

Neural basis of phonological awareness in beginning readers with familial risk of dyslexia—Results from shallow orthography



Agnieszka Dębska^{a,b}, Magdalena Łuniewska^{a,b}, Katarzyna Chyl^a, Anna Banaszekiewicz^c, Agata Żelechowska^a, Marek Wypych^c, Artur Marchewka^c, Kenneth R. Pugh^{d,e,f}, Katarzyna Jednoróg^{a,*}

^a Laboratory of Psychophysiology, Department of Neurophysiology, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland

^b Faculty of Psychology, Warsaw University, Warsaw, Poland

^c Laboratory of Brain Imaging, Neurobiology Center, Nencki Institute of Experimental Biology, Polish Academy of Sciences, Warsaw, Poland

^d Haskins Laboratories, New Haven, CT, USA

^e Department of Linguistics, Yale University, New Haven, CT, USA

^f Department of Diagnostic Radiology, Yale University School of Medicine, New Haven, CT, USA

1818

ARTICLE INFO

Article history:

Received 21 August 2015

Accepted 21 February 2016

Available online 27 February 2016

Keywords:

Children

Dyslexia

Functional MRI

Pediatric neuroimaging

Rhyme judgment

ABSTRACT

Phonological processing ability is a key factor in reading acquisition, predicting its later success or causing reading problems when it is weakened. Our aim here was to establish the neural correlates of auditory word rhyming (a standard phonological measure) in 102 young children with (FHD+) and without familial history of dyslexia (FHD−) in a shallow orthography (i.e. Polish). Secondly, in order to gain a deeper understanding on how schooling shapes brain activity to phonological awareness, a comparison was made of children who had had formal literacy instruction for several months (in first grade) and those who had not yet had any formal instruction in literacy (in kindergarten). FHD+ children compared to FHD− children in the first grade scored lower in an early print task and showed longer reaction times in the in-scanner rhyme task. No behavioral differences between FHD+ and FHD− were found in the kindergarten group. On the neuronal level, overall familial risk was associated with reduced activation in the bilateral temporal, tempo-parietal and inferior temporal–occipital regions, as well as the bilateral inferior and middle frontal gyri. Subcortically, hypoactivation was found in the bilateral thalami, caudate, and right putamen in FHD+. A main effect of the children's grade was present only in the left inferior frontal gyrus, where reduced activation for rhyming was shown in first-graders. Several regions in the ventral occipital cortex, including the fusiform gyrus, and in the right middle frontal and postcentral gyri, displayed an interaction between familial risk and grade. The present results show strong influence of familial risk that may actually increase with formal literacy instruction.

© 2016 Elsevier Inc. All rights reserved.

Introduction

To learn to read, one has to know how to manipulate and isolate phonemes, and how particular signs (graphemes) are mapped into sounds (phonemes). Phonological awareness, the ability to distinguish, identify, and manipulate the sounds of speech, is an important predictor of reading development (Torgesen et al., 1994; Ehri et al., 2001). A deficit in phonological processing remains the most consistent finding in studies of developmental dyslexia (Bradley and Bryant, 1978; White et al., 2006; Caravolas et al., 2012; Ziegler et al., 2010; Cronin and Carver, 1998; Mann and Wimmer, 2002). In addition, early intervention

focused on phonological skills may result in a significant improvement of literacy skills in children (Snowling and Hulme, 2011).

Since dyslexia is to a large extent hereditary (Castles et al., 1999; DeFries et al., 1987; Olson et al., 1989), deficits in the neural structures underlying phonological skills might be anticipated even before children start to read. Bearing in mind that dyslexia occurs in approximately 40%–60% of individuals whose first-degree relatives had a history of reading problems (Fisher and Francks, 2006), studying young children at risk for dyslexia might give important insights into functional anomalies related to reading deficits which are not, however, a result of training/remediation or compensatory mechanisms. Familial risk remains a strong predictor of dyslexia (Dandache et al., 2014). Additionally, studies have revealed a number of early cognitive markers of dyslexia related to literacy development, among which the most commonly reported are phonological awareness and rapid automatized naming (Lyytinen et al., 2005; Torppa et al., 2010). Early non-linguistic cognitive deficits were also, though less often, implicated (Bosse et al., 2007; Facioetti

* Corresponding author at: Laboratory of Psychophysiology, Department of Neurophysiology, Nencki Institute of Experimental Biology, Pasteur 3, 02-093 Warsaw, Poland.

E-mail address: k.jednorog@nencki.gov.pl (K. Jednoróg).

et al., 2010; Kevan and Pammer, 2008; Stein, 2001; Vidyasagar, 2004; Vidyasagar and Pammer, 2009).

In fact, the cognitive markers of dyslexia might be traced very early in development. The well-known Jyväskylä Longitudinal Study of Dyslexia showed poorer skills in at-risk children than in the control group in various cognitive skills known to predict reading and spelling (e.g. vocabulary, inflectional morphology, phonological processing, letter knowledge, or rapid automatized naming) with some measures different already at the age of 2 (Lyytinen et al., 2004). Considering neurophysiological markers of dyslexia, the results from event-related potential (ERP) studies in the Finnish sample (Guttorm et al., 2001, 2005; Guttorm, 2003) indicate that children with familial risk of dyslexia have attenuated brain responses to speech tokens compared with the control group at the age of 6 months, or even just after birth. These atypical patterns in newborns were shown to be related to later language development and phonological proficiency at the age of 9 (Leppänen et al., 2010). We are trying to extend this to brain organization for phonology as children begin schooling.

A number of functional magnetic resonance imaging (fMRI) studies have examined differences in phonological processing between dyslexic and typically reading children, usually employing letter and word rhyming judgments or phoneme deletion tasks. Dyslexic adolescents and children showed hypoactivation of the left tempo-parietal cortex, left superior posterior temporal sulcus, left inferior frontal gyrus, left inferior temporal gyrus and bilateral superior temporal gyrus, indicating that these regions play a role in the development of phonological processing skills (Bolger et al., 2008; Cao et al., 2006; Desroches et al., 2010; Temple et al., 2001; Van Ermingen-Marbach et al., 2013; see also Richlan et al., 2009, 2011 for a meta-analysis). However, most of these studies, when assessing phonological processing, have required children to read and compare visually presented words, which in itself might have amplified group differences as a function of reading differences. Less research has been devoted to studying phonological processing with spoken stimuli, and these have been limited to English-speaking children (Desroches et al., 2010; Kovelman et al., 2012; Raschle et al., 2012). The first two studies (Desroches et al., 2010; Kovelman et al., 2012) were performed on older (8–14 years old) typically reading or dyslexic children and found diverse results. While Desroches et al. (2010) reported group differences in the left fusiform gyrus with reduced activation in the dyslexic group, Kovelman et al. (2012) revealed the left dorsolateral prefrontal cortex (DLPFC) as the only region with significant hypoactivation in dyslexics in auditory phonological tasks. Interestingly, in the Kovelman study, a group of kindergarten pupils matched to the dyslexic children for reading level and phonological awareness showed increased activation for rhyming in the left DLPFC region, similarly to age-matched controls. Thus, the under-recruitment of the left DLPFC observed in dyslexic children did not appear to be related to overt reading or phonological performance levels with this reading age contrast, and hence may reflect a more general dyslexia marker. Finally, with regard to our focus on the link between phonological ability and familial risk, only the Raschle et al. (2012) study was performed on pre-reading children with and without a familial history for dyslexia (FHD+ and FHD–, respectively, $n = 18$ per group). The authors found that during a phonological awareness task (first phoneme matching) compared with a voice matching task, FHD+ children, when compared to FHD– children, underactivated many brain regions in bilateral occipito-temporal, left temporo-parietal areas, and the cerebellum. This could indicate that differences in brain activation are indeed present before children start to read. However, there is hardly any consistency between these three studies with respect to the brain regions involved in spoken word phonological awareness and distinguishing between typically developing children and those with dyslexia or a familial risk for dyslexia. This might be partly related to the differences in experimental and control tasks, age, instruction in literacy and reading experience of the studied participants. As

suggested by previous neuroimaging studies (Cone et al., 2008), age and orthographic knowledge influence spoken language processing in typically reading samples and we can assess this by contrasting children before and after formal schooling begins.

Nonetheless, little is known about how literacy instruction modifies brain structures involved in phonological awareness, and yet we know that learning to read has profound effects on language systems in the brain (Castro-Caldas et al., 1998; Dehaene et al., 2015). Behavioral studies indicate a strong bidirectional relation between reading and phonological awareness in children (Castles et al., 2011; Lonigan et al., 2000; Wagner et al., 1994), and hence it is important to determine how literacy modulates phonological processing. Comparative studies are needed to determine how phonological processing circuits change with emerging reading ability (Dehaene et al., 2010).

In addition, language differences could modify all this, and although orthographic depth (referring to the transparency of grapheme to phoneme mapping) is considered one of the most important environmental factors influencing typical and atypical reading development (Landerl et al., 2013; Richlan, 2014), systematic studies on the neural correlates of phonological awareness in typically developing and at-risk children in shallow orthographies are largely missing. English has been referred to as an “outlier” orthography with especially opaque grapheme–phoneme correspondences (Share, 2008). In consequence, for English-speaking children, learning to read is generally more demanding and slower than for German, Greek, Finnish, or Italian children who can benefit from the shallow orthography one-to-one relation between letters and sounds (Aro and Wimmer, 2003; Seymour et al., 2003). Thus the learning path for readers in deep/shallow orthographies may proceed somewhat differently, given the different challenges that need to be faced in order to acquire orthography and phonology (however, see Caravolas et al., 2013 for counter-arguments). Nevertheless, early positron emission tomography (PET) study performed on French, British, and Italian adults with developmental dyslexia showed similar (irrespective of orthography) pattern of reduced activation in the left middle and inferior temporal regions during a reading task (Paulesu et al., 2001). Subsequently, on the same sample, Silani et al. (2005) reported similar cortical disorganization in grey and white matter suggesting a universal pattern of brain dysfunction in dyslexics across deep and shallow orthographies (but see Hadzibeganovic et al., 2010 for a critical opinion). However, evidence in favor for a different scenario, where a core universal dysfunction is present in dyslexia with additional language-related variations (Richlan, 2014) can be found in studies comparing brain activity in typically reading adults of contrasting orthographies (Paulesu et al., 2000; Rueckl et al., in press). The current study examines precursors for the first time in a shallow orthography since previous studies focused on English only.

Our aim here has been to address the gaps in the literature alluded to in the previous sections. We examined the neural correlates of phonological awareness in beginning readers with and without familial risk for dyslexia in a shallow orthography (i.e. Polish). Secondly, we tested two groups of children, one that had been receiving formal literacy instruction for a few months (in first grade) and one that had not yet had any formal literacy instruction (in kindergarten), in order to gain a more precise picture of how reading experience shapes brain activity to create phonological awareness. If the orthographic depth of the language does not qualify risk markers associated with family history, then we expect a decrease in brain activation in FHD+ children compared to FHD– in those brain areas implicated in previous studies performed on English-speaking children (i.e. left tempo-parietal, occipito-temporal, and inferior frontal/dorsolateral prefrontal cortex) for both pre- and post-reading instruction cohorts. Moreover, since formal literacy learning clearly changes spoken language organization and competence (Dehaene et al., 2010; Castro-Caldas et al., 1998), it might be associated with a complex interaction between grade and family history on this spoken phonological awareness measure.

Materials and methods

Participants

One hundred twenty healthy, native Polish-speaking children were recruited from schools and kindergartens via announcements on parent–teacher conferences, website, and social media. Parents had to complete an online questionnaire in order to qualify their child to the study. The inclusion criteria were normal IQ (≥ 25 th percentile in Raven's Colored Progressive Matrices), birth at term (≥ 37 weeks), right-handedness, monolingualism, normal hearing, receiving regular classes at school or kindergarten, no history of neurological illness, or brain damage and no symptoms of ADHD. The study was approved by the Warsaw University Ethical Committee and all children and their parents gave written informed consent to the study.

Since the study was conducted during the introduction of educational reforms (primary school now starts at age 6 instead of age 7, as previously), some of the 6-year-old children were in the first grade and some were in the kindergarten (based on parental decision). All of them were a part of large cohort from a longitudinal study on the early predictors of dyslexia. However, due to either excessive motion during fMRI scanning (8 subjects), failure to complete 2 runs (2 subjects) or not following fMRI task instructions, i.e. more than 40% missing answers (8 subjects), 102 were included in the present study.

Thirty children were in kindergarten, involving 17 with a family history of dyslexia (FHD+): 9 F, 8 M, age in months: $M = 79.7$, $SD = 4.7$ and 13 without a family history of dyslexia (FHD−): 8 F, 5 M, age in months: $M = 78.9$, $SD = 4.9$. The second group consisted of 72 first-graders including 45 FHD+ children: 26 F, 19 M, age in months: $M = 84.7$, $SD = 6.4$, and 27 FHD− children: 19 F, 8 M, age in months: $M = 84.4$, $SD = 6.3$. Children from the FHD+ group had at least one parent who reported reading difficulties and scored greater than 0.4 points in the Adult Reading History Questionnaire (ARHQ, Lefly and Pennington, 2000) as specified in Black et al. (2012) (37.1% of children), or a first-degree relative with certified (clinical) diagnosis of developmental dyslexia (62.9% of children). Both the interclass correlation with reading scores ($ICC = 0.67$) and receiver operating characteristic (ROC) curve analysis with sensitivity of 100% and specificity of 77.1% for 0.385 cut-off indicate that the ARHQ score is a good indicator of past and current reading ability in adults (Black et al., 2012).

The mean duration of the literacy instruction measured as the time to which first-grade students have been exposed to before performing fMRI varied from 70 to 238 days and followed normal distribution (mean = 147.9, $SD = 48.8$; Skewness = 0.24, $SEM = 0.28$; Kurtosis = -1.16 , $SEM = 0.56$, Kolmogorov–Smirnov test = 0.10, $p = 0.06$). The FHD+ and FHD− groups did not differ significantly in the duration of literacy instruction, which had a normal distribution in both groups (mean FHD+ = 155 days, $SD = 49.5$ min = 70, max = 238; Skewness = 0.13, $SEM = 0.35$; Kurtosis = -1.25 , $SEM = 0.69$, Kolmogorov–Smirnov test = 0.09, $p = 0.2$; mean FHD− = 136 days, $SD = 45.9$, min = 70, max = 219; Skewness = 0.38, $SEM = 0.45$; Kurtosis = -1.04 , $SEM = 0.87$, Kolmogorov–Smirnov test = 0.14, $p = 0.18$).

Behavioral measures

We used a battery of tests measuring early reading and phonological skills: letter knowledge, simple word and pseudo-word reading (outcome measure: number of words and pseudo-words read in a minute), elision (outcome measure: number of items solved in a minute), and phoneme analysis (Szczerbiński and Pelc-Pękała, 2013). These tasks constitute the Decoding Test [Test Dekodowania] and have been standardized and normalized for first-grade pupils independently from age; however, since kindergarten children were included in the present study, raw scores were used.

Early print skills were assessed using an orthographic awareness test, in which children were presented with pairs of trigraphs and quatergraphs and had to choose the one which exists in Polish (for instance trigraph DAG exists in Polish orthography, while DGA does not) (Awramiuk and Krasowicz-Kupis, 2014); the outcome measure was the raw number of correctly assigned graphs. This test was specifically designed to test the intuition regarding potential letter combination in Polish in children who have not yet started school education. Two computerized non-standardized tests were used to measure accuracy in auditory rhyme and alliteration judgment on pseudo-words. In the computer game, children were presented with two aliens who spoke single pseudo-words. Participants' task was to assess whether the two pseudo-words rhymed (in the first game) or whether they started with the same phoneme (in the second game). The outcome measures were the percentage of correct responses in each task.

Rapid automatized naming (RAN) was tested, with subtests of object and color naming (Fecenc et al., 2013). The outcome measure was the amount of time to name all stimuli in a given subtest. As this test has been standardized and normalized for children aged 5;0–12;11, we used standard age scores for further analysis. Raven's Colored Progressive Matrices (Szustrowa and Jaworowska, 2003) were used to control non-verbal IQ. The test has been standardized for children aged 4;0–10;11 and we used percentile scores. Picture vocabulary test: Comprehension served for testing size of passive vocabulary (Haman et al., 2012). This test is based on the standard picture-choice procedure and has been standardized and normalized for children aged 2;0–6;11. As we studied also older children in the sample, we used raw scores for the analysis. Digit and syllable span were measured with tasks in which series of increasing length (from three up to ten elements) were repeated by participants. The total number of correctly repeated series was used as the outcome measure.

In the case of behavioral measures where standard scores were not available, raw scores adjusted for age (by saving standardized residuals after running a regression analysis) were submitted to further analyses, including two-way ANOVA, behavioral and brain-behavior correlations.

Hollingshead's (1975) index of social position was used to measure parental socioeconomic status (SES). Since in the case of 10 families it was impossible to contact the child's father, there are missing data in paternal ARHQ (p_{ARHQ}) and SES.

The behavioral tests were performed earlier than fMRI but the sessions were no more than 4 months apart (on average 46 days). A series of two-way ANOVAs were used to examine the effects familial risk and grade as well as the interaction of these factors on behavioral performance. Even though scores from word reading test significantly deviated from normality distribution, we nevertheless applied two-way ANOVA, since no violation of homogeneity of variance occurred and there is general consensus that violations of normality assumption do not seriously affect the probabilities needed for statistical decision-making. We considered a statistically significant result as one in which the observed p value is less than 5%.

fMRI tasks

Twenty common object word pairs were presented via headphones accompanied by pictures depicting the words. After each pair, the child had to decide whether the words rhymed or not (Rhyme task), similarly to Kovelman et al. (2012). The control experiment included exactly the same stimuli (object word pairs) but the participants' task was to assess whether the words were spoken by speakers of the same gender or not (Voice task), similarly to Raschle et al. (2012). The yes/no decision was made by pressing corresponding button. Both tasks were contrasted with a rest condition. During the rest condition, children were asked to look at a fixation cross for the duration of the block. The accuracy and reaction times were analyzed in both tasks separately using a series of two-way ANOVAs and the results are reported at $p < 0.05$. The

relationship between the in-scanner rhyme task and behavioral tests done outside the scanner were examined for the total sample and for FHD+ and FHD− children using Pearson's correlations implemented in the SPSS software package, version 22.

Procedure

Children were familiarized with the task in a mock-scanner using different items from those used in the scanning session. The experimental scheme was analogous to Raschle et al. (2012) with two functional runs: one with the experimental rhyme judgment task and one with the control voice matching task. The timing and duration of tasks were identical and the order of runs was counterbalanced between the children. The participant heard a word in the headphones and at the same time saw the picture of its referent on the screen for 2 s. After that, the second word was played and the second picture appeared for 2 s. Then a question mark appeared for 2 s prompting the child to give an answer. Each run consisted of 10 blocks: 5 blocks with stimulation and 5 with rest condition, each lasting 24 s. In experimental and control task there were 4 trials per block. 50% of trials matched regarding rhyme and 50% of words were spoken by the female/male voice. Stimuli were presented using Presentation software (Neurobehavioral Systems).

fMRI Data Acquisition and Analyses

Neuroimaging data were acquired on a 3 T Siemens Trio scanner using whole-brain echo planner imaging sequence with 12-channel head coil (34 slices, slice-thickness 3.5 mm, TR = 2 s, TE = 30 ms, flip angle = 90°, FOV = 214 mm², matrix size: 64 × 64, voxel size 3.5 × 3.5 × 3.5 mm). Anatomical data were acquired using a T1-weighted sequence (176 slices, slice-thickness 1 mm, TR = 2.53 s, TE = 3.32 ms, flip angle = 7°, matrix size: 256 × 256, voxel size 1 × 1 × 1 mm).

The data pre-processing and analyses were performed using Statistical Parametric Mapping (SPM8, Wellcome Trust Center for Neuroimaging, London, UK) running on MATLAB R2013b (The Math-Works Inc. Natick, MA, USA). First, all images were realigned to the first functional volume. Then structural images from single subjects were co-registered to the mean functional image. Co-registered anatomical images were segmented using pediatric tissue probability maps (for this purpose, Template-O-Matic toolbox was used with the matched pairs option). Next, high-dimensional Diffeomorphic Anatomical Registration through Exponentiated Lie Algebra (DARTEL) was used to create a group-specific template and flow fields based on segmented tissue from T1w images (Ashburner, 2007). The functional images were normalized using compositions of flow fields and a group-specific template. Finally, the normalized functional images were smoothed with an 8 mm isotropic Gaussian kernel. The data were modeled for each fMRI run, using the canonical hemodynamic response function convolved with the experimental conditions. Besides adding movement regressors to the design matrix, ART toolbox was used to reject motion-affected volumes. Artfactual volumes were identified using a movement threshold of 3 mm and a rotation threshold of 0.05 rad (similarly to Raschle et al., 2012). Subjects were included if a minimum 80% of volumes were artifact-free. There were no differences between the kindergarten pupils and the first-graders, nor between FHD+ and FHD− children in the number of rejected volumes (kindergarten: mean = 5.61 and 8.62 for FHD+ and FHD−, respectively; first grade: mean = 5.75 and 5.35 for FHD+ and FHD−, respectively).

The general linear approach implemented in SPM8 was used to analyze the data contrasting experimental and control blocks (Rhyme > Voice) in each subject. For the second-level analysis, a full factorial model was used with grade (kindergarten pupils vs. first-graders) and familial history (FHD− vs. FHD+) as factors. Results are reported at a significance level of $p < 0.005$ uncorrected, and extent threshold

of 50 voxels, as specified in Raschle et al. (2012). This corresponds to cluster threshold of $p < 0.05$, corrected for multiple comparisons using a cluster size algorithm based on Monte Carlo simulations (3dClustSim, AFNI, <http://afni.nimh.nih.gov>).

In case of a significant interaction between grade and familial risk, we further investigated the source of this interaction with post hoc tests in each cluster. Contrast estimates from significantly activated clusters were extracted using MarsBar toolbox (Brett et al., 2002). Previous research has shown an involvement of left ventral occipito-temporal cortex during reading and reading-related tasks in typical reading individuals as well as its consistent hypoactivation in children and adults with a diagnosis of dyslexia (Hoeft et al., 2007; Paulesu et al., 2014). Therefore, contrast estimates were extracted from left ventral occipito-temporal regions and correlation analysis (within groups of FHD+/FHD− children and for the total sample) was used to relate brain function with phonological processing skills (phonemic analysis, phonological deletion, pseudo-word alliteration, and pseudo-word rhyme) using the SPSS software package, version 22. Results with a p value below 0.05 are reported as significant.

Results

Behavioral results

Table 1 presents results from behavioral measures. There were no differences between the groups in IQ and SES. Children from first grade were significantly older than the kindergarten pupils; however, there were no age differences between FHD+ and FHD−.

First-graders compared to kindergarten pupils had significantly higher letter knowledge and were significantly better in word and pseudo-word reading as well as phoneme analysis. Significant interaction between grade and familial risk was revealed for early print task; FHD+ children performed worse than FHD− children but only in the group of first-graders. Moreover, first-graders performed better than kindergarten pupils but only in the FHD− group.

In-scanner performance

Two two-way ANOVAs were performed separately for experimental (Rhyme) and control (Voice) tasks to examine the effects of familial risk and grade on accuracy and reaction times (see Fig. 1). In the case of the Rhyme task, a significant familial risk effect ($F(3.97) = 7.21$, $p = 0.009$) as well as an interaction of familial risk and grade ($F(3.97) = 8.39$, $p = 0.005$) were revealed for the reaction times. FHD+ children had longer reaction times than FHD− children; however, the difference was significant only in case of first-graders ($M = 1.49$ s, $SD = 0.24$ and $M = 1.94$ s, $SD = 0.42$ for FHD− and FHD+ respectively, $p < 0.001$), but not in kindergarten pupils ($M = 1.81$ s, $SD = 0.43$ and $M = 1.79$ s, $SD = 0.31$ for FHD− and FHD+, respectively). In the FHD− group, there was also a grade effect ($p = 0.011$) with kindergarten pupils performing the task slower than first-graders. There were no significant group effects in the Rhyme task accuracy or in the reaction times and accuracy of the control Voice task.

The accuracy in the in-scanner Rhyme task was significantly correlated with behavioral tasks done outside the scanner—reading (letter knowledge— $r = 0.28$, $p = 0.005$; pseudo-word reading— $r = 0.21$, $p = 0.035$) and phonological awareness (phonemic analysis— $r = 0.26$, $p = 0.008$; phoneme deletion— $r = 0.29$, $p = 0.004$, RAN objects— $r = 0.21$, $p = 0.039$, RAN colors— $r = 0.25$, $p = 0.011$, pseudo-word alliteration— $r = 0.24$, $p = 0.014$, and pseudo-word rhyme— $r = 0.44$, $p < 0.001$) in the total sample. These correlations were mostly driven by the FHD+ group (letter knowledge— $r = 0.32$, $p = 0.012$; phonemic analysis— $r = 0.31$, $p = 0.016$; phoneme deletion— $r = 0.34$, $p = 0.007$, RAN objects— $r = 0.29$, $p = 0.026$, RAN colors— $r = 0.32$, $p = 0.013$, pseudo-word alliteration— $r = 0.35$, $p = 0.006$, and pseudo-word rhyme— $r = 0.52$, $p < 0.001$), whereas they were not significant in the

Table 1
Demographics and task performance characteristics of each group, ns—not significant.

	FHD – kindergarten	FHD + kindergarten	FHD – 1st grade	FHD + 1st grade	Main effect of grade	Main effect of risk	Interaction	Post hoc
Age	78.87 (± 4.93)	79.71 (± 4.73)	84.41 (± 6.28)	84.73 (± 6.37)	F(3,98) = 16.19, p < 0.001	ns	ns	1st grade > kindergarten
IQ (percentile)	82.62 (± 14.47)	75.12 (± 22.93)	78.29 (± 13.73)	76.98 (± 20.33)	ns	ns	ns	–
SES	45.63 (± 10.41)	49.00 (± 12.92)	50.22 (± 10.48)	46.38 (± 11.39)	ns	ns	ns	–
ARHQ_m	0.20 (± 0.08)	0.40 (± 0.15)	0.23 (± 0.08)	0.38 (± 0.14)	ns	F(3,98) = 42.79, p < 0.001	ns	FHD – < FHD +
ARHQ_p	0.29 (± 0.06)	0.42 (± 0.21)	0.24 (± 0.07)	0.42 (± 0.12)	ns	F(3,89) = 26.49, p < 0.001	ns	FHD – < FHD +
Letter knowledge ^a	–0.46 (± 1.04)	–0.24 (± 1.29)	0.16 (± 0.89)	0.13 (± 0.88)	F(3,98) = 5.06, p = 0.024	ns	ns	1st grade > kindergarten
Word reading ^a	–0.49 (± 0.27)	–0.19 (± 0.78)	0.32 (± 1.40)	0.27 (± 0.85)	F(3,98) = 5.77, p = 0.018	ns	ns	1st grade > kindergarten
Pseudo-word reading ^a	–0.48 (± 0.40)	–0.23 (± 0.83)	0.24 (± 1.24)	0.09 (± 0.96)	F(3,98) = 5.76, p = 0.018	ns	ns	1st grade > kindergarten
Phonemic analysis ^a	–0.47 (± 0.89)	–0.35 (± 1.09)	0.39 (± 0.91)	0.03 (± 0.96)	F(3,98) = 8.55, p = 0.004	ns	ns	1st grade > kindergarten
Phoneme deletion ^a	–0.55 (± 0.45)	–0.05 (± 1.05)	0.19 (± 1.17)	0.07 (± 0.95)	ns	ns	ns	–
RAN objects ^b	5.46 (± 2.15)	6.22 (± 2.62)	6.33 (± 2.06)	6.98 (± 1.72)	ns	ns	ns	–
RAN colors ^b	6.08 (± 2.43)	6.33 (± 2.47)	6.48 (± 1.81)	6.86 (± 1.82)	ns	ns	ns	–
Vocabulary ^a	–0.36 (± 1.09)	0.01 (± 0.93)	–0.01 (± 1.12)	0.10 (± 0.92)	ns	ns	ns	–
Print task ^a	–0.60 (± 1.07)	0.01 (± 0.80)	0.47 (± 0.88)	–0.11 (± 1.01)	F(3,98) = 5.12, p = 0.026	ns	F(3,98) = 8.02, p = 0.006	1st grade > kindergarten; FHD – > FHD + but only in 1st grade (p = 0.014); 1st grade > kindergarten in FHD – (p = 0.001)
Digit span ^a	–0.09 (± 0.99)	–0.38 (± 0.50)	0.29 (± 0.92)	–0.01 (± 1.14)	ns	ns	ns	–
Syllable span ^a	–0.17 (± 0.87)	–0.16 (± 0.92)	0.36 (± 1.05)	–0.10 (± 1.00)	ns	ns	ns	–
Pseudo-word alliteration ^a	–0.53 (± 0.82)	–0.06 (± 1.09)	0.13 (± 1.02)	0.10 (± 0.97)	ns	ns	ns	–
Pseudo-word rhyme ^a	–0.03 (± 0.97)	–0.29 (± 1.24)	0.28 (± 0.84)	–0.05 (± 0.97)	ns	ns	ns	–

^a Standardized residuals of raw test scores adjusted for age.

^b Standardized test scores.

FHD – group, since most of FHD – children performed the in-scanner task at ceiling. Reaction time in the in-scanner rhyme task was correlated only with maternal and paternal ARHQ ($r = 0.24$, $p = 0.015$; and $r = 0.20$, $p = 0.053$) in the total sample, while it was not significant when the group was split to FHD + and FHD – children.

fMRI results

Whole-brain analysis (with one-sample t-test) showed increased activation for Rhyme > Voice tasks in FHD – kindergarten pupils in a number of brain regions, including bilateral cerebellum, frontal lobe (bilateral middle frontal and precentral gyrus, left superior frontal gyrus), parietal lobe (bilateral inferior parietal lobule), temporal lobe (bilateral middle temporal gyrus and right superior temporal), occipital lobe (bilateral fusiform and lingual gyri), left limbic lobe, and subcortical

structures (left caudate and bilateral putamen). FHD + kindergarten children did not show any supra-threshold activation for the same contrast. However, at a lower threshold of $p < 0.05$ (uncorrected), the activation appeared in bilateral insula, left superior temporal gyrus, left putamen and left middle cingulate. FHD – children from first grade activated a few regions in Rhyme > Voice contrast, such as the bilateral temporal lobe (right inferior temporal gyrus, right and left superior temporal gyrus), as well as the insula bilaterally. FHD + first-graders did not show any significant activation during Rhyme > Voice contrast at $p < 0.005$. When the threshold was relaxed to $p < 0.05$ (uncorrected), the activity was found in the left cerebellum (lobule IV and V) and left middle frontal gyrus. Fig. 2 depicts brain activity for Rhyme > Voice contrast in each studied group.

In order to examine the effect of familial risk, grade and their interaction, a full factorial analysis was performed (see Fig. 3A and

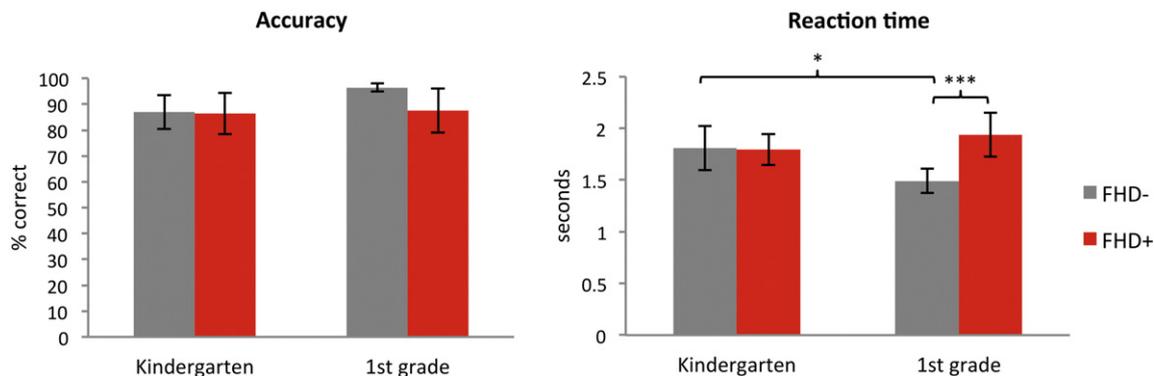


Fig. 1. Performance in the rhyme task during fMRI scanning. Error bars represent standard deviation. * $p < 0.05$, *** $p < 0.001$.

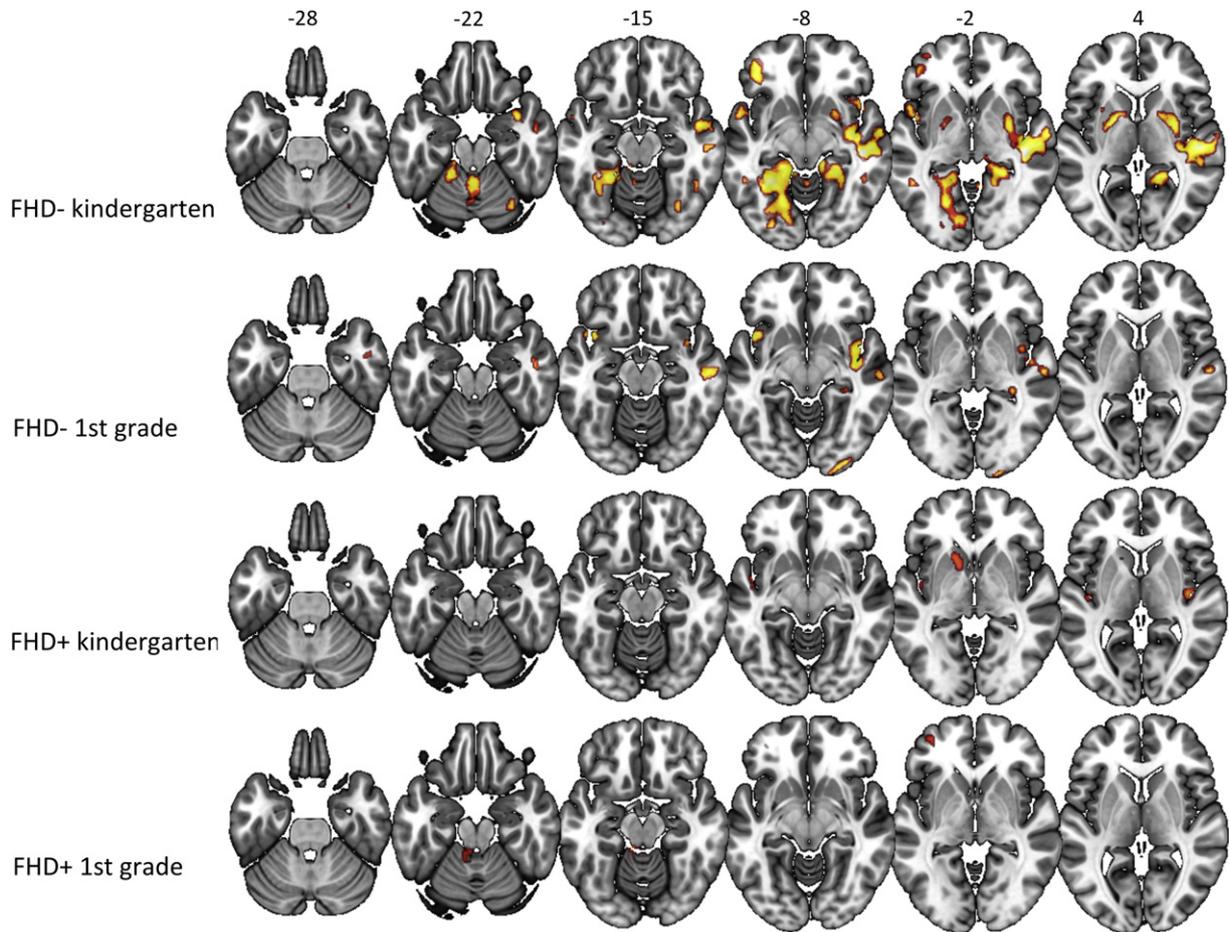


Fig. 2. Activation for Rhyme > Voice tasks for FHD – and FHD + children in kindergarten and first grade.

Table 2). The effect of risk was seen in many regions including bilateral temporal, tempo-parietal, and inferior temporal–occipital regions, as well as bilateral inferior and middle frontal gyri. Subcortically, the effect was present in the bilateral thalami, caudate, and the right putamen. In all of these regions, FHD + children showed hypoactivation compared to FHD – children. The effect of grade was restricted to one cluster in the left inferior frontal and precentral gyri. Here, the kindergarten pupils had increased activation compared to first-graders.

The interaction between risk and grade was found in several regions including right middle frontal and postcentral gyrus, three clusters in the left ventral occipital cortex including lingual, inferior, middle occipital and fusiform gyri as well as left inferior and middle orbital gyri. Fig. 3B presents contrast estimates for each group for 6 clusters showing the interaction effect. Post hoc tests on the extracted contrast estimates revealed significant grade effect that was present almost exclusively in FHD – children (besides right middle frontal gyrus, where it was present also in FHD + group). It was related to decreased activation in first-graders compared to kindergarten pupils, besides right postcentral gyrus in FHD – children and right middle frontal gyrus in FHD + children. Additionally, significant difference between FHD + and FHD – children was revealed in kindergarten pupils in all regions besides the right postcentral gyrus, where the difference was significant for first-graders. In all cases, the FHD + children had lower activation than FHD – children.

The activity in two regions in the left ventral occipito-temporal cortex (the left inferior occipital, fusiform, and lingual gyri and left fusiform gyrus) correlated with accuracy in the pseudo-word rhyming task but only in the FHD + group ($r = 0.34$, $p = 0.006$ and $r = 0.36$, $p = 0.004$, respectively, see Fig. 4). The first correlation remained significant also for the total sample ($r = 0.21$, $p = 0.035$).

Discussion

The present study investigated the relation between neuronal mechanisms underlying phonological awareness, the impact of schooling, and familial risk for developmental dyslexia in beginning Polish readers.

At the behavioral level, no major differences between FHD + and FHD – children on standard reading and reading-related tests were found. However, in the older cohort (first-graders), differences emerged on a simple orthographic awareness (print task) and on the in-scanner rhyme task. FHD + children compared to FHD – children in the first grade had lower accuracy in the early print task as well as longer reaction times in the in-scanner rhyme task. What is more, in these tasks, only in the FHD – group was there a significant progress in performance in first-graders compared to kindergarten pupils. Of course any behavioral differences with a print task would be more likely to emerge after the onset of formal reading instruction and, while this is interesting, we need to be cautious since differences were modest and did not show up on a number of standardized measures. With regard to rhyming, we might speculate that the effect of family risk on latencies for the in-scanner phonological task could reflect a subtle feedback effect of slightly better reading on auditory phonological processing only in first-graders.

As to why familial effects on print (and rhyming) behavioral performance would emerge only after formal instruction has begun, findings from behavioral genetics twin studies encourage an intriguing speculation. The impact of heritability relative to shared environment increases after children enter school on a number of tests (Byrne et al., 2005; Petrill et al., 2007), and it has been argued that school reduces environmental variance and hence reveals more clearly, subtle genetic influences. To the degree that familial history reflects genetics in some

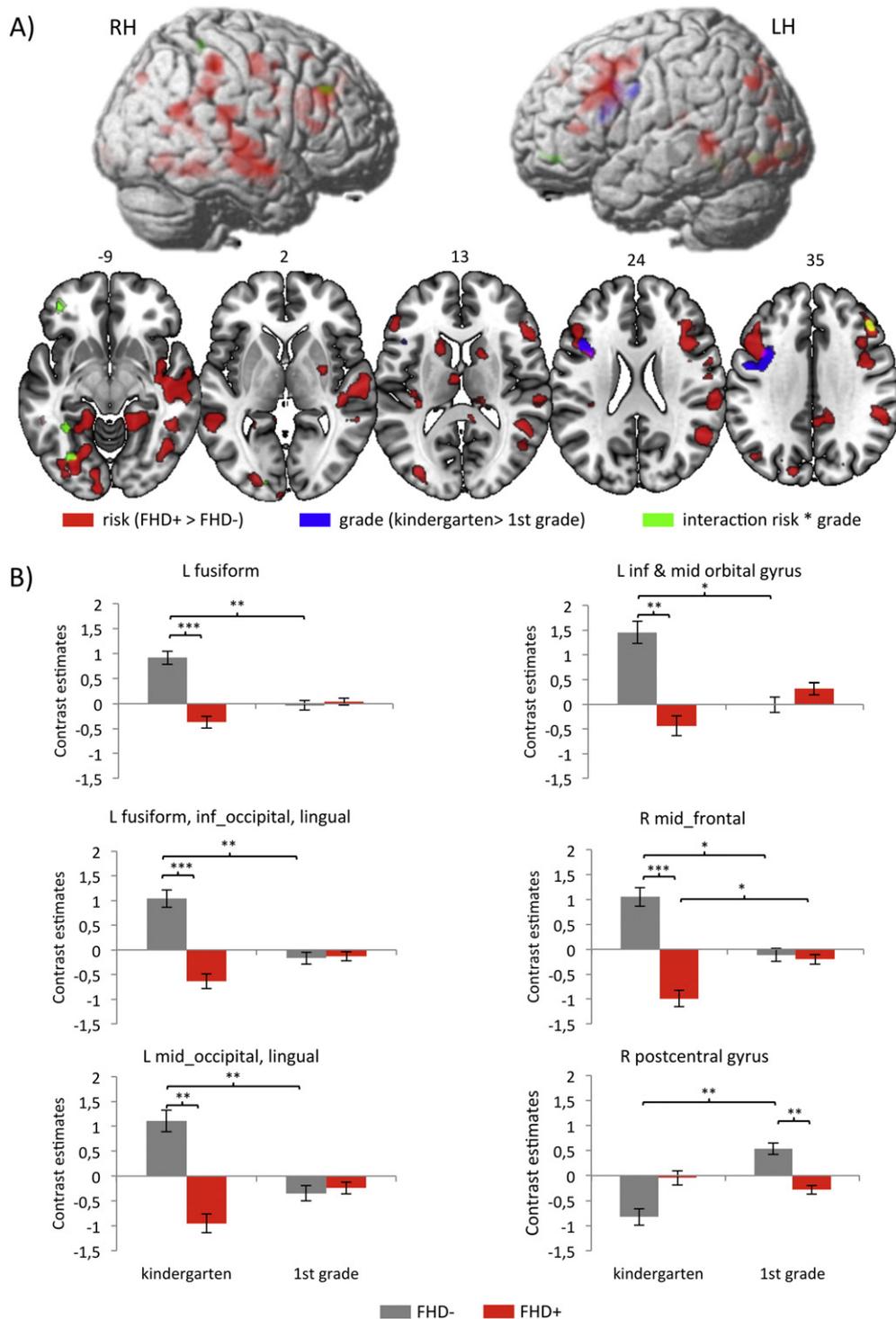


Fig. 3. A) Main effects of familial risk of dyslexia, grade and the interaction of these two factors in the Rhyme > Voice contrast; B) contrast estimates from clusters showing significant risk*grade interaction. Error bars represent standard error of mean, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

direct manner there could be parallels here. In any case, these data might be taken to suggest that risk associated with family history could be amplified by schooling and if this result holds up in future investigations it points to a complex genetic environmental interaction that dyslexia models are not well structured to predict at present.

With regard to cross-language behavioral comparisons, previous studies on English-speaking pre-schoolers of similar age have reported lower scores in at-risk children on different phonological (Kovelman et al., 2012; Pennington and Lefly, 2001; Raschle et al., 2012) and reading-related tests (Gallagher et al., 2000; Im et al. in press). The

pattern of results from shallower orthographies is less consistent. While Finnish-speaking FHD+ pre-schoolers showed problems with early reading and phonological awareness tasks (Lyytinen et al., 2006), Italian-speaking FHD+ kindergartens performed worse only in syllabic segmentation and visual attention, but did not differ from FHD- children in phonological processing (Facoetti et al., 2010). Finally, in a Norwegian longitudinal study, at-risk children performed significantly lower in reading and spelling tests but only when they reached second grade, while in preschool and first grade no significant differences were present (Specht et al., 2009). Thus, the lack of strong

Table 2
Significant brain activation for the main effect of familial risk of dyslexia, main effect of grade and their interaction.

Brain region	Hemisphere	x	y	z	F	Voxels
<i>Main effect of familial risk</i>						
Superior & middle temporal gyrus	R	51	-18	-18	19.56	3538
Middle frontal gyrus, precentral gyrus, inferior frontal gyrus (tri and oper)	L	-46	16	32	18.06	2053
Middle cingulate, precuneus	R	14	-39	45	17.14	596
Inferior temporal gyrus, fusiform gyrus, lingual gyrus	R	51	-45	-13	17.22	1597
Supramarginal gyrus, superior and middle temporal gyrus, inferior parietal lobule, angular gyrus,	R	54	-57	21	16.39	1562
Middle frontal gyrus	R	33	19	54	16.02	71
Precentral gyrus, Inferior frontal gyrus (tri and oper), Middle frontal gyrus	R	46	30	32	15.91	1989
Middle temporal gyrus	L	-56	-45	-1	15.63	548
Angular gyrus, middle occipital gyrus	L	-44	-72	38	13.53	242
Lingual gyrus, calcarine	L	-3	-102	-2	13.18	282
Thalamus (pulvinar)	R	10	-18	18	13.03	84
Inferior frontal gyrus (tri)	L	-52	30	11	12.61	114
Thalamus (ventral anterior)	L	-9	-14	17	12.75	147
Rolandic operculum, Heschl's gyrus, insula	L	-34	-32	21	12.67	172
Medial superior frontal gyrus	L&R	2	39	39	12.88	266
Inferior occipital gyrus, lingual gyrus, fusiform gyrus	L	-20	-68	-6	12.25	1009
Lingual gyrus, fusiform gyrus	L	-16	-44	-7	12.02	502
Superior occipital gyrus, cuneus	R	26	-80	40	11.16	148
Rolandic operculum, postcentral and precentral gyri	R	54	-8	20	11.28	176
Middle temporal gyrus	R	46	-63	11	11.57	106
Middle occipital gyrus	L	-36	-84	15	11.53	187
Precuneus, posterior cingulate, calcarine	R	8	-39	18	10.75	139
Precuneus, posterior cingulate, calcarine	L	-8	-41	5	10.84	78
Caudate	L	-18	12	11	10.60	83
Caudate	R	16	9	15	10.46	75
Superior occipital gyrus, superior parietal lobule, cuneus	L	-22	-77	53	9.94	173
Putamen	R	30	-3	2	9.87	52
Superior occipital gyrus, cuneus	L	-16	-84	33	9.72	135
<i>Main effect of grade</i>						
Precentral gyrus, inferior frontal gyrus (tri and oper)	L	-44	16	21	13.31	735
<i>Familial risk × grade interaction</i>						
Middle frontal gyrus	R	46	31	35	16.04	70
Fusiform gyrus, inferior occipital gyrus, lingual gyrus	L	-30	-72	-6	11.22	93
Middle occipital gyrus, lingual gyrus	L	-15	-89	-3	11.26	67
Inferior and middle orbital gyrus	L	-38	49	-7	10.80	79
Fusiform gyrus	L	-33	-48	-6	10.71	89
Postcentral gyrus	R	22	-42	60	10.63	94

behavioural differences between FHD+ and FHD- children in the present study could be related to orthographic transparency, as the Polish language has rather shallow orthography. This is consistent with the

results showing that phonological awareness, although being the strongest predictor of reading success in childhood, is moderated by language transparency, being stronger in deep orthographies and weaker in more

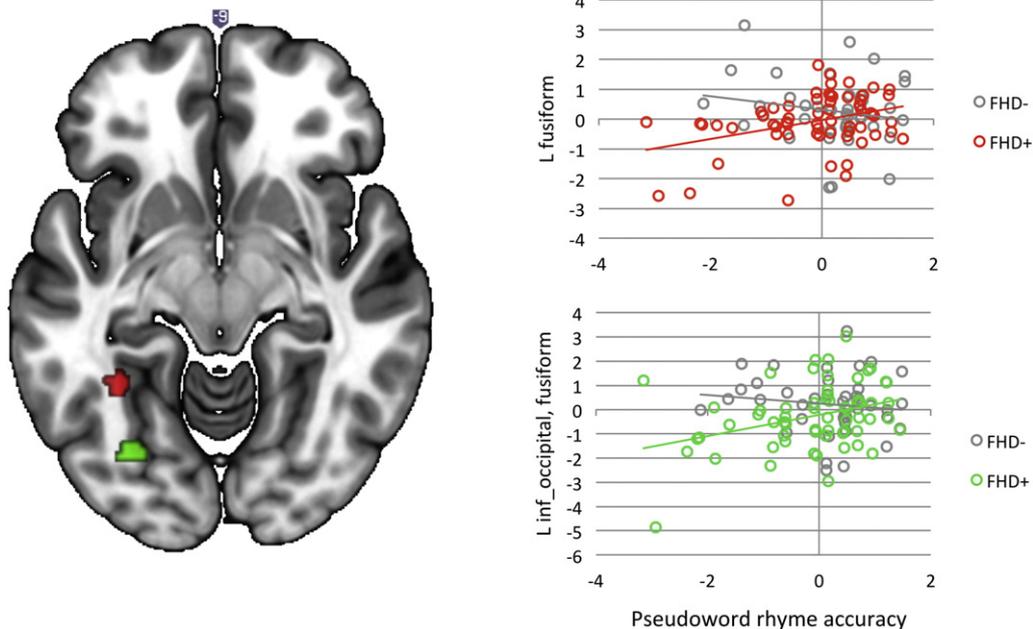


Fig. 4. Correlation between the activity in the ventral occipito-temporal cortex for the Rhyme > Voice contrast and the accuracy in the pseudo-word rhyming in FHD+ and FHD- children.

transparent ones (Richlan, 2014; Ziegler et al., 2010). Last but not least, since some behavioral differences emerged in the first-graders, it is possible that only when formal literacy instruction begins can one differentiate between FHD+ and FHD− children in shallow orthography and that would be consistent with the Norwegian data (Specht et al., 2009).

At the neuronal level, a very different story emerged. The Rhyme > Voice contrast failed to produce significant brain activity in FHD+ children at the conventional statistical threshold. This result is consistent with previous studies conducted on English-speaking readers (Kovelman et al., 2012) and pre-readers (Raschle et al., 2012). One explanation might be that FHD+ children failed to engage additional phonological processing brain regions in the Rhyme task beyond the ones engaged during Voice task. This might seem in contrast to Desroches et al.'s (2010) findings, where dyslexic children showed brain activity of similar strength and extent as the controls. However, this study, instead of a Voice or word matching task, used a low-level control to which rhyming was contrasted. On the other hand, several brain areas in the frontal, temporal, and parietal lobes were engaged in FHD− children. The pattern of activation was much more extended in the group of kindergarten pupils than in the first-graders, involving both cortical and subcortical structures. These results might be related to other studies in English, showing more widely distributed reading-related circuitry in emergent readers than in older cohorts in general. With increased experience in phonological decoding, the circuitry becomes more specialized and the functional role of a given region is shaped by its activity-dependent connections with other regions (Pugh et al., 2013; Johnson et al., 2002; Church et al., 2008).

With regard to specific main effects of age, only one cluster in the left inferior frontal and precentral gyri showed a significant grade effect, with higher activity in the kindergarten pupils than first-graders. This region has been widely implicated in phonological tasks (Burton, 2001; Zatorre et al., 1996) and some studies differentiate between its dorsal and ventral parts showing preferential activation for phonological and semantic processing, respectively (Bokde et al., 2001; Devlin et al., 2003; Poldrack et al., 1999). With respect to the current study, the cluster displaying grade effect was close to previously reported coordinates of the dorsal part of the inferior frontal gyrus associated with phonological processing. This area presented a developmental increase in activation in an auditory rhyme task in a group of 9- to 15-year-old children, but only for conflicting (orthographically similar but phonologically dissimilar conditions) compared to non-conflicting non-rhyming trials (Cone et al., 2008). In Polish, the rhymes always have orthographically similar representations, so it is never the case that orthography can interfere with phonology. Hence, it is possible that older children, thanks to reading training, can already profit from a similar representation of rhyme in the orthographic domain and therefore rely less on inferior frontal gyrus recruitment in phonological processing. Support for such an interpretation comes from behavioral studies illustrating the influence of orthographic information on the speed of spoken word recognition during auditory rhyme judgment (Donnenwerth-Nolan et al., 1981; Seidenberg and Tanenhaus, 1979).

In the current study, familial risk was associated with extensive hypoactivation in many brain areas, including cortical inferior frontal, temporal, tempo-parietal, and occipital regions, as well as subcortical regions. Our results thus indicate that despite the advantages that transparent orthography can offer at the behavioral level, Polish beginning readers with familial risk for dyslexia present a typical pattern of hypoactivations in the left hemispheric regions, previously seen in dyslexia (i.e. the left tempo-parietal region, left occipito-temporal cortex, and the left inferior frontal/dorsolateral prefrontal cortex, see Richlan et al., 2011) and consistent with English studies of similar populations (Raschle et al., 2012). Moreover, we found that the activity in the left occipito-temporal cortex correlated with the pseudo-word rhyming test (performed outside the scanner), suggesting that this region makes an important contribution to phonological awareness, in line

with previous English studies (Shaywitz et al., 2002). Interestingly, the correlation was driven mostly by the FHD+ children, whereas in the FHD− group, it was not significant. This result is somewhat similar to what Raschle et al. (2012) found in pre-readers, where correlation between brain activity in an alliteration judgment task and non-word repetition (performed outside the scanner) in the left middle temporal gyrus was significant only in the FHD+ group. They argued that the fact that there was no significant correlation with phonological skills in FHD− children suggests that this region has been fully developed and an increased skill level does not lead to increase in activation in this region. In contrast, the significant correlation in FHD+ children would indicate emerging specialization of the left occipito-temporal cortex.

In several regions, including the left inferior occipito-temporal and fusiform cortex, a significant interaction between familial risk and grade was revealed. In these regions, the effect of familial risk was present only in kindergarten pupils with decreased activation in FHD+ compared to FHD− children, coupled with a grade effect (lower activity in first-graders compared to kindergarten pupils) present only in the FHD− group. Efficient reading in adults is typically associated with lower reading activation (Heim et al., 2013; Twomey et al., 2013) but increased anatomical connectivity within the reading network (Lebel et al., 2013). Perhaps several language processing brain regions, which in the kindergarten pupils are involved in phonological awareness, are not so essential when both phonological awareness and reading become more accurate and fluent in the first grade (and specifically as greater print knowledge actually feeds back on phonological skills (see Castles and Coltheart, 2004 for discussion of bidirectional relations)). These results seem also in line with previous studies on English children. In the pre-reading group, the activity of many more regions distinguished between FHD+ and FHD− children, including also the left occipito-temporal cortex (Raschle et al., 2012), whereas in the older readers, the dyslexic group showed hypoactivation only in the left DLPFC (Kovelman et al., 2012). Again while family history may have increased impacts on behaviour after formal reading instruction, data like these suggest that the core circuits become more circumscribed with this learning. Thus the impact of schooling on risk markers is quite distinct at the behavioral and brain levels of analysis in the current data.

To conclude, Polish children with familial risk for dyslexia show subtle behavioral weaknesses compared to control children, but only after the onset of schooling. We might expect these differences to increase as we track children through a longer period of formal reading instruction, but this awaits further studies. Despite this small behavioural advantage (compared to previous findings in less transparent orthographies), they present a typical pattern of hypoactivations in the left tempo-parietal region, left occipito-temporal cortex, and the left inferior frontal/dorsolateral prefrontal cortex, as previously seen in dyslexia. Formal reading instruction (schooling) affects both behaviour and brain activation related to phonological processing.

Limitations

The present results should be treated cautiously, as it remains to be determined which children with familial risk for developmental dyslexia will develop reading disability. Since at the time when this study was carried out, Polish adaptation of Adult Reading History Questionnaire was not yet available, we administered the original ARHQ (Lefly and Pennington, 2000) translated into Polish and applied conservative cut-off established for English-speaking population (Black et al., 2012). Even though one could speculate that ARHQ questions are culturally universal, one of the limitations is the lack of cut offs calculated and tested in the Polish population. Additionally, the schooling/age effects were interpreted based on a cross-sectional study design instead of a longitudinal, which can be more influenced by the cohort effects and is therefore less representative for the population of interest. The variability of

duration of exposure to literacy instruction in the first-grade students was also somewhat high with 22.2% of children being exposed to 70–100 days of literacy instruction, which might have been too low to observe significant changes in BOLD signal. Last but not least, even though the total sample size was relatively large in the present study, the groups were unbalanced and there were only 13 FHD – children in the kindergarten group, which constitutes a relatively small sample, although comparable with previous studies (Kovelman et al., 2012).

Acknowledgments

We would like to thank all the families which participated in the current study. This work was funded by grants from the Polish Ministry of Science and Higher Education (IP2011 020271) and the National Science Center (DEC-2011/03/D/HS6/05584). The project was realized with the aid of CePT research infrastructure purchased with funds from the European Regional Development Fund as part of the Innovative Economy Operational Programme, 2007–2013.

References

- Aro, M., Wimmer, H., 2003. Learning to read: English in comparison to six more regular orthographies. *Appl. Psychol.* 24, 621–635.
- Ashburner, J., 2007. A fast diffeomorphic image registration algorithm. *NeuroImage* 38, 95–113.
- Awramiuk, E., Krasowicz-Kupis, G., 2014. Reading and spelling acquisition in Polish: educational and linguistic determinants. *L1-Educ. Stud. Lang. Lit.* 14, 1–24.
- Black, J.M., Tanaka, H., Stanley, L., Nagamine, M., Zakerani, N., Thurston, A., Kesler, S., Hulme, C., Lyytinen, H., Glover, G.H., Serrone, C., Raman, M.M., Reiss, A.L., Hoefl, F., 2012. Maternal history of reading difficulty is associated with reduced language-related gray matter in beginning readers. *NeuroImage* 59, 3021–3032.
- Bokde, A.L., Tagamets, M.A., Friedman, R.B., Horwitz, B., 2001. Functional interactions of the inferior frontal cortex during the processing of words and word-like stimuli. *Neuron* 30, 609–617.
- Bolger, D.J., Minas, J., Burman, D.D., Booth, J.R., 2008. Differential effects of orthographic and phonological consistency in cortex for children with and without reading impairment. *Neuropsychologia* 46, 3210–3224.
- Bosse, M.L., Tainturier, M.J., Valdois, S., 2007. Developmental dyslexia: the visual attention span deficit hypothesis. *Cognition* 104, 198–230.
- Bradley, L., Bryant, P.E., 1978. Difficulties in auditory organisation as a possible cause of reading backwardness. *Nature* 271, 746–747.
- Brett, M., Anton, J.-L., Valabregue, R., Poline, J.-B., 2002. Region of interest analysis using an SPM toolbox. *NeuroImage* 16, S497.
- Burton, M.W., 2001. The role of the inferior frontal cortex in phonological processing. *Cogn. Sci.* 25, 695–709.
- Byrne, B., Wadsworth, S., Corley, R., Samuelsson, S., Quain, P., DeFries, J.C., et al., 2005. Longitudinal twin study of early literacy development: preschool and kindergarten phases. *Sci. Stud. Read.* 9, 219–235.
- Cao, F., Bitan, T., Chou, T.L., Burman, D.D., Booth, J.R., 2006. Deficient orthographic and phonological representations in children with dyslexia revealed by brain activation patterns. *J. Child Psychol. Psychiatry* 47, 1041–1050.
- Caravolas, M., Lervåg, A., Mousioku, P., Efrim, C., Litavsky, M., Onochie-Quintanilla, E., Salas, N., Schöffelová, M., Defior, S., Mikulajová, M., Seidlová-Málková, G., Hulme, C., 2012. Common patterns of prediction of literacy development in different alphabetic orthographies. *Psychol. Sci.* 23, 678–686.
- Caravolas, M., Lervåg, A., Defior, S., Seidlová Málková, G., Hulme, C., 2013. Different patterns, but equivalent predictors, of growth in reading in consistent and inconsistent orthographies. *Psychol. Sci.* 24, 1398–1407.
- Castles, A., Coltheart, M., 2004. Is there a causal link from phonological awareness to success in learning to read? *Cognition* 91, 77–111.
- Castles, A., Datta, H., Gayan, J., Olson, R.K., 1999. Varieties of developmental reading disorder: genetic and environmental influences. *J. Exp. Child Psychol.* 72, 73–94.
- Castles, A., Wilson, K., Coltheart, M., 2011. Early orthographic influences on phonemic awareness tasks: evidence from a preschool training study. *J. Exp. Child Psychol.* 108, 203–210.
- Castro-Caldas, A., Peterson, K.M., Reis, A., Stone-Elender, S., Ingvar, M., 1998. The illiterate brain: learning to read and write during childhood influences the functional organization of the adult brain. *Brain* 121, 1053–1063.
- Church, J.A., Coalson, R.S., Lugar, H.M., Petersen, S.E., Schlaggar, B.L., 2008. A developmental fMRI study of reading and repetition reveals changes in phonological and visual mechanisms over age. *Cereb. Cortex* 18, 2054–2065.
- Cone, N.E., Burman, D.D., Bitan, T., Bolger, D.J., Booth, J.R., 2008. Developmental changes in brain regions involved in phonological and orthographic processing during spoken language processing. *NeuroImage* 41, 623–635.
- Cronin, V., Carver, P., 1998. Phonological sensitivity, rapid naming and beginning reading. *Appl. Psychol.* 19, 447–461.
- Dandache, S., Wouters, J., Ghesquière, P., 2014. Development of reading and phonological skills of children at family risk for dyslexia: a longitudinal analysis from kindergarten to sixth grade. *Dyslexia* 20, 305–329.
- DeFries, J.C., Plomin, R., LaBuda, M.C., 1987. Genetic stability of cognitive development from childhood to adulthood. *Dev. Psychol.* 23, 4–12.
- Dehaene, S., Pegado, F., Braga, L.W., Ventura, P., Nunes Filho, G., Jobert, A., Dehaene-Lambertz, G., Kolinsky, R., Morais, J., Cohen, L., 2010. How learning to read changes the cortical networks for vision and language. *Science* 330, 1359–1364.
- Dehaene, S., Cohen, L., Morais, J., Kolinsky, R., 2015. Illiterate to literate: behavioural and cerebral changes induced by reading acquisition. *Nat. Rev. Neurosci.* 16, 234–244.
- Desroches, A.S., Cone, N.E., Bolger, D.J., Bitan, T., Burman, D.D., Booth, J.R., 2010. Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Res.* 1356, 73–84.
- Devlin, J.T., Matthews, P.M., Rushworth, M.F., 2003. Semantic processing in the left inferior prefrontal cortex: a combined functional magnetic resonance imaging and transcranial magnetic stimulation study. *J. Cogn. Neurosci.* 15 (1), 71–84.
- Donnenwerth-Nolan, S., Tanenhaus, M.K., Seidenberg, M.S., 1981. Multiple code activation in word recognition: evidence from rhyme monitoring. *J. Exp. Psychol. Hum. Learn. Mem.* 7, 170–180.
- Ehri, L., Nunes, S., Willows, D., Schuster, B., Yaghoub-Zadeh, Z., Shanahan, T., 2001. Phonemic awareness instruction helps children learn to read: evidence from the National Reading Panel's meta-analysis. *Read. Res. Q.* 36, 250–287.
- Facchetti, A., Corradi, N., Ruffino, M., Gori, S., Zorzi, M., 2010. Visual spatial attention and speech segmentation are both impaired in preschoolers at familial risk for developmental dyslexia. *Dyslexia* 16, 226–239.
- Fecenc, D., Jaworowska, A., Matczak, A., Stańczak, J., Zalewska, E., 2013. Test szybkiego nazywania (TSN). *Podręcznik. Pracownia Testów Psychologicznych Polskiego Towarzystwa Psychologicznego, Warszawa (Poland).*
- Fisher, S.E., Francks, C., 2006. Genes, cognition and dyslexia: learning to read the genome. *Trends Cogn. Sci.* 10, 250–257.
- Gallagher, A., Frith, U., Snowling, M.J., 2000. Precursors of literacy delay among children at genetic risk of dyslexia. *J. Child Psychol. Psychiatry* 41, 203–213.
- Guttorm, T., 2003. Newborn brain responses measuring feature and change detection and predicting later language development in children with and without familial risk for dyslexia. *Jyväskylä Studies in Education, Psychology and Social Research. Jyväskylä Studies in Education, Psychology and Social Research*, p. 225.
- Guttorm, T.K., Leppänen, P.H.T., Richardson, U., Lyytinen, H., 2001. Event-related potentials and consonant differentiation in newborns with familial risk for dyslexia. *J. Learn. Disabil.* 34, 534–544.
- Guttorm, T.K., Leppänen, P.H., Poikkeus, A.M., Eklund, K.M., Lyytinen, P., 2005. Lyytinen H, Brain event-related potentials (ERPs) measured at birth predict later language development in children with and without familial risk for dyslexia. *Cortex* 41, 291–303.
- Hadzibeganovic, T., Van Den Noort, M., Bosch, P., Perc, M., Van Kralingen, R., Mondt, K., Coltheart, M., 2010. Cross-linguistic neuroimaging and dyslexia: a critical view. *Cortex* 46, 1312–1316.
- Haman, E., Fronczyk, K., Łuniewska, M., 2012. *Obrazkowy Test Słownikowy – Rozumienie (OTS)*. *Podręcznik. Pracownia Testów Psychologicznych, Gdansk (Poland).*
- Heim, S., Wehnelt, A., Grande, M., Huber, W., Amunts, K., 2013. Effects of lexicality and word frequency on brain activation in dyslexic readers. *Brain Lang.* 125, 194–202.
- Hoefl, F., Meyler, A., Hernandez, A., Juel, C., Taylor-Hill, H., Martindale, J.L., McMillon, G., Kolchugina, G., Black, J.M., Faizi, A., Deutsch, G.K., Siok, W.T., Reiss, A.L., Whitfield-Gabrieli, S., Gabrieli, J.D., 2007. Functional and morphometric brain dissociation between dyslexia and reading ability. *Proc. Natl. Acad. Sci. U. S. A.* 104, 4234–4239.
- Hollingshead AB (1975): *Four-Factor Index of Social Status*. Unpublished manuscript, Yale University, New Haven, CT.
- Im, K., Raschle, N.M., Smith, S.A., Ellen Grant, P., Gaab, N., 2016. Atypical sulcal pattern in children with developmental dyslexia and at-risk kindergarteners. *Cereb. Cortex* <http://dx.doi.org/10.1093/cercor/bhu305> (in press).
- Johnson, M.H., Halit, H., Grice, S.J., Karmiloff-Smith, A., 2002. Neuroimaging of typical and atypical development: a perspective from multiple levels of analysis. *Dev. Psychopathol.* 14, 521–536.
- Kevan, A., Pammer, K., 2008. Visual processing deficits in preliterate children at familial risk for dyslexia. *Vis. Res.* 48, 2835–2839.
- Kovelman, I., Norton, E.S., Christodoulou, J.A., Gaab, N., Lieberman, D.A., Triantafyllou, C., Wolf, M., Whitfield-Gabrieli, S., Gabrieli, J.D., 2012. Brain basis of phonological awareness for spoken language in children and its disruption in dyslexia. *Cereb. Cortex* 22, 754–764.
- Landerl, K., Ramus, F., Moll, K., Lyytinen, H., Leppänen, P.H., Lohvansuu, K., et al., 2013. Predictors of developmental dyslexia in European orthographies with varying complexity. *J. Child Psychol. Psychiatry* 54, 686–694.
- Lebel, C., Shaywitz, B., Holahan, J., Shaywitz, S., Marchione, K., Beaulieu, C., 2013. Diffusion tensor imaging correlates of reading ability in dysfluent and non-impaired readers. *Brain Lang.* 125, 215–222.
- Lefly, D., Pennington, B.F., 2000. Reliability and validity of the adult reading history questionnaire. *J. Learn. Disabil.* 33, 286–296.
- Leppänen, P.H.T., Hämäläinen, J.A., Salminen, H.K., Eklund, K.M., Guttorm, T.K., Lohvansuu, K., et al., 2010. Newborn brain event-related potentials revealing atypical processing of sound frequency and the subsequent association with later literacy skills in children with familial dyslexia. *Cortex* 46, 1362–1376.
- Lonigan, C.J., Burgess, S.R., Anthony, J.L., 2000. Development of emergent literacy and early reading skills in preschool children: evidence from a latent-variable longitudinal study. *Dev. Psychol.* 36, 596–613.
- Lyytinen, H., Aro, M., Eklund, K., Erskine, J., Guttorm, T., Laakso, M.L., Leppänen, P.H., Lyytinen, P., Poikkeus, A.M., Torppa, M., 2004. The development of children at familial risk for dyslexia: birth to early school age. *Ann. Dyslexia* 54, 184–220.
- Lyytinen, H., Guttorm, T.K., Huttunen, T., Paavo, J.H., Leppänen, H.T., Vesterinen, M., 2005. Psychophysiology of developmental dyslexia: a review of findings including studies of children at risk for dyslexia. *J. Neurolinguistics* 18, 167–195.

- Lyytinen, H., Erskine, J., Tolvanen, A., Torppa, M., Poikkeus, A.M., Lyytinen, P., 2006. Trajectories of reading development: a follow-up from birth to school age of children with and without risk for dyslexia. *Merrill-Palmer Q.* 52, 514–546.
- Mann, V., Wimmer, H., 2002. Phoneme awareness and pathways into literacy: a comparison of German and American children. *Read. Writ.* 15, 653–682.
- Olson, M., Hood, L., Cantor, C., Botstein, D., 1989. A common language for physical mapping of the human genome. *Science* 245, 1434–1435.
- Paulesu, E., McCrory, E., Fazio, F., Menoncello, L., Brunswick, N., Cappa, S.F., Cotelli, M., Cossu, G., Corte, F., Lorusso, M., Pesenti, S., Gallagher, A., Perani, D., Price, C., Frith, C.D., Frith, U., 2000. A cultural effect on brain function. *Nat. Neurosci.* 3, 91–96.
- Paulesu, E., Démonet, J.F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., 2001. Dyslexia: cultural diversity and biological unity. *Science* 291, 2165–2167.
- Paulesu, E., Danelli, L., Berlinger, M., 2014. Reading the dyslexic brain: multiple dysfunctional routes revealed by a new meta-analysis of PET and fMRI activation studies. *Front. Hum. Neurosci.* 8, 830.
- Pennington, B.F., Lefly, D.L., 2001. Early reading development in children at family risk for dyslexia. *Child Dev.* 72, 816–833.
- Petrill, S.A., Deater-Deckard, K., Thompson, L.A., Schatschneider, C., DeThorne, L.S., Vandenberg, D.J., 2007. Longitudinal genetic analyses of early reading: the Western Reserve Reading Project. *Read. Writ. Interdiscip. J.* 20, 127–146.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D., 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* 10, 15–35.
- Pugh, K.R., Landi, N., Preston, J.L., Mencl, W.E., Austin, A.C., Sibley, D., Fulbright, R.K., Seidenberg, M.S., Grigorenko, E.L., Constable, R.T., Molfese, P., Frost, S.J., 2013. The relationship between phonological and auditory processing and brain organization in beginning readers. *Brain Lang.* 125, 173–183.
- Raschle, N.M., Zuk, J., Gaab, N., 2012. Functional characteristics of developmental dyslexia in left-hemispheric posterior brain regions predate reading onset. *Proc. Natl. Acad. Sci. U. S. A.* 109, 2156–2161.
- Richlan, F., 2014. Functional neuroanatomy of developmental dyslexia: the role of orthographic depth. *Front. Hum. Neurosci.* 8, 347.
- Richlan, F., Kronbichler, M., Wimmer, H., 2009. Functional abnormalities in the dyslexic brain: a quantitative meta-analysis of neuroimaging studies. *Hum. Brain Mapp.* 30, 3299–3308.
- Richlan, F., Kronbichler, M., Wimmer, H., 2011. Meta-analyzing brain dysfunctions in dyslexic children and adults. *NeuroImage* 56, 1735–1742.
- Rueckl, J.G., Paz-Alonso, P.M., Molfese, P.J., Kuo, W.J., Bick, A., Frost, S.J., Hancock, R., Wu, D.H., Mencl, W.E., Duñabeitia, J.A., Lee, J.R., Oliver, M., Zevin, J.D., Hoefft, F., Carreiras, M., Tzeng, O.J., Pugh, K.R., Frost, R., 2016. Universal brain signature of proficient reading: evidence from four contrasting languages. *Proc. Natl. Acad. Sci. U. S. A.* (in press).
- Seidenberg, M.S., Tanenhaus, M.K., 1979. Orthographic effects on rhyme monitoring. *J. Exp. Psychol. Hum. Learn. Mem.* 5, 546–554.
- Seymour, P.H.K., Aro, M., Erskine, J.M., 2003. Foundation literacy acquisition in European orthographies. *Br. J. Psychol.* 94, 143–174.
- Share, D.L., 2008. On the anglocentricities of current reading research and practice: the perils of overreliance on an “outlier” orthography. *Psychol. Bull.* 134, 584–615.
- Shaywitz, B.A., Shaywitz, S.E., Pugh, K.R., Mencl, W.E., Fulbright, R.K., Skudlarski, P., et al., 2002. Disruption of posterior brain systems for reading in children with developmental dyslexia. *Biol. Psychiatry* 52, 101–110.
- Silani, G., Frith, U., Demonet, J.F., Fazio, F., Perani, D., Price, C.J., 2005. Brain abnormalities underlying altered activation in dyslexia: a voxel based morphometry study. *Brain* 128, 2453–2461.
- Snowling, M.J., Hulme, C., 2011. Evidence-based interventions for reading and language difficulties: creating a virtuous circle. *Br. J. Psychol.* 81, 1–23.
- Specht, K., Hugdahl, K., Ofte, S., Nygård, M., Bjørnerud, A., Plante, E., Helland, T., 2009. Brain activation on pre-reading tasks reveals at-risk status for dyslexia in 6-year-old children. *Scand. J. Psychol.* 50, 79–91.
- Stein, J.F., 2001. The magnocellular theory of developmental dyslexia. *Dyslexia* 7, 12–36.
- Szczerbiński, M., Pelc-Pekala, O., 2013. Zestaw metod do diagnozy trudności w czytaniu – Test Dekodowania (The Decoding Test – A Set of Tools for Diagnosing Reading Difficulties). PTPiP, Gdansk (Poland).
- Szustrowa, T., Jaworowska, A., 2003. TMK – Test Matryc Ravena w wersji kolorowej. Pracownia Testów Psychologicznych, Warszawa (Poland).
- Temple, E., Poldrack, R.A., Salidis, J., Deutsch, G.K., Tallal, P., Merzenich, M.M., Gabrieli, J.D.E., 2001. Disrupted neural responses to phonological and orthographic processing in dyslexic children: an fMRI study. *Neuroreport* 12, 299–307.
- Torgesen, J., Wagner, R., Rashotte, C., 1994. Longitudinal studies of phonological processing and reading. *J. Learn. Disabil.* 27, 276–286.
- Torppa, M., Lyytinen, P., Erskine, J., Eklund, K., Lyytinen, H., 2010. Language development, literacy skills and predictive connections to reading in Finnish children with and without familial risk for dyslexia. *J. Learn. Difficulties* 43, 308–321.
- Twomey, T., Kawabata Duncan, K.J., Hogan, J.S., Morita, K., Umeda, K., 2013. Dissociating visual form from lexical frequency using Japanese. *Brain Lang.* 125, 184–193.
- Van Ermingen-Marbach, M., Pape-Neumann, J., Grande, M., Grabowska, A., Heim, S., 2013. Distinct neural signatures of cognitive subtypes of dyslexia: effects of lexicality during phonological processing. *Acta Neurobiol. Exp.* 73, 404–416.
- Vidyasagar, T.R., 2004. Neural underpinnings of dyslexia as a disorder of visuo-spatial attention. *Clin. Exp. Optom.* 87, 4–10.
- Vidyasagar, T.R., Pammer, K., 2009. Dyslexia: a deficit in visuo-spatial attention, not in phonological processing. *Trends Cogn. Sci.* 14, 57–63.
- Wagner, R.K., Torgesen, J.K., Rashotte, C.A., 1994. Development of reading-related phonological processing abilities: new evidence of bidirectional causality from a latent variable longitudinal study. *Dev. Psychol.* 30, 73–87.
- White, S., Milne, E., Rosen, S., Hansen, P., Swettenham, J., Frith, U., Ramus, F., 2006. The role of sensorimotor impairments in dyslexia: a multiple case study of dyslexic children. *Dev. Sci.* 9, 237–255.
- Zatorre, R.J., Meyer, E., Gjedde, A., Evans, A.C., 1996. PET studies of phonetic processing of speech: review, replication, and reanalysis. *Cereb. Cortex* 6 (1), 21–30.
- Ziegler, J.C., Bertrand, D., Tóth, D., Csépe, V., Reis, A., Faisca, L., Saine, N., Lyytinen, H., Vaessen, A., Blomert, L., 2010. Orthographic depth and its impact on universal predictors of reading: a cross-language investigation. *Psychol. Sci.* 21, 551–559.