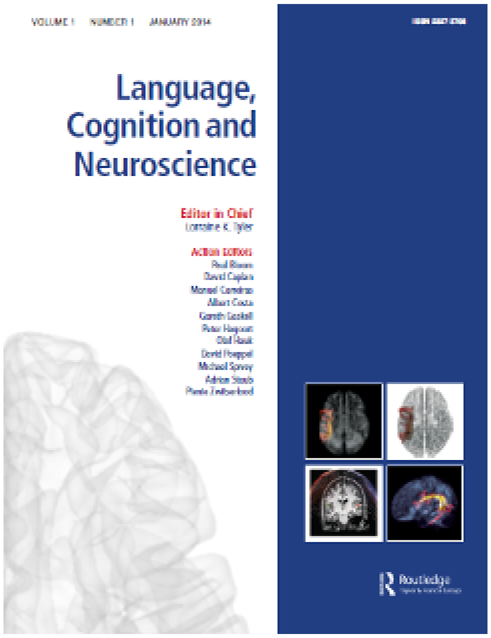

A meta-analysis of functional neuroimaging studies on developmental dyslexia across European orthographies: the ADOD model

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A meta-analysis of functional neuroimaging studies on developmental dyslexia across European orthographies: the ADOD model

Abstract

According to the “classic” and the “new” model, developmental dyslexia (DD) is associated with dysfunctions of the left temporoparietal (TP), ventral occipitotemporal (vOT) and frontal brain circuits. However, these models make different anatomo-functional predictions about the effects of age and orthographic depth on the neural correlates of DD.

To test the influence of age and orthographic depth and their interaction on the neurobiology of reading we meta-analyzed 34 fMRI studies by combining the CluB and the GingerALE methods.

Our meta-analytic results challenged both models and allowed us to generate a refined neurocognitive framework called the “Anatomo-functional, Developmental, and Orthographic Depth (ADOD) model of DD”. The ADOD model describes the interacting effects of age and orthography on the neurobiology of DD and suggests brand new conceptions on the role of the left TP cortex in reading together with a subtler parcellation of the vOT areas according to a rostro-caudal gradient.

Keywords

Developmental Dyslexia, reading, orthographic depth, meta-analysis, neuroimaging

1. INTRODUCTION

The cognitive and neurobiological origins of developmental dyslexia (DD) – a disorder "characterized by problems with accurate or fluent written word recognition, poor decoding and poor spelling abilities" (DSM-5; American Psychiatric Association, 2013) – are still a matter of debate (Frith, 1999; Peterson & Pennington, 2015; Pugh et al., 2000; Richlan, 2012, 2014).

Indeed, during the last 15 years, an increasing number of reviews (Démonet et al., 2004; Grigorenko, 2001; Habib, 2000; Heim & Keil, 2004; McCandliss & Noble, 2003; Pugh et al., 2000; Sandak et al., 2004; Shaywitz & Shaywitz, 2005; Temple, 2002) and quantitative meta-analysis on the structural (Linkersdörfer et al., 2012; Richlan et al., 2013) and functional (Maisog et al., 2008; Paulesu et al., 2014; Richlan et al., 2009, 2011) changes associated with DD have been published.

One of the highly replicated findings in the functional neuroimaging literature on dyslexia is the under-recruitment of both the left dorsal temporoparietal (TP) and the left ventral occipitotemporal (vOT) cortices (Cao et al., 2006; Hoeft et al., 2006; Kronbichler et al., 2006; McCrory et al., 2005; Paulesu et al., 2001). These results were interpreted assuming a universal neurocognitive dysfunctional mechanism in dyslexia.

However, some considerable orthography-specific differences emerged both at a behavioural and anatomo-functional level when orthography features were considered, mainly when the grapheme-to-phoneme correspondence of each orthographic system was taken into account, in line with the *orthographic depth hypothesis*. Readers who belong to shallow orthographies such as German (Seymour, Aro, & Erskine, 2003) showed better reading fluency and accuracy than readers belonging to "deep" orthographies such as English. This result has been replicated both with dyslexic and non-impaired readers (Aro & Wimmer, 2003; Frith et al., 1998; Frost et al., 1987; Georgiou et al., 2012; Landerl et al., 1997; Paulesu et al., 2001; Paulesu et al., 2000; Seymour et al., 2003; Wimmer & Goswami, 1994; Wimmer & Schurz, 2010; Zoccolotti et al., 2009; Zoccolotti et al., 2005). Further, at the anatomo-functional level, these behavioural differences are accompanied by specific brain activation patterns as a function of a language's orthographic depth.

In such an articulated scenario, two major neurofunctional models of reading development in non-impaired and dyslexic readers have been proposed in literature: (i) the "classic" model by Pugh and colleagues (2000) (Pugh et al., 2000), and (ii) the "new" reading model by Richlan (2014). Interestingly, Richlan (2014) suggests that the two models may come to different predictions about the between-group differences, the impact of orthographic depth on the neurofunctional correlates of reading, and their development.

In what follows, we first describe the aforementioned models regarding their predictions about the effects of age and orthographic depth on the anatomo-functional correlates of reading, both in healthy controls and DD. These predictions are further described to highlight limits, differences, and commonalities between the two perspectives. This qualitative review has been accompanied by a quantitative coordinate-based meta-analysis of neurofunctional studies on reading in DD.

1.1. WHICH PRIMARY NEUROFUNCTIONAL DEFICIT? THE EFFECT OF AGE ON DYSLEXIA

The most accredited serial developmental model of reading acquisition assumes that children become fluent readers by passing through three different stages, each one characterized by a particular reading strategy (Frith, 1985): (i) in the *logographic* stage, children rely on their basic memory skills in order to recognize the whole word through their graphic features, using an association strategy similar to the one used for images; (ii) in the *alphabetic* stage, children learn the rules for the grapheme-phoneme conversion and start to adopt a serial decoding strategy (Liberman et al., 1977); and finally, (iii) during the *orthographic* stage, children acquire the ability to instantly analyse whole words at the orthographic level (Sterling, 1983), without employing phonological recoding (Ziegler & Goswami, 2005). This developmental model postulates that each newly learned strategy capitalises on the others after initial drawbacks in performance.

Moreover, Frith (1985) hypothesised that DD could be a consequence of the failure to access the *alphabetic* stage. It follows that the brain regions supporting the conversion of graphemes to phonemes will be dysfunctional in dyslexic compared to non-impaired readers. In line with this prediction, the “classic” model (Démonet et al., 2004; McCandliss & Noble, 2003; Pugh et al., 2000; Pugh et al., 2005; Sandak et al., 2004) postulates (i) a primary engagement of the left dorsal TP cortex in reading – including the dorsal inferior parietal lobule (IPL) and the posterior region of the superior temporal gyrus (STG) – associated with phonology-based processes and (ii) a late involvement of the vOT cortex associated with memory-based orthographic word recognition, once an enough rich orthographic lexicon has become available. According to these predictions, the under-recruitment of the left dorsal TP cortex in dyslexic children and the left vOT in adult readers with dyslexia are expected (Pugh et al., 2000). In line with this hypothesis, a recent meta-analysis by Paulesu et al. (2014) suggested that the posterior inferior temporal cluster was specifically associated with normal readers, and with the adult group. These results support the idea of a late involvement of the vOT cortex in the normal development of the reading process. Moreover, according to the “classic” model, children with DD would be characterized by an age-dependent increase of activation of the left

Inferior Frontal Gyrus (IFG) to cope with the phonological demands through articulatory processes. The same pattern of results should also emerge for the homologues areas of the right hemisphere (Pugh et al., 2000).

Differently by Pugh et al. (2000), Richlan and colleagues (2012) recently proposed a new developmental model of reading, in which a secondary deficit in the STG - associated with phonological strategies and multisensory letter-speech sound integration - stems from a primary deficit in the left vOT cortex - associated, from his perspective, "*with both visual-orthographic whole-word processing and serial grapheme-phoneme conversion*" (Richlan, 2014, p. 8). According to this prediction, a recent meta-analysis (Martin et al., 2015) of neuroimaging studies on non-impaired adult and children readers revealed a significant age-effect in the left vOT and the left IFG regions, suggesting an early involvement of these areas during reading acquisition.

1.2. ORTHOGRAPHY-SPECIFIC EFFECT ON DYSLEXIA: THE NEURAL INFLUENCE OF ORTHOGRAPHIC DEPTH ON DYSLEXIA

According to the *orthographic depth hypothesis* (Frost et al., 1987; Katz & Frost, 1992), orthographic depth refers to the degree to which a 1:1 grapheme-to-phoneme mapping characterizes an alphabetic language. Based on the transparency and of the degree of syllabic complexity, Seymour and colleagues (2003) classified European orthographies on a 5-level continuum from the most (shallow orthographies) to the less consistent (deep orthographies).

As widely observed, at the behavioural level, readers in shallow orthographies displayed a more fluent and accurate reading, with faster time and a smaller number of errors, compared to readers in deep orthographies (Aro & Wimmer, 2003; Frith et al., 1998; Goswami et al., 1998; Landerl et al., 1997; Paulesu et al., 2000; Seymour et al., 2003; Ziegler et al., 2003). This shallow-specific advantage in reading abilities is evident in both healthy (Aro & Wimmer, 2003; Bergmann & Wimmer, 2008; Ziegler et al., 2003) and dyslexic readers (Landerl et al., 1997; Ziegler et al., 2003), specifically in the first stages of reading acquisition.

At the anatomo-functional level, converging evidence links the TP under-recruitment in dyslexic readers to their impairment in phonological processing, and grapheme-to-phoneme mapping (Paulesu et al., 2001; Rumsey et al., 1992; Rumsey et al., 1997; Shaywitz et al., 1998). To support this, researchers found a marked hypo-activation of the posterior regions (i.e., posterior superior temporal sulcus, angular and supramarginal gyri) during non-word rhyme matching task (Simos et al., 2000) and a reduction of connectivity between the angular gyrus and frontal and mid-temporal areas during non-word reading (Horwitz et al., 1998). Interestingly, while in the study by Pugh et al. (2000), there is not a specific prediction about the impact of orthographic depth on the neurofunctional manifestation of DD, in his theoretical paper Richlan (2014) states that in these brain regions (i.e., dorsal TP) the Pugh's model would predict, in shallow orthographies, "*reading-related activation in non-impaired children and adults and underactivation in dyslexic readers. For deep orthographies, in contrast, one would expect activation only in non-impaired children or in tasks requiring phonology-based reading or explicit phonological analysis*" (Richlan, 2014, p. 6).

In addition to the left TP reading system, the classic model also makes predictions on the role of the left vOT cortex. The activation of this region during reading has been associated either with fast memory-based whole-word processing (Cohen et al., 2002; Price & Devlin, 2003; Pugh et al., 2000; Turkeltaub et al., 2002; Turkeltaub et al., 2003) or with the integration between bottom-up visual information and top-down predictions (Danelli et al., 2013; Price & Devlin, 2011). If the former is true, a certain degree of activation is expected in this region in non-impaired readers of shallow orthographies, whereas little activation is expected in impaired readers (see Richlan, 2014). Given the complex grapheme-phoneme mapping in deep orthographies, significant activation of the vOT system is expected in skilled adult readers and occasionally in children who have already built an orthographic lexicon (Richlan, 2014 in revisiting the model of Pugh et al., 2000). Dyslexic adult readers and children will both show under-recruitment of the same system in deep orthographies. Conversely, if the OT cortex underlies the integration between bottom-up and top-down information (Danelli et al., 2013; Price & Devlin, 2011), dyslexic readers would show vOT under-recruitment, regardless of orthographic depth (Richlan, 2014).

The classic model postulates the involvement of a third region, the IFG, which is supposed to underlie speech-gestural articulatory recoding of orthographic stimuli; based on Richlan (2014) review, this region would be hyper-activated by dyslexic readers in both orthographies, reflecting compensatory phenomena increasingly used with age.

Once discussed the classic model and its hypothetical implications for shallow and deep orthographies, Richlan (2014) explains the impact of his new model on this issue. In particular, the author assumes that: (i) the left inferior parietal lobule (IPL) might be involved in serial decoding (Cabeza et al., 2012; Taylor et al., 2013) and attentional shifting during sub-lexical grapheme-to-phoneme processing (Danelli et al., 2015), while (ii) the left posterior STG would be involved in the multisensory letter-speech sound integration (Richlan, 2014; Richlan, 2019; Van Atteveldt et al., 2004; Wallace & Stevenson, 2014) and in the phonological-lexical aspects of reading (Danelli et al., 2015). Moreover (iii) the left dorsal precentral gyrus (PreG – Richlan, 2014) would be engaged during articulatory recoding of print, while (iv) the left IFG, would be involved in the access to output phonological representations. Considering the functional specialization within the anterior frontal and posterior TP circuits in the new model, it has been hypothesized that orthographic depth would modulate the activation of IPL during reading in non-impaired readers but should not have an effect on the STG and the vOT cortex activation (see Richlan, 2014 for a review). Finally, the new model predicts the failure in recruiting the left IPL (particularly in shallow orthographies) and of the vOT cortex and IFG in dyslexic readers, regardless of orthographic depth. Finally, the model predicts an over-recruitment of the precentral cortex in dyslexic readers, regardless of orthographic depth (Richlan, 2014).

1.3. READING AND PHONOLOGICAL PROCESSING

Based on Wagner and Torgesen (1987), Phonological Processing “refers to the use of phonological information (i.e., the sounds of one's language) in processing written and oral language.” (Wagner & Torgesen, 1987, p. 192) This high-order process *includes*, but is not correspondent to, phonological awareness, which refers to detecting and manipulating language sounds. The definition of phonological processing also entails phonological recoding in lexical access, i.e., the ability to recode a print symbol in a sound-based representation, and phonetic recoding, i.e., the ability to maintain this sound-based representation in working memory. Phonological awareness can be tested through phoneme deletion, blending and manipulation tasks, while the second can be measured through object naming and RAN (Wagner & Torgesen, 1987). Taken together, these sub-processes are considered crucial to become proficient readers.

According to this conception, we decided to take apart what we will define as “Phonological Processing” from reading and consider these two processes into two separate meta-analyses.

It is worthy to note that neither of the two models makes specific predictions about the neurobiological signatures of phonological processing, independently by the reading process. Nonetheless, specific under-recruitment of dyslexic readers was found in the left inferior frontal gyrus, superior temporal gyrus, middle temporal gyrus, and fusiform gyrus during bimodal visual-auditory phonological processing tasks (Bitan et al., 2009; Bitan et al., 2007; Bolger, Hornickel, et al., 2008; Bolger, Minas, et al., 2008; Booth et al., 2004; Cao et al., 2006; Hoeft et al., 2006; McCandliss & Noble, 2003; Shaywitz et al., 2004; Shaywitz et al., 2007; Temple et al., 2001). Unsurprisingly, these areas are commonly activated also by unimodal visual reading tasks (see Figure 1), thus suggesting, from the neurocognitive point of view, the notion that phonological processes play a role in reading. The collinearity between the two processes makes it difficult to explore a univocal neurofunctional correlate (i.e., phonological recoding in reading and phonological processing) unless specific phonological tasks based on auditory stimuli are employed. Unfortunately, few studies focused on the exclusive auditory basis of phonological awareness (Danelli et al., 2017; Eden et al., 2004; Heim et al., 2010; Kovelman et al., 2012), even if it is considered a significant predictor of reading performance (Demonet et al., 1996; Kirby et al., 2003; Leather & Henry, 1994; Parrila et al., 2004). Due to the complexity of the matter at stake, and due to the variety of experimental paradigms employed, the precise neurobiological underpinnings of phonological processing are still a matter of debate, even though both frontal (Danelli et al., 2017; Heim et al., 2010; Kovelman et al., 2012) and temporo-parietal activations (Eden et al., 2004) have been reported. From a behavioral point of view, a systematic deficit in phonological awareness tasks has been largely reported in dyslexia (Vellutino, 1979), and it is thus considered one of the universal cognitive marker of reading disorder, regardless of age and orthography (Landerl et al., 2013; Moll et al., 2014; Ziegler et al., 2010, Carioti et al., 2021). In light of this highly replicated behavioral evidence, which involved both phonological-based processing in reading and phonological awareness *per se*, we decided to explore the neuro-dysfunctional effects of DD in phonological processing by isolating the activation peaks extracted from phonological tasks in a separate dataset.

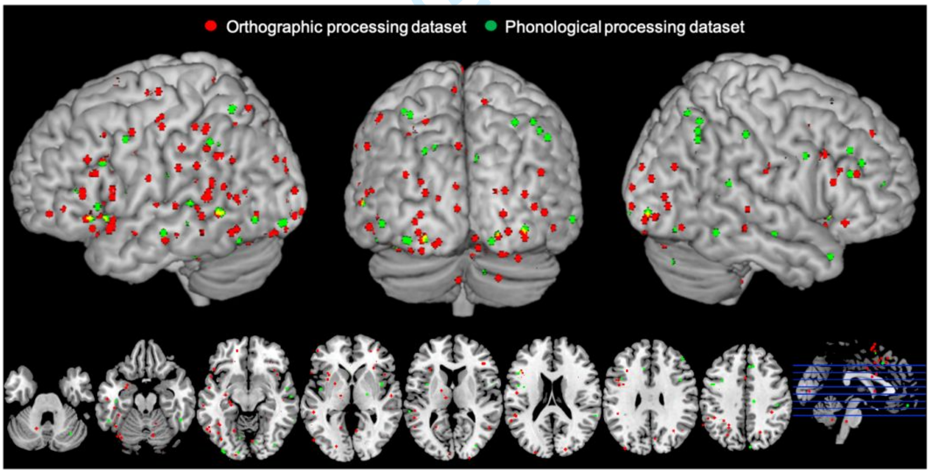


Figure 1 | Anatomical distribution of control-related peaks included in the two datasets. Stereotaxic coordinates (MNI) coming from simple effects in control readers and from [controls > dyslexics] contrasts in the orthographic dataset (red) and phonological processing dataset (green) are overlaid on a 3D rendering of the brain (top). Axial slices are provided from z = -30 to z = + 40 in MNI stereotaxic space (bottom).

2. AIMS OF THE STUDY

To date, the main focus of quantitative meta-analyses published in the literature on the reading system was to summarize previous results on the functional (for example, Maisog et al., 2008, Richlan et al., 2009, 2011, Paulesu et al., 2014) and structural (for example, Richlan et al., 2013, Linkersdörfer et al., 2012) changes associated with DD. Only a few studies have explicitly assessed the validity of the current neurofunctional models of reading development by comparing children- and adults-related activations (Martin et al., 2015; Richlan et al., 2011) or have explored the influence of orthographic depth on reading-related brain activations (Martin et al., 2016; Pollack et al., 2015).

Moreover, assessing the anatomo-functional effects of age and orthographic depth on the neurofunctional signatures of DD in the same study would require a longitudinal study with a huge sample size of dyslexic and non-impaired readers in different native languages. However, the meta-analytic approach adopted in this study allows us not only to combine the results of different single studies but also to characterize the specialization of clustered brain regions with respect to variables of interest such as group (controls vs. dyslexics), age (children vs. adults) and orthographic depth (shallow vs. deep).

Therefore, the aim of the present study is: (i) to assess the cross-orthography neurofunctional signatures of DD (group-effect), (ii) to evaluate the neurofunctional developmental trajectories in the manifestation of DD (group-by-age interaction effects), (iii) to assess the orthography-specific effects on the neurofunctional correlates of DD (group-by-orthography interaction effects), and (iv) to explore whether age and linguistic background can interact, giving rise to the specific neurofunctional manifestation of DD (group-by-age-by-orthography interaction effects). These issues will be addressed by referring to the "classic" and "new" model of reading described in the paper by Richlan (2014), that attempt to provide a description of the phenomenon along with three levels of explanation: *anatomo-functional*, *developmental*, and *orthographic depth*.

Moreover, we aimed at identifying the neural basis of phonological processing in dyslexia by comparing controls vs. dyslexic readers activation patterns during phonological tasks, regardless of age and orthography, by performing a separate meta-analysis on the phonological processing dataset. As assessed in previous meta-analytic studies (Devoto et al., 2018; Paulesu et al., 2014; Seghezzi et al., 2019), we employed a complementary approach by combining the ALE algorithm (Eickhoff et al., 2009; Turkeltaub et al., 2012) and the unique-solution clustering algorithm (Cattinelli et al., 2013b) implemented in a meta-analytical suite called CluB (Clustering the Brain; Berlingeri et al., 2019). While the former approach allows quantifying the significance of the convergent activations across studies with reference to a normally distributed statistical process, CluB permits to assess whether each cluster shows a significant preference for a given factor (group, age, and orthographic depth) or a combination of factors (i.e., interaction effects).

2.1. PREDICTIONS

As briefly reviewed in the previous sections, each neurocognitive account, i.e., the classic and the new reading model, comes with its predictions on three levels of explanation: *anatomo-functional*, *developmental,* and *orthographic depth*. It is worthy to note that these levels should not be considered in isolation since they are tightly intertwined, and they are thought to give rise to specific interactions.

First, at the ***anatomo-functional level***, they differ with respect to the parcellation of the anterior and posterior reading circuits and their underlying cognitive processes. The *classic model* (Pugh et al., 2000) relies on a gross anatomical parcellation of the reading network in three macro-areas of the left hemisphere: the temporo-parietal (TP), ventral occipito-temporal (vOT), and inferior frontal regions (IFG). From the neurofunctional point of view, the left TP cortex is assumed to underlie both grapheme-phoneme conversion and serial decoding, whereas the left vOT cortex and IFG are supposed to underlie whole-word recognition and phonological/articulatory processing, respectively. Moreover, according to the classic model, the TP regions maturation would be the *conditio sine qua non* to develop an efficient memory-based reading supported by the vOT cortices (this issue will be better described in the developmental predictions). In contrast, the *new model* by Richlan (Richlan, 2014), being more recent and hence steaming from a larger pool of empirical evidence, suggests a more fine-grained parcellation of the TP cortex with a distinction between the left Inferior Parietal lobule (IPL) (involved in serial decoding and sublexical reading (Danelli et al., 2015)) and left posterior STG (involved in phonological-lexical aspects of reading (Danelli et al., 2015), and audio-visual integration (Wallace & Stevenson, 2014; Richlan, 2019, 2020). Similarly, the anterior regions are parcellated into the left IFG (an area associated with output phonology that is supposed to be under-recruited in DD) and into the left Precentral gyrus (PreG, an area associated with articulatory processing that would be over-recruited by dyslexic readers). In contrast with the classic model, the left vOT cortex is assumed to underlie both whole-word processing and grapheme-phoneme conversion in the new model. However, it cannot be excluded that the mass of empirical evidence collected in the last 5 years may support a more fine-grained parcellation of the vOT cortex activation, dovetailing also with our previous studies on adults with and without DD (Danelli et al., 2017; Danelli et al., 2013; Danelli et al., 2015).

Second, at the ***developmental level***, the classic and new models make different predictions. The *classic model* clearly postulates that the development of the memory-based word-recognition strategy is mediated by the so-called "*ventral word form circuit"*, which depends *"on the integrity of analytic processing that occurs in the temporo-parietal or dorsal circuit*" (Pugh et al, 2000, p. 12). If this was the case, one may expect that children should rely more on the TP cortices, while adults should activate the vOT regions predominantly. Moreover, they suggest that DD would be associated with a dysfunction of the temporo-parietal region that, in turn, would disrupt the development of memory-based reading and its specific neural correlate, the vOT region. Accordingly, as children mostly rely on phonological strategies in the initial stage of the learning processes, one should find TP under-recruitment in dyslexic readers as compared with controls in children only, while adult dyslexics should be characterized by an under-recruitment of both the TP and vOT cortices. Finally, dyslexic adult readers are expected to show over-recruitment of the left IFG, probably reflecting overreliance on fine-grained articulatory processing (Pugh et al., 2000).

While the developmental predictions are clearly reported in the original paper by Pugh and colleagues (2000), in the paper by Richlan (2014), the age-related effects are less clear for a number of methodological reasons. First, the "new model" mainly relies on the results of a meta-analysis of 9 studies on adults and 9 studies on children with DD (Richlan et al., 2011); however, the authors did not formally test the effect of age as the two sets of studies were separately meta-analyzed. From the methodological point of view, this implies that the neurofunctional manifestation of reading acquisition in skilled and impaired readers, and its developmental trajectories, can be just described at the hypothetical level, as a formal comparison between children and adults is lacking. Moreover, in the 2011 meta-analysis, Richlan et al. included only stereotactic coordinates that corresponded to significant direct comparisons between skilled readers and dyslexics. This implies that their results can be adopted to describe the neurofunctional dysfunctions in DD, but nothing can be said about skilled readers and how the reading system would develop in this population.

Notwithstanding these methodological issues, the "new model" (Richlan, 2014) suggests that the left ventral OT cortex is associated with both visual-orthographic whole-word processing and serial grapheme-phoneme conversion. As a consequence, one may speculate that DD is associated with a primary left vOT dysfunction that, in turn, causes a left STG deficit. Finally, while the classic model predicts IFG over-recruitment in dyslexic adults (reflecting phonological/articulatory-based compensatory processes), the "new model" postulates a more fine-grained parcellation of the anterior circuit. Accordingly, dyslexic readers should manifest an under-recruitment of the left IFG (supporting the access to phonological output representations) coupled with an over-recruitment of the left PreG (supporting articulatory phonological recoding), regardless of age. Notably, the same cognitive process (articulatory phonological recoding) is attributed to two different brain structures in the two models: IFG in the classic and PreG in the new model.

To conclude, we describe the predictions about the ***orthographic depth*** effect. Here, it is worth noting that in the original paper by Pugh and colleagues (2000), the orthographic depth hypothesis has not been mentioned at all. However, based on the interpretation of the classic model by Richlan (2014), and according to the new model itself, we can argue that both models share the following assumptions: readers in shallow orthographies are expected to rely more on rule-based grapheme-phoneme conversion strategies, whereas readers in deep orthographies are expected to rely more on memory-based whole-word recognition strategies. At the neuroanatomical level, this converging point is represented by the role attributed to the left TP cortex and IPL in the classic and new model, respectively (i.e., the predominant activity of brain regions underlying phonological processing and serial decoding). Nonetheless, the precise characterization of the orthography-specific effects in the two models concerning the vOT cortex is tightly linked to both the neurofunctional and developmental levels, giving rise to different neuroanatomical predictions. According to the paraphrase of the classic model in Richlan (2014), while intermediate activation of the vOT circuit is expected in shallow orthographies, vOT activity is expected to increase with age in deep orthographies, in agreement with the role of this region in memory-based whole-word recognition. On the contrary, according to the new model, the vOT cortex would also be involved in grapheme-to-phoneme conversion, and it would also be engaged by children in shallow orthographies. As such, vOT deficit in dyslexia would not represent a secondary dysfunction but would be rather at the basis of the difficulties in early reading acquisition, regardless of orthography.

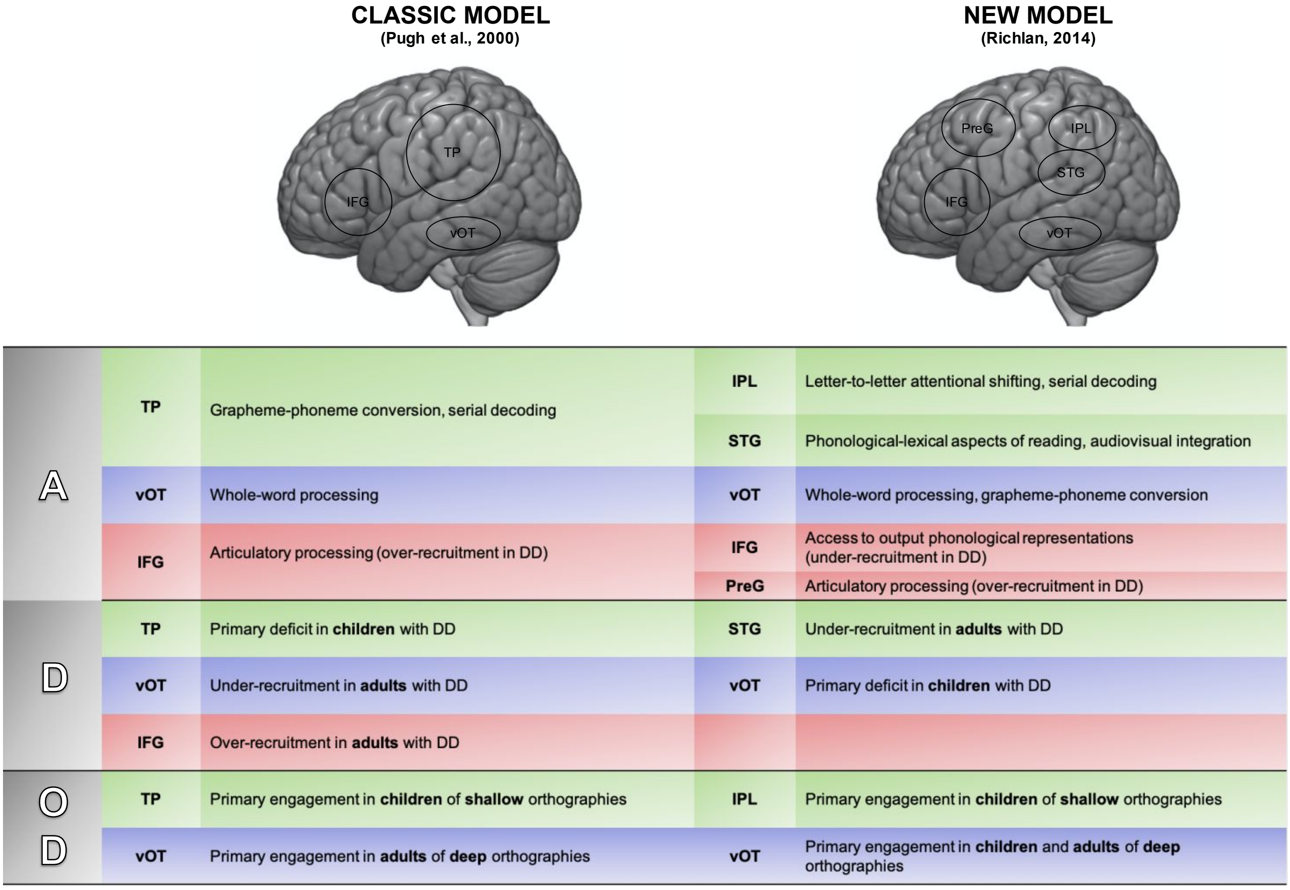
Finally, neither of the models makes orthography-specific predictions about the role of the anterior frontal reading circuit. However, since the IFG is involved in several of cognitive and emotional processes (Price, 2012; Richlan et al., 2014), we cannot *a priori* exclude that at least some of its functional/anatomical subdivisions are sensitive to orthographic depth.

For what concerns ***phonological processing***, we moved a step further in the knowledge of which regions involved in the reading process are specific for phonological processing. As a matter of fact, analyzing the classic and the new model, it is easy to identify what specific regions are involved in phonologic-based reading processes (TP cortex in the Pugh's model (Pugh et al., 2000), dorsal IPL, STG and also OT cortex in Richlan's one (Richlan, 2014)): conversely, it is challenging to understand which of these regions is specifically involved in phoneme elaboration and integration (i.e., in the phonological processing).

The grapheme-to-phoneme conversion is indeed a complex strategy characterized by attentional, visual, phonological, and integrative processes that were hardly characterized at the anatomo-functional level in the previous literature. Nevertheless, some predictions about this specific aspect can be found in the new model. Referring to the temporal-parietal region, Richlan (2014) assumes that the dorsal portion of IPL could be "*involved in shifting attention from letter to letter within a string*" (Richlan, 2014, p. 8), while the STG would be more involved in multisensory letter-speech sound integration or when the explicit phonological analysis is required. Finally, the vOT region would be further associated with serial grapheme-to-phoneme conversion.

In other words, only the involvement of the left STG in phonological processing would prove in favour of the new model, as it is the only brain region associated with "*explicit fine-grained phonological analysis"* (Richlan, 2014, p. 8).

A summary of the two theoretical models and their predictions about the three levels of explanations is reported in Figure 2.



A	**TP**	Grapheme-phoneme conversion, serial decoding	**IPL**	Letter-to-letter attentional shifting, serial decoding
			STG	Phonological-lexical aspects of reading, audiovisual integration
	vOT	Whole-word processing	**vOT**	Whole-word processing, grapheme-phoneme conversion
	IFG	Articulatory processing (over-recruitment in DD)	**IFG**	Access to output phonological representations (under-recruitment in DD)
			PreG	Articulatory processing (over-recruitment in DD)
D	**TP**	Primary deficit in **children** with DD	**STG**	Under-recruitment in **adults** with DD
	vOT	Under-recruitment in **adults** with DD	**vOT**	Primary deficit in **children** with DD
	IFG	Over-recruitment in **adults** with DD		
OD	**TP**	Primary engagement in **children** of **shallow** orthographies	**IPL**	Primary engagement in **children** of **shallow** orthographies
	vOT	Primary engagement in **adults** of **deep** orthographies	**vOT**	Primary engagement in **children** and **adults** of **deep** orthographies

Figure 2 | Graphical representation of the two models and of their predictions across the three levels of explanations. We summarized the main anatomo-functional predictions of the classic (left) and new (right) models of developmental dyslexia across the three levels of explanation (Anatomo-functional (A), Developmental (D), and Orthographic Depth (OD)) with respect to three brain circuits involved in reading: the posterior temporo-parietal (green), the posterior ventral occipito-temporal (blue), and the anterior frontal (red). IFG, Inferior Frontal Gyrus; IPL, Inferior Parietal Lobule; PreG, Precentral Gyrus; TP, Temporo-Parietal cortex; vOT, ventral Occipito-Temporal cortex.

3. METHODS

3.1. DATA COLLECTION AND PREPARATION

This meta-analytical study included 34 neuroimaging PET and fMRI studies published on DD until February 2018. The studies were selected by querying the Pubmed database (http://www.ncbi.nlm.nih.gov/pubmed/) with the keywords: "Neuroimaging and developmental dyslexia", "fMRI and developmental dyslexia", "functional Magnetic Resonance Imaging and developmental dyslexia", "PET and developmental dyslexia", and "Positron Emission Tomography and developmental dyslexia". From the initial search, 695, 794, 751, 44 and 56 entries were found, respectively, for each keyword. After duplicates removal, 1155 papers were primarily screened based on titles and abstracts, and finally, 587 full-texts were inspected (Figure S1). These were screened based on the following inclusion criteria:

(1) each study must include both a sample of skilled readers and participants with an official diagnosis of DD provided by a professional neuropsychologist, speech therapist or other professionals in compliance with each country's provisions. Studies including poor readers or subjects without an official diagnosis of dyslexia were excluded;

(2) mean age of the sample population inferior or equal to 12 years old for children and superior or equal to 18 years old for adults (studies that included adolescent participants - mean age range: 13-17 – were excluded);

(3) If the focus of the paper was on remediation interventions (Eden et al. 2004, Farris et al. 2016, Heim et al. 2015), only pre-intervention data were included in the meta-analysis[1];

(4) imaging technique: PET or fMRI;

(5) whole-brain analyses using stereotactic coordinates (Montreal Neurological Institute, MNI or Talairach coordinates);

(6) only data emerged from massively univariate statistical analyses (studies with region-of-interest analyses or single-case studies were excluded);

(7) only task-related activation paradigms;

(8) only two categories of tasks: (i) *orthographic tasks* such as letter matching or string comparison, letter, word, pseudoword and sentence reading (silently, aloud), lexical decision, semantic judgement; (ii) *phonological processing tasks* administered via auditory and/or

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[1] Remediation status of the participants was explicitly declared only in few studies (e.g., Hernandez et al. 2013, Kovelman et al. 2012, Boros et al. 2016), in these cases, participants had received reading intervention, but still had persistent reading difficulty. For this reason, it was impossible to account for this effect in the current meta-analysis.

visual modalities, such as rhyming (picture, word, nonword), phoneme discrimination, phoneme deletion, and phonological short-term memory tasks;

(9) only data for either within-group or between-group comparisons, or both, while interactions and conjunction effects were excluded;

(10) only studies including European languages belonging to the level 1, 2, 4 and 5 of Seymour's model (by design, studies in Dutch, Swedish and Portuguese were not included).

As a result, we selected 34 neuroimaging studies including 1016 activation peaks overall: 795 coordinates were associated with orthographic tasks and 321 with phonological tasks (Table 1). 21 out of the 34 selected papers were included in the orthographic dataset (Adult: 8 (38%) studies, Children: 13 (62%); Shallow: 11 (52%), Deep: 10 (48%)) and 21 in the phonological processing dataset (Adult: 9 (60%) studies, Children: 6 (40%); Shallow: 5 (33%), Deep: 10 (67%)). In the orthographic tasks' dataset, 319 controls (206 children, 113 adults) and 324 dyslexics participants (204 children, 120 adults) were studied, with a mean age of 10.7 years (range: 9.5 - 12) for children and 23.1 years (range: 18 – 33) for adults. In the phonological processing dataset, 196 controls (80 children, 116 adults) and 183 dyslexics participants (75 children, 108 adults) were studied, with a mean age of 10 years (range: 9 – 11.5) and 25.3 (range: 18 – 40) years for children and adults, respectively.

(Table 1 about here)

3.2. CLASSIFICATION OF THE RAW DATA PRIOR TO CLUSTERING ANALYSES

Each activation peak was characterized considering three different variables:

- *Group*: each peak was classified in two categories (i) *Controls,* when the peak belongs to healthy controls or comes from a "Controls > Dyslexics" contrast and (ii) *Dyslexics,* when the peak belongs to participants with DD or comes from a "Dyslexics > Controls" contrast.
- *Age:* each peak was classified in two categories (i) *Children,* when the peak belongs to groups of participants with an average age of 12 years or younger; (ii) *Adults,* when the peak belongs to groups of participants with an average age of 18 years or older. This binary classification (and as a consequence the exclusion of adolescent participants) was adopted to maximize the between-group age-related differences in terms of reading acquisition and automatization;
- *Orthographic depth*: it refers to the degree to which the grapheme-phoneme mapping of the language is based on a one-to-one or a one-to-many correspondence (Frost et al., 1987; Seymour et al., 2003). In particular, we collapsed the 5-point-continuum of Seymour et al. (2003) (Table 1, p.

146) to obtain two main categories of European Languages: (i) *Shallow* (Finnish, Greek, Italian, Spanish, German, Norwegian or Icelandic; i.e., orthographies corresponding to level 1 and 2 in Seymour's model); (ii) *Deep orthographies* (French, Danish or English; i.e., orthographies corresponding to levels 4 and 5 in Seymour's model). This binary classification was adopted to maximize the differences in orthographic consistency between the groups of readers (shallow vs. deep). Moreover, for each activation peak, we reported the scanning technique (PET or fMRI), the stereotactic space (MNI or Talairach and Tournoux template), the statistical threshold and the correction for multiple comparisons applied.

Since some of the studies entered in the meta-analysis reported peaks in Talairach and Tournoux stereotactic space, all the foci (208 for the orthographic dataset, and 154 for the phonologic one) were transformed into the MNI (Montreal Neurological Institute) stereotactic space by using Matthew Brett's script (http://imaging.mrc-cbu.cam.ac.uk/imaging/MniTalairach) implemented in the GingerALE software (Eickhoff et al., 2009). Accordingly, 13 foci (7 from the orthographic and 6 from the phonological processing dataset) were excluded because they fell outside the boundaries of the MNI stereotactic space (as assessed by the Ginger ALE software, version 3.6.6 (Eickhoff et al., 2009)).

3.3. CLUSTERING PROCEDURE

The same clustering procedure was applied for the two datasets (orthographic processing and phonological processing) separately. In particular, we employed the software *CluB* (Clustering the Brain; Berlingeri et al., 2019) to extract the principal clusters of regional effects from the studies included in each dataset. CluB is a Matlab toolbox to perform coordinate-based meta-analysis of neuroimaging through a hierarchical clustering algorithm (hierarchical clustering analysis), in addition to post-hoc statistical testing to explore cluster composition (cluster composition analysis). In the Clustering Analysis module, CluB implements a hierarchical clustering analysis on the activation peaks by means of a unique-solution clustering algorithm (Cattinelli et al., 2013b). After the Euclidean distance between each pair of the input foci is computed, activation peaks with the minimal distance are recursively merged into clusters using Ward's criterion (Ward, 1963), which minimises the total intra-cluster variance after each merging step. This procedure leads to a tree-like structure called dendrogram: in a "bottom-up" clustering algorithm as the one by Cattinelli et al. (2013b), the leaves of the dendrogram represent clusters composed of a single activation peak, while the top represents one large cluster made up of all the activation foci submitted to the procedure.

To increase the power of detecting significant associations in the cluster composition analysis (see next section for further details), we chose an a priori threshold of 7 mm (Berlingeri et al., 2019). This spatial threshold is justified by our interest in relatively wide cortical structures, as described in the introduction.

CluB automatically labelled the clusters obtained through a query of the Anatomic Automatic Labelling (AAL) template available in the MRIcron software and through visual inspection (Rorden & Brett, 2000).

It is worthy to note that hierarchical clustering analysis does not quantify the significance of each cluster location with reference to a normally distributed statistical process. To overcome this issue, the hierarchical clustering analysis output was overlapped with the maps generated by the GingerALE algorithm (version 3.0.2) (Eickhoff et al., 2009; Turkeltaub et al., 2002). The ALE maps were generated by setting a cluster-forming threshold of $p < .001$ uncorrected and $p < .05$ FWE-corrected at the cluster level. Adjustment for multiple contrasts was made by pooling together in a single experiment all the coordinates belonging to the relevant contrasts. Only the clusters that fell within the Ginger ALE maps were considered for further discussion. For the small subcortical structures, we accepted as significant also clusters converging on an ALE map thresholded at the slightly more liberal $p < 0.001$ uncorrected threshold. Finally, the intra-cluster peaks distribution was used for post-hoc analyses to assess whether each cluster shows a significant age-, group- and orthography-specific effect, or an interaction between these factors, as implemented in the cluster composition analysis module of CluB. This approach has been previously employed on DD in Paulesu et al. (2014).

3.4. CLUSTER COMPOSITION ANALYSIS

In the cluster composition analysis module, CluB permits to determine statistically significant associations of the clusters to a specific group (children vs. adults, controls vs. dyslexics) or characteristic (readers in shallow vs. deep orthographies), or even two- and three-way interactions among the factors considered. This approach has been previously employed by meta-analytical reviews in different domains (language: Crepaldi et al., 2013; reading and dyslexia: Cattinelli et al., 2013a; Paulesu et al., 2014; food perception and obesity: Devoto et al., 2018; intention and sense of agency: Seghezzi et al., 2019; neural drug cue-reactivity: Devoto et al., 2020).

To determine the age-, group- and orthography-specific effects on the clusters returned by the HCA, we employed the *binomial test*: for example, we tested if the distribution of control- and dyslexic-related peaks within each cluster ($p0$ = observed probability) was significantly higher from the overall proportion of control- and dyslexic-related peaks present in the whole dataset (PL = prior likelihood). A cluster was considered as *group-specific* only when the probability of observing a specific number of peaks associated with a given group was higher than the prior probability ($p0 > PL$, $alpha < .05$). Similar analyses were made to assess whether the activation peaks included in each cluster were predominantly related to a given age group (children vs. adults) or with a specific orthography (shallow vs. deep).

To assess whether there was any significant 2 x 2 interaction effect, we used *Fisher's exact test* (Fisher, 1970) implemented in CluB to compute age-by-group, group-by-orthography, and age-by-orthography interactions. Similarly, to what was done for the binomial tests, the odds ratio under the Fisher's test null hypothesis was corrected to reflect the PL ($or0 = PL$). In line with we calculated the ratio between the proportion of observed foci and the total number of foci within the cluster (p0) to interpret the directionality of the significant interaction effects. Then, we divided this value for the proportion of foci belonging to the same factors considering the entire dataset (PL). This computation (i.e., p0/PL) results in an index that indicates the degree to which the distribution of activation peaks belonging to a specific combination of factors within a cluster exceeds the expected probability. Values greater than one indicate a higher probability for the cluster to be specific for that particular combination of factors.

Finally, we used the *Mantel-Haenszel test* to explore group-by-age-by-orthography interactions on each cluster. The Mantel-Haenszel test can be considered an extension of Fisher's exact test that can be applied to explore 2 x 2 x 2 interactions by identifying the factor that, according to the specific users' hypotheses, can be considered the moderator. In particular, we used the factor *group* (controls versus dyslexic readers) to stratify the analysis since we considered reading dyslexia as the main moderator of age- and orthography-effects (i.e., the effects of age and orthography are likely to manifest differently within each group of participants).

Considering the paucity of the foci belonging to the phonological processing dataset (i.e., 315), we decided to test only the association for the factor group, given the relatively balanced PL between the levels ($PL_{controls} = .61$; $PL_{dyslexics} = .39$), as opposed to the disproportion of foci in the factors age ($PL_{children} = .28$; $PL_{adults} = .72$) and orthography ($PL_{shallow} = .22$; $PL_{deep} = .78$). Moreover, considering the limited number of foci of the returned clusters (i.e., characterized by a small cardinality), we did not correct for the PL to test group-specific associations ($p0 > .50$, $alpha < .05$).

Finally, to limit the impact of any given study on our inferences, we considered for further discussion only clusters that included at least 4 contributing studies (number of contributing studies equal or greater than the 25th percentile of the total contributing papers). Moreover, we discarded those clusters with cardinality (i.e., the number of peaks) inferior to the 25th percentile (< 7) of the total cardinality of clusters.

4. RESULTS

4.1. ORTHOGRAPHIC PROCESSING

In the orthographic dataset, the HCA identified 63 clusters with an average extension of 6 mm, 6.3 mm and 7 mm along the x, y and z axes. These clusters are referred to as *Orthographic Processing (OP)* and numbered according to the clustering solution computed by CluB. 12 clusters were removed because their cardinality fell under the 25th percentile (i.e., 7 foci) of the total cardinality distribution. This threshold was adopted to perform a reliable post-hoc composition analysis. Of the remaining 51 clusters, 19 overlapped with the ALE-map resulted from the same orthographic dataset. On average, 8 different studies contributed to these clusters (min = 5, max = 14).

The clusters showing a significant effect in the binomial, Fisher's exact test and/or Mantel-Haenszel test are reported in Table 2. The full list of the 19 overlapping clusters is available in the Supplementary Materials (Table S1).

(Table 2 about here)

Group-specific clusters

Of the 5 group-specific clusters, 4 were predominantly activated by controls and 1 by dyslexic readers (Table 2). The controls-specific clusters were located in the left inferior temporal gyrus (ITG) [OP59], middle temporal gyrus (MTG) [OP23], superior temporal gyrus (STG) [OP42] and in the left IOG [OP24] (Figure 3, in red). The dyslexics-specific cluster was located in the right pars triangularis of the IFG (IFGtri) [OP45] (Figure 3, in cyan).

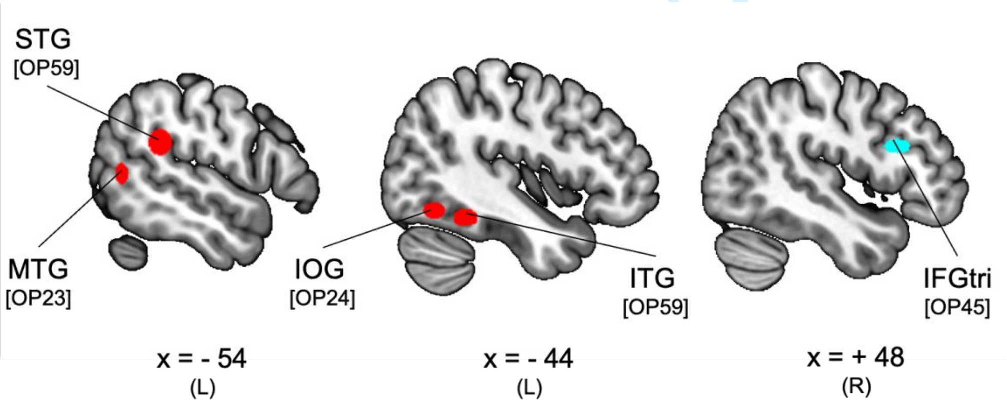

Figure 3 | Clusters showing a significant main effect of group in the orthographic dataset. Brain regions predominantly activated by control readers are shown in red, whereas brain regions predominantly activated by dyslexic readers are shown in cyan. Coordinates in MNI stereotaxic space. L, Left hemisphere; R, Right hemisphere.

Age-specific clusters

Of the 4 age-specific clusters, 1 was predominantly activated by children and 3 by adult readers (Table 2). The children-specific clusters were located in the left lingual gyrus [OP17] and in the right inferior occipital gyrus (IOG) [OP28] (Figure 4, in green), whereas the adults-specific clusters were located in the right IFGtri [OP22, OP45] and the left putamen [OP44] (Figure 4, in blue).

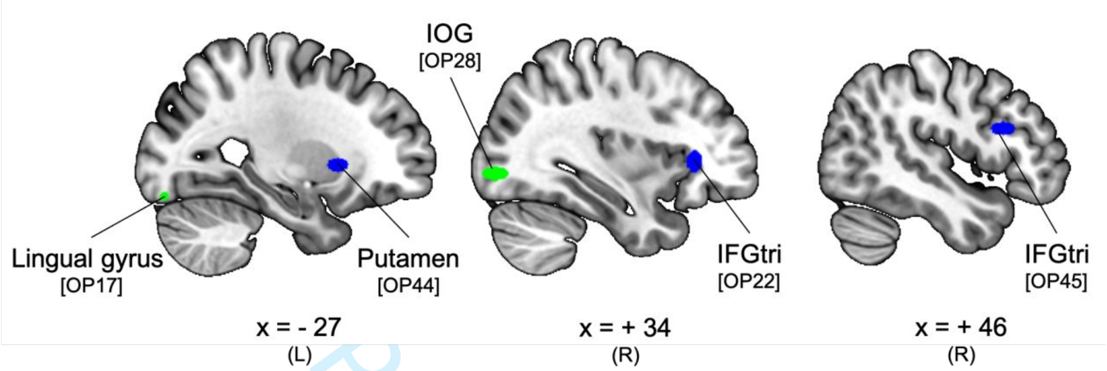

Figure 4 | Clusters showing a significant main effect of age in the orthographic dataset. Brain regions predominantly activated by children are shown in green, whereas brain regions predominantly activated by adult readers are shown in blue. Coordinates in MNI stereotaxic space. L, Left hemisphere; R, Right hemisphere.

Orthography-specific clusters

Of the 6 orthography-specific clusters, 5 were predominantly activated by readers in shallow orthographies and 1 by readers in deep orthographies (Table 2). The shallow-specific clusters were located in the left IFGtri [OP30, OP31], right IFGtri [OP22, OP45] and in the right supplementary motor area (SMA) [OP53] (Figure 5, in yellow). The deep-specific cluster was located in the left fusiform gyrus (FFG) [OP16] (Figure 5, in violet).

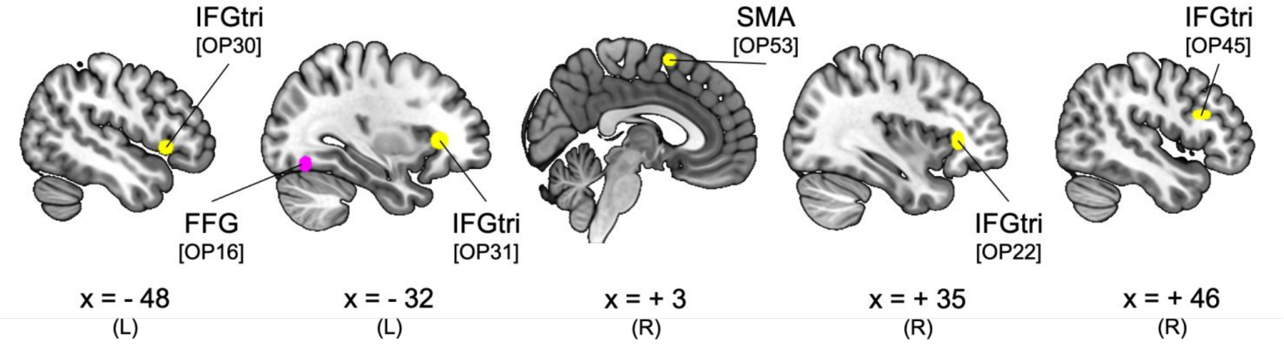

Figure 5 | Clusters showing a significant main effect of orthographic depth in the orthographic dataset. Brain regions predominantly activated by readers in shallow orthographies are shown in yellow, whereas brain regions predominantly activated by readers in deep orthographies are shown in violet. Coordinates in MNI stereotaxic space. L, Left hemisphere; R, Right hemisphere.

Group x Age interactions

No significant age-by-group interaction was observed.

Group x Orthography interactions

Two clusters, located in the left SMA [OP14] and in the right IFGtri [OP31] displayed a significant group-by-orthography interaction (Table 2 and Figure 6, in brown).

The inspection of the interaction plots in Figure 6 suggests that the left SMA [OP14] was predominantly activated by dyslexic readers in deep orthographies, whereas control readers in shallow orthographies predominantly activated the left IFGtri [OP31].

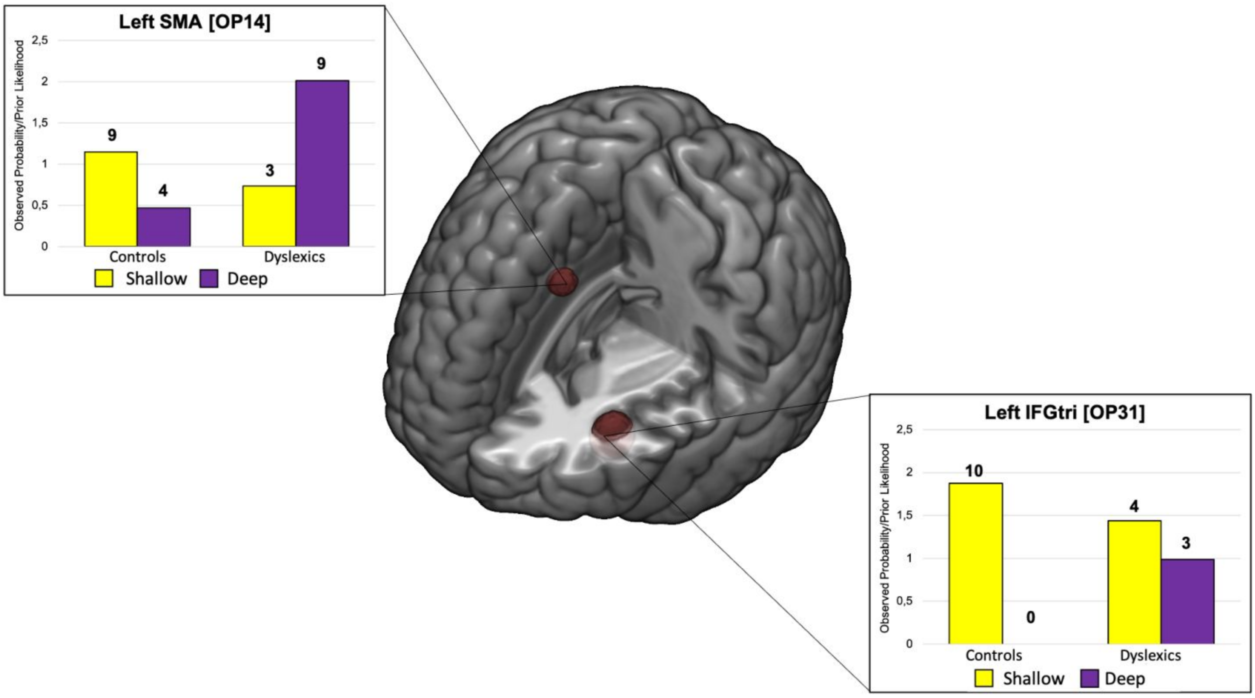

Figure 6 | Clusters showing a significant group-by-orthographic depth interaction in the orthographic dataset. Bar plots of the clusters displaying a significant two-way interaction. In the plots, the y-axis represents the ratio between observed probability and prior likelihood (p0/PL, see methods section). The raw number of foci is reported above each bar.

Age x Orthography interactions

No significant age-by-group interaction was observed.

Age x Group x Orthography interactions

Seven clusters, located in the left IFG pars opercularis [OP56], right IFGtri [OP22], left STG [OP42], MTG [OP61], ITG [OP59], FFG [OP16], and putamen [OP44] displayed a significant group-by-age-by-orthography interaction (Figure 7, in pink).

The inspection of the plots in Figure 6 suggests that the left IFGtri [OP22], the left STG [OP42] and left ITG [OP59] were predominantly activated by adult control readers in shallow orthographies. In contrast the left FFG [OP16] was predominantly activated by children control readers in deep orthographies, and the putamen [OP44] was predominantly associated with adult readers in shallow orthographies.

Finally, in the left MTG [OP61] and the left IFG pars opercularis [OP56] an opposite activation pattern between children and adult control readers emerged for deep orthographies and shallow orthographies, i.e., adult control readers in shallow orthographies recruited these regions more frequently than children, while a higher number of activation peaks was reported for children controls than proficient adult readers in deep orthographies.

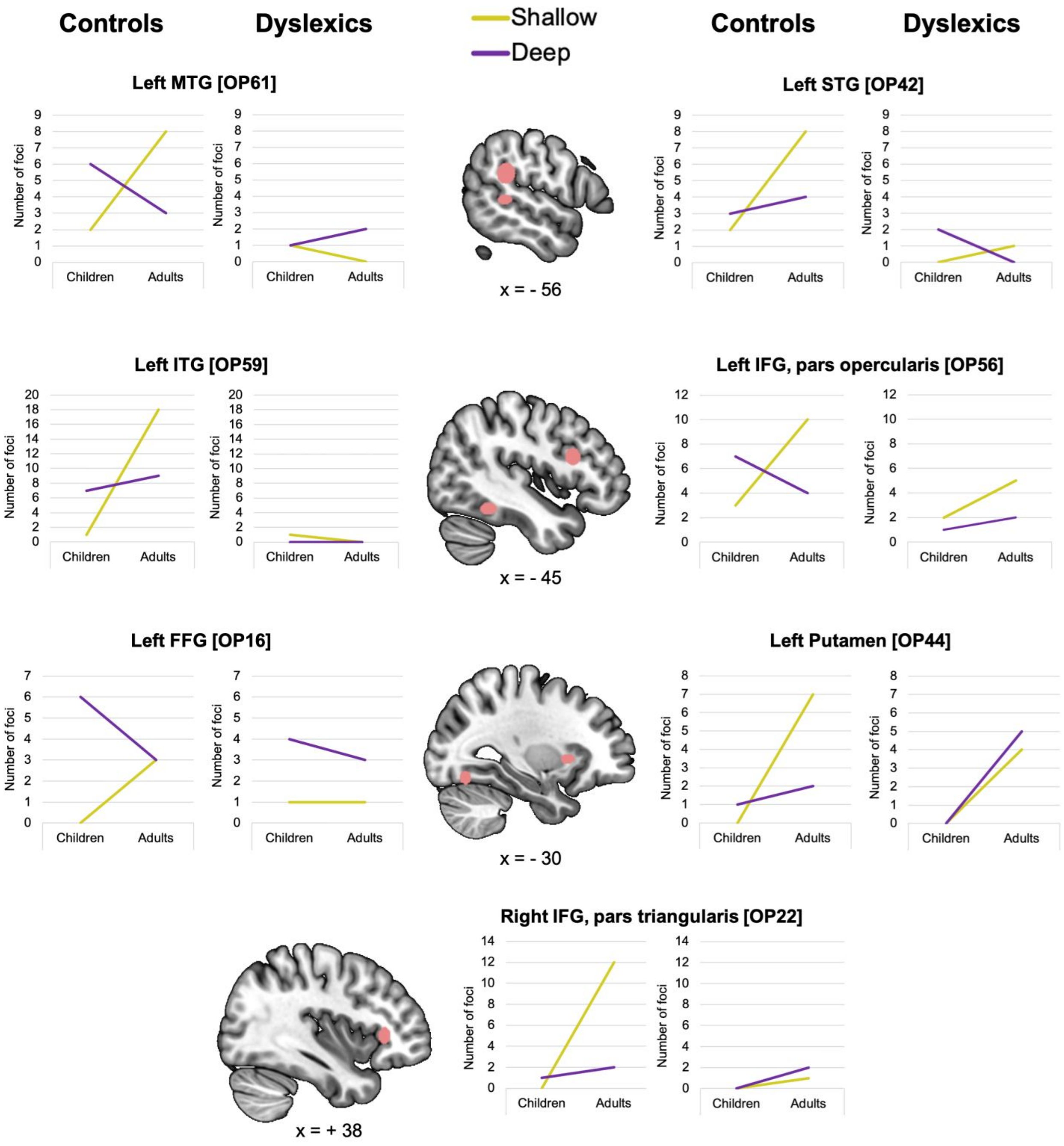

Figure 7 | Clusters showing a significant group-by-age-by-orthographic depth interaction in the orthographic dataset. Line plots of the clusters displaying a significant three-way interaction. In the plots, the y-axis represents the raw number of foci of each combination of factors for controls and for dyslexic readers separately. MNI coordinates in stereotaxic space.

4.2. PHONOLOGICAL PROCESSING

In the phonological processing dataset, the hierarchical clustering analysis identified 45 clusters with an average extension of 6.9 mm, 6.7 mm and 6.7 mm along the x, y and z axes. These clusters are referred to as *Phonological Processing (PP)* and numbered according to the clustering solution computed by CluB. 7 clusters were removed because their cardinality fell under the 25th percentile (i.e., 4 foci) of the total cardinality distribution. This threshold was adopted to perform a reliable post-hoc composition analysis. Of the remaining 38 clusters, 12 overlapped with the ALE-map resulted from the same phonological dataset. On average, 6 different studies contributed to these clusters (min = 4, max = 10). The clusters showing a significant effect of group in the binomial test are reported in Table 3. The full list of the 12 overlapping clusters is available in Supplementary Materials (Table S2).

(Table 3 about here)

Group-specific clusters

Controls predominantly activated two clusters, and no cluster was predominantly activated by dyslexic readers (Table 3). The controls-specific clusters were located in the left inferior parietal lobule (IPL) [PP45] and the left SMA [PP36] (Figure 8, in red).

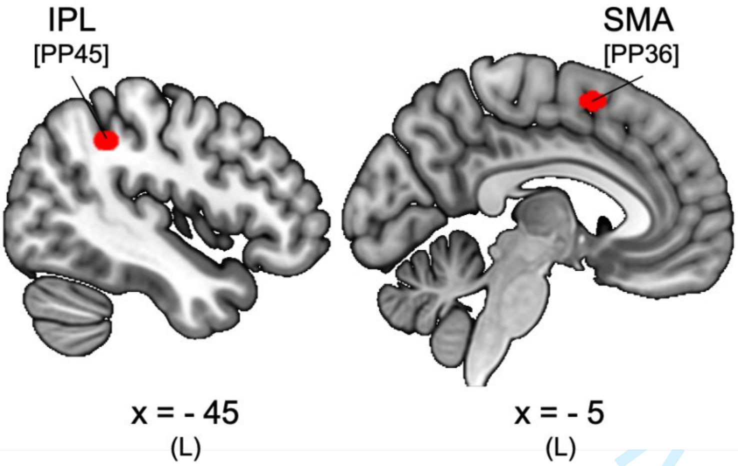

Figure 8 | Clusters showing a significant effect of group in the phonological processing dataset. Brain regions predominantly activated by control readers are shown in red. No brain region was predominantly activated by dyslexic readers. Coordinates in MNI stereotaxic space. L, Left hemisphere; R, Right hemisphere.

5. DISCUSSION

As we described in the introduction, the “classic” (Pugh et al., 2000) and the “new” models (Richlan, 2014) make different predictions on the three levels of explanation of DD: *anatomo-functional*, *developmental* and *orthographic depth*. In what follows, we first discuss our results in light of the predictions of the previous models by analyzing each level of explanation separately, to finally provide a revised neurocognitive model, the “Anatomo-functional, Developmental, Orthographic Depth” (ADOD) model of DD. This new model integrates previous theoretical perspectives with our meta-analytic findings on the three levels of explanation considered in this study. In particular, the ADOD model focuses on the interactions between the three levels of explanation, something that has never been attempted for the time being.

Before proceeding into the details of our discussion, we want to point out that the interpretation of the results will be limited to those meta-analytic clusters that showed at least (i) a significant main effect or (ii) a significant main and interaction effect (iii) in the three brain circuits described in the introduction (i.e., temporo-parietal, occipito-temporal, and frontal). Indeed, clusters that did not show a significant effect for any factor of interest would be deprived of any value, as they would represent the mere anatomical convergence of reading-related activations[2] regardless of group, age and orthographic depth. Conversely, clusters showing a significant main and/or interaction effect but localized outside the three brain circuits considered by previous models deserve further consideration. While being uninformative about the theoretical models considered in the present study, they can still provide further insights into the neurobiology of DD.

5.1. THE ANATOMO-FUNCTIONAL LEVEL

The first level of the ADOD model that we want to describe is the Anatomo-functional, and, in particular, we will start our discussion from the posterior TP circuit. According to the classic model (Pugh et al., 2000) the TP circuit comprises the posterior STG, the supramarginal and the angular gyri of the IPL, and it would be associated with phonological processing in reading. The new model by Richlan (2014), as described in the introduction, provides a more fine-grained parcellation of this circuit: the STG region would be involved in explicit phonological processing and audio-visual integration, while the IPL region would be involved in letter-to-letter attentional shifting and general

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[2] A detailed anatomical distribution of the pool of brain regions associated with reading processes is depicted in Figure S2 in the Supplementary Materials. The ALE map obtained by meta-analyzing with GingerALE 3.0.2 the entire pool of activations peaks included in our meta-analysis was passed to the cognitive decoder tool of Neurosynth (https://neurosynth.org/decode/). The results of the decoding procedure are reported in Table S3 in the Supplementary Materials.

attentional processes not strictly related to reading. Irrespectively by these differences, the two models suggest that this set of brain regions would be under-recruited in DD. Overall the results of our two meta-analyses (the one on reading tasks and the one specific for the activations elicited by phonological tasks) are in line with this prediction.

Nonetheless, from a purely neuro-anatomical point of view, our results support the idea of a subtler parcellation of the TP circuit into a dorsal and a ventral portion, with the former including IPL, and the latter including activations peaks distributed between STG and the Supramarginal gyrus (with the centroid of the cluster located in the STG at the border with the parietal regions). However, notwithstanding the anatomo-functional overlap between Richlan's model and the ADOD model, our results do not completely fit the cognitive roles ascribed by the author to these regions. In particular, our results suggest a prominent role of the left IPL [PP45] in phonological processing and its under-recruitment in dyslexic readers only when engaged in tasks posing higher demands on phonological processing (Cao et al., 2008; Danelli et al., 2017; Danelli et al., 2015; Eden et al., 2004), as the under-recruitment of IPL [PP45] in DD emerged from the phonological processing dataset only. Anyhow, further studies are needed to specifically test whether this brain region might play a role also in letter-to-letter attention shifting as suggested by Richlan (2014).

A more cautious approach must be adopted to discuss the STG cluster. According to Richlan (2014, p. 8), the "*activation of this region is predicted when the task involves unimodal auditory or bimodal audiovisual processing*". However, according to our meta-analytic findings, STG [OP42] is systematically activated in tasks with unimodal visual input requiring explicit orthographic-phonological integration by controls and under-recruited by dyslexic readers. Consequently, we suggest that STG plays a crucial role in the orthographic-phonological manipulation elicited by reading tasks, but based on our results, we cannot exclude it has a role in unimodal auditory processing.

Concerning the vOT circuit, which comprises the posterior portion of the ITG [OP59] and the FFG [OP16], both models predict their under-recruitment by dyslexic readers, but they ascribe it to different functions. According to the classic model, the OT circuit would be involved in whole-word orthographic processing, while the new model suggests that these regions would be associated both with whole-word orthographic processing *and* serial grapheme-phoneme conversion (Richlan, 2014). Of note, none of the models provides a subtler anatomo-functional subdivision of this circuit, thus assuming that the two regions included in the OT circuit would support the same cognitive processes. On the contrary, according to our ADOD model, when the three levels of explanation are considered, the picture becomes more intriguing. Indeed, the two portions of the OT circuit show opposite activation patterns: while the ITG [OP59] is more frequently activated in *adult* control readers in *shallow orthographies* (an effect that will be further discussed in the next section, see paragraph 5.2), the FFG [OP16] is predominantly associated with activations from *children* control readers in *deep orthographies*. As a first remark, the OT cortex parcellation in different neurofunctional sub-portions is in line with previous evidence (Danelli et al., 2013; Lerma-Usabiaga et al., 2018) in which a neurofunctional rostro-caudal gradient in the vOT cortex was reported. In the study by Danelli et al. (2013), the most anterior portion of the vOT cortex (in the posterior ITG) corresponded to the area of overlap between the auditory rhyming map and the *reading per se* map and represented the neurofunctional marker of the integration between orthography, phonology, and semantics (Danelli et al., 2013). The most posterior portion of the vOT cortex was located in a region of the posterior FFG and represented the overlap between the visuo-magnocellular and the pseudoword reading map. According to the authors, this region represented the neurofunctional underpinning of the visual-attentional processes related to reading (Danelli et al., 2013). Interestingly, in our meta-analysis we were able to partially replicate these results, as the anatomical location of our ITG cluster (OP59 - centroid in MNI coordinates: x = -43 ± 5, y = -46 ± 7, z = -17 ± 5, Table 2) roughly corresponds to the interface area between orthography and phonology (MNI coordinates: x = -50, y = -54, z = -18) found in Danelli et al. (2013), whereas the location of our FFG cluster (OP16 - centroid in MNI coordinates: x = -32 ± 5, y = -69 ± 5, z = -14 ± 6, Table 2) is very close to the most posterior overlap in Danelli et al. (2013) (MNI coordinates: x = -42, y = -70, z = -16). In line with these results, the dual role of the OT circuit in both phonological recoding and lexical recognition (Richlan, 2014) could be retained if one considers a subtler anatomo-functional parcellation of the vOT cortex as suggested above. Moreover, we identified the cross-linguistic under-recruitment in DD in a cluster that may represent a transition area between the more posterior FFG part (OP16, visual-orthographic processing) and the most anterior ITG part (OP59, visual-phonological processing), and that is located in the left IOG (OP24; centroid in MNI coordinates: x = - 47 ± 6, y = - 63 ± 7, z = - 13 ± 5), i.e., in a region that may benefit from short-range connectivity with the ITG [OP59] and FFG [OP16] clusters, see Figure 9. In particular, the left IOG [OP24] cluster is located in a region referred to as VWFA (see Table 4) and that, according to our meta-analytic findings, it is less frequently recruited by DD in reading tasks regardless of age and orthography. For the first time this finding was pictured in the paper by Paulesu et al. (2000) in a cross-linguistic study with adult dyslexic readers. Here we further support the universal marker of dyslexia by suggesting that this specific under-recruitment should be detectable also in children irrespectively by the orthographic context. Our result suggests that this region underlies a cognitive process primary needed in reading (Danelli et al., 2013) and that, according to previous meta-analyses (Martin et al., 2016; Paulesu et al., 2014), would be specifically impaired in DD.

This hypothesis is further supported by the results of the cross-linguistic study by Rueckl et al. (2015) in which this same brain region represents the only portion of cortex that is specifically activated for reading in proficient reading. Taken together, these results support once again the key-role of the VWFA for the development of reading skills.

Here it is worth noting that, according to the selection criteria implemented for this meta-analysis (reading tasks only), we cannot explicitly test whether: (i) the activation of the so-called VWFA in proficient readers and its under-recruitment in dyslexic readers is specific for reading tasks only (as suggested by), or (ii) the activation of the VWFA represents an interface between different domains (Behrmann & Plaut, 2013; Chen et al., 2019; Price & Devlin, 2003; Vogel et al., 2014; Xue et al., 2006).

Anyway, VWFA under-recruitment in DD is a well-replicated finding, and we suggest that it may be translated into clinical practice by adopting it as a reliable neurofunctional marker of dyslexia.

(Table 4 about here)

Again, for what concerns the anterior reading circuit, the new model suggests a subdivision into an IFG part, under-recruited in DD and that underlies the access to phonological output representations, and into a PreG part, over-recruited in DD and probably reflecting an overload of articulatory processes to compensate for posterior dysfunctions (Richlan, 2014). Conversely, articulatory recoding of print in the classic model is generally attributed to the left IFG, and it is assumed to be over-recruited in adult dyslexic readers (Pugh et al., 2000). Our results challenged this hypothesis, as only one cluster located in the left IFG [OP31] displayed a significant result in the post-hoc analysis. In particular, the left IFG [OP31] was less frequently associated with dyslexic readers in shallow orthographies compared to deep ones. No cluster associated with dyslexic under- or over-recruitment was found in the PreG. This result suggests that left IFG (pars triangularis; OP31) activation underlies a process that is deficient in dyslexic readers of shallow orthographies, contrarily from what expected by the classic model (Pugh et al., 2000): this would imply that left IFG activity reflects phonology-based processes of reading (Richlan, 2014). On the other hand, the lack of any dyslexic over-recruitment in left frontal and/or premotor regions challenges the finer parcellation of the anterior circuit in the new model, as well as the notion that the recruitment of left frontal regions is associated with overreliance on articulatory processes to compensate for the dysfunction of the posterior circuits (Pugh et al., 2000, Richlan, 2014). Of note, only two clusters showed dyslexic over-recruitment in our meta-analysis, and they were located in the dorsal part of the right IFGtri [OP45] (with no further orthography-specific effects), and in the left SMA [OP14], particularly in dyslexic readers of deep orthographies. Activation of right hemisphere regions has been associated with compensatory phenomena (Pugh et al., 2000; Rueckl et al., 2015; Shaywitz & Shaywitz, 2005; Waldie et al., 2013) and, in particular, inferior frontal regions have been associated with processes not necessarily related to reading (Paulesu et al., 2014), such as task demands (Cattinelli et al., 2013a). In sum, our data confirm the crucial role of the left posterior TP (STG and IPL), vOT (ITG, IOG, and FFG), and anterior circuit (IFG) in reading and their neurofunctional alterations in DD. However, it is worthy to note that a finer parcellation of both the posterior TP and OT cortices emerges when also the developmental and orthographic depth levels are considered.

5.2. THE DEVELOPMENTAL LEVEL

From the developmental perspective, an engagement of bilateral posterior occipital regions (left lingual gyrus, right IOG – OP28) was found in children, whereas adult readers showed a greater engagement of right inferior frontal regions and the left putamen. The overall pattern of findings may suggest a progression from the recruitment of more posterior visual areas in children (Church et al., 2008; Poldrack et al., 1998) - irrespective of orthography and group. This reflects an early visual analysis of the printed stimuli that would shift to a more anterior frontal recruitment with growth, line with the notion that cognitive development implies a progression from sensory-based processes to higher-level cognitive processes supported by a progressive fine-tuning of associative cortices (see Casey et al., 2005 for a review).

With this respect, the two models have competing predictions: the classic model predicts an early TP dysfunction in dyslexic readers followed by a late dysfunction of the vOT cortex (Pugh et al., 2000), whereas the new model predicts a vOT dysfunction from an early age on (Richlan, 2014).

Based on our results, an under-recruitment of adult dyslexics in shallow orthographies was found in both the left STG [OP42] and ITG (OP59; i.e., the anterior portion of the OT cortex), whereas dyslexic children under-recruitment emerged in the left FFG [OP16], specifically in readers of deep orthographies. These results may hint at the possibility that STG and ITG are increasingly recruited with age in reading and, as a consequence, dyslexic readers under-recruitment of these regions emerges only once they become skilled readers. However, this perspective is not well supported and by the literature (see, for example, Turkeltaub et al., 2003). Moreover, it is worth noting that this latter result may be influenced by the relatively low number of entries associated with explicit grapheme to phoneme conversion. Indeed, while lexical-based and phonological-based reading tasks were equally distributed in adults, data reported for children in both orthographies were associated with a lower proportion of phonological-based reading tasks (see Figure S3 in Supplementary Materials). Consequently, we cannot exclude that the recruitment of STG and ITG would be already detectable in childhood when a phonology-based strategy is explicitly required (e.g., low-frequency words and pseudowords reading).

Second, a primary dysfunction of the posterior vOT cortex (i.e., left FFG [OP16]) emerged, particularly when readers have to face a deeper orthography. Apparently, this pattern of results fits well with the predictions of the new model (Richlan, 2014), especially for what concerns the dual role of the vOT cortex in both phonological recoding and orthographic reading strategies; nonetheless, a word of caution is needed, as these developmental effects were only evident when the orthography was considered.

While the dysfunction of regions involved in grapheme-to-phoneme conversion (i.e., STG) is evident for shallow orthographies, an early deficit in the visual analysis of the stimulus (reflected by FFG under-recruitment) seems to affect children of deep orthographies to a greater extent. In other words, children cannot take advantage of the phonological mapping to achieve accurate word decoding due to the specific properties of their orthography. Indeed, the degree of transparency of the orthography, as argued by the orthographic depth hypothesis (Katz & Frost, 1992), forces the reader to rely on different strategies, particularly in the first stages of reading acquisition; accordingly, the grapheme-to-phoneme conversion strategy would be more suitable in shallow, rather than in deep orthographies (Ziegler & Goswami, 2006). Conversely, orthographic whole-word processing would represent a more suitable decoding strategy in deep orthographies, making the acquisition of reading in a deep orthography more challenging even in typical readers.

Crucially, another cluster of convergent under-recruitment common to both children and adult dyslexic readers across orthographies was observed in the left IOG [OP24]. The lack of both developmental and orthographic effects (as discussed in the previous section) is in line with the prediction of a primary and cross-linguistic deficit associated with the vOT cortex in the new model (Richlan, 2014), but only if it is considered a subtler parcellation of this circuitry. Moreover, this scenario supports the view of "*a primary left ventral OT dysfunction*" but does not provide evidence for the fact that it *"results in a secondary left STG dysfunction in dyslexia*" (Richlan, 2014, p. 8) as, through our meta-analytic method, it was not possible to test the developmental spreading of the neurofunctional deficit directly. Moreover, we cannot exclude that our IPL finding is sensitive to developmental and/or orthography-specific effects, since dyslexic under-recruitment of this region emerged in the phonological processing dataset, i.e., in the dataset whereby we could not test the developmental and orthographic effects (see the methods section).

Finally, concerning the anterior reading circuit, the classic model predicts dyslexic over-recruitment of the left IFG in adult readers, reflecting a greater reliance on articulatory processing that would increase with age (Pugh et al., 2000). Again, the developmental predictions of the classic model are not supported by the present findings: the only left IFG cluster [OP31] showing a group-effect in our meta-analysis was also modulated by orthographic depth (see the next paragraph for further details), being more specific for control readers in shallow orthographies; in any case, it was not modulated by age, as expected by Pugh et al. (2000).

5.3. THE ORTHOGRAPHIC DEPTH LEVEL

The converging point on the orthography-specific effects between the two models lies in the assumption that readers in shallow orthographies rely more on phonological conversion-based strategies, whereas those of deep orthographies are expected to rely more on whole-word orthographic processing. This effect is further modulated by task requirements, as adult readers in shallow orthographies may take advantage of visual strategies, particularly in some situations (e.g., during high-frequency word reding), while adult readers in deep orthographies would be less prone to adopt phonological conversion-based strategies unless explicitly required by the task, such as in low-frequency words and pseudowords reading.

It is worthy to recall that in the original paper by Pugh et al. (2000), the orthography-specific effects are not mentioned at all. Rather, Richlan (2014) attributed to the classic model some predictions about the neurofunctional effects of orthographic depth in the manifestation of DD. In particular, according to Richlan's (2014) interpretation of the classic model, proficient readers in shallow orthographies should exhibit higher activity of the TP cortex compared to readers in deep orthographies, as these latter are expected to rely less on phonological-based processes. Conversely, the vOT cortex would be predominantly engaged by non-impaired adult readers in deep orthographies, as they are more likely to rely on visual-orthographic strategies. Consequently, Richlan (2014) suggested that, according to the classic model, readers in shallow orthographies are expected to show as intermediate level of activity of the vOT cortex unless explicit orthographic processing is required. On the contrary, the new model assumes that this region's engagement would be expected regardless of age and orthography (Richlan, 2014). Further, according to the role attributed to the left IPL (i.e., serial attentional letter-to-letter shift) and left TP (i.e., grapheme-phoneme conversion) in the new and classic model, respectively, the orthography-specific predictions are the same. No orthography-specific effects are expected for the anterior reading circuit (left IFG, PreG) in either of the two models (Richlan, 2014).

Interestingly, our meta-analytic results challenge both models when considering the orthographic depth effects only, at least for what concerns the pool of European languages included in this meta-analysis. Readers of shallow orthographies activated more frequently anterior regions (i.e., bilateral dorsal and ventral IFG [OP30, OP31, OP45, OP22], right SMA [OP53]), whereas readers of deep orthographies are characterized by the more frequent activity of the left FFG [OP16] only. This result suggests that readers of shallow orthographies rely more on the anterior circuit (bilaterally), presumably reflecting orthography-specific demands on phono-articulatory processing. On the contrary, readers in deep orthographies would rely more on the posterior circuit (i.e., posterior part of the vOT cortex), probably reflecting a greater reliance on whole-word visual analysis (Danelli et al., 2015; Fiebach et al., 2002).

As already described, the left IOG [OP24], corresponding to the VWFA (see Table 4 for details), was found to be under-recruited in dyslexic readers irrespectively of age and orthography. This finding may suggest the existence of a cross-linguistic neurobiological deficit in DD, as already reported in a recent meta-analysis of neurofunctional abnormalities in DD across shallow and deep orthographies (Martin et al., 2016; Paulesu et al., 2014; Richlan, 2020) and in the seminal paper by Paulesu et al. (2001). Nonetheless, orthography strongly modulates the neural correlates of reading when also the developmental course of non-impaired and dyslexic readers is considered. Indeed, when also group and age are considered in interaction with orthography, predominant activity in adult controls of shallow orthographies was observed in the left STG [OP42], ITG (OP59; i.e., anterior part of the vOT cortex), and right IFG pars triangularis [OP45]. A more specific activation for children of deep orthographies was found in the left FFG [OP16], in line with the idea that early recruitment of lexical-orthographic processes represents the best strategy to achieve efficient and effortful decoding in deep orthographies. In our view, this result challenges the notion of a universal progression from phonology-based to orthography-based strategies during reading acquisition. In other words, in the future developmental reading models should better accommodate the orthographic depth level to fully describe reading acquisition across orthographies, as already suggested by Ziegler & Goswami (2005; 2006).

Concerning the left anterior reading circuit, we observed a cluster in the left IFG [OP31] showing a significant group-by-orthography interaction, being specific for readers of shallow compared to deep orthographies, but only when considering non-impaired readers. In other words, non-impaired readers of deep orthographies seem not to rely on IFG activity. This result is in line with the suggestion that the left IFG is sensitive to spelling-sound regularity/consistency of words (Pugh et al., 2000), particularly when there is a 1:1 grapheme to phoneme mapping. When considering the effect of age, a cluster located in the right IFGtri [OP22] displayed a significant group-by-age-by-orthography interaction, being more specific for non-impaired adult readers of shallow orthographies. The role of right brain regions in reading has always been somehow neglected. However, the centroid coordinates of this cluster (MNI: x = 36, y = 30, z = 3) in Neurosynth is often associated with "readers" (posterior probability = .77) and with "orthography" (posterior probability = .76), further suggesting that the activation of this region in reading task is unlikely to be a false positive finding. With this regard, a further inspection of the papers that contributed to the Neurosynth result suggests that this region is associated with reading fluency (Christodoulou et al., 2014) and with spelling-sound consistency (Malins et al., 2016), and that, therefore, may represent the neurofunctional counterpart of an efficiently developed reading system, at least in shallow orthographies.

5.4. A NEW ANATOMO-FUNCTIONAL DEVELOPMENTAL AND ORTHOGRAPHIC DEPTH MODEL OF DEVELOPMENTAL DYSLEXIA: THE ADOD MODEL

The results of the current meta-analysis, together with the integration with the classic and new model, allowed us to generate a refined neurocognitive model that merges both the strengths of the former models and the most replicated results in the available neuroimaging literature: the ADOD model (Figure 9). The ADOD model has been conceptualized based on the empirical evidence collected for the relatively small pool of European languages. Future studies should test whether its predictions and external validity can go beyond the border of this set of languages.

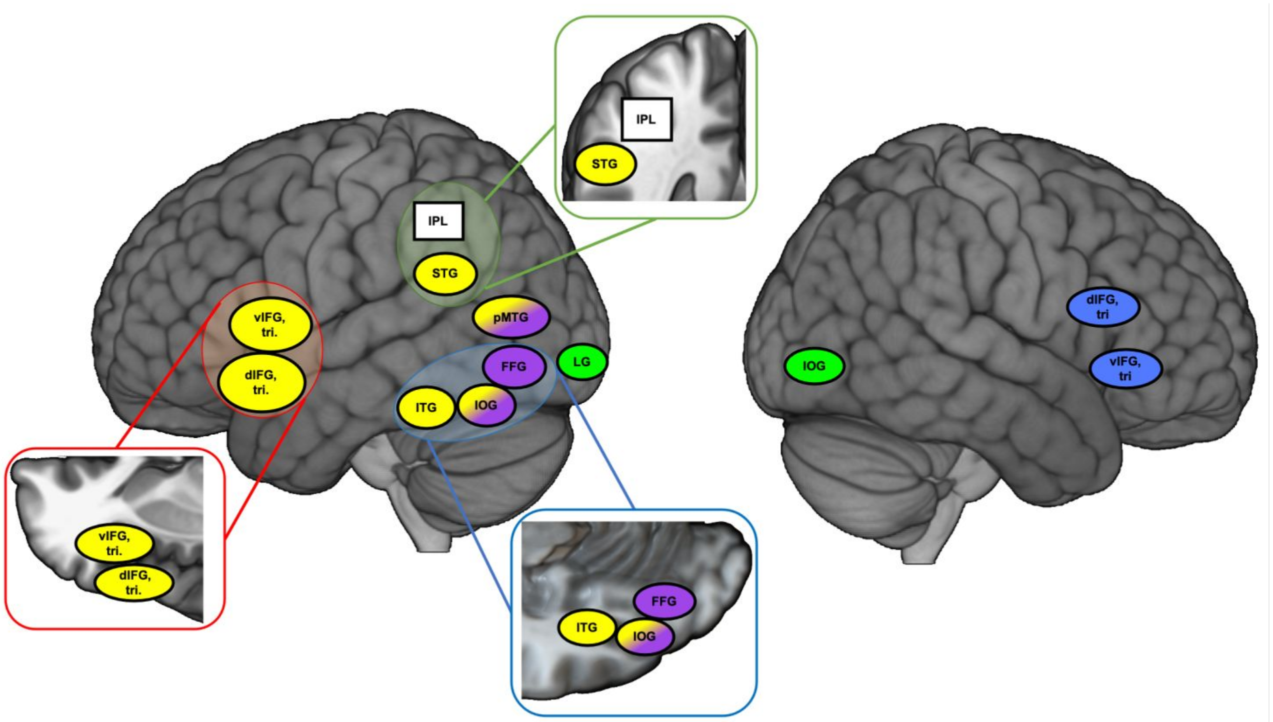

Figure 9 | The ADOD model of developmental dyslexia. Brain rendering displaying the three main reading circuits in the left hemisphere. The clusters falling within the three circuits mentioned by the main neurocognitive models of DD are grouped into color areas: the temporo-parietal circuit (green) - involved in phonological recoding and phonological processing; the occipito-temporal circuit (blue) – involved in both phonological recoding and lexical recognition; the anterior frontal circuit (red) – involved in the access to phonological output representations. All clusters in the figure represent dyslexic under-recruitment, except for the dIFG cluster [OP30] that displayed only an orthography-specific effect, and the right dIFG [OP45] that represent dyslexic over-recruitment. Each reading circuit can be further parcellated into different subregions based on the effects identified by the current meta-analysis (brain slices within the rectangular boxes). Clusters of the orthographic processing dataset are represented by ellipsoids, whereas the white square represents the cluster identified in the phonological processing dataset (SMA cluster PP36 not reported in the figure). Orthography-specific effects are represented as follows: yellow = shallow orthographies; violet = deep orthographies; yellow and violet = no orthography-specific effects; blue = adults (ventral and dorsal right IFG; Putamen cluster [OP44] is not reported in the figure); green = children (LG and IOG). The most important and novel feature of the ADOD model is the fine-grained parcellation of the ventral occipito-temporal cortex into three subregions: (i) the most anterior part (ITG), involved in visual-phonological processing, (ii) a posterior part (FFG), involved in visual-orthographic processing, and (iii) a middle part (IOG, VWFA – see section 5.1. in the discussion), representing a transition area involved in both visual-phonological and visual-orthographic processing. Note that clusters may show additional significant effects (e.g., main, interaction) not represented in the figure. See the main text for the full list of clusters and their significant effects dIFG, dorsal part of the inferior frontal gyrus; FFG, fusiform gyrus; IOG, inferior occipital gyrus; IPL, inferior parietal lobule; ITG, inferior temporal gyrus; STG, superior temporal gyrus; vIFG, ventral part of the inferior frontal gyrus.

The most important and novel feature of the ADOD model is a subtler anatomo-functional parcellation of the occipitotemporal cortex into three subdivisions that reflects a rostro-caudal gradient (Figure 9): anterior FFG (our ITG cluster [OP59]), middle FFG (our IOG cluster [OP24]), and posterior FFG [OP16]. In particular, we propose that the under-recruitment of the middle portion of the fusiform gyrus [OP24] in dyslexic readers represents the core neurobiological marker of this neurodevelopmental condition across age and orthographies in alphabetic systems. This region is part of the so-called visual word form area (VWFA) (Cohen et al., 2002; Cohen et al., 2004; Dehaene &

Cohen, 2011) and it may represent one of the earliest and most prominent neurofunctional markers of the processes involved in reading. In our model, the most anterior part of the FFG [OP59] is more prominently recruited by skilled readers of shallow orthographies (Martin et al., 2016), and thus it is proposed to underlie the explicit analysis of sub-lexical units (Danelli et al., 2017; Danelli et al., 2013; Danelli et al., 2015), that is optimized once become proficient readers. Conversely, the most posterior region of the left FFG [OP16] exhibits an orthography-specific effect in interaction with age: readers in deep orthographies engaged this region from early childhood, thus suggesting that the process supported is associated with a reading strategy more suitable for readers of deep orthographies since the very beginning of reading acquisition.

Concerning the temporoparietal cortex, the ADOD model proposes a brand-new conception of the role of left inferior parietal lobule [PP45] in reading: while no considerations can be put forward for age and orthographic depth, the engagement of this area in explicit phonological tasks highlights the need of taking phonologic-orthographic mapping in reading apart from phonological processing (e.g., phonological manipulation, rhyming). In other words, the results of our meta-analysis further suggest that DD is characterized by a dysfunction of the neural circuits underlying explicit phonological processing; this, in turn, supports the idea that phonological processing plays a crucial role in reading and some of the behavioural manifestations of DD (Brambati et al., 2006; Danelli et al., 2017; Maurer et al., 2011; Paulesu et al., 2001; Richlan et al., 2010; Schulz et al., 2008, 2009; Wimmer et al., 2010).

An additional region of the temporoparietal cortex, the posterior portion of the superior temporal gyrus (STG) [OP42], is mainly engaged by skilled adult readers of shallow orthographies, and it is thought to underlie phonology-based reading processes in the ADOD model (Figure 9). A deeper analysis of the left STG cluster composition (see Table S4 in the Supplementary Materials) suggested that, while adult readers of shallow orthographies engage this region predominantly when the reading task requires an explicit phonological recoding, children activate this area during orthographic processing, as it is the primary strategy available before acquiring reading proficiency (Ziegler & Goswami, 2006).

Finally, the recruitment of inferior frontal regions [OP30, OP31] in the ADOD model is strongly associated with reading in shallow orthographies and, in line with Richlan (2014), it may represent the neurofunctional correlate of the access to phonological output representations (Figure 9).

It is worth noting that our approach identified additional brain regions that showed either a significant main or an interaction effect, even if they lie outside the three main circuits described in the classic and new model. Nonetheless, these further regions represent the anatomo-functional convergence across different studies on the reading process, and thus should be integrated in a new revised model like the ADOD. We believe that the annexation of the following brain regions to our neurocognitive account of DD may prove beneficial to the literature: as the reader shall see below, while being reported in most of the meta-analyses of functional and structural neuroimaging studies cited in the present work (see, for example, Richlan et al., 2009, 2011, Paulesu et al., 2014), they are still underrepresented by the main neurocognitive theories of DD.

In particular, a cluster centred in the posterior left MTG [OP23] was more frequently engaged by control compared to dyslexic readers, regardless of age and orthographic depth. Posterior left MTG activation has been mainly associated with semantic processing during reading (Blumenfeld et al., 2006; Booth et al., 2006), and its involvement in normal reading, together with its under-recruitment in dyslexic readers, is a common finding in previous meta-analyses of neuroimaging studies (Paulesu et al., 2014; Jobard et al., 2003). Our result does not only align with previous meta-analytical literature for what concerns the left posterior MTG under-recruitment in DD, but it also suggests that engagement of this region is neither influenced by age-specific nor by orthography-specific effects. Indeed, both the left inferior occipitotemporal [OP24] and middle temporal [OP23] under-recruitment in dyslexic readers may be considered as a cross-linguistic neurofunctional marker of reading disability.

We also identified a cluster in the basal ganglia (putamen [OP44]) more frequently activated in adults than children and showing a significant three-way interaction effect. The role of the putamen - part of a circuit comprising the SMA, cingulate gyrus, insula - in language and reading is traditionally linked to articulatory-motor processing (Paulesu et al., 2014; Martin et al., 2015; Meschyan & Hernandez, 2006; Alario et al., 2006). Further, basal ganglia over-recruitment was consistently associated with dyslexic readers and interpreted as reflecting reliance on covert/overt articulatory processes (Richlan et al., 2009; 2011). Interestingly, the role of putamen in reading has been deeply analysed in the study by Oberhuber et al. (2013), in which the authors proposed a rostro-caudal functional subdivision of this region during reading. In particular, they showed that the anterior portion of the putamen is more active in pseudoword compared to word reading, whereas the posterior portion showed the opposite pattern (Oberhuber et al., 2013). Our cluster [OP44], lying in the anterior portion of the putamen, was more frequently engaged by adult control readers in shallow compared to deep orthographies, whereas dyslexic adult readers activated this region more frequently than children, regardless of orthography. Even if the spatial resolution of our clustering solution does not fully permit a fine-grained parcellation of small sub-cortical structures, this last result is in line with the view proposed by Oberhuber et al. (2013) and dovetails with the evidence that the putamen is one of the major structures involved in articulatory processing and, thus, phonological recoding (Meschyan & Hernandez, 2006; Oberhuber et al., 2013). Another interpretation of the basal ganglia role in DD was proposed by Ullman and Pierpont (2005) (see Ullman et al., 2020 for a review). The authors suggested that functional and structural basal ganglia abnormalities may be responsible for deficits in procedural memory and, consequently, for the lack of automatization of reading skills and other language-related disorders. Crucially, our finding is in contrast with those of previous studies and meta-analyses where more frequent activation in dyslexic readers in the basal ganglia was found (Paulesu et al., 2014, Richlan et al., 2009; Richlan, 2010). A more detailed analysis of the papers included in our meta-analysis, and in other studies, should help in clarifying this inconsistency.

By considering all these results and looking to orthographic-specific effects that characterized reading processing and its developmental trajectory, we can conclude that some different strategies are needed for the acquisition and automation of reading, based on orthographic depth.

Indeed, as supported by our results concerning STG and IFG, the access to phonological output representations is virtually needed during all reading tasks for readers of shallow orthographies, regardless of age. This result, together with the evidence of a prominent engagement of the left posterior FFG by readers of deep orthographies, suggests that reading is a linguistic process highly influenced by orthography. This implies the development of different cognitive and orthographic-specific strategies that, in turn, rely on different brain areas. At least for what concerns alphabetic orthographies, the influence of orthographic depth in characterizing different reading acquisition patterns and brain activation forces the researchers to evaluate the reading process in the light language and age, both in behavioural (Carioti et al. 2021) and neuroimaging studies. However, we acknowledge that considering age and orthographic depth as dichotomous limits the generalization of our results to age ranges and languages that lie in-between the two extreme poles. Further studies should address this limitation, overcoming this polarization and extending the neurocognitive bases of reading and DD to non-alphabetic writing systems.

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Conflict of interest

The authors report no conflict of interest.

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Table 1 | List of the studies included in the current meta-analysis. For each study, first author's name and year of publication, as well as the sample size, age of participants, orthography, imaging modality, sensory modality of presentation and the experimental paradigms included are reported. Paradigms included in the orthographic processing dataset are marked by *, whereas experimental studies included in the phonological processing dataset are marked by #. A description of the main reading processes required by the task are reported within squared brackets. C, controls; D, dyslexics; fMRI, functional magnetic resonance imaging; GPC, grapheme-phoneme conversion; MR, main effect of reading task in functional studies (word and pseudoword/non-word reading); OP, orthographic processing; PET, positron emission tomography.

Study	Sample size	Age of participants (average years)	Orthography	Imaging tecnique	Modality of stimulation	Experimental paradigm inlcuded in our meta-analysis
(Backes et al., 2002)	16 (8 C, 8 D)	Children (11.5)	German (shallow orthography)	fMRI	Visual	Semantic judgement* [OP] String comparison* [OP] Non word-rhyming#
(Booth et al., 2007)	26 (13 C, 13 D)	Children (10)	English (deep orthography)	fMRI	Visual	Semantic judgement* [OP]
(Boros et al., 2016)	33 (18 C, 15 D)	Children (11.5)	French (deep orthography)	fMRI	Visual	Pseudoword reading* [GPC]
(Cutting et al., 2013)	39 (19 C, 20 D)	Children (12)	English (deep orthography)	fMRI	Visual	Lexical decision task* [OP]
(Grande et al., 2011)	45 (25 C, 20 D)	Children (9.5)	German (shallow orthography)	fMRI	Visual	Low-frequency word reading* [GPC]

(Heim et al., 2015)	43 (10 C, 33 D)	Children (10)	German (shallow orthography)	fMRI	Visual	Reading (word and pseudoword reading)* [MR]
(Langer et al., 2015)	30 (15 C, 15 D)	Children (10)	English (deep orthography)	fMRI	Visual	Sentence reading (slow, medium, fast)* [OP] Letter reading (slow, medium, fast)* [GPC]
(Maurer et al., 2011)	27 (16 C, 11 D)	Children (11)	German (shallow orthography)	fMRI	Visual	Word recognition* [OP]
(Monzalvo et al., 2012)	46 (23 C, 23 D)	Children (10)	French (deep orthography)	fMRI	Visual	Implicit word reading* [OP]
(Morken et al., 2014)	29 (18 C, 11 D)	Children (11)	Norwegian (shallow orthography)	fMRI	Visual	Alphabetic processing* [GPC] Orthographic processing* [OP] Sentence processing* [OP]

(Olulade et al., 2015)	28 (12 C, 16 D)	Children (10)	English (deep orthography)	fMRI	Visual	Implicit word reading* [OP]
(Schulz et al., 2008)	34 (22 C, 12 D)	Children (11.5)	German (shallow orthography)	fMRI	Visual	Semantic judgement* [OP]
(Schulz et al., 2009)	30 (15 AMC, 15 D)	Children (11)	German (shallow orthography)	fMRI	Visual	Semantic judgement* [OP]
(Brambati et al., 2006)	24 (11 C, 13 D)	Adults (33)	Italian (shallow orthography)	fMRI	Visual	Word reading* [OP] Non-word reading* [GPC] Reading (word and non-word reading)* [MR]
(Brunswick et al., 1999)	12 (6 C, 6 D)	Adults (23)	English (deep orthography)	PET (H2-15O)	Visual	Reading aloud (word and pseudoword reading)* [MR] Implicit reading (word and pseudoword reading)* [MR]
(Christodoulou et al., 2014)	24 (12 C, 12 D)	Adults (22.5)	English (deep orthography)	fMRI	Visual	Semantic judgement (fast, medium, slow)* [OP]
(Danelli et al., 2017)	43 (23 C, 20 D)	Adults (21)	Italian (shallow orthography)	fMRI	Visual Auditory	Pseudoword reading* [GPC] Rhyming (letters)#

(McCrory et al., 2005)	18 (10 C, 8 D)	Adults (20)	English (deep orthography)	PET (H2-15O)	Visual	Word reading* [OP]
(Richlan et al., 2010)	33 (18 C, 15 D)	Adults (18)	German (shallow orthography)	fMRI	Visual	Lexical decision task (pseudoword)* [GPC] Lexical decision task (word)* [OP]
(Rumsey et al., 1997)	31 (14 C, 17 D)	Adults (27)	English (deep orthography)	PET (H2-15O)	Visual	Reading aloud (low-frequency words)* [GPC] Reading aloud (non-words)* [GPC]
(Wimmer et al., 2010)	39 (19 C, 20 D)	Adults (20)	German (shallow orthography)	fMRI	Visual	Lexical decision task (non-words)* [GPC] Lexical decision task (pseudo-homophones)* [OP]
(Cao et al., 2006)	28 (14 C, 14 D)	Children (11)	English (deep orthography)	fMRI	Visual	Word rhyming (conflicting, non conflicting trials)#
(Farris et al., 2016)	31 (16 C, 15 D)	Children (9)	English (deep orthography)	fMRI	Visual	Object rhyming#
(Heim et al., 2010)	36 (20 C, 16 D)	Children (9.5)	German (shallow orthography)	fMRI	Auditory	Phoneme discrimination#

(Hoeft et al., 2006)	20 (10 AMC, 10 D)	Children (10)	English (deep orthography)	fMRI	Visual	Word rhyming#
(Kovelman et al., 2012)	24 (12 C, 12 D)	Children (9)	English (deep orthography)	fMRI	Auditory	Word rhyming#
(Conway et al., 2008)	22 (11 C, 11 D)	Adults (35)	English (deep orthography)	fMRI	Auditory	Pseudo-word segmentation#
(Eden et al., 2004)	38 (19 C, 19 D)	Adults (40)	English (deep orthography)	fMRI	Auditory	Phoneme deletion#
(Hernandez et al., 2013)	31 (16 C, 15 D)	Adults (21)	French (deep orthography)	fMRI	Visual	Word rhyming#
(MacSweeney et al., 2009)	14 (7 C, 7 D)	Adults (24)	English (deep orthography)	fMRI	Visual	Picture rhyming#
(Olulade et al., 2012)	15 (9 C, 6 D)	Adults (20)	English (deep orthography)	fMRI	Visual	Word rhyming# Non-word rhyming#

(Paulesu et al., 1996)	10 (5 C, 5 D)	Adults (25)	English (deep orthography)	PET (H2-15O)	Visual	Letter rhyming# Phonological short-term memory#
(Pecini et al., 2011)	26 (13 C, 13 D)	Adults (24)	Italian (shallow orthography)	fMRI	Visual	Rhyme generation#
(Vasic et al., 2008)	25 (13 C, 12 D)	Adults (18)	German (shallow orthography)	fMRI	Visual	Phonological short-term memory#

Table 2 | Results of the cluster composition analysis for the orthographic processing (OP) dataset. For each cluster, the ID number, the anatomical labeling according to the AAL (Brodmann area, BA), the centroid coordinates (and standard deviations) in MNI space, number of foci and of the contributing studies are reported. The p-values of the binomial tests for the effect of group (GR), age (A), and orthography (O) are also reported, along with the respective two and three-way interactions. Clusters showing at least a significant simple effect or a simple *and* interaction effect are reported in bold. Trends towards significance are marked by #.

Ad., adults; C, controls; Ch., children; D, dyslexics; De., deep; Sh., shallow.

		Left hemisphere			**Right hemisphere**					**Group (GR) effects**		**Age (A) effects**		**Orthography (O) effects**		**Interactions**			
Cluster ID	**Centroid label (BA)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**# of foci**	**# of contributing studies**	**C**	**D**	**Ch.**	**Ad.**	**Sh.**	**De.**	**GR x A**	**GR x O**	**A x O**	**GR x A x O**
OP56	Inferior frontal gyrus, pars opercularis (48)	-48 (7)	16 (6)	21 (7)				34	14	.345	.779	.465	.671	.13	.929	1	.468	.285	**.002**
OP45	**Inferior frontal gyrus, pars triangularis (48)**				46 (6)	19 (7)	22 (4)	18	5	.982	*.052#*	1	**.003**	**.032**	.991	1	.313	1	.886
OP31	**Inferior frontal gyrus, pars triangularis (47)**	-36 (7)	29 (8)	3 (8)				17	8	.806	.357	.795	.381	**.004**	.999	.122	*.051#*	1	.868
OP22	**Inferior frontal gyrus, pars triangularis (47)**				36 (5)	30 (5)	3 (7)	18	5	.088	.973	1	**.003**	**.032**	.991	1	.171	.359	**.000**
OP30	**Inferior frontal gyrus, pars triangularis (45)**	-49 (3)	18 (6)	-2 (6)				22	8	.181	.918	.572	.602	**.000**	1	.569	.557	.564	.232

OP53	**Supplementary motor area (6)**				2 (7)	8 (5)	62 (5)	23	10	.765	.385	.171	.914	**.001**	1	.674	.128	.285	.194
OP14	Supplementary motor area (32)	-1 (5)	15 (5)	46 (4)				25	10	.949	.11	.934	.144	.567	.591	.141	**.047**	.659	.686
OP42	**Superior temporal gyrus (48)**	-56 (5)	-42 (7)	24 (8)				20	6	*.051#*	.986	.626	.558	.334	.809	.117	.565	.35	**.022**
OP23	**Middle temporal gyrus (37)**	-51 (6)	-63 (4)	7 (7)				8	5	**.035**	1	.319	.88	.315	.883	1	1	.502	.641
OP61	Middle temporal gyrus (22)	-54 (6)	-43 (6)	4 (4)				23	13	.064	.979	.299	.829	.577	.588	.558	.59	.412	**.046**
OP59	**Inferior temporal gyrus (20)**	-43 (5)	-46 (7)	-17 (5)				37	14	**.000**	1	.911	.162	.175	.897	.158	1	.265	**.000**
OP16	**Fusiform gyrus (19)**	-32 (5)	-69 (5)	-14 (6)				21	8	.855	.27	.095	.96	.993	**.022**	.386	1	.324	**.013**
OP24	**Inferior occipital gyrus (37)**	-47 (6)	-63 (7)	-13 (5)				19	9	**.000**	1	.739	.439	.601	.58	1	1	1	.512
OP28	**Inferior occipital gyrus (19)**				38 (7)	-85 (9)	-4 (5)	13	7	.735	.477	*.056#*	.984	.236	.899	1	.565	.6	.296

OP17	**Lingual gyrus (18)**	-29 (4)	-87 (3)	-17 (3)	9	5	.13	.977	**.014**	.998	.699	.556	1	.445	1	.876
OP44	**Putamen**	-27 (9)	13 (6)	1 (4)	19	6	.923	.167	1	**.002**	.255	.868	1	.369	1	**.02**

Table 3 | Results of the cluster composition analysis for the phonological processing (PP) dataset. For each cluster, the ID number, the anatomical labeling according to the AAL (Brodmann area, BA), the centroid coordinates (and standard deviations) in MNI space, number of foci and of the contributing studies are reported. The p-values of the binomial test for the effect of group (GR) are also reported. The effect of age, orthography, along with the respective two and three-way interactions were not tested (see the methods section for further details). Clusters showing at least a significant simple effect, or a simple *and* interaction effect are reported in bold. Trends towards significance are marked by #.
C, controls; D, dyslexics.

		Left hemisphere			**Right hemisphere**					**Group (GR) effects**	
Cluster ID	**Centroid label (BA)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**# of foci**	**# of contributing studies**	**C**	**D**
PP36	**Supplementary motor area (6)**	-2 (7)	8 (7)	58 (5)				10	5	*.055#*	.989
PP45	**Inferior parietal lobule (40)**	-41 (7)	-44 (7)	40 (6)				13	8	**.046**	.989

Table 4 | Comparison between the original coordinates of the putative VWFA and the coordinates extracted by our previous experiments and meta-analyses with the hierarchical clustering algorithm implemented. *, coordinates were transformed by means of the Brett's algorithm implemented in the GingerALE software.

Author and year (Table from which the coordinates were extracted)	**Article type**	**Talairach coordinates**			**MNI coordinates**			**Additional notes**
		X	**Y**	**Z**	**X (SD)**	**Y (SD)**	**Z (SD)**	
Cohen et al. 2000 (Table 2, average of five controls)	Experimental	-43	-54	-12	*-42.57*	*-52.9*	*-7.8**	*Original location of the VWFA*
Cohen et al. 2002 (Table 1)	Experimental	-39	-57	-9	*-38.61*	*-55.66*	*-5.16**	*Original location of the VWFA*
Danelli et al. 2013 (Table 5)	Experimental	-	-	-	-40	-56	-16	*Healthy controls*
Danelli et al. 2013 (Table 5)	Experimental	-	-	-	-40	-58	-12	*Healthy controls*
Danelli et al. 2015 (Table 1)	Experimental	-	-	-	-38	-44	-20	*Healthy controls*
Danelli et al. 2015 (Table 1)	Experimental	-	-	-	-38	-48	-18	*Healthy controls*
Danelli et al. 2017 (Table 4c)	Experimental	-	-	-	-34	-46	-22	*Under-recruitment of dyslexic readers*
Danelli et al. 2017 (Table 4c)	Experimental	-	-	-	-40	-50	-20	*Under-recruitment of dyslexic readers*
Cattinelli et al. 2013a (Table 3)	Meta-analysis	-	-	-	-28 (6)	-39 (6)	-12 (6)	*Meta-analysis using the hierarchical clustering method implemented in CluB*
Cattinelli et al. 2013a (Table 4)	Meta-analysis	-	-	-	-36 (4)	-80 (4)	-12 (4)	*Meta-analysis using the hierarchical clustering method implemented in CluB*
Paulesu et al. 2014 (Table 2)	Meta-analysis	-	-	-	-41 (3)	-60 (3)	-18 (4)	*Meta-analysis using the hierarchical*

								clustering method implemented in CluB
Current study (Table 2)	Meta-analysis	-	-	-	-47 (6)	-63 (7)	-13 (5)	*Meta-analysis using the hierarchical clustering method implemented in CluB*

A meta-analysis of functional neuroimaging studies on developmental dyslexia across European orthographies: the ADC model

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Supplementary Materials

1. Supplementary tables

2. Supplementary figures

1. Supplementary tables

1.1. Table S1

Table S1 | Clusters of the orthographic processing (OP) dataset that overlapped with the ALE map. For each cluster, the ID number, the anatomical labeling according to the AAL (Brodmann area, BA), the centroid coordinates (and standard deviations) in MNI space, number of foci and of the contributing studies are reported.

		Left hemisphere			**Right hemisphere**				
Cluster ID	**Centroid label (BA)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**# of foci**	**# of contributing studies**
OP56	Inferior frontal gyrus, pars opercularis	-48 (7)	16 (6)	21 (7)				34	14
OP31	Inferior frontal gyrus, pars triangularis (47)	-36 (7)	29 (8)	3 (8)				17	8
OP22	Inferior frontal gyrus, pars triangularis (47)				36 (5)	30 (5)	3 (7)	18	5
OP45	Inferior frontal gyrus, pars triangularis (47)				46 (6)	19 (7)	22 (4)	18	5
OP30	Inferior frontal gyrus, pars triangularis (45)	-49 (3)	18 (6)	-2 (6)				22	8
OP14	Supplementary motor area (32)	-1 (5)	15 (5)	46 (4)				25	10
OP53	Supplementary motor area (6)				2 (7)	8 (5)	62 (5)	23	10

OP46	Precentral gyrus (6)				43 (7)	6 (7)	37 (8)	19	7
OP55	Precentral gyrus (6)	-46 (5)	3 (5)	38 (7)				17	10
OP21	Insula (47)				39 (7)	19 (4)	-9 (6)	16	6
OP42	Superior temporal gyrus (42)	-56 (5)	-42 (7)	24 (8)				20	6
OP23	Middle temporal gyrus (37)	-51 (6)	-63 (4)	7 (7)				8	5
OP61	Middle temporal gyrus (22)	-54 (6)	-43 (6)	4 (4)				23	13
OP59	Inferior temporal gyrus (20)	-43 (5)	-46 (7)	-17 (5)				37	14
OP16	Fusiform gyrus (19)	-32 (5)	-69 (5)	-14 (6)				21	8
OP24	Inferior occipital gyrus (37)	-47 (6)	-63 (7)	-13 (5)				19	9
OP28	Inferior occipital gyrus (19)				38 (7)	-85 (9)	-4 (5)	13	7
OP17	Lingual gyrus (18)	-29 (4)	-87 (3)	-17 (3)				9	5
OP44	Putamen	-27 (9)	13 (6)	1 (4)				19	6

1.2. Table S2

Table S2 | Clusters of the phonological processing (PP) dataset that overlapped with the ALE map. For each cluster, the ID number, the anatomical labelling according to the AAL (Brodmann Area, BA), the centroid coordinates (and standard deviations) in MNI space, number of foci and of the contributing studies are reported.

		Left hemisphere			Right hemisphere				
Cluster ID	**Centroid label (BA)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**X (SD)**	**Y (SD)**	**Z (SD)**	**# of foci**	**# of contributing studies**
PP37	Superior medial frontal gyrus (32)	-1 (9)	23 (6)	44 (7)				19	9
PP42	Inferior frontal gyrus, pars triangularis (48)	-44 (5)	16 (6)	27 (5)				17	10
PP38	Inferior frontal gyrus, pars triangularis (45)	-41 (7)	37 (9)	15 (6)				8	5
PP19	Inferior frontal gyrus, pars triangularis (45)	-49 (6)	18 (5)	0 (8)				8	5
PP36	Supplementary motor area (6)	-2 (7)	8 (7)	58 (5)				10	5
PP3	Precentral gyrus (6)	-47 (4)	-3 (7)	50 (5)				7	4
PP4	Precentral gyrus (6)	-43 (10)	3 (4)	36 (4)				12	8
PP10	Insula (47)	-32 (7)	24 (7)	2 (5)				12	5
PP20	Rolandic operculum (6)	-48 (9)	5 (5)	15 (3)				10	5
PP32	Superior parietal lobule (7)	-31 (6)	-61 (11)	56 (7)				8	6
PP45	Inferior parietal lobule (40)	-41 (7)	-44 (7)	40 (6)				13	8
PP31	Superior occipital gyrus (19)	-22 (5)	-78 (8)	40 (6)				7	4

1.3. Table S3

Table S3 | List of terms identified through the decoder function of Neurosynth. Results obtained by loading into Neurosynth the GingerALE map of the orthographic processing (A) and phonological processing (B) datasets. Numeric values represent Pearson's correlation coefficient (i.e., the magnitude of correlation between the Neurosynth map generated for the specific term and the ALE input image).

A) Orthographic dataset

Term	Correlation
reading*	0.488
orthographic*	0.471
word*	0.468
visual word*	0.440
words*	0.436
word form*	0.428
readers*	0.404
phonological*	0.403
written*	0.367
form*	0.361
lexical*	0.355
language*	0.338
chinese*	0.333
inferior	0.320
characters*	0.318
inferior frontal	0.314
english*	0.314
semantic*	0.312
temporal cortex	0.305
languages*	0.296
occipito temporal	0.296
fusiform gyrus	0.295
letter*	0.293
verb*	0.275
occipitotemporal cortex	0.275
word recognition*	0.274
bilinguals*	0.273
occipito	0.272
occipitotemporal	0.270

B) Phonological processing dataset

Term	Correlation
frontal	0.393
demands*	0.374
verbal*	0.374
word*	0.349
inferior	0.344
phonological*	0.335
inferior frontal	0.334
task*	0.305
ba 44	0.301
languages*	0.301
frontal gyrus	0.300
language*	0.300
judgment*	0.298
tasks*	0.285
lexical*	0.283
verb*	0.278
broca	0.272
ba	0.267
working memory*	0.262
semantic*	0.260
working*	0.260
words*	0.258
english*	0.256
reading*	0.253
ifg	0.251
semantically*	0.244
pre supplementary	0.230
gyrus ifg	0.221
pre sma	0.216

frontal	0.268
fusiform	0.268
pre sma	0.240
pseudowords*	0.240
demands*	0.233
broca	0.229
recognition*	0.227
verbal*	0.223
pre supplementary*	0.220
verbs*	0.215
fusiform gyri*	0.214
linguistic*	0.213
frontal gyrus*	0.211
syntactic*	0.211
read*	0.210
speakers*	0.209
decision task*	0.206
sentences*	0.197
task*	0.197
sentence*	0.196
inferior temporal*	0.194

difficulty*	0.216
orthographic*	0.211
bilinguals*	0.210
syntactic*	0.199
performance*	0.191
fluency*	0.189
memory*	0.187
linguistic*	0.186
stroop*	0.186
load*	0.181
asd*	0.177
speakers*	0.173
verbs*	0.171
chinese*	0.170
sentence comprehension*	0.168
task difficulty	0.166
motor pre	0.165
sentence*	0.165
memory wm*	0.163
conflict*	0.163
interference*	0.163

**Non-anatomical terms included in the Figure S2, panel B.*

1.4. Table S4

Table S4 | Task composition of the left STG cluster [OP42]. Raw number of foci coming from contrasts associated with grapheme-phoneme conversion strategies (GPC; low-frequency word reading, pseudoword reading, nonword reading), orthographic whole-word processing (OP; sentence judgement, sentence reading, word reading and recognition, lexical decision), and main effect of reading task in functional studies (MR; word and pseudoword or nonword reading) for control and dyslexic readers.

	Control readers					**Dyslexic readers**				
	Children		**Adults**			**Children**		**Adults**		
	Shallow	**Deep**	**Shallow**	**Deep**	*Total*	**Shallow**	**Deep**	**Shallow**	**Deep**	*Total*
GPC	0	0	5	2	7	0	0	0	0	0
OP	2	3	0	2	7	0	2	0	1	3
MR	0	0	3	0	3	0	0	0	0	0
Total	2	3	8	4	17	0	2	0	1	3

2. Supplementary figures

2.1. Figure S1

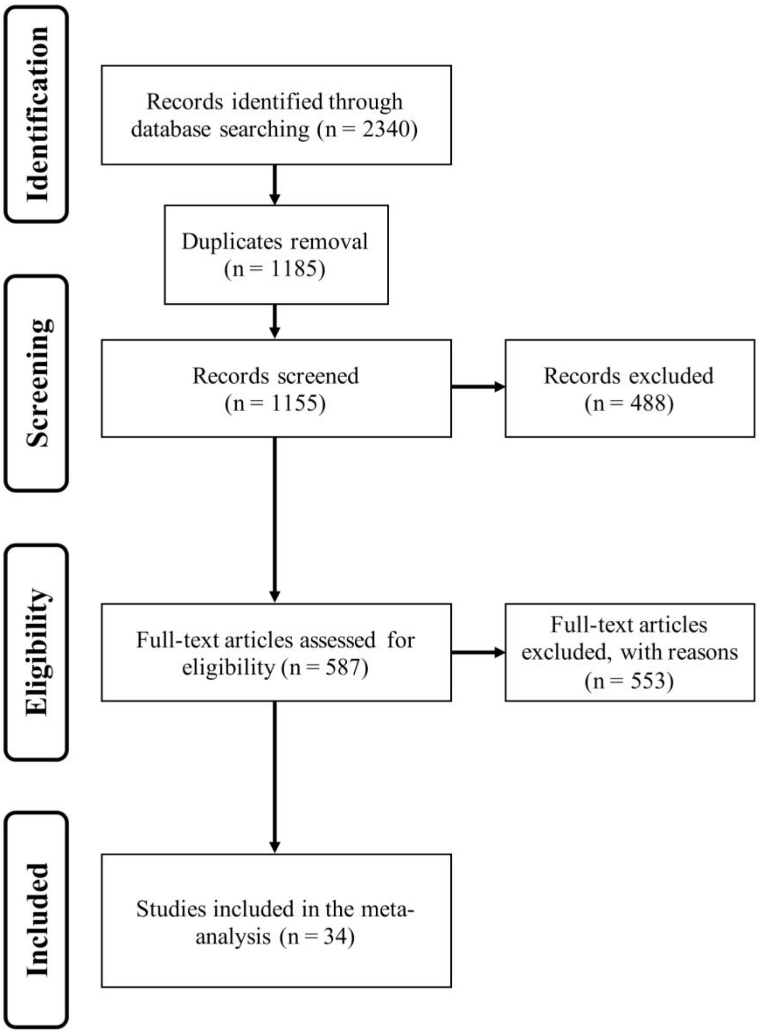

Figure S1 | Flowchart of the study identification and selection process.

2.2. Figure S2

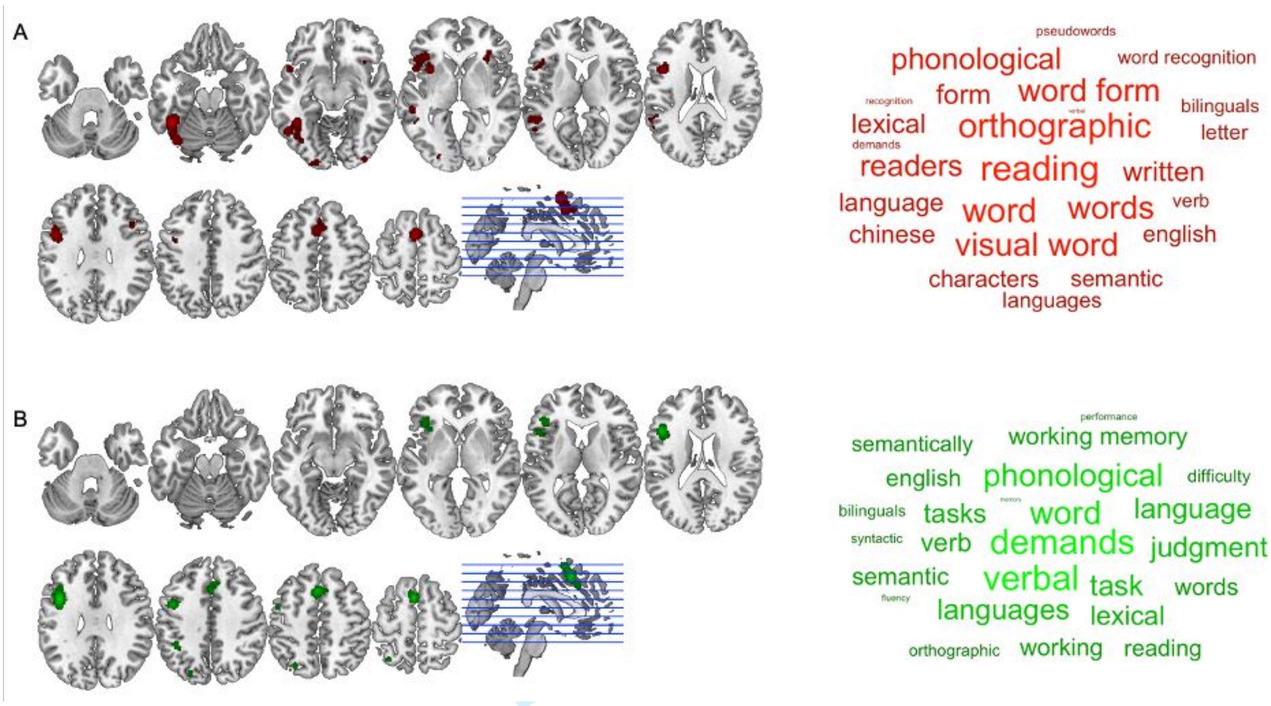

Figure S2 | Results of the ALE meta-analyses and cognitive decoding through Neurosynth. Panel A. Results of the orthographic processing dataset. **Panel B.** Results of the phonological processing dataset.

2.3. Figure S3

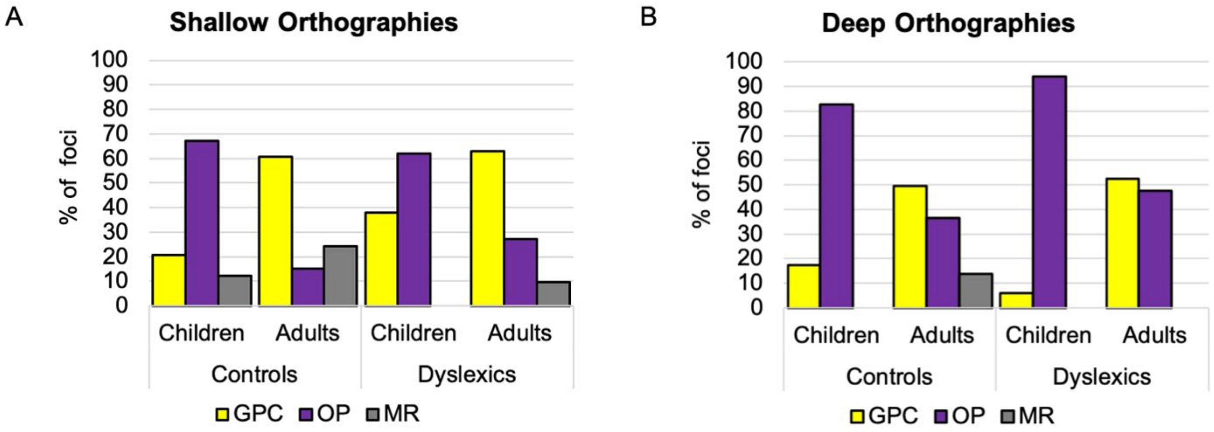

Figure S3 | Proportion of task type in the orthographic dataset. Panel A. Proportion of activation foci coming from contrasts associated with grapheme-phoneme conversion strategies (GPC; low-frequency word reading, pseudoword reading, nonword reading), orthographic whole-word processing (OP; sentence judgement, sentence reading, word reading and recognition, lexical decision), and main effect of reading task in functional studies (MR; word and pseudoword or nonword reading) in shallow orthographies. **Panel B.** Proportion of activation foci coming from contrasts associated with GPC, OP, and MR in deep orthographies. The proportion of foci belonging to each category of task was computed within age groups separately for visualization purposes.