Convergent and divergent structural and functional brain abnormalities associated with developmental dyslexia: a cross-linguistic meta-analysis of neuroimaging studies

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Abstract

Brain abnormalities in the reading network have been repeatedly reported in individuals with developmental dyslexia (DD); however, it is still not totally understood where and why the structural and functional abnormalities are consistent/inconsistent across languages. In the current multimodal meta-analysis, we found convergent structural and functional alterations in the left superior temporal gyrus across languages, suggesting a neural signature of DD. We found greater reduction in grey matter volume and brain activation in the left inferior frontal gyrus in morpho-syllabic languages (e.g. Chinese) than in alphabetic languages, and greater reduction in brain activation in the left middle temporal gyrus and fusiform gyrus in alphabetic languages than in morpho-syllabic languages. These language differences are explained as consequences of being DD while learning a specific language. In addition, we also found brain regions that showed increased grey matter volume and brain activation, presumably suggesting compensations and brain regions that showed inconsistent alterations in brain structure and function. Our study provides important insights about the etiology of DD from a cross-linguistic perspective with considerations of consistency/inconsistency between structural and functional alterations.

Keywords: dyslexia, fMRI/PET, VBM, meta-analysis, multimodal, alphabetic language, morpho-syllabic language
Introduction

Individuals with developmental dyslexia (DD) encounter difficulty in learning to read even with normal intelligence and adequate educational guidance (Peterson & Pennington, 2012). DD affects a large number of individuals across writing systems, and the prevalence is about 5-10% in alphabetic writing systems (e.g., English and German) (Döhla & Heim, 2016; Katusic et al., 2001; Shaywitz, 1996) and about 4-7% in morpho-syllabic writing systems (e.g., Chinese and Japanese Kanji) (Sun et al., 2013; Uno et al., 2009; Zhao et al., 2016). A phonological deficit in DD has been documented across languages (Gu & Bi, 2020; Snowling & Melby-Lervag, 2016). Individuals with DD show deficient phonological ability including phonological representation, manipulation and retrieval even when compared to reading-level controls (Melby-Lervag et al., 2012; Parrila et al., 2020). However, the common phonological deficit may manifest differently in reading behavior depending on the specific requirements of the writing system. For example, phonological deficit in English is associated with lower accuracy in phonological decoding (Landerl et al., 1997; Ziegler et al., 2003), and it is associated with slower reading speed in transparent orthographies with relatively intact accuracy in phonological decoding (Wimmer & Schurz, 2010). In Chinese, phonological deficit is associated with a higher rate of semantic errors during character reading (Shu et al., 2005), because children with DD over-rely on the semantic cue in the character during reading due to the inability to use the phonological cue. According to research, 80% of Chinese characters have a semantic radical and a phonetic radical.
providing semantic cues and phonological cues of the character, respectively (Honorof & Feldman, 2006).

At the neurological level, individuals with DD are associated with dysfunction in the left reading network (Richlan, 2012), including the occipitotemporal cortex (OT), the temporoparietal cortex (TP) and the inferior frontal cortex. The left TP area, including the posterior superior temporal gyrus (STG) and inferior parietal lobule (IPL), is a key area related to phonological representation and phonological conversion (Petersen & Fiez, 1993; Richlan, 2012). This region tends to show reduced brain activation in alphabetic languages as demonstrated in a cross-linguistic study of English, Italian and French (Paulesu et al., 2001) and several meta-analysis studies in alphabetic languages (Maisog et al., 2008; Martin et al., 2016; Paulesu et al., 2014; Richlan et al., 2009, 2011). The left OT area, including the middle occipital gyrus (MOG), inferior temporal gyrus (ITG) and fusiform gyrus, has been consistently found to show reduced activation in individuals with DD across morpho-syllabic and alphabetic languages (Bolger et al., 2008; Cao et al., 2020; Centanni et al., 2019; Chyl et al., 2018; Paz-Alonso et al., 2018). This region is associated with visuo-orthographic processing during reading (Glezer et al., 2016, 2019). The left inferior frontal gyrus (IFG) has been known to be involved in phonological and semantic retrieval, lexical selection and integration (Booth et al., 2007a, 2007b; Costafreda et al., 2006; Szatkowska et al., 2000). However, the nature of dysfunction in the left IFG in individuals with DD remains controversial. Although reduced activation in the left IFG was confirmed by many fMRI studies
and meta-analysis studies (Booth et al., 2007a; Cao et al., 2006; Richlan et al., 2010; Wimmer et al., 2010), increased activation in the left IFG was also reported in many fMRI studies (Grunling et al., 2004; Kronbichler et al., 2006; Waldie et al., 2013; Wimmer et al., 2010). The inconsistent results may be related to task difficulty (Waldie et al., 2013; Wimmer et al., 2010), orthographic transparency (Martin et al., 2016) and age of participants (Chyl et al., 2018).

From a cross-linguistic perspective, quite a few studies have found language-universal deficits associated with DD. Paulesu et al. (2001) found that readers with DD in English, Italian and French showed similar brain abnormality during an explicit word reading task and an implicit reading task, namely, reduced brain activation at the left middle/superior temporal gyrus, ITG and MOG. Hu et al. (2010) found that both Chinese and English children with DD showed reduced brain activation at the left middle frontal gyrus (MFG), middle temporal gyrus (MTG), angular gyrus and OT area, suggesting language-universal deficits. Feng et al. (2020) found that children with DD in both Chinese and French showed common reduction of brain activation in the left fusiform gyrus and STG.

Even though language-universal deficits in the brain have been suggested in several studies (Feng et al., 2020; Hu et al., 2010; Paulesu et al., 2001), language specificity has been demonstrated as well (Martin et al., 2016; Siok et al., 2004). In a meta-analysis study (Martin et al., 2016), researchers directly compared brain deficits associated with DD between transparent and opaque orthographies and found that functional abnormalities in the brain vary with orthographic depth in alphabetic
languages. Specifically, consistent reduction of brain activation was found in a left OT area regardless of orthographic depth including the left ITG, MTG, and inferior occipital gyrus, whereas greater reduction was found in the left fusiform gyrus, left TP and left IFG pars orbitalis in transparent orthographies than in opaque orthographies, and greater reduction in the bilateral intraparietal sulcus, left precuneus and left IFG pars triangularis was found in opaque orthographies than in transparent orthographies. In a recent study on Chinese-English bilingual children with DD, researchers also found both language-universal deficits at the left ITG, the precuneus and dorsal IFG and language-specific deficits at the left IPL for Chinese and the left ventral IFG for English (Cao et al., 2020). These findings suggest that there are both language-universal and language-specific deficits across languages. The language-universal deficits might be related to the causal risk of DD while the language-specific deficits tend to be interpreted as the result of interaction between DD and the specific language system that one studies.

Research on DD in Chinese has revealed different patterns of brain abnormalities from alphabetic languages. Significant alteration in the left MFG or dorsal IFG has been consistently reported in different studies while the alteration in the left TP areas has been reported in only a few studies. Siok et al. (2004, 2008) found that Chinese children with DD showed reduced activation at the left MFG during a homophone judgment task. Cao et al. (2017, 2020) also found reduced activation in the left dorsal IFG in Chinese children with DD compared to age-matched controls and reading-matched controls during an auditory rhyming task and
a visual rhyming judgment task. A similar hypoactivation in the left dorsal IFG was also reported in morphological tasks in Chinese (Liu et al., 2012, 2013b). The left dorsal IFG in Cao et al.’s study (2020) was proximal to the left MFG in Siok et al.’s study (2004). In contrast, reduced activation in the left TP area has been found in only a few studies so far (Cao et al., 2017, 2018; Hu et al., 2010).

As a morpho-syllabic language, Chinese characters map to syllables and there are no grapheme-to-phoneme correspondence rules. Each character represents a morpheme and there are many homophones in Chinese; therefore, during Chinese reading, the direct mapping from orthography to semantics plays a very important role. These features of Chinese could help explain why the left TP is less affected and the left dorsal IFG is more affected in Chinese. The left TP has been believed to be essential in rule-based conversion between orthography and phonology and more involved in transparent orthographies than opaque orthographies, while the left dorsal IFG appears to be more involved in whole-word reading in opaque orthographies than in transparent orthographies (Fiez, 2000; Martin et al., 2016; Paulesu et al., 2000). It has also been found that the left TP is more involved in English reading and the left dorsal IFG is more involved in Chinese reading (Bolger et al., 2005; Tan et al., 2005). Therefore, the greater deficit in the left dorsal IFG than in the left TP areas in Chinese is consistent with the features of Chinese. Chinese characters also have complex visuo-spatial configurations, which require an increasing involvement of visual-orthographic analysis at the bilateral precuneus (Cao et al., 2013). That explains the fact that the precuneus showed consistent deficit
in Chinese DD (Cao et al., 2018, 2020). Ziegler (2006) argued that Chinese readers with DD should share a common neurocognitive deficit that DD readers have in alphabetic languages, because Chinese reading is essentially the process of mapping from orthography to phonology and meaning as alphabetic languages do and Chinese readers with DD also show phonological deficits (Goswami et al., 2011; Hu et al., 2010). However, despite a universal phonological deficit across languages, different parts of the brain might be affected, because different strategies might be used when mapping orthography to phonology depending on the features of the language.

A large number of studies have been conducted in investigating structural alterations associated with DD; however, none of them has taken language difference into account. In a meta-analysis, Linkersdorfer et al. (2012) gathered nine voxel-based morphometry (VBM) studies in alphabetic languages and found consistent grey matter reduction in the left OT area and TP area, but failed to find reliable evidence in the left IFG. In another two meta-analysis studies in alphabetic languages, researchers only found consistent grey matter reduction in the left TP area but failed to find reduction in the OT area (McGrath & Stoodley, 2019; Richlan et al., 2013). These three meta-analytic studies echo findings from functional studies by showing abnormal brain structures within the classic reading network. However, studies also showed abnormal brain structures outside the reading network. For example, studies have found reduced grey matter volume (GMV) at the left putamen in Chinese children with DD (Wang et al., 2019), at the cerebellum in Spanish (Adrian-Ventura et al., 2020), Italian (Brambati et al., 2004) and English (Brown et
al. 2001), at the thalamus in English (Brown et al., 2001), French, German and Polish (Jednorog et al., 2015), and at the caudate nucleus in English (Brown et al., 2001; Jagger-Rickels et al., 2018). In summary, previous inconsistent findings in brain structure might be due to the lack of differentiation in participants’ language. It is important to differentiate language-universal structural alterations as a core deficit which might be related to the cause of DD and language-specific structural alterations as a consequence of being DD in a specific language. While brain structural deficits may cause reading disability, learning experience may also shape brain development. Learning a specific language with DD may affect brain development in language-specific regions (Mechelli et al., 2004).

DD is associated with altered brain structure and function, but very few studies have investigated whether brain structural alterations and brain functional alterations are consistent or inconsistent. In a study by Siok et al. (2008), researchers examined both structural and functional alterations in Chinese children with DD, and found reduced GMV and brain activation in the left MFG, which underscores the association between the left MFG and DD in Chinese. Another study located a key region in the left IPL, which showed reduced GMV and activation in English-speaking readers with DD (Hoeft et al., 2007). There is a paucity of research to examine brain regions that show increased GMV but decreased brain function or vice versa, and neither is there discussion about the neurocognitive implications of such patterns. Simultaneously considering structural and functional abnormalities with a focus on cross-linguistic comparison would provide a comprehensive
perspective to understand the neural mechanisms of DD.

In this meta-analysis study, we aimed to explore how structural and functional impairment of DD converge or diverge and whether this pattern is similar or different across writing systems. We expected to find brain regions that show decreased brain structure and function, indicating insufficient neuronal resources for certain cognitive computations. For regions that show increased brain structure and function, we believe they develop to an unusually high degree for compensation.

For brain regions with increased structure but decreased function or decreased structure and increased function, it may be due to brain structures receiving inhibitory input from other regions. We also expected to find language-universal as well as language-specific neurological abnormalities. For language-universal deficits, we tend to believe that they are related to the cause of DD, while the language-specific deficits tend to be consequences of DD in different languages.

**Methods**

*Literature retrieval and data extraction*

We searched in “PubMed” (http://www.pubmed.org) and “Web of science” using a combination of “dyslexia”, “reading disorder”, “reading impairment” or “reading disability” and “fMRI”, “PET”, “voxel-based morphometry”, “VBM” or “neuroimaging” as key words for neuroimaging studies published from January 1986 to January 2020. Additionally, we manually added studies by checking the references of the selected papers that were missed in the search. The inclusion criteria were: (1)
PET, fMRI, voxel-based morphometry (VBM) studies or structural studies using a volumetric FreeSurfer pipeline, (2) whole-brain results were reported, (3) direct group comparisons between readers with DD and age control readers were reported, (4) coordinates were reported in Talairach or MNI stereotactic space, and (5) studies on DD in the first language. The exclusion criteria were (1) studies with only ROI analysis, (2) resting-state studies, (3) studies that only included readers with DD or did not report group differences, (4) studies with direct group comparisons only between readers with DD and reading level control readers, (5) studies on children at

Figure 1. PRISMA flowchart of the selection process for included articles.
risk for dyslexia, and (6) studies focused on non-linguistic tasks (Evans et al., 2014a; Margolis et al., 2019; Menghini et al., 2006; Yang et al., 2013). Finally, 119 experiments from 110 papers were included in this meta-analysis comprising 92 brain functional experiments (from 87 papers) and 27 brain structural experiments (from 23 papers) (see Table 1, Table 2 and Figure 1 for detail). From the original publications, we extracted peak coordinates, where there is a significant difference between controls and individuals with DD either in brain activation or regional GMV. We also extracted effect sizes and other information from the publications.

Voxel-wise meta-analysis

After data acquisition, we conducted a voxel-wise meta-analysis using the anisotropic effect-size version of Signed Differential Mapping software (AES-SDM version 5.14, see http://www.sdmproject.com) separately for functional studies and structural studies. Unlike other coordinate-based meta-analysis methods such as Activation likelihood estimation (ALE) or Multilevel peak Kernel density analysis (MKDA), AES-SDM combined the peak coordinates with the statistical parameter maps to increase the sensitivity of the analysis (Radua et al., 2012a). Data were first preprocessed with the statistical parameter maps and the peak coordinates were convolved with a fully anisotropy un-normalized Gaussian kernel (\(\alpha=1\)) (full width at half maximum = 20 mm) to recreate the effect size map and the corresponding variance map for each study (Radua et al., 2012a, 2014). Then, a random-effect model was set up to calculate the differences between the DD group and the control group. Five hundred permutations were performed to ensure the stability of the
Finally, the results of the standard meta-analysis were thresholded at peak height of the mean effect size SDM-$Z=1$, uncorrected $p=.005$ at the voxel level and 150 voxels at the cluster level, which is stricter than the advised threshold by Radua et al. (Radua et al., 2012a) (peak height SDM-$Z=1$, uncorrected $p=.005$ at the voxel level and 10 voxels at the cluster level) in order to avoid false-positive results.

To test the stability of the meta-analysis results, we conducted a whole-brain jack-knife sensitivity analysis. The standard meta-analysis was repeated $n$ times ($n=92$ for functional studies, $n=27$ for structural studies) but leaving out one study each time, to determine whether the results remained significant.

**Multimodal meta-analysis**

Because we were interested in the convergence between functional deficits and structural deficits, a multimodal meta-analysis was conducted, which provided an efficient way to combine two meta-analyses in different modalities. The union probabilities of the meta-analytical maps of functional studies and structural studies were estimated and then thresholded at the peak height $p=0.00025$, with a voxel level uncorrected $p=0.0025$ and 150 voxels at the cluster level, which was stricter than the one suggested by Radua et al. (2012b, 2013) (peak height $p=0.00025$, with a voxel level uncorrected $p=0.0025$ and 10 voxels at cluster level).

**Subgroup meta-analysis**

In order to explore the language effect, we conducted a subgroup meta-analysis. According to the native language of the participants, the functional and
structural studies were subdivided into an alphabetic language group in which writing symbols represent phonemes, and a morpho-syllabic language group in which each writing symbol represents a morpheme with a syllable, which resulted in 79 functional and 21 structural studies for alphabetic languages and 12 functional (including a Japanese study focused on Kanji) and 6 structural studies for morpho-syllabic languages. First, a standard functional and structural meta-analysis was conducted for alphabetic languages and morpho-syllabic languages, separately. Then multimodal meta-analysis was conducted to find the convergence between functional and structural deficits separately for each language group. The threshold for the separate structural and functional maps and multimodal analysis was the same as mentioned above. Next, we conducted a direct comparison between the alphabetic language and morpho-syllabic language group for functional studies and structural studies separately to find the difference between the two language groups. The threshold was set at peak height SDM-Z=1, voxel level uncorrected p=.005 and 150 voxels at the cluster level.

**Confirmation study**

Because there were many more functional studies included in the alphabetic group than in the morpho-syllabic group, and most of the morpho-syllabic studies focused on children, the language difference may be due to these differences in the two groups of studies. To avoid influences of these factors, we selected ten English studies (Booth et al., 2007a; Cao et al., 2008; Farris et al., 2016; Hancock et al., 2016; Hu et al., 2010; Langer et al., 2015; Meyler et al., 2008; Olulade et al., 2015;
Rimrodt et al., 2009; Temple et al., 2001) and ten Chinese studies (Cao et al., 2018, 2020; Feng et al., 2017; Hu et al., 2010; Liu et al., 2012, 2013b; Siok et al., 2004, 2008, 2009; Yang & Tan, 2020) for further confirmation analysis. The two subgroups were matched on participants’ age (mean age = 10.95 years for English studies, mean age = 11.40 years for Chinese studies) and task (visual word tasks). Then, we conducted a direct comparison between the Chinese studies and English studies. The threshold was set at peak height SDM-Z=1 and voxel level uncorrected p=.005 with 150 voxels at the cluster level.

Results

Description of the included studies

For the functional studies, a total of 2746 participants (controls:1377, DD:1369) were included, and the mean age was 16.55 years for controls and 16.23 years for participants with DD. For the structural studies, a total of 1183 participants (controls:588, DD:595) were included, and the mean age was 16.88 years for controls and 16.97 years for participants with DD.

Meta-analysis results

Functional impairment associated with DD across all languages

In the meta-analysis of all functional studies, hypoactivation in DD was found in a large cluster peaked at the left IPL which extended to the inferior frontal cortex, occipitotemporal cortex and cerebellum, and a cluster peaked at the right MOG (Table S1 and Figure S1). Hyperactivation in DD was found in the right cerebellum,
right precentral/postcentral gyrus and bilateral caudate nucleus. The jack-knife sensitivity analysis showed that all results reported above were replicable (Table S1).

**Structural impairment associated with DD across all languages**

In the meta-analysis of all structural studies, readers with DD showed a decrease in GMV in the left inferior frontal cortex and right STG (Table S2 and Figure S2). In contrast, readers with DD showed an increase in GMV in the right MTG and left IPL. The jack-knife sensitivity analysis showed that all results reported were replicable (Table S2).

**Multimodal analysis across all languages**

As shown in Table 3 and Figure 2, decreased GMV and hypoactivation in DD were found in the left IFG, and left TP which peaked at the left STG and extended to the left IFG and precentral gyrus. Increased GMV and hyperactivation in DD were found in the right anterior MTG/ITG. Increased GMV and hypoactivation in DD were found in the left IPL and left cerebellum which extended to FG. Decreased GMV and hyperactivation in DD were found in bilateral caudate.

Figure 2. Structural and functional deficits in DD across all languages (red-yellow:
decreases in DD in both structural and functional, blue: increases in DD in both structural and functional studies, purple: increases in DD in structural studies and decreases in DD in functional studies, green: decreases in DD in structural studies and increases in DD in functional studies).

We also found brain regions that had normal structure but altered function. We found normal brain structure but reduced brain activation at the right MOG and a large cluster peaked at left supramarginal gyrus, which extended to the left ITG, MTG and IFG. We found normal brain structure but increased activation at the right cerebellum and right precentral gyrus (Figure S7 and Table S7). There are also regions that had altered structure but normal function. We found normal brain activation but reduced GMV at the left IFG and right STG, as well as normal brain function but increased GMV at the right MTG (Figure S8 and Table S8).

Subgroup analysis results – comparison between alphabetic and morpho-syllabic languages

For the direct comparison between the morpho-syllabic and alphabetic languages in functional studies, we found greater reduction of brain activation in alphabetic languages than in morpho-syllabic languages in the right STG, left MTG and left fusiform gyrus. We found greater reduction of brain activation in morpho-syllabic languages than in alphabetic languages in the left IFG and greater increase of brain activation in DD in morpho-syllabic languages than in alphabetic languages in the right precentral gyrus (Table 4, Figure 3).
Figure 3. Direct comparison between alphabetic languages and morpho-syllabic languages in structural and functional deficits. A, Language differences in functional deficits. B, Language differences in structural deficits. C, Conjunction of language differences between functional and structural deficits, which is due to greater reduction in brain activation and GMV in morpho-syllabic languages than in alphabetic languages in the left dorsal IFG. (red-yellow: greater decreases in DD in alphabetic languages than in morpho-syllabic languages; blue-green: greater decreases in DD in morpho-syllabic languages than in alphabetic languages; purple: greater increases in DD in morpho-syllabic languages than in alphabetic languages).

For the direct comparison between the morpho-syllabic and alphabetic languages in structural studies, we found greater reduction of GMV in DD in
morpho-syllabic languages than in alphabetic languages in the left STG, left IFG, left MFG, left supramarginal gyrus, left superior occipital gyrus (SOG) and left insula. We also found greater increase of GMV in DD in morpho-syllabic languages than in alphabetic languages in the right STG and left ITG (Table 5, Figure 3). We found no regions that showed greater GMV changes in alphabetic languages than in morpho-syllabic languages.

To identify the common language differences across both structural and functional studies, we conducted a conjunction analysis of the thresholded language difference maps. This produced an overlap of 387 voxels in the left IFG, which peaked at (-48, 8, 26), indicating greater reduction of both GMV and brain activation in morpho-syllabic languages than in alphabetic languages (Figure 3).

**Subgroup analysis results – multimodal analysis**

Multimodal meta-analysis in alphabetic languages showed that decreased GMV and hypoactivation in DD were found in the bilateral TP and left IFG; no regions showed increased GMV and hyperactivation; increased GMV and hypoactivation in DD were found in left IPL and left cerebellum; decreased GMV and hyperactivation in DD were found in bilateral caudate and right cerebellum (Table 6, Figure 4). Multimodal meta-analysis in morpho-syllabic languages showed that decreased GMV and hypoactivation in DD were found in the left TP and left IFG; increased GMV and hyperactivation in DD were found in the right MTG; decreased GMV and hyperactivation in DD were found in left STG; no regions
showed increased GMV and hypoactivation (Table 7, Figure 4).

Figure 4. Structural and functional deficits in DD for alphabetic languages and morpho-syllabic languages. A, Structural and functional deficits in DD for alphabetic languages. B, Structural and functional deficits in DD for morpho-syllabic languages. C, Conjunction of structural and functional deficits in alphabetic and morpho-syllabic languages, which is driven by decreased GMV and brain activation in the left STG in both alphabetic and morpho-syllabic languages. (red-yellow: decreases in DD in both structural and functional studies, blue: increases in DD in both structural and functional studies, purple: increases in DD in structural studies and decreases in functional studies, green: decreases in DD in structural studies and increases in functional studies).

To identify the common structural and functional deficit in alphabetic
languages and morpho-syllabic languages, we conducted a conjunction analysis of the thresholded multimodal maps of the two types of writing systems. This procedure produced an overlap of 482 voxels in the left STG, which peaked at (-56, -32, 20), indicating shared reduction of GMV and hypoactivation in both types of writing systems (Figure 4).

Subgroup analysis results – confirmation analysis

Confirmation analysis of two well-matched subgroups showed greater reduction of brain activation in DD in English than in Chinese in the left ITG and left MOG and greater reduction of brain activation in DD in Chinese than in English in the left precentral gyrus. Greater increase of brain activation in English than in Chinese was found in the right supramarginal gyrus, right hippocampus, and right supplementary motor area; greater increase of brain activation in Chinese than in English was found in the right precentral gyrus (Table S9, Figure S9). Conjunction analysis of the difference maps between alphabetic and morpho-syllabic languages and the difference maps between English and Chinese showed consistent greater reduction of brain activation in DD in alphabetic languages/English than in morpho-syllabic languages/Chinese in the left ITG (-50, -42, -24) and left MTG (-50, -66, 8) with a cluster size of 76 voxels and 147 voxels, respectively; there was consistent greater reduction of brain activation in DD in morpho-syllabic languages/Chinese than in alphabetic languages/English in the left IFG (-46, 8, 30) with a cluster size of 1999 voxels. Consistent greater increase of brain activation in morpho-syllabic languages/Chinese than in alphabetic languages/English was also found in the right...
precentral gyrus (42, -20, 52), and the cluster size was 791 voxels. The results from
the well-matched subgroup analysis confirmed findings from the comparison
between alphabetic languages and morpho-syllabic languages.

**Discussion**

In this meta-analysis study, we examined the relationship between structural
and functional deficits associated with DD as well as whether the deficits are
consistent across languages. We found that readers with DD showed both GMV
reduction and functional hypoactivation in the left TP and inferior frontal cortex,
among which, the left STG was a shared impairment across all languages, and the
left IFG showed a greater impairment in morpho-syllabic languages than in
alphabetic languages, suggesting both language-universal and language-specific
deficits in the brain. We also found GMV increase and functional hyperactivation in
the right anterior MTG/ITG region across all languages; however, conjunction
analysis between morpho-syllabic languages and alphabetic languages did not reveal
any overlap. In addition to the consistent structural and functional alterations, we
also detected inconsistent structural and functional alterations. Individuals with DD
showed increased GMV and hypoactivation in the left IPL and left cerebellum, and
decreased GMV and hyperactivation in the bilateral caudate. However, when we
subdivided the data into alphabetic and morpho-syllabic languages, these
inconsistent structural and functional changes only existed in alphabetic languages.

*Convergent structural and functional impairment across writing systems*
Across writing systems, convergent structural and functional deficits were found around the left perisylvian region (i.e., left IFG, left supramarginal gyrus and left STG) due to reduced GMV and brain activation. The left perisylvian region is a very important component in the language network, which shows structural and functional abnormality in individuals with DD as suggested in previous meta-analysis studies (Linkersdorfer et al., 2012; Maisog et al., 2008; McGrath & Stodley, 2019; Paulesu et al., 2014; Richlan et al., 2013). The left STG and the dorsal IFG are two core regions in the language model proposed by Friederici (2012), and by Hickok and Poeppel (2007). These two brain regions are involved in phonological processing during both spoken language processing and reading (Bolger et al., 2005; Enge et al., 2020; Tan et al., 2005). Furthermore, proficient reading is characterized by convergence between speech and print at these two regions regardless of languages, because multivariate brain activity patterns are similar for speech and print at these regions (Chyl et al., 2021). These findings suggest that the reading network may develop based on the built-in language circuit, as reading is a skill that humans acquire too late in the course of human evolution to have a brain network dedicated to it. Our finding suggests that dyslexia is associated with structural and functional abnormalities of the language network regardless of language. Recently, a growing number of studies have investigated early signs of dyslexia before the onset of reading and found that structural and functional deficits in the left TP area and left inferior frontal cortex appear before reading onset (Clark et al., 2014; Hosseini et al., 2013; Plewko et al., 2018; Raschle et al., 2012, 2014;
Vandermosten et al., 2019). It further suggests that DD might be due to early abnormality in the language network.

Furthermore, our conjunction analysis of the two language subgroups confirmed that the left STG is a site for a common deficit in both language groups with reduced GMV and decreased brain activation. The evidence suggests that this is a neural signature of DD. The STG is where the auditory cortex is located, which is responsible for auditory perception and phonological analysis of words and sentences (Friederici, 2012). Recently, Skeide et al. (2018) found hypermyelination in the left auditory cortex in readers with DD using ultra-high-field MRI at 7T, and disrupted neural firing induced by hypermyelination in the layer IV of the auditory cortex, which may cause hypoactivation in the left STG. In summary, we found structural and functional alterations at the left STG in individuals with DD regardless of languages, which supports the phonological deficit hypothesis.

However, we failed to find consistent structural and functional deficits in the OT area. The main reason was that there was no structural alteration but only functional reduction at this area. The OT area is a key region for orthographic recognition during visual word processing (Glezer et al., 2009, 2016; Hirshorn et al., 2016; Nobre et al., 1994) and was reported to be impaired in individuals with DD (McCrorry et al., 2005; Richlan et al., 2010; Wandell et al., 2012). The specialization of this region for orthographic processing is developed along with reading acquisition (Brem et al., 2010), and the dysfunction of the OT area in DD is possibly a result of reading failure (Pugh et al., 2000). A recent meta-analysis of VBM studies...
(McGrath & Stoodley, 2019) also failed to detect structural deficit in the OT area, which is consistent with our finding. Taken together, the lack of structural deficits with only hypoactivation at the OT area appears to suggest that the visuo-orthographic deficits at the OT might be a consequence of being DD. In contrast, the left STG which was discussed above, appears to be associated with the cause of DD. Our results provide further support for the phonological deficit hypothesis that phonological deficit is the primary deficit and other deficits may be a result of the phonological deficit (Pugh et al., 2000).

Language differences in structural and functional alterations

The left dorsal IFG which peaked at (-48, 8, 26) showed greater reduction in morpho-syllabic languages than in alphabetic languages for both GMV and brain activation, suggesting greater impairment in this region in morpho-syllabic languages than in alphabetic languages, and the greater activation reduction in morpho-syllabic languages was also verified in the confirmation analysis. Previously, many Chinese studies have reported impairment at the dorsal left IFG, for example, reduced brain activation in an auditory rhyming judgment task in children with DD at (-44, 10, 26) (Cao et al., 2017), in a lexical decision task at (-44, 3, 29) (Siok et al., 2004), in a homophone judgment task at (-55, 5, 22) (Siok et al., 2008), and in a morphological task at (-36, 8, 26) (Liu et al., 2013b). This left dorsal IFG has been believed to be more involved in Chinese reading than in alphabetic languages, with a peak at the left MFG (-46, 18, 28) as reported in a previous meta-analysis study (Tan et al., 2005). The dorsal IFG was found to be involved in
phonological processing in Chinese reading (Wu et al., 2012), and it is thought to be related to addressed phonology during Chinese character reading (Tan et al., 2005). Our study adds to the literature that not only the brain activation but also the GMV is more reduced in the left dorsal IFG in individuals with DD in morpho-syllabic languages than in alphabetic languages. This might be due to the fact that healthy Chinese readers have increased GMV and brain activation in the left dorsal IFG than healthy alphabetic readers, because the features of Chinese require greater involvement of this region in reading than alphabetic languages due to the whole-character-to-whole-syllable mapping. Actually, two cross-linguistic studies have argued that different findings of DD in different languages are actually driven by the fact that control readers show language-specific brain activation patterns (Feng et al., 2020; Hu et al., 2010), and that brain activation in individuals with DD is actually the same across languages. For example, Hu et al. (2010) found that Chinese control readers showed greater activation in the left IFG, and English control readers showed greater activation in the left superior temporal sulcus; however, children with DD in Chinese and English showed similar brain activation in these two regions. Therefore, readers with DD fail to show language specialization due to their limited reading experience and skills. In summary, this language-specific deficit is believed to be a consequence of being DD in learning morpho-syllabic languages, indicating their inability to accommodate to their own writing system.

In the direct comparison between alphabetic and morpho-syllabic languages, we also found greater hypoactivation in DD in alphabetic languages than in morpho-
syllabic languages in the left MTG, right STG and left fusiform gyrus, which was verified in the confirmation analysis. Our finding is consistent with previous neuroimaging studies that revealed reduced activation associated with DD in the posterior reading network in alphabetic languages (Paulesu et al., 2001; Richlan et al., 2010; Vandermosten et al., 2019), suggesting deficient orthographic and phonological processing. However, the novelty of the current study is to demonstrate greater severity of deficit in these regions in alphabetic languages than in morpho-syllabic languages. In a previous meta-analysis study of alphabetic languages, it was found that there was greater hypoactivation in the left fusiform gyrus (-40, -42, -16) in shallow orthographies than in deep orthographies (Martin et al., 2016). The explanation is that this region is associated with bottom-up rapid processing of letters, because it was found that at a proximal region (-38, -50, -16), there was a word length effect for German nonwords in non-impaired readers (Schurz et al., 2010). Moreover, the left fusiform gyrus has been found to be more involved in English reading than in Chinese reading in typical mature readers with a peak of the effect at (-44, -56, -12) (Tan et al., 2005). Therefore, the left fusiform gyrus is important for letter-by-letter orthographic recognition in alphabetic languages, and this explains why we found greater deficit in this region in alphabetic languages than in morpho-syllabic languages. As for the right STG, the previous meta-analysis found greater hypoactivation in deep orthographies than shallow orthographies (Martin et al., 2016). Together with our finding, it suggests that the right STG might be associated with the inconsistent mapping between graphemes and phonemes in
deep orthographic alphabetic languages. In summary, these greater deficits in alphabetic languages than in morpho-syllabic languages might be due to the inability to adapt to the special features of alphabetic languages in individuals with DD.

For the structural studies, we found greater GMV alterations in morpho-syllabic languages than in alphabetic languages, including greater GMV reduction in the left STG, left MFG, left supramarginal gyrus, left SOG and left insula, as well as greater GMV increase in the right STG and ITG. However, considering the limited number of studies included in the morpho-syllabic language group and inconsistent results with functional studies, the results should be interpreted with caution.

**Compensation mechanism**

In the multi-modal meta-analysis, we found increased GMV and hyperactivation in participants with DD in the right MTG which was mainly driven by the morpho-syllabic languages. For the functional studies, we also found greater hyperactivation in the right precentral gyrus in morpho-syllabic languages than in alphabetic languages. We believe that these findings are related to the compensation mechanism of the right hemisphere. As precentral gyri play an important role in articulation (Dronkers, 1996), overactivation in the precentral gyrus is interpreted as an articulation strategy used by individuals with DD to compensate for their deficient phonological processing (Cao et al., 2018; Shaywitz et al., 1998; Waldie et al., 2013). The compensation in the right MTG is developed in morpho-syllabic languages presumably due to the tight connection between orthography and
Substantial evidence has shown that dyslexia was often accompanied by excessive activation of the right hemisphere (Cao et al., 2017, 2018; Kovelman et al., 2012; Kronschnabel et al., 2014; Yang & Tan, 2020) and reduced left lateralization of the language network (Altarelli et al., 2014; Bloom et al., 2013). Furthermore, training studies have also found increased activation in many regions in the right hemisphere in individuals with DD after reading intervention (Barquero et al., 2014; Meyler et al., 2008), suggesting the compensatory role of the right hemisphere when the left language/reading network is deficient (Coslett & Monsul, 1994; Weiller et al., 1995). However, according to the previous meta-analysis study, different regions showed overactivation in different writing systems (Martin et al., 2016). In particular, the left anterior insula showed greater overactivation in deep orthographies while the left precentral gyrus showed greater overactivation in shallow orthographies in individuals with DD. Taken together, it suggests that different compensatory mechanisms are developed depending on the characteristics of the writing system as well as learning experiences, and the compensation in the right MTG and right precentral gyrus appears to be particularly salient in morpho-syllabic languages.

**Divergent structural and functional alterations in DD**

In the multimodal analysis, we also found divergent structural and functional changes related to DD, including the left IPL and left cerebellum where there was increased GMV and hypoactivation and bilateral caudate where there was reduced GMV and hyperactivation. These divergent structural and functional alterations in
DD were primarily driven by alphabetic languages.

The left IPL

We found increased GMV and hypoactivation in DD in the left IPL. Consistent hypoactivation in the left IPL in DD has been documented in previous studies (Maisog et al., 2008; Martin et al., 2016). Furthermore, it was found that the deficit of the left IPL was greater in children than in adults with DD (Richlan et al., 2011), suggesting that the functional impairment of the left IPL may gradually recover with development. This may be related to the transfer of the reading circuit from the dorsal pathway to the ventral pathway over development (Younger et al., 2017). Control children activate the left IPL to a greater degree than control adults because they rely more on the dorsal pathway. Therefore, children with DD show a great reduction in the left IPL in comparison to adults with DD. Alternatively, the left IPL has been found to be deactivated during language tasks (Cao et al., 2008, 2017; Meyler et al., 2008; Schulz et al., 2009), and this is due to the nature of the default mode network (Laird et al., 2009), which is deactivated during active tasks. Therefore, it might be the case that the increased GMV in individuals with DD increases inhibitory inputs received by the IPL, which results in greater deactivation.

For structural studies involving the left IPL, the results are inconsistent. The GMV of the left supramarginal gyrus around the posterior part of perisylvian cortex was found to be reduced in individuals with DD (Linkersdorfer et al., 2012; McGrath & Stoodley, 2019) and it showed a positive correlation with reading accuracy only in
normal readers (Jednorog et al., 2015). However, the GMV of the left inferior parietal cortex excluding the supramarginal and the angular was found to increase in individuals with DD (McGrath & Stoodley, 2019) and a study showed that the volume of the left inferior parietal cortex in control readers was negatively correlated with reading level (Houston et al., 2014). The IPL in the current study is outside the supramarginal and angular gyrus; therefore, it is consistent with the previous findings that there is increased GMV in individuals with DD.

The cerebella

Increased GMV and hypoactivation in DD were also found in the left cerebellum; however, in the right cerebellum, for the alphabetic language group, we found decreased GMV and hyperactivation. Previously, it was found that the right cerebellum is greater in size than the left cerebellum in healthy controls while the asymmetry is reduced in individuals with DD (Kibby et al., 2008; Rae et al., 2002). This is consistent with our finding of increased GMV in the left cerebellum and decreased GMV in the right cerebellum in individuals with DD, suggesting reduced asymmetry in cerebellum.

The cerebella have been found to play an important role in inner speech, automatization in reading and suppression of overt articulatory movement in silent reading (Ait Khelifa-Gallois et al., 2015). Functional abnormality of cerebellum in DD has been reported repeatedly; however, hyperactivation was reported more often in the right cerebellum (Feng et al., 2017; Hernandez et al., 2013; Kronschnabel et
al., 2014; Richlan et al., 2010; Rumsey et al., 1997; van Ermingen-Marbach et al., 2013a), while hypoactivation was reported more often in the left cerebellum (Christodoulou et al., 2014; McCrory et al., 2000; Olulade et al., 2012; Reilhac et al., 2013; Siok et al., 2008). This is consistent with our finding of hyperactivation in the right cerebellum and hypoactivation in the left cerebellum. Different alteration patterns in the left and right cerebellum suggest that they may play different roles in reading and dyslexia. The right cerebellum has been found to be connected with the left frontal-parietal pathway for phonological processing and with the left frontal-temporal pathway for semantic processing (Alvarez & Fiez, 2018; Gatti et al., 2020).

The left cerebellum, however, is involved in error monitoring during reading unfamiliar non-words (Ben-Yehudah & Fiez, 2008), as well as articulation related movement process, since it is activated in reading aloud but not in lexical decision (Carreiras et al., 2007). Richards et al. (2006) argued that the left cerebellum is involved in processing the morphology of word forms, and the right cerebellum is involved in phonological processing. Therefore, hyperactivation in the right cerebellum in readers with DD suggests that they may use it as a compensation for their deficient phonological processing, while hypoactivation in the left cerebellum may suggest reduced error monitoring in readers with DD. Taken together, the finding of neurological alterations in the cerebellum supports the cerebellar deficit hypothesis (Stoodley & Stein, 2011), implicating the necessity of considering DD from a broader spectrum of developmental disorders.

It is still unclear why there is increased GMV but decreased activation in some
brain regions. It may be due to the following reasons: (1) increased dendrites receiving more inhibitory input from other neurons; (2) abnormal neuronal migration deactivated the firing of neurons as a result of disrupted local microcircuits (Giraud & Ramus, 2013); (3) weaker input from other regions deactivated the target region and changed the structure of the region (Wang et al., 2019).

**The caudate**

We also found decreased GMV and hyperactivation in readers with DD in the bilateral caudate. Previous studies have reported decreased GMV (Brown et al., 2001; Jagger-Rickels et al., 2018; McGrath & Stoodley, 2019; Tamboer et al., 2015) and hyperactivation in bilateral caudate in individuals with DD (Martin et al., 2016; Olulade et al., 2012; Pekkola et al., 2006; Richlan et al., 2010, 2011; Rumsey et al., 1997), which is consistent with our finding. Furthermore, the GMV volume of the caudate in individuals with DD was found to be positively correlated with reading performance (Pernet et al., 2009; Tamboer et al., 2015), and the left caudate’s activation was correlated with longer reaction time in word reading only in individuals with DD (Cheema et al., 2018). The caudate plays an important role in procedural learning and phonological processing (Grahn et al., 2008; Tettamanti et al., 2005; Ullman et al., 2020). Decreased GMV and increased activation at the bilateral caudate might be caused by reduced dendrites and reduced inhibitory inputs received in individuals with DD (Achal et al., 2016; Finn et al., 2014). It may also be due to pre-existing local structural deficit leading to compensatory hyperactivation of the remaining part of the caudate. GMV reduction in basal ganglia was found in
many other neuropsychiatric disorders, such as attention-deficit hyperactivity disorder (Frodl & Skokauskas, 2012; Mous et al., 2015; Nakao et al., 2011), autism spectrum disorder (Nickl-Jockschat et al., 2012) and major depression disorder (Husain et al., 1991; Lu et al., 2016). Altered myelination and neurotransmitters may contribute to the structural and functional alterations related to basal ganglia (Nord et al., 2019; Wichmann & DeLong, 2012).

In addition, there are also brain regions that only showed alteration in structure but not in function or vice versa. It suggests that brain activation is only partially determined by GMV and that there are other factors influencing brain activation which might include but are not limited to myelination, synaptic processes, as well as interconnectivities between regions.

**Limitation**

In this meta-analysis, we found convergent and divergent functional and structural alterations across writing systems. However, due to limitations of neuroimaging techniques and the lack of evidence from multi-scale studies, the neurophysiology of changes in brain structure and function is unknown.

**Conclusion**

We found convergent functional and structural alterations in the left STG across different writing systems, suggesting a neural signature of DD, which might be associated with phonological deficit. We also found greater functional and structural alteration in the left dorsal IFG in morpho-syllabic languages than
alphabetic languages, suggesting a language-specific effect of DD, which might be related to the special feature of whole-character-to-whole-syllable mapping in morpho-syllabic languages.

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**References**

Achal, S., Hoeft, F., & Bray, S. (2016). Individual differences in adult reading are associated with left temporo-parietal to dorsal striatal functional connectivity. *Cerebral Cortex, 26*(10), 4069-4081. doi:10.1093/cercor/bhv214

Adrian-Ventura, J., Soriano-Ferrer, M., Fuentes-Claramonte, P., Morte-Soriano, M., Parcet, M. A., & Avila, C. (2020). Grey matter reduction in the occipitotemporal cortex in Spanish children with dyslexia: A voxel-based morphometry study. *Journal of Neurolinguistics, 53*. doi:10.1016/j.jneuroling.2019.100873

Ait Khelifa-Gallois, N., Puget, S., Longaud, A., Laroussinie, F., Soria, C., Sainte-Rose, C., & Dellatolas, G. (2015). Clinical evidence of the role of the cerebellum in the suppression of overt articulatory movements during reading. A study of reading in children and adolescents treated for cerebellar pilocytic astrocytoma. *The Cerebellum, 14*(2), 97-105. doi:10.1007/s12311-014-0612-1

Altarelli, I., Leroy, F., Monzalvo, K., Fluss, J., Billard, C., Dehaene-Lambertz, G., Galaburda, A. M., & Ramus, F. (2014). Planum temporale asymmetry in developmental dyslexia: Revisiting an old question. *Human Brain Mapping, 35*(12), 5717-5735. doi:10.1002/hbm.22579

Alvarez, T. A., & Fiez, J. A. (2018). Current perspectives on the cerebellum and reading development. *Neuroscience and Biobehavioral Reviews, 92*, 55-66. doi:10.1016/j.neubiorev.2018.05.006

Bach, S., Brandeis, D., Hofstetter, C., Martin, E., Richardson, U., & Brem, S. (2010). Early emergence of deviant frontal fMRI activity for phonological processes in poor beginning readers. *Neuroimage, 53*(2), 682-693. doi:10.1016/j.neuroimage.2010.06.039

Barquero, L. A., Davis, N., & Cutting, L. E. (2014). Neuroimaging of reading intervention: A systematic review and activation likelihood estimate meta-analysis. *PLoS One, 9*(1), e83668.
Ben-Yehudah, G., & Fiez, J. A. (2008). Impact of cerebellar lesions on reading and phonological processing. *Annals of the New York Academy of Sciences, 1145*, 260-274. doi:10.1196/annals.1416.015

Beneventi, H., Tonnessen, F. E., & Ersland, L. (2009). Dyslexic children show short-term memory deficits in phonological storage and serial rehearsal: An fMRI study. *International Journal of Neuroscience, 119*(11), 2017-2043. doi:10.1080/00207450903139671

Beneventi, H., Tonnessen, F. E., Ersland, L., & Hugdahl, K. (2010a). Executive working memory processes in dyslexia: Behavioral and fMRI evidence. *Scandinavian Journal of Psychology, 51*(3), 192-202. doi:10.1111/j.1467-9450.2010.00808.x

Beneventi, H., Tonnessen, F. E., Ersland, L., & Hugdahl, K. (2010b). Working memory deficit in dyslexia: Behavioral and fMRI evidence. *International Journal of Neuroscience, 120*(1), 51-59. doi:10.3109/00207450903275129

Blau, V., van Atteveldt, N., Ekkebus, M., Goebel, R., & Blomert, L. (2009). Reduced neural integration of letters and speech sounds links phonological and reading deficits in adult dyslexia. *Current Biology, 19*(6), 503-508. doi:10.1016/j.cub.2009.01.065

Bloom, J. S., Garcia-Barrera, M. A., Miller, C. J., Miller, S. R., & Hynd, G. W. (2013). Planum temporale morphology in children with developmental dyslexia. *Neuropsychologia, 51*(9), 1684-1692. doi:10.1016/j.neuropsychologia.2013.05.012

Bohler, D. J., Perfetti, C. A., & Schneider, W. (2005). Cross-cultural effect on the brain revisited: Universal structures plus writing system variation. *Human Brain Mapping, 25*(1), 92-104. doi:10.1002/hbm.20124

Bohler, 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*(14), 3210-3224. doi:10.1016/j.neuropsychologia.2008.07.024

Booth, J. R., Bebko, G., Burman, D. D., & Bitan, T. (2007a). Children with reading disorder show modality independent brain abnormalities during semantic tasks. *Neuropsychologia, 45*(4), 775-783. doi:10.1016/j.neuropsychologia.2006.08.015

Booth, J. R., Cho, S., Burman, D. D., & Bitan, T. (2007b). Neural correlates of mapping from phonology to orthography in children performing an auditory spelling task. *Developmental Science, 10*(4), 441-451.

Boros, M., Anton, J. L., Pech-George, C., Grainger, J., Szwed, M., & Ziegler, J. C. (2016). Orthographic processing deficits in developmental dyslexia: Beyond the ventral visual stream. *Neuroimage, 128*, 316-327. doi:10.1016/j.neuroimage.2016.01.014

Brambati, S. M., Termine, C., Ruffino, M., Stella, G., Fazio, F., Cappa, S. F., & Perani, D. (2004). Regional reductions of gray matter volume in familial dyslexia. *Neurology, 63*(4), 742-745. doi:10.1212/01.wnl.0000134673.95020.ee

Brambati, S. M., Termine, C., Ruffino, M., Danna, M., Lanzi, G., Stella, G., Cappa, S. F., & Perani, D. (2006). Neuropsychological deficits and neural dysfunction in familial dyslexia. *Brain Research, 1113*, 174-185. doi:10.1016/j.brainres.2006.06.099

Brem, S., Bach, S., Kucian, K., Guttorp, T. K., Martin, E., Lyytinen, H., Brandeis, D., & Richardson, U. (2010). Brain sensitivity to print emerges when children learn letter-speech sound correspondences. *Proceedings of the National Academy of Sciences, 107*(17), 7939-7944. doi:10.1073/pnas.0904402107
Brown, W. E., Eliez, S., Menon, V., Rumsey, J. M., White, C. D., & Reiss, A. L. (2001). Preliminary evidence of widespread morphological variations of the brain in dyslexia. *Neurology, 56*(6), 781-783. doi:10.1212/wnl.56.6.781

Brunswick, N., McCrorry, E., Price, C. J., Frith, C. D., & Frith, U. (1999). Explicit and implicit processing of words and pseudowords by adult developmental dyslexics - A search for Wernicke's Wortschatz? *Brain, 122*, 1901-1917. doi:10.1093/brain/122.10.1901

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. *Journal of Child Psychology and Psychiatry, 47*(10), 1041-1050. doi:10.1111/j.1469-7610.2006.01684.x

Cao, F., Yan, X., Wang, Z., Liu, Y. N., Wang, J., Spray, G. J., & Deng, Y. (2017). Neural signatures of phonological deficits in Chinese developmental dyslexia. *Neuroimage, 146*, 301-311. doi:10.1016/j.neuroimage.2016.11.051

Cao, F., Yan, X., Spray, G. J., Liu, Y., & Deng, Y. (2018). Brain mechanisms underlying visuo-orthographic deficits in children with developmental dyslexia. *Frontiers in Human Neuroscience, 12*, 490. doi:10.3389/fnhum.2018.00490

Carpentieri, T. M., Norton, E. S., Ozernov-Palchik, O., Park, A., Beach, S. D., Halverson, K., Gaab, N., & Gabrieli, J. D. E. (2019). Disrupted left fusiform response to print in beginning kindergartners is associated with subsequent reading. *NeuroImage: Clinical, 22*, 101715. doi:10.1016/j.nicl.2019.101715

Cheema, K., Lantz, N., & Cummine, J. (2018). Exploring the role of subcortical structures in developmental reading impairments: Evidence for subgroups differentiated by caudate activity. *Neuroreport, 29*(4), 271-279. doi:10.1097/WNR.0000000000000938

Christodoulou, J. A., Del Tufo, S. N., Lymbereis, J., Saxler, P. K., Ghosh, S. S., Triantafyllou, C., Whitfield-Gabrieli, S., & Gabrieli, J. D. E. (2014). Brain bases of reading fluency in typical reading and impaired fluency in dyslexia. *PLoS One, 9*(7), e100552. doi:10.1371/journal.pone.0100552

Chyl, K., Kossowski, B., Delska, A., Luniewska, M., Marchewka, A., Pugh, K. R., & Jednorog, K. (2018). Reading acquisition in children: Developmental processes and dyslexia-specific effects. *Journal of the American Academy of Child and Adolescent Psychiatry*. doi:10.1016/j.jaac.2018.11.007

Chyl, K., Kossowski, B., Wang, S., Delska, A., Luniewska, M., Marchewka, A., Wypych, M., van den Bunt, M., Mencl, W., Pugh, K., & Jednorog, K. (2021). The brain signature of emerging
reading in two contrasting languages. *Neuroimage*, 225.

doi:10.1016/j.neuroimage.2020.117503

Clark, K. A., Helland, T., Specht, K., Narr, K. L., Manis, F. R., Toga, A. W., & Hugdahl, K. (2014). Neuroanatomical precursors of dyslexia identified from pre-reading through to age 11. *Brain*, 137, 3136-3141. doi:10.1093/brain/awu229

Conway, T., Heilman, K. M., Gopinath, K., Peck, K., Bauer, R., Briggs, R. W., Torgesen, J. K., & Crosson, B. (2008). Neural substrates related to auditory working memory comparisons in dyslexia: An fMRI study. *Journal of the International Neuropsychological Society*, 14(4), 629-639. doi:10.1017/S1355617708080867

Coslett, H. B., & Monsul, N. (1994). Reading with the right-hemisphere: Evidence from transcranial magnetic stimulation. *Brain and Language*, 46(2), 198-211. doi:10.1006/brln.1994.1012

Costafreda, S. G., Fu, C. H. Y., Lee, L., Everitt, B., Brammer, M. J., & David, A. S. (2006). A systematic review and quantitative appraisal of fMRI studies of verbal fluency: Role of the left inferior frontal gyrus. *Human Brain Mapping*, 27(10), 799-810. doi:10.1002/hbm.20221

Cutting, L. E., Clements-Stephens, A., Pugh, K. R., Burns, S., Cao, A., Pekar, J. J., Davis, N., & Rimrodt, S. L. (2013). Not all reading disabilities are dyslexia: distinct neurobiology of specific comprehension deficits. *Brain Connectivity*, 3(2), 199-211. doi:10.1089/brain.2012.0116

Danelli, L., Berlingeri, M., Bottini, G., Borghese, N. A., Lucchese, M., Shenra, M., Price, C. J., & Paulesu, E. (2017). How many deficits in the same dyslexic brains? A behavioural and fMRI assessment of comorbidity in adult dyslexics. *Cortex*, 97, 125-142. doi:10.1016/j.cortex.2017.08.038

Desroches, A. S., Cone, N. E., Bolger, D. J., Bitan, T., Burman, D. D., & Booth, J. R. (2010). Children with reading difficulties show differences in brain regions associated with orthographic processing during spoken language processing. *Brain Research*, 1356, 73-84. doi:10.1016/j.brainres.2010.07.097

Döhla, D., & Heim, S. (2016). Developmental dyslexia and dysgraphia: What can we learn from the one about the other? *Frontiers in Psychology*, 6(2045). doi:10.3389/fpsyg.2015.02045

Dronkers, N. F. (1996). A new brain region for coordinating speech articulation. *Nature*, 384(6605), 159-161. doi:10.1038/384159a0

Dufor, O., Serniclaes, W., Sprenger-Charolles, L., & Demonet, J. F. (2007). Top-down processes during auditory phoneme categorization in dyslexia: A PET study. *Neuroimage*, 34(4), 1692-1707. doi:10.1016/j.neuroimage.2006.10.034

Eckert, M. A., Leonard, C. M., Wilke, M., Eckert, M., Richards, T., Richards, A., & Berninger, V. (2005). Anatomical signatures of dyslexia in children: Unique information from manual and voxel based morphometry brain measures. *Cortex*, 41(3), 304-315. doi:10.1016/S0010-9452(08)70268-5

Eden, G. F., Jones, K. M., Cappell, K., Gareau, L., Wood, F. B., Zeffiro, T. A., Dietz, N. A., Agnew, J. A., & Flowers, D. L. (2004). Neural changes following remediation in adult developmental dyslexia. *Neuron*, 44(3), 411-422. doi:10.1016/j.neuron.2004.10.019

Enge, A., Friederici, A. D., & Skeide, M. A. (2020). A meta-analysis of fMRI studies of language comprehension in children. *Neuroimage*, 215, 116858. doi:10.1016/j.neuroimage.2020.116858

Evans, T. M., Flowers, D. L., Napolitello, E. M., Olulade, O. A., & Eden, G. F. (2014a). The functional anatomy of single-digit arithmetic in children with developmental dyslexia. *Neuroimage*, 101,
Evans, T. M., Flowers, D. L., Napoliello, E. M., & Eden, G. F. (2014b). Sex-specific gray matter volume differences in females with developmental dyslexia. *Brain Structure and Function, 219*(3), 1041-1054. doi:10.1007/s00429-013-0552-4

Farris, E. A., Ring, J., Black, J., Lyon, G. R., & Odegard, T. N. (2016). Predicting growth in word level reading skills in children with developmental dyslexia using an object rhyming functional neuroimaging task. *Developmental Neuropsychology, 41*(3), 145-161. doi:10.1080/87565641.2016.1158264

Feng, X., Li, L., Zhang, M., Yang, X., Tian, M., Xie, W., Lu, Y., Liu, L., Belanger, N. N., Meng, X., & Ding, G. (2017). Dyslexic children show atypical cerebellar activation and cerebro-cerebellar functional connectivity in orthographic and phonological processing. *Cerebellum, 16*(2), 496-507. doi:10.1007/s12311-016-0829-2

Feng, X., Altarelli, I., Monzalvo, K., Ding, G., Ramus, F., Shu, H., Dehaene, S., Meng, X., & Dehaene-Lambertz, G. (2020). A universal reading network and its modulation by writing system and reading ability in French and Chinese children. *Elife, 9*. doi:10.7554/eLife.54591

Fiez, J. A. (2000). Sound and meaning: How native language affects reading strategies. *Nature Neuroscience, 3*(1), 3-5. doi:10.1038/71078

Finn, E. S., Shen, X., Holahan, J. M., Scheinost, D., Lacadie, C., Papademetris, X., Shaywitz, S. E., Shaywitz, B. A., & Constable, R. T. (2014). Disruption of functional networks in dyslexia: A whole-brain, data-driven analysis of connectivity. *Biological Psychiatry, 76*(5), 397-404. doi:10.1016/j.biopsych.2013.08.031

Francisco, A. A., Takashima, A., McQueen, J. M., van den Bunt, M., Jesse, A., & Groen, M. A. (2018). Adult dyslexic readers benefit less from visual input during audiovisual speech processing: fMRI evidence. *Neuropsychologia, 117*, 454-471. doi:10.1016/j.neuropsychologia.2018.07.009

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Sciences, 16*(5), 262-268. doi:10.1016/j.tics.2012.04.001

Frodl, T., & Skokauskas, N. (2012). Meta-analysis of structural MRI studies in children and adults with attention deficit hyperactivity disorder indicates treatment effects. *Acta Psychiatrica Scandinavica, 125*(2), 114-126. doi:10.1111/j.1600-0447.2011.01786.x

Gaab, N., Gabrieli, J. D., Deutsch, G. K., Tallal, P., & Temple, E. (2007). Neural correlates of rapid auditory processing are disrupted in children with developmental dyslexia and ameliorated with training: An fMRI study. *Restorative Neurology and Neuroscience, 25*(3-4), 295-310.

Gatti, D., Van Vugt, F., & Vecchi, T. (2020). A causal role for the cerebellum in semantic integration: A transcranial magnetic stimulation study. *Scientific Reports, 10*(1), 18139. doi:10.1038/s41598-020-75287-z

Georgiewa, P., Rzanny, R., Hopf, J. M., Knab, R., Glauche, V., Kaiser, W. A., & Blanz, B. (1999). fMRI during word processing in dyslexic and normal reading children. *Neuroreport, 10*(16), 3459-3465. doi:10.1097/00001756-199911080-00036

Giraud, A. L., & Ramus, F. (2013). Neurogenetics and auditory processing in developmental dyslexia. *Current Opinion in Neurobiology, 23*(1), 37-42. doi:10.1016/j.conb.2012.09.003

Glezer, L. S., Jiang, X., & Riesenhuber, M. (2009). Evidence for highly selective neuronal tuning to whole words in the “Visual Word Form Area”. *Neuron, 62*(2), 199-204. doi:10.1016/j.neuron.2009.03.017
Glezer, L. S., Eden, G., Jiang, X., Luetje, M., Napoletti, E., Kima, J., & Riesenhuber, M. (2016). Uncovering phonological and orthographic selectivity across the reading network using fMRI-RA. *Neuroimage*, 138, 248-256. doi:10.1016/j.neuroimage.2016.05.072

Glezer, L. S., Jiang, X., Luetje, M. M., Napoletti, E. M., Kim, J., Riesenhuber, M., & Eden, G. F. (2019). An fMRI-adaptation study of phonological and orthographic selectivity to written words in adults with poor reading skills. *Brain Lang.*, 191, 1-8. doi:10.1016/j.bandl.2019.01.002

Goswami, U., Wang, H. L. S., Cruz, A., Fosker, T., Mead, N., & Huss, M. (2011). Language-sensory deficits in developmental dyslexia: English, Spanish, and Chinese. *Journal of Cognitive Neuroscience*, 23(2), 325-337. doi:10.1162/jocn.2010.21453

Grahn, J. A., Parkinson, J. A., & Owen, A. M. (2008). The cognitive functions of the caudate nucleus. *Progress in Neurobiology*, 86(3), 141-155. doi:10.1016/j.pneurobio.2008.09.004

Grande, M., Meffert, E., Huber, W., Amunts, K., & Amunts, K. (2010). Interaction of phonological awareness and 'magnocellular' processing during normal and dyslexic reading: Behavioural and fMRI investigations. *Dyslexia*, 16(3), 258-282. doi:10.1002/dys.409

Heim, S., Wehnelt, A., Grande, M., Huber, W., & Amunts, K. (2013). Effects of lexicality and word frequency on brain activation in dyslexic readers. *Brain and Language*, 125(2), 194-202. doi:10.1016/j.bandl.2011.12.005

Hickok, G., & Poeppel, D. (2007). The cortical organization of speech processing. *Nature Reviews Neuroscience*, 8(5), 393-402. doi:10.1038/nrn2113

Hirshorn, E. A., Li, Y., Ward, M. J., Richardson, R. M., Fiez, J. A., & Ghuman, A. S. (2016). Decoding
and disrupting left midfusiform gyrus activity during word reading. Proceedings of the National Academy of Sciences, 113(29), 8162. doi:10.1073/pnas.1604126113

Hoeft, F., Hernandez, A., McMillon, G., Taylor-Hill, H., Martindale, J. L., Meyer, A., Keller, T. A., Siok, W. T., Deutsch, G. K., Just, M. A., Whitfield-Gabrieli, S., & Gabrieli, J. D. (2006). Neural basis of dyslexia: A comparison between dyslexic and nondyslexic children equated for reading ability. Journal of Neuroscience, 26(42), 10700-10708. doi:10.1523/JNEUROSCI.4931-05.2006

Hoeft, 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. Proceedings of the National Academy of Sciences, 104(10), 4234-4239. doi:10.1073/pnas.0609399104

Honorof, D., & Feldman, L. (2006). The Chinese character in psycholinguistic research: Form, structure, and the reader. In P. Li, L. H. Tan, E. Bates, & O. J. L. Tzeng (Eds.), The Handbook of East Asian Psycholinguistics (Vol. 1, pp. 195-208). Cambridge, U.K.: Cambridge University Press.

Horowitz-Kraus, T., Buck, C., & Dorrmann, D. (2016). Altered neural circuits accompany lower performance during narrative comprehension in children with reading difficulties: an fMRI study. Annals of Dyslexia, 66(3), 301-318. doi:10.1007/s11881-016-0124-4

Hosseini, S. M. H., Black, J. M., Soriano, T., Bugescu, N., Martinez, R., Raman, M. M., Kesler, S. R., & Hoeft, F. (2013). Topological properties of large-scale structural brain networks in children with familial risk for reading difficulties. Neuroimage, 71, 260-274. doi:10.1016/j.neuroimage.2013.01.013

Houston, S. M., Lebel, C., Katzir, T., Manis, F. R., Kan, E., Rodriguez, G. G., & Sowell, E. R. (2014). Reading skill and structural brain development. Neuroreport, 25(5), 347-352. doi:10.1097/WNR.0000000000000121

Hu, W., Lee, H. L., Zhang, Q., Liu, T., Geng, L. B., Seghier, M. L., Shakeshaft, C., Twomey, T., Green, D. W., Yang, Y. M., & Price, C. J. (2010). Developmental dyslexia in Chinese and English populations: Dissociating the effect of dyslexia from language differences. Brain, 133, 1694-1706. doi:10.1093/brain/awq106

Husain, M. M., McDonald, W. M., Doraismwamy, P. M., Figiel, G. S., Na, C., Escalona, P. R., Boyko, O. B., Nemeroff, C. B., & Krishnan, K. R. R. (1991). A magnetic resonance imaging study of putamen nuclei in major depression. Psychiatry Research: Neuroimaging, 40(2), 95-99. doi:10.1016/0925-4927(91)90001-7

Ingvar, M., af Trampe, P., Greitz, T., Eriksson, L., Stone-Elander, S., & von Euler, C. (2002). Residual differences in language processing in compensated dyslexics revealed in simple word reading tasks. Brain and Language, 83(2), 249-267. doi:10.1016/S0093-934X(02)00055-X

Jaffe-Dax, S., Kimel, E., & Ahissar, M. (2018). Shorter cortical adaptation in dyslexia is broadly distributed in the superior temporal lobe and includes the primary auditory cortex. Elife, 7. doi:10.7554/eLife.30018

Jagger-Rickels, A. C., Kibby, M. Y., & Constance, J. M. (2018). Global gray matter morphometry differences between children with reading disability, ADHD, and comorbid reading disability/ADHD. Brain and Language, 185, 54-66. doi:10.1016/j.bandl.2018.08.004

Jednorog, K., Gawron, N., Marchewka, A., Heim, S., & Grabowska, A. (2014). Cognitive subtypes of dyslexia are characterized by distinct patterns of grey matter volume. Brain Structure and...
Jednorog, K., Marchewka, A., Altarelli, I., Lopez, A. K. M., van Ermingen-Marbach, M., Grande, M., Grabowska, A., Heim, S., & Ramus, F. (2015). How reliable are gray matter disruptions in specific reading disability across multiple countries and languages? Insights from a large-scale Voxel-Based Morphometry study. *Human Brain Mapping*, 36(5), 1741-1754. doi:10.1002/hbm.22734

Kast, M., Bezzola, L., Jancke, L., & Meyer, M. (2011). Multi- and unisensory decoding of words and nonwords result in differential brain responses in dyslexic and nondyslexic adults. *Brain and Language*, 119(3), 136-148. doi:10.1016/j.bandl.2011.04.002

Katusic, S. K., Colligan, R. C., Barbaresi, W. J., Schaid, D. J., & Jacobsen, S. J. (2001). Incidence of reading disability in a population-based birth Cohort, 1976–1982, Rochester, Minn. Mayo Clinic Proceedings, 76(11), 1081-1092. doi:10.4065/76.11.1081

Kibby, M. Y., Fancher, J. B., Markanen, R., & Hynd, G. W. (2008). A quantitative magnetic resonance imaging analysis of the cerebellar deficit hypothesis of dyslexia. *Journal of Child Neurology*, 23(4), 368-380. doi:10.1177/0888307307309235

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. *Cerebral Cortex*, 22(4), 754-764. doi:10.1093/cercor/bhr094

Krafnick, A. J., Flowers, D. L., Luetje, M. M., Napoliello, E. M., & Eden, G. F. (2014). An investigation into the origin of anatomical differences in dyslexia. *Journal of Neuroscience*, 34(3), 901-908. doi:10.1523/JNEUROSCI.2092-13.2013

Kronbichler, M., Hutzler, F., Staffen, W., Mair, A., Ladurner, G., & Wimmer, H. (2006). Evidence for a dysfunction of left posterior reading areas in German dyslexic readers. *Neuropsychologia*, 44(10), 1822-1832. doi:10.1016/j.neuropsychologia.2006.03.010

Kronbichler, M., Wimmer, H., Staffen, W., Hutzler, F., Mair, A., & Ladurner, G. (2008). Developmental dyslexia: Gray matter abnormalities in the occipitotemporal cortex. *Human Brain Mapping*, 29(5), 613-625. doi:10.1002/hbm.20425

Kronschnabel, J., Schmid, R., Maurer, U., & Brandeis, D. (2013). Visual print tuning deficits in dyslexic adolescents under minimized phonological demands. *Neuroimage*, 74, 58-69. doi:10.1016/j.neuroimage.2013.02.014

Kronschnabel, J., Brem, S., Maurer, U., & Brandeis, D. (2014). The level of audiovisual print-speech integration deficits in dyslexia. *Neuropsychologia*, 62, 245-261. doi:10.1016/j.neuropsychologia.2014.07.024

Laird, A. R., Eickhoff, S. B., Li, K., Robin, D. A., Glahn, D. C., & Fox, P. T. (2009). Investigating the functional heterogeneity of the default mode network using coordinate-based meta-analytic modeling. *The Journal of Neuroscience*, 29(46), 14496. doi:10.1523/JNEUROSCI.4004-09.2009

Landerl, K., Wimmer, H., & Frith, U. (1997). The impact of orthographic consistency on dyslexia: A German-English comparison. *Cognition*, 63(3), 315-334. doi:10.1016/S0010-0277(97)00005-X

Landi, N., Mencl, W. E., Frost, S. J., Sandak, R., & Pugh, K. R. (2010). An fMRI study of multimodal semantic and phonological processing in reading disabled adolescents. *Annals of Dyslexia*, 60(1), 102-121. doi:10.1007/s11881-009-0029-6
Langer, N., Benjamin, C., Minas, J., & Gaab, N. (2015). The neural correlates of reading fluency deficits in children. *Cerebral Cortex, 25*(6), 1441-1453. doi:10.1093/cercor/bht330

Linkersdorfer, J., Lonnemann, J., Lindberg, S., Hasselhorn, M., & Fiebach, C. J. (2012). Grey matter alterations co-localize with functional abnormalities in developmental dyslexia: An ALE meta-analysis. *PLoS One, 7*(8). doi:10.1371/journal.pone.0043122

Liu, L., Wang, W., You, W., Li, Y., Awati, N., Zhao, X., Booth, J. R., & Peng, D. (2012). Similar alterations in brain function for phonological and semantic processing to visual characters in Chinese dyslexia. *Neuropsychologia, 50*(9), 2224-2232. doi:10.1016/j.neuropsychologia.2012.05.026

Liu, L., You, W., Wang, W., Guo, X., Peng, D., & Booth, J. (2013a). Altered brain structure in Chinese dyslexic children. *Neuropsychologia, 51*(7), 1169-1176. doi:10.1016/j.neuropsychologia.2013.03.010

Maisog, J. M., Einbinder, E. R., Flowers, D. L., Turkeltaub, P. E., & Eden, G. F. (2008). A meta-analysis of functional neuroimaging studies of dyslexia. *Annals of the New York Academy of Sciences, 1145*, 237-259. doi:10.1196/annals.1416.024

Margolis, A. E., Pagliaccio, D., Davis, K. S., Thomas, L., Banker, S. M., Cyr, M., & Marsh, R. (2019). Neural correlates of cognitive control deficits in children with reading disorder. *Brain Imaging and Behavior*. doi:10.1007/s11682-019-00083-x

McCrory, E. J., Mechelli, A., Frith, U., & Price, C. J. (2005). More than words: A common neural basis for reading and naming deficits in developmental dyslexia? *Brain, 128*, 261-267. doi:10.1093/brain/awh340

McGrath, L. M., & Stoodley, C. J. (2019). Are there shared neural correlates between dyslexia and...
ADHD? A meta-analysis of voxel-based morphometry studies. *Journal of Neurodevelopmental Disorders*, 11(1), 31. doi:10.1186/s11689-019-9287-8

Mechelli, A., Crinion, J. T., Noppeney, U., O'Doherty, J., Ashburner, J., Frackowiak, R. S., & Price, C. J. (2004). Neurolinguistics: Structural plasticity in the bilingual brain. *Nature*, 431(7010), 757. doi:10.1038/431757a

Melby-Lervag, M., Lyster, S. A. H., & Hulme, C. (2012). Phonological skills and their role in learning to read: A meta-analytic review. *Psychological Bulletin*, 138(2), 322-352. doi:10.1037/a0026744

Menghini, D., Hagberg, G. E., Caltagirone, C., Petrosini, L., & Vicari, S. (2006). Implicit learning deficits in dyslexic adults: An fMRI study. *Neuroimage*, 33(4), 1218-1226. doi:10.1016/j.neuroimage.2006.08.024

Menghini, D., Hagberg, G. E., Petrosini, L., Bozzali, M., Macaluso, E., Caltagirone, C., & Vicari, S. (2008). Structural correlates of implicit learning deficits in subjects with developmental dyslexia. *Annals of the New York Academy of Sciences*, 1145, 212-221. doi:10.1196/annals.1416.010

Meyler, A., Keller, T. A., Cherkassky, V. L., Gabrieli, J. D., & Just, M. A. (2008). Modifying the brain activation of poor readers during sentence comprehension with extended remedial instruction: a longitudinal study of neuroplasticity. *Neuropsychologia*, 46(10), 2580-2592. doi:10.1016/j.neuropsychologia.2008.03.012

Monzalvo, K., Fluss, J., Billard, C., Dehaene, S., & Dehaene-Lambertz, G. (2012). Cortical networks for vision and language in dyslexic and normal children of variable socio-economic status. *Neuroimage*, 61(1), 258-274. doi:10.1016/j.neuroimage.2012.02.035

Mous, S. E., Hammerschlag, A. R., Polderman, T. J. C., Verhulst, F. C., Tiemeier, H., van der Lugt, A., Jaddoe, V. W., Hofman, A., White, T., & Posthuma, D. (2015). A population-based imaging genetics study of inattention/hyperactivity: Basal ganglia and genetic pathways. *Journal of the American Academy of Child and Adolescent Psychiatry*, 54(9), 745-752. doi:10.1016/j.jaac.2015.05.018

Nakao, T., Radua, J., Rubia, K., & Mataix-Cols, D. (2011). Gray matter volume abnormalities in ADHD: Voxel-based meta-analysis exploring the effects of age and stimulant medication. *American Journal of Psychiatry*, 168(11), 1154-1163. doi:10.1176/appi.ajp.2011.11020281

Nickl-Jockschat, T., Habel, U., Maria Michel, T., Manning, J., Laird, A. R., Fox, P. T., Schneider, F., & Eickhoff, S. B. (2012). Brain structure anomalies in autism spectrum disorder—a meta-analysis of VBM studies using anatomic likelihood estimation. *Human Brain Mapping*, 33(6), 1470-1489. doi:10.1002/hbm.21299

Nobre, A. C., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature*, 372(6503), 260-263. doi:10.1038/37260a0

Nord, C. L., Kim, S.-G., Callesen, M. B., Kvamme, T. L., Jensen, M., Pedersen, M. U., Thomsen, K. R., & Voon, V. (2019). The myeloarchitecture of impulsivity: Premature responding in youth is associated with decreased myelination of ventral putamen. *Neuropsychopharmacology*, 44(7), 1216-1223. doi:10.1038/s41386-019-0343-6

Olulade, O. A., Gilger, J. W., Talavage, T. M., Hynd, G. W., & McAteer, C. I. (2012). Beyond...
phonological processing deficits in adult dyslexics: Atypical fMRI activation patterns for spatial problem solving. Developmental Neuropsychology, 37(7), 617-635. doi:10.1080/87565641.2012.702826

Oulade, O. A., Flowers, D. L., Napolietto, E. M., & Eden, G. F. (2015). Dyslexic children lack word selectivity gradients in occipito-temporal and inferior frontal cortex. NeuroImage: Clinical, 7, 742-754. doi:10.1016/j.nicl.2015.02.013

Parrila, R., Dudley, D., Song, S., & Georgiou, G. K. (2020). A meta-analysis of reading-level match dyslexia studies in consistent alphabetic orthographies. Annals of Dyslexia, 70(1), 1-26. doi:10.1007/s11881-019-00187-5

Paulesu, E., Frith, U., Snowling, M., Gallagher, A., Morton, J., Frackowiak, R. S. J., & Frith, C. D. (1996). Is developmental dyslexia a disconnection syndrome?: Evidence from PET scanning. Brain, 119(1), 143-157. doi:10.1093/brain/119.1.143

Paulesu, E., McCrory, E., Fazio, F., Menoncillo, L., Brunswick, N., Cappa, S. F., Cotelli, M., Cosso, 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. Nature Neuroscience, 3(1), 91-96. doi:10.1038/71163

Paulesu, E., Démonet, J. F., Fazio, F., McCrory, E., Chanoine, V., Brunswick, N., Cappa, S. F., Cossu, G., Habib, M., Frith, C. D., & Frith, U. (2001). Dyslexia: Cultural diversity and biological unity. Science, 291(5511), 2165-2167. doi:10.1126/science.1057179

Paulesu, E., Danelli, L., & Berlingeri, M. (2014). Reading the dyslexic brain: Multiple dysfunctional routes revealed by a new meta-analysis of PET and fMRI activation studies. Frontiers in Human Neuroscience, 8. doi:10.3389/fnhum.2014.00830

Paz-Alonso, P. M., Oliver, M., Lerma-Usabiaga, G., Caballero-Gaudes, C., Quinones, I., Suarez-Coalla, P., Dunabeitia, J. A., Cuetos, F., & Carreiras, M. (2018). Neural correlates of phonological, orthographic and semantic reading processing in dyslexia. NeuroImage: Clinical, 20, 433-447. doi:10.1016/j.nicl.2018.08.018

Pecini, C., Biagi, L., Brizzolara, D., Cipriani, P., Di Lieto, M. C., Guzzetta, A., Tosetti, M., & Chilosi, A. M. (2011). How many functional brains in developmental dyslexia? When the history of language delay makes the difference. Cognitive and Behavioral Neurology, 24(2), 85-92. doi:10.1097/WNN.0b013e318222a4e2

Pekkola, J., Laasonen, M., Ojanen, V., Autti, T., Jaaskelainen, I. P., Kujala, T., & Sams, M. (2006). Perception of matching and conflicting audiovisual speech in dyslexic and fluent readers: An fMRI study at 3 T. Neuroimage, 29(3), 797-807. doi:10.1016/j.neuroimage.2005.09.069

Pernet, C., Andersson, J., Paulesu, E., & Demonet, J. F. (2009). When all hypotheses are right: A multifocal account of dyslexia. Human Brain Mapping, 30(7), 2278-2292. doi:10.1002/hbm.20670

Perrachione, T. K., Del Tufo, S. N., Winter, R., Murtagh, J., Cyr, A., Chang, P., Halverson, K., Ghosh, S. S., Christodoulou, J. A., & Gabrieli, J. D. E. (2016). Dysfunction of rapid neural adaptation in dyslexia. Neuron, 92(6), 1383-1397. doi:10.1016/j.neuron.2016.11.020

Petersen, S. E., & Fiez, J. A. (1993). The processing of single words studied with positron emission tomography. Annual Review of Neuroscience, 16(1), 509-530. doi:10.1146/annurev.ne.16.030193.002453

Peterson, R. L., & Pennington, B. F. (2012). Developmental dyslexia. Lancet, 379(9830), 1997-2007. doi:10.1016/S0140-6736(12)60198-6
Peyrin, C., Demonet, J. F., N'Guyen-Morel, M. A., Le Bas, J. F., & Valdois, S. (2011). Superior parietal lobule dysfunction in a homogeneous group of dyslexic children with a visual attention span disorder. *Brain and Language, 118*(3), 128-138. doi:10.1016/j.bandl.2010.06.005

Plewko, J., Chyl, K., Bola, L., Luniewska, M., Debksa, A., Banaszkiewicz, A., Wypych, M., Marchewka, A., van Atteveldt, N., & Jednorog, K. (2018). Letter and speech sound association in emerging readers with familial risk of dyslexia. *Frontiers in Human Neuroscience, 12*, 393. doi:10.3389/fnhum.2018.00393

Prasad, S., Sagar, R., Kumaran, S. S., & Mehta, M. (2020). Study of functional magnetic resonance imaging (fMRI) in children and adolescents with specific learning disorder (dyslexia). *Asian Journal of Psychiatry, 50*. doi:10.1016/j.ajp.2020.101945

Pugh, K. R., Mencl, W. E., Jenner, A. R., Katz, L., Frost, S. J., Lee, J. R., Shaywitz, S. E., & Shaywitz, B. A. (2000). Functional neuroimaging studies of reading and reading disability (developmental dyslexia). *Mental Retardation and Developmental Disabilities Research Reviews, 6*(3), 207-213.

Radua, J., Mataix-Cols, D., Phillips, M. L., El-Hage, W., Kronhaus, D. M., Cardoner, N., & Surguladze, S. (2012a). A new meta-analytic method for neuroimaging studies that combines reported peak coordinates and statistical parametric maps. *European Psychiatry, 27*(8), 605-611. doi:10.1016/j.eurpsy.2011.04.001

Radua, J., Borgwardt, S., Crescini, A., Mataix-Cols, D., Meyer-Lindenberg, A., McGuire, P. K., & Fusar-Poli, P. (2012b). Multimodal meta-analysis of structural and functional brain changes in first episode psychosis and the effects of antipsychotic medication. *Neuroscience and Biobehavioral Reviews, 36*(10), 2325-2333. doi:10.1016/j.neubiorev.2012.07.012

Radua, J., Romeo, M., Mataix-Cols, D., & Fusar-Poli, P. (2013). A general approach for combining voxel-based meta-analyses conducted in different neuroimaging modalities. *Current Medicinal Chemistry, 20*(3), 462-466.

Radua, J., Rubia, K., Canales-Rodriguez, E. J., Pomarol-Clotet, E., Fusar-Poli, P., & Mataix-Cols, D. (2014). Anisotropic kernels for coordinate-based meta-analyses of neuroimaging studies. *Frontiers in Psychiatry, 5*, 13. doi:10.3389/fpsyt.2014.00013

Rae, C., Harasty, J. A., Dzendrowskyj, T. E., Talcott, J. B., Simpson, J. M., Blamire, A. M., Dixon, R. M., Lee, M. A., Thompson, C. H., Styles, P., Richardson, A. J., & Stein, J. F. (2002). Cerebellar morphology in developmental dyslexia. *Neuropsychologia, 40*(8), 1285-1292. doi:10.1016/S0028-3932(01)00216-0

Raschle, N. M., Zuk, J., & Gaab, N. (2012). Functional characteristics of developmental dyslexia in left-hemispheric posterior brain regions predate reading onset. *Proceedings of the National Academy of Sciences, 109*(6), 2156-2161. doi:10.1073/pnas.1107721109

Raschle, N. M., Stering, P. L., Meissner, S. N., & Gaab, N. (2014). Altered neuronal response during rapid auditory processing and its relation to phonological processing in prereading children at familial risk for dyslexia. *Cerebral Cortex, 24*(9), 2489-2501. doi:10.1093/cercor/bht104

Reilhac, C., Peyrin, C., Demonet, J. F., & Valdois, S. (2013). Role of the superior parietal lobules in letter-identity processing within strings: fMRI evidence from skilled and dyslexic readers. *Neuropsychologia, 51*(4), 601-612. doi:10.1016/j.neuropsychologia.2012.12.010

Richards, T. L., Aylward, E. H., Berninger, V. W., Field, K. M., Grimme, A. C., Richards, A. L., & Nagy, W. (2006). Individual fMRI activation in orthographic mapping and morpheme mapping after orthographic or morphological spelling treatment in child dyslexics. *Journal of
Richlan, F., Kronbichler, M., & Wimmer, H. (2009). Functional abnormalities in the dyslexic brain: A quantitative meta-analysis of neuroimaging studies. *Human Brain Mapping, 30*(10), 3299-3308. doi:10.1002/hbm.20752

Richlan, F., Sturm, D., Schurz, M., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A common left occipito-temporal dysfunction in developmental dyslexia and acquired letter-by-letter reading? *PLoS One, 5*(8), e12073. doi:10.1371/journal.pone.0012073

Richlan, F., Kronbichler, M., & Wimmer, H. (2011). Meta-analyzing brain dysfunctions in dyslexic children and adults. *Neuroimage, 56*(3), 1735-1742. doi:10.1016/j.neuroimage.2011.02.040

Richlan, F. (2012). Developmental dyslexia: Dysfunction of a left hemisphere reading network. *Frontiers in Human Neuroscience, 6*. doi:10.3389/fnhum.2012.00120

Richlan, F., Kronbichler, M., & Wimmer, H. (2013). Structural abnormalities in the dyslexic brain: A meta-analysis of voxel-based morphometry studies. *Human Brain Mapping, 34*(11), 3055-3065. doi:10.1002/hbm.22127

Rimrodt, S. L., Clements-Stephens, A. M., Pugh, K. R., Courtney, S. M., Gaur, P., Pekar, J. J., & Cutting, L. E. (2009). Functional MRI of sentence comprehension in children with dyslexia: Beyond word recognition. *Cerebral Cortex, 19*(2), 402-413. doi:10.1093/cercor/bhn092

Ruff, S., Cardebat, D., Marie, N., & Demonet, J. F. (2002). Enhanced response of the left frontal cortex to slowed down speech in dyslexia: An fMRI study. *Neuroreport, 13*(10), 1285-1289. doi:10.1097/00001756-200207190-00014

Rumsey, J. M., Nace, K., Donohue, B., Wise, D., Maisog, J. M., & Andreasen, P. (1997). A positron emission tomographic study of impaired word recognition and phonological processing in dyslexic men. *Archives of Neurology, 54*(5), 562-573. doi:10.1001/archneur.1997.00550170042013

Schulz, E., Maurer, U., van der Mark, S., Bucher, K., Brem, S., Martin, E., & Brandeis, D. (2008). Impaired semantic processing during sentence reading in children with dyslexia: Combined fMRI and ERP evidence. *Neuroimage, 41*(1), 153-168. doi:10.1016/j.neuroimage.2008.02.012

Schulz, E., Maurer, U., van der Mark, S., Bucher, K., Brem, S., Martin, E., & Brandeis, D. (2009). Reading for meaning in dyslexic and young children: Distinct neural pathways but common endpoints. *Neuropsychologia, 47*(12), 2544-2557. doi:10.1016/j.neuropsychologia.2009.04.028

Schurz, M., Sturm, D., Richlan, F., Kronbichler, M., Ladurner, G., & Wimmer, H. (2010). A dual-route perspective on brain activation in response to visual words: Evidence for a length by lexicality interaction in the visual word form area (VWFA). *Neuroimage, 49*(3), 2649-2661. doi:10.1016/j.neuroimage.2009.10.082

Shaywitz, S. E. (1996). Dyslexia. *Scientific American, 275*(5), 98-104.

Shaywitz, S. E., Shaywitz, B. A., Pugh, K. R., Fulbright, R. K., Constable, R. T., Mencl, W. E., Shankweiler, D. P., Liberman, A. M., Skudlarski, P., Fletcher, J. M., Katz, L., Marchione, K. E., Lacadie, C., Gatenby, C., & Gore, J. C. (1998). Functional disruption in the organization of the brain for reading in dyslexia. *Proceedings of the National Academy of Sciences, 95*(5), 2636-2641. doi:10.1073/pnas.95.5.2636

Shu, H., Meng, X. Z., Chen, X., Luan, H., & Cao, F. (2005). The subtypes of developmental dyslexia in Chinese: Evidence from three cases. *Dyslexia, 11*(4), 311-329. doi:10.1002/dys.310

Silani, G., Frith, U., Demonet, J. F., Fazio, F., Perani, D., Price, C., Frith, C. D., & Paulesu, E. (2005).
Brain abnormalities underlying altered activation in dyslexia: A voxel based morphometry study. Brain, 128, 2453-2461. doi:10.1093/brain/aws579

Siok, W. T., Perfetti, C. A., Jin, Z., & Tan, L. H. (2004). Biological abnormality of impaired reading is constrained by culture. Nature, 431(7004), 71-76. doi:10.1038/nature02865

Siok, W. T., Niu, Z., Jin, Z., Perfetti, C. A., & Tan, L. H. (2008). A structural-functional basis for dyslexia in the cortex of Chinese readers. Proceedings of the National Academy of Sciences, 105(14), 5561-5566. doi:10.1073/pnas.0801750105

Siok, W. T., Spinks, J. A., Jin, Z., & Tan, L. H. (2009). Developmental dyslexia is characterized by the co-existence of visuospatial and phonological disorders in Chinese children. Current Biology, 19(19), R890-892. doi:10.1016/j.cub.2009.08.014

Skeide, M. A., Bazin, P. L., Trampel, R., Schafer, A., Mannel, C., von Kriegstein, K., & Friederici, A. D. (2018). Hypermyelination of the left auditory cortex in developmental dyslexia. Neurology, 90(6), e492-e497. doi:10.1212/WNL.0000000000004931

Snowling, M. J., & Melby-Lervag, M. (2016). Oral language deficits in familial dyslexia: A meta-analysis and review. Psychological Bulletin, 142(5), 498-545. doi:10.1037/bul0000037

Steinbrink, C., Vogt, K., Kastrup, A., Muller, H. P., Juengling, F. D., Kassubeck, J., & Riecker, A. (2008). The contribution of white and gray matter differences to developmental dyslexia: Insights from DTI and VBM at 3.0 T. Neuropsychologia, 46(13), 3170-3178. doi:10.1016/j.neuropsychologia.2008.07.015

Steinbrink, C., Groth, K., Lachmann, T., & Riecker, A. (2012). Neural correlates of temporal auditory processing in developmental dyslexia during German vowel length discrimination: An fMRI study. Brain Lang, 121(1), 1-11. doi:10.1016/j.bandl.2011.12.003

Stoodley, C. J., & Stein, J. F. (2011). The cerebellum and dyslexia. Cortex, 47(1), 101-116. doi:10.1016/j.cortex.2009.10.005

Sun, Z., Zou, L., Zhang, J. J., Mo, S. N., Shao, S. S., Zhong, R., Ke, J. T., Lu, X. Z., Miao, X. P., & Song, R. R. (2013). Prevalence and associated risk factors of dyslexic children in a middle-sized city of China: A cross-sectional study. PLoS One, 8(2). doi:10.1371/journal.pone.0056688

Szatkowska, I., Grabowska, A., & Szymańska, O. (2000). Phonological and semantic fluencies are mediated by different regions of the prefrontal cortex. Acta Neurobiologiae Experimentalis, 60(4), 503-508.

Tamboer, P., Scholte, H. S., & Vorst, H. C. (2015). Dyslexia and voxel-based morphometry: correlations between five behavioural measures of dyslexia and gray and white matter volumes. Annals of Dyslexia, 65(3), 121-141.

Tan, L. H., Laird, A. R., Li, K., & Fox, P. T. (2005). Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: A meta-analysis. Human Brain Mapping, 25(1), 83-91. doi:10.1002/hbm.20134

Temple, E., Poldrack, R. A., Protopapas, A., Nagarajan, S., Salz, T., Tallal, P., Merzenich, M. M., & Gabrieli, J. D. (2000). Disruption of the neural response to rapid acoustic stimuli in dyslexia: Evidence from functional MRI. Proceedings of the National Academy of Sciences, 97(25), 13907-13912. doi:10.1073/pnas.240461697

Temple, E., Poldrack, R. A., Salidis, J., Deutsch, G. K., Tallal, P., Merzenich, M. M., & Gabrieli, J. D. (2001). Disrupted neural responses to phonological and orthographic processing in dyslexic children: An fMRI study. Neuroreport, 12(2), 299-307.
Tettamanti, M., Moro, A., Messa, C., Moresco, R. M., Rizzo, G., Carpinelli, A., Matarrese, M., Fazio, F., & Perani, D. (2005). Basal ganglia and language: Phonology modulates dopaminergic release. *Neuroreport, 16*(4), 397-401. doi:10.1097/00001756-200503150-00018

Ullman, M. T., Earle, F. S., Walenski, M., & Janacsek, K. (2020). The neurocognition of developmental disorders of language. *Annual Review of Psychology, 71*(1), 389-417. doi:10.1146/annurev-psych-122216-011555

Uno, A., Wydell, T. N., Haruhara, N., Kaneko, M., & Shinya, N. (2009). Relationship between reading/writing skills and cognitive abilities among Japanese primary-school children: Normal readers versus poor readers (dyslexics). *Reading and Writing, 22*(7), 755-789. doi:10.1007/s11145-008-9128-8

van der Mark, S., Bucher, K., Maurer, U., Schulz, E., Buckelmuller, J., Kronbichler, M., Loenneker, T., Klaver, P., Martin, E., & Brandeis, D. (2009). Children with dyslexia lack multiple specializations along the visual word-form (VWF) system. *Neuroimage, 47*(4), 1940-1949. doi:10.1016/j.neuroimage.2009.05.021

van Ermingen-Marbach, M., Grande, M., Pape-Neumann, J., Sass, K., & Heim, S. (2013a). Distinct neural signatures of cognitive subtypes of dyslexia with and without phonological deficits. *NeuroImage: Clinical, 2*, 477-490. doi:10.1016/j.nicl.2013.03.010

van Ermingen-Marbach, M., Pape-Neumann, J., Grande, M., Grabowska, A., & Heim, S. (2013b). Distinct neural signatures of cognitive subtypes of dyslexia: Effects of lexicality during phonological processing. *Acta Neurobiologiae Experimentalis (Wars), 73*(3), 404-416.

Vandermosten, M., Correia, J., Vanderauwera, J., Wouters, J., Ghesquiere, P., & Bonte, M. (2019). Brain activity patterns of phonemic representations are atypical in beginning readers with family risk for dyslexia. *Developmental Science, e12857*. doi:10.1111/desc.12857

Vasic, N., Lohr, C., Steinbrink, C., Martin, C., & Wolf, R. C. (2008). Neural correlates of working memory performance in adolescents and young adults with dyslexia. *Neuropsychologia, 46*(2), 640-648. doi:10.1016/j.neuropsychologia.2007.09.002

Vinckenbosch, E., Robichon, F., & Eliez, S. (2005). Gray matter alteration in dyslexia: converging evidence from volumetric and voxel-by-voxel MRI analyses. *Neuropsychologia, 43*(3), 324-331. doi:10.1016/j.neuropsychologia.2004.06.023

Waldie, K. E., Haigh, C. E., Badzakova-Trajkov, G., Buckley, J., & Kirk, I. J. (2013). Reading the wrong way with the right hemisphere. *Brain Sciences, 3*(3), 1060-1075. doi:10.3390/brainsci3031060

Wandell, B. A., Rauschecker, A. M., & Yeatman, J. D. (2012). Learning to see words. *Annual Review of Psychology, 63*, 31-53. doi:10.1146/annurev-psych-120710-100434

Wang, X. J., Yang, J. F., Yang, J., Mencl, W. E., Shu, H., & Zevin, J. D. (2015). Language differences in the brain network for reading in naturalistic story reading and lexical decision. *PLoS One, 10*(5). doi:10.1371/journal.pone.0124388

Wang, Z., Yan, X., Liu, Y., Spray, G. J., Deng, Y., & Cao, F. (2019). Structural and functional abnormality of the putamen in children with developmental dyslexia. *Neuropsychologia, 130*, 26-37. doi:10.1016/j.neuropsychologia.2018.07.014

Weiller, C., Isensee, C., Rijnjtes, M., Huber, W., Müller, S., Bier, D., Dutschka, K., Woods, R. P., Noth, J., & Diener, H. C. (1995). Recovery from wernicke's aphasia: A positron emission tomographic study. *Annals of Neurology, 37*(6), 723-732. doi:10.1002/ana.410370605

Weiss, Y., Katzir, T., & Bitan, T. (2016). When transparency is opaque: Effects of diacritic marks and vowel letters on dyslexic Hebrew readers. *Cortex, 83*, 145-159.
Wichmann, T., & DeLong, M. R. (2012). Neurotransmitters and disorders of the basal ganglia. In S. T. Brady, G. J. Siegel, R. W. Albers, & D. L. Price (Eds.), Basic Neurochemistry (Eighth Edition) (pp. 856-871). New York: Academic Press.

Wimmer, H., Schurz, M., Sturm, D., Richlan, F., Klackl, J., Kronbichler, M., & Ladurner, G. (2010). A dual-route perspective on poor reading in a regular orthography: An fMRI study. Cortex, 46(10), 1284-1298. doi:10.1016/j.cortex.2010.06.004

Wimmer, H., & Schurz, M. (2010). Dyslexia in regular orthographies: Manifestation and causation. Dyslexia, 16(4), 283-299. doi:10.1002/dys.411

Wu, C. Y., Ho, M. H. R., & Chen, S. H. A. (2012). A meta-analysis of fMRI studies on Chinese orthographic, phonological, and semantic processing. Neuroimage, 63(1), 381-391. doi:10.1016/j.neuroimage.2012.06.047

Xia, Z., Hoeft, F., Zhang, L., & Shu, H. (2016). Neuroanatomical anomalies of dyslexia: Disambiguating the effects of disorder, performance, and maturation. Neuropsychologia, 81, 68-78. doi:10.1016/j.neuropsychologia.2015.12.003

Yang, J., & Tan, L. H. (2020). Whole-brain functional networks for phonological and orthographic processing in Chinese good and poor readers. Frontiers in Psychology, 10. doi:10.3389/fpsyg.2019.02945

Yang, Y., Bi, H. Y., Long, Z. Y., & Tao, S. (2013). Evidence for cerebellar dysfunction in Chinese children with developmental dyslexia: an fMRI study. International Journal of Neuroscience, 123(5), 300-310. doi:10.3109/00207454.2012.756484

Yang, Y. H., Yang, Y., Chen, B. G., Zhang, Y. W., & Bi, H. Y. (2016). Anomalous cerebellar anatomy in Chinese children with dyslexia. Frontiers in Psychology, 7. doi:10.3389/Fpsyg.2016.00324

Younger, J. W., Tucker-Drob, E., & Booth, J. R. (2017). Longitudinal changes in reading network connectivity related to skill improvement. Neuroimage, 158, 90-98. doi:10.1016/j.neuroimage.2017.06.044

Zhao, H., Zhang, B. P., Chen, Y., Zhou, X., & Zuo, P. X. (2016). Environmental risk factors in Han and Uyghur Children with dyslexia: A comparative study. PLoS One, 11(7). doi:10.1371/journal.pone.0159042

Ziegler, J. C., Perry, C., Ma-Wyatt, A., Ladner, D., & Schulte-Korne, G. (2003). Developmental dyslexia in different languages: Language-specific or universal? Journal of Experimental Child Psychology, 86(3), 169-193. doi:10.1016/S0022-0965(03)00139-5

Ziegler, J. C. (2006). Do differences in brain activation challenge universal theories of dyslexia? Brain Lang, 98(3), 341-343. doi:10.1016/j.bandl.2005.05.002

Zuk, J., Perdue, M. V., Becker, B., Yu, X., Chang, M., Raschle, N. M., & Gaab, N. (2018). Neural correlates of phonological processing: Disrupted in children with dyslexia and enhanced in musically trained children. Developmental Cognitive Neuroscience, 34, 82-91. doi:10.1016/j.dcn.2018.07.001
**Table 1. Functional studies included in the meta-analysis**

| Studies                          | N(TD) | N(DD) | Mean age in months | Language | Writing system | Subject type       | Tasks                                                                 |
|----------------------------------|-------|-------|--------------------|----------|----------------|-------------------|----------------------------------------------------------------------|
| (Bach et al., 2010)              | 18    | 14    | 99.6               | German   | alphabetic     | children          | Covert reading task                                                  |
| (Beneventi et al., 2009)         | 13    | 11    | 160.4              | Norwegian| alphabetic     | children          | Sequential verbal working memory task                               |
| (Beneventi et al., 2010a)        | 13    | 11    | 160.4              | Norwegian| alphabetic     | children          | n-back task (Letter)                                                 |
| (Beneventi et al., 2010b)        | 14    | 12    | 160.3              | Norwegian| alphabetic     | children          | n-back task (Picture)                                                |
| (Blau et al., 2009)              | 13    | 13    | 301.8              | Dutch    | alphabetic     | adult              | Letter–speech-sound integration task                                |
| (Booth et al., 2007a)            | 13    | 13    | 126.0              | English  | alphabetic     | children          | Word judgment task                                                   |
| (Boros et al., 2016)             | 18    | 15    | 130.1              | French   | alphabetic     | children          | String detection and passive reading task                           |
| (Brambati et al., 2006)          | 11    | 13    | 368.5              | Italian  | alphabetic     | adult and adolescent | Word reading and pseudoword reading                                 |
| (Brunswick et al., 1999)         | 6     | 6     | 277.2              | English  | alphabetic     | adult              | Explicit reading task                                                |
| (Brunswick et al., 1999)         | 6     | 6     | 294.0              | English  | alphabetic     | adult              | Implicit reading task                                                |
| (Cao et al., 2008)               | 12    | 12    | 148.2              | English  | alphabetic     | children          | Visual word rhyming task                                             |
| (Cao et al., 2017)               | 13    | 17    | 134.0              | Chinese  | morpho-syllabic| children          | Auditory rhyming task                                                |
| (Cao et al., 2018)               | 19    | 23    | 132.9              | Chinese  | morpho-syllabic| children          | Visual spelling task                                                 |
| (Cao et al., 2020)               | 17    | 16    | 137.3              | Chinese  | morpho-syllabic| children          | Visual rhyming task                                                  |
| (Chył et al., 2018)              | 25    | 25    | 105.4              | Polish   | alphabetic     | children          | Visual word reading                                                  |
| (Conway et al., 2008)            | 11    | 11    | 420.0              | English  | alphabetic     | adult              | Auditory working memory task                                        |
| (Cutting et al., 2013)           | 19    | 20    | 147.02             | English  | alphabetic     | adolescent        | Lexical decision task                                                |
| (Danelli et al., 2017)           | 23    | 20    | 250.55             | Italian  | alphabetic     | adult              | Pseudoword reading, auditory letter-name rhyming task, visual motion stimulation task and motor sequence learning task |
| (Desroches et al., 2010)         | 12    | 12    | 137.4              | English  | alphabetic     | children          | Auditory rhyming task                                                |
| (Dufor et al., 2007)             | 16    | 14    | 344.6              | French   | alphabetic     | adult              | Auditory phoneme categorization task                                |
| (Eden et al., 2004)              | 19    | 19    | 512.4              | English  | alphabetic     | adult              | Word repetition task and initial sound deletion task                  |
| (Farris et al., 2016)            | 16    | 15    | 112.2              | English  | alphabetic     | children          | Object rhyming task                                                  |
| Study                                | Age 1 | Age 2 | Age 3 | Language  | Script Type | Group | Task(s)                                                                 |
|--------------------------------------|-------|-------|-------|-----------|-------------|-------|------------------------------------------------------------------------|
| Feng et al., 2017                    | 20    | 14    | 123.1 | Chinese   | morpho-syllabic | children | Character spelling task and character rhyming task                  |
| Francisco et al., 2018               | 20    | 21    | 303.7 | Dutch     | alphabetic   | adult  | 1-back task                                                            |
| Gaab et al., 2007                    | 23    | 22    | 127.8 | English   | alphabetic   | children | Sound discrimination task                                             |
| Georgiewa et al., 1999               | 17    | 17    | 168.0 | German    | alphabetic   | children | Letter reading task, nonwords reading task, words reading task and phonological transformation task |
| Grande et al., 2011                  | 25    | 20    | 115.1 | German    | alphabetic   | children | Picture naming task and words reading task                            |
| Grunling et al., 2004                 | 21    | 17    | 162.8 | German    | alphabetic   | adolescent | Slash patterns matching task, letters matching task, words matching task, pseudoword matching task and pseudoword rhyming task |
| Hancock et al., 2016                  | 11    | 16    | 125.0 | English   | alphabetic   | children | Word rhyming task                                                     |
| Heim et al., 2010                     | 20    | 20    | 114.0 | German    | alphabetic   | children | First sound detection task, motion detection task, Posner attention task, auditory discrimination task |
| Heim et al., 2013                     | 15    | 11    | 435.4 | German    | alphabetic   | adult  | Overt word reading                                                    |
| Heim et al., 2015                     | 10    | 33    | 118.9 | German    | alphabetic   | children | Overt word reading                                                    |
| Hernandez et al., 2013                | 16    | 15    | 252.7 | French    | alphabetic   | adult  | Word rhyming task and font matching task                              |
| Higuchi et al., 2020                  | 14    | 11    | 172.7 | Japanese  | morpho-syllabic | adolescent | Character/picture passive viewing task                              |
| Hoefft et al., 2006                   | 10    | 10    | 133.9 | English   | alphabetic   | children | Visual word rhyming task                                              |
| Hoefft et al., 2007                   | 19    | 19    | 172.8 | English   | alphabetic   | adolescent | Visual word rhyming task                                             |
| Horowitz-Kraus et al., 2016          | 9     | 10    | 120.5 | English   | alphabetic   | children | Narrative comprehension task                                          |
| Hu et al., 2010                       | 8     | 8     | 171.6 | Chinese   | morpho-syllabic | children | Semantic match task, word/ picture naming task                       |
| Hu et al., 2010                       | 10    | 11    | 164.5 | English   | alphabetic   | children | Semantic match task, word/ picture naming task                       |
| Ingvar et al., 2002                   | 9     | 9     | 287.0 | Swedish   | alphabetic   | adult  | Word reading task and nonword reading task                            |
| Jaffe-Dax et al., 2018                | 19    | 20    | 302.2 | Hebrew    | alphabetic   | adult  | Tone frequency discrimination task                                   |
| Kast et al., 2011                     | 13    | 12    | 314.5 | German    | alphabetic   | adult  | Lexical decision task                                                 |
| Study                          | N  | N  | Mean  | Language | Alphabetic | Age Group | Task Description                                                                 |
|-------------------------------|----|----|-------|----------|------------|-----------|----------------------------------------------------------------------------------|
| (Kovelman et al., 2012)       | 12 | 12 | 108.4 | English  | alphabetic | children  | Auditory words rhyming task and auditory words matching task                      |
| (Kronbichler et al., 2006)    | 15 | 13 | 187.9 | German   | alphabetic | adolescent| Sentence verification task                                                        |
| (Kronschnabel et al., 2013)   | 22 | 13 | 191.7 | German   | alphabetic | adolescent| Rapid serial visual stimulation detect task                                       |
| (Kronschnabel et al., 2014)   | 22 | 13 | 190.9 | German   | alphabetic | adolescent| Target detection task                                                            |
| (Landi et al., 2010)          | 13 | 13 | 157.8 | English  | alphabetic | adolescent| Rhyming task and semantic categorization task                                     |
| (Langer et al., 2015)         | 15 | 15 | 119.4 | English  | alphabetic | children  | Sentence reading task                                                            |
| (Liu et al., 2012)            | 11 | 11 | 142.8 | Chinese  | morpho-syllabic | children  | Word rhyming task and semantic judgment task                                      |
| (Liu et al., 2013b)           | 14 | 14 | 141.8 | Chinese  | morpho-syllabic | children  | Lexical match task and character rhyming task                                    |
| (Lobier et al., 2014)         | 12 | 12 | 129.6 | French   | alphabetic | adult     | visual categorization of character task                                          |
| (MacSweeney et al., 2009)     | 7  | 7  | 343.5 | English  | alphabetic | adult     | Picture rhyming task                                                            |
| (Maurer et al., 2011)         | 16 | 11 | 136.6 | German   | alphabetic | children  | Word matching task, pseudoword matching task, picture matching task              |
| (McCrorry et al., 2000)       | 6  | 8  | 275.0 | English  | alphabetic | adult     | Words and pseudowords production                                                 |
| (McCrorry et al., 2005)       | 10 | 8  | 242.0 | English  | alphabetic | adult     | Words reading and pictures naming                                                |
| (Meyler et al., 2008)         | 12 | 23 | 129.6 | English  | alphabetic | children  | Sentence comprehension                                                          |
| (Monzalvo et al., 2012)       | 23 | 23 | 130.0 | French   | alphabetic | children  | Passive picture/word viewing task and passive sentence listening task            |
| (Olulade et al., 2012)        | 9  | 6  | 247.7 | English  | alphabetic | adult     | Word rhyme task                                                                |
| (Olulade et al., 2015)        | 12 | 16 | 120.5 | English  | alphabetic | children  | 3-D spatial rotations                                                           |
| (Paulesu et al., 2001)        | 36 | 36 | 286.4 | English, | alphabetic | adult     | Implicit word reading                                                           |
| (Paulesu et al., 1996)        | 5  | 5  | 314.5 | English  | alphabetic | adult     | Word and non-word reading task                                                   |
| (Pecini et al., 2011)         | 13 | 13 | 276.0 | Italian  | alphabetic | adult     | Letter rhyming and letter memory                                                 |
| (Pekkola et al., 2006)        | 10 | 10 | 330.6 | Finnish  | alphabetic | adult     | Rhyme-generation task                                                           |
| (Perrachione et al., 2016)    | 19 | 19 | 279.6 | English  | alphabetic | adult     | Audio-visual speech perception                                                  |
| Reference                                | Subjects       | Language  | Orthography | Group  | Task                                                                 |
|-----------------------------------------|----------------|-----------|-------------|--------|----------------------------------------------------------------------|
| Perrachione et al., 2016                | 24/23/26       | English   | alphabetic  | adult  | Spoken words listening, Written words, objects, and faces viewing    |
| Perrachione et al., 2016                | 25/26/7.0      | French    | alphabetic  | children| Categorical matching task                                             |
| Prasad et al., 2011                     | 12/12/120.0    | Hindi     | syllabic    | children| Auditory rhyming task, picture-naming task and semantic tasks        |
| Reilhac et al., 2013                    | 12/12/306.6    | French    | alphabetic  | adult and adolescent | Perceptual matching task |
| Richlan et al., 2010                    | 18/15/215.8    | German    | alphabetic  | adult and adolescent | Phonological decision task |
| Rimrodt et al., 2009                    | 15/14/141.0    | English   | alphabetic  | children| Sentence comprehension task                                           |
| Ruff et al., 2002                       | 11/6/348.7     | French    | alphabetic  | adult  | Passive listening task                                               |
| Rumsey et al., 1997                     | 14/17/313.2    | English   | alphabetic  | adult  | Pronunciation task and lexical decision task                          |
| Schulz et al., 2008                     | 22/12/137.7    | German    | alphabetic  | children| Sentence reading task                                                |
| Schulz et al., 2009                     | 15/15/138.0    | German    | alphabetic  | children| Sentence reading task                                                |
| Siok et al., 2004                       | 8/8/132.0      | Chinese   | morpho-syllabic | children| Homophone judgement task and lexical decision task                   |
| Siok et al., 2008                       | 12/12/131.5    | Chinese   | morpho-syllabic | children| Character rhyming task                                               |
| Siok et al., 2009                       | 12/12/131.5    | Chinese   | morpho-syllabic | children| Font size judgment task                                              |
| Steinbrink et al., 2012                 | 16/17/223.7    | German    | alphabetic  | adult and adolescent | Syllable discrimination |
| Temple et al., 2000                     | 10/8/362.7     | English   | alphabetic  | adult  | Pitch discrimination task                                             |
| Temple et al., 2001                     | 15/24/127.5    | English   | alphabetic  | children| Letter rhyming task, letter matching task                             |
| van der Mark et al., 2009               | 24/18/136.1    | German    | alphabetic  | children| Phonological lexical decision task                                    |
| van Ermingen-Marbach et al., 2013a      | 13/17/117.2    | German    | alphabetic  | children| Phoneme detection task                                               |
| van Ermingen-Marbach et al., 2013a      | 13/14/116.4    | German    | alphabetic  | children| Phoneme detection task                                               |
| van Ermingen-Marbach et al., 2013b      | 10/32/117.0    | German    | alphabetic  | children| Initial phoneme deletion task                                        |
| Vasic et al., 2008                      | 13/12/219.6    | German    | alphabetic  | adult  | Verbal working memory task                                           |
| Study                          | Age Range | Mean Response Time | Language Type       | Age Group         | Task Type                                      |
|-------------------------------|-----------|--------------------|---------------------|-------------------|-----------------------------------------------|
| (Waldie et al., 2013)         | 16-12     | 365.1              | English alphabetic  | Adult             | Go/no-go lexical decision task               |
| (Weiss et al., 2016)          | 22-21     | 325.1              | Hebrew alphabetic   | Adult             | Word reading task                             |
| (Wimmer et al., 2010)         | 19-20     | 247.6              | German alphabetic   | Adult and Adolescent | Phonological lexical decision task          |
| (Yang & Tan, 2020)            | 16-16     | 123.5              | Chinese morpho-syllabic | Children       | Homophone judgments task and component judgments task |
| (Zuk et al., 2018)            | 13-11     | 114.0              | English alphabetic  | Children          | First sound matching task                    |
Table 2. Structural studies included in the meta-analysis

| Study                        | N(TD) | N(DD) | Mean age in months | Language | Writing system  | Subject type                  |
|------------------------------|-------|-------|--------------------|----------|----------------|-------------------------------|
| (Adrian-Ventura et al., 2020)| 12    | 13    | 146.2              | Spanish  | alphabetic     | children                      |
| (Brambati et al., 2004)     | 11    | 10    | 352.8              | Italian  | alphabetic     | adult and adolescent          |
| (Brown et al., 2001)        | 14    | 16    | 288.0              | English  | alphabetic     | adult                         |
| (Eckert et al., 2005)       | 13    | 13    | 136.5              | English  | alphabetic     | children                      |
| (Evans et al., 2014b)       | 14    | 14    | 505.8              | English  | alphabetic     | adult                         |
| (Evans et al., 2014b)       | 13    | 13    | 371.4              | English  | alphabetic     | adult                         |
| (Evans et al., 2014b)       | 15    | 15    | 107.4              | English  | alphabetic     | children                      |
| (Evans et al., 2014b)       | 17    | 17    | 115.2              | English  | alphabetic     | children                      |
| (Hoeft et al., 2007)        | 19    | 19    | 172.8              | English  | alphabetic     | children and adolescent       |
| (Jagger-Rickels et al., 2018)| 32    | 17    | 114.2              | English  | alphabetic     | children                      |
| (Jednorog et al., 2014)     | 35    | 46    | 123.5              | Polish   | alphabetic     | children                      |
| (Jednorog et al., 2015)     | 106   | 130   | 123.9              | French, German, Polish | alphabetic | children                      |
| (Kraftnick et al., 2014)    | 15    | 15    | 118.2              | English  | alphabetic     | children                      |
| (Kronbichler et al., 2008)  | 15    | 13    | 187.9              | German   | alphabetic     | adolescent                   |
| (Liu et al., 2013a)         | 18    | 18    | 141.4              | Chinese  | morpho-syllabic | children                      |
| (Menghini et al., 2008)     | 10    | 10    | 489.0              | Italian  | alphabetic     | adult                         |
| (Moreau et al., 2019)       | 12    | 12    | 352.2              | English  | alphabetic     | adult                         |
| (Pernet et al., 2009)       | 39    | 38    | 336.0              | French   | alphabetic     | adult                         |
| (Siok et al., 2005)         | 32    | 32    | 304.5              | Italian, French, English | alphabetic | adult                         |
| (Siok et al., 2008)         | 16    | 16    | 132.0              | Chinese  | morpho-syllabic | children                      |
| (Steinbrink et al., 2008)   | 8     | 8     | 262.8              | German   | alphabetic     | adult                         |
| (Tamboer et al., 2015)      | 57    | 37    | 245.3              | Dutch    | alphabetic     | adult                         |
| (Vinckenbosch et al., 2005) | 10    | 13    | 282.0              | French   | alphabetic     | adult                         |
| (Wang et al., 2019)         | 17    | 27    | 134.0              | Chinese  | morpho-syllabic | children                      |
| (Xia et al., 2016)          | 12    | 12    | 132.0              | Chinese  | morpho-syllabic | children                      |
| (Xia et al., 2016)          | 12    | 12    | 169.2              | Chinese  | morpho-syllabic | children                      |
| (Yang et al., 2016)         | 14    | 9     | 149.0              | Chinese  | morpho-syllabic | children                      |
### Table 3. Multi-modal structural and functional abnormalities in individuals with DD across all languages

| Regions | MNI coordinate | Voxels | Cluster breakdown (Voxels) |
|---------|----------------|--------|---------------------------|
| **Decreased GMV and hypoactivation in DD** | | | |
| Left STG | -54,-34,20 | 3597 | Left rolandic operculum, BA 48 (388)  
Left STG, BA 48 (313)  
Left supramarginal gyrus, BA 48 (282)  
Left STG, BA 42 (262)  
Left insula, BA 48 (240)  
Left MTG, BA 21 (170)  
Left IFG, opercular part, BA 48 (152) |
| Left IFG | -46,42,0 | 354 | |
| **Increased GMV and hypoactivation in DD** | | | |
| Left IPL | -40,-38,38 | 1439 | Left IPL, BA 40 (822)  
Left fusiform gyrus, BA 19 (196)  
Left cerebellum, crus I, BA 19 (162) |
| Left cerebellum | -42,-68,-24 | 709 | |
| **Decreased GMV and hyperactivation in DD** | | | |
| Right caudate | 8,8,10 | 559 | Right anterior thalamic projections (204)  
Right caudate nucleus (180) |
| Left caudate | -18,10,10 | 519 | Left anterior thalamic projections (323) |
| **Increased GMV and hyperactivation in DD** | | | |
| Right MTG | 48,-8,-24 | 669 | Right inferior network (238)  
Right ITG, BA 20 (166)  
Right MTG, BA 21 (151) |
Table 4. Direct comparison between alphabetic languages and morpho-syllabic languages in functional studies

| Regions                      | MNI coordinate | SDM-Z | P       | Voxels | Cluster breakdown (Voxels)                                      |
|------------------------------|----------------|-------|---------|--------|-----------------------------------------------------------------|
| **Hypoactivation in DD**     |                |       |         |        |                                                                 |
| Alphabetic languages > Morpho-syllabic languages |                |       |         |        |                                                                 |
| Right STG                    | 60,-18,4       | 1.059 | 0.0000  | 2448   | Right STG, BA 22 (436)                                          |
|                             |                |       |         |        | Corpus callosum (381)                                          |
|                             |                |       |         |        | Right STG, BA 48 (287)                                          |
|                             |                |       |         |        | Right insula, BA 48 (271)                                       |
| Left fusiform gyrus          | -38,-42,-22    | 1.215 | 0.0000  | 846    | Left fusiform gyrus, BA 37 (187)                                |
| Left MTG                     | -50,-66,8      | 1.121 | 0.0000  | 732    | Left MTG, BA 37 (396)                                          |
| **Morpho-syllabic languages > Alphabetic languages** | |       |         |        |                                                                 |
| Left IFG                     | -48,8,28       | -4.282| 0.0000  | 2179   | Left precentral gyrus, BA 6 (524)                               |
|                             |                |       |         |        | Left IFG, opercular part, BA 44 (284)                           |
|                             |                |       |         |        | Left precentral gyrus, BA 44 (191)                              |
|                             |                |       |         |        | Left IFG, triangular part, BA 48 (174)                          |
|                             |                |       |         |        | Corpus callosum (167)                                          |
| **Hyperactivation in DD**    |                |       |         |        |                                                                 |
| Morpho-syllabic languages > Alphabetic languages |                |       |         |        |                                                                 |
| Right precentral gyrus       | 40,-20,54      | -2.262| 0.0000  | 1518   | Right precentral gyrus, BA 6 (525)                              |
|                             |                |       |         |        | Right precentral gyrus, BA 4 (306)                              |
|                             |                |       |         |        | Right postcentral gyrus, BA 3 (286)                             |
|                             |                |       |         |        | Right postcentral gyrus, BA 4 (171)                             |
Table 5. Direct comparison between alphabetic languages and morpho-syllabic languages in structural studies

| Regions                          | MNI coordinate | SDM-Z | P      | Voxels | Cluster breakdown (Voxels) |
|----------------------------------|----------------|-------|--------|--------|---------------------------|
| **Decreased GMV in DD**          |                |       |        |        |                           |
| Morpho-syllabic languages > Alphabetic languages |                |       |        |        |                           |
| Left STG                         | -50,10,-18     | -3.139| 0.0000 | 1218   | Left STG, BA 38 (322)     |
| Left IFG                         | -52,10,24      | -2.253| 0.0008 | 409    |                           |
| Left MFG                         | -28,16,44      | -2.888| 0.0001 | 346    |                           |
| Left supramarginal gyrus         | -48,-44,24     | -2.761| 0.0001 | 344    |                           |
| Left SOG                         | -20,-72,20     | -2.911| 0.0001 | 287    | Corpus callosum (187)     |
| Left insula                      | -32,14,8       | -2.046| 0.0015 | 179    |                           |
| **Increased GMV in DD**          |                |       |        |        |                           |
| Morpho-syllabic languages > Alphabetic languages |                |       |        |        |                           |
| Right STG                        | 34,6,-28       | -1.893| 0.0001 | 1397   | Right STG, BA 38 (246)    |
| Left ITG                         | -54,-58,-16    | -1.120| 0.0018 | 161    | Right inferior network (239) |
Table 6. Multi-modal structural and functional abnormalities in individuals with DD in alphabetic languages

| Regions                          | MNI coordinate | Voxels | Cluster breakdown (Voxels)                        |
|---------------------------------|----------------|--------|--------------------------------------------------|
| **Decreases of GMV and hypoactivation in DD** |                |        |                                                   |
| Left supramarginal gyrus        | -50,-30,20     | 1087   | Left MTG, BA 21 (236)                             |
| Right STG                       | 62,-32,14      | 328    |                                                   |
| Left IFG                        | -46,42,0       | 240    |                                                   |
| **Increased GMV and hypoactivation in DD** |               |        |                                                   |
| Left IPL                        | -46,-40,38     | 1692   | Left IPL, BA 40 (942)                             |
| Left cerebellum                 | -40,-70,-24    | 433    | Left cerebellum, crus I, BA 19 (154)             |
| **Decreases of GMV and hyperactivation in DD** |                |        |                                                   |
| Right cerebellum                | 28,-52,-34     | 1313   | Right cerebellum, lobule VI, BA 37 (75)          |
|                                 |                |        | Middle cerebellar peduncles (272)                |
|                                 |                |        | Right cerebellum, lobule VI, BA 19 (207)        |
|                                 |                |        | Right cerebellum, crus I (155)                  |
| Right caudate                   | 8,8,12         | 600    | Right anterior thalamic projections (214)        |
|                                 |                |        | Right caudate nucleus (189)                      |
| Left caudate                    | -16,8,14       | 595    | Left anterior thalamic projections (353)         |
Table 7. Multimodal structural and functional abnormalities in individuals with DD in morpho-syllabic languages

| Regions                                      | MNI coordinate | Voxels | Cluster breakdown (Voxels)                                |
|----------------------------------------------|----------------|--------|----------------------------------------------------------|
| Decreases of GMV and hypoactivation in DD    |                |        |                                                          |
| Left TP                                      | -58,-38,22     | 1566   | Left supramarginal gyrus, BA 48 (254)                    |
|                                              |                |        | Left STG, BA 42 (253)                                    |
|                                              |                |        | Left supramarginal gyrus, BA 40 (153)                    |
| Left IFG                                     | -56,2,10       | 1052   | Left IFG, opercular part, BA 44 (151)                    |
| Decreases of GMV and hyperactivation in DD   |                |        |                                                          |
| Left STG                                     | -44,16,-22     | 854    | Left STG, BA 38 (394)                                    |
| Increases of GMV and hyperactivation in DD   |                |        |                                                          |
| Right MTG                                    | 48,-6,-26      | 493    | Right MTG, BA 21 (178)                                   |
|                                              |                |        | Right inferior network (155)                             |
Convergent and divergent structural and functional brain abnormalities associated with developmental dyslexia: a cross-linguistic meta-analysis of neuroimaging studies

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Table S1. Convergent functional deficits in individuals with DD across all languages (JK represents the results of jack-knife sensitivity analysis)

| Regions                                      | MNI coordinate | SDM-Z | P    | Voxels | Cluster breakdown (Voxels)                          | JK  |
|----------------------------------------------|----------------|-------|------|--------|-----------------------------------------------------|-----|
| Hypoactivation in DD                        |                |       |      |        |                                                    |     |
| Left IPL                                     | -54,-44,30     | 5.427 | 0.0000 | 12510  | Left IPL, BA 40 (1011)                              |     |
|                                              |                |       |      |        | Left MTG, BA 21 (694)                               |     |
|                                              |                |       |      |        | Left MTG, BA 37 (620)                               |     |
|                                              |                |       |      |        | Left ITG, BA 37 (608)                               |     |
|                                              |                |       |      |        | Left fusiform gyrus, BA 37 (467)                    |     |
|                                              |                |       |      |        | Left inferior network, inferior longitudinal fasciculus (429) |     |
|                                              |                |       |      |        | Left ITG, BA 20 (389)                               |     |
|                                              |                |       |      |        | Left STG, BA 48 (372)                               |     |
|                                              |                |       |      |        | Left supramarginal gyrus, BA 48 (354)               |     |
|                                              |                |       |      |        | Left rolandic operculum, BA 48 (314)               |     |
|                                              |                |       |      |        | Left angular gyrus, BA 39 (312)                    |     |
|                                              |                |       |      |        | Left MTG, BA 22 (301)                               |     |
|                                              |                |       |      |        | Left STG, BA 42 (290)                               |     |
|                                              |                |       |      |        | Left precentral gyrus, BA 6 (271)                  |     |
|                                              |                |       |      |        | Left arcuate network, posterior segment (261)       |     |
|                                              |                |       |      |        | Left cerebellum, lobule VI, BA 37 (260)            |     |
|                                              |                |       |      |        | Left IFG, opercular part, BA 44 (256)              |     |
|                                              |                |       |      |        | Left superior parietal gyrus, BA 7 (250)           |     |
|                                              |                |       |      |        | Left superior longitudinal fasciculus III (229)    |     |
|                                              |                |       |      |        | Left STG, BA 22 (215)                               |     |
|                                              |                |       |      |        | Left cerebellum, crus I, BA 37 (214)               |     |
|                                              |                |       |      |        | Left supramarginal gyrus, BA 40 (202)              |     |
|                                              |                |       |      |        | Left IFG, triangular part, BA 45 (197)             |     |
|                                              |                |       |      |        | Left IPL, BA 2 (194)                                |     |
|                                              |                |       |      |        | Left fusiform gyrus, BA 19 (171)                   |     |
|                                              |                |       |      |        |                                                    |     |
|                                              |                |       |      |        |                                                    |     |
Left IFG, opercular part, BA 48 (170)
Corpus callosum (159)
Left precentral gyrus, BA 44 (155)

Table S2. Convergent structural deficits in individuals with DD across all languages (JK represents the results of jack-knife sensitivity analysis)

| Regions                      | MNI coordinate | SDM-Z | P      | Voxels | Cluster breakdown (Voxels) | JK  |
|------------------------------|----------------|-------|--------|--------|-----------------------------|-----|
| **Decreased GMV in DD**      |                |       |        |        |                             |     |
| Left IFG                     | -38,44,-16     | 2.275 | 0.0001 | 494    | Left IFG, orbital part, BA 47 (182) | 26/27 |
| Right STG                    | 56,-44,18      | 2.027 | 0.0006 | 365    |                             | 25/27 |
| **Increased GMV in DD**      |                |       |        |        |                             |     |
| Right MTG                    | 46,-4,-22      | -1.658| 0.0001 | 747    | Right inferior network (210) | 26/27 |
| Left IPL                     | -42,-36,36     | -1.817| 0.0000 | 235    | Left IPL, BA 40 (151)      | 26/27 |

Table S3. Convergent functional deficits in individuals with DD across alphabetic languages

| Hypoactivation in DD         | Regions                      | MNI coordinate | SDM-Z | P      | Voxels | Cluster breakdown (Voxels) |
|------------------------------|------------------------------|----------------|-------|--------|--------|----------------------------|
|                              | Right middle occipital gyrus | 42,-86,6       | 1.988 | 0.0008 | 178    |                             | 91/92 |
| **Hyperactivation in DD**    | Right cerebellum             | 24,-56,-30     | -1.500| 0.0000 | 1968   | Right cerebellum, lobule VI, BA 37 (359) | 92/92 |
|                              | Right postcentral gyrus      | 40,-26,56      | -1.347| 0.0001 | 951    | Right postcentral gyrus, BA 3 (246) | 92/92 |
|                              | Right caudate nucleus        | 10,2,14        | -1.224| 0.0002 | 450    | Right anterior thalamic projections (176) | 92/92 |
|                              | Left caudate nucleus         | -16,12,6       | -1.253| 0.0002 | 413    | Left anterior thalamic projections (269) | 92/92 |
| Region | Coordinates | t-value | p-value | MNI | Description |
|--------|-------------|---------|---------|-----|-------------|
| Left IPL | -52,-44,40  | 5.039   | 0.0000  | 10625 | Left IPL, BA 40 (990) |
|         |             |         |         |     | Left MTG, BA 21 (714 ) |
|         |             |         |         |     | Left MTG, BA 37 (629) |
|         |             |         |         |     | Left ITG, BA 37 (591) |
|         |             |         |         |     | Left fusiform gyrus, BA 37 (484) |
|         |             |         |         |     | Left inferior network (449) |
|         |             |         |         |     | Left ITG, BA 20 (408) |
|         |             |         |         |     | Left STG, BA 48 (376) |
|         |             |         |         |     | Left supramarginal gyrus, BA 48 (327) |
|         |             |         |         |     | Left angular gyrus, BA 39 (314) |
|         |             |         |         |     | Left MTG, BA 22 (300) |
|         |             |         |         |     | Left cerebellum, lobule VI, BA 37 (289) |
|         |             |         |         |     | Left STG, BA 42 (281) |
|         |             |         |         |     | Left rolandic operculum, BA 48 (258) |
|         |             |         |         |     | Left arcuate network (256) |
|         |             |         |         |     | Left cerebellum, crus I, BA 37 (210) |
|         |             |         |         |     | Left STG, BA 22 (200) |
|         |             |         |         |     | Left supramarginal gyrus, BA 40 (198) |
|         |             |         |         |     | Left superior longitudinal fasciculus III (185) |
|         |             |         |         |     | Left IPL, BA 2 (167) |
| Right STG | 60,-16,4   | 1.995   | 0.0009  | 444  | Right STG |
| Right MOG | 42,-86,6    | 2.273   | 0.0002  | 394  | Right MOG, BA19 (218) |
| **Hyperactivation in DD** | | | | | |
| Right cerebellum | 24,-62,-28 | -1.567 | 0.0000  | 1612 | Right cerebellum, lobule VI, BA 37 (361) |
|         |             |         |         |     | Right cerebellum, lobule VI, BA 19 (239) |
|         |             |         |         |     | Middle cerebellar peduncles (217) |
| Left caudate nucleus | -16,12,6 | -1.458 | 0.0000  | 608  | Left anterior thalamic projections (363) |
| Right caudate nucleus | 10,2,14 | -1.315 | 0.0001  | 519  | Right caudate nucleus (184) |
Right anterior thalamic projections

Table S4. Convergent structural deficits in individuals with DD across alphabetic languages

| Regions          | MNI coordinate | SDM-Z  | P      | Voxels | Cluster breakdown (Voxels)                      |
|------------------|----------------|--------|--------|--------|------------------------------------------------|
| **Decreased GMV in DD** |                |        |        |        |                                                |
| Left IFG         | -38,42,-16     | 2.306  | 0.0001 | 611    | Left IFG, orbital part, BA 47 (217)            |
| Right STG        | 56,-44,18      | 2.024  | 0.0003 | 560    | Right STG, BA 42 (156)                         |
| Right caudate    | 6,14,2         | 1.695  | 0.0022 | 166    |                                                |
| **Increased GMV in DD** |            |        |        |        |                                                |
| Left IPL         | -42,-36,36     | -1.976 | 0.0000 | 237    | Left IPL, BA 40 (237)                         |
| Right MTG        | 50,-12,-14     | -1.040 | 0.0014 | 174    |                                                |

Table S5. Convergent functional deficits in individuals with DD across morpho-syllabic languages

| Regions                          | MNI coordinate | SDM-Z  | P      | Voxels | Cluster breakdown (Voxels)                      |
|----------------------------------|----------------|--------|--------|--------|------------------------------------------------|
| **Hypoactivation in DD**         |                |        |        |        |                                                |
| Left IFG                         | -48,10,28      | 4.071  | 0.0000 | 2527   | Left precentral gyrus, BA 6 (623)              |
|                                 |                |        |        |        | Left IFG, opercular part, BA 44 (278)          |
|                                 |                |        |        |        | Left precentral gyrus, BA 44 (195)            |
|                                 |                |        |        |        | Corpus callosum (178)                          |
|                                 |                |        |        |        | Left MFG, BA 44 (162)                          |
| Left supramarginal gyrus         | -58,-42,26     | 2.149  | 0.0001 | 1001   | Left IPL, BA 40 (271)                         |
|                                 |                |        |        |        | Left STG, BA 42 (153)                         |
|                                 |                |        |        |        | Left supramarginal gyrus, BA 48 (144)         |
| Left ITG                         | -48,-56,-18    | 1.761  | 0.0008 | 326    | Left ITG, BA37 (166)                          |
**Hyperactivation in DD**

Right precentral gyrus

52, -16, 44  
-2.035  
0.0000  
2201  
Right precentral gyrus, BA 6 (640)  
Right postcentral gyrus, BA 3 (447)  
Right precentral gyrus, BA 4 (350)  
Right postcentral gyrus, BA 4 (215)

Right MTG

56, -10, -18  
-1.453  
0.0013  
298

| Regions                      | MNI coordinate | SDM-Z | P     | Voxels | Cluster breakdown (Voxels)                                                                 |
|------------------------------|----------------|-------|-------|--------|------------------------------------------------------------------------------------------|
| **Decreased GMV in DD**      |                |       |       |        |                                                                                           |
| Left STG                     | -50, 4, -4     | 2.466 | 0.0000| 2948   | Left insula, BA 48 (539)  
Left STG, BA 38 (392)  
Left Rolandic operculum, BA 48 (226)  
Left MTG, BA 21 (215)  
Left STG, BA 48 (186) |
| Left temporoparietal cortex  | -56, -40, 18   | 2.102 | 0.0002| 900    | Left supramarginal gyrus, BA 48 (188)  
Left STG, BA 42 (171) |
| Left Calcarine Cortex        | -20, -66, 14   | 2.447 | 0.0000| 449    | Corpus callosum (297) |
| Left MFG                     | -32, 26, 40    | 2.319 | 0.0001| 438    |                                                                                           |
| **Increased GMV in DD**      |                |       |       |        |                                                                                           |
| Right STG                    | 34, 6, -26     | -1.572| 0.0001| 1829   | Right inferior network (273)  
Right STG, BA 38 (261)  
Right ITG, BA 20 (250)  
Right MTG, BA 20 (212) |
| Right precuneus              | 12, -52, 42    | -1.254| 0.0014| 156    |                                                                                           |

**Table S7.** Convergent deficits in individuals with DD only in functional studies not in structural studies
| Regions                      | MNI coordinate | SDM-Z | Voxels | Cluster breakdown (Voxels)                                      |
|------------------------------|----------------|-------|--------|----------------------------------------------------------------|
| **Hypoactivation in DD**     |                |       |        |                                                                |
| Left supramarginal gyrus     | -56,-44,38     | 5.581 | 7946   | Left MTG (1694)                                                |
|                              |                |       |        | Left ITG (1108)                                                |
|                              |                |       |        | Left fusiform gyrus (745)                                     |
|                              |                |       |        | Left IPL (496)                                                 |
|                              |                |       |        | Left supramarginal gyrus (428)                                |
|                              |                |       |        | Left STG (372)                                                 |
|                              |                |       |        | Left precentral gyrus (366)                                   |
|                              |                |       |        | Left inferior occipital gyrus (312)                           |
|                              |                |       |        | Left angular gyrus (282)                                      |
|                              |                |       |        | Left superior Parietal gyrus (275)                            |
|                              |                |       |        | Left IFG (274)                                                 |
|                              |                |       |        | Left cerebellum Crus (256)                                    |
|                              |                |       |        | Left IFG (213)                                                 |
| Right middle occipital gyrus | 42,-86,6       | 1.988 | 178    |                                                                |
| **Hyperactivation in DD**    |                |       |        |                                                                |
| Right Cerebellum             | 24,-56,-30     | -1.500| 1968   | Right cerebellum, Anterior Lobe (1356)                        |
| Right precentral gyrus       | 46,-26,56      | -1.347| 951    | Right postcentral gyrus (466)                                  |
|                              |                |       |        | Right precentral gyrus (437)                                  |
Table S8. Convergent deficits in individuals with DD only in structural studies not in functional studies

| Regions                | MNI coordinate | SDM-Z  | Voxels | Cluster breakdown (Voxels)                      |
|------------------------|----------------|--------|--------|------------------------------------------------|
| **Decreased GMV in DD**|                |        |        |                                                |
| Left IFG               | -38,44,-16     | 2.275  | 362    | Left IFG, orbital part (190)                   |
| Right STG              | 56,-44,18      | 2.027  | 365    | Right STG, BA 42 (196)                        |
| **Increased GMV in DD**|                |        |        |                                                |
| Right MTG              | 42,-2,-20      | -1.584 | 582    | Right MTG (154)                               |

Table S9. Confirmation study results when matched language, age and number of studies

| Regions                                      | MNI coordinate | SDM-Z  | P       | Voxels | Cluster breakdown (Voxels)          |
|----------------------------------------------|----------------|--------|---------|--------|-------------------------------------|
| **Hypoactivation in DD**                     |                |        |         |        |                                     |
| Alphabetic languages > Morpho-syllabic languages |                |        |         |        |                                     |
| Left ITG                                     | -60,-38,4      | 1.665  | 0.0001  | 1044   | left ITG, BA 20 (569)               |
|                                              |                |        |         |        | left MTG, BA 20 (185)               |
| Left MOG                                     | -20,-88,-20    | 1.785  | 0.0001  | 606    | Corpus callosum (222)               |
| Left MOG                                     | -48,-88,4      | 1.489  | 0.0005  | 200    |                                     |
| **Morpho-syllabic languages > Alphabetic languages** |                |        |         |        |                                     |
| Left precentral gyrus                        | -56,4,26       | -2.865 | 0.0000  | 2311   | Left precentral gyrus, BA 6 (592)   |
|                                              |                |        |         |        | Left IFG, opercular part, BA 44 (286)|
|                                              |                |        |         |        | Left precentral gyrus, BA 44 (182)  |
|                                              |                |        |         |        | Corpus callosum (173)               |
| **Hyperactivation in DD**                    |                |        |         |        |                                     |
| Alphabetic languages > Morpho-syllabic languages |                |        |         |        |                                     |
| Right supramarginal gyrus                    | 60,-48,26      | -1.133 | 0.0004  | 715    |                                     |
| Right hippocampus                            | 26,-10,-12     | -1.304 | 0.0001  | 585    |                                     |
| Right supplementary motor area               | 4,8,48         | -1.105 | 0.0005  | 390    |                                     |
| **Morpho-syllabic languages > Alphabetic languages** |                |        |         |        |                                     |
| Right precentral gyrus                       | 40,-20,54      | -1.536 | 0.0001  | 792    | Right precentral gyrus, BA 6 (236)  |
| Region                                | Abbreviation | ID |
|--------------------------------------|--------------|----|
| Right precentral gyrus                | BA 4         | 208|
| Right postcentral gyrus               | BA 3         | 180|
Figure S1. Functional deficits in individuals with DD across all languages (red-yellow: decreased activation in individuals with DD than in controls, blue-green: increased activation in individuals with DD than in controls).
Figure S2. Structural deficits in individuals with DD across all languages (red-yellow: decreased GMV in individuals with DD than in controls, blue-green: increased GMV in individuals with DD than in controls).
**Figure S3.** Functional deficits in individuals with DD in alphabetic languages (red-yellow: decreased activation in individuals with DD than in controls, blue-green: increased activation in individuals with DD than in controls).
Figure S4. Structural deficits in individuals with DD in alphabetic languages (red-yellow: decreased GMV in individuals with DD than in controls, blue-green: increased GMV in individuals with DD than in controls).
Figure S5. Functional deficits in individuals with DD in morpho-syllabic languages (red-yellow: decreased activation in individuals with DD than in controls, blue-green: increased activation in individuals with DD than in controls).
Figure S6. Structural deficits in individuals with DD in morpho-syllabic languages (red-yellow: decreased GMV in individuals with DD than in controls, blue-green: increased GMV in individuals with DD than in controls).
Figure S7. Convergent deficits in individuals with DD only in functional studies not in structural studies (red: TD>DD, blue: TD<DD).
Figure S8. Convergent deficits in individuals with DD only in structural studies not in functional studies (red: TD>DD, blue: TD<DD).

Figure S9. Direct comparison between alphabetic languages/English and morpho-syllabic languages/Chinese in fMRI/PET studies. Figure S9A. Direct comparison between alphabetic languages and morpho-syllabic languages. Figure S9B. Confirmation study results when matched language, age and number of studies. Figure S9C. Overlap of the two difference maps. (red-yellow: greater decreases in DD in alphabetic languages/English than in morpho-syllabic languages/Chinese; blue-green: greater decreases in DD in morpho-syllabic languages/Chinese than in alphabetic languages/English; purple: greater increases in DD in morpho-syllabic languages/Chinese than in alphabetic languages/English; cyan: greater increases in DD in alphabetic languages/English than in morpho-syllabic languages/Chinese).