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Prereader to beginning reader: changes induced by reading acquisition in print and speech brain networks

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Background: Literacy acquisition is a demanding process that induces significant changes in the brain, especially in the spoken and written language networks. Nevertheless, large-scale paediatric fMRI studies are still limited. **Methods:** We analyzed fMRI data to show how individual differences in reading performance correlate with brain activation for speech and print in 111 children attending kindergarten or first grade and examined group differences between a matched subset of emergent-readers and prereaders. **Results:** Across the entire cohort, individual differences analysis revealed that reading skill was positively correlated with the magnitude of activation difference between words and symbol strings in left superior temporal, inferior frontal and fusiform gyri. Group comparisons of the matched subset of pre- and emergent-readers showed higher activity for emergent-readers in left inferior frontal, precentral, and postcentral gyri. Individual differences in activation for natural versus vocoded speech were also positively correlated with reading skill, primarily in the left temporal cortex. However, in contrast to studies on adult illiterates, group comparisons revealed higher activity in prereaders compared to readers in the frontal lobes. Print-speech coactivation was observed only in readers and individual differences analyses revealed a positive correlation between convergence and reading skill in the left superior temporal sulcus. **Conclusions:** These results emphasise that a child's brain undergoes several modifications to both visual and oral language systems in the process of learning to read. They also suggest that print-speech convergence is a hallmark of acquiring literacy. **Keywords:** fMRI; literacy; prereaders; reading acquisition; print-speech convergence.

Introduction

Literacy acquisition is a demanding process that induces significant changes in brain structure and function (Dehaene, Cohen, Morais, & Kolinsky, 2015). In adults with varied literacy skills, reading performance has been shown to modulate responses to written words in left hemisphere (LH) language areas, including the visual word form area (VWFA) in left ventral occipito-temporal (vOT) cortex, superior temporal sulcus (STS), temporal pole, premotor cortex, inferior frontal gyrus (IFG), and supplementary motor area (Dehaene et al., 2010). Literacy skill has also been shown to affect activation patterns for spoken language processing, with some language areas showing greater activation (left posterior STS, bilateral middle temporal gyri [MTG], anterior cingulate), and others showing less activation (bilateral posterior superior temporal gyri [STG]) for literate relative to illiterate participants (Dehaene et al., 2010; see also Castro-Caldas, Petersson, Reis, Stone-Elander, & Ingvar, 1998).

Although the fMRI literature on literacy acquisition in children is growing, it is still relatively small and most of the studies have been conducted in a single language – English. In a cross-sectional study with beginning to expert readers ranging from 6 to 22 years of age, Turkeltaub, Gareau, Flowers, Zeffiro, and Eden (2003) report positive correlations between reading and brain activity to print in multiple LH areas, including left inferior and middle temporal areas, whereas activation of the right posterior cortical areas was negatively related to reading outcomes. A similar study by Shaywitz et al. (2002) also showed increased left posterior activity and a general reduction in right hemisphere (RH) involvement in typical readers; however, the posterior LH shift was not observed in the reading disabled cohort. Moreover, successful remediation of reading skill was associated both with increased left posterior and decreased RH involvement (Shaywitz et al., 2004; see also Simos et al., 2002, 2007 for similar intervention results with MEG). In another longitudinal study of children aged 7–12, Ben-Shachar, Dougherty, Deutsch, and Wandell (2011) also observed age-related increases in the sensitivity to printed words in posterior left vOT

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cortex with the magnitude of change further correlated with word reading efficiency gains. In one of the few fMRI studies looking at literacy acquisition in a language other than English, Brem et al. (2010) showed that print sensitivity in the VWFA emerged after only 4 hours of grapheme-phoneme correspondence training in German-speaking, nonreading kindergarten children. Studies looking at children with risk for dyslexia have failed to observe this pattern of print sensitivity in the LH posterior regions. Six-year-old children with dyslexia risk exhibited lower activation for words in bilateral vOT regions and higher activation in insula, thalamus and several right temporal regions relative to children without the risk for dyslexia (Specht et al., 2009). In another study, kindergarten pupils with behavioural risk of dyslexia had reduced activation for letters compared to false fonts in bilateral tempo-parietal regions (Yamada et al., 2011). In sum, these developmental studies suggest that successful literacy learning is associated with increased reading specialization in LH ventral cortex and generally less RH and frontal involvement with experience and skill (Pugh et al., 2013; Richlan, Kronbichler, & Wimmer, 2009).

Besides studying the relationship between literacy skills and activation patterns for print, we propose that in learning to read a critical measure should entail focus on changes in the neural correlates of speech and print-speech integration. The impact of literacy on speech processing has been documented in adult literates and illiterates, described above, as well as in a study of reading and prereading 6-year-old children showing that reading performance was positively correlated with spoken language processing in the left IFG, left posterior STS, and left temporal pole (Monzalvo & Dehaene-Lambertz, 2013). Surprisingly, greater activation for prereaders than readers was observed in left anterior insula and precental gyrus in an additional group contrast.

Our focus on convergence (spatial coactivation) of print and speech networks is further motivated by theory regarding the relationship between spoken and written language (Liberman, 1992) and research indicating that individual differences in reading abilities, longitudinal outcomes in children, and print comprehension in adults closely depend upon the ability to reorganize speech sensitive networks in the LH to become responsive to print (Frost et al., 2009; Preston et al., 2016; Shankweiler et al., 2008). In 6–10-year-old readers, reading readiness (as indexed by phonological awareness) was strongly correlated with the degree to which LH voxels relevant to spoken word processing were coactivated by print (Frost et al., 2009). Reinforcing the importance of print-speech integration for skilled reading, Preston et al. (2016) found that the extent to which 6–10-year-old readers engage common voxels for print and speech in LH predicts performance on standardized reading tests 2 years later above and beyond total activation for either print or speech alone. In addition, regions such as STS and STG have been found to preferentially respond to converging multisensory input (Van Atteveldt, Formisano, Goebel, & Blomert, 2004) and show reduced activation in dyslexic compared to control children and adults (Blau, van Atteveldt, Ekkebus, Goebel, & Blomert, 2009; Blau et al., 2010).

Despite a growing body of evidence on how learning to read at different ages modifies brain systems for print, speech and their relation, we need more information at the earliest stages of literacy acquisition in other languages than English. Because, unlike other alphabetic orthographies, the English orthography has a very high degree of irregularity in spelling-sound mappings, previous research may have a limited relevance for a universal science of reading (Share, 2008). Our study addresses this gap directly testing Polish beginning readers from kindergarten and first grade. We selected children who could read at least one word and performed regression analysis to examine how reading performance correlates with the activation for print and speech as well as print-speech convergence in the first year of reading acquisition. On the basis of previous research in English, for better readers, we expect to find higher activation for print in LH language areas including IFG, temporal, and temporo-parietal areas. These regions should show print-speech convergence in more skilled readers. We hypothesize that the first stage of literacy acquisition affects also activation patterns for spoken language processing, but because we study implicit processing, higher activation in better readers is expected in the left temporal and IFG areas, but not in the vOT cortex (Dehaene & Cohen, 2011). To the extent that print and speech processing changes reflect less effort and attentional resources for better readers, we expect negative correlations with skill in anterior cingulate and anterior prefrontal cortex.

We also test if the onset of literacy induces a distinction in print and speech networks between beginning readers and prereaders matched for age, sex and socioeconomic status (SES). For print, we expect to observe higher activation in begining readers mainly in the LH temporal, tempo-parietal and frontal cortical areas, given findings from previous studies (with exception of Brem et al., 2010) suggesting that in the VWFA the specificity for print emerges relatively late in childhood. However, it is possible that it may develop earlier in a language such as Polish that has more transparent print-speech mappings than English. Differences between readers and prereaders in speech processing has been less extensively studied and thus predictions are not as clear though Monzalvo and Dehaene-Lambertz (2013) study suggests decreased involvement of left precentral/insular cortex in readers compared to prereaders.

Methods

Participants

Data from 111 children (*M* age = 6.90, *SD* = 0.55, min = 5.51, max = 8.06, 65 girls, 46 boys) out of 120 were included in the current analyses (for details see Supporting Information); data from nine subjects were excluded due to excessive motion in scanner. Seventy-eight children were in first grade of elementary school and 33 attended kindergarten. All children met the following criteria: typical IQ, being born at term (>37 weeks) and right-handedness. None of the children had any history of neurological illness or brain damage and no symptoms of ADHD. The study was approved by the University of Warsaw Ethics Committee. All parents gave written informed consent to the study and children agreed orally.

Prereader/reader analysis subsample. Thirty-three children were not able to read a single word in 60 s. For categorical group comparisons, these prereaders were matched pairwise for age, sex, IQ and SES with 33 readers. Subjects were matched to reduce total distance using the Hungarian optimization algorithm (Kuhn, 1955) to minimize the cost function: $d_{ij} = W_1 * (age_i - age_j)^2 + W_2 * (IQ_i - IQ_j)^2 + W_3 * (SES_i - SES_j)^2$ with weightings $W_1 = 2$; $W_2 = W_3 = 1$. See Table 1 for sample and subsample demographics. Although the time of school/kindergarten year when children were tested did not differ between the groups, there was a significant difference in the formal reading instruction time: there were more first graders in the readers group.

Reading skill analysis subsample. The inclusion criterion for the regression analysis was a score of at least one word read aloud in a timed sight word reading task (Szczerbiński & Pelc-Pękała, 2013). Seventy-eight children fulfilled this criterion (*M* age = 7.04 years, *SD* = 0.53, min – 5.94, max = 8.06): 66 first graders, 48 girls, 30 boys and 47 children with family history of dyslexia (FHD+). Reading performance ranged from one to 74 sight words read in 60 s (*M* = 22.65, *SD* = 18.50, *Mdn* = 16).

Behavioural measures

Forty-seven days on average (min = 4, max = 144) before the neuroimaging session participants performed a sight word reading test, a subtest of the Decoding Test (Szczerbiński & Pelc-Pękała, 2013; see Supporting information for details), including also: letter knowledge, pseudoword reading, elision and phoneme analysis. The delay between behavioural and fMRI testing did not differ between the groups and did not affect the pattern of fMRI results. Early print skills were assessed using an orthographic awareness test (Awramiuk & Krasowicz-Kupis, 2014). Rapid automatized naming (RAN) was tested with object and color naming subtests (Fecenec, Jaworowska, Matczak, Stańczak, & Zalewska, 2013). Raven's Coloured Progressive Matrices (Polish adaptation: Szustrowa & Jaworowska, 2003) provided a measure of nonverbal IQ and the Picture Vocabulary Test: Comprehension indexed receptive vocabulary (Haman, Fronczyk, & Łuniewska, 2012). The behavioural data were analyzed in IBM SPSS Statistics v. 23.0.0.1.

fMRI task and procedure

Children received a short language localizer task in an event-related design with four stimulus conditions: (1) printed real words, (2) spoken real words, (3) printed symbol strings, and (4) spoken words vocoder processed to minimize phonetic content (for details, see Supporting Information and Table S1). Conditions (3) and (4) can be considered as low-level nonlinguistic *control* conditions that are matched in physical characteristics to the printed linguistic stimuli (length and visual complexity on screen) and to the spoken linguistic stimuli (dynamic frequency and amplitude content). However, linguistic content has been eliminated (orthographic and phonetic, respectively). This design evokes robust activation of the language network, and is sensitive to individual differences in reading skill in adults (Malins et al., 2016). Children were asked to pay attention to the stimuli – no explicit task was given to the participants. However, in such tasks reading occurs implicitly even without explicit instruction to read (Price, Wise, & Frackowiak, 1996).

On each trial, four different stimuli from the same condition were presented in rapid succession in a 'tetrad', designed to evoke strong activation with a relatively short imaging time.

Table 1 Demographics and test performance in prereaders and matched readers

Characteristic	Matched readers	Prereaders	Test	*p*-value
N	33	33		
Age (months)	80.68 ± 4.72	79.01 ± 5.73	$t = 1.29$	ns
Sex	14 M, 19 F	16 M, 17 F	$\chi^2 = 0.24$	ns
Grade	7 K, 26 E	21 K, 12 E	$\chi^2 = 12.16$	<.001
FHD status	13 FHD-, 20 FHD+	12 FHD-, 21 FHD+	$\chi^2 = 0.06$	ns
SES	48.40 ± 10.37	43.43 ± 12.01	$t = 1.75$	ns
Raven IQ[a]	7.33 ± 1.30	7.03 ± 1.40	$t = 0.91$	ns
Articulation[b] (% of correctly pronounced words)	89.7 ± 18.03	77.57 ± 32.78	$t = 1.87$	.067
Sight word reading[b] (words per minute)	21.03 ± 17.77	0	$t = 6.80$	<.001
Letter knowledge[b] (identification of 64 lower & upper case letters)	57.7 ± 10.69	25.27 ± 14.61	$t = 9.34$	<.001
Pseudoword reading[b] (pseudowords per minute)	16.72 ± 11.99	0	$t = 8.01$	<.001
Phoneme analysis[b] (*N* of correctly analyzed words)	8.84 ± 2.57	2.12 ± 2.84	$t = 10.06$	<.001
Phoneme elision[b] (*N* of correctly deleted phonemes)	5.39 ± 3.9	0.79 ± 1.65	$t = 6.25$	<.001
Rapid automatized naming[a] (average time in object and color subtests)	6.98 ± 2.04	5.78 ± 1.93	$t = 2.44$	.017
Picture vocabulary task[b] (*N* of correctly recognized pictures)	79.72 ± 5.61	73.3 ± 6.60	$t = 4.26$	<.001
Orthographic awareness[b] (% of correctly identified items)	66.56 ± 15.11	52.71 ± 13.05	$t = 3.92$	<.001

M, male; F, female; K, kindergarten; E, elementary school; FHD, familial history of dyslexia; SES, socioeconomic status.

[a] Standard values.

[b] Raw values.

Each visual stimulus was presented for 250 ms, followed by a 200 ms blank screen, whereas each auditory stimulus was allowed 800 ms to play out. 'Jittered' intertrial intervals were employed with occasional 'null' trials resulting in ITIs ranging from 4 to 13 s (6.25 s on average). The task was performed in two runs, each lasting 5:02. All conditions were presented in each run, with 48 trials per run presented pseudorandomly, with no condition allowed to repeat more than three times in a row. This results in 24 total trials per condition, and 96 total stimuli per condition. Stimuli were presented using Presentation software (Neurobehavioral Systems, Albany, CA). Before the scanning session children were familiarized with the task in a mock-scanner using different items.

fMRI data acquisition and analyses

fMRI data were acquired on a 3T Siemens Trio scanner using a whole-brain echoplanar imaging sequence with 12-channel head coil (32 slices, slice-thickness 4 mm, TR = 2,000 ms, TE = 30 ms, flip angle = 80°, FOV = 220 mm^2, matrix size = 64 × 64, voxel size = 3 × 3 × 4 mm). Anatomical data was acquired using a T1 weighted MP-RAGE sequence (176 slices, slice-thickness = 1 mm, TR = 2,530 ms, TE = 3.32 ms, flip angle = 7°, matrix size = 256 × 256, voxel size = 1 × 1 × 1 mm).

The preprocessing and analyses were performed using SPM8 (Welcome Trust Center for Neuroimaging, London, UK). Images were realigned to the first functional volume. Then structural images from single subjects were coregistered to the mean functional image. Coregistered anatomical images were segmented using paediatric tissue probability maps (generated with Template-O-Matic toolbox). Next, DARTEL was used to create a group-specific template and flow fields based on segmented tissues (Ashburner, 2007). Functional images were normalized using compositions of flow fields and a group-specific template and smoothed with an 8 mm isotropic Gaussian kernel. The data were modelled for each fMRI run, using the canonical hemodynamic response function convolved with the experimental conditions and fixation periods. Besides adding movement regressors to the design matrix, ART toolbox was used to reject motion-affected volumes (for details, see Supporting Information).

The general linear approach was used to analyze the data, contrasting experimental and rest trials in each subject. For each subject, contrasts were computed to examine word (print>rest and speech>rest) and word-specific effects for print and speech (print>symbol strings and speech>vocoded speech). For the results of brain activity to control conditions relative to rest, or reversed contrasts (i.e., symbol strings>print and vocoded speech>speech), see Supporting Information (Figures S1 and S2). At the second level, using one-sample *t*-tests we studied word and word-specific activation to print and speech in three groups: prereaders, matched readers and total sample of readers. To uncover print-speech convergence regions we computed a null (AND) conjunction between word and word-specific activation to print and speech. For multiple regression analyses, the neural response for word-specific activation to print and speech was correlated with sight word reading skill, controlling for age as a variable of no interest. Here again, a conjunction analysis for positive correlations was computed by examining the intersection between the two contrasts. Using two-sample *t*-tests, we compared word-specific brain activity to print and speech between prereaders and matched readers. Results are reported at a significance level of $p < .005$ uncorrected, and an extent threshold of 50 voxels (Raschle, Zuk, & Gaab, 2012), corresponding to the threshold of $p < .05$, corrected for multiple comparisons using a cluster size algorithm resulting from Monte Carlo simulations (3dClustSim, AFNI, http://afni.nimh.nih.gov). Significant clusters were labelled using Automated Anatomical Labeling (AAL) Atlas implemented in xjView toolbox (http://www.alivelearn.net/xjview).

Results

Behavioural results: Prereaders/readers analysis

Independent samples *t*-tests showed significant differences between matched readers and prereaders in letter knowledge task, pseudoword reading, phoneme analysis, phoneme elision, orthographic awareness, vocabulary size, and rapid automatized naming. For means, standard deviations and *t*-statistics see Table 1.

Behavioural results: Beginning readers

Using Pearson correlations, we found that sight word reading correlated with pseudoword reading ($r = .87$; $p < .001$) and several tests measuring reading-related skills, such as letter knowledge ($r = .58$; $p < .001$), phoneme analysis ($r = .42$; $p < .001$), elision ($r = .72$; $p < .001$), orthographic awareness ($r = .51$; $p < .001$), and verbal working memory ($r = .31$; $p = .006$). Reading score did not correlate with vocabulary size or RAN. We observed a significant correlation with nonverbal IQ ($r = .34$; $p = .002$). The reading score did not correlate with age and SES. The independent samples *t*-test revealed no differences in reading score between boys and girls or FHD+ and FHD- children.

fMRI results: Prereaders/readers analysis

Prereaders versus matched readers. Figure 1 illustrates word (A: print>rest and speech>rest) and word-specific (B: print>symbol strings and speech>vocoded speech) activation for prereaders and matched readers (see Tables S2 and S3 for the location of cluster maxima). Regions in which printed words elicited significantly higher activity than symbol strings were exclusively found in the LH in both groups. Prereaders activated two small clusters in the left caudate and lingual gyrus, whereas matched readers showed activation in the IFG, precentral, and postcentral gyri. Neural response for speech>vocoded speech in prereaders and matched readers was present mainly in bilateral superior, middle temporal, and inferior frontal cortex.

While we observed a coactivation for print>rest and speech>rest in bilateral IFG, insula, and STG/MTG/STS (see Table S4 for coordinates and spatial extent) in readers, this coactivation was absent in prereaders. Neither did we observe word-specific coactivation in any of the groups.

The results of two-sample *t*-test on word-specific activation for print and speech are presented in Figure 2 and Table 2. For print, prereaders had higher activation in the left caudate than matched readers. The opposite contrast showed enhanced activation in the left IFG, precentral and postcentral gyri in matched readers. In the prereading children, speech induced larger activation in the bilateral precentral gyrus, left IFG and right Rolandic

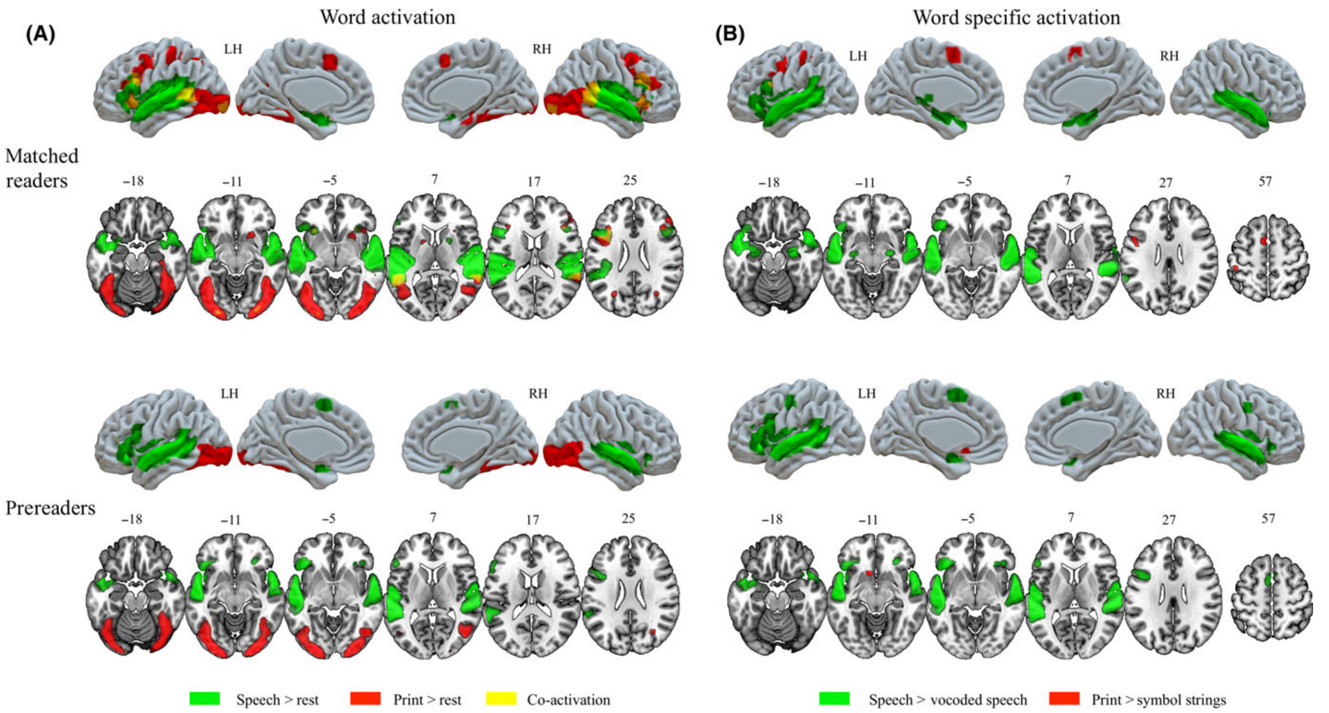

Figure 1 (A) Word (print>rest and speech>rest) and (B) word-specific (print>symbol strings and speech>vocoded speech) activation in matched readers and prereaders ($p < .05$ cluster-corrected; $p < .005$ height threshold) [Colour figure can be viewed at wileyonlinelibrary.com]

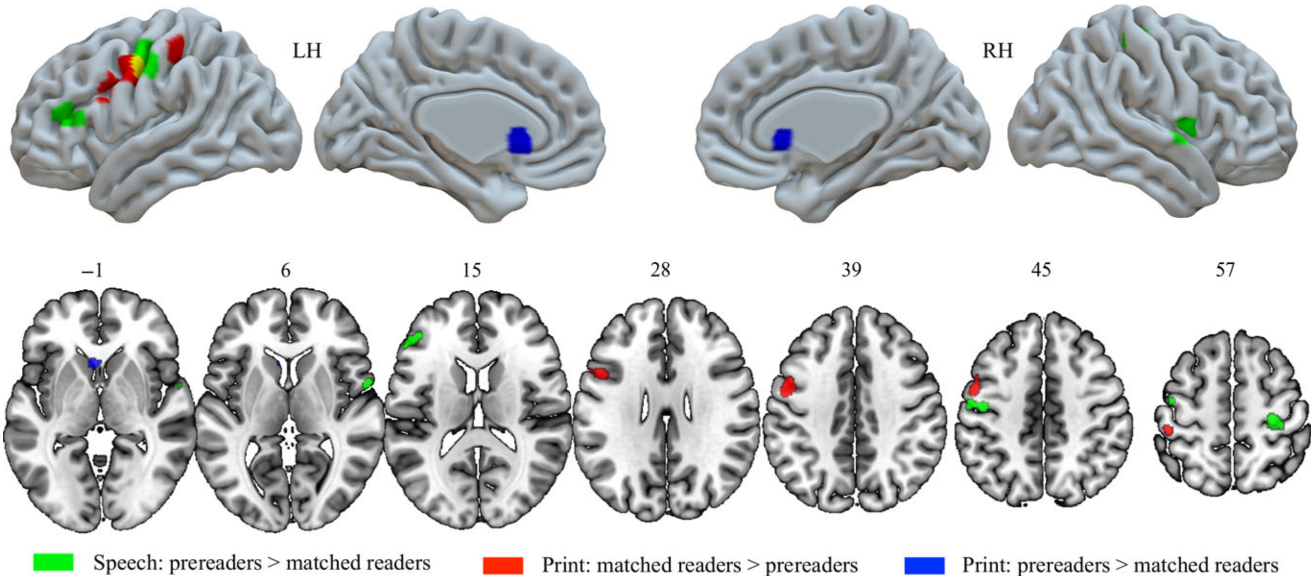

Figure 2 Differences between prereaders and matched readers in word-specific brain response to print (words>symbol strings) and speech (speech>vocoded speech) ($p < .05$ cluster-corrected; $p < .005$ height threshold) [Colour figure can be viewed at wileyonlinelibrary.com]

operculum. The reverse contrast (matched readers>prereaders) yielded no significant activations.

Beginning readers. For full description of the larger reading sample, we also computed word and word-specific activation analyses with all 78 readers (see Figure 3 and Tables S5 and S6). Word-specific activation for print was observed in the left IFG and precentral gyri, and also in left tempo-parietal and vOT cortex. Speech-specific activation was present mainly in bilateral superior, middle temporal and inferior frontal cortex. Print and speech coactivation was found in bilateral IFG/insula, left precentral gyrus, and the bilateral STG/MTG/STS. Word-specific coactivation of print and speech was restricted to two left IFG clusters, right insula and left STG/STS (see Table S4).

An additional analysis in which control conditions are contrasted with experimental conditions or rest can be found in the Supporting Information

Table 2 Comparison of word-specific brain activity to print (print>symbol strings) and speech (speech>vocoded speech) in readers and prereaders

Brain region	Hemisphere	*x*	*y*	*z*	*t*	Voxels
Print: prereaders>matched readers						
Caudate	L	−4	20	0	3.52	71
Print: matched readers>prereaders						
Precentral	L	−52	−3	42	3.90	257
Precentral, Inferior frontal (oper)	L	−48	9	30	3.52	105
Postcentral	L	−48	−32	57	3.10	64
Speech: prereaders> matched readers						
Precentral	R	32	−24	58	3.43	174
Postcentral	L	−56	−12	46	3.38	211
Inferior frontal (tri)	L	−51	34	16	3.14	92
Rolandic operculum	R	58	3	3	2.99	80

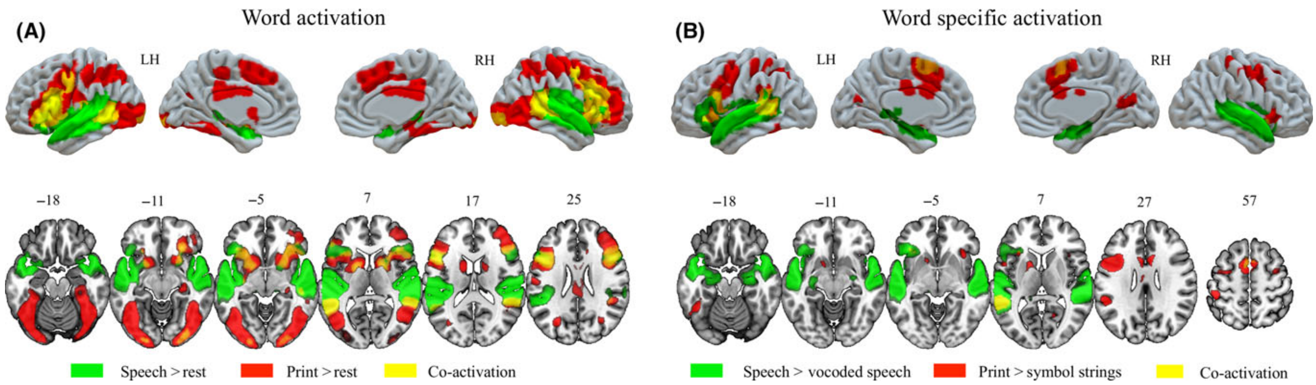

Figure 3 (A) Word (print>rest and speech>rest) and (B) word-specific (print>symbol strings and speech>vocoded speech) activation in 78 readers ($p < .05$ cluster-corrected; ($p < .005$ height threshold) [Colour figure can be viewed at wileyonlinelibrary.com]

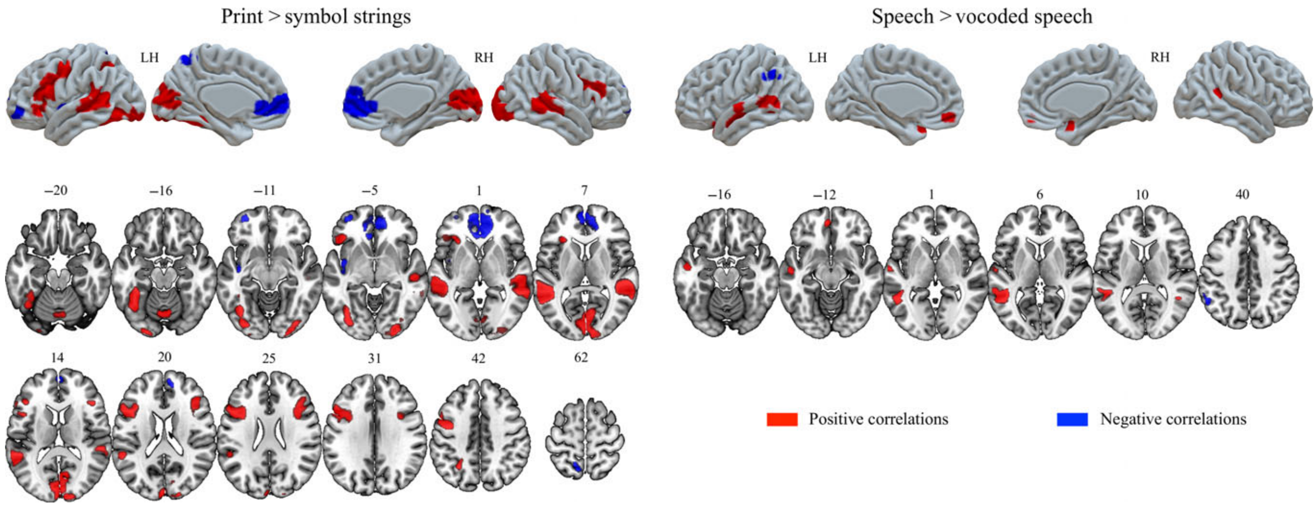

Figure 4 Correlations between sight word reading and word-specific brain response to print (words > symbol strings) and speech (speech > vocoded speech) ($p < .05$ cluster-corrected; $p < .005$ height threshold) [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure S1, prereaders and matched readers; Figure S2, all readers).

fMRI Results: Reading skill analysis

Next, we correlated sight word reading skill with word-specific activation for print and speech (see Figure 4 and Table 3).

Better performance was related to enhanced activity for print in bilateral STG and MTG, calcarine and cuneus, left fusiform and inferior occipital gyri, left superior parietal lobule, left precentral gyrus, and bilateral IFG. Negative correlations were present in the bilateral medial part of superior frontal gyrus, anterior cingulate, left precuneus, insula, and middle frontal gyrus. Reading efficiency was related to

Table 3 Correlations between sight word reading and brain response to print (print>symbol strings) and speech (speech>vocoded speech)

Brain region	Hemisphere	*x*	*y*	*z*	*t*	Voxels
Print – positive correlations						
Middle & Superior temporal	L	−58	−36	4	6.34	2,383
Middle & Superior temporal	R	54	−32	6	4.99	2,173
Calcarine (L&R), Cuneus (L&R)	L&R	10	−102	12	4.98	2,640
Precentral, Inferior frontal (tri, oper)	L	−42	−3	40	4.86	2,750
Inferior occipital	R	28	−93	−4	4.63	666
Inferior frontal (orb, tri)	L	−44	30	−4	4.37	554
Fusiform, Inferior occipital	L	−39	−63	−15	4.31	1,439
Lingual	L	−22	−98	−16	4.26	170
Vermis (VI), cerebellum (VI)	R	2	−72	−18	3.76	281
Inferior frontal (tri, oper)	R	42	30	20	3.56	946
Inferior & Superior parietal	L	−28	−57	46	3.33	307
Print – negative correlations						
Superior medial frontal (L&R), Anterior cingulum (L&R), Medial orbital frontal (L)	L&R	6	46	0	4.87	2,803
Insula	L	−40	−3	−4	3.69	193
Middle orbital frontal	L	−33	56	−9	3.22	221
Precuneus (L)	L	−9	−62	62	3.22	123
Speech – positive correlations						
Middle temporal	L	−44	−45	3	3.76	741
Superior temporal	L	−63	−10	2	3.18	67
Medial orbital frontal	L	−6	50	−14	3.16	76
Middle temporal	L	−54	−8	−18	3.10	209
Superior temporal pole	R	26	6	−22	3.08	52
Superior temporal pole	L	−36	18	−24	3.06	64
Middle temporal	R	46	−51	12	3.02	75
Speech – negative correlations						
Inferior parietal	L	−56	−57	42	3.10	75

stronger word-specific activation for speech in bilateral STG and MTG. Negative correlations were observed only in the left inferior parietal lobule. An intersection of positive correlations (conjunction) for print and speech was found exclusively in the left MTG/STS ($x = -47$, $y = -45$, $z = 0$; 580 voxels, see Figure 5).

Additional regression analyses of experimental conditions relative to rest are reported in Table S7.

Discussion

Neural structures processing print

Prereaders and matched readers, when implicitly processing printed words, engaged partially nonoverlapping neuronal networks. In prereaders, activation levels did not differentiate words from symbol strings: they showed activation only in the left caudate and lingual gyrus. In matched readers, words triggered implicit reading even though no linguistic decisions were required, as shown by the involvement of higher order language areas only for words (see Figure S1 for brain activity to control conditions and to reversed contrasts). In agreement with our expectations, readers relative to prereaders showed higher activation for print than for symbol strings in several LH frontal structures such as IFG, precentral, and postcentral gyri. Greater engagement of these areas, specifically the IFG, has been associated with phonological recoding during reading (Pugh et al., 2010) and possibly related to top-down cognitive control relevant to reading (Pollack, Luk, & Christodoulou, 2015). Left precentral and postcentral gyri are essential for convergence between the oral and written language networks and are typically activated when speech is produced, connecting visual words with articulatory representations (Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012; Price, 2010). This pattern of results would be supported by most theories of reading acquisition, where at the beginning greater reliance on segmentation and letter decoding rather than lexical processing is observed. According to the dorsal-ventral model (Pugh et al., 2001), left inferior occipital areas play an increasingly important role in the processing of print in beginners as they become more skilled (Blomert, 2011; Shaywitz et al., 2002; Turkeltaub et al., 2003).

No word-specific activation was observed in the VWFA in either group, as both words and symbol strings activated the left ventral occipito-temporal cortex (Price et al., 1996; Turkeltaub et al., 2003) with even higher magnitude of response for symbol strings in the posterior medial part (see Figure S1; Brem et al., 2006, 2009; Van der Mark et al., 2009). These results therefore do not support the hypothesis that the occipito-temporal print sensitivity is established in transparent languages during the earliest phase of reading acquisition in

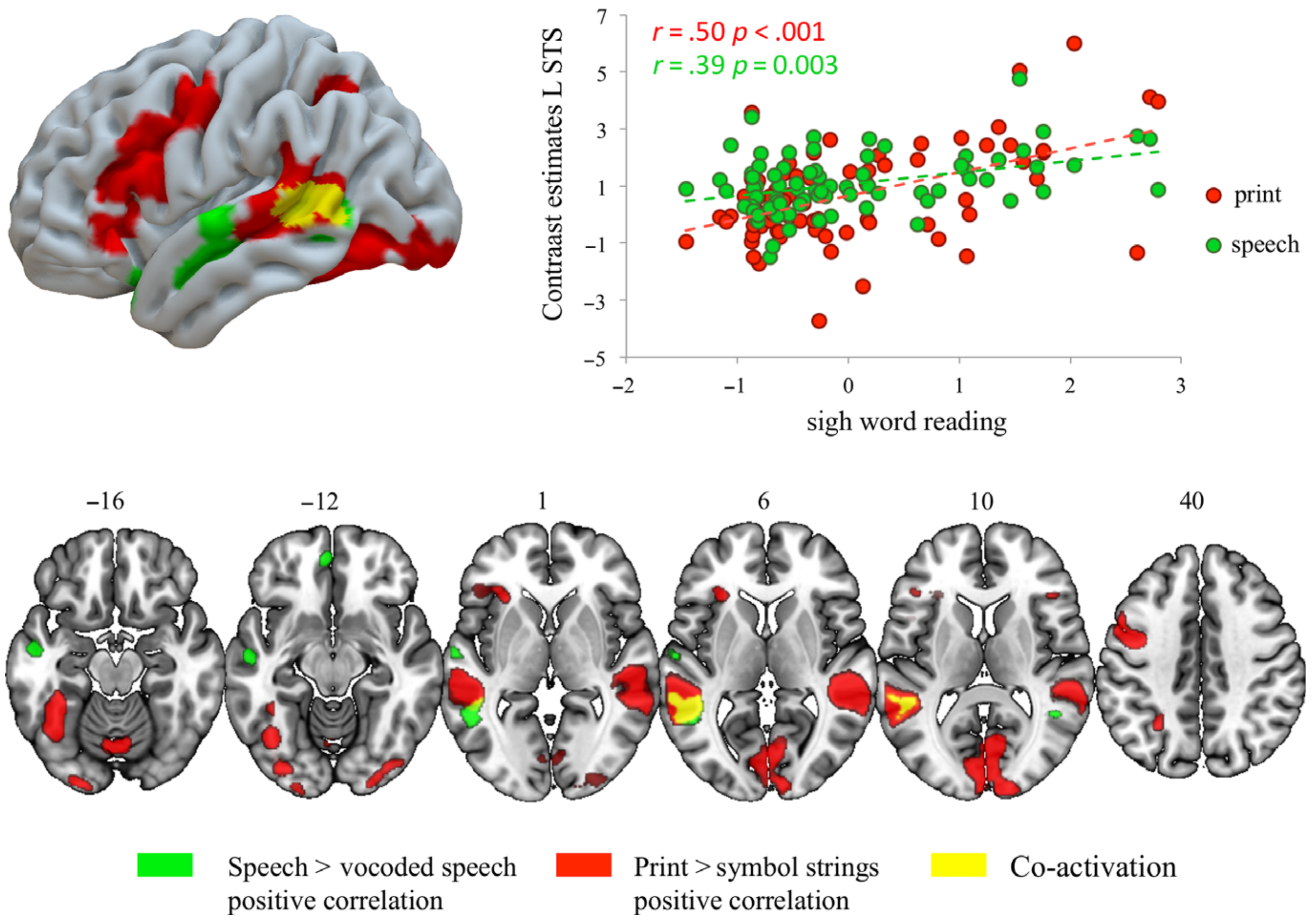

Figure 5 Overlap between positive correlations of reading skill and word-specific activation to print and speech. Scatterplots present contrast estimates from left MTG/STS and standardized sight word reading score controlled for age [Colour figure can be viewed at wileyonlinelibrary.com]

childhood (Brem et al., 2010), but rather agree with the notion that print-specific tuning emerges after children master basic reading abilities (Maurer et al., 2006). Reinforcing the idea that VWFA comes in at a somewhat later point in learning, for the whole sample of readers (including older, more skilled readers) word-specific activation in VWFA was observed (see Table S4). The local maximum of the VWFA activation ($x = -45$, $y = -48$, $z = -20$) was very close to the classical VWFA location ($x = -45$, $y = -57$, $z = -12$) with an Euclidean distance of 12 mm and with more anterior and lateral location than symbol specific activation. This pattern of results suggests that brain activity to words relative to symbol strings changes gradually as reading skill increases. In line with previous research, prereaders show almost no difference in activity for print and symbol strings (Cantlon, Pinel, Dehaene, & Pelphrey, 2011), whereas poorer/younger readers show higher activity for symbol strings than print (see Figure S1), and better/older readers show word specific activation (print > symbols, Figure S2). So it seems that VWFA selectivity to words is highly dependent on reading experience and requires more than a brief exposure to print (in contrast to Brem et al., 2010).

In agreement with these observations, when the group of readers was considered as a whole (ranging from inexperienced to more experienced readers), the positive correlation between reading skill and the word-specific neural response to print was present in VWFA and a number of bilateral (inferior and middle temporal, IFG, calcarine, cuneus, inferior occipital gyri) areas. Activity of the VWFA is known to correlate with reading proficiency in both young and adult readers (Dehaene et al., 2015; Shaywitz et al., 2002). Here, we show that even at the onset of reading acquisition (and in contrast to Turkeltaub et al., 2003), reading skill correlates with the magnitude of word-specific brain activation in the left vOT cortex, reinforcing the evidence that specialization for print in this region emerges with higher reading expertise. Although studies diverge on the concept of contribution of this area to nonreading tasks, they converge on an idea that it is generally involved in expert perception (Price & Devlin, 2003), including visual word processing (Langer et al., 2017). As predicted, literacy acquisition allows the left-hemispheric spoken language network to be activated by print because correlation was also observed in language processing LH areas including inferior frontal, temporal and temporo-parietal areas. These areas mature early in the acquisition of literacy (Turkeltaub et al., 2003) and display stronger activation during reading in control versus dyslexic subjects (Richlan, 2012; Shaywitz et al., 2002) and are important for phonological processing, letter-sound integration, and lexical-semantic processes (Cao, Bitan, Chou, Burman, & Booth, 2006; Van Atteveldt et al., 2004).

In contrast to Turkeltaub et al. (2003), which included older readers, we did not observe disengagement of the RH inferotemporal cortical areas in better readers, which has been taken to indicate decreasing reliance on nonlexical form recognition for word identification. Instead, less proficient readers in response to print employed bilateral anterior cingulate and anterior prefrontal regions, supporting our hypothesis of increased attentional resources and higher effort to perform the task (Shaywitz et al., 1998) and in line with studies on late literates (Dehaene et al., 2010).

Neural structures processing speech

Specialization of the LH structures (including STG, temporal pole and planum temporale) in speech processing was reported already in 3 month-old infants (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002) and can be also observed in both prereaders and beginning readers in this study. When prereaders and matched readers were directly compared, in contrast to previous studies on adults (Dehaene et al., 2010) we did not find heightened word-specific activation to speech in readers compared to prereaders. Only a reversed contrast showed increased activation of the right precentral gyrus and rolandic operculum as well as left IFG and postcentral gyrus in the prereading group compared to matched readers. These results are in line with Monzalvo and Dehaene-Lambertz (2013), where only left precentral/insular cortex distinguished prereading from reading children, and suggest greater involvement of articulatory processes (covert repetition) in prereaders (Price, 2010), possibly to compensate for their comprehension difficulties.

At the same time, as expected, in the whole sample of beginning readers, literacy refined spoken language processing by enhancing activation in the temporal cortex to speech consistently with adult (Dehaene et al., 2010) and child (Monzalvo & Dehaene-Lambertz, 2013) studies. This pattern of results therefore supports a continuous effect of reading practice on the oral network instead of a sudden change after the onset of literacy acquisition and might reflect increased phonemic processing that accompanies reading acquisition. In addition, activation of the left inferior parietal lobule was negatively correlated with reading skill. This structure plays a role in sublexical speech perception tasks (i.e., attention to phonemic segments) and its activation has been attributed to the phonological working memory system that uses articulatory mechanisms to keep phonemic representations active (Hickok & Poeppel, 2000). This result would therefore agree with our prediction of less effortful speech comprehension in better readers.

Print and speech coactivation

Coactivation for print and speech was observed in readers only, in bilateral MTG/STG/STS and IFG. In the total sample of readers additionally a word-specific coactivation was present only in left MTG/STG/STS and IFG. Moreover, in the left STS we found an overlapping positive correlation between reading skill and neural activity to spoken and written words. These results are in line with previous studies in English with somewhat older children (Frost et al., 2009) and adults, showing a relation between reading or phonological awareness skills and convergent activation for print and speech in LH language areas. They are also coherent with additional findings that this integration in left perisylvian regions is associated with higher skills concurrently and better reading outcomes 2 years later (Preston et al., 2016). Here, we show that even in emerging 6–8-year-old readers (with maximally 1 year of reading instruction), the acquisition of reading enables access from vision to language processing system. At the same brain response to speech becomes enhanced, perhaps due to increased phonemic awareness. Therefore, the print-speech convergence in the language cortex emerges already at the early steps of acquiring literacy, possibly being a prerequisite for the later-developing word-specific tuning in more experienced readers.

Limitations

More than half of examined children had familial risk of dyslexia since they were recruited for the study on the early predictors the disorder (Dębska et al., 2016). Around 30% of them will become dyslexic (Snowling & Melby-Lervag, 2016), resulting in an 18% prevalence of dyslexia in the current sample, which is somewhat higher than in general population (5%–17%). Another concern is the educational stage which differed between prereaders and matched readers and might have affected their exposure to print, although the groups were matched for age. Finally, because a number of children were still prereaders, we employed a passive task to study implicit processing related to print and speech. Thus, we cannot exclude that in such task the observed findings are a mixture of specific effects related to reading processes and nonspecific effects related to attention or engagement with the task. Indeed, we found increased activity in prefrontal and parietal areas belonging to the default mode network (DMN) in poor readers for speech relative to rest (see

Table S7), which suggests a specific failure to disengage the DMN during task, already described in dyslexic children (Boros et al., 2016).

Conclusions

In summary, we have shown how literacy acquisition in a transparent orthography affects patterns of activation for print, speech, and their overlap. In emerging readers, reading skill was positively correlated both with word-specific activation to print and speech in language-related areas, and with print-specific activation of the VWFA. Literacy was associated with activation of the left-hemispheric spoken language network by print and at the same time enhanced activation in the temporal cortex to speech. Young readers compared to prereaders of Polish showed word-specific activation to print only in the left anterior dorsal regions including IFG, which argues against the idea of the rapid specialization in the ventral occipital cortex in transparent orthographies. When listening to speech prereaders showed increased activation compared to readers in speech production cortical areas, suggestive of greater involvement of covert articulation. Finally, print and speech convergent activation was observed only in readers, with greater convergence correlated with increased reading skill. We suggest that print-speech convergence is a hallmark of acquiring literacy and should be further tested as a possible early marker of reading acquisition failure.

Supporting information

Additional Supporting Information may be found in the online version of this article:

Figure S1. (A) Symbol strings>rest and vocoded speech>rest as well as (B) reversed contrast (symbol strings>print and vocoded speech >speech) activation in matched readers and prereaders ($p < .05$ cluster-corrected; $p < .005$ height threshold).

Figure S2. (A) Symbol strings>rest and vocoded speech>rest as well as (B) reversed contrast (symbol strings>print and vocoded speech >speech) activation in 78 readers ($p < .05$ cluster-corrected; $p < .005$ height threshold).

Appendix S1. Participants – whole sample.

Appendix S2. fMRI task.

Appendix S3. fMRI results – head movement artefacts.

Tables S1. Lexical parameters across two experimental conditions.

Tables S2. Brain areas active for print > rest and speech > rest in prereaders and matched readers.

Tables S3. Word specific brain activations for print (print > symbol strings) and speech (speech > vocoded speech) in prereaders and matched readers.

Tables S4. Word and word specific coactivation for print and speech.

Tables S5. Brain areas activated for print (print > rest) and speech (speech > rest) in 78 readers.

Tables S6. Word specific brain activations for print (print > symbol strings) and speech (speech > vocoded speech) in 78 readers.

Tables S7. Correlations between sight word reading and brain response to print>rest and speech>rest.

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Key points

- Literacy acquisition induces significant brain reorganization of the language network.
- In emerging readers reading skill correlates with the word-specific activation to print and speech in a number of brain areas.
- Nonetheless, only in the left IFG, precentral and postcentral gyri did readers show higher activity to print than prereaders, suggesting that specialization for print over other visual symbols begins in the dorsal network.
- Print and speech converging activation can be only found in readers in left-hemispheric language areas, while reading skill enhances such convergence in the left STS.

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