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Exploring the neurofunctional underpinnings of dyslexia: A review focusing on dyslexic children

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ABSTRACT Dyslexia is a hereditary impairment characterized by effortful and slow reading acquisition that is often accompanied by severe difficulties in writing and spelling. Inconsistencies regarding the definition and assessment of dyslexia have led to considerable variation in prevalence rates and gender-ratios. However, it is agreed upon that dyslexia affects between 3 and 17% of school-aged children who mostly display deficits in pre-literacy skills already at pre-school age. Since neuroimaging provides a unique opportunity to shed light on potential anomalies in neural functioning underlying this impairment, reviewing the most recent results of fMRI studies of affected children can help us better understand this impairment. The present chapter provides a review of 24 functional magnetic resonance imaging (fMRI) studies (conducted between 2000 and 2016) investigating reading-related processing in children diagnosed with dyslexia (age: 8–15 years). The results suggest a clear underactivation in almost all areas designated as core reading areas (left-hemispheric occipito-temporal, temporo-parietal and frontal circuits) during orthographic, phonological and auditory tasks. Different and reduced patterns of activation were also found in the inferior frontal cortex, with a peak in the inferior frontal gyrus. Moreover, numerous studies reported a large network of compensatory activation in right-hemispheric and bilateral reading-related areas in dyslexic children, which was particularly active in more demanding tasks (e.g., rhyming of words and non-words). These findings support the hypothesis that children with dyslexia often also display deficits in auditory comprehension of speech input and generally struggle with the processing of phonological properties of words and non-words as well as simpler units like letters and symbols.

KEYWORDS auditory processing, developmental dyslexia, dyslexic children, fMRI, phonological processing, reading circuits

1 INTRODUCTION

Becoming literate is a crucial milestone in every child's life. It opens doors to education, employment, career, social contacts and possibly even adult well-being (Snowling & Hume, 2012). However, not every child manages to master this task. Numerous children face severe difficulties in literacy acquisition and consequently fail to develop age-appropriate reading skills for no obvious reason. Many of these children suffer from a disorder termed *developmental dyslexia* (henceforth *dyslexia*).

Even though dyslexia has been explored in much depth in the past decades, the neural underpinnings of this impairment remain largely unknown to date. Moreover, a considerable number of studies, but very few of the meta-analyses and reviews about dyslexia so far, have explicitly addressed reading processing in children with a diagnosis of dyslexia. Therefore, the following chapter reviews the most recent results on deficient reading processing in children with dyslexia, aged 8–15 years. First, a basic understanding of the symptoms, causes and the prevalence of this impairment will be given. Second, we will have a closer look at reading processing more generally in order to understand possible differences in brain activation in dyslexic individuals in contrast to non-impaired readers. Before analyzing the selected studies, the findings of other meta-analyses that primarily investigated adults and teenagers suffering from dyslexia will briefly be discussed. Finally, the findings of 24 functional magnetic resonance imaging (fMRI) studies conducted between

2000 and 2016 investigating children with dyslexia will be summarized and interpreted accordingly.

1.1 Developmental dyslexia

Dyslexia is a specific reading disorder marked by substantial deficits in reading achievement below the expected level given a child's chronological age (World Health Organization, 2015). It also usually affects spelling and writing in spite of normal intelligence and educational opportunity (Bishop & Snowling, 2004; Snowling & Göbel, 2010). Dyslexia is said to affect about 5–10% of the population (Landerl, Fussenegger, Moll, & Willburger, 2009; Siegel, 2006), but numbers ranging from 2.28%-3.9% (Miles, Haslum, & Wheeler, 1998; Sun et al., 2013) to 7.49% (Jepkoech, Mathai, & Kumar, 2015) and even 17–20% (as mentioned in Ozernov-Palchik & Gaab, 2016) have been reported. Prevalence rates vary mostly due to inconsistencies in assessing and defining dyslexia and differences due to the language and writing system being acquired. In addition, gender-ratio remains a highly debated issue. Studies with dyslexic children have reported gender ratios between 2:1 and 15:1, with girls usually being less frequently diagnosed and less severely affected (Hawke, Wadsworth, Olson, & Defries, 2007; Miles et al., 1998; Shaywitz, Shaywitz, Fletcher, & Escobar, 1990; Sun et al., 2013).

Even if prevalence rates vary and the gender-ratio is debatable, there is clear indication for the heredity of dyslexia because family history is considered the strongest risk factor. Research has shown that 68% of identical twins and 40–60% of children with one parent suffering from dyslexia are affected (Fisher & Francks, 2006; Francks, MacPhie, & Monaco, 2002). However, it seems that the interplay of various genes is responsible for the development of this impairment and the search for a specific causative agent is therefore extremely challenging (for a summary see Mascheretti et al., 2017). Recently, for instance, phonological deficits in dyslexics were linked to genetic anomalies of the temporal lobe (Giraud & Ramus, 2013), but more research is needed to confirm this finding. Regarding behavioral deficits, pre-literacy skills (skills at the intersection of phonology and written language) remain the most robust predictor among kindergarten children, including *letter-sound knowledge*, *phonological awareness* (awareness of the sound structure of syllables, words and sentences) and *rapid automatized naming* (rapid naming of words) (Landerl et al., 2009; Landerl & Wimmer, 2008; Olzernov-Palchik & Gaab, 2016).

Theories concerning the origin of dyslexia are diverse and still hotly debated (Goswami, 2015) and despite the contributions of neuroimaging methods to this debate, no simple common ground can be found so far (Ziegler, 2006). While earlier studies considered a visual processing deficit, it is now mainly believed that dyslexics have incomplete or deficient representation, storage and retrieval of phonological input, which leads to faulty *grapheme-phoneme correspondences* (Ramus et al., 2003). However, this so-called *phonological awareness theory* cannot account for the variety of sensory deficits (e.g., visual, auditory, motor skills) frequently observed in dyslexics (Eden & Zeffiro, 1998; Goswami, 2015). A comprehensive review by Hämäläinen, Salminen and Leppänen (2013), for instance, has even revealed that up to half of all children diagnosed with dyslexia display major auditory deficits. Moreover, since not all children display the same visual, auditory or phonological deficits, there has been discussion as to whether dyslexia could be present in a variety of subtypes or should generally be considered a multi-deficit disorder (Fostick & Revah, 2018).

1.2 Reading and the brain

Learning to read fluently is a long and complex process that requires a highly organized brain system specialized for the integration of the four subcomponents related to reading: pre-lexical, phonological, orthographic and lexico-semantic processing[1] (Liebig et al., 2017; Sandak, Mencl, Frost, & Pugh, 2004). Furthermore, metacognitive resources, instructional factors and individual differences, such as motivation, practice and experience, also heavily influence literacy acquisition (Snowling & Göbel, 2010).

1 The four subcomponents of reading designate the basic processes taking place when an individual is reading. While pre-lexical refers to the processing of units smaller than words, lexico-semantic processing refers to the stage at which whole words are processed and their semantic information is retrieved automatically (Sandak et al., 2004).

According to the classical neurological model of reading (Pugh et al., 2001), the highly intertwined reading network comprises three core areas: (1) a left dorsal temporo-parietal network [including superior temporal areas and the inferior parietal lobule (IPL)], (2) a left ventral occipito-temporal network [involving extrastriate cortex, fusiform gyrus (FG), inferior temporal areas and the visual word form area (VWFA)] and (3) a left inferior circuit [inferior frontal gyrus (IFG) and precentral gyri (PrCG)]. The first area is believed to be involved in phonology-based reading (grapheme-phoneme conversion, phonological assembly), whereas the second plays an essential role in visual-orthographic word recognition. The third circuit in the frontal lobe is linked to speech-gestural articulatory recoding of written words (Liebig et al., 2017; Martin et al., 2015; Pugh et al., 2001).

Liebig et al. (2017) state that it has often been assumed that each basic subcomponent of reading can be linked to one specific neural network. Identifying letters, for instance, is primarily linked to the occipital cortex (more specifically to the VWFA), while whole words would be more likely to be computed in the ventral stream only [inferior temporal gyrus (ITG), middle temporal gyrus (MTG) and IFG]. When dyslexic children have difficulties with literacy acquisition, they would possibly rely more on the dorsal stream [superior temporal gyrus (STG) and parietal cortex], since grapheme-to-phoneme conversion and phonological analysis are performed therein. Adding difficulty to this process, both routes (ventral and dorsal) rely on the IFG and the insula, which are thought to be of great importance for the integration of information and adding semantic knowledge to what has been read (Binder, Desai, Graves, & Conant, 2009) as well as for processing and making decisions. In other words, even though one or the other processing stage might be more linked to one network or circuit, they cannot function properly without one another. Furthermore, it has only partly been revealed what happens when specific parts are deficient and have to be compensated for and how this affects later processing stages.

Although studies have provided evidence that these core circuits are already spatially restricted and lateralized in children, e.g., during single-word reading (Brem et al., 2010; Church, Coalson, Lugar, Petersen, & Schlaggar, 2008), age-related changes have only been marginally addressed so far. A decreased reliance on phonological mechanisms com-

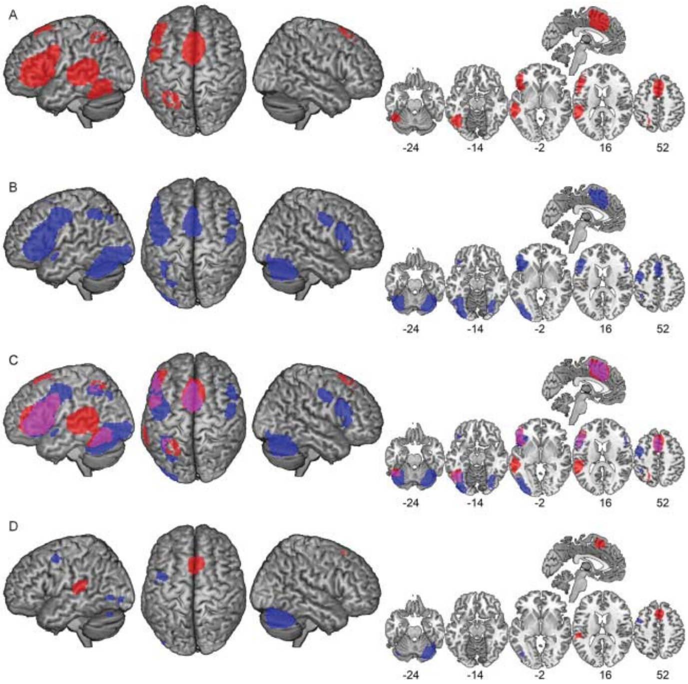

Figure 1. A comparison of brain activation in two age groups in 40 fMRI studies during reading-related tasks. (A) Brain activation in children (7–12 years) in red. (B) Brain activation in adults in blue. (C) Overlapping activation between both age groups shown in pink. (D) Direct comparison between adults and children (Martin et al., 2015, p. 1970).

bined with an increased reliance on visual mechanisms could be one age-related change from child- to adulthood (Church et al., 2008; Pugh et al., 2001). A meta-analysis by Martin, Schurz, Kronbichler and Richlan (2015) has also found differences between reading processing in adults and children, which may highlight developmental processes and possible adjustments due to reading experience and practice. Martin and colleagues extended Houdé, Rossi, Lubin and Joliot's (2010) meta-analysis on reading processing in healthy adults and children, analyzing 20 fMRI studies with adults and 20 with children (7–12 years). Despite a very common pattern of brain activation in both groups in left ventral occipito-temporal, inferior frontal and parietal areas, within-group convergence was found in many reading-related areas in both groups. Differences between children and adults were evident in both the extent and location of the reading-related activation clusters in the core reading circuits (e.g., the inferior frontal cortex including the motor cortex, the superior temporal lobe, small areas in the superior parietal lobe and

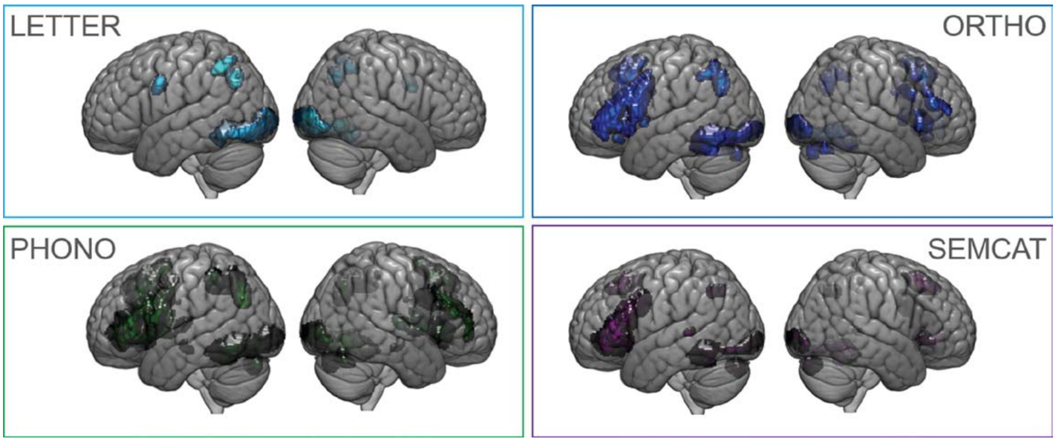

Figure 2. Differences in brain activation in children when performing different tasks: letter identification, orthographic decision, phonological decision and semantic categorization (Liebig et al., 2017, p. 49).

the temporo-occipital area; see Figure 1). Moreover, the shift of the more temporal focus towards the dorsal areas (the occipital lobe) in the left hemisphere from child- to adulthood is clearly visible.

In a single study, Liebig et al. (2017) intended to shed light on differences in reading processing in children applying four different tasks related to the four subcomponents of reading. They applied *letter identification* (processing stage: pre-lexical; task: detect letters in words/non-words), *orthographic decision* (processing stage: orthographic; judge whether a presented letter string is a correctly spelled word or a pseudo-homophone[2]), *phonological decision* (processing stage: phonological; judge whether a visually presented word sounds like a real word or not) and *semantic categorization* (processing stage: lexico-semantic; decide if a word is a living or non-living object). The results confirm differential activation according to task type (see Figure 2). Regardless of the specific task, however, engagement primarily involved the core reading circuits with the exception of the cerebellum, which is known to play an extraordinary role in language processing and dyslexia.

2 *Pseudohomophone* refers to a word that sounds like a real word but is spelled differently (e.g., 'Haus vs. Hauß' in German – only the first is a German word but both are pronounced exactly the same way; Liebig et al., 2017).

To summarize, reading relies on the interconnection and general functioning of a number of areas designated as core reading circuits. These areas are engaged in a similar fashion in both children and adults, but there are slight age-related differences concerning extent and location of activations (Figure 1). Additionally, the specific task and processing stage in a study may lead to very distinct activation profiles (Figure 2). When investigating functioning of these reading circuits in dyslexics, it is thus inevitable to pay close attention to the precise age of the individuals and the employed tasks.

1.3 Reading processing in dyslexics

Behavioral differences between impaired and non-impaired readers have been thoroughly explored up to now (e.g., Landerl et al., 2013), but little is known about the underlying neural deficits or anomalies that characterize this reading impairment. Since there are three main reading circuits that need to work in concert for successful reading (Pugh et al., 2001), it seems plausible to argue that at least one of the three, or the interaction between them, must somehow be deficient in dyslexics. So far, quite a large number of single studies with small sample sizes but few meta-analyses have focused on uncovering differences in brain activation between children suffering from dyslexia as compared to healthy controls.

As a first step, let us briefly examine the few meta-analyses that have attempted to explore the suspected anomalies in brain activation in dyslexic children and adults. With regard to terminology, it is noteworthy to state that authors usually report under-/overactivation when talking about significantly less or more activation of dyslexics in contrast to non-impaired peers (i.e., the two terms do not designate increasing or decreasing activation as the name might imply).

Maisog, Einbinder, Flowers, Turkeltaub and Eden (2008) performed a meta-analysis on dyslexia focusing on teenagers and adults. They reported overactivation in dyslexics in right thalamus and insula, and underactivation in left ventral extrastriate cortex, ITG, FG, precuneus and right FG. They concluded that left-hemispheric areas are more active in non-impaired readers, while greater right-hemispheric activity (seen as compensatory activation) is indicative of dyslexia.

Richlan, Kronbichler and Wimmer (2009) analyzed 17 fMRI studies in which dyslexic children, adolescents and adults performed reading-related tasks. They reported significant underactivation in dyslexic individuals (regardless of age) in left-hemispheric IPL, STG, MTG, ITG and FG. Moreover, they reported more activation in inferior frontal regions (mostly IFG) in controls while motor areas were activated more strongly in dyslexics. The studies included in Richlan et al. were further included in a larger meta-analysis by Paulesu, Danelli and Berlingeri (2014; 53 fMRI studies altogether), who reported very similar findings. They emphasized that single-word reading is marked by dysfunction of left occipito-temporal areas and/or left temporo-parietal areas, the latter assumed to display an early dysfunction of phonological processing. Through their meta-analysis, Paulesu et al. (2014) confirmed the importance of left occipito-temporal cortex in normal populations alongside a lack of such engagement in dyslexic individuals.

Major drawbacks of the last two meta-analyses, however, are that they compared the results of studies with children even if they were not diagnosed as dyslexic but referred to as *poor readers*, and these meta-analyses only differentiated between two age groups, namely adults (18 or older) and children (18 or younger). This is not an ideal approach as the groups are inhomogeneous and Martin et al. (2015) have shown that between adults and children reading activation differences exist. Therefore, only half of the studies with children in Paulesu et al. (2014) were considered suitable for the present review. Additionally, one of the major issues that arises when working with dyslexic children is that training and practice may significantly affect (and supposedly improve) reading performance and brain activation. Therefore, including teenagers of 17 years and comparing their results to children aged 8–12, for instance, should certainly be avoided.

In contrast, a small meta-analysis (18 studies) by Richlan, Kronbichler and Wimmer (2011) examined studies with children between 9 and 11 years of age and compared them to young adults (nine studies for each age group). They found that dyslexic children had less activation compared to peers in left IPL and supramarginal gyrus (SMG). Additionally, they reported a small cluster in the right IPL and in the left ventral occipito-temporal cortex (VWFA). Slight overactivation in dyslexic children was only found in the frontal lobe (IFG) and PrCG. To summarize the findings by Richlan et al. (2011), substantial differences exist when comparing adults and children with dyslexia in a more controlled manner. This is a clear indication that mixing different groups of adults, teenagers and children may obliterate important developmental age-related differences.

2 METHODOLOGY

The major aim of this review is to provide the reader with a wide-ranging overview of studies involving dyslexic children of the past two decades. Such a review is needed to finally pinpoint the neural underpinnings of dyslexia, while eliminating the major drawbacks encountered in earlier analyses. In contrast to the aforementioned meta-analyses, only a rather limited age range (8–15 years) and only reading-related and auditory tasks were included. Overall, this review summarizes 24 fMRI studies investigating different processing mechanisms related to reading in dyslexic children. fMRI studies were first collected through Google Scholar and PubMed using the key words “dyslexia AND fMRI”, “reading processing AND dyslexia” and “children AND fMRI AND dyslexia”.[3] Studies were included if they met the following criteria:

1. Participants are children (8–15 years) with an official diagnosis of dyslexia and without any comorbidities (e.g., dyscalculia, attention deficit disorder).
2. Participants are monolingual speakers of alphabetic languages.
3. The study applies one or more reading-related tasks (i.e., reading, rhyming or auditory tasks) during an fMRI session.
4. At least one control group, either age-matched or reading-matched, is present.
5. Whole-brain analysis is performed (i.e., no mere region of interest analyses).

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3 A list of abbreviations of brain regions commonly used in the following sections is provided at the end of the chapter.

6. If the study uses intervention or remediation, only the results before treatment are taken into account.

In total, 24 studies conducted between 2000 and 2016 fulfilled these criteria and were thus included in the review. A time span between 2000 and 2016 was chosen because neuroimaging has been widely used since 2000, in particular with children, and dyslexia has received increasing interest in the cognitive neurosciences at the end of the 20th century.

It should be mentioned again that this chapter provides a review and not a meta-analysis. Sample size and statistical significance are usually not taken into account in a review, and thus the results have to be treated with some caution.

2.1 Tasks

The aforementioned meta-analyses differentiated mainly between reading-related and non-reading-related tasks. For the sake of simplicity, all non-reading related tasks were excluded and all relevant tasks were categorized into two umbrella categories, namely (1) auditory processing and (2) reading processing (including all phonological, orthographic and semantic tasks). A further differentiation of tasks only seems meaningful in the latter category, where three specific task categories, namely *rhyming* (focus on phonological aspect), *reading* and *other tasks* are distinguished (see Table 1 for a general overview of all tasks used in the studies). It is important to note that many tasks are merely applied to guarantee that subjects pay attention to the stimuli, and the main task is just reading. For instance, lexical decision tasks require subjects to read a word (e.g., cat) or non-word (e.g., cit) and to decide whether it is a real word in the native language or not. In this case, what researchers are really interested in, is the activation for reading the word or non-word and not the decision subjects make, even if this might lead to activation for decision-making processes.

Table 1. Summary of all tasks employed in the studies of this review together with a brief instruction of what participants were asked to do

Task	What did participants have to do?
Auditory discrimination	Listen to and discriminate between given acoustic stimuli/ sounds (e.g., /ba/ vs. /da/ or /b/ vs. /p/)
False font reading	Read false fonts
Letter rhyming	Decide whether given letters rhyme (e.g., b and t)
Lexical decision	Decide whether a given presented word/non-word is a real word or not (e.g., cat vs. cit)
Morpheme mapping	Make associations between elements (affixes) that carry grammatical information and the meaning attached to them (e.g., build and builder)
Non-word reading	Read non-words/pseudo-words[4]
Non-word rhyming	Decide whether non-words rhyme (e.g., hime and brime)
Passive listening	Listen passively to acoustic stimuli, such as speech sounds, words or non-speech sounds
Phoneme/orthographic mapping	Make associations between sounds and letters or letter combinations
Semantic judgment	Decide whether two presented items are semantically (meaning-wise) related (e.g., table and desk; anger and floor)
Sentence reading	Read full sentences
Silent/overt word generation	Generate words (either silent or overt) after having seen a given image/word
Symbol reading	Read a symbol
Word reading	Read single words
Word rhyming	Decide whether presented words rhyme (e.g., mine and fine)

4 The terms non-word and pseudo-word refer to words that do not actually exist in a language but follow the phonotactic rules of the language (for instance, ‘brime’ is not an English word although one could probably imagine it being one because it follows the phonotactic rules of English). The two words are used interchangeably in studies.

2.2 Studies and participants

All children had alphabetic languages (German, Swiss German, English, Dutch, French or Norwegian) as their native languages. Initially, the age range was set to 8–12 years, but since Hoeft et al. (2007) and Shaywitz et al. (2002) included an impressive number of participants and applied highly relevant reading-related tasks, these two studies were included as well, which led to a redefinition of the age group to 8–15 years. For a complete list of all studies and the used tasks, as well as information on the number and age of participants, see Table 2.

Table 2. Complete list of all studies selected for the review including number of participants, number of dyslexics, mean age of participants and tasks applied (differentiating between auditory and reading tasks)

Study	Year	Participants		Task(s) (A/R)
		Number (D)	*Mean age*	
Aylward et al.	2003	21 (10)	11.6	Phoneme mapping, morpheme mapping (R)
Backes et al.	2002	16 (8)	11.5	Non-word rhyming, semantic judgment (R)
Baillieux et al.	2009	22 (15)	11.4	Silent word generation (R)
Blau et al.	2010	34 (18)	9.4	Passive listening (A)
Boros et al.	2016	33 (15)	11.5	Non-word reading, false font reading (R)
Cao et al.	2006	28 (14)	11.6	Word rhyming (R)
Corina et al.	2001	16 (8)	10.8	Word rhyming, non-word rhyming, lexical decision (R)
Gaab et al.	2007	45 (22)	10.5	Passive listening (A)
Georgiewa et al.	2002	17 (9)	12.6	Word reading, non-word reading (R)
Heim et al.	2010a	40 (20)	9.6	Auditory discrimination (A), phonological decision (R)
Heim et al.	2010b	37(18)	9.4	Overt word reading (R)
Hoeft et al.	2006	30 (10)	10.4	Word rhyming (R)
Hoeft et al.	2007	53 (23)	14.4	Word rhyming (R)
Kovelman et al.	2012	39 (12)	9.0	Word rhyming (R)
Maurer et al.	2011	27 (11)	11.4*	Word reading, symbol reading (R)

Study	Year	Participants		Task(s) (A/R)
		Number (D)	*Mean age*	
Monzalvo et al.	2012	46 (23)	9.9	Word reading (R), passive listening (A)
Morken et al.	2014	29 (11)	11.8	Word reading, sentence reading (R)
Olulade et al.	2015	28 (16)	10.0	False font reading (R)
Richards et al.	2006	39 (18)	10.9	Phoneme mapping, morpheme mapping, orthographic mapping (R)
Schulz et al.	2008	52 (16)	11.6	Sentence reading (R)
Schulz et al.	2009	45 (15)	11.6	Sentence reading (R)
Shaywitz et al.	2002	144 (70)	13.3	Letter rhyming, non-word rhyming, semantic judgment (R)
Temple et al.	2000	39 (24)	10.7	Letter rhyming, letter matching (R)
Van der Mark et al.	2009	42 (18)	11.3	Phonological decision (R)

Note. D dyslexics; *rough estimates as not indicated in the study (e.g., due to exclusion of participants); Tasks: (A) auditory processing, (R) reading processing.

Given the lack of a larger review of studies investigating brain activation differences in dyslexic children only, I have decided to make an attempt to fill this gap. There is no doubt that behavioral differences are of great significance for understanding dyslexia but (1) there is already an impressive body of research on this topic and (2) behavioral differences cannot help us uncover the underlying impairment in terms of anomalies in the human brain (be it structurally or functionally). It is often argued that the brains of dyslexics function differently, and many fMRI studies have tried to investigate these differences. Still, small-scale studies do not allow a proper evaluation of the nature of this impairment and only reviews and meta-analyses can provide us with a clearer picture.

Of the 24 studies I considered suitable after the first screening, I investigated every single study looking at the participants (diagnosis, age, first language) and the tasks applied in the study (see Table 1), and made sure they analyzed the results of whole brain analyses. The behavioral findings are only of marginal interest for me in this review, and therefore they will only be addressed in a brief, separate section. The major focus lies on the neural findings in the form of brain activation during certain linguistic and non-linguistic tasks.

3 RESULTS

3.1 Behavioral findings

In all reading-related measures and auditory tasks (see Table 1 and 2 for a complete overview of tasks), the control group significantly outperformed the dyslexic group. Very few studies failed to detect differences between the two groups. Concerning the control tasks (line orientation, visual tasks or letter detection), no differences were reported between dyslexics and their age-matched peers, except for auditory tasks involving tone judgment or passive listening.

3.1.1 *Accuracy and reaction time*

Almost all studies reported that during reading-related tasks (e.g., reading pseudo-words, words, pseudohomophones or sentences), controls outperformed dyslexics with respect to accuracy (Blau et al., 2010; Hoeft et al., 2007; Shaywitz et al., 2002; Schulz et al., 2008; Van der Mark et al., 2009). Monzalvo, Fluss, Billard, Dehaene and Dehaene-Lambertz (2012) reported that more generally, reading time was faster and error rate was considerably lower in controls as compared to dyslexics. Interestingly, they could also link a low socio-economic status to a tendency to produce more reading errors.

Dyslexics were particularly less accurate and slower during the non-word rhyming and the semantic categorization tasks (Backes et al., 2002). In Boros et al. (2016), reaction times did not differ, but dyslexic children were also less accurate in letter and digit reading. However, no interaction was found between group (impaired vs. non-impaired) and stimuli (letters vs. digits) presented. Mainly, a lack of engagement in a variety of areas and an activation of the *default-mode network*[5] instead might be responsible for the difficulties encountered (Boros et al., 2016).

The more difficult the task, the larger the discrepancy between the performances of the groups. Increasing difficulty in conflicting trials led

[5] The default-mode network is a resting state network that shows a decrease in activation as soon as a task is performed by an individual. It comprises the precuneus, posterior cingulate cortex, anterior cingulate cortex and temporo-parietal junction areas (Heine et al., 2012).

to less accuracy and delayed responses in impaired readers, although dyslexics were slower and less accurate more generally in all tasks as reported by Cao, Bitan, Chou, Burman and Booth (2006). This increasing difficulty for dyslexics was confirmed by greater activation in conflicting vs. non-conflicting trials in bilateral IFG and left-hemispheric regions in temporal areas, FG and the parietal lobe. In other words, the increasing complexity and difficulty of the task led to overactivation in a large network of areas, especially in IFG, the region responsible for making decisions, executing and joining orthographic and phonological information.

Although most studies found delayed responses and worse accuracy in dyslexics, a number of studies did not detect differences in response times or failed to detect any group-related differences at all. In Morken, Helland, Hugdahl and Specht (2014), accuracy and response time did not differ between the two groups during alphabetic and sentence processing, but differed significantly between the groups in the orthographic processing task (reading of long and irregular words). This is interesting because brain engagement showed large discrepancies in all three processing stages, that is, during all tasks, which could not be confirmed behaviorally.

Similarly, applying false font reading and letter detection, Olulade, Flowers, Napoliello and Eden (2015) failed to detect an effect due to condition (accuracy during tasks), but they observed a group effect regarding response times with dyslexics responding more slowly than the control children. They reported that both groups actually scored very high in the real word and false font reading tasks, which might indicate ceiling effects. On the other hand, the behavioral findings do not support the differences in engagement detected with the help of fMRI because differences between controls and dyslexics were confirmed in both tasks. Furthermore, Van der Mark et al. (2009) reported that false-font and word reading did not reveal any differences between the performances of the two groups.

In sum, while reaction times between the two groups did not often differ significantly (e.g., Boros et al., 2016; Corina et al., 2001), accuracy was far worse in dyslexic children with very few exceptions (Morken et al., 2014; Olulade et al., 2015). The more complex the task, the larger the differences in behavioral performance.

3.1.2 *Auditory processing*

The *auditory deficit hypothesis* is supported by Gaab, Gabrieli, Deutsch, Tallal and Temple (2007), reporting that even in a pitch discrimination task of a non-linguistic nature, dyslexics respond less accurately compared to age-matched peers. Measures of language and reading ability led to significant differences between the two groups. Even after remediation and improvement in dyslexics as compared to constant results in the non-impaired group, dyslexics significantly underperformed controls. In another study by Temple, Poldrack, Protopapas, Nagarajan and Salz (2000), controls were more accurate for rapid and slow non-speech analogues than dyslexics and, not surprisingly, accuracy was greater for the slow stimuli more generally. However, no interaction between group and stimulus type and no difference in response time was reported. Specifically, phonological awareness and phonological decoding revealed significant deficits in the reading-impaired children (Blau et al., 2010). Also in Corina et al. (2001), dyslexics were less accurate in lexical decision and tone judgment tasks (mainly requiring auditory processing). Still, brain activation differences reflected discrepancies during both tasks, and more specifically, tone judgment difficulties were related to a lack of engagement of the parietal cortex.

3.1.3 *Performance of control groups*

Interestingly, the studies that included two control groups (Hoeft et al., 2006; Hoeft et al., 2007), namely one age-matched group and one reading-level-matched (younger children) group, showed that there were no differences in response time and accuracy between the latter and the dyslexics. In fact, only the age-matched peers outperformed the reading-impaired children and the reading-matched group. Hoeft et al. (2006) highlighted reading deficits regarding receptive vocabulary and IQ in the dyslexics. However, their study also revealed that nonsense word decoding and comprehension showed differences between dyslexics and their age-matched peers but not with their reading-matched peers. In other words, reaction time and accuracy were only significant between impaired readers and their age-matched peers. This confirms that dyslexics fail to develop age-appropriate reading skills, but there is nothing that distinguishes dyslexic children from those of the same reading-level. Dyslexics suffer from a severe developmental delay and their deficits might indicate a lack of reading exposure and experience, but this is usually not the case.

3.1.4 *Visual tasks*

During all kinds of control tasks, such as visual tasks (line orientation and string comparison), no differences between dyslexics and non-impaired readers were found. It has been a matter of debate whether dyslexia is mainly a visual deficit, but this could not be supported by the behavioral results of this review. With regard to differences in brain activation, line orientation led to higher activation in parietal cortex in control and in left lateral extrastriate cortex in dyslexics, but the behavioral performance was not affected.

In sum, behavioral deficits and discrepancies were confirmed in almost all studies with respect to slower response and higher accuracy for the control groups compared with the dyslexics. Most strikingly, even if studies found large differences on the neural level (i.e., significantly more or less activation in a number of areas or compensatory activation), some studies only found minor or no differences in behavioral performance between the groups. Furthermore, only age-matched peers significantly outperformed dyslexics, while those studies introducing reading-matched groups reported no differences.

3.2 **fMRI findings**

3.2.1 *Group-related differences in auditory processing*

Gaab et al. (2007), Monzalvo et al. (2012), Blau et al. (2010) and Heim et al. (2010a) focused on auditory processing and found (1) less activation differentiation for slow and fast stimuli, (2) weaker auditory incongruency effects in auditory cortex (AC), (3) reduced right and left frontal activation during phonological awareness and (4) small regions of compensatory activation in the dyslexic population (in particular in the right hemisphere).

Gaab et al. (2007) investigated passive listening to acoustic stimuli with either slow or fast transitions. The control group showed higher activation for rapid vs. slow stimuli in the left prefrontal cortex primarily in superior and medial frontal gyrus (SFG, MFG) and right-hemispheric areas (including peri-sylvian regions). In dyslexics, the left MTG was the only region showing activation for the fast vs. slow distinction, which indicates a lack of specialization for this particular task.

In the study of Blau et al. (2010), children had to listen to speech sounds while reading Dutch letters (pairs were either matched or deviant). They found that children with dyslexia had significantly weaker activity for processing speech sounds in anterior STG and for processing letters in FG bilaterally. Moreover, they observed that fluent readers showed a congruency effect close to the primary AC (Heschl's sulcus), which was absent in all dyslexics.

In the study by Heim et al. (2010a), a variety of tasks was applied. For testing phonological awareness, participants heard words and pseudo-words and had to indicate the initial sound of each word (single choice). The auditory discrimination task included words and non-lexicalized syllables, and the participants were required to indicate if the speech sound pairs were identical or not (e.g., /ba/ – /pa/). According to their findings, dyslexics showed higher activation in the left inferior frontal lobe (inferior frontal sulcus and MFG) during auditory sound discrimination tasks. Additionally, dyslexics had more activation in frontal areas during this task, whereas phonological awareness was linked to reduced activation in the left frontal cortex (only at uncorrected level, however) and reduced activation in the right fronto-medial wall (superior medial gyrus).

Finally yet importantly, Monzalvo et al. (2012) investigated both visual and auditory processes in dyslexic children. In their visual experiment, houses, faces, words and a checkerboard were presented. In their auditory task, on the other hand, 40 sentences in the subjects' native language (French) and in a foreign language were presented. They discovered that the control group had higher activation in supplementary motor area (SMA) bilaterally and the right temporal region when listening to the short French sentences. Only marginal clusters were found in the left hemisphere, for instance, in planum temporale (PT) and insula, and slight activation asymmetries were found in the temporal cortex (e.g., normal readers were more right lateralized in auditory areas extending to SMG).

3.2.2 *Reading processing in dyslexic children*

3.2.2.1 Rhyming tasks

The variety of rhyming tasks used by the selected studies led to under- and overactivation in several regions. Non-word rhyming, on the one hand, led to significant overactivation in all reading-relevant brain regions, with little or no activation in areas that were not engaged in the control group. Word and letter rhyming, on the other hand, were marked by more frequent compensatory activation (right-hemispheric and bilaterally) together with a lack of engagement of the core reading circuits as reported in the non-word rhyming tasks.

Backes et al. (2002) and Shaywitz et al. (2002) used non-word rhyming tasks. Dyslexics exhibited less activation in left inferior prefrontal regions and left cingulate gyrus, and in contrast to controls, did not activate the superior temporal cortex (bilaterally) at all. Instead, dyslexics activated the left extrastriate cortex (Backes et al., 2002). In Shaywitz et al. (2002), controls exhibited more activation in core left hemisphere regions, namely IFG, posterior STG, MTG and right-hemispheric IFG, STG, MTG and medial orbital gyrus. No compensatory activation was found in dyslexics.

Corina et al. (2001) applied both non-word and word rhyming and suggest that dyslexics differ in auditory language processes (rhyming) and attention processes. They reported asymmetry during rhyming in ITG (left > right in controls, vice versa in dyslexics) and PT (left more in controls), and underactivation of dyslexics in PrCG, MFG. Altogether, the lexical task they applied additionally engaged more regions in both groups, resulting in many regions of difference, such as less bilateral insula, left ITG and IFG.

The following four studies relied on word-rhyming tasks only. Cao et al. (2006) included non-conflicting (easy) and conflicting (difficult) trials, which posed heavy demands on phonological processing. Only the more challenging trials led to different activation patterns, namely more activation in controls in bilateral IFG and left-hemispheric ITG, FG, IPL and MTG (i.e., areas in all core circuits involved in reading). Without considering difficulty levels, Hoeft et al. (2006) found that age-matched controls engaged the left parieto-temporal cortex, right parieto-temporal regions, two frontal regions and right occipito-temporal cortex more than dyslexics. They state that the core differences between groups can be found in three regions, namely the frontal lobe, the parietal lobe and the temporal lobe. In a follow-up study, Hoeft et al. (2007) reported more activation in control children in left IPL, bilateral FG and lingual gyri. The dyslexics, on the other hand, engaged the left IFG, left MFG, left caudate and right thalamus more often. Kovelman et al. (2012) had rather opposing findings to those observed in previous studies. Dyslexics showed greater activation in the right temporo-parietal region including STG, MTG and angular gyri (AG). In contrast, controls activated more strongly the left dorso-lateral prefrontal cortex for rhyming in contrast to the baseline task.

Several studies applied word or non-word rhyming tasks known to elicit phonological processing areas. Temple et al. (2000) employed the simplest task, namely letter rhyming. Whereas the control group activated the left temporo-parietal cortex, dyslexics did not engage this region at all. Dyslexics, however, had higher activation in many regions, for example, in the bilateral SFG, right IFG, right MTG, bilateral PrCG and postcentral gyri and right-hemispheric occipital areas [middle occipital gyrus (MOG) and inferior occipital gyrus (IOG)], as well as in bilateral basal ganglia and right vermis.

3.2.2.2 Reading tasks

The majority of studies included in this review laid their focus on silent or overt reading of linguistic material, such as reading words, letters, symbols, digits, non-words and sentences. In the following subsections, studies involving words and sentences will be discussed separately due to the large number of studies employing these tasks. The other types of stimuli, namely letters, symbols, false fonts and non-words, will be presented in a separate section.

LETTERS, SYMBOLS, FALSE FONTS AND NON-WORDS. Using a letter-reading task, Boros et al. (2016) found that controls exhibited more activation in right STG and bilateral MOG. Dyslexics, on the other hand, had more default-mode-network activation bilaterally in parietal, temporal and frontal lobes. Similarly, controls activated left FG (peak in left occipital-temporal cortex) anterior to VWFA and right MFG more strongly during false font reading (Olulade et al., 2015). Also in Boros et al. (2016), false font reading led to higher activation in temporal and occipital areas (MOG) bilaterally. Reading symbols, on the other hand, led to higher activation in the left ventral visual stream, temporal areas bilaterally and frontal areas in controls. In accordance with the letter reading task, the default mode network showed higher activation in the dyslexics. During non-word reading, mainly temporal (ITG, MTG) and occipital gyri (IOG, MOG) bilaterally showed higher activation in controls (Boros et al., 2016).

WORDS. Most studies applied silent reading of words. Georgiewa et al. (2002) reported that the three core areas of activation in dyslexics were (1) left IFG, insula and STG, (2) left thalamus and (3) left nucleus caudatus. Additionally, contrasting words vs. pseudohomophones led to stronger engagement of left IPL, STG and insula, whereas pseudo-words vs. words led to no significant distinction between the groups (Van der Mark et al., 2009). Contrary results were found by Heim et al. (2010a), who reported differences in word vs. pseudo-word reading mainly in the right fronto-medial wall and left IFG.

Maurer et al. (2011) observed increased activation for controls in inferior occipito-temporal regions extending to VWFA when subjects had to read normal words. Also in Van der Mark et al. (2009), processing words vs. false fonts led to more activation in inferior and occipital regions in the left hemisphere, plus bilateral cingulate and right-hemispheric cuneus activations. Only one study reported hyperactivation in left IFG, insula and lingual gyrus in dyslexics (Georgiewa et al., 2002); the other studies found no word-specific overactivation in impaired readers (Van der Mark et al., 2009).

Morken et al. (2014) added some complexity to the design by using regular and irregular words and found differences in several regions (involving bilateral frontal areas, SMA, cerebellum, thalamus etc.) but mostly in the form of hyperactivations of dyslexic children due to increasing difficulty. Generally, they argued that six regions were related to increasing processing demands, namely right SFG, left pre-SMA, left nucleus caudatus and right SFG and MFG. They therefore stated that these areas may show considerable differences in activation between dyslexics and controls.

In the study by Baillieux et al. (2009), subjects had to generate words from cues. The authors reported more diffuse and widespread left-hemispheric activations in temporo-occipital, temporo-parietal and occipital areas in dyslexics. Additionally, they found that activation in the cerebellum differed extensively between the two groups. In Heim et al.'s study (2010b), overt word reading activated frontal, parietal AG and temporal regions in both hemispheres, as well as the right hippocampus and the left cerebellum. Dyslexics activated very similar regions, but different tasks were associated with different strengths of activation in dyslexics and controls.

To sum up, reading of single words and smaller units led to striking differences in all core reading circuits, in particular in frontal areas, but few studies reported compensatory activation. Compensatory activation was only reported in two studies (Georgiewa et al., 2002; Morken et al., 2014), one of which applied irregular words and thus added difficulty to the task. It can be argued that simple word reading does not lead to any overactivation due to the simplicity of the task, but if complexity is added, for example by using irregular or infrequent words, additional areas are engaged.

SENTENCES. Differences in sentence reading were not only found between dyslexics and age-matched controls (controls > dyslexics: left IPL, frontal, temporal and fusiform areas) but also between dyslexics and reading-matched controls (controls > dyslexics: bilateral IPL, frontal, temporal and cingulate; Schulz et al., 2009). In an earlier study, Schulz et al. (2008) found similar results, where controls engaged left-hemispheric regions (frontal, IPL) more strongly. In another study by Morken et al. (2014), both groups showed a widespread network of activation, but the control group also activated right MTG and thalamus. The sentence condition generally led to increased activation in dyslexics (the control group showed a decrease, instead) in right SFG and left pre-SMA. Overall, Morken et al. reported hyperactivation due to increasing processing demands in dyslexic children, particularly in sentence processing.

Only three out of the 34 studies applied sentence reading but all reported slight underactivation in frontal, parietal and temporal areas, with minor compensatory areas (right MTG and thalamus). What is more, one study further reported increased activation in dyslexics interpreted to be due to the increasing demand in sentence reading compared with single word reading.

3.2.2.3 Other tasks

This section deals with phonological, orthographic and morpheme mapping tasks and semantic aspects of word and sentence reading, which were specifically addressed in a number of studies. In Aylward et al. (2003), controls showed more activation in left frontal regions (IFG, MFG), bilateral (left > right) superior parietal regions and slight differences in bilateral AG, SFG, FG and temporal regions (ITG, MTG) during phoneme mapping. Morpheme mapping led to more activation in controls in right FG, right superior parietal regions, bilateral occipito-parietal junction and left MFG, which was not statistically significant, however. Using the same tasks and criteria for groups, Richards et al. (2006) found different activation patterns during all tasks. During morpheme and orthographic mapping, dyslexics only activated about half of the regions that controls activated, but they instead also activated several compensatory regions. Only in phoneme mapping did the two groups engage a similar number of regions, but with different activation profiles (e.g., additional activation of left STG or bilateral activation in controls of thalamus and PrCG, whereas dyslexics only activated one hemisphere).

During semantic categorization in Schulz et al. (2008), dyslexic children showed reduced incongruency effects in the parietal lobe and precuneus. Shaywitz et al. (2002), who found more activation in left parietal, temporal and occipital and right temporal and occipital areas in controls, reported a larger difference for semantic judgment. Wide-spread compensatory activation in dyslexics was reported by Backes et al. (2002), in particular in the right inferior frontal areas as well as in bilateral prefrontal and extrastriate cortex.

It is not possible to summarize these findings in a uniform manner, but to put it in a nutshell, semantic categorization tasks and specifically mapping tasks led to striking differences in neuronal activation, even though they are not the primary focus of most studies investigating dyslexia. The mapping tasks especially are very complex and investigate core principles when it comes to reading acquisition. Discrepancies in these tasks on the behavioral and neural level highlight the enormous difficulties dyslexic children encounter during literacy acquisition.

4 DISCUSSION

In summary, all studies of this review reported different activation patterns in dyslexic children compared with controls in a variety of areas during auditory or reading-related tasks. The most striking differences were a lack of engagement of all core reading areas, namely inferior frontal cortex (including IFG and MFG), the parieto-occipital network (including inferior parietal areas and FG) and temporo-parietal areas (including STG, MTG and PT) together with a network of compensatory activation in bilateral and right-hemispheric areas. The latter, however, was only found in more demanding tasks (e.g., rhyming, mapping and semantic tasks and in some reading tasks). The results of this review should be regarded with some caution, as statistical effect sizes were not taken into consideration, which limits the comparability of the studies included. Nonetheless, the overall findings suggest a tendency towards a large network of engaged regions that seem to be deficient in dyslexic children.

The findings favor the belief that dyslexics engage fewer and/or different brain areas in contrast to non-impaired readers in all tasks related to reading and at different processing stages. In addition, a large number of studies reported bilateral and particularly right-hemispheric compensatory activation in reading-related areas (inferior frontal lobe, inferior parietal areas, FG, temporo-parietal regions). In other words, the compensatory activation was predominant in the right hemisphere, but not limited to it. The areas showing the most striking underactivation in dyslexics during reading processing are primarily those of the left-hemisphere, the so-called core reading circuits as presented in the Introduction. It is interesting to see that rather simple tasks like false font reading, symbol or word reading do not lead to additional engagement of brain areas. This might be due to the simplicity of the task and the fact that the dyslexic children are already familiar with most words which therefore does not pose major challenges to them anymore. Rhyming tasks, on the other hand, require explicit phonological information and are more complex, in particular when rhyming non-words. Furthermore, sentence processing or processing of irregular words led to additional activation, which is most likely to be due to increasing complexity as well.

In the auditory tasks, differences in activation and asymmetry were reported most often in the classical auditory areas, that is STG, MTG and PT. Since phonological processing deficits are often assumed to be predominant in dyslexics, basic auditory processing has received minor attention in past years. Still, as already mentioned, a comprehensive review has revealed that auditory deficits affect about 30–50% of dyslexic individuals (Hämäläinen et al., 2013), and it therefore seems necessary to investigate different aspects of elementary auditory processing in dyslexics as well. There seems to be poor differential activation for slow vs. fast auditory stimuli in dyslexic children. Segmenting and decoding speech requires engagement of the temporal and prefrontal cortex, and there is evidence for a lack of corresponding IFG integration in dyslexics (Tallal & Gaab, 2006). They are very likely to be impaired in the "ability to track brief, rapidly successive, dynamic acoustic changes within the complex acoustic waveform of speech" (Tallal & Gaab, 2006, p. 382). As a consequence, the processing of single speech sounds and letters is also impaired in dyslexic children. The lack of response to incongruous speech-letter pairs may reflect an insufficient integration of these speech sounds (Heim et al., 2010a). The findings of this review support the hypothesis that many children with dyslexia also experience major difficulties when categorizing, discriminating and integrating single speech sounds. Even if not all children display auditory deficits, these deficits may heavily influence subsequent literacy acquisition. Furthermore, a very impressive longitudinal study (Serrallach et al., 2016) has clearly linked differences in auditory cortex (functionally and structurally) to dyslexia, but it remains to be seen whether developmental changes and improvements might influence these anomalies. To summarize the findings on auditory processing, I argue that auditory processing does not deserve to be overlooked as basic auditory processing may have a considerable impact on literacy acquisition, and the present review clearly speaks for a striking role of deficient auditory processing in dyslexic children. Even if auditory processing deficits are not as striking as phonological and orthographic integration deficits, they have to be taken into account when further exploring the underpinnings of developmental dyslexia.

Phonological processes are at the core of all reading-related tasks explored in the numerous studies of this review. The capacity to immediately understand the phonological value of a sound or letter (e.g., rhyming letters) in words requires efficient processing in the left and right parieto-temporal cortex, frontal areas and the occipito-temporal cortex. Letter, non-word and word rhyming have been found to mostly engage the three core circuits with a focus in the temporo-parietal region. In dyslexics, letter rhyming revealed deficits mainly in temporo-parietal areas combined with a large compensatory network in right and bilateral areas in occipital and frontal lobes and motor areas. Apart from these findings, reduced functional connectivity was confirmed in Hoeft et al. (2006) in the left occipito-temporal cortex and middle occipital cortex, left MTG, STG and insula, that is affecting all areas relevant for mapping auditory and visual input. Non-word rhyming, in contrast, led to compensatory activation in dyslexic children in the left extrastriate cortex. Significantly less activation was found in the prefrontal cortex (IFG) and temporal areas and additionally, dyslexics failed to engage bilateral temporal areas and IPL. Also word rhyming requires the three core circuits for reading, namely parieto-temporal, frontal and occipito-temporal cortex. Especially IFG bilaterally and right-hemispheric temporal cortices (MTG and ITG) led to differential activation in dyslexics (Kovelman et al., 2012). Furthermore, the more phonologically demanding the word pairs, the more differences found between dyslexics and controls (Cao et al., 2006).

To summarize, rhyming tasks led to striking underactivation as well as overactivation (i.e., compensatory activation; bilaterally and on the right) possibly due to the more challenging nature of the task. Both the occipito-temporal and the temporo-parietal cortex seem to be heavily involved and thus severely impaired in dyslexics, which would explain their significantly worse performance on all rhyming tasks and their slower response times. Hand in hand with the significant underactivation in the variety of areas, the rhyming tasks led to compensatory activation in right and bilateral areas and the left extrastriate cortex. In fact, rhyming is a complex task that requires an immediate phonological analysis of a given orthographic cue, not the word itself. During normal single word or sentence reading, children are not required to process single units and their smallest elements. During rhyming tasks, however, concrete phonological knowledge is required, which was also highlighted in the large behavioral differences in accuracy and reaction times between the impaired and non-impaired readers. It seems, thus, that the more demanding a reading-related process, the more impaired readers try to compensate their deficits by engaging a large variety of brain areas. This might be due to the insufficient integration of speech sounds and their correspondence to letters in the impaired group.

In overt word reading, however, deficits could only be attributed to the extent but not the location of activation. Slight differences were further found between word reading vs. reading of pseudo-homophones and pseudo-words and between regular and irregular words, which could be linked to the increasing processing demands, which may be more difficult to cope with for dyslexic children. Both letter and non-word reading typically showed deficient processing in occipital (visual) and temporal (STG; auditory) areas in dyslexics (Backes et al., 2002). For letter and symbol reading, less deactivation was found in dyslexics in areas associated with the default mode network. In addition, false-font reading, related to the other three categories, led to activation differences in visual (VWFA) and occipito-temporal areas (Backes et al., 2002; Olulade et al., 2015).

Interestingly, there were also major differences between sentence reading and single word reading with the first leading to compensatory activation. For both tasks, sentence and word reading engaged core reading circuits and large differences in extent and intensity of activation were found in the left frontal regions, the IPL, temporal areas (mostly MTG) and occipital areas. It may be speculated that the higher complexity of sentences as compared to words – which represents a higher cognitive load – leads to a higher activation in frontal areas relevant for working memory functions but has very little effect on the reading circuits. In the studies, however, overactivation in additional areas was further spread and not limited to the frontal areas but rather to the core reading circuits. Still, this finding has to be treated with much caution as sentence reading was only applied in three studies and only one directly compared word and sentence reading. It has to be considered, however, that differences in age might lead to very different results in sentence reading. More reading exposure and practice consequently lead to much greater ease while reading. Therefore, reading sentences or words might be much easier than reading non-words or pseudohomophones, for instance. It is also interesting that studies apply simpler tasks like word reading or reading of letters rather than more challenging ones like non-word or sentence reading. Reading words might be a process that can become automatized even in dyslexic children, who undoubtedly struggle with this process. Therefore, reading single words might even be very simple for them, especially if very easy, regular words are used.

With regard to the brain areas most often found to be over- or under-activated during the reading tasks, only one single study found an under-activation of the cerebellum, which has been a topic of its own with respect to dyslexia in the past years. Therefore, I would argue at this point that the cerebellum is not essential for literacy acquisition to the extent that the brain has to rearrange according to the difficulties encountered. It might also have been a coincidence that none of the other studies found over- or underactivation in the cerebellum. Another explanation would be that the cerebellum plays a bigger role in adults and teenagers, which is why no cerebellar activation was found in the studies analyzed in this review.

I would like to briefly mention the behavioral findings and how far they can relate to the neural findings. It is interesting that no behavioral differences could be found between reading-matched control children and the dyslexics, whereas the age-matched clearly outperformed both groups with ease. Interestingly, brain activation showed a very different picture. During sentence reading, for instance, there were striking differences between reading-matched controls and dyslexics and not only between age-matched and dyslexics, as would have been expected. It might be the case that the differences between the reading-matched groups and the dyslexics are so subtle that behavioral measures fail to detect them at all, while minor differences on the neural level are visible and found to be significant in the studies. This was confirmed throughout the review and even though reaction times did not add much to the picture (if one needs longer to relate a sound and a letter or to read a word it seems logical that it takes one longer to respond), accuracy did. There were very few tasks that did not reveal differences between dyslexic readers and the non-impaired group and among them was false font reading, which is not strongly related to reading and the result is therefore somewhat expected.

To the best of my knowledge, Richlan et al. (2011) are the only ones so far who have looked at studies investigating reading-related processing through fMRI in dyslexic children with a strictly-defined age group. The main aim of Richlan et al. was to explore whether the predominant phonological deficit of temporo-parietal regions in children progresses towards a visual-orthographic left occipito-temporal dysfunction in adults. The results of their meta-analysis, however, were quite complex and could not fully confirm their primary hypothesis. They reported that the visual-orthographic deficit assumed to be predominant in dyslexic adults might have been underestimated in dyslexic children in the past. In particular, a lack of studies involving pseudo-words and pseudohomophones could have caused this underestimation (also in the current review, only a limited number of studies applied pseudo-word reading or rhyming). Moreover, they reported marginal overactivation in dyslexics, which is not in accordance with what the studies analyzed in this review have found.

In the present review, I extended Richlan et al.'s sample (9 fMRI studies with children) and limited and extended Paulesu et al.'s sample. The findings of this extended review support the results reported by Maisog et al. (2008), who found a small but significant network of compensatory activation in the right hemisphere and a lack of engagement in the core reading areas, namely FG, precuneus and ITG. Furthermore, Richlan et al.'s (2009) study reported very similar results as the ones I found. The only difference is that they also highlighted overactivation of motor areas in dyslexic individuals, which cannot be supported by this review.

I have to agree with Richlan et al. (2009) that more pseudo-word/non-word reading tasks need to be applied to help uncover the deficient mechanisms behind dyslexia. Even if single word or letter reading are slower and less accurate tasks for dyslexics, the brain activation patterns behind this process will probably reveal a focus on grapheme-phoneme conversion due to insufficient integration of the word or not reveal differences at all if the child has adapted adequately. When reading pseudo-words, on the other hand, the child has no knowledge to rely on and it allows us to a certain extent to investigate how encoding and grapheme-to-phoneme conversion take place at the same time. I therefore encourage those researchers dedicating their career to exploring dyslexia to become more creative and to increase difficulty levels while conducting fMRI.

All in all, the behavioral and fMRI findings are far from uniform and many specific regions reported in one study are not found in another although they apply the same task. Still, all reading-related tasks led to considerable underactivation in dyslexic children, while at the same time, dyslexics engaged a large network of compensatory areas instead, in particular during phonological tasks (e.g., rhyming). Thus, the review supports the findings from the other meta-analyses that dyslexic children between 8–15 years old fail to engage the typical reading-related areas during reading processing (also found in adults, see Maisog et al., 2008). Furthermore, and possibly in some contrast to adults, they use strikingly large right-hemispheric and bilateral compensatory networks to make up for the lack of engagement of the core reading circuits, which were only marginally reported in Richlan et al. (2009, 2011).

In general, I aimed at creating strict and homogenous criteria for the inclusion of relevant studies, and I tried to include as many studies as possible. Since only experimental paradigms with phonological, orthographic and auditory tasks were included, no inferences can be drawn with regard to visual processing. This does not imply that visual deficits are marginal and not worthy of discussion. Furthermore, I am well aware that reviews do not take into account statistical effect sizes. However, the review does show a clear picture and even if the findings have to be treated with some caution, they support previous meta-analyses and highlight the lack of engagement of core reading areas in dyslexics paired with networks of compensatory activation due to increasing task difficulty.

5 CONCLUSION

Given the results of the present review, I have to partly agree with Ramus, Altarelli, Jednoróg, Zhao and di Covella (2018), who criticize that small-scale studies and reviews tend to show a rather homogeneous picture, which cannot be confirmed in large-scale meta-analyses and studies. Mostly, large-scale analyses reveal few robust results and highlight inconsistencies instead. Likewise, the results of the review show a small number of robust patterns found in dyslexic children. Still, it remains debatable whether these small-scale studies with few participants not only report false positives but also blur the overall picture. However, one finding that will survive any criticism is the fact that activation in reading circuits differs between children with a diagnosis of dyslexia and non-impaired readers – even if the extent and location of differences vary with task, severity of the disorder and concrete age of the participants. Additionally, right-hemispheric and bilateral compensatory activation has been confirmed in such a large variety of studies that one could argue that this finding is also quite robust and reliable. It seems that dyslexic children show processing deficits in all core reading circuits and the more challenging the task, the more likely it is that they need engagement of additional regions to compensate for those deficits.

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ABBREVIATIONS

AG	Angular gyrus	MTG	Middle temporal gyrus
FG	Fusiform gyrus	PrCG	Precentral gyrus
IFG	Inferior frontal gyrus	PT	Planum temporale
IOG	Inferior occipital gyrus	SFG	Superior frontal gyrus
IPL	Inferior parietal lobule	SMA	Supplementary motor area

ITG	Inferior temporal gyrus	SMG	Supramarginal gyrus
MFG	Middle frontal gyrus	STG	Superior temporal gyrus
MOG	Middle occipital gyrus	VWFA	Visual word form area

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