



How reading acquisition changes children's spoken language network



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ABSTRACT

To examine the influence of age and reading proficiency on the development of the spoken language network, we tested 6- and 9-years-old children listening to native and foreign sentences in a slow event-related fMRI paradigm. We observed a stable organization of the peri-sylvian areas during this time period with a left dominance in the superior temporal sulcus and inferior frontal region. A year of reading instruction was nevertheless sufficient to increase activation in regions involved in phonological representations (posterior superior temporal region) and sentence integration (temporal pole and pars orbitalis). A top-down activation of the left inferior temporal cortex surrounding the visual word form area, was also observed but only in 9 year-olds (3 years of reading practice) listening to their native language. These results emphasize how a successful cultural practice, reading, slots in the biological constraints of the innate spoken language network.

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1. Introduction

Language in humans has both early and protracted development. From birth onward, infants show complex language capacities and begin to learn their native language (Dehaene-Lambertz, Hertz-Pannier, & Dubois, 2006; Kuhl, 2004). These early capacities rely on a set of perisylvian brain regions, close to what has been described in adults (Dehaene-Lambertz, Dehaene, & Hertz-Pannier, 2002). In particular, a left dominance for language processing is observed at the level of the *planum temporale* already during the first months of life (Dehaene-Lambertz et al., 2010; Pena et al., 2003) and even before term (Mahmoudzadeh et al., 2013); and activation in the left inferior frontal region is detected when infants are engaged in a short-term verbal memory task (Dehaene-Lambertz, Hertz-Pannier, Dubois et al., 2006).

Although the main rules of human verbal communication are acquired within the first three years of life (Bernal, 2001; Gertner & Fisher, 2012; Mills, Coffey-Corina, & Neville, 1993), children continue to improve their language expertise until adulthood, increasing their vocabulary and their syntactic skills. Several functional magnetic resonance imaging (fMRI) studies report that activation increases correlate with age in several regions of the perisylvian network (Brauer & Friederici, 2007; Lidzba, Schwilling, Grodd,

Krageloh-Mann, & Wilke, 2011; Schmithorst, Holland, & Plante, 2006; Szaflarski, Holland, Schmithorst, & Byars, 2006; Szaflarski et al., 2012). These sustained changes can be explained by the heterogeneous calendar of myelination and of synaptogenesis/pruning in the different perisylvian areas, spread over several years (Paus et al., 1999; Sowell et al., 2003; Yakovlev & Lecours, 1967) and by an increased mastery of spoken language, but another cultural factor, rarely marked out in studies of normal language development might also affect neural responses in this network: reading. Especially in the case of alphabetic writing, readers develop better metaphonological capacities and short-term verbal memory than those who are illiterate (Morais & Kolinsky, 2005). Their speech perception becomes influenced by orthography (Ventura, Morais, Pattamadilok, & Kolinsky, 2004; Ziegler & Ferrand, 1998) and they better retained the meaning of new words when they are exposed to their orthography, even incidentally (Ricketts, Bishop, & Nation, 2009). They also have access to more complex syntactical structures and can acquire a richer and more diverse vocabulary through books. Thus reading has an unquestionable influence on oral language processing, and certainly plays a role in the neural changes observed during childhood.

Comparisons of the neural bases of spoken language between literate and illiterate adults have revealed higher activations in the left parieto-temporal region and involvement of supplementary regions, such as the visual word form area (VWFA) in tasks involving spoken language (Carreiras et al., 2009; Castro-Caldas, Petersson, Reis, Stone-Elander, & Ingvar, 1998; Dehaene et al., 2010; Li et al., 2006). Similar differences have been obtained when

Abbreviations: VWFA, visual word form area; STS, superior temporal sulcus.

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comparing normal adult readers and dyslexics (Blomert, 2011; Paulesu et al., 2001). Similarly normal child readers have larger activation in the left posterior temporal region than impaired readers and recruit the VWFA, when performing auditory spelling and rhyming tasks (Booth et al., 2004; Desroches et al., 2010), as well as when merely listening to their native language (Monzalvo, Fluss, Billard, Dehaene, & Dehaene-Lambertz, 2012).

Our goal was thus to study the early impact of reading on the spoken language network using fMRI. We used a slow event-related design to test normal 6- and 9-year-old children listening to short sentences in their native language and a foreign language (one sentence every 12 s, repeated once). The subtraction of the responses to the foreign sentences from the native sentences aimed at disentangling specific linguistic effects from the general effects of age and education on the auditory system whereas sentence repetition aimed at parceling the superior temporal regions. Stimulus repetition has been used to separate different regions depending on the temporal decay of mental representations computed from the stimulus (Henson, Shallice, & Dolan, 2000). In adults, when the same sentence is repeated 14.4s later, the superior temporal sulcus, which hosts abstract linguistic representations (Davis & Johnsrude, 2003; Pallier, Devauchelle, & Dehaene, 2011), but not the upper regions in the superior temporal gyrus, displayed a decrease of amplitude of the BOLD response (Dehaene-Lambertz, Dehaene et al., 2006). In infants, a similar repetition effect was observed but only when the sentence was immediately repeated (Dehaene-Lambertz et al., 2010) and not when the same delay than in adults was used (Dehaene-Lambertz, Dehaene et al., 2006). Working memory and sentence intelligibility are crucial factors in the lengthening of the temporal delay. Reading notably improves working memory, thanks to a better phonological loop. We have thus examined whether the neural impact of reading goes beyond the early stages of phonological coding and change the whole sentence integration in the superior temporal sulcus facilitating a repetition suppression effect.

The effects of age and education are difficult to separate, as the academic curriculum is generally homogeneous in a given country, especially for fundamental acquisitions such as reading. Thus older children following a normal curriculum are by default more expert readers than younger children. We thus specifically examined the impact of reading in our 6-year-olds by taking advantage of the gap between the academic and the civil year. We set up two groups of approximately the same age but with a one-year difference in reading instruction. This comparison aimed to examine whether reading quickly modifies the spoken language system from the first year of teaching onward. In particular, we wondered whether the changes in the posterior temporal region for native sentences and the recruitment of the VWFA, described in the studies that compared literate and illiterate adults, would already be visible after a few months of reading practice.

2. Methods

2.1. Subjects

Forty-nine children, 25 boys and 24 girls, were recruited in the Paris area and divided into two groups based on age (6- and 9-year-old children) or three groups based on reading abilities (pre-readers, beginners and advanced readers). All parents and children gave their written consent. The study was approved by the local ethical committee for biomedical research.

Children with cognitive, neurological or behavioural disorders, hearing deficit, not corrected visual problem and mental retardation were excluded from the study. At the time of the study, we checked with the parents and teacher that the child was following

a normal academic curriculum without difficulties. We confirmed his/her normal intellectual development with two subtests of the WISC (the block design and the similarities subtests). If a child performed poorly (scaled score below 8 corresponding to percentile rank of 25) in one of these subtests (usually because of shyness at the beginning of the test), he/she was also tested with the picture completion and the vocabulary subtests. We also examined their handedness, verbal memory, verbal and reading abilities (Table 1).

The oldest group or advanced readers (23 children, 9 years, 7 months \pm 6 months) had three complete years of reading experience. Eleven children in this group came from a low socio-economical background (SES) and among them 7 were bilingual (only one spoke a romance language, i.e. Romanian). These 7 children were from migrant families (Pakistan, Mali, Algeria, Yugoslavia and Romania), but all, except one, were born in France. They were all following the normal French academic curriculum since kindergarten (i.e. around 6 years in a French teaching environment). According to the parents who filled a questionnaire on cultural habits, their children showed a marked preference to speak French even at home suggesting that French was probably their dominant language. Their fluency in French was confirmed by their normal performances in our French verbal and reading tests. In a previous published paper focused on this question (Monzalvo et al., 2012), we analyzed the effects of SES in these same 23 children. Our low-SES children had lower verbal and reading performances than their higher SES peers as noted in numerous studies (Hackman & Farah, 2009; Noble, McCandliss, & Farah, 2007), but they all remained in the normal range (see complete results in Monzalvo et al., 2012, and in Table 1 here). No significant functional difference related to SES/bilingualism was observed in the brain responses to speech at the group level. This result is congruent with studies in adults showing only weak differences, if any, between monolinguals and proficient bilinguals in MRI activations during speech listening (Abutalebi, 2008). Therefore, we merge here these two groups to increase our statistical power to detect differences between ages and to have a better coverage of the normal range of oral and written language capacities.

None of the 6-year-old children was coming from low-SES family and only one was bilingual. This child was fluent in French and German, performing above average in all French verbal and reading tests. For the 6-year-olds, we tried to recruit children of approximately the same age but with one year of difference in reading instruction by taking advantage of the gap between the civil and academic years. We thus divided the 6-year-olds into two groups: 13 children in kindergarten with no reading instruction, called “pre-readers” (6 boys, 7 girls; mean age: 6 years 2 months, 70–80 months) and 13 children tested at the end of the first grade year, called “beginners” (7 boys, 6 girls; mean age: 6 years 10 months, 70–87 months). Children in this group were tested 8–16 months (mean = 11 months) after their entrance in first grade. However, despite an overlap between the two groups, a significant age difference remained. As expected, the number of words read in 1 min (Khomsi, 1999) was significantly lower in the pre-readers relative to the beginners (4 [0–10] vs. 40 [22–54] w/mn, $p < .001$). This test is a standardized list of 105 words with increased difficulties. The first 15 words are monosyllabic and frequent, and comprise articles (e.g. “le”), pronouns (e.g. “il”) or simple open-class words (e.g. “nu”). All pre-readers were able to read and write their first name. Some of them were also able to read the first words of this list but 9 on 13 were reading less than 5 words in 1 min, and the remaining 4 children, between 5 and 10. The reading performance within the 6-year-old group was correlated with age ($R^2 = 0.48$, $F(1,24) = 24$, $p < .001$). When the effect of age was discarded by using the residuals of the linear regression between age and the number of words read by minute, a significant difference was still observed

Table 1
Characteristics of the groups (mean \pm standard deviation), significant *p* values are in bold.

	6-Year-olds		9-Year-olds advanced readers		Non readers versus beginners (<i>p</i> value)	Beginners versus advanced (<i>p</i> value)
	Pre-readers	Beginner readers				
Age (months) (min–max)	74 (70–80)	82 (70–87)	Low-SES	115 (107–129)	<.001	<.0001
			Normal SES	116 (107–130)		
Handedness (left handed/total)	3/13	2/13	Low-SES	1/11		
			Normal SES	1/12		
Sex (girls/total)	7/13	6/13	Low-SES	3/11		
			Normal SES	8/12		
PIQ estimation ^a (min–max)	12.1 (9–18)	11.8 (8–15)	Low-SES	9.4 (8–13)	0.7	0.005^c
			Normal SES	9.8 (8–15)		
VIQ estimation ^a (min–max)	11 (6–16) ^b	12.3 (8–15)	Low-SES	11 (8–14)	0.19	0.56
			Normal SES	12.6 (8–19)		
Number of words read in one minute (LUMtest) (min–max)	4 (0–10)	40 (22–54)	Low-SES	74 (56–98)	<.001	<.001
			Normal SES	85 (67–98)		
Phonological awareness (% of correct responses) (\pm 27.1)	41.2 (\pm 27.1)	78.8 (\pm 12.6)	Low-SES	91.4 (\pm 10.7)	<.001	0.006
			Normal SES	90.7 (\pm 12)		
Rapid automatic naming (time in s) (7.7)	26.4 (7.7)	20 (\pm 5.2)	Low-SES	17 (\pm 3.3)	0.02	0.01
			Normal SES	15.5 (\pm 2.7)		
Forward digit span (maximum length of the correctly repeated sequence of numbers) (\pm 0.7)	4.4 (\pm 0.7)	5.1 (\pm 1.1)	Low-SES	4.9 (\pm 0.5)	0.09	0.44
			Normal SES	5.8 (\pm 0.9)		
Backward digit span (\pm 0.7)	2.3 (\pm 0.7)	2.9 (\pm 0.8)	Low-SES	3.3 (\pm 0.7)	0.03	0.15
			Normal SES	3.4 (\pm 0.8)		
Sentence span (number of words in the last correctly repeated sentence) (\pm 3.4)	13.8 (\pm 3.4)	15.5 (\pm 3.4)	Low-SES	16.1 (\pm 3.5)	0.21	0.04
			Normal SES	21.1 (\pm 4.2)		
Number of correctly named images (/48) (\pm 3.6)	33.1 (\pm 3.6)	36.5 (\pm 3.5)	Low-SES	34.4 (\pm 5)	0.02	0.61
			Normal SES	40 (\pm 3.5)		

^a PIQ and VIQ are estimated with subtests of the WISC: Block design or picture completion for PIQ estimation, similarities or vocabulary subtests for VIQ estimation (see subjects description).

^b One pre-reader was very shy and refused to answer for the verbal subtests. His school records were excellent and his performances in the other tests in the average, notably the number of correctly named images.

^c Note that here contrary to the other tests, it is the advanced readers who have the weaker scores.

($t(19.15) = 3.12, p = .006$), demonstrating that beyond the small but significant age difference, reading experience was indeed, as expected, different between our groups. Unsurprisingly, reading experience had also an effect on phonological abilities, rapid automatic naming, backward digit span and vocabulary. The beginners significantly outperformed the pre-readers in all these tests (Table 1).

2.2. Stimuli and task

Forty short sentences in French (native language) and Japanese (a foreign language that none of the children understood) were produced by two different female native speakers using a highly intoned voice. The mean sentence duration was similar in both languages (2707 vs. 2724 ms). These sentences were randomly presented every 12 s in a slow event-related design and repeated once to study the effect of repetition (Dehaene-Lambertz, Dehaene et al., 2006). Children were asked to press a button with their right hand as fast as possible at the end of each sentence, but not before the end of the sentence. This incidental task was planned to maintain the child's attention to the auditory stimuli.

Each functional run comprised four different sentences in each language, repeated one time for a total duration of 3'12" (16 sentences). Children listened to four runs (except for two pre-readers, who had only three runs; in both cases, the experiment was stopped on the child's request). Stimulus presentation and behavioral response collection were performed with E-prime1.

2.3. Image acquisition

MRI structural (TR = 2.3, TE = 4.18, matrix 256 \times 256 \times 176, voxel size = 1 \times 1 \times 1 mm) and functional (TR = 2.4 s, TE = 30,

matrix 64 \times 64 \times 40, voxel size = 3 \times 3 \times 3 mm) data of the whole brain were acquired on a 3.0-T scanner (Siemens Tim Trio). Each auditory run comprised 80 volumes. Children were protected with noise-protection earphones and a mirror system above the child's head allowed them to see visual stimuli presented on a screen at the end of the tunnel. No visual stimuli were presented during the auditory runs, but children viewed cartoons during structural acquisition. Visual fMRI sequences (Monzalvo et al., 2012) and diffusion tensor magnetic resonance imaging were also collected. These data are not presented here.

2.4. Data preprocessing

Preprocessing and analyses of the data were conducted using SPM5. Images were first realigned to the first functional image and co-registered with the individual anatomical image. T1 images were non-linearly normalized to the adult MNI brain space using the default procedure proposed in spm5 with gray matter, white matter, and CSF default templates proposed by this software (see Kang, Burgund, Lugar, Petersen, & Schlaggar, 2003 for a discussion of the comparability of anatomical localization of functional responses across ages). The normalization matrix computed in each child was then applied to the coregistered EPI images, which were finally spatially smoothed using a 5-mm Gaussian kernel to take into account residual movement between images.

During the functional runs, the children moved an average of 1.5 mm in translation and 3.2° in rotation. Movements decreased with age (mean maximal translation amplitude in the *z* direction: 3.6 vs. 2.8 vs. 1.6 mm, $F(1,47) = 5.20, p = .027$; mean maximal pitch rotation angle: 7.3 vs. 7.5 vs. 2.9 d°, $F(1,47) = 6.49, p = .014$; no other significant difference between groups was

observed in the other directions). When the child's movement during a run was superior to 2 mm in translation and/or 1 degree in rotation, all functional images were visually screened to detect volumes with movement present during the volume acquisition and showing hyper- or hypo-intense slices in the image (outlier volumes). Artprepair5, an SPM5 toolbox (Mazaika, Whitfield-Gabrieli, & Reiss, 2007), was used to further detect outlier volumes in which the global intensity of the volume was greater than 2.5% of the global mean during the time series. Outlier volumes were replaced by interpolation between the preceding and following correct images. This procedure was used in 17/49 children (6 9-year-olds, 6 pre-readers and 5 beginners) with an average of 2.85% interpolated volumes (less than 5.3% in all children except for one pre-reader whose 10.6% of the acquired volumes (34/320) were interpolated).

2.5. Statistical analyses

The data were modeled within each fMRI run using the canonical SPM hemodynamic response function and its time derivative convolved with the experimental conditions (first and second presentation of the native and foreign sentences). The 6 movement parameters were entered as regressors of non-interest. A second-level group ANOVA was performed with a between-factor of group (advanced, beginner and pre-readers) and within-subject factors of language (foreign and native sentences) and repetition (first and second presentation) using the individual contrast images. To account for minor individual differences in exact localization of

corresponding functional responses, these contrast images were smoothed with a 8-mm Gaussian kernel.

To examine group differences, we first considered the regions activated by speech (i.e. grouping all conditions in a speech contrast). We limited our statistical reports to the clusters positively activated in this contrast across all children at $p < .001$ at the peak level and $p < .05$ at the cluster level. We subsequently identified the regions that were more involved in native language processing by masking the results of this analysis with the regions that were significantly more activated ($p < .001$) by the native than by the foreign language across all children (i.e. native language mask). We reported all significant results when voxels were significant at $p < 0.001$ and formed a contiguous cluster whose extent was significant at $p < 0.05$, corrected for the multiple comparisons done within the spatial mask of analysis (the cluster-level corrected p value is denoted as pc_cor).

We also tested left–right differences by subtracting voxel by voxel the right activation from the corresponding left hemisphere activation (Dehaene-Lambertz et al., 2002; Pinel & Dehaene, 2009). Because of the known structural asymmetries affecting particularly the superior temporal regions (e.g. the right sylvian fissure is steeper and shorter than the left (Toga & Thompson, 2003), flipping the images along the x axis is not sufficient to align the corresponding left and right structures. We thus used the procedure reported in Didelot et al. (2010) to create a symmetrical anatomical template. This procedure comprised the following steps. We flipped the MNI template along the x axis, and summed the original (orMNI) and flipped (fMNI) images to create a symmetrical image (orfMNI). We coregistered the original (orMNI) and flipped (fMNI) images on orfMNI, then computed the mean of these two images creating cMNI. We flipped this last image (fcMNI) and computed the mean of cMNI and fcMNI to obtain the final symmetrical template (sMNI). For each child, we flipped the anatomical image and then computed the spatial transformation appropriate to align the original and flipped anatomical image to the symmetrical MNI template (sMNI). We then similarly flipped each original contrast and applied the appropriate normalization matrix on the original and flipped contrast images. Finally, we computed a left–right activation difference image by subtracting the normalized flipped from the normalized original contrast image. These images were submitted to the same ANOVA models as above in order to estimate the hemispheric differences for each effect of interest.

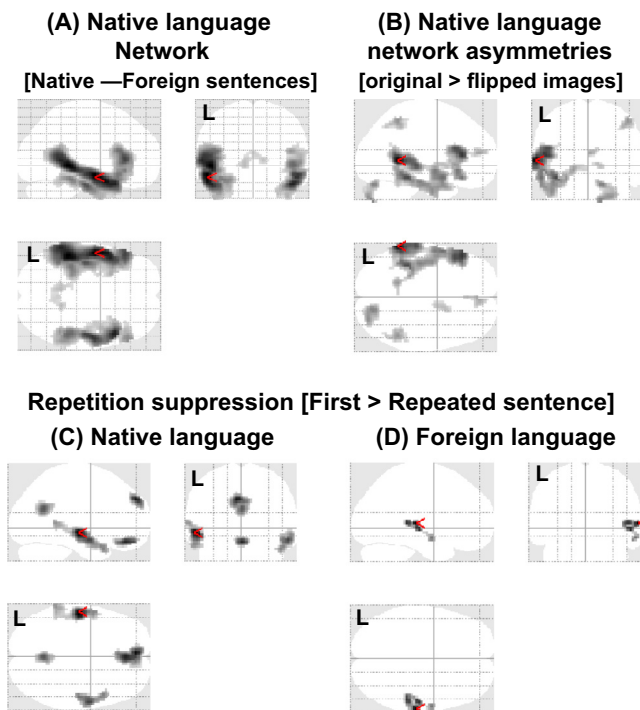


Fig. 1. Differences in fMRI activation computed across all children presented on a glass-brain (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level): (A) native > foreign sentences; (B) asymmetries of the native language network (original > flipped images); (C and D) first > second presentation for the native and foreign sentences. The red arrow is located at the global maximum in each analysis (A) left anterior STS [$-54 -6 -15$], z inf; (B) left posterior STS (sMNI) [$-63 -48 6$], $z = 7.50$; (C) left STS [$-57 -15 -6$], $z = 5.52$ and (D) right STS [$-63 -21 6$], $z = 3.84$). Coordinates are given in the MNI space except for B (sMNI: symmetrical MNI space). L = left hemisphere. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3. Results

3.1. Behavioral results

Children were instructed to press a button at the end of each sentence. The task was easily performed by each subject. Because of technical issues, behavioral data from two participants (one pre-reader and one beginner) were lost. There was no effect of group (653 ± 64 ms/ 671 ± 58 ms/ 667 ± 34 ms for the pre/beginner/advanced readers, respectively, $F(2,44) < 1$). As expected, children were faster at detecting the end of the sentence at the second presentation (570 vs. 759 ms: $F(1,44) = 98.19$, $p < .0001$) with no main effect of language ($F(1,44) < 1$) and no interaction among language, repetition or group.

3.2. FMRI results

We first present analyses performed across all children and in each group. Second, we examine the differences between the 6 and 9 year-olds. Finally, we restrict our analyses to the 6-year-olds to investigate the early impact of reading instruction.

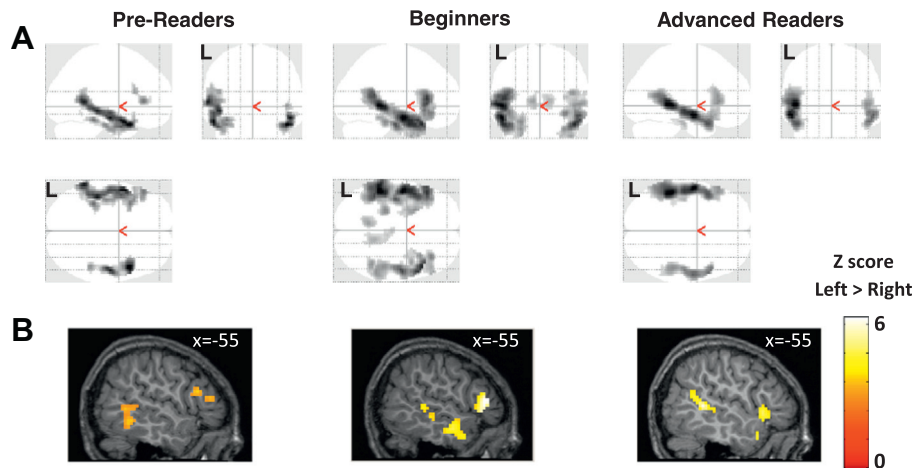


Fig. 2. The native language network. (A) [native–foreign sentences] contrast in each group presented on a glass-brain (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level) (B) Significant asymmetries of the native language network (left > right) presented on a sagittal slice of an individual child ($x = -55$ mm, sMNI space). The inferior frontal region and the posterior superior sulcus are asymmetric toward the left hemisphere in each group.

3.2.1. A common linguistic network

We first performed analyses across all children. The response to speech stimuli was bilateral, with a large set of regions more

activated by the native than by the foreign sentences (inferior frontal, insula, superior temporal and inferior temporal regions Fig. 1 A). Most of the regions preferentially activated by the native

Table 2
Regions of significant activations in each of the three groups.

Analysis	Area	MNI coordinates			SPM <i>t</i> -tests					
		<i>x</i>	<i>y</i>	<i>z</i>	No. of voxels in cluster	Cluster-level <i>p</i> value (corrected)	<i>z</i> Value at local maximum			
<i>Advanced readers</i>										
Native language network [native–foreign sentences]	Left	Anterior STS	–54	–6	–12	1315	<0.001	7.45		
		Posterior STS	–51	–36	0			7.41		
		Temporal pole	–48	15	–24			6.04		
	Right	Inferior frontal	–57	30	6			4.91		
		Inferior temporal	–42	–18	–24			4.2		
		Fusiforme gyrus	–36	–33	–18			3.39		
Repetition effect (first > second presentation)	Left	Anterior STS	–57	–6	–9	486	<0.001	6.05		
		Posterior STS	–51	–42	6			3.81		
		Temporal pole	–45	21	–24			3.32		
Right	Right STS	57	–6	–12	397	<0.001	5.98			
		51	18	–21			4.53			
<i>Beginner readers</i>										
Native language network [native–foreign sentences]	Left	Posterior STS	–51	–36	0	2108	<.001	7.46		
		Anterior STS	–51	–6	–15			7.27		
		Inferior frontal	–51	27	9			6.64		
		Inferior temporal	–42	–15	–24			6.13		
		Fusiforme gyrus	–27	–30	–21			5.03		
	Right	Temporal pole	48	21	–24			1079	<.001	6.84
		Anterior STS	51	–9	–12					6.27
		Inferior frontal	36	33	–9					5.14
		Posterior STS	54	–42	3					4.87
		Calcarine	–9	–54	6					116
Repetition effect (first > second)	Right	Calcarine	12	–45	6	156	0.002	4.25		
		No suprathreshold clusters								
<i>Pre-readers</i>										
Native language network [native–foreign sentences]	Right	Temporal pole	48	15	–24	336	<.001	6.79		
		Anterior STS	51	–12	–15			6.32		
		Posterior STS	45	–39	0			4.54		
	Left	Temporal pole	–54	9	–21			910	<.001	6.61
		Posterior STS	–60	–48	6					6.28
		Fusiforme gyms	–36	–36	–18					5.14
		Inferior temporal	–42	–18	–27					4.73
Repetition effect (first > second)	Left	Inferior frontal	–51	33	6	115	0.007	4.96		
		No suprathreshold clusters								

language were significantly asymmetric toward the left side (Fig. 1B; coordinates of the maxima are given relative to the symmetrical template reference (sMNI) $[-63 -486]$, $z = 7.5$, 1473 vox, $pc_cor < .001$), but some clusters presented the reverse asymmetry: in the cerebellum (sMNI $[15 -78 -45]$, $z = 5$, 206 vox, $pc_cor < .001$), anterior cingulate (sMNI $[351 15]$, $z = 4.36$, 50 vox, $pc_cor = .008$), and caudate (sMNI $[1290]$, $z = 3.83$, 46 vox, $pc_cor = .012$).

Regions showing a repetition suppression effect (first > second sentence presentation) were entirely included in the native language mask (i.e., a mask of the regions more activated by the native than by the foreign language, see methods). This effect was not significantly different between languages at our statistical threshold. However for the native sentences, the repetition effect was mainly observed along the left STS ($[-57 -15 -6]$, $z = 5.52$, 312 vox, $pc_cor < .001$), with a right cluster in the anterior STS ($[57 -315]$, $z = 4.78$, 196 vox, $pc_cor = .004$) (Fig. 1C), whereas it was only significant in a right posterior STS site for the foreign sentences ($[63 -216]$, $z = 3.84$, 103 vox, $pc_cor = .05$, Fig. 1D). The reverse comparison (second > first) isolated both insulas, extending in the left hemisphere medially to the putamen and exteriorly to the inferior frontal, central and marginal regions. None of these regions was included in the native language mask. No significant left-right differences were observed for any of these repetition effects.

Similar results were observed when each group was considered separately (Fig. 2) except that no significant cluster was detected in the analyses of the repetition effect in the 6-year-olds (Table 2). In all three groups for the [native-foreign] contrast, the left posterior superior temporal sulcus and the left inferior frontal region were significantly more activated than their right equivalent (Table 3 and Fig. 2B).

3.2.2. Changes between 6- and 9-year-olds

Second, we examined the differences between the 6- and 9-year-olds. There was no difference between groups in either direction in the native vs. foreign sentences comparison. However, when all conditions were grouped, a large set of regions (cluster size = 3409 vox) was more activated in the 9-year-old children than in the 6-year-old children (Fig. 3A and B). This cluster comprised both caudate (R: $z = 6.63$ and L: $z = 6.14$), SMAs ($z = 6.44$), pre- and post-central areas (R: $z = 6.24$; L: $z = 6.14$), cerebellum ($z = 5.49$), left insula ($z = 5.82$), and notably regions involved in reading: the left posterior superior temporal sulcus (pSTS, $z = 5.54$), and the visual word form area (VWFA, $z = 4.35$). To disentangle changes which might be more specifically related to native language processing than to general processing, we restricted the analysis to the native language mask. Only two of these clusters were included in this mask: the pSTS ($[-54 -63 15]$, $z = 5.54$, 127 vox, $pc_cor = .004$) and the VWFA ($[-39 -48 -27]$, $z = 4.35$, 53 vox, $pc_cor = .049$). This last region was also the only region of the native language network significantly more asymmetric toward the left side in the 9 than the 6-year-olds in the analyses of functional asymmetries (sMNI $[-45 -480]$, $z = 4.43$, 34 vox, $pc_cor = .045$). By contrast, a stronger left-lateralization of the pars opercularis was observed in the younger group (sMNI $[-54 1221]$, $z = 4.93$, 39 vox, $pc_cor = .025$).

As bilingual children (7 in the 9-year-old group, 1 in the 6-year-old beginner group) might have different activations to French than monolingual, we did the same analyses but discarding these children. The results remained similar with in particular no supplementary cluster differentiating the 9 and 6-year-olds (Fig. 3A). The only difference was that the VWFA was the only remaining significant cluster when the analysis was limited to the native language mask ($[-39 -45 -30]$, $z = 5.39$, 89 vox, $pc_cor = .017$). The extent of the pSTS cluster was too small to survive statistical correction ($[-57 -66 15]$, $z = 3.79$, 29 vox). This similarity is congruent with

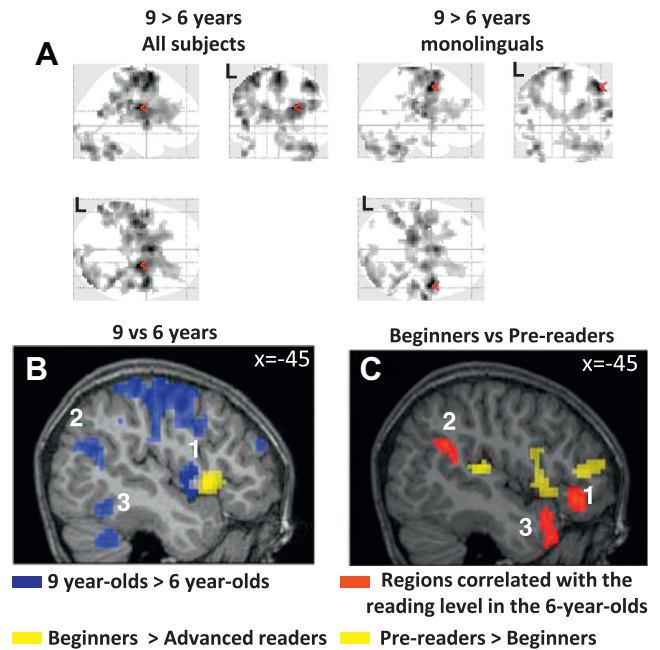


Fig. 3. Impact of age and reading on the speech network. (A) Comparison of the responses to speech in 9- vs. 6-year-olds (beginners + pre-readers) when all subjects (left) or only monolingual subjects (right) are considered. (B) The same results (all subjects) are presented on a sagittal view of an individual child ($x = -45$ mm, MNI space): A large set of regions (blue regions), notably comprising the left insula (1), the posterior STS (2) and the VWFA (3), was more activated in the older children. (C) Comparison of the responses to the contrast [native-foreign sentences] in the 6-year-olds in function of their reading level. Activation in the red regions (1: pars orbitalis, 2: posterior STS, 3: temporal pole) was positively correlated with reading performance in the 6-year-olds independently of age. The anterior insula (yellow region in B and C) was more activated in the less advanced group in two-by-two comparisons (pre-readers > beginners and beginners > advanced readers). Reading rapidly affects the oral language network, notably in integration regions (temporal pole and pars orbitalis) and phonological regions (posterior STS) whereas activation of the VWFA during speech listening needs more training and is seen only in the older children. By contrast, children might rely less on covert repetition (insula) as their sentence comprehension improves.

observations in adults, showing only minimal differences between monolinguals and fluent bilinguals listening to speech in MRI (Abutalebi, 2008; Kovelman, Baker, & Petitto, 2008).

Although no repetition effect was observed in the younger groups, there was no significant difference between ages in either direction on the first vs. second sentence presentation contrast computed across the whole brain, even when the analysis was restricted to the native language sentences and to the monolingual children.

3.2.3. Analyses of the 6-year-olds: what is the impact of a few months of reading instruction?

In the above comparisons between the 6- and 9-year-olds, it is difficult to disentangle reading and age. We therefore focused on the two groups of 6-year-olds who were approximately the same age but exhibited very different expertise in reading. As there was a small but significant difference in age between our two groups, age was entered as a regressor of non interest in all the following analyses and we used the number of words read in 1 min as representative of the children reading performances. In the Speech contrast, three clusters were positively correlated with the reading performance: the hand left motor cortex ($[-42 -24 66]$, $z = 5.75$, 104 vox, $pc_cor = .040$); the left *planum temporale* ($[-42 -30 21]$, $z = 5.31$, 101 vox, $pc_cor = .043$), extending toward the posterior

Table 3
Asymmetries in the native language network [native–foreign sentences] in each of the three groups. The peak coordinates are given relatively to the symmetrical MNI template (sMMI).

Area	sMMI coordinates			SPMt-tests			
	x	y	z	No. of voxels in cluster	Cluster-level <i>p</i> value (corrected)	<i>z</i> Value at local maximum	
<i>Advanced readers</i>							
Left > right	Posterior STS	−60	−45	6	193	<0.001	4.91
	Inferior frontal	−51	15	−27	94	<0.001	4.21
<i>Beginner readers</i>							
Left > right	Inferior frontal	−57	27	9	153	<0.001	5.18
	Inferior temporal	−39	−18	−27	319	<0.001	5.15
	Lingual gyrus	−18	−57	−6	107	<0.001	4.95
	Posterior STS	−66	−24	0	66	0.001	4.20
	Cerebellum	−21	−63	−39	38	0.028	4.02
Right > left	Caudate	0	3	3	64	0.002	4.05
<i>Pre-readers</i>							
Left > right	Inferior frontal	−45	30	12	118	<0.001	4.87
	Inferior temporal	−45	−42	−12	104	<0.001	5.31
	Posterior STS	−63	−48	3	100	<0.001	6.27
Right > left	Cuneus	0	−81	30	167	<0.001	4.63
	Cerebellum	24	−84	−33	118	<0.001	4.60
	Anterior cingulate	15	45	21	44	0.014	4.14
	Planum temporale	39	−39	21	40	0.022	3.99

STS ([−45−54 9], $z = 3.85$); and the right Heschl's gyrus, extending within the *planum temporale* and the supramarginal gyrus ([51−21 18], $z = 6$; 250 vox, $pc_cor = .001$). This same right cluster was also inversely correlated with age ([69−36 12], $z = 6.36$, 205 vox, $pc_cor = .002$), suggesting a greater reliance on the right auditory areas in the most precocious readers.

Better reading performance also induced an increase of activity in the contrast [native–foreign] sentences in three left perisylvian clusters of our native language mask (Fig. 2B): the left temporal pole ([−48 15−36], $z = 5.04$, 78 vox, $pc_cor = .021$), the left inferior frontal region (pars orbitalis [−42 33−12], $z = 4.55$, 57 vox, $pc_cor = .046$), and the left posterior STS ([−45−51 24], $z = 4.39$, 47 vox, $pc_cor = .070$). No cluster was significantly correlated with age for this comparison. No repetition effect in either direction was correlated with age or the reading performance.

When 6-year-olds were considered as two groups (pre-readers and beginners) and age was entered as a regressor of non-interest, the clusters identified in the previous analysis did not reach a significant pc_cor level. This result favors a continuous effect of reading practice on the oral network rather than a sudden change after the start of a formal teaching. By contrast, a large left region extending from Heschl's gyrus ([−39−33 9], $z = 5.88$, 1290 vox, $pc_cor < .001$) toward the insula ([−30 27 9], $z = 5.85$) and rolandic operculum ([−51 9 3], $z = 4.39$) and both anterior cingulate ([−12 9 39], $z = 4.55$, 374 vox, $pc_cor < .001$) and thalami ([9−15 9], $z = 4.62$, 142 vox, $pc_cor = .014$) was more activated in pre-readers than in beginners. Only the left insula/precentral cluster ([−30 27 9], $z = 5.85$, 129 voxels, $pc_cor = .005$) remained significant when the analysis was restricted to the native language mask.

As we were not expecting stronger activation in less expert children, we examined whether the same difference was present between beginners and advanced readers in a follow-up comparison with age as a regressor of non interest. We again observed the same cluster more activated in the 6- than the 9-year-olds although with a peak shift ([−45 9 0], $z = 5.38$, 165 vox, $pc_cor = .007$). This cluster (yellow cluster in Fig. 2) was anterior to the insula cluster which exhibited a reverse pattern (see comparisons between 6 and 9 year-olds presented above), that is more activity in 9-year-olds than in 6-year-olds (¹blue cluster in Fig. 2).

¹ For interpretation of color in Fig. 2, the reader is referred to the web version of this article.

This anterior insula cluster was comprised in the regions that were more activated by the native language (and especially when the sentence was repeated) than by the foreign language in the 6-year-olds but was not observed in the same comparison in the 9-year-olds.

4. Discussion

Through the manipulation of two orthogonal factors, repetition and speech comprehension, our goals were to study the impact of maturation and reading instruction on the spoken language network during normal development. Our results support the hypothesis of a stable set of peri-sylvian regions involved in speech processing since the early months of life with a clear left advantage to process the native language (Figs. 1 and 2). Nevertheless, during a short period of three years (6–9 years of age), but at a key time when children learn to read, several changes are induced by reading practice (Fig. 3). First, we observed an increased activation in the posterior STS/*planum temporale* region in the better readers, i.e. nine-year-old relatively to 6-year-old children but also beginners vs. pre-readers. Second, a few months of reading instruction (an of average 11 months in our children) induced larger responses in the native language network in the temporal pole and the pars orbitalis (Fig. 3C), but also decreased activity in the left insula for the native sentences (Fig. 3C). This activity further decreased in the 9-year-olds relative to the beginners (Fig. 3B). Third, a larger response in the VWFA was only observed in the comparison of 9- and 6-year-olds, but not when beginners and pre-readers were compared suggesting slower changes in this region relatively to the previous regions (Fig. 3B). Finally, a repetition suppression effect was only detected in the older group although no significant difference between ages was observed at our statistical threshold. We will discuss these points in turn.

4.1. Core regions of the language network

As expected from published studies in infants (Dehaene-Lambertz, Dehaene et al., 2006) and children (Ahmad, Balsamo, Sachs, Xu, & Gaillard, 2003; Balsamo et al., 2002; Lidzba et al., 2011; Schmithorst et al., 2006; Szaflarski et al., 2012), listening to speech and, more specifically to native language sentences, activates similar regions in children as in older ages. The network involved in native speech processing comprised the superior

temporal region around the STS, the inferior frontal regions, and inferior temporal regions (basal language area). This network was notably and significantly asymmetric toward the left side (Figs. 1 and 2) with no increase in asymmetries during this time-period (except for the VWFA). This result confirms the now numerous brain imaging studies that demonstrated that the left advantage observed during linguistic tasks is not a property of the mature adult brain but is commonly observed from infancy (Ahmad et al., 2003; Balsamo et al., 2002 in children; Berl et al., 2010; Dehaene-Lambertz et al., 2002, 2010 in infants; Lidzba et al., 2011; Schmithorst et al., 2006).

Among the native language network regions, we obtained clear activations in the inferior temporal area, a region rarely reported in adult MRI studies but already reported in children (Balsamo, Xu, & Gaillard, 2006). This multi-modal region, called basal language area in the neuropsychological literature, participates in language production and comprehension and mediates semantic retrieval from oral or visual language input (Binder et al., 1997; Demonet, Thierry, & Cardebat, 2005). Its role was principally inferred from neuropsychological studies and electrical stimulation in patients who presented with anomia and loss of understanding from oral, written and tactile speech when this region was destroyed or stimulated during surgery (Burnstine et al., 1990; Sharp, Scott, & Wise, 2004; Trebuchon-Da Fonseca et al., 2009). The difference between children and adults might be related to the well-known loss of data around the pneumatized mastoids in adults or to the children's difficulties in retrieving the semantic content of a long sentence in the noisy environment of the MRI scanner. Using PET, Sharp et al. (2004) reported a modulation of this region with the intelligibility of speech, but its activation did not increase, but decreased, when speech was less intelligible. Here, repetition, which should facilitate sentence understanding, had no significant effect on this region (Fig. 1C). There was also no difference between 6- and 9-year-old children. These three arguments do not favor the recruitment of this region as a supplementary area in children to help them understand native sentences but rather suggest a lack of MRI sensitivity in adults in the anterior basal regions. Further studies comparing adults, adolescents and children with sentences of increasing complexity should address this question.

4.2. Reading adds new regions to the oral language network: the VWFA

The basal language region connects to the higher visual regions. The peak of the specific response to written words (i.e., the VWFA) in our 9-year-old children was located at $[-42 -45 -15]$ (published result in Monzalvo et al., 2012) and thus, was part of the lateralized cluster of voxels, differentiating the 6- and the 9-year-olds listening to native sentences (point #3 in Fig. 3B). In our previous paper, comparing dyslexics and the same 9-year-olds as studied here, the dyslexics, as the 6-year-olds in the present study, did not activate this region when listening to speech. It is also one of the regions that differentiates literate and illiterate adults (Dehaene et al., 2010). These differences between groups of subjects with different reading capacities are not related to a modulation of deactivations in visual areas but to a genuine activation in this region for spoken input. In adults, selective attention to speech stimuli relative to attention to tones contour modulates the BOLD response in visual areas, but only speech drives an increase of activity in this region and solely in this region (Yoncheva, Zevin, Maurer, & McCandliss, 2010). Thus, this region, which is not a natural spoken language area, can be recruited by oral speech input but apparently only in competent readers.

Usually, adults recruit this area in demanding tasks such as lexical decision task (Dehaene et al., 2010), selective attention to ambiguous speech stimuli (Yoncheva et al., 2010) and not when they are just listening to sentences (Dehaene-Lambertz, 2006

#5733 using the same sentences than here and also Dehaene et al., 2010). The recruitment of this region may provide the neural basis for the orthographic influence on speech perception reported in lexical decision task in adults: Adults are slower to classify inconsistent words (i.e., containing sounds with several possible spellings) relative to consistent words (one single spelling) (Ventura et al., 2004; Ziegler & Ferrand, 1998). In children also, the automatic recruitment of this region might explain the better performances of more advanced readers to learn the meaning of new words when exposed to their written form, even incidentally (Ricketts et al., 2009).

Contrary to adults, speech listening was sufficient in our children to elicit response in this region. Our sentences might require more effort to be understood by children than by adults in the noise of an MRI scanner but it may also be possible that children may momentarily rely more on this area than adults. Booth et al. (2004) comparing 9- to 12-year-olds and adults reported similar activations in this region at both ages for an auditory rhyming task but greater activation in the children for the spelling task, whereas no difference between ages was observed in the same tasks when the stimuli were presented visually. Similarly, in behavioral tasks, an orthographic influence, which is obviously absent in pre-readers, was detected more widely during the first years of reading than in adults for both words and non-words in a lexical decision task (Ventura, Morais, & Kolinsky, 2007). The authors explained these u-shaped results with over-trained grapho-phonological procedures in children. The same explanation might be proposed here.

Dehaene and Cohen (2007) proposed that the success of cultural inventions relies on an efficient recycling of neural elements within the constraints of their previous functions. In this context, our result uncovers that the VWFA appears at the intersection of several key regions. It is at the posterior tip of a multimodal semantic region and at the anterior tip of a hierarchy of visual areas that code the written input more and more selectively (Vinckier et al., 2007), and is directly related to the posterior superior temporal region through the posterior branch of the arcuate fasciculus (Thiebaut de Schotten, Cohen, Amemiya, Braga, & Dehaene, 2012).

4.3. Reading increased activations in the posterior temporal region in a few months of training

Contrary to the recruitment of the VWFA which needs more than a year of training, activation rapidly increases after a few months of reading practice, in several left regions of the native language network: the posterior STS and *planum*, the temporal pole and the pars orbitalis. Literates listening to speech present larger activation in the posterior temporal region relative to illiterates (Dehaene et al., 2010), as normal-readers relative to dyslexics (Monzalvo et al., 2012; Paulesu et al., 2001). Here, this increase in activation observed in our 6-year-olds correlated with the number of words they were able to read in 1 min, independently of age and thus of a maturational calendar. The posterior STS is classically involved in the reading system (Dehaene, 2009) and is a site of integration of sounds and letters (Blau, van Atteveldt, Ekkebus, Goebel, & Blomert, 2009; Blau et al., 2010; Froyen, Bonte, van Atteveldt, & Blomert, 2009; van Atteveldt, Formisano, Goebel, & Blomert, 2004). When an incongruent letter was presented in the same time as an auditory vowel, adults, but not 8-year-old children with one year of reading instruction, presented an electrical mismatch response (Froyen, Van Atteveldt, Bonte, & Blomert, 2008). In 11-year-olds, this response was observed but only if the letter preceded the sound by 200 ms. However at both ages, a later effect at about 650 ms was recorded in children suggesting a slow and effortful grapheme-phoneme association. Our MRI result showed that even if the arbitrary associations between letters and sounds took several years to become rapid and fully automatic, reading

practice quickly transformed the posterior temporal region. The increase of activity in this region, that encompasses the *planum*, might also be related to the improvement of metaphonological capacities secondary to the explicit work on speech segmentation done during reading instruction. In any case, as a convergent region of auditory and visual information (Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004), strongly connected through the dorsal pathway to the articulatory anterior regions (Lerch et al., 2006; Leroy et al., 2011; Poeppel & Hickok, 2004), the posterior temporal region presents the suitable characteristics to be embedded in this new function, reading.

4.4. Improvement in sentence processing

The two other regions (temporal pole and pars orbitalis) which were also affected by reading in the 6-year-olds are classically related to sentence integration, and not usually reported when subjects with different reading capacities are compared. This might be related to the use of sentences instead of words in our experimental paradigm as these two regions are involved in the binding of syntactic structures with lexico-semantic representations (Dapretto & Bookheimer, 1999; Pallier et al., 2011; Price, 2010). The sentences we used, contained between 10 and 12 words, at the superior limit of the 6-years-olds' verbal words span (Table 1), combined in varied and complex syntactical structures with a rich vocabulary. They certainly required an effort to be perfectly understood by the children and the differences within the 6-year-olds might be compatible with a greater ease to process these sentences in school-children than in kindergarten children. This might be favoured by reading practice itself but also by one year of school work which in the French curriculum, concerned not only grapheme-phoneme conversion but all aspects of language with explicit exercises on vocabulary and morpho-syntactic structures. These exercises are particularly necessary because of the numerous morpho-syntactic markers present in French orthography (e.g. singular/plural markers with no difference in the oral form: "il brille" vs. "ils brillent"; mute letters in masculine forms: "vert" vs. "verte", etc.).

Finally, no repetition suppression effect was observed in the superior temporal sulcus, in the 6-year-olds contrary to the 9-year-olds, although there was a similar acceleration of the reaction times with repetition at both ages. This null effect in the younger children suggests that a stable representation of the native sentence was not maintained over the 12s delay between sentences. As in adults, the regions showing a repetition suppression effect in the 9-year-olds were the most ventral of the superior temporal region, and thus the most abstract linguistic regions, sensitive notably to intelligibility (Davis & Johnsrude, 2003; Vagharchakian, Dehaene-Lambertz, Pallier, & Dehaene, 2012). In parallel, we noticed a decrease of activation in the left anterior insula, a region involved in speech production (Ackermann & Riecker, 2004; Dronkers, 1996), as competence increased (once the effect of age canceled) suggesting a strategy of covert repetition in less competent children to compensate their comprehension difficulties. These results are in line with a decrease of activity in the cingulum with age during narrative comprehension reported by Szafarsky and colleagues. (Szafarsky et al., 2006, 2012) and illustrate the continuous progress in speech processing fluency during childhood.

5. Conclusion

Human language relies on a core of regions around the left Sylvian fissure. Several studies in infants have now uncovered the striking similarities of the speech network in infants and adults. The fact that a few months of reading instruction are sufficient to

modify these linguistic core regions is in agreement with the notion that the success of a cultural object is its efficiency in increasing and developing neural possibilities within the frame of pre-existing constraints. We postulated that the regions affected by reading acquisition (e.g. *planum*/pSTS, VWFA) are located at crucial intersection points between different systems. DTI studies should help to refine this model. The pattern of connectivity of individual voxels in these regions might help to predict these activation patterns as it has been demonstrated for the fusiform face area (Saygin et al., 2012). Finally, it is often emphasized that the main effect of reading on speech perception is an improvement of the coding and the retrieval of the speech sublexical units. It is thus noteworthy to signal that reading has a much broader effect, from sublexical sampling to sentence comprehension, during the first years of schooling and thus this observation should be taken into account when normally developing children are compared with impaired children.

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References

- Abutalebi, J. (2008). Neural aspects of second language representation and language control. *Acta Psychologica (Amsterdam)*, 128(3), 466–478.
- Ackermann, H., & Riecker, A. (2004). The contribution of the insula to motor aspects of speech production: A review and a hypothesis. *Brain and Language*, 89(2), 320–328.
- Ahmad, Z., Balsamo, L. M., Sachs, B. C., Xu, B., & Gaillard, W. D. (2003). Auditory comprehension of language in young children: Neural networks identified with fMRI. *Neurology*, 60(10), 1598–1605.
- Balsamo, L. M., Xu, B., & Gaillard, W. D. (2006). Language lateralization and the role of the fusiform gyrus in semantic processing in young children. *Neuroimage*, 31(3), 1306–1314.
- Balsamo, L. M., Xu, B., Grandin, C. B., Petrella, J. R., Branietki, S. H., Elliott, T. K., et al. (2002). A functional magnetic resonance imaging study of left hemisphere language dominance in children. *Archives of Neurology*, 59(7), 1168–1174.
- Beauchamp, M. S., Argall, B. D., Bodurka, J., Duyn, J. H., & Martin, A. (2004). Unraveling multisensory integration: Patchy organization within human STS multisensory cortex. *Nature Neuroscience*, 7(11), 1190–1192.
- Berl, M. M., Duke, E. S., Mayo, J., Rosenberger, L. R., Moore, E. N., VanMeter, J., et al. (2010). Functional anatomy of listening and reading comprehension during development. *Brain and Language*, 114(2), 115–125.
- Bernal, S. (2001). *Catégorisation des mots grammaticaux par l'enfant de 18 mois*. Rapport de maîtrise de l'ENS Lyon.
- Binder, J. R., Frost, J. A., Hammeke, T. A., Cox, R. W., Rao, S. M., & Prieto, T. (1997). Human brain language areas identified by functional magnetic resonance imaging. *Journal of Neuroscience*, 17, 353–362.
- Blau, V., Reithler, J., van Atteveldt, N., Seitz, J., Gerretsen, P., Goebel, R., et al. (2010). Deviant processing of letters and speech sounds as proximate cause of reading failure: A functional magnetic resonance imaging study of dyslexic children. *Brain*, 133(Pt 3), 868–879.
- Blau, V., van Atteveldt, N., Ekkebus, M., Goebel, R., & Blomert, L. (2009). Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. *Current Biology*, 19(6), 503–508.
- Blomert, L. (2011). The neural signature of orthographic-phonological binding in successful and failing reading development. *Neuroimage*, 57(3), 695–703.
- Booth, J., Burman, D., Meyer, J., Gitelman, D., Parrish, T., & Mesulam, M. (2004). Development of brain mechanisms for processing orthographic and phonologic representations. *Journal of Cognitive Neuroscience*, 16(7), 1234–1249.
- Brauer, J., & Friederici, A. D. (2007). Functional neural networks of semantic and syntactic processes in the developing brain. *Journal of Cognitive Neuroscience*, 19(10), 1609–1623.
- Burnstine, T. H., Lesser, R. P., Hart, J., Jr., Uematsu, S., Zinreich, S. J., Krauss, G. L., et al. (1990). Characterization of the basal temporal language area in patients with left temporal lobe epilepsy. *Neurology*, 40(6), 966–970.
- Carreiras, M., Seghier, M. L., Baquero, S., Estevez, A., Lozano, A., Devlin, J. T., et al. (2009). An anatomical signature for literacy. *Nature*, 461(7266), 983–986.

- Castro-Caldas, A., Petersson, K. M., Reis, A., Stone-Elander, S., & Ingvar, M. (1998). The illiterate brain. Learning to read and write during childhood influences the functional organization of the adult brain. *Brain*, 121(Pt 6), 1053–1063.
- Dapretto, M., & Bookheimer, S. Y. (1999). Form and content: Dissociating syntax and semantics in sentence comprehension. *Neuron*, 24(2), 427–432.
- Davis, M. H., & Johnsrude, I. S. (2003). Hierarchical processing in spoken language comprehension. *Journal of Neuroscience*, 23(8), 3423–3431.
- Dehaene, S. (2009). *Reading in the brain*. Penguin Viking.
- Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384–398.
- Dehaene, S., Pegado, F., Braga, L. W., Ventura, P., Filho, G. N., Jobert, A., et al. (2010). How learning to read changes the cortical networks for vision and language. *Science*, 330(6009), 1359–1364.
- Dehaene-Lambertz, G., Dehaene, S., Anton, J. L., Campagne, A., Ciuciu, P., Dehaene, G. P., et al. (2006). Functional segregation of cortical language areas by sentence repetition. *Human Brain Mapping*, 27(5), 360–371.
- Dehaene-Lambertz, G., Dehaene, S., & Hertz-Pannier, L. (2002). Functional neuroimaging of speech perception in infants. *Science*, 298(5600), 2013–2015.
- Dehaene-Lambertz, G., Hertz-Pannier, L., & Dubois, J. (2006). Nature and nurture in language acquisition: Anatomical and functional brain-imaging studies in infants. *Trends in Neurosciences*, 29(7), 367–373.
- Dehaene-Lambertz, G., Hertz-Pannier, L., Dubois, J., Meriaux, S., Roche, A., Sigman, M., et al. (2006). Functional organization of perisylvian activation during presentation of sentences in preverbal infants. *Proceedings of the National Academy of Sciences of the United States of America*, 103(38), 14240–14245.
- Dehaene-Lambertz, G., Montavont, A., Jobert, A., Allior, L., Dubois, J., Hertz-Pannier, L., et al. (2010). Language or music, mother or Mozart? Structural and environmental influences on infants' language networks. *Brain and Language*, 114(2), 53–65.
- Demonet, J. F., Thierry, G., & Cardebat, D. (2005). Renewal of the neurophysiology of language: Functional neuroimaging. *Physiological Reviews*, 85(1), 49–95.
- Desroches, A. S., Cone, N. E., Bolger, D. J., Bitan, T., Burman, D. D., & Booth, J. R. (2010). Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Research*, 1356, 73–84.
- Didelot, A., Mauguier, F., Redoute, J., Bouvard, S., Lothe, A., Reilhac, A., et al. (2010). Voxel-based analysis of asymmetry index maps increases the specificity of 18F-MPPF PET abnormalities for localizing the epileptogenic zone in temporal lobe epilepsies. *Journal of Nuclear Medicine*, 51(11), 1732–1739.
- Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature*, 384(6605), 159–161.
- Froyen, D. J., Bonte, M. L., van Atteveldt, N., & Blomert, L. (2009). The long road to automation: Neurocognitive development of letter-speech sound processing. *Journal of Cognitive Neuroscience*, 21(3), 567–580.
- Froyen, D., Van Atteveldt, N., Bonte, M., & Blomert, L. (2008). Cross-modal enhancement of the MMN to speech-sounds indicates early and automatic integration of letters and speech-sounds. *Neuroscience Letters*, 430(1), 23–28.
- Gertner, Y., & Fisher, C. (2012). Predicted errors in children's early sentence comprehension. *Cognition*, 124(1), 85–94.
- Hackman, D. A., & Farah, M. J. (2009). Socioeconomic status and the developing brain. *Trends in Cognitive Sciences*, 13(2), 65–73.
- Henson, R., Shallice, T., & Dolan, R. (2000). Neuroimaging evidence for dissociable forms of repetition priming. *Science*, 287(5456), 1269–1272.
- Kang, H. C., Burgund, E. D., Lugar, H. M., Petersen, S. E., & Schlaggar, B. L. (2003). Comparison of functional activation foci in children and adults using a common stereotactic space. *Neuroimage*, 19(1), 16–28.
- Khomi, A. (1999). *Epreuve d'évaluation de la compétence en lecture révisée (LMC-R)*. Paris: les Editions du Centre de Psychologie Appliquée.
- Kovelman, I., Baker, S. A., & Petitto, L. A. (2008). Bilingual and monolingual brains compared: A functional magnetic resonance imaging investigation of syntactic processing and a possible "neural signature" of bilingualism. *Journal of Cognitive Neuroscience*, 20(1), 153–169.
- Kuhl, P. K. (2004). Early language acquisition: Cracking the speech code. *Nature Reviews Neuroscience*, 5(11), 831–843.
- Leitch, J. P., Worsley, K., Shaw, W. P., Greenstein, D. K., Lenroot, R. K., Giedd, J., et al. (2006). Mapping anatomical correlations across cerebral cortex (MACACC) using cortical thickness from MRI. *Neuroimage*, 31(3), 993–1003.
- Leroy, F., Glasel, H., Dubois, J., Hertz-Pannier, L., Thirion, B., Mangin, J. F., et al. (2011). Early maturation of the linguistic dorsal pathway in human infants. *Journal of Neuroscience*, 31(4), 1500–1506.
- Li, G., Cheung, R. T., Gao, J. H., Lee, T. M., Tan, L. H., Fox, P. T., et al. (2006). Cognitive processing in Chinese literate and illiterate subjects: An fMRI study. *Human Brain Mapping*, 27(2), 144–152.
- Lidzba, K., Schwilling, E., Grodd, W., Krageloh-Mann, I., & Wilke, M. (2011). Language comprehension vs. language production: Age effects on fMRI activation. *Brain and Language*, 119(1), 6–15.
- Mahmoudzadeh, M., Dehaene-Lambertz, G., Fournier, M., Kongolo, G., Goudjil, S., Dubois, J., et al. (2013). Syllabic discrimination in premature human infants prior to complete formation of cortical layers. *Proceedings of the National Academy of Sciences of the United States of America*, 110(12), 4846–4851.
- Mazaika, P., Whitfield-Gabrieli, S., Reiss, A. (2007). Artifact repair for fMRI data from high motion clinical subjects. *Paper presented at the 13th annual meeting of the Organization for Human, Brain Mapping*.
- Mills, D. L., Coffey-Corina, S. A., & Neville, H. J. (1993). Language acquisition and cerebral specialization in 20-month-old infants. *Journal of Cognitive Neuroscience*, 5, 317–334.
- Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., & Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *Neuroimage*, 61(1), 258–274.
- Morais, J., & Kolinsky, R. (2005). Literacy and cognitive change. In M. Snowling & C. Hulme (Eds.), *The science of reading: A handbook* (pp. 188–203). Oxford: Blackwell.
- Noble, K. G., McCandliss, B. D., & Farah, M. J. (2007). Socioeconomic gradients predict individual differences in neurocognitive abilities. *Developmental Science*, 10(4), 464–480.
- Pallier, C., Devauchelle, A. D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences of the United States of America*, 108(6), 2522–2527.
- Paulesu, E., Demonet, J. F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., et al. (2001). Dyslexia: Cultural diversity and biological unity. *Science*, 291(5511), 2165–2167.
- Paus, T., Zijdenbos, A., Worsley, K., Collins, D. L., Blumenthal, J., Giedd, J. N., et al. (1999). Structural maturation of neural pathways in children and adolescents: In vivo study. *Science*, 283(5409), 1908–1911.
- Pena, M., Maki, A., Kovacic, D., Dehaene-Lambertz, G., Koizumi, H., Bouquet, F., et al. (2003). Sounds and silence: An optical topography study of language recognition at birth. *Proceedings of the National Academy of Sciences of the United States of America*, 100(20), 11702–11705.
- Pinel, P., & Dehaene, S. (2009). Beyond hemispheric dominance: Brain regions underlying the joint lateralization of language and arithmetic to the left hemisphere. *Journal of Cognitive Neuroscience*, 22(1), 48–66.
- Poeppel, D., & Hickok, G. (2004). Towards a new functional anatomy of language. *Cognition*, 92(1–2), 1–12.
- Price, C. J. (2010). The anatomy of language: A review of 100 fMRI studies published in 2009. *Annals of the New York Academy of Sciences*, 1191(1), 62–88.
- Ricketts, J., Bishop, D. V., & Nation, K. (2009). Orthographic facilitation in oral vocabulary acquisition. *Quarterly Journal of Experimental Psychology (Hove)*, 62(10), 1948–1966.
- Saygin, Z. M., Osher, D. E., Koldewyn, K., Reynolds, G., Gabrieli, J. D., & Saxe, R. R. (2012). Anatomical connectivity patterns predict face selectivity in the fusiform gyrus. *Nature Neuroscience*, 15(2), 321–327.
- Schmithorst, V. J., Holland, S. K., & Plante, E. (2006). Cognitive modules utilized for narrative comprehension in children: A functional magnetic resonance imaging study. *Neuroimage*, 29(1), 254–266.
- Sharp, D. J., Scott, S. K., & Wise, R. J. (2004). Retrieving meaning after temporal lobe infarction: The role of the basal language area. *Annals of Neurology*, 56(6), 836–846.
- Sowell, E. R., Peterson, B. S., Thompson, P. M., Welcome, S. E., Henkenius, A. L., & Toga, A. W. (2003). Mapping cortical change across the human life span. *Nature Neuroscience*, 6(3), 309–315.
- Szaflarski, J. P., Altaye, M., Rajagopal, A., Eaton, K., Meng, X., Plante, E., et al. (2012). A 10-year longitudinal fMRI study of narrative comprehension in children and adolescents. *Neuroimage*, 63(3), 1188–1195.
- Szaflarski, J. P., Holland, S. K., Schmithorst, V. J., & Byars, A. W. (2006). fMRI study of language lateralization in children and adults. *Human Brain Mapping*, 27(3), 202–212.
- Thiebaut de Schotten, M., Cohen, L., Amemiya, E., Braga, L. W., & Dehaene, S. (2012). Learning to read improves the structure of the Arcuate Fasciculus. *Cerebral Cortex*.
- Toga, A. W., & Thompson, P. M. (2003). Mapping brain asymmetry. *Nature Reviews Neuroscience*, 4(1), 37–48.
- Trebuchon-Da Fonseca, A., Benar, C. G., Bartolomei, F., Regis, J., Demonet, J. F., Chauvel, P., et al. (2009). Electrophysiological study of the basal temporal language area: A convergence zone between language perception and production networks. *Clinical Neurophysiology*, 120(3), 539–550.
- Vagharchakian, L., Dehaene-Lambertz, G., Pallier, C., & Dehaene, S. (2012). A temporal bottleneck in the language comprehension network. *Journal of Neuroscience*, 32, 9089–9102.
- van Atteveldt, N., Formisano, E., Goebel, R., & Blomert, L. (2004). Integration of letters and speech sounds in the human brain. *Neuron*, 43(2), 271–282.
- Ventura, P., Morais, J., & Kolinsky, R. (2007). The development of the orthographic consistency effect in speech recognition: From sublexical to lexical involvement. *Cognition*, 105(3), 547–576.
- Ventura, P., Morais, J., Pattamadilok, C., & Kolinsky, R. (2004). The locus of the orthographic consistency effect in auditory word recognition. *Language and Cognitive Processes*, 19, 57–95.
- Vinckier, F., Dehaene, S., Jobert, A., Dubus, J. P., Sigman, M., & Cohen, L. (2007). Hierarchical coding of letter strings in the ventral stream: Dissecting the inner organization of the visual word-form system. *Neuron*, 55(1), 143–156.
- Yakovlev, P., & Lecours, A. R. (1967). The myelogenetic cycles of regional maturation of the brain. In A. Minkovski (Ed.), *Regional development of the brain in early life* (pp. 3–69). Oxford and Edinburgh: Blackwell.
- Yoncheva, Y. N., Zevin, J. D., Maurer, U., & McCandliss, B. D. (2010). Auditory selective attention to speech modulates activity in the visual word form area. *Cerebral Cortex*, 20(3), 622–632.
- Ziegler, J. C., & Ferrand, L. (1998). Orthography shapes the perception of speech: The consistency effect in auditory word recognition. *Psychonomic Bulletin and Review*, 5, 683–689.