Deficient orthographic and phonological representations in children with dyslexia revealed by brain activation patterns

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Background: The current study examined the neuro-cognitive network of visual word rhyming judgment in 14 children with dyslexia and 14 age-matched control children (8- to 14-year-olds) using functional magnetic resonance imaging (fMRI). **Methods:** In order to manipulate the difficulty of mapping orthography to phonology, we used conflicting and non-conflicting trials. The words in conflicting trials either had similar orthography but different phonology (e.g., pint-mint) or similar phonology but different orthography (e.g., jazz-has). The words in non-conflicting trials had similar orthography and phonology (e.g., gate-hate) or different orthography and phonology (e.g., press-list). **Results:** There were no differences in brain activation between the controls and children with dyslexia in the easier non-conflicting trials. However, the children with dyslexia showed less activation than the controls in left inferior frontal gyrus (BA 45/44/47/9), left inferior parietal lobule (BA 40), left inferior temporal gyrus/fusiform gyrus (BA 20/37) and left middle temporal gyrus (BA 21) for the more difficult conflicting trials. For the direct comparison of conflicting minus non-conflicting trials, controls showed greater activation than children with dyslexia in left inferior frontal gyrus (BA 9/45/46) and medial frontal gyrus (BA 8). Children with dyslexia did not show greater activation than controls for any comparison. **Conclusions:** Reduced activation in these regions suggests that children with dyslexia have deficient orthographic representations in ventral temporal cortex as well as deficits in mapping between orthographic and phonological representations in inferior parietal cortex. The greater activation for the controls in inferior frontal gyrus could reflect more effective top-down modulation of posterior representations. **Keywords:** Brain imaging, dyslexia, learning difficulties, magnetic resonance imaging, phonological processing, reading disorder. **Abbreviations:** IPL: inferior parietal lobule; IFG: inferior frontal gyrus; FG: fusiform gyrus; ITG: inferior temporal gyrus; MeF: medial frontal gyrus; BA: Brodmann Area; EPI: echo planar imaging; SPGR: spoiled gradient recalled acquisitions in the steady state; SPM2: statistical parametric mapping; HRF: hemodynamic response function; TE: Time of echo; TR: Time of repetition.

Dyslexia is perhaps the most common neuro-behavioral disorder in children, with prevalence rates ranging from 5 to 17.5% (Shaywitz et al., 1998). Converging behavioral evidence suggests that a central problem in patients with dyslexia is a deficit in phonological processing, especially in identifying and manipulating the sound structure of a word (Brady & Shankweiler, 1991; Bruck, 1992; Stanovich & Siegel, 1994; Shankweiler et al., 1995). Neuroimaging studies show that patients with dyslexia exhibit less intense activation than controls in left temporo-parietal regions, including the posterior part of the superior temporal gyrus and inferior parietal cortex (Rumsey et al., 1997a, 1997b; Shaywitz et al., 1998; Brunswick, McCrory, Price, Frith, & Frith, 1999; Helenius, Uutela, & Hari, 1999; Pugh et al., 2000b; Simos et al., 2000b; Shaywitz et al., 2002, 2003). Under-activation in these regions may reflect deficits that patients with dyslexia have in phonological processing in superior temporal gyrus

and in mapping from orthographic to phonological representations in inferior parietal cortex.

Neuroimaging studies have also found that patients with dyslexia show less activation than controls in left fusiform gyrus (Rumsey et al., 1997b; Shaywitz et al., 1998; Brunswick et al., 1999; Paulesu et al., 2001; Shaywitz et al., 2002, 2003). Research suggests that left fusiform gyrus is important for processing the orthographic structure of well-learned visual word forms (Price, Wise, & Frackowiak, 1996; Tarkiainen, Helenius, Hansen, Cornelissen, & Salmelin, 1999; Cohen et al., 2000; Xu et al., 2001; Cohen et al., 2002). Although there is a debate on whether the left fusiform gyrus is sensitive to lexicality or just familiarity, most agree that this region includes orthographic representations that are linguistically structured (Pugh et al., 2000b). Although reduced activation in left fusiform gyrus for patients with dyslexia may reflect a deficit in orthographic processing, some studies have shown normal activation in this region during letter rhyming judgment (Temple et al., 2001) or non-word reading (Georgiewa et al., 1999, 2002).

In addition to the activation deficits described above, neuroimaging studies of adults with dyslexia show either greater activation (Shaywitz et al., 1998; Brunswick et al., 1999) or no difference (Rumsey et al., 1997b; Paulesu et al., 2001; Shaywitz et al., 2003) from controls in left inferior frontal gyrus. This over-activation in the left inferior frontal gyrus has been interpreted as a compensatory mechanism involving sub-vocal phonological rehearsal by adults with dyslexia. In children with dyslexia, however, only one study found greater activation in the left inferior frontal gyrus (Georgiewa et al., 2002), whereas most studies show either less activation (Georgiewa, 1999; Shaywitz et al., 2002) or no difference (Georgiewa et al., 1999; Temple et al., 2001; Shaywitz et al., 2002). One study showed that there was a positive correlation between activation in left inferior frontal gyrus and age during a nonword rhyming judgment task in children with dyslexia (Shaywitz et al., 2002). Taken together, these studies suggest that adults with dyslexia show over-activation whereas children with dyslexia show under-activation in the left inferior frontal gyrus.

In the current study, we manipulated the difficulty of a visual rhyming task by including word pairs with conflicting (e.g., pint-mint, jazz-has) or non-conflicting (e.g., gate-hate, press-list) orthographic and phonological information in children. Research generally shows that spelling and rhyming judgments are more difficult for conflicting than for non-conflicting pairs (Polich, McCarthy, Wang, & Donchin, 1983; Johnston & McDermott, 1986; Kramer & Donchin, 1987; Rugg & Barrett, 1987; Levinthal & Hornung, 1992) and that patients with dyslexia have greater difficulty with conflicting pairs as compared to non-conflicting pairs (Rack, 1985; McPherson, Ackerman, & Dykman, 1997), but no neuroimaging studies have compared patients with dyslexia to controls on conflicting versus non-conflicting pairs. The goal of this study was to determine if trials that placed greater demands on orthographic and phonological processing would produce larger group differences. We expected the more difficult conflicting trials to generate greater behavioral and activation differences between children with dyslexia and controls as compared to the non-conflicting trials. Consistent with previous reports, we expected children with dyslexia to show less activation in left temporo-parietal cortex, left fusiform gyrus, and left inferior frontal gyrus.

Materials and methods

Participants

Fourteen children with dyslexia (M age = 11.6, range: 8.8–14.10; 12 males, 2 females) and fourteen chronological age-matched children (M age = 11.5, range: 8.9–14.11; 8 males, 6 females) participated in this study. Children with dyslexia met the following inclusionary criteria: (1) full scale IQ (Wechsler, 1999) was above 75, (2) mean on word and nonword reading accuracy and naming speed tests (Torgesen, Wagner, & Rashotte, 1999; Woodcock, McGrew, & Mather, 2001) was below 95. All dyslexics had a diagnosis in the past of learning disability by an appropriate professional. However, some dyslexics had received remediation and this may account for their relatively high scores on some of the standardized tests. The chronological age-matched control children met the following criteria: (1) difference of age with matched children with dyslexia was less than four months (M = 1.8 months, range: 0–4 months), (2) full scale IQ (Wechsler, 1999) was above 75, (3) mean on word and nonword reading accuracy and naming speed tests (Torgesen et al., 1999; Woodcock et al., 2001) was above 95. There were significant differences between children with dyslexia and controls in IQ and reading achievement (see Table 1). Because of the significant difference between groups in full scale IQ, this was used as a covariate of no interest for the fMRI data analysis. Parents of all children were given an informal interview to insure that the children met the following inclusionary criteria: (1) native English speaker, (2) right-handedness, (3) free of neurological disease or psychiatric disorders, and (4) no attention deficit hyperactivity disorder (ADHD). The Institutional Review Board at Northwestern University and Evanston Northwestern Healthcare Research institute approved the informed consent procedures.

Functional activation task

Rhyming task. Two words were visually presented in sequential order and the participant had to determine whether the two words rhymed (Table 2). If the word pair rhymed, the participant pressed a button with the

Table 1 Means (standard deviations, ranges) for the standardized tests for children with dyslexia and controls

	Dyslexia	Control
Verbal IQ (WASI)*	96 (14, 71–127)	109 (11, 79–123)
Performance IQ (WASI)**	96 (10, 79–112)	109 (11, 79–124)
Full Scale IQ (WASI)**	95 (12, 76–115)	110 (12, 85–124)
Word Identification (WJ-III)***	86 (7, 72–102)	112 (9, 96–126)
Word Attack (WJ-III)***	85 (9, 74–101)	104 (7, 93–112)
Single Word Reading Efficiency (TOWRE)***	85 (6, 77–99)	105 (8, 93–118)
Pseudoword Decoding Efficiency (TOWRE)***	78 (10, 59–96)	101 (7, 89–110)
Reading Average***	83 (7, 73–94)	106 (6, 98–112)

***: $p < .001$; **: $p < .01$; *: $p < .05$ in independent-sample t-tests. Reading average: average of four standardized reading tests.

Table 2 Examples of stimuli in four lexical trial types for the visual rhyming task. Stimuli with similar orthography and dissimilar phonology or vice versa were the conflicting trials

	Similar phonology (P+)	Dissimilar phonology (P−)
Similar orthography (O+)	Gate-hate	Pint-mint
Different orthography (O−)	Has-jazz	Press-list

right index finger; if the word pair did not rhyme, the participant pressed another button with the right middle finger. Each word was presented for 800 msec followed by a 200 msec blank interval. A red fixation-cross appeared on the screen after the second word, indicating the need to make a response during the subsequent 2,600 msec interval.

Half of the word pairs rhymed and half did not. Half of the word pairs had similar orthography and the other half did not. The combination of these factors resulted in four trials, namely: similar orthography similar phonology (O+P+), similar orthography different phonology (O+P−), different orthography similar phonology (O−P+) and different orthography different phonology (O−P−) (see Table 2). There were 24 word pairs for each trial type. The four trial types were matched for their written word frequency based on child and adult norms (Educators Word Frequency Guide, 1996). All words and symbols (see below) were presented in lower case, at the center of the screen, with a .5 letter offset of position between the first and second stimulus.

Control trials. Two perceptual control trial types were used in which two symbol strings were presented visually in sequential order and the participant had to determine whether the strings matched. In the 'Simple' trials, the symbol string consisted of a single symbol, while in the 'Complex' trials the symbol string consisted of three different symbols. Timing parameters were the same as for the lexical trials. Twenty-four items were presented in each perceptual trial type, with half of them matching. In addition to the perceptual control trials, 72 fixation trials were included as null events. In the null trials, a black fixation-cross was presented for the same duration as the stimuli in the lexical and perceptual trials and participants were instructed to press a button when the black fixation-cross turned red. We used null trials as the baseline for our fMRI analysis because the difference in behavioral performance between groups was the smallest for these trials.

Experimental procedure

After standardized tests were administered, participants were given a practice session in which they performed one run experimental task in a simulator. Different stimuli were used for the practice session. Scanning took place within a week from the practice session. In the scanning session, the task was administered in two 108 trial runs (8 minute), in which the order of lexical, perceptual and fixation trials and was optimized for event-related design using OptSeq (http://surfer.nmr.mgh.harvard.edu/

optseq) (Burock, Buckner, Woldorff, Rosen, & Dale, 1998). The order of stimuli within task was fixed for all subjects.

MRI data acquisition

Images were acquired using a 1.5 Tesla GE scanner, using a standard head coil. The BOLD functional images were acquired using the EPI (echo planar imaging) method. The following parameters were used for scanning: TE = 35 msec, flip angle = 90°, matrix size = 64 × 64, field of view = 24 cm, slice thickness = 5 mm, number of slices = 24; TR = 2000 msec. Two runs, with 240 repetitions each, were administered for the functional images. In addition, structural T1 weighted 3D images were acquired (SPGR, TR = 21 ms, TE = 8 msec, flip angle = 20°, matrix size = 256 × 256, field of view = 22 cm, slice thickness = 1 mm, number of slices = 124).

Image analysis

Data analysis was performed using SPM2 (Statistical Parametric Mapping) (http://www.fil.ion.ucl.ac.uk/spm). The images were spatially realigned to the first volume to correct for head movements. No individual runs had more than 3 mm maximum displacement in either X, Y or Z translation (M = 1.41, SD = .92 for children with dyslexia; M = .87, SD = .45 for controls). Movement was not significantly different between children with dyslexia and controls ($t = 1.96$, $p = .06$). Sinc interpolation was used to minimize timing-errors between slices. The functional images were co-registered with the anatomical image, and normalized (12 linear affine parameters for brain size and position, 8 non-linear iterations and $2 \times 2 \times 2$ nonlinear basis functions) to the standard T1 template volume (MNI). The data was then smoothed with a 10 mm isotropic Gaussian kernel (Xiong et al., 2000). Statistical analyses at the first level were calculated using an event-related design, separately for each task, with 4 lexical trial types, 2 perceptual trial types, and null trial types as trials of interest. A high pass filter with a cutoff period of 128 seconds was applied. Word pairs were treated as individual events for analysis and modeled using a canonical HRF. We used global normalization to scale the mean of each scan to a common value. Both correct and incorrect trials were used in the statistical analysis.

Parameter estimates from contrasts in single subject models were entered into random-effects analysis using one-sample t-tests across all participants in each group to determine whether activation within a group was significant and using two-sample t-tests across groups (children with dyslexia, controls) to determine whether there were reliable group differences. We also examined the correlation between behavioral performance and activation separately in controls and children with dyslexia by adding accuracy as a covariate of interest. All reported areas of activation were significant using $p < .001$ uncorrected at the voxel level and containing a cluster size greater than 20 voxels for the contrasts within each group and greater than 15 voxels for the contrasts between groups.

Results

Behavioral performance

Table 3 presents accuracy and reaction time for controls and children with dyslexia on the visual rhyming judgment in the scanner. We calculated trial type (conflicting, non-conflicting) by group (controls, children with dyslexia) ANOVAs separately for accuracy and reaction time on correct trials. There were significant main effects for group showing that children with dyslexia were less accurate, $F(1,26) = 94.16$, $p < .001$, and slower, $F(1,26) = 9.437$, $p < .01$, than controls. There were significant main effects for trial type showing that the conflicting trials were less accurate, $F(1,26) = 81.09$, $p < .001$, and slower, $F(1,26) = 18.44$, $p < .001$, than the non-conflicting trials. There was a significant interaction between group and trial type for accuracy, $F(1,26) = 9.35$, $p < .01$, but not for reaction time. Although the difference between controls and children with dyslexia was clearly larger for the conflicting trials, t-tests showed that children with dyslexia were less accurate than controls in non-conflicting trials, $t(26) = 5.00$, $p < .001$, as well as conflicting trials, $t(26) = 9.50$, $p < .001$. Although children with dyslexia were near chance on the conflicting trials, the fact that they had slower reaction times than for the non-conflicting trials suggests that they were not just responding randomly.

Brain activation patterns

Table 4 shows reliable activation for conflicting minus null and non-conflicting minus null contrasts within each group, and Figures 1 and 2 shows the brain activation maps for these comparisons. Table 5 shows greater activation for controls than for children with dyslexia on conflicting trials, and Figure 3 shows the brain activation maps for this comparison. Controls showed greater activation than children with dyslexia in the left (BA 45/47/46/9) and right (BA 9) inferior frontal gyrus, left inferior temporal gyrus extending into the fusiform gyrus (BA 20/37), left inferior parietal lobule (BA 40), and left middle temporal gyrus (BA 21). Controls did not show significantly different activation than children with dyslexia for

Table 3 Means (and standard deviations) for accuracy and reaction time in children with dyslexia and controls in the conflicting and non-conflicting trials

	Conflicting	Non-conflicting
Accuracy (%)		
Controls	79.5 (7.3)	94.5 (5.2)
Dyslexia	44.8 (11.5)	75.2 (13.5)
Reaction time (ms)		
Controls	1240 (351)	1119 (348)
Dyslexia	1593 (272)	1480 (282)

the non-conflicting trials. Table 5 also shows greater activation for controls than for children with dyslexia on the conflicting minus non-conflicting using the inclusive mask of brain activation for the controls on the conflicting minus null, and Figure 4 shows the brain activation maps for this comparison. Controls showed greater activation than children with dyslexia in left inferior and middle frontal gyrus (BA 9/45/46), medial frontal gyrus (BA8) and lingual gyrus. Children with dyslexia did not show greater activation than controls for any contrast. We also correlated behavioral performance with activation for controls and children with dyslexia for the more difficult conflicting trials. None of the correlations overlapped with the effect of greater activation for controls compared to children with dyslexia in the conflicting trials, suggesting that the effect of differential activation between groups may not be due to differences in accuracy on this specific lexical task.

We recalculated group differences for the conflicting minus null, non-conflicting minus null and the conflicting minus non-conflicting contrasts for correct trials only. Table 6 shows that the similar group differences emerged for all contrasts and in all regions, except for inferior parietal lobule, when a more liberal significance threshold was applied ($p < .01$ uncorrected, 10 or greater voxels). Inferior parietal lobule showed a group difference at $p < .05$ uncorrected, 10 or greater voxels.

Discussion

In the conflicting trials, both children with dyslexia and controls activated a network that has been previously implicated in lexical processing, including bilateral inferior frontal gyrus, inferior temporal/fusiform gyrus and medial frontal gyrus. Only controls showed activation in inferior parietal lobule and this activation was significantly greater than that of children with dyslexia for the conflicting trials compared to baseline. Controls also showed significantly greater activation in bilateral inferior frontal gyrus, left middle temporal gyrus and left fusiform gyrus for the conflicting trials compared to baseline and greater activation in left inferior frontal gyrus and medial frontal gyrus for the conflicting trials compared to non-conflicting trials. All significant differences in the magnitude of brain activation between controls and children with dyslexia appeared for the more difficult conflicting word pairs (e.g., pint-mint, has-jazz) and not for the non-conflicting pairs (e.g., gate-hate, press-list). This is consistent with previous research that has shown smaller group differences in activation for easier phonological tasks (Shaywitz et al., 1998). It is also consistent with behavioral results showing larger group differences in conflicting compared to non-conflicting pairs (Rack, 1985; McPherson et al., 1997). Although there was

Table 4 Activations in controls and children with dyslexia in conflicting minus null (Conflict) and non-conflicting minus null (Non) contrasts

Contrast	Region	H	BA	z-test	voxels	x	y	z
Control (Conflict)	**Inferior**/middle frontal gyrus	L	**47**/45/44/46/9/6/8	5.99	1503	−42	24	−3
	Inferior frontal gyrus	R	**47**	5.26	334	36	27	−3
	Middle frontal gyrus	R	**9**	3.87	27	39	6	27
	Medial frontal gyrus/ superior frontal gyrus/ anterior cingulate	L/R	**8**/32	5.68	687	9	18	48
	Inferior parietal lobule	L	40	3.65	38	−36	−33	45
	Fusiform/middle occipital/ inferior temporal gyrus	L	**37**/19/18	5.28	391	−42	−54	−18
	Middle occipital/fusiform/ inferior temporal gyrus	R	**18**/19/37	5.13	421	36	−90	−3
	Cuneus/posterior cingulate	R/L	**18**/19/30	4.26	331	15	−75	12
	Caudate nucleus/thalamus	R/L	–	5.48	290	9	12	6
Dyslexia (Conflict)	Inferior frontal gyrus	L	**45**/44/9	4.16	252	−33	33	6
	Medial frontal gyrus/ superior frontal gyrus/ anterior cingulate	L/R	32	3.59	29	0	18	42
	Fusiform/inferior occipital gyrus	L	**37**/19	3.89	134	−39	−54	−12
Control (Non)	Inferior frontal gyrus	L	**45**/44/46/47	4.37	302	−42	27	12
	Inferior frontal gyrus	L	**9**/6	4.08	124	−45	6	33
	Superior frontal gyrus	L	**6**/8	4.07	48	−3	12	60
	Middle occipital/fusiform/ inferior temporal gyrus	L	**19**/37/18	4.95	349	−36	−81	−3
	Inferior/middle occipital gyrus	R	19	4.84	281	36	−81	−9
Dyslexia (Non)	**Precentral**/inferior frontal gyrus	L	**6**/9	4.16	76	−57	0	36
	Inferior occipital/fusiform gyrus	L	**19**/37	4.92	308	−39	−75	−6
	Inferior occipital/fusiform gyrus	R	**19**/37	4.68	133	42	−75	−6
	Lingual gyrus	R	18	3.63	22	12	−81	0

Note: Peaks of activation are listed in bold for areas spanning different regions; H = hemisphere, L = left, R = right; BA = Brodmann Area.
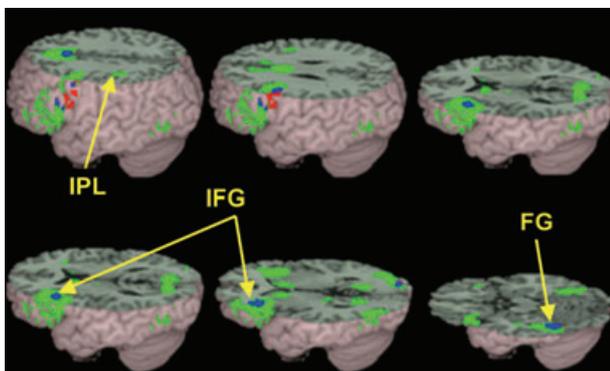

Figure 1 Brain activations for the conflicting versus 'null' trials in controls group (green) and in children with dyslexia (red). The overlap between the groups is represented in blue. Both controls and children with dyslexia showed activation in left inferior frontal gyrus (IFG) and left fusiform gyrus (FG). Only controls showed activation in left inferior parietal lobule (IPL). See Table 3 for a full listing of activations

Figure 2 Brain activations for non-conflicting versus 'null' trials in controls (green) and in children with dyslexia (red). The overlap between the groups is represented in blue. Both controls and children with dyslexia showed activation in left inferior frontal gyrus (IFG) and left fusiform gyrus (FG). See Table 3 for a full listing of activations

no difference between children with dyslexia and controls for the non-conflicting trials in brain activation, there was a difference in behavioral performance. It could be that there were differences in functional or effective connectivity between brain regions that caused differences in behavioral performance (Pugh et al., 2000a).
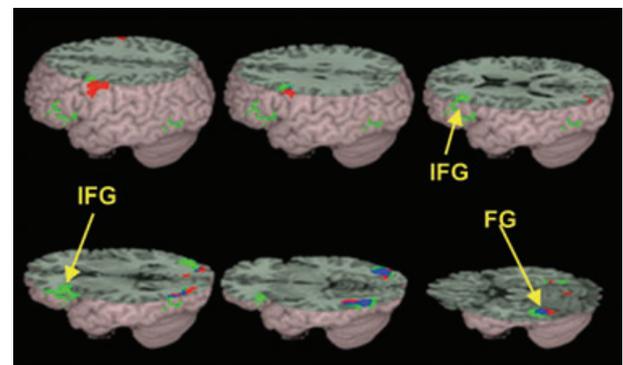
Inferior temporal gyrus/fusiform gyrus

Previous research has implicated the inferior temporal gyrus and fusiform gyrus in orthographic processing. Dehaene et al. (2004) suggested that moving in a posterior-to-anterior progression within the ventral occipito-temporal cortex results in progressively larger units, from visual features in

Table 5 Direct comparisons between controls and children with dyslexia during conflicting minus null, nonconflicting minus null, and conflicting minus non-conflicting

Contrast	Region	H	BA	z-test	voxels	x	Y	z
Conflicting – Null	**Inferior**/middle frontal gyrus	L	**45**/47/46	4.73	203	−57	21	6
	Precentral/inferior frontal gyrus	L	**6**/9	4.14	79	−42	3	36
	Middle/inferior frontal gyrus	R	**10**/9	3.55	19	36	36	18
	Inferior parietal lobule	L	40	3.65	18	−30	−39	33
	Inferior temporal/fusiform gyrus	L	**20**/37	4.18	20	−42	−21	−21
	Middle temporal gyrus	L	21	3.94	27	−60	−54	3
Non-conflicting – Null	–	–	–	–	–	–	–	–
Conflicting – Non-conflicting	**Middle**/inferior frontal gyrus	L	**9**,45,46	3.73	82	42	9	30
	Medial frontal gyrus	L/R	8	3.50	25	−3	21	48
	Lingual gyrus	R	**17**/18	3.85	47	12	−39	−12

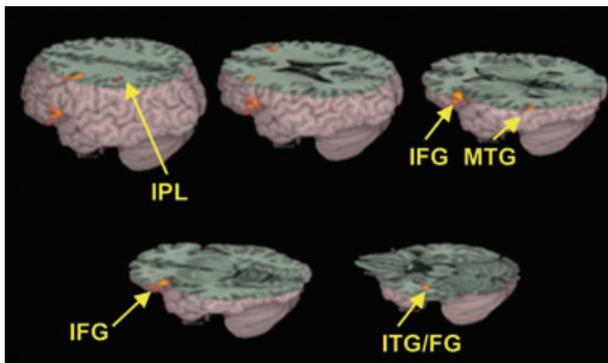*Note*: See Table 4 note.

Figure 3 Significantly greater activations for controls than for children with dyslexia in conflicting versus 'null' trials included the left inferior frontal gyrus (IFG), left inferior parietal lobule (IPL) and left inferior temporal gyrus/fusiform gyrus (ITG/FG). See Table 4 for a full listing of activations
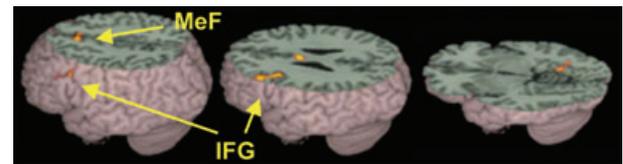

Figure 4 Significantly greater activations for controls than for children with dyslexia in conflicting versus the non-conflicting trials (masked by controls conflicting – 'null' trials) included left inferior frontal gyrus (IFG) and medial frontal gyrus (MeF). See Table 5 for a full listing of activations

extrastriate cortex to graphemes, syllables, and eventually entire words in temporal cortex. Posterior areas have been suggested to contain location specific letter detectors because they show case-invariant, location-specific priming. Middle areas have been suggested to encode partial words because they show significant priming effects for words only when they are repeated at the same location. Anterior regions have been suggested to encode whole words because they show both location-independent and

case-invariant repetition effects. Anterior regions in the banks of the inferior temporal sulcus have also been shown to respond to both visual and auditory word forms. This has been referred to as 'lateral inferotemporal multimodal area' (LIMA) and has been suggested to be involved in supramodal word processing (Cohen, Jobert, Le Bihan, & Dehaene, 2004). Our study found that children with dyslexia produced less activation in an anterior region of the ventral temporal cortex than is probably involved in whole word or supramodal word processing. The lack of differences in posterior regions suggests that children with dyslexia in our study may have intact orthographic processing for letters and partial words, with an orthographic deficit only for whole word representations. However, some research have argued that left fusiform gyrus may be involved in

Table 6 Direct comparisons between controls and children with dyslexia during conflicting minus null, non-conflicting minus null, and conflicting minus non-conflicting for correct trials only

Contrast	Region	H	BA	z-test	voxels	x	Y	z
Conflicting – Null	**Inferior frontal**/middle frontal/ precentral gyrus	L	**47**/45/46/6/9	3.68	388	−48 −42	21 3	−3 36
	Inferior/middle frontal gyrus	R	**10**/9	2.84	33	36	33	15
	*Inferior parietal lobule	L	40	2.36	102	−36	−36	39
	Inferior temporal/fusiform gyrus	L	**20**/37	3.22	48	−42	−24	−21
	Middle temporal gyrus	L	21	4.01	70	−60	−57	3
Non-conflicting – Null	–	–	–	–	–	–	–	–
Conflicting – Non-conflicting	**Inferior**/middle frontal gyrus	L	**9**/45/46	3.06	28	−39	6	27
	Medial frontal gyrus	L/R	8	3.03	38	3	33	48
	Culmen/Lingual Gyrus	R	20	3.36	67	12	−42	−21

Note: See Table 4 note. *: inferior parietal lobule was only activated at $p < .05$ uncorrected.

semantic processing because activation in this region was correlated with performance accuracy on an auditory semantic decision task in young children (5–10 years) (Balsamo, Xu, & Gaillard, in press).

Inferior parietal lobule

Our study revealed that children with dyslexia produced less activation than controls in left inferior parietal lobule. Our findings are consistent with previous studies that have found under-activation in left inferior parietal cortex in children with dyslexia (Simos et al., 2000b; Temple et al., 2001). The inferior parietal lobule has been implicated in mapping between orthographic and phonological representations (Xu et al., 2001; Booth et al., 2002, 2003), and is sensitive to conflict between orthographic and phonological information (Bitan et al., in press). Control children produced greater activation in this region during rhyming judgments for conflicting pairs (e.g., pint-mint, has-jazz) than for non-conflicting pairs (e.g., gate-hate, press-list) (Bitan et al., in press). Group differences between children with dyslexia and controls may only emerge when the demands on mapping orthographic to phonological representations are enhanced (Shaywitz et al., 1998; Pugh et al., 2000b) as in the case of conflicting pairs.

Inferior frontal gyrus

Activation in the dorsal left inferior frontal gyrus (BA 44) has been found in tasks that involve effortful selection, retrieval or manipulation of phonological representations such as reading of pseudo-words (Fiez, Balota, Raichle, & Petersen, 1999; Fiebach, Friederici, Müller, & von Cramon, 2002). The inferior frontal gyrus may act as an executive system that controls the access, retrieval, selection and gating of information by the modulation or reactivation of representations in posterior brain regions (Wagner, Desmond, Demb, Glover, & Gabrieli, 1997; Poldrack et al., 1999). Studies of children with dyslexia have found either under-activation or normal activation in left inferior frontal gyrus (Georgiewa et al., 1999; Temple et al., 2001; Shaywitz et al., 2002). Under-activation in children seems to be most pronounced in tasks that involve difficult phonological processing (Shaywitz et al., 2002). Our finding of less activation in inferior frontal gyrus for children with dyslexia during the difficult conflicting pairs is consistent with this previous literature. The location of the difference between the controls and children with dyslexia in our study is close to a region that was sensitive to the conflict effect in a large group of control children (Bitan et al., in press), consistent with a deficit specific to difficult phonological processing. Effective connectivity analysis of the rhyming task has shown that the inferior frontal gyrus is involved in the top-down modulation of posterior regions involved in task-specific integration (Bitan

et al., 2005). Children with dyslexia may not effectively recruit the inferior frontal gyrus for this top-down modulation of phonological representations in posterior temporal cortex. The reduced activation could therefore be a neural correlate of the well-established behavioral deficits in phonological processing in patients with dyslexia (Brady & Shankweiler, 1991; Bruck, 1992; Stanovich & Siegel, 1994; Shankweiler et al., 1995).

Middle temporal gyrus

Children with dyslexia in our study produced less activation than controls in the posterior region of the middle temporal gyrus. This finding is consistent with previous neuroimaging studies of patients with dyslexia (Rumsey et al., 1997b; Simos et al., 2000a; Paulesu et al., 2001; Shaywitz et al., 2002). Left middle temporal gyrus activation has been shown during a variety of semantic tasks (Pugh et al., 1996; Price, Moore, Humphreys, & Wise, 1997; Friederici, Opitz, & von Cramon, 2000). In addition, increases in accuracy have been associated with greater activation in middle temporal gyrus during association judgments (Blumenfeld, Booth, & Burman, 2006) and improvement in accuracy during semantic training has similarly resulted in greater activation in middle temporal gyrus (Sandak et al., 2004). The conflicting word pairs in our experiment were difficult to process, so perhaps the control children relied more on semantics for accessing the phonological representation in order to perform the rhyming judgment. Behavioral studies have shown increasing involvement of semantics for linguistic tasks when word reading becomes more difficult as when processing low frequency words (Becker, 1979; Stanovich & West, 1981; Borowski & Besner, 1993). Children with dyslexia may not have been able to effectively use their semantic representations as a compensatory mechanism because of their lower verbal abilities.

Conclusion

This study demonstrates that children with dyslexia have a deficit in a left hemisphere network involved in reading, including inferior frontal gyrus, inferior parietal lobule, and middle and ventral temporal cortex. The reduction of activation in the temporal regions could reflect deficits in orthographic representations and less reliance on semantic representations when processing the difficult conflicting pairs. The reduction in the parietal and frontal regions could reflect deficits in mapping between orthographic and phonological representations and in top-down modulation of these representations. Significant group differences were noted only for the more difficult conflicting trials, suggesting that task difficulty may be an

important consideration for experimental designs intending to identify abnormal activation patterns in dysfunctional groups.

Acknowledgements

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