually interfere with spoken word processing because of the lack of systematic mapping between orthography and phonology, and this may underlie the lack of neuroimaging evidence for the involvement of orthographic representations in auditory processing of language.

The central goal of this study was to determine whether the acquisition of a written script has differential effects in Chinese as compared to previous reports in alphabetic languages. Behavioral studies in alphabetic languages show greater orthographic effects in spoken language tasks for higher skill readers (Zecker, 1991, Bruck, 1992), suggesting that proficiency is associated with automatic activation of orthographic representations due to the relatively systematic mapping between phonemes and graphemes. In support of this, neuroimaging studies show that typical children show greater activation in fusiform gyrus than children with dyslexia in rhyming judgment to auditorily presented words (Desroches, In press). Developmental or skill differences in the influence of orthographic representations on spoken language processing have not been investigated in Chinese. Early in acquisition, Chinese children will have relatively few characters in their orthographic lexicon, so the problem of homophony should not be extensive. However, when children learn more characters, there will be more ways to spell a single spoken syllable so that the mapping from phonology to orthography will be one-to-many. This one-to-many mapping may actually interfere with spoken language processing tasks in skilled readers, and therefore, we expect developmental decreases in activation in regions associated with orthographic processing for a rhyming task to auditorily presented words.

Two other nodes of the language network that seem to be critical for processing spoken word forms are superior temporal gyrus and inferior frontal gyrus. Left superior temporal gyrus has been associated with the perceptual representation of phonology. This region has been found to be activated in Chinese for rhyming (Liu et al., 2009), semantic (Liu et al., 2009), spelling (Lin et al., 2007), and lexical decision tasks (Xiao et al., 2005) to auditorily presented words. Previous studies on alphabetic languages found age-related increases in activation in left superior temporal gyrus in rhyming and spelling tasks to auditorily presented words (Booth et al., 2004). This is consistent with behavioral studies that have found increases in the elaboration of phonological representations with age in alphabetic languages (Fowler, 1991), which also seems to be a characteristic of development in Chinese (Jiang, 1999, Xu, 2004). These findings suggest that left superior temporal gyrus is involved in representing phonological forms and that these representations may become more elaborated early in development across languages.

Another critical node of the language processing network involved in processing spoken word forms is inferior frontal gyrus. Recent studies suggest that the anterior portion of left inferior frontal gyrus is involved in controlled retrieval and that the dorsal portion of left inferior frontal gyrus is involved in post-retrieval selection of representations (Badre, Poldrack et al. 2005; Badre and Wagner 2007). Consistent with this, effective connectivity studies suggest that there is top-down modulation from left inferior frontal gyrus to posterior task-specific language areas in adults (Bitan et al., 2005). One of the most consistent findings in the developmental neuroimaging literature is age-related increases in activation of and connection with left inferior frontal gyrus. Increased activation for alphabetic languages has been found in a variety of tasks in both the visual and auditory modality (Holland, Plante et al. 2001; Schlaggar, Brown et al. 2002; Shaywitz, Shaywitz et al. 2002; Turkeltaub, Garaeu et al. 2003; Booth, Burman et al. 2004; Szaflarski, Schmithorst et al. 2006; Booth, Cho et al. 2007; Cone, Burman et al. 2008; Bitan 2009). Increased connectivity between left inferior frontal gyrus and left superior temporal gyrus has been found for alphabetic languages in auditory tasks (Karunanayaka 2007; Schmithorst, Holland et al. 2007; Booth, Mehdiratta et al. 2008), and in phonological tasks in the visual modality (Bitan, Burman et al. 2006; Bitan 2009). Previous Chinese studies have also found skillrelated increases in left inferior frontal gyrus in rhyming (Cao et al., 2009), homophone judgment (Siok et al., 2004), and lexical decision tasks (Siok et al., 2004) in the visual modality. Taken together, studies suggest that there are prolonged developmental changes in left inferior frontal gyrus across lexical tasks and across languages.

The current study explored whether the acquisition of a writing system in Chinese has an effect on the nature of spoken language processing. We recruited three groups of participants, a group of adults, a group of third-grade (9-year-olds) elementary school children and a group of fifth-grade (11-year-olds) elementary school children. Including 9year-olds and 11-year-olds allowed us to examine early changes, because previous behavioral studies suggest that this is an important transition point in the development of fluent reading (Peng, 1985; Song, 1995). We included a task with orthographic demands (i.e. spelling judgment to auditorily presented words) and a task without orthographic demands (i.e. rhyming judgment to auditorily presented words) to determine if orthographic involvement was affected by task. We expected developmental increases of activation in visuo-orthographic regions in the spelling task, due to greater access to more elaborated orthographic representations. However, we expected developmental decreases in visuoorthographic regions in the rhyming task, because access to orthographic representations may interfere with spoken word processing because of the large number of homophones in Chinese. For both tasks, and consistent with previous literature, we expected to find developmental increases of activation in left superior temporal gyrus due to more elaborated representations of perceptual phonology, and developmental increases of activation in left inferior frontal gyrus due to the greater engagement of controlled retrieval and selection mechanisms.

Methods

Participants

20 adults (\underline{M} age = 21.5, range, 19–28; 7 males) participated in the rhyming and spelling tasks. 13 third-grade children (\underline{M} age = 9.2, range, 8–10; 7 males) participated in the rhyming and 12 third-grade children (\underline{M} age = 9.2, range, 8–10; 6 males) participated in the spelling task. 8 of them participated in both tasks. 14 fifth-grade children (\underline{M} age = 11.6, range, 10–12; 8 males) participated in the rhyming task. 10 of them participated in both tasks. Adult participates were undergraduate or graduate students at Beijing Normal University. Children participants were from a public elementary school in Baoding, Hebei

province of China. According to an informal interview, all participants met the following criteria, (1) native Mandarin Chinese speaker, (2) right-handed, (3) free of neurological disease or psychiatric disorders, (4) no attention deficit hyperactivity disorder (ADHD), and (5) no learning disability.

Cognitive tasks

Rhyming and spelling judgment—Two words were presented sequentially in the auditory modality and participants were asked to determine whether the second syllable of the words rhymed in the rhyming judgment or whether the second character had a similar orthography by sharing a phonetic radical in the spelling judgment. All words consisted of two characters. In order to eliminate the possibility of making decisions based solely on orthographic, phonological or tone information, we controlled for the similarity of the orthography, phonology, and tone of the second character in the first and the second word. There were 24 trials in each of 4 conditions, similar orthography and rhyming (O+P+, e.g. $\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}$), different orthography and rhyming (O-P+, e.g. $\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}$), different orthography and rhyming (O-P+, e.g. $\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2}\frac{1}{2$

Stimulus characteristics—All words used in this experiment did not have homophones. The two character words were matched on several variables across tasks, conditions, and presentation orders using analysis of variance (ANOVA) models of 2 task (rhyming and spelling) \times 4 condition (O+P+, O+P-, O-P+ and O-P-) \times 2 presentation order (first word and second word). These variables were adult written frequency (Beijing Language and Culture University, 1990), number of strokes, word familiarity in third-graders, and word familiarity in fifth-graders. Word familiarity was assessed in an independent study on 50 third-graders and 50 fifth-graders through a 7-point scale.

The second characters of words were also matched on several variables across tasks, conditions, and presentation orders using ANOVA models of 2 task (rhyming and spelling) \times 4 condition (O+P+, O+P-, O-P+ and O-P-) \times 2 presentation order (first word and second word). The variables were adult written frequency (Beijing Language and Culture University, 1990), and number of strokes.

Control trials—For the perceptual control trials, three-tone auditory stimuli, where all the component tones were ranging from 300–875 Hz (in 25 Hz increments), were presented sequentially and the participant was asked to determine whether the tone pairs were identical. Each tone in the three-tone stimuli was 200 ms in duration witha 50 ms linear fade in and out. The perceptual control had 24 trials with half of them matched and half unmatched. There were also 48 null trials in which a black cross turned red indicating the need to press a button with the right index finger.

Experimental procedure

We used an event-related design with four 6 min 44 seconds runs for each subject including two runs of each task. In each run, there were 12 seconds for a `dummy' period at the beginning, and 22 seconds at the end in order to get the whole hemodynamic response function (HRF) for the last trial. In each run, there were 48 experimental trials, 12 perceptual control trials, and 24 null trials. For the experimental trials, the two spoken words were presented in sequential order and a black fixation-cross appeared throughout the trial. The duration of each word was between 500 and 800 ms, with the second word beginning 1000 ms after the onset of the first. A 2600 ms response interval occurred 800 ms after the onset

of the second word. The start of the response interval was signified by a red fixation-cross and indicated the need to make a response. In the spelling task, if the second character of the two words shared one phonetic radical, the participant was asked to press a button with the index finger; if they did not share a phonetic radical, the participant was asked to press a different button with the middle finger. In the rhyming task, if the second syllable of the two words rhymed, the participant was asked to press a button with the index finger; if they did not rhyme, the participant was asked to press a different button with the participant was asked to press a different button with the middle finger. We presented the perceptual control trials in the same procedure as we did for the experimental trials. For 48 null trials, there was a black fixation cross (+) presented for 1800 ms and then a red cross was presented for 2600 ms indicating the need to press a button with the right index finger. Stimuli were presented in the same order for all subjects, optimized for random order using OptSeq (http://surfer.nmr.mgh.harvard.edu/optseq).

MRI data acquisition

After informed consent was obtained, participants were administered an informal interview and a practice session to become familiarized with the tasks. The participant practiced a half-length version of the experimental task. Different stimuli (matched in their stimulus characteristics) were used in the practice and fMRI sessions. Within a week, the participant was administered the MRI session.

All images were acquired using a 3 Tesla Siemens scanner. Gradient-echo localizer images were acquired to determine the placement of the functional slices. For the functional imaging studies, a susceptibility weighted single-shot EPI (echo planar imaging) method with BOLD (blood oxygenation level-dependent) was used. Functional images were interleaved from bottom to top in a whole brain EPI acquisition. The following scan parameters were used, TR = 2000 ms, TE = 20 ms, flip angle = 80°, matrix size = 128×128, field of view = 220 mm, slice thickness = 3 mm, number of slices = 33. These scanning parameters resulted in a $1.7 \times 1.7 \times 3$ mm voxel size. At the end of the functional imaging session, a high resolution, T1 weighted 3D image was acquired (MPRAGE, TR = 2390 ms, TE = 2.9 ms, TI = 900 ms, flip angle = 20°, matrix size = 256×256 , field of view = 256 mm, slice thickness = 1 mm, number of slices = 160). The orientation of the 3D volume was identical to the functional slices.

Image data analysis

Data analysis was performed using SPM5 (Statistical Parametric Mapping) (http,//www.fil.ion.ucl.ac.uk/spm). The functional images were corrected for differences in slice-acquisition time to the middle volume and are realigned to the last volume in the scanning session using affine transformations. No individual runs had more than 4 mm maximum movement for any subject in the x-plane, y-plane or z-plane. Furthermore, no individual runs had more than 3° of maximum displacement in rotation for pitch, yaw or roll. All statistical analyses were conducted on these movement-corrected images. Coregistered images were normalized to the MNI (Montreal Neurological Institute) average template (12 linear affine parameters for brain size and position, 8 non-linear iterations and $2\times2\times2$ nonlinear basis functions). Statistical analyses were calculated on the smoothed data ($4\times4\times8$ mm isotropic Gaussian kernel).

Data from each subject were entered into a general linear model using an event-related analysis procedure (Josephs & Henson, 1999). Word pairs were treated as individual events for analysis and modeled using a canonical HRF. Statistics was calculated with a high pass filter (128 seconds cutoff period). We used global normalization to scale the mean of each scan to a common value. Parameter estimates from contrasts of the canonical HRF in single

subject models were entered into random-effects analyses. All whole brain results are reported at p < .001 uncorrected and contain 12 or greater voxels.

In order to determine the group differences, we employed analysis of covariance (ANCOVA) of age group with accuracy as a covariate in a whole brain analysis on the contrast of lexical minus null separately for the rhyming and the spelling task. In one analysis, we combined third- and fifth-graders, and compared them to adults. In another analysis, we compared fifth-graders to third-graders. Due to the imbalance of sample size in these two analyses, early developmental changes (differences between third- and fifthgraders) might be underestimated. Based on developmental effects, we extracted the average of HRF values from volumes of interest (VOIs) (6 mm radius spheres) for each age group in each task centered on the peak voxel in the whole brain analysis. For both tasks, this consisted of nearly identical regions of left dorsal inferior frontal gyrus (dIFG) and left anterior inferior frontal gyrus (aIFG). We also included a VOI in left superior temporal gyrus (STG) for both tasks based on a study that showed a developmental decrease in this region for Chinese word processing in the visual modality (Cao et al., 2010). Superior temporal gyrus has been implicated in the perceptual representation of phonology in spoken language studies (Xiao, Zhang et al. 2005; Lin, Xiao et al. 2007; Liu, Deng et al. 2009), and this region showed a developmental increase during auditory word processing in studies of English (Booth et al., 2003b, Booth et al., 2004). In order to determine whether there were different developmental trajectories for frontal and temporal regions, ANOVAs of group (adults, third-graders, and fifth-graders) by task (rhyming, spelling) by region (STG, dIFG, aIFG) were calculated.

We also employed an ANCOVA of age group (adults versus combined group of third- and fifth-graders) with accuracy as a covariate in a whole brain analysis on the contrast of perceptual control minus null separately for each task, so that we were able to distinguish brain regions that showed developmental effects specific to lexical tasks from those that showed developmental effects in perceptual processing.

In order to determine whether there were developmental differences in conflict effects, we compared adults to children (combined third and fifth-graders) in a whole brain analysis using two-sample t-tests separately for each task. This was done for the lexical trials with conflicting orthographic and phonological information (O-P+, O+P-) compared to non-conflicting information (O-P-, O+P+) and for lexical trials with conflicting tone compared to non-conflicting tone information.

Results

Behavioral performance

Table 1 presents accuracy and reaction time for adults and children on the lexical and perceptual for the rhyming and spelling tasks in the scanner. We calculated condition (lexical and perceptual) by group (adults, third-graders and fifth-graders) ANOVAs separately for accuracy and reaction time in each task. There were significant main effects of condition for accuracy ($\underline{F}(1,44) = 34.890$, $\underline{p} = .000$ for the rhyming task; $\underline{F}(1,42) = 103.743$, $\underline{p} = .000$ for the spelling task), and for reaction time ($\underline{F}(1,44) = 192.117$, $\underline{p} = .000$ for the rhyming task; $\underline{F}(1,42) = 278.342$, $\underline{p} = .000$ for the spelling task). In both tasks, the accuracy was lower and the reaction time was slower on the lexical trials than on the perceptual trials. There were significant main effects of group for accuracy ($\underline{F}(2,44) = 10.605$, $\underline{p} = .000$ for the rhyming task; $\underline{F}(2,42) = 18.781$, $\underline{p} = .000$ for the spelling task), and for reaction time ($\underline{F}(2,44) = 5.797$, $\underline{p} = .006$ for the rhyming task; $\underline{F}(2,42) = 18.797$, $\underline{p} = .006$ for the rhyming task; $\underline{F}(2,42) = 18.797$, $\underline{p} = .006$ for the rhyming task; $\underline{F}(2,42) = 9.505$, $\underline{p} = .000$ for the spelling task).

Multiple comparisons (P<.017=.05/3) on the group effect for reaction time found that adults were faster than third-graders for the rhyming (t(31)=3.112, p=.004) and for the spelling task (t(30)=3.292, p=.003). Adults were faster than fifth-graders for the spelling task (t(31)=3.581, p=.001). Fifth-graders were faster than third-graders for the rhyming task (t(25)=3.036, p=.006)

The interaction between group and condition was significant for accuracy on the rhyming task ($\underline{F}(2,44) = 6.188$, $\underline{p} = .004$) and on the spelling task ($\underline{F}(2,42) = 3.280$, $\underline{p} = .047$). Multiple comparisons (corrected at p<.017= .05/3) found that adults were more accurate than third-graders on lexical trials in the rhyming task ($\underline{t}(31) = 5.272$, $\underline{p} = .000$). Adults were more accurate than third-graders on lexical trials and perceptual trials in the spelling task ($\underline{t}(30) = 5.299$, $\underline{p} = .000$; $\underline{t}(30) = 4.127$, $\underline{p} = .000$, respectively). Adults were more accurate than fifth-graders on lexical trials and perceptual trials in the spelling task ($\underline{t}(31) = 3.292$, $\underline{p} = .003$; $\underline{t}(31) = 3.291$, $\underline{p} = .002$, respectively). There was no significant difference between fifth-graders and third-graders on the accuracy in either condition in either task.

Brain activation patterns

Brain activation in children and adults for each task—Table 2 lists brain activation in children (combined fifth-graders and third-graders) and adults for the rhyming and spelling task. A wide spread network was activated including auditory phonological processing, orthographic processing and lexical control and selection. We focus our reporting of the results within groups for the language tasks compared to the null condition on regions that showed significant differences between groups (see below). Both children and adults showed extensive activation in both tasks in bilateral superior temporal gyrus and left inferior frontal gyrus. In the rhyming task, children showed extensive activation in bilateral occipito-temporal cortex (including middle occipital gyrus and fusiform gyrus), whereas activation in this region was much more limited in adults. In the spelling task, both groups showed activation in occipital cortex, however this extended down into the inferior temporal cortex in adults only.

Adults versus children (combined third and fifth graders)—We conducted comparisons between adults and both groups of children separately for each task on the contrast of experimental trials minus null trials. Table 3 lists these results, and Figure 1 shows the major effects for adults greater than children (green) and children greater than adults (red). In the rhyming task, adults showed greater activation than children in bilateral anterior inferior frontal gyri (BA 45/46) and left dorsal inferior frontal gyrus (BA 9). Children showed greater activation than adults in left fusiform gyrus (BA 37) and left middle occipital gyrus (BA 19). In the spelling task, adults showed greater activation than children in bilateral anterior inferior frontal gyri (BA 45/46) and left dorsal inferior frontal gyrus (BA 37) and left middle occipital gyrus (BA 19). In the spelling task, adults showed greater activation than children in bilateral anterior inferior frontal gyri (BA 45/46) and left dorsal inferior frontal gyrus (BA 37) and right inferior occipital gyrus (BA 19). There were no regions that showed greater activation in children than in adults for the spelling task. In summary, these results show similar changes across tasks in inferior frontal gyrus, but regions involved in visuo-orthographic processing showed age-related increases in the auditory spelling task, but decreases in the auditory rhyming task.

Fifth-graders versus third-graders—There were no significant differences between fifth-graders and third-graders on either task.

VOI analysis—For both tasks, 2 VOIs were identified including left aIFG ((-48, 18, 16) for the rhyming task and (-48, 16, 16) for the spelling task), and left dIFG ((-48, 10, 32) for the rhyming task and (-48, 10, 34) for the spelling task). Left STG (-54, -42, 16) was also included as a VOI for both tasks, based on a previous study that found developmental decreases at this peak during visual word processing and because this region has been implicated in phonology (Booth et al., 2004, Cao et al., 2010). Figure 2 presents beta values at these 3 VOIs for each group in each task.

Because the peaks of left aIFG and left dIFG were close across the two tasks and because we used the same peak for left STG across tasks based on a previous study (Cao et al., 2010), we performed a group (adults, third-graders and fifth-graders) by task (rhyming and spelling) by region (aIFG, dIFG and STG) ANOVA to examine early versus late developmental effects. The interaction of task by region was significant ($\underline{F}(2,84)=7.797$, $\underline{p}=$. 001). Multiple comparisons found that the spelling task produced greater activation than the rhyming task in dIFG ($\underline{t}(44)=2.552$, $\underline{p}=.014$), but the task difference was not significant in aIFG or STG. The main effect of group was significant ($\underline{F}(2,42)=22.462$, $\underline{p}=.000$). However, this was qualified by a significant interaction of region by group ($\underline{F}(4,84)=3.038$, $\underline{p}=.022$). Multiple comparisons (corrected at p<.017= .05/3) found that in aIFG and dIFG, adults showed greater activation than third-graders ($\underline{t}(31)=4.042$, $\underline{p}=.000$; $\underline{t}(31)=5.099$, $\underline{p}=.000$, respectively), and fifth-graders ($\underline{t}(32)=2.767$, $\underline{p}=.009$; $\underline{t}(32)=4.103$, $\underline{p}=.000$, respectively). In STG, fifth-graders showed greater activation than third-graders ($\underline{t}(25)=2.842$, $\underline{p}=.009$). In summary, these results show that frontal regions exhibited later developmental increases, whereas STG showed earlier developmental increases.

Perceptual control effects—No regions showed greater activation in adults than in children (combined third and fifth graders) for the perceptual control task; however left middle occipital gyrus (-28, -94, 12, z=3.94, cluster=12) showed greater activation in children than in adults in the rhyming task. Therefore, the age-related decrease in left middle occipital gyrus for the rhyming task does not appear to be specific to lexical processing.

Conflict effects—There were no developmental differences for either the rhyming or spelling task when comparing the trials with conflicting orthographic and phonological information (O+P-, O-P+) to trials with non-conflicting information (O+P+, O-P-). There were also no developmental differences for either task when comparing trials with conflicting tonal information to trials with non-conflicting tonal information. Therefore, age related differences for the rhyming and spelling task reported above do not seem to be driven by trials that have conflicting information.

Discussion

The current study found that, with the acquisition of reading, involvement of orthography showed differential effects on spoken language tasks in Chinese. Consistent with alphabetic languages, there was increased involvement of orthography during spelling judgments to auditorily presented words in Chinese. In contrast to studies on alphabetic languages, there was decreased involvement of orthography in rhyming judgments to auditorily presented words in Chinese. This suggests that the one-to-many mapping between phonology and orthography in Chinese results in less involvement of orthography during spoken language processing. In addition, we found different developmental trajectories in two regions crucial to language processing, with early changes in left superior temporal gyrus thought to be involved in phonological representations and later changes in left inferior frontal gyrus thought to be involved in controlled retrieval and selection.

The role of visuo-orthographic representations in spoken language processing

We found that the role of visuo-orthographic representations in spoken language processing was task specific. When the task required access to these representations for correct performance (i.e. spelling), adults showed greater activation than children in left inferior temporal gyrus and right inferior occipital gyrus. This is likely due to the fact that adults have a larger vocabulary and more elaborated orthographic representations. This is broadly consistent with a previous study on alphabetic languages (i.e. English) showing skill-related increases in activation in ventral visual cortex in a spelling task in the auditory modality (Booth et al., 2003a). The left inferior temporal gyrus has been associated with letter/letter string representations in alphabetic scripts in the visual modality centered at $(-43\pm5, -54\pm5, -54$ -12 ± 5 (Cohen et al., 2000), and in the auditory modality centered at (-52, -56, -12)(Cohen et al., 2004). This region has also been associated with radical recognition in Chinese characters, with pseudo characters invoking greater activation than artificial characters at (-45±5, -54±4, -15±5) (Liu et al., 2008). Our finding of developmental increases of activation at (-50, -54, -16) is similar to these previous three studies, perhaps because our auditory spelling task required judgments of information about components of characters, i.e. radicals, and therefore, brain regions involved in processing sub-lexical information may be engaged to a greater degree with development. Right inferior occipital gyrus has been associated with holistic visual processing in Chinese visual word recognition (Bolger et al., 2005, Tan et al., 2005). This region has also shown age-related and skillrelated increases during Chinese visual word processing (Cao, Peng et al. 2009; Siok, Spinks et al. 2009; Cao, Lee et al. 2010). Our study suggests that during the auditory spelling task, brain regions involved in holistic visual configuration of Chinese characters are more engaged in adults than in children.

We found that when the task did not require access to visual-orthographic representations for correct performance, adults showed less activation in visual-orthographic regions than children, presumably because extensive homophony in adults interferes with their spoken language processing. We found developmental decreases in the rhyming task in regions implicated in visuo-orthographic analysis including left middle occipital gyrus and left fusiform gyrus. However, only the effect in left fusiform gyrus was specific to the lexical task, as the left middle occipital gyrus also showed decreases during the perceptual trials. The left fusiform gyrus has been implicated in processing whole word representations centered at $(-37\pm4, -54\pm8, -11\pm6)$ (Glezer et al., 2009). The developmental decrease in fusiform activation at (-28, -58, -12) in our study suggests reduced automatic activation of orthography at the character level in adults during a task that can be performed solely based on accessing auditory word forms.

Our study suggests that in comparison to alphabetic languages, acquisition of the written script actually reduces the involvement of orthography in spoken language processing in Chinese. Because of the one-to-many mapping from phonology to orthography in Chinese, activation of orthography might interfere with the phonological processing that is demanded by the rhyming task. With acquisition of reading, Chinese adults face greater interference of orthography than children, because they have more spellings corresponding to one single syllable in their lexicon. Therefore it is more crucial for adults to ignore the orthographic information during these tasks. However in alphabetic languages, the mapping between phonology and orthography is more systematic and reading proficiency is marked by greater automatic activation of orthography during spoken language processing.

Phonological representations and frontal cortex

We found developmental increases in activation of left superior temporal gyrus in both the rhyming and the spelling tasks, suggesting increases in the elaboration of phonological

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representations. This is consistent with behavioral studies showing greater elaboration of phonological representations in older Chinese children (Jiang, 1999, Xu, 2004). These behavioral studies found that older children had higher performance than younger children on syllable awareness, onset/rime awareness and phoneme awareness tests. This finding is also consistent with fMRI studies of alphabetic languages that found developmental increases of activation in superior temporal cortex during spelling and rhyming tasks in the auditory modality (Booth et al., 2004). Our study further suggests that activation in the superior temporal gyrus during spoken language processing approaches adult levels in Chinese at around 11 years of age. Chinese is a tone language with all characters being mono-syllabic. Previous behavioral studies suggest that tone awareness develops early and reaches near adult levels before school (Xu, 2004). Therefore, early developing tone awareness combined with the relatively simple syllabic structure of Chinese may contribute to early developing phonological representations. In a previous study, we found age-related decreases of activation in the same cluster in superior temporal gyrus in Chinese during a rhyming task in the visual modality (Cao et al., 2010), presumably because phonology becomes less important while orthography becomes more important in Chinese reading. This conclusion is supported by behavioral studies on reading that showed greater reliance on orthography in adults and greater reliance on phonology in third-graders, with fifthgraders at the turning point of this reliance (Peng, 1985, Song, 1995). Phonology may become less important in visual word processing because of the existence of multiple homophones in Chinese. Multiple characters that share the same phonology can have different meanings, therefore the mapping from phonology to semantics is one-to-many which makes phonology an unreliable pathway in accessing semantics for single characters. However this ambiguity can be resolved in context. The context of natural speech provides constraints which is why illiterate people and young children have no difficulty understanding Chinese spoken language.

We also found developmental increases in both left dorsal and left anterior inferior frontal gyrus in both the rhyming and the spelling tasks. This is consistent with our previous neuroimaging study of rhyming and spelling judgment tasks to visually presented Chinese words (Cao et al., 2010). This finding is also consistent with previous studies on alphabetic languages using rhyming (Cone et al., 2008) and spelling tasks (Booth et al., 2007) in the auditory modality. Previous studies suggest that left anterior inferior frontal gyrus is associated with controlled retrieval whereas left dorsal inferior frontal gyrus is associated with post-retrieval selection (Badre, Poldrack et al. 2005; Badre and Wagner 2007). Our dorsal inferior frontal gyrus (-48, 10, 34) is close to the dorsal inferior frontal gyrus in Badre's study (-51, 15, 33), suggesting that this region is involved in general selection. Although our anterior inferior frontal gyrus (-48, 18, 16) is more dorsal than the anterior inferior frontal gyrus in Badre's study (-45, 27, -15), it is still relatively close. Our finding of developmental increases in these two regions suggests greater engagement of controlled retrieval and selection processes with age. Our findings of task differences also seem to support the distinction between the anterior and dorsal regions of inferior frontal gyrus. Anterior inferior frontal gyrus was equally involved in both tasks, whereas dorsal inferior frontal gyrus showed greater activation in the spelling compared to the rhyming task. Both tasks require controlled retrieval, but the spelling task requires greater selection among competing alternatives to a greater degree because there are multiple spellings corresponding to a single syllable.

In contrast to the relatively early developmental changes in left superior temporal gyrus, our study suggests that there is prolonged development in left inferior frontal gyrus. The late development of left inferior frontal gyrus compared to temporal regions is consistent with previous structural studies that show grey matter density matures later in frontal cortex compared to auditory cortex (Reiss, Abrams et al. 1996; Gogtay, Giedd et al. 2004), and that

show the development of both the axons and dendrites of frontal areas seems to lag chronologically behind that of other cortical areas (Huttenlocher, 1990, Scheibel et al., 1990). Several previous functional imaging studies have indirectly suggested that activation in superior temporal gyrus shows earlier changes as compared to inferior frontal gyrus. Turkeltaub et al (2003) showed that both children and adults exhibit activation in left superior temporal gyrus whereas only adults revealed activation in left inferior frontal gyrus during an implicit word reading task (Turkeltaub et al., 2003). In a word generation task to visually or auditorily presented words, others have found developmental increases in inferior frontal gyrus, but no developmental differences in superior temporal gyrus (Brown et al., 2005). Brauer et al. (2008) also found greater difference between children and adults in left inferior frontal gyrus than in left superior temporal cortex in the latency to peak activation during sentence listening (Brauer, 2008). The later age-related changes of inferior frontal gyrus may underlie the development of highly integrative functions, such as controlled retrieval and selection that continue to change into adulthood.

Educational implications

This study uncovered what appears to be an interesting cross-linguistic difference. Our study showed that the activation of visuo-orthographic representations decreases over development in Chinese during a task that relies solely on phonological representations, whereas previous studies in alphabetic languages have shown developmental increases in the activation of visuo-orthographic representations during phonological tasks. This crosslinguistic difference is likely due to the fact that alphabetic scripts have a semi-regular mapping between phonology and orthography, whereas Chinese has a more arbitrary mapping with many spoken word forms that can be spelled in different ways (i.e. homophones). This cross-linguistic difference has implications for instruction, as phonological processing in alphabetic languages may benefit from multisensory approaches that encourage the co-activation of phonological and orthographic representations. Intervention studies in alphabetic languages have found that after phonologically-based training, there is increased activation in left hemisphere language areas including fusiform gyrus, superior/middle temporal gyrus, inferior parietal lobule and inferior frontal gyrus (Richards, Corina et al. 2000; Eden, Jones et al. 2004; Shaywitz, Shaywitz et al. 2004; Odegard, Ring et al. 2008) This widespread effect on the brain suggests that multiple processes are affected by intervention in alphabetic languages. In contrast, the co-activation of visuo-orthographic information in Chinese may actually interfere with phonological processing and spoken language instruction may benefit from a uni-sensory approach.

We also found significant developmental increases in brain regions involved in orthographic processing from fifth-grade to adulthood in the spelling task. Although some behavioral studies in Chinese suggest that orthographic and visual skills are only important for beginning learners (Shu, 2003b, McBride-Chang, 2005), our findings suggest that greater instructional emphasis should be placed on writing, even after the fifth-grade. Due to the complex visual forms of Chinese characters, writing may be a good strategy to enhance the quality of orthographic representations. Indeed, one previous study argued that reading depends on writing in Chinese (Tan et al., 2005). This may be because of the crucial role that orthography plays in Chinese reading due to extensive homophony.

Conclusion

Reading acquisition seems to have fundamentally different effects in alphabetic compared to logographic languages such as Chinese. Previous studies in alphabetic languages have shown developmental increases in activation in visual-orthographic regions during spoken language tasks that can be performed solely based on access to phonological representations. This automatic activation of orthography over reading acquisition presumably results from

the systematic mapping between phonology and orthography in alphabetic languages. However, the existence of prevalent one-to-many mappings between phonology and orthography in Chinese means that as reading acquisition proceeds children learn more and more homophones. The learning of these homophones suggests that the activation of orthographic representations during phonological processing in spoken language tasks may actually interfere with processing, and therefore, may explain the developmental reduction of activation in left fusiform gyrus in Chinese. Our study also demonstrated that inferior frontal gyrus is relatively late to mature compared to superior temporal cortex. Inferior frontal cortex is implicated in controlled retrieval and selection. It may be the case that developmental increases in top-down modulation from frontal cortex allow for greater task specialization in posterior regions (Bitan et al., 2006).

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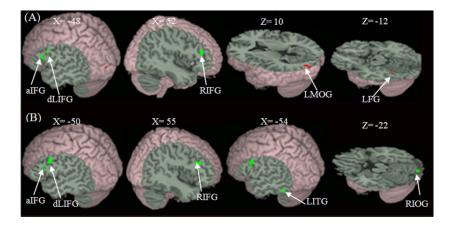


Figure 1.

Developmental changes in the auditory rhyming A and auditory spelling B tasks. In the auditory rhyming task, adults green showed greater activation than children in dorsal left inferior frontal gyrus dIFG, anterior left inferior frontal gyrus aIFG, and right inferior frontal gyrus RIFG. Children red showed greater activation than adults in left middle occipital gyrus LMOG and left fusiform gyrus LFG. In the auditory spelling task, adults green showed greater activation than children in dorsal left inferior frontal gyrus dIFG, anterior left inferior frontal gyrus aIFG, right inferior frontal gyrus RIFG, left inferior temporal gyrus LITG and right inferior occipital gyrus RIOG. Children did not show greater activation than adults in the spelling task.

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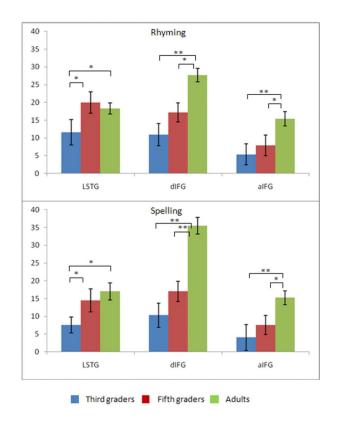


Figure 2.

Brain activity beta values at three VOIs in each group of participants in the rhyming and spelling task. One asterisk indicates significant group differences at P<.05, and two asterisks indicate significant differences at p<.01. LSTG = left superior temporal gyrus, dIFG = left dorsal inferior frontal gyrus, aIFG = left anterior inferior frontal gyrus. The STG VOI was taken from a previous study that showed developmental increases in Chinese during a rhyming task in the visual modality (Cao et al., 2010).

Table 1

Means (and standard deviations) for accuracy and reaction time for adults and children (third- and fifthgraders) in the lexical and perceptual conditions of the rhyming and spelling tasks.

	Rhy	ming
Accuracy (%)	Lexical	Perceptual
Third-graders	67.9 (16.7)	83.6 (17.8)
Fifth-graders	77.5 (2.3)	89.9 (7.7)
Adults	90.2 (8.7)	92.6 (2.7)
Reaction time (ms)		
Third-graders	1618 (231)	1166 (116)
Fifth-graders	1475 (170)	998 (159)
Adults	1377 (244)	1023 (158)
	Spe	lling
Accuracy (%)	Lexical	Perceptual
Third-graders	64.7 (10.0)	87.6 (6.6)
Fifth-graders	72.3 (9.5)	87.2 (10.1)
Adults	82.7 (8.9)	95.6 (4.5)
Reaction time (ms)		
Third-graders	1802 (187)	1305 (150)
Fifth-graders	1856 (192)	1301 (248)
Adults	1613 (256)	1026 (220)

Table 2

Brain activation in children and adults in the rhyming and spelling task.

Contrast	Region	Η	BA	z-test	voxels	x	Y	z
Rhyming > null Children	Superior temporal gyrus, Heschl's gyrus, middle temporal gyrus	Г	22,41, 42, 21	7.80	1793	-40	-30	8
	Superior temporal gyrus, Heschl's gyrus, middle temporal gyrus	R	22 , 41, 21	inf	1771	64	-10	-2
	Inferior occipital gyrus, Middle occipital gyrus, lingual gyrus, cuneus	L/R	19	6.95	3581	-8	-64	-4
	Inferior temporal gyrus, fusiform gyrus	L	37,19	4.99	18	-46	-34	-18
	Dorsal inferior frontal gyrus	Г	6	5.85	39	-46	12	28
	Anterior inferior frontal gyrus	Г	45 ,46	5.23	52	-48	32	8
	Inferior frontal gyrus	R	47	5.42	160	32	30	-2
	Precentral gyrus	R	9	5.40	156	54	0	48
	Postcentral gyrus	Г	2,3	4.30	18	-26	-34	46
	Middle frontal gyrus	R	9	4.21	36	28	-2	54
	Superior parietal lobule	Г	5,7	4.08	311	-22	-48	64
	Parahippocampal gyrus	R	:	4.87	107	30	4	-34
Adults	Superior temporal gyrus, Heschl's gyrus, middle temporal gyrus	Г	22 , 41, 42, 21	7.39	1132	-56	-4	-2
	Superior temporal gyrus, middle temporal gyrus	R	22 , 21	7.67	2901	64	-10	-2
	Inferior temporal gyrus	L	37	4.94	304	-44	-42	-14
	Cuneus	L	18	4.89	31	-2	-96	2
	Cuneus	R	18 , 19	5.39	50	4	-88	12
	Dorsal inferior frontal gyrus	L	9	6.69	487	-48	12	30
	Anterior inferior frontal gyrus	L	45 ,46	5.82	121	-36	30	6
	Precentral gyrus	L	6	5.90	17	-48	-2	54
	Insula	R	13	5.65	14	32	24	2
	Inferior parietal lobule	L	40	4.38	107	-30	-58	44
	Superior parietal lobule	L	7	4.08	82	-20	-64	60
Spelling > null Children	Superior temporal gyrus, Heschl's gyrus, middle temporal gyrus	L	22 , 41, 42, 21	7.11	3992	-58	-4	-6
	Superior temporal gyrus, middle temporal gyrus	R	22 , 21	7.53	2875	64	-16	0
	Lingual gyrus, fusiform gyrus	L	19, 37	5.91	235	-18	-66	-6
	Cuneus, lingual gyrus	L/R	23, 18	5.53	142	-8	-74	8

Contrast	Region	Н	BA	z-test	voxels	x	Y	z
	Dorsal inferior frontal gyrus	Г	9 , 46	5.68	268	-44	4	28
	Anterior inferior frontal gyrus	Г	47 , 45	4.00	299	-36	32	-16
	Insula	Г	13	5.36	119	-28	28	0
	Insula	R	13	5.53	50	32	28	0
Adults	Superior temporal gyrus, Heschl's gyrus	Г	22, 41, 42	6.44	718	-56	-8	-4
	Superior temporal gyrus, middle temporal gyrus	R	22, 21	6.77	574	99	-10	0
	Inferior temporal gyrus	Г	19, 37	5.13	246	-54	-62	-14
	Cuneus	Г	18 , 19	4.88	37	-22	06-	22
	Cuneus, inferior occipital gyrus, lingual gyrus	R	18 , 19	5.60	150	2	06-	22
	Dorsal inferior frontal gyrus	Г	6	6.91	480	-48	12	32
	Anterior Inferior frontal gyrus	Г	46	6.22	:	-46	32	12
	Inferior frontal gyrus	R	47	69.9	74	32	26	5
	Inferior parietal lobule	Г	40, 39	5.46	58	-30	-56	38
	Precentral gyrus	L	4	5.66	32	-48	-14	50

<u>Note</u>: Brain regions and BAs listed in bold are the peak coordinate for areas spanning different regions; Coordinates (X, Y, Z) listed are significant at P<.0001 FDR corrected. H = hemisphere, L = left, R = right; BA = Brodmann's Area.

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Table 3

Direct comparisons between children and adults in the spelling task and the rhyming task.

Rhyming Adults>Children Inferior frontal gyrus R Anterior inferior frontal gyrus Anterior inferior frontal gyrus 1 Children>Adults Dorsal inferior frontal gyrus, cuneus 1 Children>Adults Middle occipital gyrus, cuneus 1 Texiform gyrus Inferior frontal gyrus 1 Children>Adults Middle frontal gyrus 1 Declive Declive 1 1 Spelling Adults>Children Middle frontal gyrus, inferior frontal gyrus 1 Spelling Adults>Children Middle frontal gyrus, inferior frontal gyrus 1 Contart gyrus, inferior frontal gyrus 1 1 Middle frontal gyrus, inferior frontal gyrus 1 1 Midel frontal gyrus, inferior frontal gyrus 1 1 Midel frontal gyrus, inferior frontal gyrus 1 1 Midel frontal gyrus 1 1 1 Mider orcipital gyrus, inferior frontal gyrus 1 1 Mider orcipital gyrus 1 1 1 Mider orcipital gyrus 1 1 1 Mider orcipital gyrus 1 1 1 <th></th> <th></th> <th></th> <th></th> <th></th> <th>•</th> <th>4</th>						•	4
Anterior inferior frontal gyrus Dorsal inferior frontal gyrus Pusiform gyrus Fusiform gyrus Inferior frontal gyrus Declive Middle frontal gyrus, inferior frontal gyrus Declive Middle frontal gyrus, inferior frontal gyrus Declive Inferior frontal gyrus, inferior frontal gyrus	R	46	3.82	34	48	34	16
Dorsal inferior frontal gyrusMiddle occipital gyrus, cuneusFusiform gyrusInferior frontal gyrusInferior frontal gyrusDecliveMiddle frontal gyrus, inferior frontal gyrusDorsal inferior frontal gyrusInferior temporal gyrusInferior frontal gyrus	Г	45	3.74	25	-48	18	16
Middle occipital gyrus, cuneus Fusiform gyrus Inferior frontal gyrus Declive Middle frontal gyrus, inferior frontal gyrus Declive Middle frontal gyrus, inferior frontal gyrus Inferior temporal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Inferior frontal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Inferior frontal gyrus Inferior frontal gyrus Inferior frontal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Inferior frontal gyrus Inferior frontal gyrus	Г	6	3.54	14	-48	10	32
Fusiform gyrus Inferior frontal gyrus Declive Declive Middle frontal gyrus, inferior frontal gyrus Dorsal inferior frontal gyrus Inferior temporal gyrus, fusiform gyrus, lingual gyrus Inferior footal gyrus Inferior temporal gyrus Inferior temporal gyrus Inferior footal gyrus	Г	19	3.90	43	-28	-94	10
Inferior frontal gyrus Declive Declive Middle frontal gyrus, inferior frontal gyrus Dosal inferior frontal gyrus Anterior inferior frontal gyrus Inferior temporal gyrus, fusiform gyrus, lingual gyrus Inferior occipital gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Inferior frontal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Inferior frontal gyrus Inferior frontal gyrus	Г	37, 19	3.22	23	-28	-58	-12
Declive Middle frontal gyrus, inferior frontal gyrus Dorsal inferior frontal gyrus Anterior inferior frontal gyrus Inferior temporal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Cingulate gyrus	R	47	3.90	16	52	12	-2
Middle frontal gyrus, inferior frontal gyrus Dorsal inferior frontal gyrus Anterior inferior frontal gyrus Inferior temporal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus, fusiform gyrus, lingual gyrus Inferior frontal gyrus Cingulate gyrus	Г	:	3.70	15	-42	-64	-30
l gyrus tal gyrus us rus, fusiform gyrus, lingual gyrus	yrus R	6	5.12*	127	48	24	26
tal gyrus us rus, fusiform gyrus, lingual gyrus	L	6	4.53*	101	-48	10	34
us rus, fusiform gyrus, lingual gyrus	Г	45	3.72*	73	-48	16	16
rus, fusiform gyrus, lingual gyrus	L	20, 37	4.49*	104	-50	-54	-16
	s, lingual gyrus R	19 , 37, 17	3.99^{*}	142	18	-88	-22
	Я	45	3.75*	58	34	26	16
	L/R	32	4.30^{*}	16	-4	12	38
	L	7	3.94^{*}	16	9–	-66	62
Parahippocampal gyrus	R	28	3.49^{*}	28	22	-24	-10

* indicates regions that are significant at P<:05 FDR corrected. Coordinates (X, Y, Z) listed in bold are peaks from which we did VOI analyses in Figure 2. H = hemisphere, L = left, R = right; BA = Brodmann's Area.