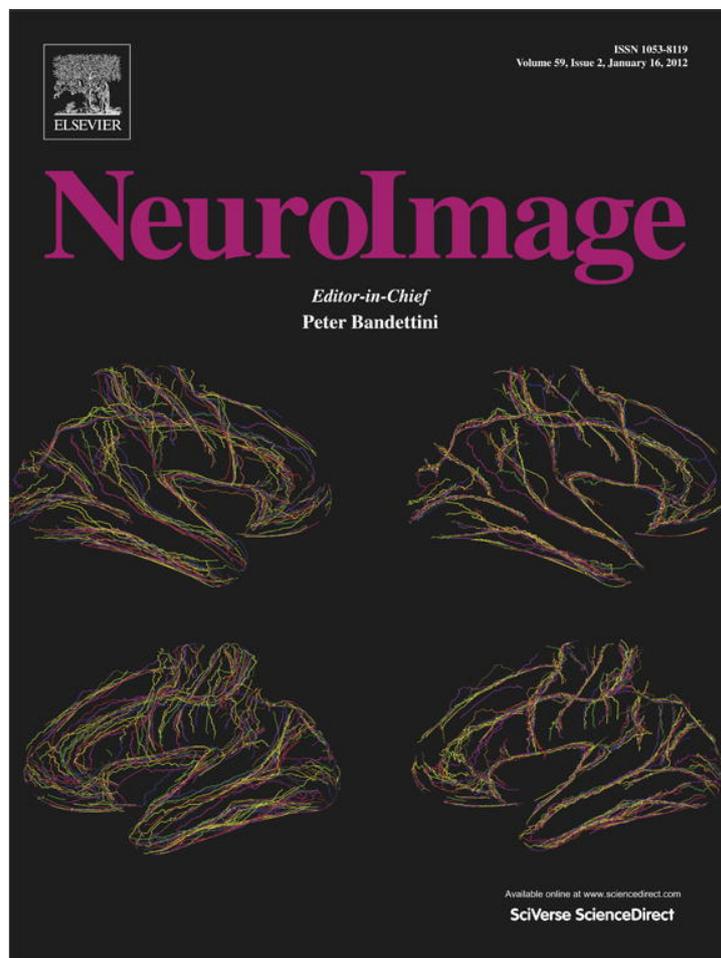


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Full Length Article

Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status

Karla Monzalvo^{a,b,c}, Joel Fluss^{c,d,e}, Catherine Billard^{c,d},
Stanislas Dehaene^{a,b,c,f}, Ghislaine Dehaene-Lambertz^{a,b,c,*}

^a INSERM, Cognitive Neuroimaging Unit, Gif sur Yvette, 91191 France

^b CEA, DSV, I2BM, Neurospin center, Gif sur Yvette, 91191 France

^c University Paris 11, Orsay, France

^d Assistance Publique-Hôpitaux de Paris, 94 Le Kremlin-Bicêtre, France

^e Neurologie pédiatrique, Hôpitaux Universitaires Genève, Suisse

^f Collège de France, Paris, France

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ABSTRACT

In dyslexia, anomalous activations have been described in both left temporo-parietal language cortices and in left ventral visual occipito-temporal cortex. However, the reproducibility, task-dependency, and presence of these brain anomalies in childhood rather than adulthood remain debated. We probed the large-scale organization of ventral visual and spoken language areas in dyslexic children using minimal target-detection tasks that were performed equally well by all groups. In 23 normal and 23 dyslexic 10-year-old children from two different socio-economic status (SES) backgrounds, we compared fMRI activity to visually presented houses, faces, and written strings, and to spoken sentences in the native or in a foreign language. Our results confirm a disorganization of both ventral visual and spoken language areas in dyslexic children. Visually, dyslexic children showed a normal lateral-to-medial mosaic of preferences, as well as normal responses to houses and checkerboards, but a reduced activation to words in the visual word form area (VWFA) and to faces in the right fusiform face area (FFA). Auditorily, dyslexic children exhibited reduced responses to speech in posterior temporal cortex, left insula and supplementary motor area, as well as reduced responses to maternal language in subparts of the *planum temporale*, left basal language area and VWFA. By correlating these two findings, we identify spoken-language predictors of VWFA activation to written words, which differ for dyslexic and normal readers. Similarities in fMRI deficits in both SES groups emphasize the existence of a core set of brain activation anomalies in dyslexia, regardless of culture, language and SES, without however resolving whether these anomalies are a cause or a consequence of impaired reading.

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Introduction

During reading acquisition, the child's brain must learn to identify a new category of visual stimuli, written words, and to connect it with the already developed spoken language network. Acquisition of this new capacity deeply affects anatomical and functional brain organization, as shown by studies comparing illiterate and literate adults (Carreiras et al., 2009; Castro-Caldas et al., 1998; Dehaene et al., 2010; Li et al., 2006). In particular, it leads to the development of a specific brain site in the left visual occipito-temporal cortex, the “visual word form area” (VWFA), that strongly responds to orthographic stimuli in the learned

script, as well as to efficient integration in the superior temporal areas between letters and the sounds they represent (Blomert and Froyen, 2010; van Atteveldt et al., 2004).

Dyslexic children exhibit functional deficits in both of these brain systems (Maisog et al., 2008; Richlan et al., 2009, 2011). Impaired phonological representations have been proposed as the main causal mechanism of developmental reading impairments (Blau et al., 2009, 2010; Paulesu et al., 2001; Ramus, 2004; Shaywitz, 1998; Temple, 2002; Torgesen et al., 1994; Vellutino et al., 2004). Brain imaging studies have indeed revealed hypo-activations in adult and children dyslexics in regions involved in phonetic computations, particularly the left temporo-parietal region, often accompanied by an increase in the inferior frontal regions which is interpreted as a compensatory response (Chandrasekaran et al., 2009; Dufor et al., 2007; Hoeft et al., 2011; Maisog et al., 2008; Paulesu et al., 2001; Richlan et al., 2009; Ruff et al., 2003; Shaywitz et al., 2003). Particular impressive are recent studies revealing basic anomalies in processing individual

Abbreviations: FFA, fusiform face area; VWFA, visual word form area; PPA, parahippocampal place area.

* Corresponding author at: Laboratoire de Neuroimagerie Cognitive INSERM U992, CEA/SAC/DSV/DRM/NeuroSpin, Bat 145, point courrier 156, F-91191 GIF/YVETTE, France. Fax: +33 1 69 08 79 73.

E-mail address: ghislaine.dehaene@cea.fr (G. Dehaene-Lambertz).

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speech sounds and letter–sound correspondences in the left superior temporal gyrus (Blau et al., 2009, 2010).

Nevertheless, a recent meta-analysis (Richlan et al., 2011) indicates that such activation anomalies in dyslexics' left temporo-parietal cortex are not always reproducible. In particular, while frequently seen in fMRI studies of adult dyslexics, they are often absent when scanning dyslexic children (but see Blau et al., 2010 and Maurer 2011). Instead, the most reproducible site of hypo-activation in adult and children dyslexics appears to be the left occipito-temporal cortex, at the site of the VWFA (Richlan et al., 2011). Because this region is unresponsive to written words in non-readers (Dehaene et al., 2010), and quickly increases its response during reading acquisition (Maurer et al., 2005b, 2010; Schlaggar and McCandliss, 2007), its reduced activation in dyslexics might reflect a consequence rather than a cause of reading impairment. Nevertheless, across distinct studies, anomalies in the VWFA area can occur without any superior temporal deficit (McCroary et al., 2005) or vice-versa (Blau et al., 2009).

In this context, the main goal of the present study was to probe the functional organization of the large-scale maps for vision and spoken language in normal and dyslexic children. Within the same children, we mapped the mosaic of ventral regions responsive to distinct categories of visual stimuli (faces, houses, words, checkerboards) as well as the entire perisylvian areas responsive to spoken language, allowing us to evaluate the existence of correlated deficits in these two domains. Furthermore, we aimed to assess whether these functional anomalies may still be observed in the absence of any complex task. Many previous neuroimaging studies of dyslexia relied on reading, metaphonological, or orthographic tasks that present difficulties for dyslexic children. Only a handful of studies have revealed persistent anomalies in functional activation during tasks requiring only minimal passive exposure to letter strings (Brunswick et al., 1999a), single letters (Blau et al., 2010), or speech sounds corresponding to single letters (Blau et al., 2009, 2010; Froyen et al., 2011). Our design fell in the latter category: by requiring only a minimal detection task, we aimed to probe functional brain architecture in the absence of differences potentially induced by poorer performance or greater effort in the dyslexic group.

In the first half of our experiment, children were presented with visual words, faces, buildings and moving checkerboards while their task was to detect a rare target star. This design allowed us to probe the overall organization of the lateral-to-mesial mosaic of activations to visual categories (Golarai et al., 2007; Hasson et al., 2003; Haxby et al., 2001; Ishai et al., 1999), as well the presence of specific anomalies in the response to each category, either relative to rest, to the checkerboard baseline, or to each other. Because face responses were recently found to be modulated by literacy (Dehaene et al., 2010), we were particularly interested in the possibility that the fusiform face (FFA) might be anomalous in dyslexia.

In the second half of our experiment, the children listened to sentences in their native or in a foreign language, while their task was to press a button at the end of each sentence. Following the design of our earlier study (Dehaene-Lambertz et al., 2006a), each sentence was repeated twice at a 14 s interval. This simple design proved powerful in adults (Dehaene-Lambertz et al., 2006a) and infants (Dehaene-Lambertz et al., 2006a) in order to activate the entire perisylvian spoken-language network, including but not restricted to regions involved in the phonological processing of connected speech, and dissect it into three levels, any of which might be deficient in dyslexic children: (1) activations to all speech stimuli relative to rest; (2) activation specific to the native language and absent to foreign language; (3) areas responsive to the native language and whose activation decreases with sentence repetition, thus probing short-term linguistic memory.

Finally, one last goal of our study was to probe the invariance of functional brain anomalies in dyslexic children in the face of large variations in socio-economic background. To this end, within both

the normal and the dyslexic groups, we constituted two subgroups of children with low versus high socio-economic status (SES). The dominant view of dyslexia suggests that it reflects mainly a neurobiological impairment that should reveal itself identically in all affected children, regardless of their cultural or social background (e.g. Paulesu et al., 2001). Yet this issue remains largely untested, since the majority of dyslexia studies have involved middle to high-SES children. Reading difficulties are known to be compounded by a lower SES (Noble et al., 2006a), but interestingly meta-phonological competence remains the most important predictor of reading difficulties even in low SES children, with SES itself predicting only 9% of the variance in reading scores (Fluss et al., 2009; Frederickson and Frith, 1998). Noble et al. (2006a) therefore proposed a model where phonological deficits interact with SES, a low SES preventing the natural compensation available to high-SES children through parental input, early education and print exposure, larger vocabulary and superior executive functions (Hackman and Farah, 2009). Here, because we used simple and nearly passive tasks, differences in executive functions should minimally influence our results. We tested the prediction that a shared cerebral substrate for dyslexia should exist in both high- and low-SES readers, in spite of the low-SES children's lower vocabularies.

Methods

Subjects

46 dyslexics and normal readers (25 boys and 21 girls, 8 y 11 m to 10 y 10 m) were recruited in the Paris area from two different socio-economic backgrounds (Table 1). Children with co-morbid cognitive, neurological or behavioral disorders, hearing deficit, not corrected visual problem and $IQ < 80$ were excluded from the study. Half of the children were coming from a district classified as an educational priority zone because of multiple social and demographic indicators of a disadvantaged family background such as a high rate of unemployment, a weak proportion of native French speakers and low or very low family income. The other half came from a highly educated area, due to the proximity of a university and of numerous public and private research laboratories. All children, except one, were born in France and all had been following the normal French academic cursus. All the participants, their parents, school directors and teachers were orally informed about the aims of the project in personal or/and collective meetings at schools, and received a printed information booklet about MRI scanning. All parents and every child gave their written informed consent for the behavioral tests and fMRI scanning. The study was approved by the local ethical committee for biomedical research.

In each SES group, half of the children were dyslexics, as previously diagnosed by a dedicated learning disability center (Dr. Billard, CHU Bicêtre) based on extensive behavioral testing with nationally established criteria following INSERM recommendations (2007) (clinical examination, full-scale IQ, standardized tests for working memory, meta-phonology, spelling, rapid automatic naming, words, non-words and passage reading, etc.). At the time of the study, we checked their current reading level with "L'alouette", a standardized reading test classically used to detect dyslexia in French speaking children. It consists in reading as fast and accurately as possible a meaningless text of 265 words within 3 min (Lefavrais, 1967). The resulting score is commonly translated in a reading age and a delay of more than 18 months is an accepted criterion for dyslexia in children between 8 and 12 years. All the dyslexic children included in this study had a persisting and pronounced reading delay in their reading skills (-50 to -22 months corresponding to -2.77 to -0.83 SD, mean delay: -35 months or -1.95 SD) whereas our normal readers were between -13 and $+28$ months corresponding to $+0.16$ to 2.33 SD (mean: $+6$ months, or 0.98 SD). Thus there was no overlap between the two groups (Table 1). We also checked the number of isolated words read in 1 min (LUM), handedness, verbal

Table 1
Characteristics of the four groups. Significant p-values are in bold.

| | Low-SES | | Dysl vs NR | High-SES | | Dysl vs NR | High vs Low SES (pvalue) | Dysl vs NR (pvalue) | Reading SES (pvalue) |
|--|------------------|----------------|------------------|-----------------|-----------------|------------------|--------------------------|---------------------|----------------------|
| | Dyslexics | Normal readers | t-tests (pvalue) | Dyslexics | Normal readers | t-tests (pvalue) | | | |
| Age (months) | 118 (±6) | 115 (±6) | 0.19 | 120 (±6) | 116 (±6) | 0.13 | 0.57 | 0.046 | 0.88 |
| Sex (boys) | 7/12 | 8/11 | | 8/11 | 4/12 | | | | |
| SES Score | −4.0 (±1.5) | −3.6 (±2.3) | | 3.3 (±1.2) | 4.1 (±0.7) | | | | |
| Bilingualism at home (bilinguals) | 10/12 | 7/11 | | 1/11 | 0/12 | | | | |
| Handedness (Edimburgh) | 67.3 | 83.5 | 0.82 | 73.2 | 77.2 | 0.83 | 0.99 | 0.43 | 0.64 |
| PIQ | 87 | 91 | 0.55 | 98 | 108 | 0.26 | 0.014 | 0.64 | 0.2 |
| VIQ | 87 | 104 | 0.032 | 105 | 126 | 0.046 | 0.002 | 0.002 | 0.78 |
| Number of correctly named images (/48) | 30 | 34 | 0.13 | 36 | 40 | 0.021 | 0.001 | 0.006 | 0.84 |
| Reading lag relative to age (months and age normed standard score) | −38.25 (−2.3 SD) | −1 (+0.6 SD) | <.0001 | −30.8 (−1.6 SD) | +11.8 (+1.3 SD) | <.0001 | 0.001 | <.001 | 0.35 |
| Reading Speed: Number of words read in 1 min | 21 | 74 | <.0001 | 32 | 86 | <.0001 | 0.003 | <.001 | 0.88 |
| RAN (time in sec) | 22 | 17 | 0.059 | 20 | 15 | 0.002 | 0.23 | 0.001 | 0.85 |
| Phonological awareness (% of correct responses) | 69.10% | 91.40% | 0.006 | 76.70% | 90.70% | 0.01 | 0.44 | <.001 | 0.35 |
| Forward Digit Span (normalized scores relative to age) | 9 | 12 | 0.016 | 10 | 14 | 0.005 | 0.19 | <.001 | 0.38 |
| Backward Digit Span (normalized scores relative to age) | 9 | 11 | 0.067 | 10 | 11 | 0.4 | 0.33 | 0.063 | 0.62 |
| Sentence span (number of words) | 13 | 16 | 0.039 | 15 | 21 | 0.002 | 0.003 | <.001 | 0.2 |
| Visual cancellation task (number of bells/35 found in 2 min) | 28 | 28 | 0.86 | 28 | 30 | 0.14 | 0.32 | 0.25 | 0.42 |
| Strings comparisons (% of correct responses) | 95% | 95% | 0.9 | 95% | 95% | 0.86 | 0.31 | 0.8 | 0.99 |
| Strings comparisons (time in sec to complete the task) | 97 | 87 | 0.53 | 99 | 81 | 0.09 | 0.88 | 0.13 | 0.64 |

abilities, and other abilities that have been proven to be predictive of reading difficulties (phonological awareness, verbal short-term memory, visual attention, rapid automated naming). Phonological awareness was tested with a French standardized test (EVALEC) consisting of the deletion of the first syllable in 10 trisyllabic words, then of the first phoneme in 12 CVC words, finally in 12 CCV words (Sprengrer-Charolles et al., 2005). Verbal short-term memory was assessed with forward and backward digit span and a sentence span (correct repetition of sentences of increasing length), visual attention with a cancellation task in which the number of 35 bells found on a page in 2 min was measured, and with a task in which children detected the differences in 20 pairs of 3 to 5 letters strings. Vocabulary level was determined with DEN48, consisting in the number (on 48) of pictures correctly named (Jambaqué and Dellatolas, 2000). Rapid automatic naming (RAN) for pictures was measured. Finally, IQ was estimated using the verbal and perceptual subtests of Wechsler's WISC III or IV.

Parents were asked to complete a questionnaire about their education and employment level as well as the presence of a second language spoken at home and reading habits (number of books at home and number of books owned by the child). Children completed another questionnaire concerning their own reading habits, family life and other social and cultural activities. For each child, a composite SES score was determined. This score took into account the school location as a surrogate for neighborhood SES, and the parent's level of education because a previous study undertaken in the city of Paris demonstrates that these two factors were the most predictive environmental variables of the reading score (Fluss et al., 2009). We added also bilingualism at home, which was present in almost all families coming from the educational priority zone (but was unconfounded with dyslexia).

The children were sorted into four groups according to their SES background and reading scores, as shown in Table 1, and each score was submitted to a 2×2 ANOVA with factors of SES and reading group. Dyslexic children were slightly older than normal readers. As can be seen in Table 1, the profile of impairment of the dyslexic children in the low SES group was very similar to that of the high SES dyslexia group as proven by the absence of any significant reading by SES interaction whenever a main effect of the reading group factor

was present. More specifically, besides reading, phonological awareness (EVALEC), verbal short-term memory (forward digit span and sentence span) and lexical access (RAN) were significantly worse in dyslexics than in normal readers, and this was significant within each SES group. In the low SES group, reading lag was significantly correlated with phonological awareness ($p=0.002$), forward digit span ($p=0.02$) and RAN ($p=0.04$). The same correlations were observed in the high SES group (phonological awareness, $p=0.006$; forward digit span, $p=0.001$ and RAN $p=0.005$).

As previously noted in numerous studies (Hackman and Farah, 2009; Noble et al., 2007), low SES children showed a lower verbal performance than their higher SES peers, as reflected here by a weaker verbal IQ, smaller vocabulary and smaller sentence span. However, none of these scores made this main effect of SES interact with the reading group factor ($ps>0.2$). Post-hoc comparisons restricted to normal readers showed that vocabulary and sentences span were significantly lower in low relative to high SES children ($ps<.01$) and that their reading abilities, although in the normal range were less developed than their counterparts with higher SES (-1 vs $+11.8$ months; $F(1, 21) = 5.88$, $p=0.024$). Note that there was no difference in phonological awareness ($F(1,21) <1$). In dyslexics, reading scores were significantly lower in low compared to high SES children (-38.25 vs -30.8 months; $F(1, 21) = 10.211$, $p=0.004$) but no other verbal difference related to SES was significant except for vocabulary ($p=0.047$): low SES dyslexics had a smaller lexical repertoire than their high SES peers.

Many of the low SES children, although born in France and provided with their entire schooling in France (at least 4 years in our groups), were also exposed to another language at home. Our groups were too small to disentangle SES from bilingualism. However, Noble et al. (2007) studying a group of 168 first-graders reported that SES rather than exposure to a second language, was the pertinent variable to explain reading competencies. Three distinct studies, by Frederickson and Frith (1998), Fluss et al. (2009), and Lesaux and Siegel (2003), all note that bilingualism does not have any negative consequences on reading per se: even within migrant bilingual populations, what matters to reading difficulties is phonological competence in the target language. In fact, Frederickson and Frith (1998) note that, beyond two

years of exposure to English, mono and bilingual populations exhibited similar phonological competence. Here too, phonological awareness did not differ between the low-SES, primarily bilingual children, versus the high-SES, primarily monolingual ones ($p = 0.44$).

Stimuli and task

Two functional experiments, one assessing the organisation of the visual ventral pathway, the second assessing the spoken language network, were performed.

1) Visual experiment

Four categories of visual stimuli (houses, faces, words and a revolving checkerboard) were presented in a block paradigm. 30 different black and white pictures of unknown people and places and 30 four-letter regular French words were used. The words were frequent regular words encountered by young readers, as specified in Manulex, a lexical database compiling the frequency of occurrence of words in 54 French scholar reading books (Lété et al., 2004).

10 pairs of different images of the same category (200 ms presentation for the first picture/word, 200 ms inter-stimulus, 500 ms presentation for the second picture/word) were successively presented (inter-pairs interval: 600 ms) followed by a cross fixation image during 10.5 s (total bloc duration 28.5 s). The stimuli were projected onto a translucent screen, 640 pixel wide (VGA mode), subtending 42.5 cm width and viewed through a mirror from a distance of 125 cm, for an overall angular size of 19.3°. For an entire block, images in a pair were either repeated or different, with a size-factor difference for pictures, and an upper-lower case transformation for words (the goal was to study repetition effects, but this manipulation gave no significant results and therefore is not reported further). For the checkerboard category, a round black and white checkerboard picture was smoothly rotated during 18 s followed by a cross fixation image during 10.5 s. In each block, two stars were randomly inserted during the visual stimuli presentation, either on the right or the left side of the screen. The child was instructed to press the left button as soon as detected. This incidental task was planned to keep the child's attention toward the visual stimuli. In a run, two blocks of each category were randomly presented except the checkerboard block that was presented only once. The total run duration was 3' 21" and the children saw 4 runs.

2) Language experiment

40 short sentences in French (native language) and Japanese (a foreign language that none of the children understood) were randomly presented every 12 s in a slow-event design. Each sentence was repeated one time in a row to study repetition effect (Dehaene-Lambertz et al., 2006a). Children were asked to press a right button at the end of the sentence. This incidental task was planned to keep the child's attention toward the auditory stimuli. For comparison purposes, we presented the same set of French sentences previously used in infants (Dehaene-Lambertz et al., 2006b), and thus produced by a native female speaker with a highly intonated voice. The Japanese sentences were produced with the same characteristics. The mean sentence duration was similar in both languages (2707 vs 2724 ms). Each functional run comprised 4 different sentences in each language, repeated one time for a total duration of 3' 12" (16 sentences). Children listened to 4 runs.

Procedure

Before MRI acquisition, the children's reading performance for all the words presented during the fMRI experiment was assessed. Children were instructed to read as fast and accurately as possible the words presented on a computer screen either in upper or in lower case. Words appeared 500 ms after the vocal response. Then

each child was trained in a mock MRI scanner: the real experiment was simulated using recorded MRI noises and shortened versions of the two different types of functional runs, and the child was trained to remain absolutely still.

MR imaging parameters

Magnetic resonance was performed on a Siemens Tim Trio 3.0 Tesla scanner. Stimulus presentation and behavioral responses collection were done with E-prime1. Children were protected with noise-protection ear-phones and a mirror system above the child's head allowed them to see the visual stimuli presented on a screen at the end of the tunnel. T1 images were acquired for anatomical reference. For functional imaging, 84 EPI volumes ($TR = 2.4$ s, $TE = 30$ ms matrix $64 \times 64 \times 40$, voxel size = $3 \times 3 \times 3$ mm) were acquired for each visual run and each 80 volumes for each auditory run. A diffusion tensor magnetic resonance imaging was finally acquired but these data are not presented here. During the structural acquisition, children were looking at cartoons. To reduce head motion, the quality of the MRI images was checked after each acquisition and feed-back was given to the child.

Statistical analyses

Preprocessing and analyses of the data were done using SPM5. Images were first realigned to the first functional image. During the functional visual runs, the children moved in an average of 0.9 mm in translation and 1° in rotation (1.2 mm and 1.8° for the auditory runs). There was no group difference in the auditory experiment. In the visual experiment, the low-SES kids moved significantly more than the high-SES group (mean maximal translation amplitude in the x direction: 0.5 vs 0.6 mm, $F(1,42) = 17$, $p < .001$; z direction: 1.4 vs 3.2 mm, $F(1,42) = 12$, $p = .001$; mean maximal rotation angle: 1.2 vs 1.5 d°, $F(1,42) = 13$, $p < .001$). The most restless group was the normal-readers low-SES group. When the child's movement during a run was superior to 2 mm in translation and/or 1° in rotation, all functional images were visually screened to detect volumes with movement present during the volume acquisition detected as hyper- or hypo-intense slices in the image. Artrepair5, an SPM5 toolbox (Mazaika et al., 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 applied to 7 children for the visual runs (in the low-SES groups: 3 normal readers and 2 dyslexics, in the high-SES groups: one child in each reading group), and to 13 children for the auditory runs (in the low-SES groups: 4 normal readers and 5 dyslexics, in the high-SES groups: two in each reading group).

Images were then coregistered with the individual anatomical image, normalized toward the adult MNI brain space, and spatially smoothed using a 5 mm Gaussian kernel. The data were modeled, within each fMRI run and for each experiment, using the canonical SPM hemodynamic response function and its time derivative convolved with the experimental conditions (5 in the visual experiment: Words, Faces, Houses, Checkerboard and Targets; 4 in the auditory experiment: French first and second presentation of the sentences, Japanese first and second presentation of the sentences). The 6 movement parameters were entered as regressors of non-interest. For testing left-right differences, we computed the spatial transformation appropriate in each child to align his/her flipped anatomical image to the MNI template. We then applied this transformation to each original contrast image, and computed a left-right difference image by subtracting the flipped from the contrast image. These images were submitted to the same ANOVA model as with the original fMRI images, in order to estimate the hemispheric differences for each effect of interest.

A second-level group ANOVA was performed with a between-factor of group (4 levels, defined by the combinations of impaired

versus normal readers, and normal versus low SES), and within-subject factors of experimental conditions, using the individual contrast images smoothed with a 8 mm Gaussian kernel. To better understand the effect of reading on brain activations, we also computed analyses with reading performance entered as a regressor. All reading performances being correlated, we choose the advance or delay of the reading age relative to the chronological age on the “Alouette” test (hereafter called “reading lag regressor”) as representative of the level of reading proficiency attained. In independent fMRI analyses, we also performed regressions with the other behavioral performance measures that predict reading proficiency such as RAN, metaphonological performance, and memory spans.

Unless otherwise specified, significant results are reported when voxels were significant at $p < 0.001$ and formed a contiguous cluster whose extent was significant at $p < 0.05$, corrected for multiple comparisons across the entire brain volume (the cluster-level corrected p value is denoted as $p_{c,cor}$). Occasionally, we report focussed analyses where the search for significant voxels was restricted to a pre-specified region of interested, e.g. the ventral occipito-temporal cortex.

For the visual experiment, we first examined the ventral maps of preferential activations to one category relative to all others. While these contrasts are useful in order to produce figures of categorical preference in ventral visual cortex, for group comparison purposes, they do not properly test each category independently of the others. For instance, in the faces-others contrast, a superior response in normal readers relative to dyslexics might indicate a greater response to faces, or a lower response to one or more of the categories mixed within the ‘other’ group, e.g. words. To perform truly independent tests, we thus first compared normal readers and dyslexics on the contrasts of each visual category relative to the blank screen. Second, since we were specifically interested in testing, independently, whether dyslexia affects fMRI response to words and to faces, we contrasted each of these categories to the two remaining ones (houses and checkerboards).

For the auditory experiment, we compared the two groups on their responses to all stimuli versus silence, native versus foreign language, and first versus second sentence presentation. We again complemented the categorical distinction between poor and good readers by a continuous regressor (reading lag). We characterized the role of the significant clusters by intersecting these analyses first with a mask of the native language network (Native–Foreign language contrast computed across all children and thresholded at voxel $p < .05$) and second, with a mask of the repetition suppression effect in the native language (First–Second presentation of a native sentence computed across all children and thresholded at $p < .05$).

Finally we explored the correlations between the activation to written words in the visual experiment and the speech responses in the auditory experiment. We first probed the relations between written and spoken language networks in young readers by intersecting the contrast Words versus others categories during the visual runs, and the contrast native versus foreign language during the spoken runs. Second, we examined whether a cortical marker of inter-individual variability in reading achievement, the level of activation of the VWFA to written words, was correlated with the fMRI activation evoked by spoken language—and, crucially, whether this correlation with VWFA activation arose from the same brain regions in controls and in dyslexics. To this end, we extracted, for each subject, the activation of the five best voxels responding more to words than to houses and checkerboards within the left fusiform region, and entered this activation as a regressor of interest in the speech experiment. To check for differences between groups, we entered this variable separately for each reading group, and used SPM to test whether the slope of the regression differed in the two groups.

Results

1) Visual experiment

Behavioral results

Before the MRI experiment, we tested reading performance for the words used in the paradigm. The mean reading time was significantly faster (894 vs 2506 ms: $F(1,42) = 22.4$, $p < .001$) and the percentage of errors lower (1 vs 7% $F(1,42) = 32$, $p < .001$) in normal-readers compared to dyslexic children confirming the reading impairment. Reading time was also significantly correlated with the children's reading level as measured with standardized tests (e.g. with the number of words read in one minute: $R^2 = 0.47$, $p < .001$). Reading time was not affected by SES ($F < 1$) but the low SES children tended to make more reading errors (12 vs 7% $F(1,42) = 3.2$, $p = 0.07$). The SES \times reading interaction was not significant, neither for reading time nor for errors.

Within the scanner, no difference between groups nor interaction was observed in the RT to the target star (normal readers: 713 ms; dyslexics: 716 ms) confirming that all subjects were similarly engaged in the task.

fMRI results

Neither the main effect of SES nor the interactions of SES with reading were significant in any analyses of the visual runs. We thus present the results with both SES groups merged.

Group analysis

We first examined the mosaic of ventral visual activations to each category relative to all others. As shown in Fig. 1, the different categories elicited activations localized successively along a medial–lateral axis from checkerboard in the primary visual and surrounding areas, lined externally with houses then faces. In the left hemisphere, only in normal readers, a response to words bordered externally the response to faces (Table 2).

We compared the two groups on the responses to each visual category relative to the blank screen (see Methods). No difference between groups was observed for checkerboards or for houses minus blank. The words minus blank and the faces minus blank comparisons identified respectively a left and a right cluster more activated in controls than in dyslexics in the fusiform regions. These clusters were not significant when corrected for repeated measures across the whole brain, but became significant when the analyses were restricted to a mask comprising the fusiform and inferior temporal gyri based on the AAL atlas (Tzourio-Mazoyer et al., 2002): We observed a difference normal readers $>$ dyslexics both for words minus rest ($[-45 -45 -15]$, $z = 4.3$, 25 vox, $p_{c,cor} = .048$) and for faces minus rest ($[39 -42 -15]$, $z = 3.9$, 57 vox, $p_{c,cor} = .007$).

Whole brain asymmetry analyses revealed only one significant difference between the two groups in the lateralization of the responses to faces (Table 3 and Fig. 2). The response to faces minus blank was significantly more right-lateralized in normal than in impaired readers ($[42 -39 -18]$, $z = 4.22$, 49 vox, $p_{c,cor} = .012$). No difference of lateralization between groups was observed for the other conditions (houses, checkerboards, and even words minus blank).

To examine whether normal readers and dyslexics specifically differed within ventral visual regions specialized for words and for faces, we also examined the responses to words and faces relative to the mean of houses and checkerboard stimuli, with small volume correction over the bilateral fusiform and inferior temporal gyri. For the Word minus [House,Checkerboard] contrast, a significant difference favoring normal readers over dyslexics was observed around the peak of the VWFA ($[-42 -45 -15]$, $z = 4.6$, 46 voxels, small-volume $p_{c,cor} = .038$). For the Face minus [House,Checkerboard] contrast, a

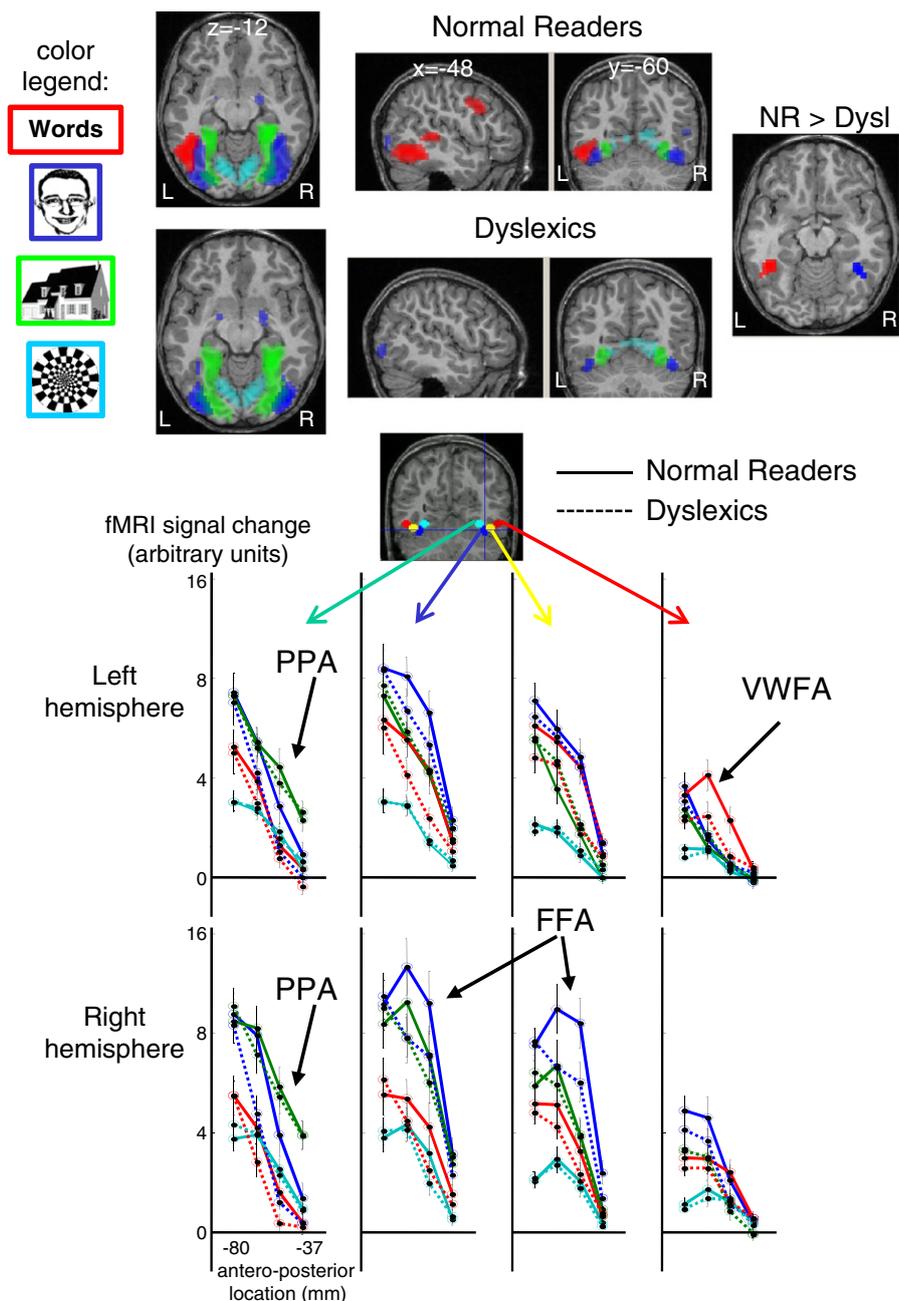


Fig. 1. Mosaic of preference for different visual categories in ventral visual cortex: the three orientation slices on top show the activation differences between a given category and all the others in normal readers (NR) and dyslexics (Dysl) (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparison at the whole-brain level). Graphs below shows the fMRI signal change relative to rest in both groups in successive spheres of 5 mm regularly spaced along an anterior–posterior (x axis, -80 to -37 mm) and a medial–lateral axis (color code on the coronal slice: ± 27 to ± 50 mm). Note the differences between normal (plain lines) and impaired readers (dotted lines) in their response to words (red lines) on the left side, but also to faces (blue lines) on the right side, whereas the responses to houses (green lines) and checkerboard (cyan lines) are similar in the two groups.

significantly greater activation in normal readers relative to dyslexics was observed in a right cluster around the peak of the FFA ($[39-51 - 15]$, $z = 4.1$, 15 voxels, small-volume $p_{c,cor} = .026$). No suprathreshold cluster was detected in the converse direction (dyslexics > normal readers). No significant lateralization differences were observed with these contrasts.

While the above analyses were based on a categorical distinction between normal readers and dyslexics, they were also replicated, with slightly increased significance, when replacing the binary group distinction by a continuous variable of reading lag for each child (where a negative value indicates retardation relative to

normal) (see Fig. 3). In the analyses of words minus blank, reading scores were well predicted by fMRI activation only in the left VWFA ($[-42 - 45 - 18]$, $z = 5.34$, 85 vox, and a similar correlation was found when analyzing the Word minus [House,Checkerboard] contrast ($[-42 - 48 - 15]$, $z = 5.64$, 85 vox, $p_{c,cor} = .022$). For faces minus blank, the regression with reading scores identified a right cluster within the FFA ($[45-57 - 18]$, $z = 4.12$, 88 vox, $p_{c,cor} = .020$), and a second more dorsal and posterior cluster putatively corresponding to the occipital face area (OFA; $[21-81 15]$, $z = 3.98$, 74 vox, $p_{c,cor} = .039$). When using the Face minus [House,Checkerboard] contrast, only the anterior FFA cluster remained ($[39-51 - 12]$, $z = 4.34$,

Table 2
Regions of significant activations for each visual category vs all others in normal readers and dyslexics groups.

| | Area | MNI coordinates | | | SPM t-tests | | | | | |
|------------------|-----------------------|--------------------------------|-----|-----|-----------------------------------|--------------------------|--------------------------|-------|------|------|
| | | x | y | z | Cluster-level P value (corrected) | No. of voxels in cluster | Z value at local maximum | | | |
| Normal readers | Checkerboard > others | Right calcarine sulcus | 9 | -75 | -3 | <.001 | 1807 | Inf | | |
| | | Left calcarine sulcus | -9 | -75 | 0 | | | Inf | | |
| | | Left cuneus | -3 | -84 | 39 | | | 5.27 | | |
| | Houses > others | Right cuneus | 6 | -84 | 39 | <.001 | 883 | 4.23 | | |
| | | Right fusiform gyrus | 30 | -45 | -9 | | | Inf | | |
| | | | 30 | -63 | -6 | | | 5.95 | | |
| | | Right middle occipital gyrus | 33 | -81 | 9 | | | 6.25 | | |
| | | Left fusiform gyrus | -27 | -48 | -9 | | | <.001 | 693 | 7.75 |
| | | Left middle occipital gyrus | -27 | -90 | 9 | | | 5.95 | | |
| | Faces > others | Left inferior occipital gyrus | -24 | -84 | -9 | <.001 | 722 | 5.77 | | |
| | | Right fusiform gyrus | 39 | -51 | -15 | | | Inf | | |
| | | Right Inferior occipital gyrus | 42 | -81 | -9 | | | 6.5 | | |
| | | Left fusiform gyrus | -39 | -60 | -15 | | | <.001 | 457 | 6.42 |
| | Words > others | Left inferior occipital gyrus | -39 | -84 | -3 | <.001 | 384 | 6.31 | | |
| | | Left Inferior temporal gyrus | -51 | -57 | -12 | | | 5.71 | | |
| | | Left fusiform gyrus | -45 | -48 | -15 | | | 5.49 | | |
| | | Left superior temporal sulcus | -54 | -33 | 3 | | | 5.59 | | |
| | | Left Precentral | -45 | 9 | 30 | | | 0.006 | 115 | 4.31 |
| | | | | | | | | | | |
| Impaired readers | Checkerboard > others | Right calcarine sulcus | 9 | -75 | 0 | <.001 | 1856 | Inf | | |
| | | Left calcarine sulcus | -6 | -81 | 0 | | | Inf | | |
| | | Right cuneus | 12 | -87 | 15 | | | 7.39 | | |
| | | Left cuneus | -12 | -90 | 15 | | | 6.89 | | |
| | Houses > others | Right fusiform gyrus | 30 | -48 | -9 | <.001 | 1288 | Inf | | |
| | | | 27 | -81 | -9 | | | 6.76 | | |
| | | Right middle occipital gyrus | 36 | 84 | 12 | | | 6.6 | | |
| | | Left fusiform gyrus | -27 | -48 | -9 | | | <.001 | 1103 | 7.32 |
| | | Left middle occipital gyrus | -30 | -90 | 12 | | | 6.19 | | |
| | | Left inferior occipital gyrus | -24 | -84 | -9 | | | 6.09 | | |
| | Faces > others | Right Inferior occipital gyrus | 42 | -78 | -9 | <.001 | 363 | 7.04 | | |
| | | Right fusiform gyrus | 39 | -48 | -21 | | | 6.12 | | |
| | | Left fusiform gyrus | -39 | -48 | -18 | | | <.001 | 336 | 6.02 |
| | | Left inferior occipital gyrus | -39 | -84 | -12 | | | 5.72 | | |
| | Words > others | No suprathreshold clusters | | | | | | | | |

42 vox, $p_{c_uncor} = .024$, small-volume $p_{c_cor} = .045$). No correlation with reading score was observed in the fMRI activation to houses or checkerboards.

Similar results were observed when the regressor was the number of words read in one minute. No significant area was identified by regression with the other behavioral measures (vocabulary size,

metaphonological awareness, rapid automatic naming, digit and sentence spans).

Individual subject analyses

SPM group analyses leave open the possibility of a selective but spatially more variable response to words and faces in dyslexics

Table 3
Regions of significant asymmetries for each visual category vs blank in normal readers and dyslexics groups.

| | Area | MNI coordinates | | | SPM t-tests | | | |
|---------------------------|------------------------------|--------------------------------|-----|-----|-----------------------------------|--------------------------|--------------------------|-------|
| | | x | y | z | Cluster-level p value (corrected) | No. of voxels in cluster | Z value at local maximum | |
| Normal readers | Houses vs blank | Right middle occipital gyrus | 33 | -78 | 9 | <.001 | 608 | Inf |
| | | Right parahippocampal gyrus | 33 | -33 | -15 | | | 5.28 |
| | | Right fusiform gyrus | 36 | -45 | -18 | | | 5.14 |
| | Faces vs blank | Right fusiform gyrus | 48 | -57 | -15 | <.001 | 453 | 7.35 |
| | | Right fusiform gyrus | 42 | -39 | -21 | | | 5.66 |
| | | Right middle occipital gyrus | 33 | -81 | 9 | | | <.001 |
| | Words vs blank | Right lingual gyrus | 24 | -87 | -9 | 0.005 | 58 | 4.65 |
| | | Right lingual gyrus | 24 | -87 | -9 | | | 4.57 |
| | | Left precentral | -39 | 0 | 33 | | | <.001 |
| Impaired readers | Checkerboard vs blank | Right lingual gyrus | 9 | -72 | 0 | <.001 | 118 | 4.90 |
| | | Right middle occipital gyrus | 36 | -81 | 3 | | | 4.81 |
| | Houses vs blank | Right middle occipital gyrus | 39 | -78 | 9 | <.001 | 336 | 7.31 |
| | | Right fusiform gyrus | 33 | -48 | -9 | | | 0.001 |
| | Faces vs blank | Right inferior occipital gyrus | 33 | -90 | 9 | <.001 | 203 | 6.90 |
| | | Right lingual gyrus | 21 | -87 | -3 | | | 6.22 |
| Words vs blank | Right middle occipital gyrus | 36 | -87 | 9 | <.001 | 86 | 4.89 | |
| Normal > Impaired readers | Checkerboard vs blank | No suprathreshold clusters | | | | | | |
| | Houses vs blank | No suprathreshold clusters | | | | | | |
| | Faces vs blank | Right fusiform Gyrus | 42 | -39 | -18 | 0.012 | 49 | 4.22 |
| | | Right inferior temporal gyrus | 48 | -54 | -15 | | | 4.19 |
| | Words vs blank | No suprathreshold clusters | | | | | | |

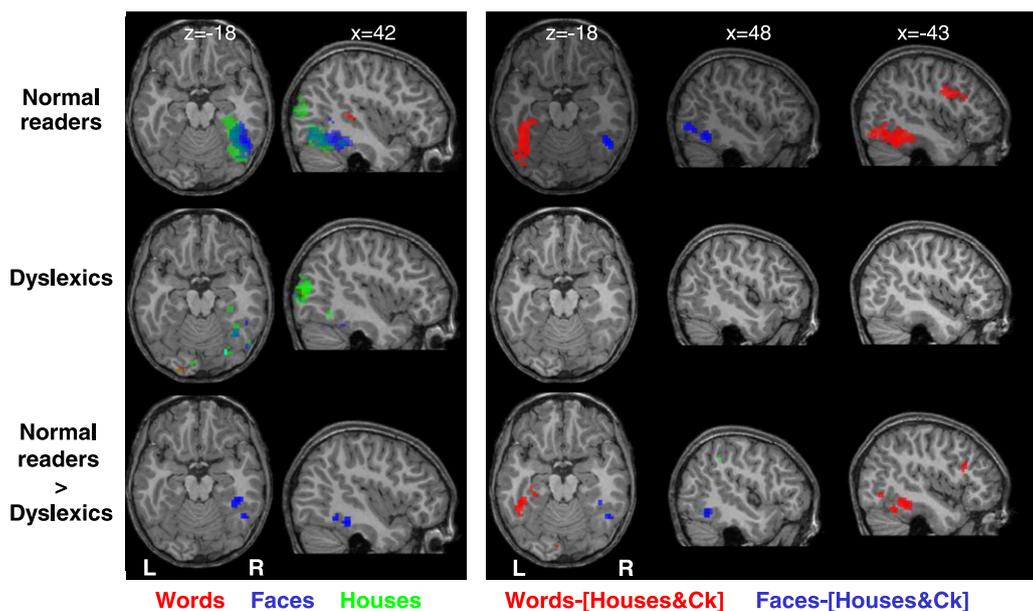


Fig. 2. Hemispheric asymmetry in functional activation patterns. Left, analyses of each category relative to rest (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparison at the whole-brain level). Right, analysis of words and faces relative to the mean of houses and Checkerboards (Ck). In each case, images show regions where activation was larger in the left hemisphere than in the right (left-hemisphere voxels) or vice-versa (right-hemisphere voxels), superimposed over axial and sagittal slices of an individual child. The threshold was lowered to $p < .01$ for images in the bottom right row, as no difference between normal and impaired readers was present at $p < .001$.

than in normal readers, which would explain the weaker activation found in dyslexics at the group level. We thus searched, within each child, for the location of the most responsive voxel to Words versus [Houses,Checkerboards] and, separately, to Faces versus [Houses,Checkerboards], within 10 mm of the left VWFA and right FFA peaks obtained across all children (similar results were obtained with 20 mm). For words, the Euclidean distance between each individual peak and the group mean did not differ significantly between the two groups (7.98 vs 7.96 mm; $F(1,44) < 1$). Thus, the spatial dispersion of the responses was not greater in dyslexics. Furthermore, even after searching for the best voxel in the vicinity of the VWFA, the amplitude of the peak activation to words remained systematically correlated with reading proficiency ($p < .0001$). Similarly, in the vicinity of the right FFA, although the Euclidean distance between each individual peak and the mean peak tended to be more important in the dyslexic group (6.4 vs 7.8 mm), this effect did not quite reach significance ($F(1,44) = 3.54$; $p = .07$), and the amplitude of the peak activation to faces remained positively correlated with reading proficiency ($p = .046$). These analyses suggest that our results could not be imputed to a group difference in inter-individual variability: reading proficiency still affected the amplitude of the response to words in the left fusiform, as well as the amplitude of the face response in the right fusiform, even when the best voxel was selected in each child.

Regions of interest

Finally, we probed whether the antero-posterior and medial-lateral organization of the extrastriate maps was similar in the two groups. To this aim, we averaged activations for the three contrasts House, Face and Words minus Checkerboard within 5 mm spheres regularly spaced along the anterior-posterior axis of the ventral regions (eight y coordinates, ranging from -80 to -37 mm) at each of four medial-lateral x locations (± 27 to ± 50 mm) on each side. These regions corresponded to the pattern of activations for houses, faces and words when all children were considered. We submitted them to separate ANOVAs at each of the 8 y positions, with Group as a between-subjects factor and Hemisphere (left, right), lateral

position (4 levels) and condition (3 levels corresponding to House-Checkerboard, Face-Checkerboard and Words-Checkerboard contrast) as within-subject factors.

If categorical specificity varies along the medial-to-lateral axis, then a significant interaction of Categories \times Lateral position should be found. Such was the case at each of the eight anterior-posterior y coordinates (-80 to -37 mm) and within each hemisphere (all p s $< .001$). To determine if this gradient of categorical preferences differed between normal readers and dyslexics, we then probed the triple interaction of Group \times Categories \times Lateral Position. This triple interaction reached significance only in the left hemisphere at four y coordinates extending from -65.5 to -44.5 mm (respectively $p = .02, .001, < .001, .021$). This effect was primarily due to a reduced response to words in dyslexic children around the x coordinate of the VWFA (see Fig. 1). Nevertheless, even after removing the word condition, a triple interaction was still observed at $y = -37$ mm in the left hemisphere ($F(6,132) = 3.69$, $p = 0.014$). Post-hoc analyses revealed that this effect was due to stronger activation to faces in the innermost sphere at $x = -27$ mm, ($F(1,44) = 5.22$, $p = 0.027$) in normal readers relative to dyslexics. Thus, besides their reduced activation to words, dyslexics had an essentially similar medial-lateral gradient than normal readers, but the face response extended slightly more medially in normal than in impaired readers in the left hemisphere.

2) Spoken language experiment

Behavioral results

As expected, the detection of the end of the sentence was faster for the second presentation of the same sentence (573 vs 739 ms: $F(1,45) = 139$, $p < .001$). This facilitation with repetition tended to be stronger for the foreign than for the native language (-190 vs -143 ms: $F(1,45) = 4$, $p = .051$). There was no difference between normal-readers and dyslexics ($F(1,42) < 1$), but the low SES children tended to be slower (main effect of SES: $F(1,42) = 3.98$, $p = .053$). The latter effect was due to a few very slow subjects. Four children

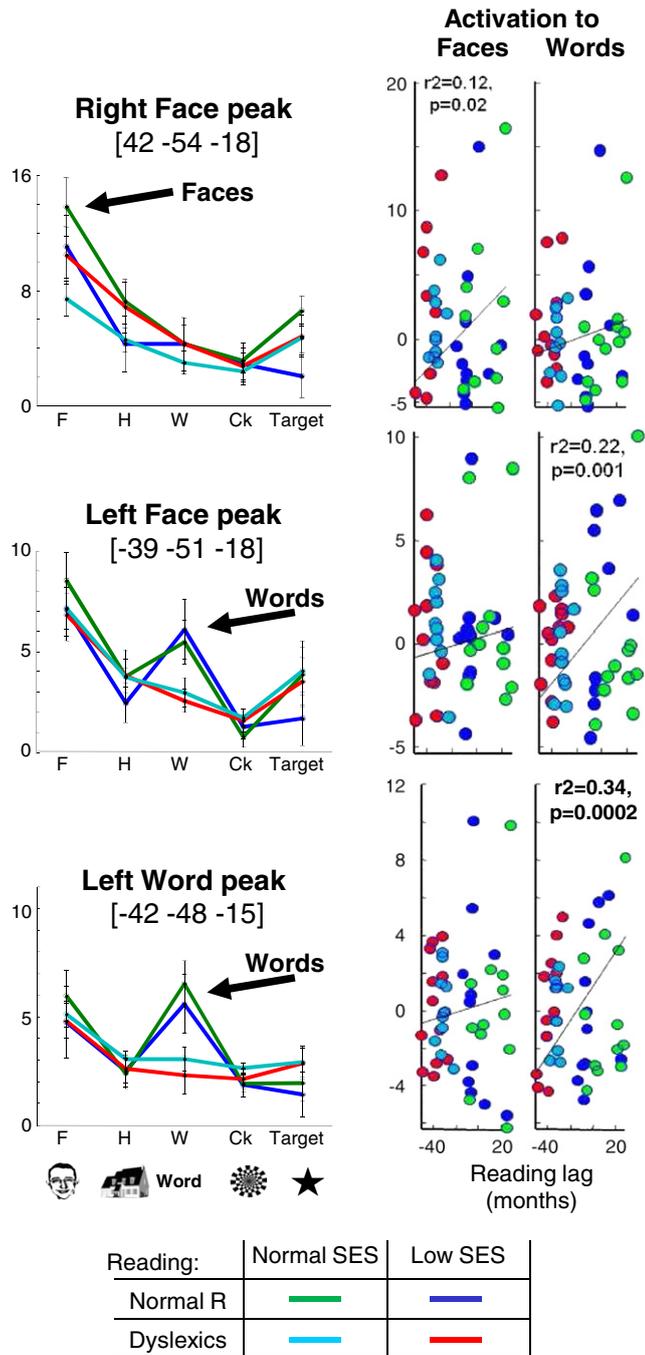


Fig. 3. Correlation between reading performance and responses to words and faces. Left: Mean percentage of signal change in the four groups at the peak of the face and the word responses minus [Houses-Checkerboard]. Note that the coordinates were determined by a contrast orthogonal to reading score (peak computed across all subjects). Right: Scatter plots illustrating the correlation between reading performance and the fMRI response to faces and words at these peaks. In the left hemisphere, the response to words develops laterally to faces and increases with reading performance (bottom rows). In the right hemisphere, the response to faces also increases with reading performance (top row). Arrows indicate the condition which is significantly correlated with reading performance at each location.

(three low-SES normals and one high-SES dyslexic) had a mean reaction time of 1340 ms whereas the mean reaction of the remaining children was 590 ms (± 174 ms). When these four children were removed, neither main effect of reading, SES, nor any interaction between reading, SES, repetition and language were present.

fMRI results

Both the dyslexic and the normal-readers groups presented a bilateral response to speech stimuli, with significantly stronger responses to the native than to the foreign language, as well as to the first rather than the second presentation of the sentence (Table 4). In both groups, the network of native-language regions identified by the native minus foreign language subtraction was significantly asymmetric along the STS and inferior frontal areas.

When the responses to all stimuli vs silence were considered, normal readers showed significant stronger activations than impaired readers in both SMAs ([0 6 66], $z = 6.07$, 263 vox, $p_{c_cor} = .003$) and in the right temporal region ([48 0 51], $z = 5.84$, 1025 vox, $p_{c_cor} < .001$). Two marginally significant clusters were also observed on the left side, in the *planum temporale* ([-39 -39 18], $z = 5.33$, 118 vox, $p_{c_cor} = .059$) and in the insula ([-48 6-6], $z = 5.23$, 123 vox, $p_{c_cor} = .052$). The converse comparison (dyslexic > normal readers) isolated two occipital clusters, due to a lesser deactivation in dyslexic relative to normal readers ([-18 -81 30] $z = 4.58$, 157 vox, $p_{c_cor} = .025$ and [-45 -72 0] $z = 4.24$, 130 vox, $p_{c_cor} = .045$).

The two groups also differed in their activation asymmetries differences: normal readers were significantly more right lateralized than dyslexics in Heschl's gyrus ([54-12 12], $z = 7.57$, 230 vox, $p_{c_cor} < .001$) and in a posterior region going from the superior temporal gyrus till the supramarginal gyrus ([66-36 12], $z = 5.48$, 64 vox, $p_{c_cor} = .037$). These two clusters surrounded the left *planum temporale* cluster observed in the previous analysis, which tended to be more activated on the left than the right in normal readers than in dyslexic ([-42 -39 18], $z = 4.75$, 33 vox, $p_{c_uncor} = .027$). Last but not least, controls showed a greater left-hemispheric lateralization than dyslexics in a left ventral temporal cluster coinciding with the basal language area and extending posteriorly towards the VWFA (controls > dyslexics: [-42 -30 -21], $z = 5.25$, 286 vox, $p_{c_cor} < .001$). Indeed, this cluster of abnormal lateralization to speech in dyslexia overlapped significantly with the cluster of reduced activation to written words in dyslexics reported above (intersection = 21 voxels, peak coordinates at [-39 -51 -12] and [-42 -42 -15]).

Analyses where the binary distinction between normal-readers and dyslexics was replaced by a continuous reading-lag regressor confirmed a relation between reading lag and activations to speech in the same clusters: SMAs, right precentral, right posterior temporal region and three clusters in the left hemisphere: *planum temporale* ([-42 -39 18], $z = 4.96$ and [-45 -51 12], $z = 3.88$, 126 vox, $p_{c_cor} = .048$), insula ([-48 6-6], $z = 5.59$, 239 vox, $p_{c_cor} = .005$) and ventral inferior temporal cortex, corresponding to the basal temporal language area and again extending posteriorly to a point just anterior to the VWFA ([-45 -27 -21], $z = 4.60$ to [-36 -45 -27], $z = 4.23$, 137 vox, $p_{c_cor} = .037$). To clarify the role of these regions in speech processing, we first intersected this image with a mask of the regions significantly more active for the native than for the foreign language ($p < .05$) across all children. Within this mask, clusters significantly more activated in controls were now limited to the inferior temporal cluster just anterior to the VWFA (same coordinates as above, 73 vox, $p_{c_cor} = .026$), the left *planum temporale* ([-42 -42 18], $z = 4.59$, 49 vox, $p_{c_cor} = .053$) and the right posterior STG ([60-33 9], $z = 5.77$, 48 vox, $p_{c_cor} = .054$). Second, when we intersected the initial contrast image with a mask of the regions significantly more active for the first than for the second presentation of the native sentences ($p < .05$) across all children, the only remaining significant region was the cluster located in the inferior temporal cortex (same coordinates as above, 103 vox, $p_{c_cor} = .016$). These effects were nevertheless weak, as no significant difference between groups was observed, in either direction, on the native versus foreign contrast, and on the first versus second presentation contrast computed across the whole brain (Tables 4 and 5).

Contrary to the visual experiment, several areas also showed significant correlations with other behavioral variables for the speech

Table 4
Regions of significant activations in the linguistic network in normal and impaired readers.

| | | Area | MNI coordinates | | | SPM t-tests | | | |
|---|--|------------------------------|----------------------------|--------------------|-----|----------------------------------|--------------------------|--------------------------|------|
| | | | x | y | z | Clusterlevel p value (corrected) | No. of voxels in cluster | Z value at local maximum | |
| Normal readers | Native vs foreign language | Left anterior STS | -57 | -6 | -12 | <.001 | 1477 | Inf | |
| | | Left posterior STS | -48 | -39 | 3 | | | Inf | |
| | | Left temporal pole | -48 | 15 | -21 | | | 7.02 | |
| | | Left IFG | -57 | 30 | 9 | | | 5.84 | |
| | | Right anterior STS | 57 | -6 | -12 | <.001 | | 530 | 6.28 |
| | | Right temporal pole | 51 | 18 | -21 | | | | 5.82 |
| | Foreign vs native language First > repeated | Right posterior STS | 45 | -33 | 0 | | 5.50 | | |
| | | Right inferior parietal lobe | 54 | -57 | 36 | 0.054 | 125 | 4.35 | |
| | | Left anterior STS | -57 | -6 | -9 | <.001 | 604 | 6.63 | |
| | | Left posterior STS | -51 | -42 | 3 | | | 4.31 | |
| | | Right anterior STS | 57 | -3 | -12 | <.001 | 513 | 6.56 | |
| | | Right posterior STS | 48 | -36 | 3 | | | 4.14 | |
| | | Repeated > first | No suprathreshold clusters | | | | | | |
| | | Impaired readers | Native vs foreign language | Left temporal pole | -54 | 6 | -18 | <.001 | 1125 |
| Left posterior STS | -54 | | | -42 | 6 | | 7.51 | | |
| Right temporal pole | 48 | | | 15 | -24 | <.001 | 532 | 6.51 | |
| Foreign vs native First > repeated | No suprathreshold clusters | | | | | | | | |
| | Left anterior superior temporal sulcus | | -51 | -9 | -12 | 0.012 | 198 | 5.25 | |
| Repeated > first | Right anterior middle temporal gyrus | | 57 | 9 | -15 | 0.015 | 188 | 3.34 | |
| | no suprathreshold clusters | | | | | | | | |
| Normal vs impaired readers and impaired vs normal readers/all contrasts: no suprathreshold clusters | | | | | | | | | |

versus silence contrast. Regression with vocabulary level isolated significant clusters in the left *planum temporale* ($[-39 -36 12]$, $z = 5.66$, 143 vox, $p_{c,cor} = .032$) and in the left ventral region adjacent to the VWFA ($[-33 -42 -45]$, $z = 5.09$, 118 vox, $p_{c,cor} = .057$). Both *planum temporale* (Right: $[57-12 9]$, $z = 6.67$, 1475 vox, $p_{c,cor} < .001$; Left: $[-54 -24 9]$, $z = 5.78$, 343 vox, $p_{c,cor} = .001$) and bilateral SMA ($[3 6 63]$, $z = 5.08$, 158 vox, $p_{c,cor} = .024$) were correlated with metaphonological performance. The left *planum* region related to metaphonological performance was anterior and lateral to the cluster correlated with vocabulary level and reading lag. Finally, forward and backward digit span performance was again correlated with *planum* clusters (Right: $[48-18 6]$, $z = 5.18$, 342 vox, $p_{c,cor} = .001$; Left: $[-45 -33 12]$, $z = 5.71$, 192 vox, $p_{c,cor} = .012$) and a right precentral cluster ($[30 0 51]$, $z = 4.57$, 137 vox, $p_{c,cor} = 0.039$). These clusters were embedded in the clusters correlated with metaphonological performance. Similar but smaller clusters than for digit span were

observed for sentence span. Thus the *planum* was the main structure whose activation correlated with several behavioral performance measures, with a partial segregation into subregions differently sensitive to the different competences targeted by these measures.

Finally, we probed the effect of SES on spoken language processing. On the speech minus silence contrast, high-SES children showed stronger activation than low-SES children in the right superior temporal gyrus encompassing *planum temporale* and Heschl's gyrus, bilateral putamen extending on the right side into the right insula, and right middle frontal gyrus (Table 6). None of these clusters were part of the native-language network, as they disappeared when the analysis was restricted to regions showing more activation to native than to foreign sentences. Furthermore, no effect of SES was observed for the native language versus silence contrast. By contrast, the same clusters plus the left SMA were observed for the foreign language versus silence contrast (Table 6). In all these analyses, the SES effect

Table 5
Regions of significant asymmetries in the linguistic network.

| | | Area | MNI coordinates | | | SPM t-tests | | |
|--------------------------------------|---------------------------|--|-------------------------------|-----|------|----------------------------------|--------------------------|--------------------------|
| | | | x | y | z | Clusterlevel p value (corrected) | No. of voxels in cluster | Z value at local maximum |
| Normal readers | Native > foreign language | Left posterior middle temporal gyrus | -48 | -45 | 3 | <.001 | 157 | 5.26 |
| | | Left superior frontal gyrus | -9 | 57 | 27 | 0.046 | 59 | 4.99 |
| | | Left inferior frontal gyrus | -54 | 21 | 18 | | | 4.21 |
| Impaired readers | Native > foreign language | No suprathreshold clusters | | | | | | |
| | | Left inferior frontal gyrus | -51 | 27 | 3 | <.001 | 307 | 5.31 |
| | | Left putamen | -18 | 9 | 9 | | | 4.70 |
| Left posterior middle temporal gyrus | -66 | -30 | 6 | | 3.23 | | | |
| Normal vs impaired readers | First > repeated | No suprathreshold clusters | | | | | | |
| | | Native > foreign language | No suprathreshold clusters | | | | | |
| | | First > repeated | No suprathreshold clusters | | | | | |
| Low SES | Native > foreign | Left middle temporal gyrus | -57 | -45 | 6 | <.001 | 219 | 5.87 |
| | | Left inferior frontal gyrus | -48 | 12 | 9 | <.001 | 255 | 4.65 |
| Normal SES | Native > foreign language | No suprathreshold clusters | | | | | | |
| | | Left posterior middle temporal gyrus | -51 | -42 | 3 | 0.026 | 69 | 4.71 |
| | | Right middle frontal gyrus | 30 | 45 | 24 | 0.029 | 67 | 4.50 |
| | | Right superior frontal sulcus | 21 | 36 | 30 | | | 3.61 |
| | | Left inferior frontal gyrus | -48 | 24 | 3 | <.001 | 162 | 4.48 |
| | | Left anterior superior temporal sulcus | 54 | -3 | -12 | 0.050 | 57 | 4.07 |
| | | Right <i>planum temporale</i> | 45 | -33 | 12 | 0.013 | 81 | 5.11 |
| Normal vs low SES | First > repeated | No suprathreshold clusters | | | | | | |
| | | Native > foreign | Right <i>planum temporale</i> | 42 | -30 | 9 | 0.039 | 62 |

Table 6
Regions of significant differences between low and high SES groups.

| | | Area | x y z | | | SPM t-tests | | |
|----------------|---|-------------------------------|-------------------------------|-----|-------|----------------------------------|--------------------------|--------------------------|
| | | | x | y | z | Clusterlevel p value (corrected) | No. of voxels in cluster | Z value at local maximum |
| High > low SES | Speech vs silence | Right <i>planum temporale</i> | 54 | -27 | 9 | 0.003 | 276 | 6.81 |
| | | Right putamen | 24 | 15 | 3 | <.001 | 496 | 5.12 |
| | | Right insula | 33 | 30 | 3 | | | 4.51 |
| | | Right middle frontal gyrus | 48 | 45 | 6 | | | 3.66 |
| | | Left putamen | -21 | 9 | 6 | 0.010 | 200 | 4.04 |
| | Native language vs silence | No suprathreshold clusters | | | | | | |
| | | Foreign language vs silence | Right <i>planum temporale</i> | 54 | -27 | 9 | 0.041 | 134 |
| | Right putamen | | 24 | 15 | 3 | <.001 | 440 | 5.21 |
| | Right insula | | 30 | 27 | 6 | | | 4.29 |
| | Left putamen | | -24 | 9 | 6 | 0.002 | 301 | 4.63 |
| Left SMA | -6 | | -18 | 60 | 0.041 | 134 | 4.37 | |
| Low > high SES | No suprathreshold clusters for any of the above contrasts | | | | | | | |

remained similar when analyses were restricted to the dyslexic children, but disappeared when restricted to the normal readers group. It was not related to the children's lexical level (which was one of the main behavioral differences between the two SES groups), as the same clusters remained significant when lexical level was entered as a regressor of non-interest in the analyses. As shown in Fig. 4, at the relevant cortical sites, the high-SES dyslexic group showed similar or even stronger activation than the normal readers group whereas the low-SES dyslexic group showed weaker activation for all speech conditions. These results are consistent with a reduced activation in dyslexia that was partially compensated in high-SES children.

3) Relations between spoken and written language networks

Because the same children participated in the visual and auditory experiments, we could examine which regions were common to

spoken and written language at this age. To this aim, we intersected the contrast “words versus others categories” during the visual runs, and the contrast “native versus foreign language” during the spoken runs (Fig. 5). This analysis was performed only in normal readers, because there were no significant voxels for the visual comparison in dyslexics. It isolated three clusters in the left hemisphere (Fig. 5): one in the posterior STS/MTG region ([-48 -42 3]), in the inferior temporal region corresponding to the basal temporal language area ([-42 -33 -21]) and in the left precentral region ([-42 15 24]). Thus, these regions emerge as essential points of connection between written and spoken language in young readers, and which fail to appear in dyslexics.

To clarify the relations between the anomalies observed in visual and spoken language processing, we also examined whether a cortical marker of inter-individual variability in reading achievement, the level of

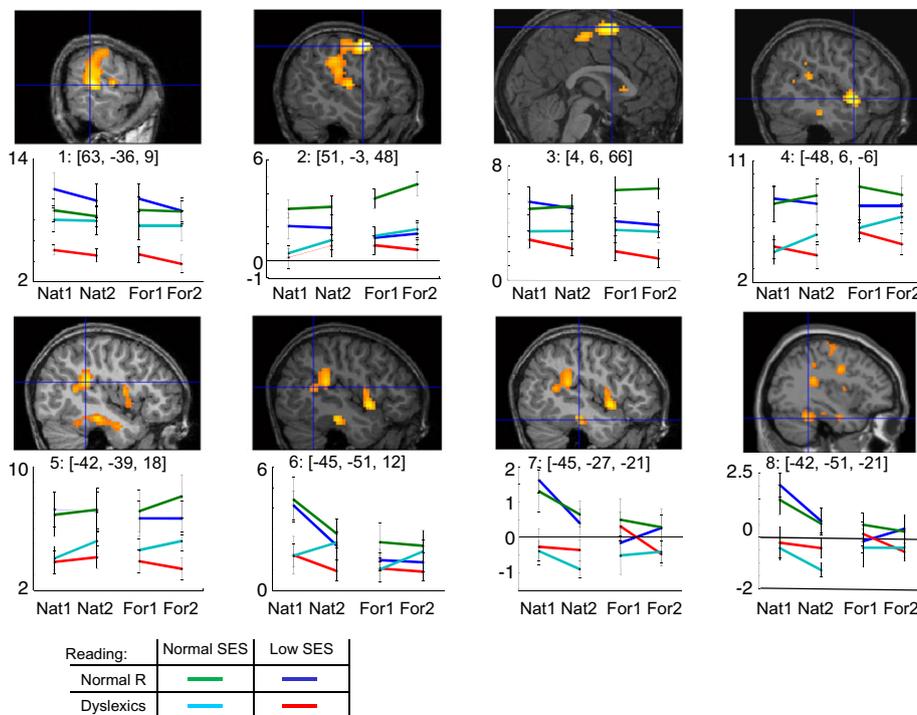


Fig. 4. Brain regions where activations to speech, relative to silence, are correlated with reading lag (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparison at the whole-brain level). The SPM map is projected on a sagittal slice of an individual child. Plots present the fMRI response in each group for the four conditions at the peak of these clusters (Nat1 Nat2 = first and second presentation of native sentences, For1 and For2 = first and second presentation of foreign sentences). At peaks 1–5 activation is similar in all conditions, and the responses are globally increased in normal readers relative to impaired readers. By contrast, at peaks 6–8 (posterior STS, basal language area and VWFA), the response is significantly increased for the first presentation of sentences in the native language, but only in normal readers. Note also at peaks 1 and 3, the effect of SES in the dyslexic groups. The low-SES dyslexic children have weaker activations than the other groups, in particular the high-SES dyslexics.

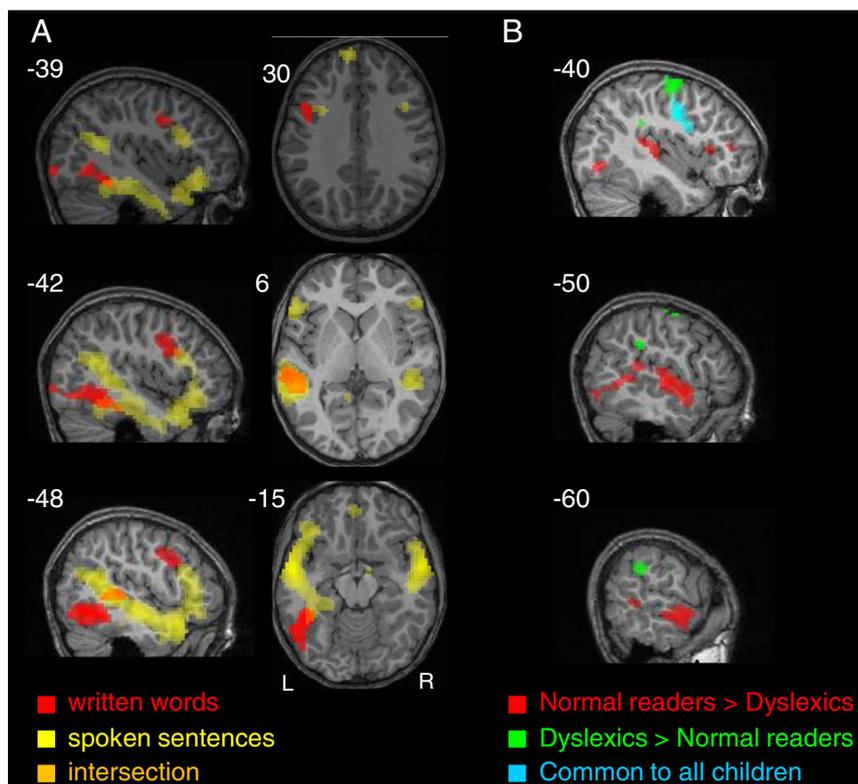


Fig. 5. Relations between written and spoken language networks. A, written and spoken language in normal readers. The figure shows, in red, the contrast “written words > other visual categories” and in yellow, the contrast “first spoken sentence in native language > all other spoken sentences” (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparison at the whole-brain level) in normal readers. The regions common to both contrasts appear in orange. The map is projected on sagittal ($x = -39/-42/-48$) and axial slices ($z = 30/6/-15$ MNI space) of an individual child. B, spoken-language predictors of VWFA activation to written words. The figure shows areas where the speech vs silence contrast was significantly correlated with the VWFA activation to written words (5 best VWFA voxels, individually extracted; voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparison at the whole-brain level). The correlation was performed separately for normal readers and dyslexics, and compared across groups. Results are projected on sagittal slices of an individual child ($x = -40/-50/-60$ MNI space).

activation of the VWFA to written words, was correlated with the fMRI activation evoked by spoken language—and, crucially, whether this correlation with VWFA activation arose from the same brain regions in normals and in dyslexics. To this end, we extracted, for each subject, the activation of the five best voxels responsive to words within the left fusiform region. We first entered this activation as a regressor of interest in the speech experiment across all children to find a common effect between reading groups. This identified a single cluster in the left precuneal cortex ($[-39 -6 36]$, $z = 5.50$, 165 vox, $p_{c_cor} = .021$). This cluster remained when the analysis was restricted to the normal readers ($[-39 -6 36]$, $z = 5.70$, 141 vox, $p_{c_cor} = .007$), but an additional cluster emerged in the left anterior STS ($[-63 -15 -3]$, $z = 6.01$, 220 vox, $p_{c_cor} = .006$). The same analysis in dyslexics isolated again a left precuneal cluster, but at a more dorsal location ($[-42 -6 60]$, $z = 5.27$, 117 vox, $p_{c_cor} = .046$). To test whether these differences were significant, we entered the individual VWFA regressor separately for each group (Fig. 5). Stronger correlations between written word and spoken language responses in normal readers than in dyslexics were observed in a wide set of regions, predominantly in classical left-hemispheric language areas of the left superior temporal gyrus, extending laterally and towards the ventral temporal cortex ($[-54 0 -9]$, $z = 5.91$; $[-45 -36 12]$, $z = 4.62$; $[-51 -72 -9]$, $z = 4.02$, 529 vox, $p_{c_cor} < .001$), but also the right superior temporal region ($[51 -15 3]$, $z = 6.54$; $[54 12 -24]$, $z = 3.90$; 339 vox, $p_{c_cor} = .001$), both vermi ($[-3 -54 -42]$, $z = 4.78$; 300 vox, $p_{c_cor} = .002$) and finally a cluster in the left insula that fell short of significance ($[-30 39 9]$, $z = 4.59$; 117 vox, $p_{c_cor} = .060$). The converse comparison isolated clusters in the left precuneal region ($[-42 -9 57]$, $z = 5.05$; 124 vox, $p_{c_cor} = .051$), and the left supra-marginal gyrus ($[-57 -36 30]$, $z = 4.38$; $p_{FDR_cor} = .017$, 63 vox, p_{c_cor} n.s.).

Discussion

In this experiment, we studied two age-homogeneous groups of dyslexic and normal readers, between 9 and 11 years, during their 4th year of reading training. Both groups were further separated by their low versus high socio-economic status (SES). Our main goal was to examine whether the ventral visual and superior temporal anomalies in fMRI activation, which have been frequently but not systematically observed in dyslexia, could be replicated with minimally demanding tasks that did not directly tax reading or meta-phonological skills. We also questioned to what extent a low-SES modulates the reading deficit.

The results revealed impairments in both visual and spoken-language systems, largely independently of SES. In the visual system, beyond the well-known reduced activation to words, a reduced activation to faces was observed in the right fusiform response in dyslexics relative to normal readers, resulting in a significant increase in the asymmetry of face responses toward the right hemisphere in normal readers relative to dyslexics. In the spoken language domain, dyslexics showed reduced activation, first in speech regions responding similarly to both languages (bilateral posterior temporal cortex, left insula and supplementary motor area), second in regions more involved in native language processing (right STG and left *planum temporale*, left basal language area extending to the VWFA), and third in regions more recruited for the first presentation of a native sentence (left basal language area extending to the VWFA). A lower SES amplified the impairment seen in dyslexic children, notably in the right hemisphere (right superior temporal region, insula, and middle frontal gyrus).

Crucially, these visual and auditory activations were correlated, differently for dyslexic and normal readers. In both groups, the activation to written words in the VWFA was well predicted by the activation to speech in the precentral gyrus, but two other sets of regions emerged as unique to each group. In normal readers, VWFA activation was predicted by the activation of the left superior and lateral temporal regions, the left insula, and both vermis, whereas in dyslexics the predictive regions comprised the left supramarginal gyrus and upper precentral region (at a site compatible with Exner's area). This suggests that reading acquisition in dyslexics might rely on a different network than in normal children. We now discuss each of these results in turn.

Dyslexia and the development of the ventral visual system

Our first goal was to probe the organization of ventral visual cortex in normal and dyslexic children, beyond the categories of strings and letter-like stimuli that were used in most prior studies. In adults, a mosaic of areas preferentially responds to different categories of visual stimuli, with a medial–lateral gradient (Golarai et al., 2007; Hasson et al., 2003; Haxby et al., 2001; Ishai et al., 2000). Medially, a region in the parahippocampal gyrus named the parahippocampal place area (PPA) responds more to buildings and landscapes than to other stimuli. This area is externally bordered by a region in the fusiform gyrus responding more to faces (fusiform face area, FFA) then by an area in the lateral occipital cortex (LOC) responding more to objects than to scramble images.

Our results indicate that this basic gradient is present in 9-year-olds and is unaffected in dyslexia. As typical in adult studies, checkerboards elicited more activation around the calcarine scissure, buildings in the parahippocampal gyri, and faces more laterally in the fusiform gyrus. Furthermore, the dyslexics' responses to checkerboards and to houses were strictly normal. For these categories, in both groups, a small but significant right lateralization was observed (Figs. 1 and 2), similar to that seen in adults using the same non-verbal visual stimuli (Dehaene et al., 2010). These findings suggest that ventral visual cortex is not disorganized as a whole in dyslexia.

With written words, we replicated the strong reduction in fMRI activation in dyslexics within the left ventral occipito-temporal cortex, at the site of the VWFA, as now observed in numerous studies (Brunswick et al., 1999b; Maisog et al., 2008; McCandliss and Noble, 2003; Richlan et al., 2009; van der Mark et al., 2009). Importantly, our findings confirm that this region differs between controls and dyslexics even when reading is implicit and not required by the task (see also Brunswick et al., 1999a, 1999b).

More surprisingly perhaps, we discovered that the response to faces is weaker in the right hemisphere in dyslexics relative to controls either when compared to rest or when compared to houses and checkerboards. Indeed, the rightward asymmetry in response to faces, present in normal readers, is not observed in dyslexics (Fig. 2). Finally, the response to faces in the left hemisphere extends more medially in normal readers than in dyslexics (Fig. 1). It seems unlikely that these results reflect a bilateral disorganization of the fusiform gyrus in dyslexia. Although neuronal migration anomalies were occasionally reported in the ventral visual cortex of dyslexics (Galaburda et al., 1985, 2006), anatomical MR analyses have been inconsistent, with Silani et al. (2005) observing increased gray matter in the left inferior temporal region, while Kronbichler et al. (2008) reported a bilateral fusiform decrease in gray matter and others in different temporal or occipital regions (e.g. Eckert et al., 2005, in the lingual gyrus; Brambati et al., 2004, in the anterior fusiform gyri). Also note that in the present results, the left-hemispheric activation to faces was similar in normal readers and dyslexics at the VWFA site (Fig. 3), confirming that this region is able to sustain a normal level of activation. Similarly, using MEG in dyslexic and control adults, Tarkiainen et al. (2003) reported that, although the dyslexics were slower and more prone to error in facial recognition

tasks, MEG signals did not differ between groups before 250 ms. In particular the specific response to faces at 150 ms was unaffected, suggesting a normal occipito-temporal encoding of faces.

The most plausible hypothesis therefore is that both script- and face-related activation anomalies are an indirect consequence of the functional reorganization of the ventral visual system required by reading acquisition, and which unfolds abnormally in dyslexics. Development fMRI studies have observed a slow maturation of ventral face responses: the peak location of the FFA is reproducible across age, culture, SES, language, expertise and training level, but its size increases with age (Aylward et al., 2005; Golarai et al., 2007; Joseph et al., 2011; Passarotti et al., 2003; Peelen et al., 2009; Scherf et al., 2007, 2011). Similarly, the left fusiform response to written words emerges rapidly around the age of six, the typical age for reading acquisition (Maurer et al., 2005a, 2010; McCandliss et al., 2003). We propose that this emerging VWFA competes with the representation of faces in the left fusiform, thus partially displacing face responses toward the right fusiform gyrus as well as more mesially in the left fusiform gyrus. Indeed, in adults with variable levels of literacy, the right-hemispheric fusiform response to faces increases with reading scores (Dehaene et al., 2010), at a location very similar to the present study. This observation suggests that changes in face responses can be a consequence of literacy (and therefore of dyslexia). Developmental studies also suggest a process of competition for cortical territory between faces and other visual categories (Cantlon et al., 2011; Joseph et al., 2011).

Dehaene et al. (2010) observed that the increase in VWFA response to written words with literacy was associated with a slightly reduced response to faces at the same location, strongly indicative of a cortical competition process. Here, no such reduction was found, as the amplitude of the left-hemispheric faces responses was similar in both groups although the topography was slightly medially shifted in normals. This null result might however reflect that dyslexics, contrary to illiterates, have been trying to learn to read for several years. Although not fully successful, such learning may have partially changed the left fusiform region.

Note that a displacement of the face response because of a competition with words in the left hemisphere is only one of the possible interpretations for the observed increase in right fusiform face responses in dyslexia. Another factor may be the enhanced efficiency at processing foveal stimuli brought about by reading acquisition. Visual response enhancements due to literacy have been observed in occipital and even primary visual cortex (Dehaene et al., 2010; Szwed et al., 2011), and such changes may putatively generalize to other non-reading stimuli that rely heavily on high-resolution foveal processing, the most prominent of which is the category of faces (Hasson et al., 2002). A third possibility worth mentioning is that alphabetic reading requires the discovery of phonetic information embedded in speech, and might therefore enhance attention to facial speech movements. Strikingly, there is a substantial increase of audio–visual integration, measured through the McGurk effect, between 6 and 8 years of age in English children but not in Japanese children (Sekiyama and Burnham, 2008). The authors did not consider reading acquisition as a potential cause of this change, but the greater phonetic demands of alphabetic reading might have enhanced attention to articulation during reading acquisition in English compared to Japanese children. Although audiovisual integration has been mainly related to the superior temporal sulcus (Beauchamp et al., 2004), while FFA is thought to be more involved in speaker identification (von Kriegstein et al., 2005), several experiments using audio–visual speech reported greater activations for speaking relative to still faces in both left and right fusiform areas (Campbell et al., 2001; Dick et al., 2010; Kawase et al., 2005; Stevenson et al., 2010; Nath et al., 2011). By causing an enhanced attention to articulation, literacy might thus benefit to both word and face responses. Future research should try to disentangle these three non-exclusive possibilities.

Dyslexia and the spoken language system

The second half of our fMRI study was dedicated to spoken language processing. Phonological competence is a key predictor of reading acquisition (Lyytinen et al., 2004; Maurer et al., 2009) and relates primarily to the left temporo-parietal region (Dehaene-Lambertz et al., 2005; Jacquemot et al., 2003), a region frequently hypoactivated in dyslexics (Blau et al., 2009, 2010; Paulesu et al., 2001; Richlan et al., 2009; Rumsey et al., 1992; Temple, 2002). However, in their meta-analysis of fMRI dyslexia studies, Richlan et al. (2011) note that this hypo-activation is typical of adult dyslexics, but is less frequent in children (Blau et al., 2010 and more recently Maurer et al., 2011). We therefore re-examined this issue by probing whether deficits would be seen even in a minimal sentence-listening task.

The results indeed revealed anomalies in activation to spoken language at several sites predominantly located in the left temporal lobe (see Fig. 4). In particular, a salient hypoactivation correlated with reading performance was seen in the left *planum temporale*. At this site, normal participants but not dyslexics showed a greater activation to native than to foreign language (see Fig. 4, region #6). This hypo-activation is likely to be a consequence of impaired reading acquisition because activation to speech, at this site, increases with literacy in adults (Dehaene et al., 2010). Indeed, this region, together with the nearby left superior temporal and supramarginal cortices, hosts native-language phonetic representations (Chang et al., 2010; Jacquemot et al., 2003) which are known to be refined by reading acquisition (Morais et al., 1979; Perre et al., 2009). As letter-sound correspondences are learned, this region becomes sensitive to letter-sound congruity (Brem et al., 2010; Perre et al., 2009; van Atteveldt et al., 2004; Yoncheva et al., 2010a), an effect which is reduced or absent in dyslexic subjects (Blau et al., 2009, 2010; Perre et al., 2009). The present research shows that this anomaly is detectable in a mere speech-listening task. Furthermore, activation in the *planum temporale* was correlated with several behavioral scores beyond reading performance: verbal memory, phoneme deletion and vocabulary. Regression with these different scores isolated slightly different subregions of the *planum* as well as distinct distant cortical areas (verbal memory with the precentral region, possibly due to articulatory planning; metaphonology with SMA, possibly related to articulatory motor selection and execution; and vocabulary with VWFA, possibly related to lexical learning). This observation points to the possibility of a fragmentation of different subparts of the *planum* into specialized subterritories, as previously pointed out (Zheng, 2009).

We also observed a reduced activation of the left ventral temporal cortex in dyslexics during spoken language processing, particularly to the first presentation of a sentence in the native language. The posterior part of this cluster overlaps with the anterior part of the VWFA, and thus may relate to the top-down recruitment of an orthographic code only in good readers. Such a top-down activation has been observed by fMRI during selective attention to auditory rhymes in adults (Yoncheva et al., 2010b) and is present in literates but not illiterate adults during a difficult spoken lexical decision task (Dehaene et al., 2010). Desroches et al. (2010) observed it in 9–15 years-old normal readers but not dyslexics during an auditory rhyming task. Here, we further observed that this area of top-down activation extends anteriorly towards the basal temporal language area, a multi-modal region involved in spoken and written language processing (Büchel et al., 1998; Burnstine et al., 1990; Luders et al., 1991; Mani et al., 2008; Papathanassiou et al., 2000). The role of this region remains uncertain, but may concern amodal lexico-semantic processing of single words, as part of the lexical route for reading (Jobard et al., 2003). Since we found its activation during language listening to correlate with reading scores, but also with vocabulary size, we suggest that the vocabulary increase induced by literacy might account for the increased activation to spoken language in this region in normals compared to dyslexics.

The SMA, right posterior temporal region and left insula also showed a decreased response to all speech stimuli in dyslexics. Although we cannot completely exclude that the normal readers were more attentive, this interpretation seems unlikely given that both groups showed the same performance in detecting the end of the sentences, and in particular the same acceleration of response times for the second presentation of the sentences. Dyslexics and controls also did not differ in their amount of motion during fMRI (the more restless participants, and thus possibly the less attentive ones, were the low-SES normal-readers). Thus, rather than inattention in dyslexics, these results are compatible with a broad auditory enhancement in normal readers, leading to an expansion of speech responses to bilateral temporal cortices and to regions involved in articulatory coding (SMA, left anterior insula) (Dronkers, 1996). These effects may tentatively relate to the enhanced phonological awareness in literates (Morais et al., 1979; Perre et al., 2009) and, conversely, to the documented difficulties of dyslexic children in perceiving speech in noise (Ziegler et al., 2009). It appears that, during speech listening in the aversive conditions caused by magnet noise, normal readers are able to recruit additional brain regions involved in articulation.

Predictors of VWFA development

By studying both visual and spoken language responses in children, our study offered a unique opportunity to evaluate the relations between these two systems. In particular, we evaluated whether the inter-individual variability in VWFA activation to written words could be predicted by the activations to spoken language. Crucially, our results suggest that the predictive regions differ for dyslexics compared to normal readers. In normal readers, the spoken-language predictors of VWFA activation during reading were found primarily in the left superior temporal gyrus and sulcus (Fig. 5). This correlation is hardly surprising since these sites activate amodally immediately after the VWFA during word reading (Marinkovic et al., 2003) and contribute decisively to letter-sound integration (Blomert and Froyen, 2010; van Atteveldt et al., 2004) as well as lexical and sentential analysis (Jobard et al., 2003, 2007). It seems logical that children with the most developed spoken-language networks also show the most responsive VWFA during reading. This finding also confirms previous research in adults which indicates that the lateralization of the VWFA is highly correlated with that of temporal lobe spoken-language areas, particularly in the STS (Cai et al., 2008, 2010; Pinel and Dehaene, 2009).

The left precentral cortex, another essential area of convergence between the oral and written language networks, also showed an activation to speech that was correlated with the response to written words in the VWFA, for both normals and dyslexics (at $z = +36$ mm). This precentral activation extends over regions controlling mouth and larynx movements (Price, 2010), and might thus connect visual words with an articulatory representation. In adults, this motor representation is accessed automatically, even for subliminal words (Dehaene et al., 2001; Nakamura et al., 2007), emphasising the fast connection between the VWFA and this region. The observed correlation suggests that, in complement to the cross-modal integration of letters and sounds which occurs in the posterior superior temporal cortex (Blomert and Froyen, 2010; van Atteveldt et al., 2004), the articulatory component of speech may play an important role in reading acquisition.

Beyond this common site in precentral cortex, dyslexics differed from normal readers by exhibiting a reduced correlation of the VWFA activation with lateral and superior temporal regions, and an increased correlation with a dorsal supra-sylvian network comprising the left supramarginal gyrus and a cluster in the upper precentral cortex ($z = +60$ mm). The latter site overlaps with a region involved in hand movement planning (e.g. finger tapping, Meister et al., 2009) and especially writing (Exner's area) (Longcamp et al., 2003; Roux

et al., 2009). A tentative interpretation is that the most successful dyslexics, who eventually develop a VWFA, rely in part on manual gestures to compensate their phonological deficit. Indeed, practice in handwriting has been shown to enhance letter and written word recognition, both in normal adults (Longcamp et al., 2008), in brain-lesioned adults with pure alexia (Seki et al., 1995), and in normal children (Bara et al., 2004; Longcamp et al., 2005). It would be interesting to examine whether a similar improvement can be seen in dyslexic children.

Socio-economic status, dyslexia, and brain activation

Finally, our results revealed a strong reproducibility of the neural correlates of impaired reading in the two SES groups (Figs. 3 and 4). As expected from the literature (Hackman and Farah, 2009), low-SES children showed lower verbal performances and reading level, even in the normal-readers group. Nevertheless, we observed almost no difference related to SES. In particular, we did not replicate Noble et al.'s (2006b) observation of a multiplicative effect of SES and phonological awareness on VWFA activation. When phonological abilities were similar, as was the case here in each reading group, there was no supplementary impairment related to a lower SES in the ventral areas (see Fig. 3). The only observed difference related to SES was observed during the auditory runs and, as discussed above, might relate to a weaker possibility of compensation in the low-SES dyslexics. Relative to their high-SES peers, they were less able to recruit right-hemispheric regions (superior temporal region, insula, and middle frontal gyrus). In particular, the reduced activation in the right frontal region might be a negative predictive factor for reading abilities in these children, as suggested by Hoefl et al. (2011). Further studies in these populations are needed to understand why they are not able to recruit these regions and how adequate rehabilitation can be proposed.

Conclusion

Our results demonstrate that near-passive fMRI, using a minimal detection task, suffices to detect localized activation differences between normal readers and dyslexics. In the visual system, we observed a hypoactivation in the VWFA to written words but also to speech listening. In the auditory system, the *planum temporale* showed a reduced response to spoken sentences in the native language. These differences between normal and impaired readers were common to both SES backgrounds, and are coherent with the numerous studies testing dyslexic adults and children. At the theoretical level, they remain consistent with two alternative interpretations. One possible scenario, in agreement with the phonological hypothesis for the origin of dyslexia, is that before reading, children at risk of dyslexia already present a reduced activation in *planum temporale*, which causes difficulties in reading acquisition and therefore impedes the normal development of an orthographic representation in the VWFA. Another scenario, however, acknowledges that the observed areas of hypo-activation in dyslexic children coincide with the sites of reduced activation in illiterate relative to literate adults (Dehaene et al., 2010). As such, they may solely be a consequence of the abnormal acquisition of literacy, rather than a cause of dyslexia. Further experiments, possibly using a longitudinal design with the same fMRI methods, will be needed to understand the causal relation between reading proficiency and brain organization.

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