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Executive working memory processes in dyslexia: Behavioral and fMRI evidence

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Dyslexia is an impairment in learning to read and write, primarily associated with a phonological core deficit. However, the manifestation of symptoms in dyslexia also includes impaired working memory (WM). The aim of this study was to investigate cortical activation related to verbal WM in dyslexic and normal readers aged around 13 years, controlling for phonological awareness processing. We used a modified WM n-back task where the participants remembered the first or last speech segment (phonemes) of the names of common objects shown as pictures. Dyslexic readers were impaired compared with the control group. Compared with the dyslexic readers, controls showed increased fMRI activation in the left superior parietal lobule and the right inferior prefrontal gyrus. Unlike controls, dyslexics did not show a significant increase in activation in WM areas with increased memory load. These findings provide support for a specific working memory deficit in dyslexic individuals.

Key words: Working memory, dyslexia, phoneme detection, n-back.

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INTRODUCTION

Although a phonological processing deficit is well established as one of the main causes of dyslexia (Høien & Lundberg, 2000; Snowling, 2000; Stanovich & Siegel, 1994), it is still unclear which factors underlie this problem and whether other deficits also impair reading acquisition. There are at least two major alternative explanations of dyslexia. One explanation focuses on a basic deficiency in rapid temporal perception of auditory and visual information (Hugdahl, Heiervang, Ersland, Lundervold & Smievoll, 2003; Stein & Walsh, 1997; Tallal, Miller & Fitch, 1993). The other suggests a basic deficiency in the automatization of skills (Nicolson, Fawcett & Dean, 1995). However, learning to read is a complex process that could be constrained by a number of cognitive factors, ranging from low-level sensory to high-level cognitive processes, such as working memory. Working memory (WM) refers to a limited-capacity memory system that is involved in the temporary storage and processing of information, maintaining, integrating and manipulating verbal and visuo-spatial information on-line. It is conceptualized as a multi-component system comprising two modality-specific slave systems: the phonological loop and the visual-spatial sketch-pad, and the modality-free central executive (Baddeley, 1990). Whereas short-term memory refers to the structure of a hypothetical memory store, WM is a broader, functional term in that it refers to processing; that is, to how memorial resources are used within a particular task (Hulme & Roodenrys, 1995). A traditional verbal short-term memory span task taps the capacity of the phonological loop. The phonological loop maintains information in a temporary phonological store through speech rehearsal. Its function is primarily associated with increased activity in the left inferior parietal lobe, posterior inferior frontal gyrus, premotor cortex and the cerebellum (Awh, Jonides, Smith, Schumacher, Koeppe & Katz, 1996; Paulesu, Frith & Frackowiak, 1993). In contrast to the passive storage requirement of simple span tasks, WM span involves the simultaneous processing of information, and thus draws on the central executive as well as the slave systems. The central executive is assumed to handle manipulation, continuous updating, temporal order, inhibition and attention shifting, and is primarily associated with increased bilateral activity in the frontal and parietal cortices, including the dorsolateral prefrontal cortex, the bilateral premotor cortex and the lateral and medial superior parietal cortex (Wager & Smith, 2003). WM deficits could undermine reading ability and reading acquisition in several ways. Reading comprehension depends on WM where sentences that are read may need to be 'held' for sufficient time for meaning to be extracted, possibly involving multiple parses of a sentence (Gathercole & Baddeley, 1993). However, it is also probable that WM processes contribute to reading acquisition. For instance, the development of phonological awareness depends not only on the ability to consciously detect but also manipulate speech sounds in WM. Furthermore, a phonological reading strategy will depend on the phonological loop to store individual phonemes of a word in order to allow blending, whereas the central executive simultaneously activates grapheme-phoneme conversion rules in long-term memory and effectively switches between phonological and orthographic processing strategies (Palmer, 2000b). Poor verbal short-term memory span in dyslexia is reported extensively in the literature

(Helland & Asbjornsen, 2004; Jorm, 1983; Mann, Liberman & Shankweiler, 1980; Palmer, 2000a, 2000b; Shankweiler, 1979; Siegel & Linder, 1984; Smith Spark, Fisk, Fawcett & Nicolson, 2003; Snowling, Nation, Moxham, Gallagher & Frith, 1997). It is still unclear whether this impairment is caused by phonological loop problems or a more basic deficit in phonological processing, and it has proved difficult to experimentally divorce phonological memory from other phonological processes (Snowling, Chiat & Hulme, 1991). This has led to some controversy over the relative contribution of phonological and memory processes in dyslexia (Gathercole, Willis & Baddeley 1991; Snowling *et al.*, 1991). However, there is also converging *behavioral* evidence for a central executive deficit in dyslexia (Asbjornsen & Bryden, 1998; de Jong, 1998; Gathercole, Pickering, Hall & Peaker, 2001; Helland & Asbjornsen, 2000; Palmer, 2000a; Reiter, Tucha & Lange, 2005; Smith Spark *et al.*, 2003), indicating that poor performance on WM tasks might not emerge from a phonological deficit alone. Thus, a major question is whether the WM impairment is secondary to phonological core deficit affecting the phonological loop only, or caused by an additional deficit involving the central executive.

Furthermore, an unsolved issue in current research is the effects of dyslexia on the neuronal correlates of working memory processes. Functional neuroimaging methods such as fMRI could reveal brain areas involved in executive versus phonological processes. Based on previous studies, an executive deficit might be predicted to reveal itself as impaired activation in dorsolateral prefrontal and parietal cortex, whereas a phonological deficit might be revealed in relation to differences in activation within inferior frontal and superior temporal brain areas. The aim of the present study was therefore to explore the effects of dyslexia on neuronal activation in brain areas involved in working memory and phonological processing in dyslexia, using a combined phoneme detection and working memory n-back task (Awh *et al*., 1996; Braver, Cohen, Nystrom, Jonides, Smith & Noll, 1997; Nystrom, Braver, Sabb, Delgado, Noll & Cohen, 2000), in a group of children with dyslexia and an age-matched control group. The n-back task requires on-line monitoring, continuous updating, and temporal order of remembered information and is therefore assumed to place greater demands on executive processes compared to memory span tasks (Braver *et al*., 1997). Various n-back tasks have been shown to broadly activate the same frontal and parietal cortical regions. However, differential activation at subregional level or in terms of hemispheric lateralization has been found. For example, verbal tasks have been associated with enhanced activation in the left ventrolateral prefrontal cortex, whereas non-verbal spatial tasks have been associated with enhanced activation in the right dorsolateral prefrontal, lateral premotor and posterior parietal cortex (Owen, McMillan, Laird & Bullmore, 2005). We used a phoneme detection task with two difficulty levels where the participants were required to identify and remember the first or last phoneme when naming common objects. Data from phonological segmentation tasks, such as comparison of a sound or sounds either in the beginning or end of words, constitute much of the empirical evidence underlying the phonological deficit hypothesis (Katzir, Misra & Poldrack, 2005). Using visual presentations of common objects as stimuli rather than auditory or written text stimuli, makes it possible to investigate both working memory and phonological processing without the confounding effects of co-existing auditory problems and differences in reading experience. Norwegian is a regular language in terms of spelling sound correspondences, and letter sounds are unambiguous. Whether the respondent chose to identify the segment to be remembered in the WM task on the basis of the spoken form or the written form of the word should not make a difference.

METHOD

Participants

The participants were 11 dyslexic and 13 control children from a south-west Norwegian municipality. Initially, 14 dyslexic and 14 control children from a previous dyslexia study volunteered for the study. The dyslexic participants were originally recruited from the poorest 5% of readers in their classes as judged by their teachers (Iversen, Berg, Ellertsen & Tonnessen, 2005). All children were rescreened with a battery of tests measuring general intelligence (IQ), reading processes and listening comprehension. Estimated full IQ was obtained with a short-form of the standardized Norwegian version of the Wechsler Intelligence Scales for Children (WISC-III). The Similarities, Vocabulary, Block design, and Picture arrangement subscales were administered. The sum of Scaled Scores were converted to a full IQ estimate using the procedure described by Kaufman, Kaufman, Balgopal and McLean (1996). Four subtests from a standardized Norwegian computerized test for reading processes (LOGOS, http://www.logos-test.no/) were administered, including a pseudoword reading test (phonological processing strategy), a reading test with rapid word presentations (orthographic processing strategy), a phoneme deletion test (phonological awareness) and a listening comprehension test. Accuracy and reaction times were recorded. In addition, a percentile score based on the accuracy/reaction time ratio was calculated for each subtest.

A child was included in the dyslexic group if the performance on either pseudoword reading test or the phoneme deletion test was below the 16th percentile, and estimated IQ quotient was within 1.5 standard deviation (*SD*) of the population mean ($M = 100$, $SD = 15$). The participants were also screened with a dichotic listening (DL) task to control for language laterality (Hugdahl, Carlsson & Eichele, 2001). DL involves presenting two different consonant-vowel (CV) syllables simultaneously in the left and right ear, asking the participant to indicate which sound she/he heard (best or most clearly). The most common result with verbal stimuli is a preponderance of reports from the right ear – or a "right ear advantage" (REA). REA is a strong indicator of left-sided language

Table 1. *Demographic data and performance of dyslexics and controls on intelligence, laterality and reading tasks*

	Group			
	Controls ($n = 13$)		Dyslexics ($n = 11$)	
	Mean	*SD*	Mean	*SD*
Age (years)	13.5	0.5	13.2	0.4
Sex				
Male	6		6	
Female	7		5	
Estimated full IQ	97	9	89	9.5
Dichotic listening test (Lat.index)	24	18	19	17
Logos-test				
Phonological reading*	54 percentile	18	11 percentile	11
Orthographic reading*	49 percentile	15	18 percentile	20
Phoneme deletion*	52 percentile	17	19 percentile	20
Listening comprehension	71 percentile	19	55 percentile	25

* Significant group differences $p = 0.01$.

lateralization (Hugdahl, 2003). One participant in the control group was excluded due to a clear left ear advantage (Laterality index < –15). Two dyslexic participants and one control participant were lefthanders. However, they all had a strong REA (Laterality index > 30) and were not excluded from the study. Demographic data and performance on intelligence, laterality and reading tasks for both groups are reported in Table 1.

All participants were native Norwegian speakers, and written informed consent was obtained from both participants and parents. All participants and their parents were asked about additional learning difficulties when they signed up for the study. One participant was excluded from the study due to additional attention problems (AD/HD). In addition, the participants with dyslexia have been assessed by school psychologists, no additional learning difficulties were reported in the participants' clinical records. In advance of the fMRI scanning the participants were instructed about the procedure and trained on the tasks to above chance performance. They were explicitly instructed to subvocally name the objects. Furthermore, in the training sessions in school all objects with corresponding name were presented, and repeated prior to fMRI scanning. This ensured familiarity with the requirements of the task prior to scanning. The participants and their parents were also interviewed by an experienced neuroradiologist about health status, including routine questions associated with MR safety screening, before the scanning, and they also signed an informed consent letter about health status disclosure. The study was approved by the Regional Ethics Committee for Medical Research (REK-Vest). Before being placed in the MR scanner the participants were given an additional short practice run of all four conditions. The instructions were repeated before each session in the scanner.

Stimuli and experimental procedure

Two modified versions of a 2-back working memory task and a 0-back control task were administered. In each trial, a picture of a common object was presented. In the "first-phoneme" version of the task, participants were required to identify the first letter-sound in the name of the presented object, whereas in the "last-phoneme" version of the task participants identified the last letter-sound. The stimuli were 33 line drawings of common objects taken from Snodgrass and Vanderwart norms (Snodgrass & Vanderwart, 1980). One-third of the objects' name were monosyllabic Norwegian words (e.g. hår) and two-thirds were bisyllabic words (e.g. plaster). Each object was repeated 2–8 times, and balanced across tasks and/or conditions.

In the first-phoneme 0-back condition, the participants responded to object names starting with the letter-sound "k" (the first letter with highest frequency in the stimuli sample). In the last-phoneme 0-back condition, participants responded to object names ending with the letter-sound "r" (the last letter with highest frequency in the stimuli sample). In the first-phoneme 2-back condition, the participants responded if the object's name started with the same letter-sound as the one presented two trials back. In the last-phoneme 2-back condition, the participants responded if the object's name ended with the same letter-sound as the one presented two trials back. There were 48 pictures presented in each condition, and the number of response targets was 16. Tasks and conditions are illustrated in Fig. 1.

The presentation of the stimuli was controlled by E-prime software (Psychology Software Tools Inc.), and stimuli were presented through MR compatible LCD "goggles" (Magnetic Resonance Technology Inc.) connected to a PC outside the MR chamber. Responses were recorded by pressing the key with the right-hand thumb on a response box located on the chest of the participant, and were only required to positive targets. The stimuli were presented in an alternating fMRI blood-oxygenation-level dependent (BOLD) ON/OFF-block (box-car) design with four separate runs. In each run there were four ON-blocks and four OFF-blocks. The duration of a block was set to 30 seconds. There were different instructions for each run, so that each run represented a different experimental condition. The OFF-blocks were without any stimulus presentations or tasks. There were 12 stimuli presented in an ON-block, with 1000 ms duration and 1500 ms blank in between stimulus presentations. The two phonological awareness difficulty levels were randomized and balanced across participants and groups and the n-back levels were presented counterbalanced as either 0-back, 2-back, or as 2-back, 0-back.

MRI scanning

Functional MRI was performed with a 1.5 T Siemens Vision Plus scanner equipped with 25 mT/m gradients. Initial scanning of anatomy was done with a T1-weighted MPRAGE pulse sequence with flip angle (FA) 10°, repetition time (TR) 9.7 ms, echo time (TE) 4 ms, field of

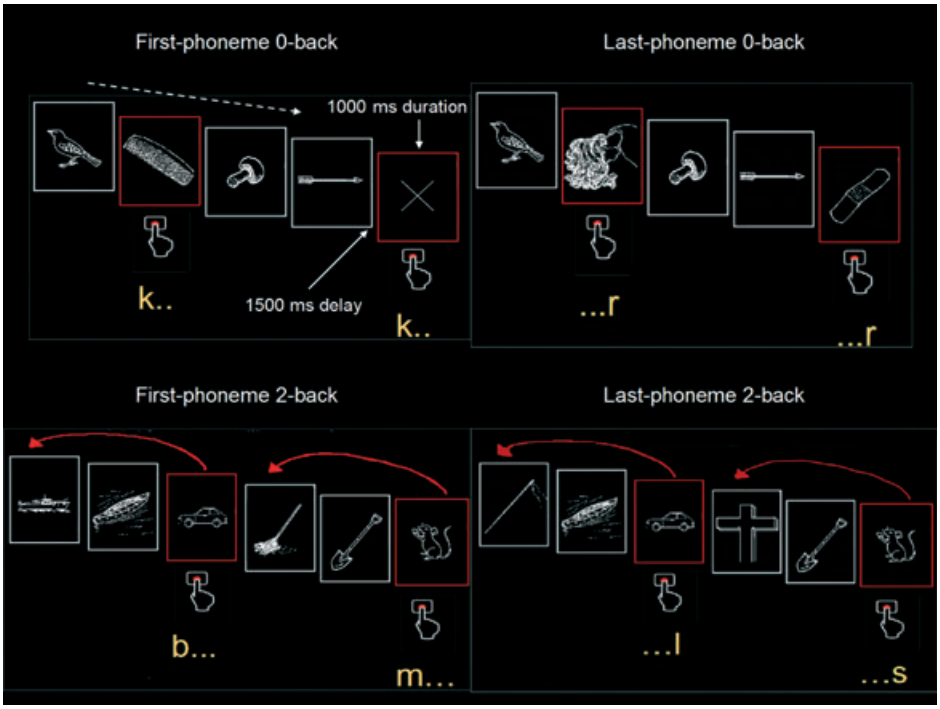

Fig. 1. A diagram for the two memory conditions of the phoneme detection tasks.

view (FOV) 256 mm × 256 mm, matrix 192 × 256 pixels, Slice thickness: 1.0 mm, Voxel size 1.0 × 1.0 × 1.0 mm. Thereafter, 384 BOLD sensitive echo planar (EPI) volume measurements were acquired for the 4 runs (96 volumes per run). The first 10 volumes of each run were excluded from the analysis. Each EPI volume consisted of 25 axial slices with 5.5 mm slice thickness, including an interslice gap of 0.5 mm. Voxel size 4.0 × 4.0 × 5.0. The EPI images were acquired in ascending order. Image parameters were: FA/TR/TA/TE/FOV/matrix = 90°/2.8s/2.6s/60ms/256 × 256mm/64 × 64 pixels. The scanner was synchronized with the presentation of the first trial of each run, with the ratio of interscan to intertrial interval ensuring that voxels were sampled at different phases relative to trial onset (Price, Veltman, Ashburner, Josephs & Friston, 1999).

Behavioral data

Response accuracy and reaction time (RT) when solving the tasks during fMRI scanning were recorded. Response accuracy was based on the rate of omissions and commission errors. A 2 (group: dyslexics, controls) × 2 (task; first, last phoneme) × 2 (condition: 0-back, 2-back) ANOVA was applied, with Group as a between-subjects factor and Task and Condition as repeated measures was used to test for main-effects and interactions for both response accuracy and reaction time for correct responses. In addition, planned comparisons were computed for pairwise comparisons between means for each condition.

fMRI data analysis

Data pre-processing and all statistical analyses were performed with the statistical parametric mapping software SPM2 (Friston, Holmes, Poline *et al*., 1995; Worsley & Friston, 1995). To correct for head movement, all images were realigned to the first image in the time series on a voxel-by-voxel basis. The realigned images were normalized to the reference space of the stereotactical standard brain from Montreal Neurological Institute (MNI), resliced to a cubic voxel size of 3 mm and smoothed by an 8 mm full width at half maximum (FWHM) isotropic Gaussian kernel. The time-series data were band-pass filtered with a high pass filter of 128 s to remove low-frequency drifts in the BOLD signal.

The fMRI data were first analyzed using a single-subject fixed-effects model where the expected hemodynamic response was modeled by a ''box-car'' stimulus function that was convolved with a canonical hemodynamic response function (hrf) (Friston, Fletcher, Josephs, Holmes, Rugg & Turner, 1998) to create covariates in a general linear model. In addition, the Weighted Least Square (WLS) toolbox was used to detect and adjust for movement artifacts in the data. The WLS toolbox weighted each image with the inverse of its variance, the higher the variance of the image, the less it would impact the results (Diedrichsen & Shadmehr, 2005). Subsequently, parameter estimates of the hrf regressor for each of the four conditions were calculated from the least mean squares fit of the model to the time series. Pooled main effects [ON-OFF] contrasts for each group were computed for the 0-back and 2-back conditions, and a pooled between conditions (2-back > 0-back) contrast was computed. Contrast images were generated from the parameter estimates and used in the random-effects group analyses.

Only voxels which survived the significance threshold in the main-effects were included in between-condition and between-group analyses. Masks including voxels which survived the main effect significance threshold in at least one of the conditions or groups were created using the Imcalc function in SPM2. Within-group statistical analyses were performed by entering the contrast images from the single-subject analyses into separate one-sample *t*-tests. Between group analyses were performed by entering the contrast images from the main effects analysis into two-sample *t*-tests. The analyses were done with a false discovery rate (FDR)-corrected significance level of < 0.05, and a cluster extent threshold of 5 voxels, unless stated otherwise. In addition, the contrast images resulting from the first-level main effects analysis were used in a multiple regression model to test for interaction effects.

Areas with statistically significant changes in signal intensity were determined by setting contrasts using the *t*-statistic (one-tailed) on a voxel-by-voxel basis. The resulting set of *t*-values constituted the statistical parametric map (SPM). The reported voxel coordinates were transformed from MNI- to Talairach space (Talairach & Tournoux, 1988) by non-linear transformations (using the ''mni2tal'' script, http://www.mrc-cbu.cam.ac.uk/imaging/mnispace.html). The peak voxel coordinates, for anatomical localization, for each condition and cluster, were validated against the Talairach-Tournoux Atlas (Talairach & Tournoux, 1988).

RESULTS

Behavioral data

The ANOVA analysis showed a main effect of group indicating that the participants with dyslexia were impaired compared to the controls ($F(1,22) = 16.86$, $p < 0.001$), with regard to response accuracy. Planned comparisons showed that the dyslexic participants performed worse than the controls in all four conditions; First phoneme 0-back ($F(1,22) = 14.56$, $p < 0.001$), Last phoneme 0-back ($F(1,22) = 14.87$, $p < 0.001$), First phoneme 2-back ($F(1,22) = 7.90$, $p = 0.01$), Last phoneme 2-back ($F(1,22) = 7.71$,

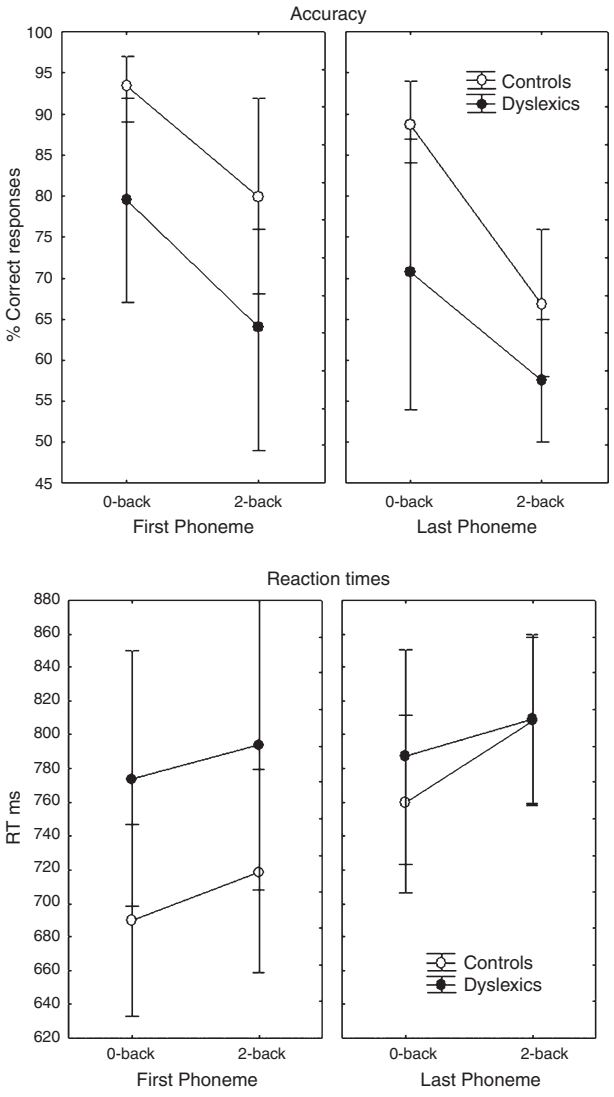

Fig. 2. Means and standard deviations for the percentage correct responses and reaction times for the different tasks split for the dyslexic and control.

$p = 0.01$). There was also a significant general decrease in performance with increasing memory load ($F(1,22) = 100.38$, $p < 0.0010$) and a generally poorer performance in the Last Phoneme conditions compared to the First Phoneme conditions ($F(1,22) = 26.60$, $p < 0.001$). There was also a non-significant trend for a 3-way interaction ($F(1,22) = 2.97$, $p = 0.1$). With regard to RT data, the ANOVA analysis showed that the dyslexic participants were significantly slower compared to the controls ($F(1,22) = 10.69$, $p = 0.004$). Planned comparisons showed that the dyslexic participants were slower in the First phoneme 0-back condition ($F(1,22) = 9.61$, $p = 0.005$) and the First phoneme 2-back ($F(1,22) = 6.23$, $p = 0.02$). There was also a significant general increase in RT with increasing memory load ($F(1,22) = 8.49$, $p = 0.008$), and RTs in the Last phoneme condition were slow compared to the First phoneme condition ($F(1,22) = 12.01$, $p = 0.002$). There was also a Group × Phoneme detection significant interaction ($F(1,22) = 5.68$, $p = 0.02$), which means that an increase in RT in the last phoneme detection task occurred for the control group, but not for the dyslexia group. The behavioral results are shown in Fig. 2.

BOLD fMRI data

Between-group comparisons: 0-back [on-off]: The control > dyslexics comparison yielded activations bilaterally in the parietal lobule and in the right posterior inferior frontal gyrus (IFG) and middle frontal gyrus (MFG). In the left parietal lobule activations were greater in both superior parietal lobule (SPL) and inferior parietal lobule (IPL), and in the right parietal lobule greater activations were found in the SPL and precuneus. The reverse comparison did not reveal any significant voxels. See Table 2 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values for peak voxels. Activations are rendered on the SPM

Table 2. *Brain regions showing significant differences in the 0-back contrast, cluster size (in number of voxel, voxel size 3 × 3 × 3 mm),* t-*values,* p-*values, and anatomical localizations*

	Statistical values			Coordinates anatomical location					
Comparisons	Cluster size	*t*-value	*p*-value	*x*	*y*	*z*	Hemisphere	Structure	Brodmann area
Controls	13159	21.97	0.000	−24	−96	−12	Left	MOG	18
		14.15	0.000	30	−48	−21	Right	Fusiform g.	37
	1458	9.47	0.000	−42	6	27	Left	IFG	44
		8.86	0.000	−39	−3	39	Left	Precentral g.	6
		8.12	0.000	−45	30	21	Left	MFG	46
	709	7.52	0.000	6	21	45	Right	Cingulate	32
		6.95	0.000	−3	15	51	Left	MeFG	6
	80	5.14	0.001	6	−33	21	Right	Cingulate	23
	104	4.30	0.004	−18	−3	9	Left	Globus Pallidus	
		2.64	0.041	−6	−18	15	Left	Thalamus	
	90	3.58	0.011	−21	3	−6	Left	Putamen	
		3.33	0.015	−21	0	−15	Left	Parahippocampal g.	
	15	2.64	0.041	18	−6	−6	Right	Globus Pallidus	
Dyslexics	227	11.43	0.009	−48	18	−3	Left	IFG	47
		6.34	0.021	−42	12	24	Left	IFG	44
		5.94	0.021	−51	15	33	Left	MFG	9
	2790	9.31	0.013	51	−69	−15	Right	MOG	19
		7.98	0.019	12	−84	−21	Right	Lingual g.	18
	116	7.91	0.019	−3	27	42	Left	MFG	6
	33	6.11	0.021	45	15	27	Right	IFG	44
	14	6.08	0.021	42	51	21	Right	MFG	46
	17	5.31	0.021	51	21	−6	Right	IFG	47
Controls> Dyslexics	135	5.42	0.014	45	3	36	Right	IFG	44
		5.34	0.014	33	12	33	Right	MFG	9
	9	5.26	0.014	−21	−60	60	Left	SPL	7
	49	4.96	0.014	−39	−36	45	Left	IPL	40
		4.12	0.025	−27	−36	45	Left	Postcentral g.	3
	44	4.39	0.020	12	−72	42	Right	Precuneus	7
		3.84	0.032	27	−69	42	Right	SPL	7
	8	4.23	0.023	9	−69	54	Right	SPL	7
	5	3.64	0.038	24	−57	48	Right	Precuneus	7
Controls> Dyslexics (65% acc.)	107	5.59	0.020	30	6	33	Right	Precentral g.	6
		5.46	0.020	33	15	36	Right	MFG	9
	6	4.70	0.027	3	−27	48	Right	Paracentral g.	31
	6	4.65	0.028	9	−69	54	Right	SPL	7

Notes: IFG = inferior frontal gyrus; IPL = inferior parietal lobule; MeFG = medial frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; SPL = superior parietal lobule. The table shows up to 2 local maxima per cluster.

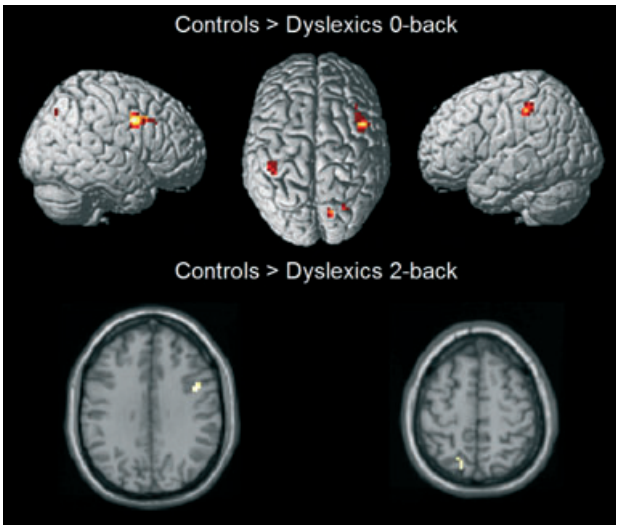

Fig. 3. Brain regions that were significantly more active in age-matched controls compared to the dyslexic group. All activations are rendered on an anatomical template in standard stereotactic space.

template brain and shown in Fig. 3. Due to chance performance in two dyslexic participants we decided to reanalyze the 0-back control > dyslexic comparison, including only participants with above chance performance (>65%) accuracy ($n = 9$). The data were reanalyzed using a mask including the frontal and the parietal lobes only, using the WFU pickatlas tool in the SPM toolbox. This comparison yielded activations in the right posterior PFC, including the MFG and the precentral gyrus, and in the SPL and paracentral gyrus.

2-back [on-off]: The control > dyslexic comparison yielded activations in the right posterior PFC and the left parietal cortex. In the right posterior PFC a cluster of significantly activated voxels covered the posterior parts of the IFG. In the left parietal cortex a cluster of significantly activated voxels was found in the superior parietal lobe. The reverse comparison did not reveal any significant voxels. See Table 3 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values for peak voxels. Activations are rendered on the SPM template brain and shown in Fig. 3. Again, we reanalyzed the 2-back control > dyslexic comparison including only participants ($n = 5$) with above chance performance (>65% accuracy). The data were reanalyzed using a mask including the frontal and the parietal lobes only. This comparison yielded bilateral activations in the frontal lobe. In the right PFC activations were found in the posterior IFG and the anterior MFG, using the WFU pickatlas tool in the SPM toolbox. In the left frontal lobe activations were found in the precentral gyrus and the cingulate gyrus.

Within-group comparisons:0-back [on-off]: In the dyslexic group a one-sample *t*-test yielded a pattern of bilateral activation in the prefrontal and occipitotemporal cortex. The bilateral prefrontal activations covered primarily the posterior parts of the MFG and the IFG, with more extensions in the left hemisphere. In addition, the anterior parts of the right MFG were activated. See Table 2 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values. Activations are rendered on the SPM template brain and shown in Fig. 4.

In the control group a one-sample *t*-test yielded a pattern of bilateral activation that included the prefrontal cortex, parietal lobule, the occipitotemporal cortex and a cluster of subcortical areas, including the thalamus and striatum. See Table 3 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values. Activations are rendered on the SPM template brain and shown in Fig. 5.

2-back [on-off]: In the dyslexic group a one-sample *t*-test yielded a pattern of activation in the prefrontal cortex, the parietal lobule and the occipitotemporal cortex. The prefrontal activations were found bilaterally in the superior frontal gyrus (SFG), in the right MFG, the right cingulate and the left insula. In the parietal cortex the activation occurred in the inferior parietal lobule (IPL). See Table 3 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values. Activations are rendered on the SPM template brain and shown in Fig. 4.

In the control group a one-sample *t*-test yielded a pattern of bilateral activation that included the prefrontal cortex, the parietal lobule, the occipitotemporal cortex and a cluster of subcortical areas, including the thalamus and striatum. See Table 3 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values. Activations are rendered on the SPM template brain and shown in Fig. 5.

2-back [on-off] > 0-back [on-off]: In the dyslexic group a one-sample *t*-test did not yield any significant activation.

In the control group a one-sample *t*-test yielded a pattern of bilateral activation that included the prefrontal cortex, the parietal lobule and the cerebellum. The bilateral prefrontal activations covered primarily the posterior parts of the MFG and SFG, with more extended clusters in the left PFC. The bilateral parietal activations were in the SPL and IPL. The reverse comparison did not reveal any significant voxels. See Table 4 for corresponding Talairach and Tournoux coordinates, and *t*- and *p*-values. Activations are rendered on the SPM template brain and shown in Fig. 5.

First phoneme versus Last phoneme detection: No significant activation differences were detected in First phoneme versus Last phoneme detection for both the 0-back and the 2-back condition in either group.

Interaction effects: There were no significant interaction effects, even at liberal thresholds ($p = 0.01$ uncorrected). However, we also performed an *F*-test with mapping significant effects of interest (FDR = 0.05) and plotted percentage signal changes for each task and condition, for each group, respectively in ROIs in the prefrontal and parietal lobe. Signal changes were stronger in the control group compared to the dyslexic group. In addition, the pattern of changes seemed to deviate for the Last phoneme 2-back task in several areas for the dyslexic group, including the left inferior parietal lobule and bilaterally in the inferior frontal gyrus. Plots of signal changes are shown in Fig. 6.

DISCUSSION

The results from the behavioral screening showed that the dyslexic group performed significantly worse on all reading tasks. Although there were slight differences in IQ between the groups, these did not reach significance and were, in any case, limited to

Table 3. *Brain regions showing significant differences in the 2-back contrast, cluster size (in number of voxel, voxel size 3 × 3 × 3 mm),* t-*values,* p-*values, and anatomical localizations*

	Statistical values			Coordinates anatomical location					
Comparisons	Cluster size	*t*-value	*p*-value	*x*	*y*	*z*	Hemisphere	Structure	Brodmann area
Controls	7384	16.48	0.000	−18	−99	9	Left	MOG	18
		13.83	0.000	12	−99	−9	Right	Lingual g.	18
		11.88	0.000	−30	−69	39	Left	SOG	19
	1236	12.67	0.000	45	6	30	Right	IFG	44
		8.28	0.000	−6	18	48	Left	Cingulate	32
		6.41	0.000	39	21	−6	Right	IFG	47
	1092	9.70	0.000	−36	0	42	Left	MFG	6
		8.91	0.000	−45	6	21	Left	IFG	44
		8.86	0.000	−51	33	21	Left	MFG	46
	106	6.30	0.000	36	54	−6	Right	MFG	10
	15	5.39	0.001	24	−27	−6	Right	Lat. Geniculum body	
	43	5.28	0.001	−12	−12	9	Left	Thalamus	
	13	4.95	0.002	36	54	27	Right	SFG	10
	24	4.89	0.002	0	−27	−15	Right	Red nucleus	
	61	4.72	0.002	12	−15	6	Right	Thalamus	
	14	4.67	0.003	−27	−30	0	Left	Thalamus	
	14	4.43	0.003	39	24	51	Right	MFG	8
	10	4.25	0.004	−45	48	6	Left	MFG	46
	21	4.22	0.004	−15	−3	−6	Left	Globus Pallidus	
Dyslexics	2426	8.28	0.031	45	−72	−9	Right	IOG	19
		7.91	0.031	24	−66	−18	Right	Fusiform g.	19
	14	5.55	0.031	51	39	24	Right	MFG	46
	95	5.12	0.031	3	24	45	Right	Cingulate	32
		5.05	0.031	−3	18	54	Left	SFG	8
	31	4.59	0.031	−39	15	18	Left	Insula	13
	16	4.01	0.036	−33	−54	45	Left	IPL	40
	11	3.91	0.038	36	15	54	Right	SFG	8
		3.89	0.039	30	12	60	Right	MFG	6
Controls > Dyslexics	14	4.08	0.001*	45	6	33	Right	IFG	44
	6	3.91	0.001*	−15	−72	54	Left	SPL	7
Controls > Dyslexics (>65% acc.)	6	5.62	0.001*	−18	−12	39	Left	Cingulate g.	32
	23	4.78	0.001*	45	9	30	Right	IFG	44
	11	4.59	0.001*	39	42	−15	Right	MFG	11
	19	4.13	0.001*	30	9	39	Right		
	5	4.10	0.001*	−39	0	39	Left	Precentral g.	6

Notes: IFG = inferior frontal gyrus; IPL = inferior parietal lobule; MeFG = medial frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; SPL = superior parietal lobule. The table shows up to 2 local maxima per cluster.
*Uncorrected *p*-values.

verbal tests. It is unlikely that the difference in performance between the groups on this demanding task simply reflected general intelligence. The behavioral results showed that the dyslexic group had significantly poorer performance in all conditions, relative to the control group, especially in the 2-back task. Overall accuracy for six dyslexic participants was at chance level, which makes it difficult to ensure that they were actually performing the task, that is, engaging working memory processes. Hence, the 2-back activation data from the dyslexic group should be interpreted with caution. In addition, accuracy in the Last phoneme condition was poorer compared to the First phoneme and poorer in the 2-back task compared to the 0-back task for both groups. The analysis did not yield any significant interactions. However, there was a tendency for a 3-way interaction indicating that the control group experienced a relative larger drop in performance in the 2-back Last phoneme condition. It is possible that large variance, in addition to small samples, could partly account for the absence of significant interactions. Another confounding factor could be individual differences in strategies which we did not control for. In addition to poorer accuracy, dyslexics showed slowed performance compared with controls – however, this was limited to the First phoneme tasks. Although significant behavioral differences were found between the First phoneme and Last phoneme conditions, comparisons of fMRI activation for the First phoneme versus the Last phoneme conditions did not yield significant differences as a main effect in either group.

The 0-back phoneme detection tasks do not require the recruitment of extensive WM resources. Thus, dyslexic deficits on this 0-back task indicate impaired phonological processing compared with controls. With regard to the fMRI data, the pooled effects from the 0-back phoneme detection tasks showed significant group differences in the left inferior parietal lobule. Differences in the left temporo-parietal areas are commonly found in other studies involving phonological processing in adults (Brunswick,

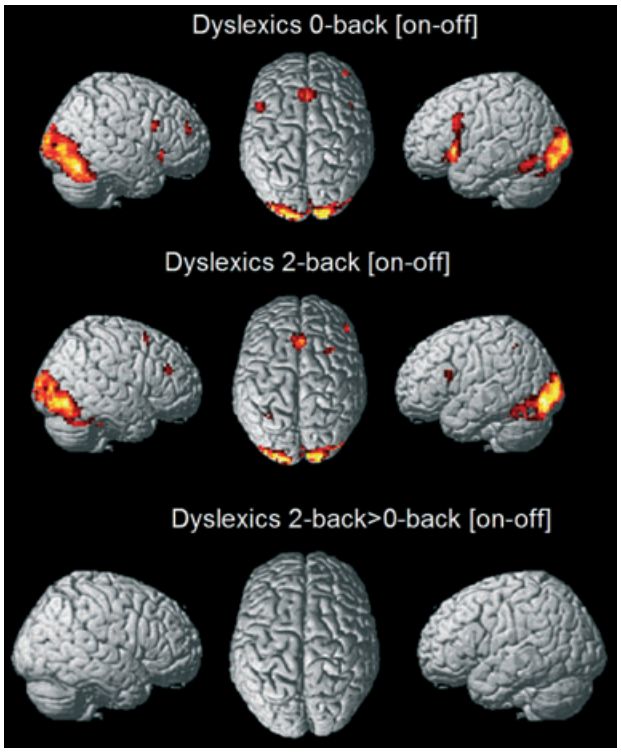

Fig. 4. Brain regions showing significant activation in the dyslexic group. All activations are rendered on an anatomical template in standard stereotactic space.

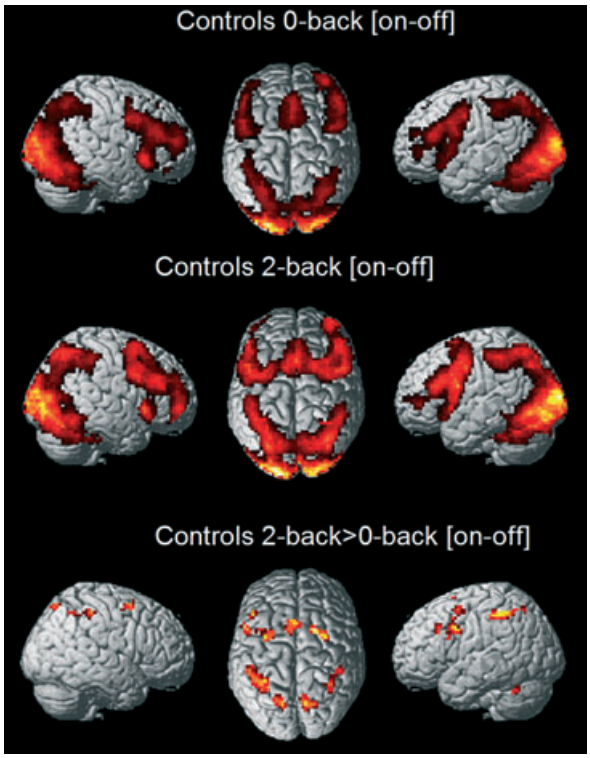

Fig. 5. Brain regions showing significant activation in the control group. All activations are rendered on an anatomical template in standard stereotactic space.

McCrory, Price, Frith & Frith, 1999; Rumsey, Horwitz, Donohue, Nace, Maisog & Andreason, 1997, 1999; Shaywitz, Shaywitz, Pugh *et al*., 1998) and children (Temple, Poldrack, Salidis *et al*., 2001) with dyslexia. These findings are in line with the phonological deficit hypothesis (Elbro & Jensen, 2005; Snowling, 2000). In addition, we also found differences in the right IFG and MFG and bilaterally in the SPL between the dyslexic readers and the control group. These fronto-parietal regions are commonly associated with executive processes in adults (Owen *et al.*, 2005; Wager & Smith, 2003) and children (Casey, Cohen, Jezzard *et al*., 1995). The results suggest that these areas are less involved in phoneme identification in the dyslexic readers. A possible explanation could be that although there are no overt memory requirements, the 0-back task nevertheless demands conscious access, attention to, and manipulation of phonological representations, that is, executive processes (Démonet, Taylor & Chaix, 2004; Ramus & Szenkovits, 2008). It should also be noted that since 0-back performance was at chance level in two dyslectic participants,

Table 4. *Brain regions showing significant differences in the 2-back > 0-back contrast, cluster size (in number of voxel, voxel size 3 × 3 × 3 mm),* t-*values,* p-*values, and anatomical localizations*

	Statistical values			Coordinates anatomical location					
Comparisons	Cluster size	*t*-value	*p*-value	*x*	*y*	*z*	Hemisphere	Structure	Brodmann area
Controls	211	6.75	0.016	−30	−51	48	Left	SPL	7
		6.15	0.016	−48	−33	48	Left	IPL	40
	15	6.58	0.016	−45	24	36	Left	MFG	9
	49	6.05	0.016	48	−33	51	Right	IPL	40
		5.29	0.016	33	−51	48	Right	SPL	7
	66	5.90	0.016	24	3	54	Right	MFG	6
		5.33	0.016	18	9	57	Right	SFG	6
	61	5.77	0.016	15	−64	58	Right	SPL	7
	123	5.68	0.016	−48	3	33	Left	Precentral g.	6
		5.11	0.016	−27	0	48	Left	MFG	6
	28	5.40	0.016	−30	−60	−33	Left	Cerebellum	
	62	5.12	0.016	−3	15	57	Left	SFG	8
		3.98	0.021	−6	21	45	Left	Cingulate g.	32
Dyslexics	*No significant voxels*								

Notes: IFG = inferior frontal gyrus; IPL = inferior parietal lobule; MeFG = medial frontal gyrus; MFG = middle frontal gyrus; SFG = superior frontal gyrus; SPL = superior parietal lobule. The table shows up to 2 local maxima per cluster.

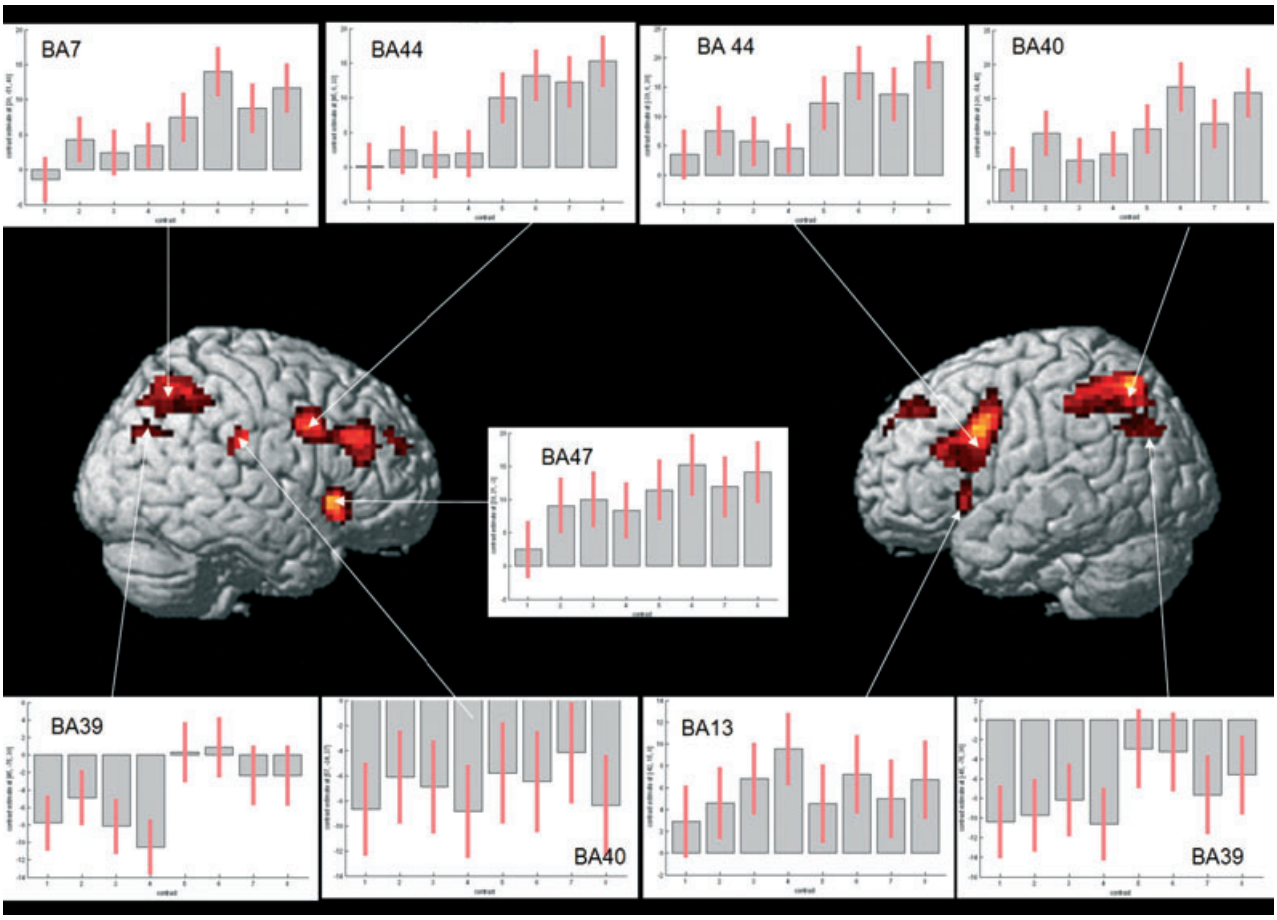

Fig. 6. Brain regions showing significant effects of interest (*F*-test, $p = 0.05$, FWE corrected). The bar-plots show the mean-corrected % signal changes for all tasks and conditions for both groups in areas of interest in the prefrontal and temporoparietal areas. The red line represents the standard errors. Bar-plots 1–4 represent the 0-back first phoneme, 2-back first phoneme, 0-back last phoneme, and 2-back last phoneme task in the dyslexic group. Bar-plots 5–8 represent the 0-back first phoneme, 2-back first phoneme, 0-back last phoneme, and 2-back last phoneme task in the control group.

reanalysis was performed excluding these participants whose data may have reflected inability/inattention to task for the control group. Significant group-differences were found in the same right MFG and SPL areas as in the original analyses, and no significant activations were found in the posterior left areas associated with phonological processing. An important question to be answered in future studies is whether neural activation in areas associated with phonological and executive processing correlates with differences in performance on phonological awareness tasks.

In the 2-back phoneme detection tasks significant group differences in brain activation were found in the right IFG and the left SPL, which suggests that these areas are less involved in dyslexic readers performing these tasks. As reported in the results section, the 2-back performance in the dyslexic group was low, and at chance level for six participants. Reanalysis on the remaining group still showed significant group differences in the same right IFG area as in the original analyses. In addition, significant differences were found in the right anterior MFG and the left cingulate gyrus and the precentral gyrus. Although the analysis was based on a small sub-sample and with an uncorrected significance threshold ($p < 0.001$), it is less likely that the originally observed differences in the right PFC reflected processes associated with chance performance. That is, variance in the dyslexic group reduced statistical sensitivity with regard to the between-group comparison. Bilateral activation in the PFC has been shown to be associated with executive processes (Wager & Smith, 2003). In addition, it is less likely that the right lateralized differences in the IFG could be attributed to phonological processing. Thus, the 2-back results reveal neuronal correlates that could be attributed to executive, rather than phonological processes, in dyslexic readers. Thus, a possible explanation could be that poor verbal WM in dyslexia could reflect two separate deficits. Neuronal activation detected with functional neuroimaging methods cannot always bear simple functional explanations, especially when it comes to the relationship between brain activation and behavioral accuracy measures. Alternative explanations could be differences in behavioral performance or alternate processing strategies in the dyslexic sub-group. Thus, functional imaging abnormalities should always be supported by other supplementary data. Furthermore, the plots of percentage signal changes showed a deviant activation pattern in the dyslexic group in the Last phoneme 2-back task when both phonological processing load and working memory load were increased. This would be predicted if two separate deficits existed. However, this was not supported in the behavioral results where an opposite pattern was found. Ramus and Szenkovits (2008) suggested that dyslexic readers have problems with phonological access rather than degraded phonological representations. By this, they mean all processes by which phonological representations

are accessed for the purpose of external computations, such as working memory, phonological awareness and rapid naming, and that these processes could be termed executive processes. This could explain why differences in areas associated with executive processes were found in both the 0-back and the 2-back conditions in our study. Further support for a central role of executive processes is provided by the within-group comparisons. In the control group, the dorsolateral PFC and SPL were activated more strongly when WM load was added to the phoneme detection task. These areas have previously been associated with executive processes in WM (Owen *et al.*, 2005; Wager & Smith, 2003). In contrast, the dyslexic group did not show significant differences. It could be that the executive processing requirements of the phoneme identification task (0-back) already approached or exceeded the capacities of the dyslexic readers, leaving no additional resources for the more demanding 2-back task. One explanation could be a reduction in the absolute amount of central executive capacity. A second explanation could be that less effective phonological processing demands relatively more central executive processing causing a relative reduction in capacity. One way to address these issues in future fMRI studies would be to equate phonological task difficulty across subjects or use non-verbal stimuli to address a possible differential implication of the central executive. However, it should be borne in mind that the lack of within-group effects could be related to chance performance of half the dyslexic students in the 2-back task and larger error variance among the dyslexic group in the behavioral data. Thus these particular fMRI results should be interpreted with caution.

Another potential confounding factor regarding the fMRI data could be differences in variance between the groups reflecting external factors. We noted more movement artifacts in the younger participants and more motor unrest in the dyslexic participants. The WLS toolbox in the SPM2 software package was used to diminish the impact of larger movement artifacts in the dyslexic group. On the other hand, larger within-group variance could be explained by the fact that dyslexia is a heterogeneous disorder. Another possible limitation could be that the phonological task also involved letter knowledge, and different amount of exposure in the control group compared to the dyslexic group. Although this is theoretically possible we consider it a remote possibility due to the fact that differences in letter knowledge or knowledge of written spellings would imply differences in the representations of visual word forms. We did not find any differences in the left posterior fusiform area which has been associated with processing of visual word forms (Cohen, Dehaene, Naccache *et al*., 2000). A confounding factor could be individual differences in naming ability. Dyslexics tend to be slower and/or more error prone in naming letters, colors and objects (see Beaton, 2004 for a review). However, the literature provides contradictory results for confrontational naming and rapid automatized naming. Normal performance has been found for confrontational naming (Trauzettel-Klosinski, Dürrwächter, Klosinski & Braun, 2006), while deficits have been found for infrequent words (Swan & Goswami, 1997), and especially when the task demands a combination of serial processing and speed. Thus, the precise nature of the naming difficulty in dyslexia is not clear and merits further attention (see also Meyer, Wood, Hart & Felton, 1998).

Overall, and despite some caveats concerning interpretation, it is possible that the impaired WM processes in dyslexia have a unique neuronal signature which may be associated with central executive processes. These processes are, in addition, involved in normal phonological awareness skills, as suggested by Ramus and Szenkovits (2008). This could indicate that executive processes are recruited when accessing phonological representations for the purpose of both working memory and phonological awareness, and that dyslexics are most vulnerable to a simultaneous increase in phonological and working memory processing demands. However, the behavioral and fMRI findings were not consistent. The current results may therefore more be seen as exploratory findings promoting future studies, than as a hypothesis confirmation. It is suggested that future studies should equate performance on a phonological control task before manipulating load for a central executive module. Alternatively, a non-verbal task could be used to avoid confounding effects of phonological processing.

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