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Original Article

Examination of common and unique brain regions for atypical reading and math: a meta-analysis

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The purpose of this study is to identify consistencies across functional neuroimaging studies regarding common and unique brain regions/networks for individuals with reading difficulties (RD) and math difficulties (MD) compared to typically developing (TD) individuals. A systematic search of the literature, utilizing multiple databases, yielded 116 functional magnetic resonance imaging and positron emission tomography studies that met the criteria. Coordinates that directly compared TD with either RD or MD were entered into GingerALE (Brainmap.org). An activation likelihood estimate (ALE) meta-analysis was conducted to examine common and unique brain regions for RD and MD. Overall, more studies examined RD ($n = 96$) than MD ($n = 20$). Across studies, overactivation for reading and math occurred in the right insula and inferior frontal gyrus for atypically developing (AD) > TD comparisons, albeit in slightly different areas of these regions; however, inherent threshold variability across imaging studies could diminish overlying regions. For TD > AD comparisons, there were no similar or overlapping brain regions. Results indicate there were domain-specific differences for RD and MD; however, there were some similarities in the ancillary recruitment of executive functioning skills. Theoretical and practical implications for researchers and educators are discussed.

Key words: fMRI; reading disabilities; math disabilities; dyslexia; dyscalculia; meta-analysis.

Introduction

Children's reading and math skills are critical to their future educational outcomes, career readiness, and overall health and well-being (DeWalt et al. 2004; Cain and Oakhill 2006; Krajewski and Schneider 2009; Geary 2011; Ritchie and Bates 2013; ACT 2020; Heilmann 2020), yet many children struggle with developing math and reading skills (National Center for Education Statistics 2020). Complexities in the derivation and behavioral presentation of learning disabilities contribute to difficulties with identification, prognosis, and treatment (Branum-Martin et al. 2013; Fletcher et al. 2019). Consequently, discrepancies in the descriptions and outcomes of atypical populations are observed across studies. Efforts to better elucidate distinctions and overlap among learning difficulties are ongoing, with the ultimate objective of developing treatments to bolster the neurocognitive mechanisms that support academic skills (Peters and Ansari 2019; Peterso et al. 2021). Much remains to be learned, particularly regarding the neurobiological underpinnings of reading and math difficulties (MD), an understanding of which could support the development of evidence-based interventions for those struggling to learn.

The multiple deficit model encompasses the complexity of multiple predictors contributing to learning disabilities, including shared risk factors that possibly account for comorbidity in learning disorders (Pennington 2006; Peterson et al. 2017). This model is supported by the behavioral literature, outlining distinct (domain-specific), and shared (domain-general) features in disorders of reading and math (Cirino et al. 2018). For instance, those with reading difficulties (RD) may display deficits in word reading, while those with MD may struggle with numerical processing. In addition, domain-general, executive function skills that are high-level cognitive processes, such as inhibition, working memory, and cognitive flexibility/shifting (Miyake et al. 2000), are recruited for complex tasks such as reading and math (Diamond 2013; Coulacoglou and Saklofske 2017). Poor executive functioning may be present for those with RD and MD (Peng and Fuchs 2014; Slot et al. 2016; Child et al. 2019). In isolation, both RD and MD have been associated with differences in neurobiology relative to typically developing (TD) learners (Kaufmann et al. 2011; Richlan et al. 2011). While a meta-analysis has compared typical reading and math functional neurobiology (Pollack and Ashby 2018), and descriptive/qualitative approaches to synthesizing across RD and MD studies have been undertaken (Grant et al. 2020), there are no published meta-analyses directly comparing RD and MD in study designs with a TD control. The current meta-analysis aims to uncover functional similarities and distinctions between RD and MD across the neuroimaging literature to advance understanding of the underlying mechanisms that contribute to learning difficulties. Findings from such a meta-analytic approach can ultimately facilitate improved methods of identification, classification, and treatment of learning difficulties.

Review of reading difficulties

Skilled readers have been studied extensively. During reading tasks, TD readers recruit brain regions in a well-established left hemisphere "reading network" (see Fig. 1) during reading (Jobard et al. 2003; Richlan et al. 2009; Price 2012; Norton et al. 2014; Martin et al. 2016; Kearns et al. 2019). The occipitotemporal region (largely within the fusiform gyrus) is understood to process

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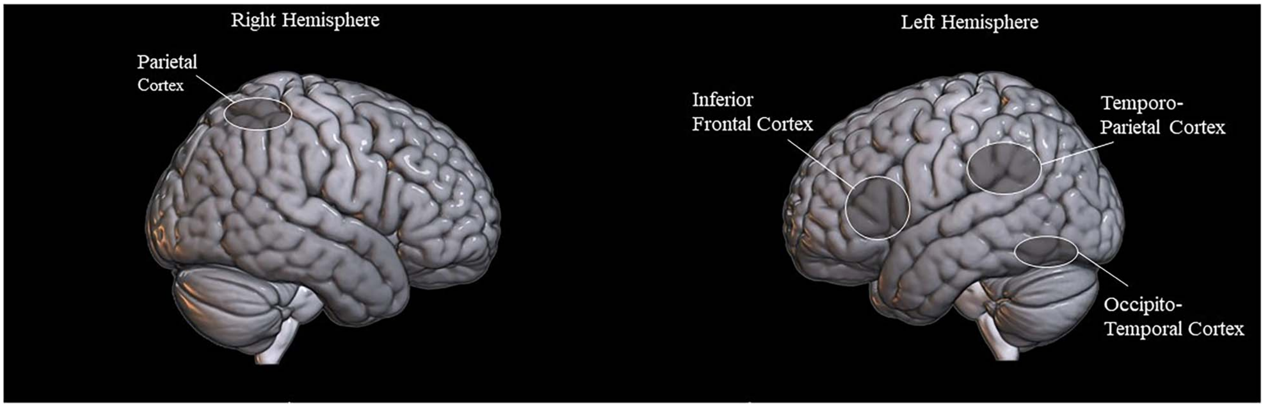

Domain-Specific Regions	Reading	Math
Right Hemisphere		**Parietal Cortex** Intraparietal Sulcus
Left Hemisphere	**Inferior Frontal Cortex** Inferior Frontal Gyrus **Temporo-Parietal Cortex** Supramarginal Gyrus, Angular Gyrus, Posterior Middle Temporal Gyrus, Superior Temporal Sulcus **Occipito-Temporal Cortex** Fusiform Gyrus, Middle Temporal Gyrus, Lingual Gyrus, Inferior Temporal Gyrus	

Fig. 1. Domain-specific brain activation for typical reading and math.

familiar visual information and contains the area referred to as the visual word form area (Kronbichler et al. 2004). The temporoparietal region (areas of the supramarginal, angular, posterior middle temporal, and superior temporal gyri) is thought to support the linkage of phonemes and graphemes for word decoding, and may also involve semantic associations (Price 2012). The inferior frontal region has multiple language-related functions, believed to be involved in sound sequencing, word representation, and articulation (Pugh et al. 2000; Richlan et al. 2011). Meta-analysis has supported a dual-route model of reading; a direct route linking prelexical processing regions with regions designated in semantic processing, and an indirect route that requires the additional recruitment of brain regions associated with executive functioning, particularly working memory (Jobard et al. 2003), with route designation presumably related to automaticity and reading fluency. Common brain signatures, with limited language-specific variation, are found across languages, suggesting that there are universal patterns of functional activation for phonological and semantic processing in tasks presented in English, Spanish, Hebrew, and Chinese (Rueckl et al. 2015). As the general reading network has been so consistently substantiated, it makes sense to explore if and how brain activity in less skilled readers differs from TD.

Reading comprehension, the ultimate goal of reading, requires the integration of word reading skills and oral language abilities (Gough and Tunmer 1986; Hoover and Gough 1990), as well as executive function skills (working memory; Cutting et al. 2015; Peng et al. 2018; Peng and Kievit 2020). Individuals with RD may display deficits in one or more of these components (Cain and Oakhill 2006; Carroll and Snowling 2004; Beneventi et al. 2010a), rendering endeavors to understand the underlying neural mechanisms of RD quite challenging. Yet, a growing number of studies have contributed to identifying neurobiological differences between RD and TD. In meta-analyses that explored the neurological biases of dyslexia, results indicated that typical readers tend to display greater functional activation of the reading network in the left hemisphere compared to those with dyslexia (Maisog et al. 2008). Additionally, compared to typical readers, readers with dyslexia were more inclined to recruit resources from the right hemisphere of the brain, perhaps as compensatory engagement (Maisog et al. 2008). Compared to TD, RD brain activation is also more varied, requiring a more nuanced interpretation than that of TD (Barquero et al. 2014; Perdue et al. 2022). It remains unclear how specific RD is to the reading network or whether it may be associated with generalized deficits that propagate impact across academic skills. The current meta-analysis offers additional critical insights as it compares atypical readers to those with atypical math abilities to determine similar and distinct mechanisms across types of learning difficulties (and in the process also provides updates of prior meta-analyses in reading with the recent literature). These could provide critical insights for educators and researchers to provide more targeted instructional strategies to students struggling to read.

Review of math difficulties

Compared to reading, much less is known about the development and mechanisms of math (Hulme and Snowling 2013). Similar to proficient readers, skilled mathematical problem solvers may employ various math-specific and domain-general skills, including math knowledge of concepts and math vocabulary, procedural calculation skills, and executive functioning (Geary 2000). Again, recent momenta in neuroimaging literature have contributed to our understanding of math. Across studies with TD populations, activation of the intraparietal sulcus (IPS; see Fig. 1) is associated with magnitude comparison tasks and solving math problems, such as addition and multiplication (Sokolowski et al. 2017;

Chochon et al. 1999). In a recent meta-analysis, frontal regions were also recruited during magnitude comparisons regardless of number format (digits, dots, size), while format specialization was observed in parietal regions (Sokolowski et al. 2017). In number and calculation tasks, recruitment of brain regions associated with executive functioning were also engaged (Arsalidou and Taylor 2011). Finally, the left fusiform gyrus, an area known more for visual word recognition, is also activated during number and calculation tasks (Arsalidou and Taylor 2011). Together these findings highlight the domain-specific, as well as domain-general, resources essential in mathematics.

Cognitive theories of MD suggest that the core deficits could be specific to math (processing quantity, number sense), or domain-general (working memory, attention) (Ashkenazi et al. 2013). Similar to the dual-route model of reading that suggests a less efficient mode for those struggling to read, those with MD may display a delayed transition, or inefficient use, of math strategies. For instance, those with MD display under activation in the left supramarginal gyrus (Evans et al. 2014), and employ greater activation in executive functioning areas (Davis et al. 2009) during calculation, suggesting increased effort. In a prior math meta-analysis, one analysis compared the math competency of MD to TD with a small sample of studies (Kaufmann et al. 2011). Activation in the left temporal and occipital regions as well as the left and right parietal and frontal regions were consistent across studies; however, whether MD displayed over or under activation varied with studies (Kaufmann et al. 2011). The current meta-analysis expands these findings to include the recent insurgence of imaging studies in math, and therefore addresses these inconsistencies, and further examines MD and RD together to extend our understanding of the underlying neural mechanisms of reading and math.

Significance of this study

Prior work in the reading and math literature indicates that each domain has designated brain regions for processing. Distinctively, while the left hemisphere “reading network” is recruited during reading tasks (Jobard et al. 2003), solving math problems employs math-specific regions in the right hemisphere (Chochon et al. 1999; Sokolowski et al. 2017). Such distinctions suggest that reading and math each have domain-specific mechanisms. On the other hand, there seems to be evidence for overlap in reading and math components (Peters et al. 2018). For instance, letters and numbers may both require the recruitment of similar visual recognition brain regions, including the left fusiform gyrus (Arsalidou and Taylor 2011). Additionally, behavioral and neurobiological findings indicate that executive functioning is crucial for both reading (Jobard et al. 2003; Peng et al. 2018; Wang et al. 2020) and math (Arsalidou and Taylor 2011; Peng et al. 2016).

In the current study, we identify consistencies across functional neuroimaging studies regarding common and unique brain regions/networks for individuals with RD and MD compared to TD individuals. This overarching goal is supported through 3 aims. First, we aim to compile the relevant studies and provide a comprehensive overview of the neurobiological correlates of RD and MD as each compare to TD. Presented as a tabular summary, such an overview allows for qualitative exploration of similitudes among studies, serving to broaden understanding of the neural patterns of RD and MD. Second, we aim to compare the neurobiological correlates of RD and MD with TD through the more quantitative approach of activation likelihood estimate (ALE) meta-analysis, revealing how activation patterns in each atypical group compare with TD. Third, also using ALE of functional activation, we aim to compare RD to MD. This aim allows us to examine common and unique underlying mechanisms of RD and MD, potentially revealing the recruitment of domain-general neural mechanisms in learning difficulties that align with behavioral recruitment of executive function skills in RD and MD. Finally, focal follow-up analyses will be conducted to address how specific types of tasks and developmental age differences may influence the activation of brain regions (Geary 2004; Tilstra et al. 2009).

Materials and methods

Data collection

Guidelines outlined for best practices in neuroimaging meta-analysis were followed (Müller et al. 2018). First, a systematic search of the literature was conducted to identify studies that examined the activation of brain regions in individuals with reading or MD while completing a task. The tasks included those specific to math or reading (domain-specific), and those that were domain-general (executive functioning). Electronic databases, including Education Database, Linguistics Database, Psychology Database, Proquest Dissertations & These Global, PsycINFO, Education Collection, and Linguistic Collection were utilized to perform the initial search. The first line of search terms targeted the appropriate methodology for the research question using the following terms: fMRI OR “functional magnetic resonance imaging” OR “brain imaging” OR neuroimaging OR “magnetic resonance imaging” OR MRI OR “positron emission tomography” OR PET. The second line of search terms attempted to capture the relevant population using the following terms: “learning disabilit*” OR dyslexia OR dyslexic* OR “reading disabilit*” OR “reading difficult*” OR dyscalculia OR “math* disabilit*” OR “math* difficult*.” Conducted in October 2019, this initial search was limited to papers available in English and those who had at least a preprint available in October 2019 or earlier. This resulted in 5095 research items which included, journal articles, book chapters, dissertations, and conference proceedings (see Fig. 2 for PRISMA flowchart). After the removal of duplicates, 4,505 research items remained. Items were then hand-sorted according to relevance, using article titles, into 2 categorical groups: no and maybe. Articles sorted into the maybe group, which consisted of 557 articles, were screened to determine fit based on the eligibility criteria.

The following criteria had to be met for a study to be included in the meta-analysis: 1) represented original research (not a review); 2) included at least 1 measure of functional whole-brain imaging; and 3) included at least 1 group of participants with atypical reading or math with a comparison to a TD sample. We included participants that were identified as at-risk or with a learning difficulty or disability in reading or math to obtain a wide spectrum of atypical reading and math. This includes participants with a family history of learning disabilities, genetic disorders specifically associated with learning disabilities (Turner syndrome; Mazzocco and Hanich 2010), and individuals that use inefficient strategies (use of counting rather than retrieval; Berteletti et al. 2014; Evans et al. 2014). Exclusion criteria included: 1) studies that included participants with learning impairment resulting from a brain injury or other disorders with varying academic profiles (autism spectrum disorder); 2) studies that did not conduct a direct atypical to typical group comparison; and 3) studies that did not disaggregate participants with learning difficulties/disabilities and TD participants in the results.

In addition to the systematic electronic search, a hand search was conducted. First, an examination of published meta-analyses

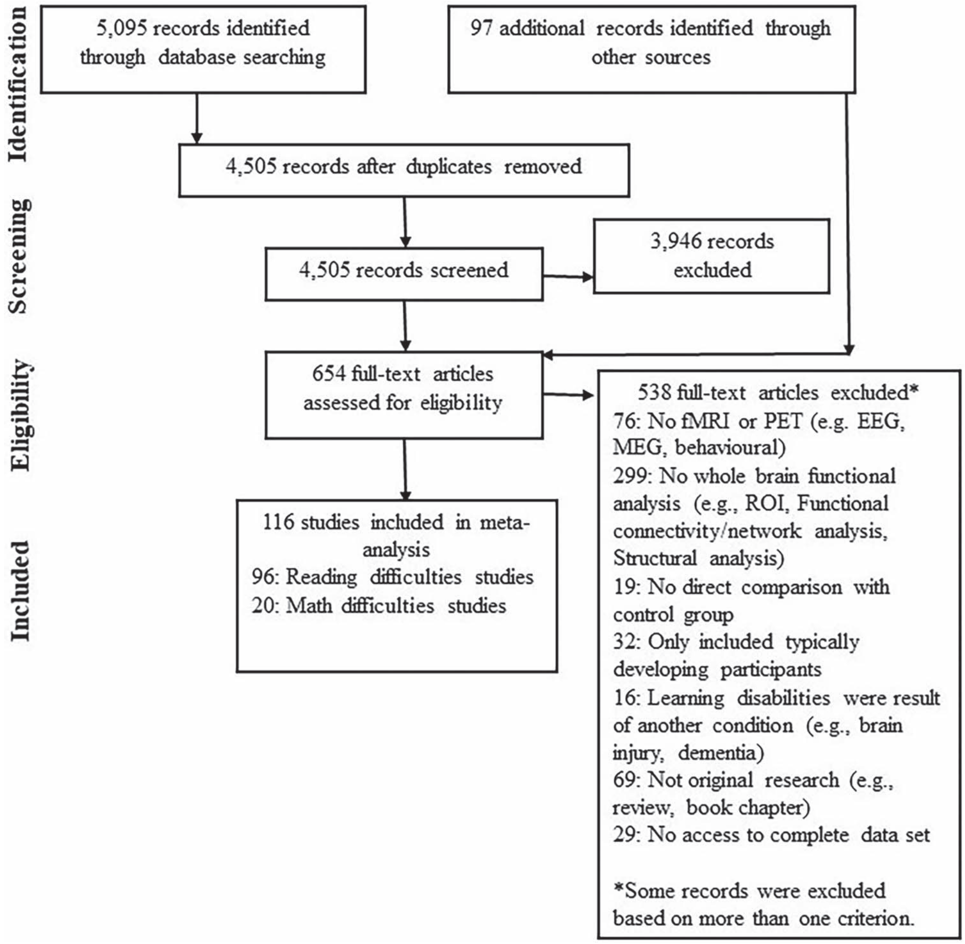

Fig. 2. PRISMA flowchart.

in reading (Maisog et al. 2008; Richlan et al. 2009, 2011; Paulesu et al. 2014; Pollack et al. 2015; Martin et al. 2016) and math (Kaufmann et al. 2011) discovered during the initial search were evaluated. A backward ancestral search examined studies cited in the reference lists of the qualifying articles to determine eligibility. Next, a forward ancestral search was completed using Google Scholar, by searching the publication list for the first author and the list of the articles that cited each of the qualifying articles. Articles obtained from the search were examined using the inclusion/exclusion criteria to determine eligibility. Finally, hand searches of reoccurring journals of the included article (*Behavioral and Brain Function, Brain, Brain and Language, Cerebral Cortex, Cortex, Developmental Cognitive Neuroscience, Developmental Neuropsychology, Journal of Cognitive Neuroscience, NeuroImage, NeuroImage: Clinical, Neuropsychologia, PLoS One, Proceedings of the National Academy of Sciences*) were reviewed for the last 5 years (from October 2014 to October 2019) to determine if any other articles would qualify to be included in the synthesis using the inclusion/exclusion criteria. The hand search resulted in the addition of 97 articles that were reviewed for inclusion. Figure 2 outlines the identification process, screening, and eligibility process, including the details of why studies were excluded.

Data analysis

Main analyses. Four initial meta-analyses were conducted using ALE (Laird et al. 2005, 2009; Turkeltaub, Eickhoff, et al. 2012): 2 for RD and 2 for MD, each being compared to TD individuals, and indicating over and under-activation. BrainMap GingerALE version 3.0.2 (Eickhoff et al. 2009, 2012; Turkeltaub, Benson, et al. 2012) was used to conduct ALE meta-analyses. In preparation for the ALE meta-analysis, coordinates in either Talairach or MNI neuroimaging were entered into a REDCap database (Harris et al. 2009, 2019) and checked by a second researcher for accuracy. These coordinates were then exported and used to create the text files entered into GingerALE for analyses. Coordinates reported in Talairach space were converted to MNI with GingerALE software. Duplicate data reported in published dissertations and journal articles were only included in the analysis once (Temple 2001; Temple et al. 2001; Kast 2011; Kast et al. 2011).

ALE aims to identify convergent clusters of foci with significantly higher activation differences as compared to a random spatial null distribution. GingerALE uses the foci coordinates reported in the studies to construct 3D Gaussian kernels, with the foci weighted by the number of participants in each study. Modeled activation maps are generated by combining the probabilities of the reported foci (Turkeltaub, Eickhoff, et al. 2012). The activation maps are used to calculate ALE scores that represent the convergence of activation foci across experiments. ALE scores are compared to a null distribution, constituted by a random spatial association among experiments. A cluster-level family-wise error (FWE) threshold of $P < 0.05$ and voxel-level of $P < 0.001$ were used, with 1,000 thresholding permutations run, in accordance with recommended thresholding (Eickhoff et al. 2012, 2016) and in line with several recent studies that employed GingerALE across multiple disciplines that have used the same thresholding

(Arioli et al. 2022). For visualization of clusters, we used Mango (http://ric.uthscsa.edu/mango/).

Post-hoc analyses. In addition to the 4 main analyses (MD vs. TD and RD vs. TD under activation and overactivation), several follow-up analyses were conducted to examine developmental and task-related differences in RD and MD. First, a post-hoc analysis was conducted to examine developmental differences between children and adults with RD compared to TD. Studies that included participants younger than 18 years of age were classified as children and those with participants 18 years of age or older were classified as adults. Studies that did not disaggregate children and adult participants were excluded from this analysis. Though there were not enough math studies with adults to examine developmental differences between children and adults with MD compared to TD, a post-hoc analysis was conducted to examine children with MD compared to TD. Second, post-hoc analyses were conducted to examine task differences in the reading studies. An analysis was conducted to examine the activation for RD on tasks that did not include reading, early literary, and oral language. This analysis included the following types of tasks: working memory, tone counting, visual/movement processing, serial reaction time, motor sequencing, spatial visualization, and implicit motor learning tasks. There were not enough studies to conduct a similar analysis for math studies. Finally, a post-hoc analysis was conducted to examine active tasks (tasks requiring a response from the participants) in reading. None of the math studies included passive tasks (tasks that did not require a response from participants), so a similar analysis was not conducted for math studies.

To further examine the similarities and distinctions between RD and MD compared to TD, two additional post-hoc analyses were conducted. First, Neurosynth (neurosynth.org), a meta-analysis tool utilized for examining consistent brain activations across studies, was employed to extract "association test" maps of brain activations to determine if any overlapping areas were linked to specific executive function components (working memory, attention, inhibition, and shifting). A voxel-level threshold of $P < 0.01$ with FDR correction (Yarkoni et al. 2011) was used. Second, given that the literature largely supports the specificity of the putative Visual Word Form Area (pVWFA) to proficiently identify words during reading (Cohen et al. 2000; Dehaene and Cohen 2011) and the IPS to adequately process numbers during math (Arsalidou and Taylor 2011), we sought to further interrogate the specificity of these 2 areas for RD vs. MD. Thus, post-hoc analyses were conducted to examine the functional specificity of pVWFA and the IPS for RD and MD, compared to TD. The pVWFA was defined as a sphere centered at ($x = -44$, $y = -58$, $z = -15$) with a radius equal to 5 mm (Vigneau et al. 2005) and the IPS was centered at ($x = 36$, $y = -48$, $z = 48$) with a 5 mm radius (Sokolowski et al. 2017).

Results

An overview of the studies ($n = 116$) included in the meta-analyses are reported in Table 1 (included studies are designated with * in the reference section). Studies were categorized as a reading or math study, based on the atypical sample included in the study. Description and grouping criteria for atypical reading (RD) and math (MD) varied across studies. There were markedly more studies with individuals with RD ($n = 96$) than studies with individuals with MD ($n = 20$). Participants included in the studies spanned in age from elementary school to adulthood, yet elementary students represented the majority of the studies in both reading and math. All of the tasks in the math studies were active, while some (~9%) of the reading studies were passive and did not require participants to respond to the stimuli (listening to letter sounds). The reading studies included tasks presented visually, auditory, or with dual-modality, yet the math studies were presented either with visually or with dual visual and auditory modality. Although most of the studies included domain-specific tasks (i.e. reading or math), other tasks were also included (working memory, tone discrimination). Baseline tasks also differed across studies (see Tables 2 and 5), ranging from passive fixation to tasks more closely aligned to the active task to control for unrelated processing.

Table 1. Summary of studies ($n = 116$).

	Atypical reading ($N = 96$)		Atypical math ($n = 20$)	
Characteristic	*n*	%	*n*	%
Age level[a]				
Elementary students	45	37.50	15	71.43
Middle school students	28	23.33	2	9.52
High school students	11	9.17	0	0.00
Adult	36	30.00	4	19.05
Modality[a]				
Visual	66	68.75	19	95.00
Auditory	23	23.96	0	0.00
Dual	7	7.29	1	5.00
Engagement[a]				
Active	87	90.63	20	100.00
Passive	9	9.37	0	0.00
Types of tasks[a]				
Language	82	82.00	0	0.00
Math	1	1.00	17	77.27
Working memory	3	3.00	2	9.09
Other	14	14.00	3	13.64

[a] Several studies included more than one category.

Reading studies

Details of included reading studies are in Table 2.

Under activation for RD (TD > RD)

There were 85 studies, representing 762 foci and 2,853 participants, that reported under activation of RD compared to TD that were entered into the first initial analysis for reading. This resulted in 2 significant clusters in the left hemisphere (see Table 3; Fig. 3, Panel A). There were 39 studies, that included participants from 5 to 63 years, that contributed to the first cluster (12,888 mm^3). This cluster in the fusiform/temporal/inferior parietal regions was from (−64, −72, −26) to (−32, −26, 52) centered at (−48.9, −53.2, 3) with a max value at (−46, −58, −16), and included early literacy, reading, oral language, working memory, visual and motion processing, and math fact verification tasks. The second cluster (3,016 mm^3) in the middle and inferior frontal, and precentral regions was from (−52, −6, 18) to (−36, 22, 46) centered at (−43.4, 6.6, 33.7) with a max value at (−44, 6, 36). There were 15 contributing studies that included participants from 8 to 38 years. Tasks represented in this cluster included early literacy, reading, oral language, motion processing, auditory discrimination, and working memory tasks.

Table 2. Studies that include individuals with RD organized by age.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
Norton (2012)	fMRI	43	Range: 4–6 Mean: 5.54	At-risk for dyslexia	Normed assessment <25%ile	Phonological task (First sound matching/voice matching)	Auditory and visual (dual-modality)	Active	Letter sounds, pictures (English)
						One-back task (Letters/false fonts)	Visual	Active	Letter, false fonts (English)
Yu et al. (2020)	fMRI	69	Range: NR Mean: TD = 5.41 AD = 5.5	Family history of dyslexia	Self-report	Phonological task (First sound matching for word and image/voice matching)	Auditory and visual (dual-modality)	Active	Spoken words, pictures (English)
Powers et al. (2016)	fMRI	50	Range: NR Mean: TD = 5.4 AD = 5.6	Family history of developmental dyslexia	Self-report	Phonological task (First sound matching/voice matching)	Auditory and visual (dual-modality)	Active	Letter sounds, pictures (English)
Raschle et al. (2012)	fMRI	36	Range: NR Mean: TD = 5.56 AD = 5.70	Family history of developmental dyslexia	Self-report	Phonological task (First sound matching/voice matching)	Auditory and visual (dual-modality)	Active	Letter sounds, pictures (English)
Yamada et al. (2011)	fMRI	27	Range: NR Mean: TD = 5.7 AD = 5.6	At-risk for later reading difficulties	Normed assessment < 35%ile	One-back task (Letters/false fonts)	Visual	Active	Letters, false fonts (English)
Raschle et al. (2013)	fMRI	28	Range: NR Mean: TD = 5.6 AD = 5.75	Family history of developmental dyslexia	Self-report	Auditory processing task (High frequency of speech sounds/low frequency) Phonological task (First sound matching/voice matching)	Auditory	Active	Speech sounds (English)
Specht et al. (2009)	fMRI	33	Range: NR Mean: 6.6	At-risk for developing dyslexia	Self-report	Semantic judgment task (Pictures/blank screen) Semantic judgment Task (Logos/blank Screen) Semantic judgment task (Words/blank screen)	Visual	Active	Pictures (Norwegian) Logos (Norwegian) Words (Norwegian)
Plewko et al. (2018)	fMRI	85	Range: 5–8 Mean: TD = 6.89 AD = 6.92	Family history of dyslexia	Self-report	Phonological task (Congruent letter & Sounds/incongruent letter & sounds)	Auditory	Passive (with attending task)	Letters, letter sounds (Polish)
Monzalvo et al. (2012)	fMRI	46	Range: 8–10 Mean: TD = 115 months AD = 118 months	Dyslexia	Dx (INSERM criteria)	Visual language task (Viewing words & pictures/blank screen)	Visual	Passive (with attending task)	Words, pictures (French)
Bach et al. (2010)	fMRI	32	Range: NR Mean: 8.3	Poor readers	Normed assessment ≤25%ile	Lexical task (Word vs. nonword) Decision task (Phonological manipulation/no phonological manipulation)	Visual	Active	Words, pseudowords (German)
Maurer et al. (2011)	fMRI	27	Range: NR Mean: T1 TD = 8.3 AD = 8.3 T3 TD = 11.3 AD = 11.5	Dyslexia	Normed assessment <10%ile	Repetition task (Words/symbols)	Visual	Active	Words, symbols (German)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
Farris et al. (2016)	fMRI	31	Range: 6–14 Mean: 9.35	Dyslexia	Dx	Rhyming task (Picture rhyming/color matching)	Visual	Active	Pictures (English)
Blau et al. (2010)	fMRI	34	Range: NR Mean: TD = 9.43 AD = 9.39	Dyslexia	IQ/performance discrepancy	Phonological task (Congruent letter sounds and letters/incongruent letter sounds and letters)	Auditory visual	Passive with attending task	Letters, letter sounds (Dutch)
Heim et al. (2010)	fMRI	40	Range: NR Mean: 9.5	Dyslexia	Dx (ICD-10 criteria)	Phonological task (First sound matching/passive fixation)	Auditory	Active	Words, pseudowords (German)
						Motion detection task (Dot pattern motion change/passive fixation)	Visual	Active	Dot patterns (German)
						Attention shifting task (Posner paradigm/passive fixation)	Visual	Active	German (symbol)
						Auditory discrimination task (Speech sound matching/passive fixation)	Auditory	Active	Speech sounds (German)
Grande et al. (2011)	fMRI	45	Range: NR Mean: TD = 9.5 AD = 9.7	Dyslexia	Normed assessment ≤10%ile	Reading and oral language task (Word reading and picture naming low frequency/word reading and picture naming high frequency)	Visual	Active	Words, pictures (German)
						Word reading task (Reading words/picture naming)	Visual	Active	Words, pictures (German)
van Ermingen-Marbach et al. (2013)	fMRI	44	Range: 8–11 Mean: TD = 9.6 AD = 9.9	Reading deficits	Normed assessment	Phonological task (Phoneme presence/auditory directional decision)	Auditory	Active	Letter sounds (German)
Heim et al. (2015)	fMRI	45	Range: 8.7–11.2 Mean: 9.9	Dyslexia	Normed assessment “on average worse”	Reading task (Word reading aloud/passive fixation)	Visual	Active	Words (German)
Langer et al. (2019)	fMRI	30	Range: 8.3–12.5 Mean: TD = 9.9 AD = 10	Reading difficulties	Dx	Reading task (Read sentence and select matching picture/letter discrimination)	Visual	Active	Words, letters (English)
You et al. (2011)	fMRI	28	Range: 8–11 Mean: TD = 10.0 AD = 9.9	Impaired readers	Normed assessment <25%ile	Orthographic task (Letter match/passive fixation)	Visual	Active	Letters (English)
						Rhyming task (Letter rhyming/crosshair fixation)	Visual	Active	Letters (English)
Roe et al. (2018)	fMRI	108	Range: 8–11 Mean: TD = 9.93 AD = 10.14	Struggling readers	Normed assessment < 25%ile	Reading task (Sentence plausibility judgment/passive fixation)	Visual	Active	Words (English)
Olulade et al. (2015)	fMRI	28	Range: NR Mean: TD = 10.1 AD = 10.0	Dyslexia	Normed assessment ≤30%ile	Visual processing task (Tall letter identification in real words/passive fixation); (Tall letter identification in false fonts/passive fixation)	Visual	Active	Words (English)
Langer et al. (2015)	fMRI	30	Range: NR Mean: TD = 10.5 AD = 9.8	Reading disabilities	Dx	Phonological task (First sound matching/voice gender matching)	Auditory	Active	Words (English)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
Evans (2013)	fMRI	28	Range: NR Mean: TD = 10.2 AD = 10.4	Developmental dyslexia	Childhood history of dyslexia; normed assessment ≤30%ile	Visual processing task (Tall letter identification in words/tall letter identification in false fonts)	Visual	Active	Words (English)
Hoeft et al. (2006)	fMRI	30	Range: 8–12 Mean: 10.4	Dyslexia	Normed assessment ≤1 SD	Rhyming task (Word rhyming/passive fixation)	Visual	Active	Words (English)
Hancock et al. (2016)	fMRI	45	Range: 8–12 Mean: TD = 10 AD = 10.7	Poor readers	IQ/performance discrepancy	Rhyming task (Word rhyming/passive fixation)	Visual	Active	Words (English)
Evans et al. (2014)	fMRI	28	Range: NR Mean: TD = 10.21 AD = 10.37	Developmental dyslexia	Dx normed assessment ≤30%ile	Math verification task (Single digit addition & subtraction/pseudofont matching before and after equal sign)	Visual	Active	Digits, pseudo font characters (English)
Gaab et al. (2007)	fMRI	45	Range: NR Mean: TD = 10.5 AD = 10.8	Developmental dyslexia	Dx normed assessment ≤16%ile	Auditory processing task (Rapid or slow frequency of speech sounds determination)	Auditory	Active	Speech sounds (English)
Meyler et al. (2008)	fMRI	35	Range: NR Mean: TD = 10.8 AD = 10.8	Poor readers	Normed assessment <30%ile	Reading task (Sentence plausibility judgment/passive fixation)	Visual	Active	Words (English)
Meng et al. (2015)	fMRI	25	Range: 9.3–12.1 Mean: 10.85	Reading impaired	Normed assessment <25%ile	Rhyming task (Word rhyming/tone discrimination)	Auditory	Active	Words (English)
Siok et al. (2008)	fMRI	24	Range: NR Mean: TD = 11 AD = 10	Dyslexia	School performance	Rhyming task (Character rhyming/font size judgment)	Visual	Active	Characters (Chinese)
Temple et al. (2001)	fMRI	39	Range: 8–12 Mean: TD = 10.5 AD = 10.7	Dyslexia	History of reading difficulty; normed assessment	Letter match task (Letter matching/line matching)	Visual	Active	Letters, lines (English)
Siok et al. (2004)	fMRI	16	Range: 10–12 Mean: TD = 11.08 AD = 10.92	Reading impaired	School performance	Phonological task (Homophone judgment/font size judgment)	Visual	Active	Characters (Chinese)
						Lexical decision task (Character, non-character/passive fixation)	Visual	Active	Characters (Chinese)
Cao et al. (2018)	fMRI	58	Range: 10.11–12.03 Mean: TD = 11.03 AD = 11.11	Developmental dyslexia	Normed assessment ≤1 SD	Lexical task (Second character matching/crosshair color change detection)	Visual	Active	Words (Chinese)
						Perceptual task (Symbol matching/crosshair color change detection)	Visual	Active	Tibetan symbols (Chinese)
van der Mark et al. (2009)	fMRI	42	Range: 9–12 Mean: TD = 11.3 AD = 11.4	Dyslexia	Normed assessment <10%ile	Lexical decision task (Pseudohomophones/ passive fixation) (False-fonts/words) (Pseudohomophones/ words)	Visual	Active	Words, nonwords (German)
Schulz et al. (2008)	fMRI	45	Range: NR Mean: TD = 11.4 AD = 11.6	Dyslexia	Normed assessment <10%ile	Reading task (Sentence plausibility judgment task congruent items/passive fixation); (Sentence plausibility judgment congruent items/incongruent items)	Visual	Active	Words (German)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
Schulz et al. (2009)	fMRI	52	Range: 10–12 Mean: 11.5	Dyslexia	Normed assessment <10%ile	Reading task (Sentence plausibility judgment congruent items/passive fixation); (Sentence plausibility judgment congruent items/incongruent items)	Visual	Active	Words (German)
Bolger et al. (2008)	fMRI	24	Range: 8–15 Mean: TD = 11.06 AD = 11.9	Impaired readers	Normed assessment ≤25%ile	Rhyming task (Word rhyming with orthographic match/letter string matching) Rhyming task (Word rhyming with phonological match/letter string matching)	Visual	Active	Words (English)
Cao et al. (2017)	fMRI	43	Range: 10.47–12.03 Mean: TD = 11.20 AD = 11.14	Developmental dyslexia	Normed assessment ≤1 SD	Rhyming task (Second syllable word rhyming/tone matching)	Auditory	Active	Words (Chinese)
Norton et al. (2014)	fMRI	90	Range: 8.2–12.6 Mean: NR	Developmental dyslexia	Normed assessment <25%ile	Rhyming task (Word rhyming/word semantic judgment)	Visual	Active	Words (English)
Rimrodt et al. (2008)	fMRI	29	Range: 9–14 Mean: TD = 11.81 AD = 11.69	Reading difficulties	Normed assessment ≤25%ile	Reading task (Sentence plausibility judgment/word 1-back paradigm)	Visual	Active	Words (English)
Mohl et al. (2015)	fMRI	38	Range: NR Mean: TD = 11.7 AD = 12.2	Reading disabilities	IQ/performance discrepancy	Rhyming task (Word rhyming/passive fixation)	Visual	Active	Words (English)
Liu et al. (2012)	fMRI	22	Range: NR Mean: TD = 11.75 AD = 12.05	Reading disabilities	Normed assessment	Rhyming task (Character rhyming/character matching)	Visual	Active	Characters (Chinese)
Yang et al. (2013)	fMRI	21	Range: NR Mean: TD = 12.24 AD = 12.63	Developmental dyslexia	Normed assessment ≤1.5 SD	Motor task (Serial reaction time sequential block/random block)	Visual	Active	Pictures (Chinese)
Cao et al. (2008)	fMRI	24	Range: 8.9–14.11 Mean: 12.3	Reading difficulties	Dx	Rhyming task (Word rhyming/symbol string matching)	Visual	Active	Words (English)
Cutting et al. (2013)	fMRI	51	Range: 10–14 Mean: 12.06	Dyslexia	Normed assessment ≤25%ile	Lexical decision task (Low-frequency/high-frequency words)	Visual	Active	Words, pseudowords (English)
Booth et al. (2007)	fMRI	30	Range: 9–15 Mean: NR	Reading disorder	Dx of learning disability	Semantic related judgment task (Words/passive fixation)	Visual	Active	Words (English)
Tanaka et al. (2011)	fMRI	131	Range: 7.7–16.9 Mean: 13.4	Poor readers	Normed assessment ≤25%ile	Rhyming task (Word rhyming/passive fixation)	Visual	Active	Words (English)
Beneventi et al. (2010b)	fMRI	26	Range: NR Mean: TD = 13.5 AD = 13.2	Dyslexia	Normed assessment ≤25%ile	Working memory task (n-back/blank screen)	Visual	Active	Letters (Norwegian)
Beneventi et al. (2009)	fMRI	24	Range: NR Mean: TD = 13.5 AD = 13.2	Dyslexia	Normed assessment ≤16%ile	Working memory task (Sequence order probe/blank screen)	Visual	Active	Letters (Norwegian)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
Beneventi et al. (2010a)	fMRI	24	Range: NR Mean: TD = 13.5 AD = 13.2	Dyslexia	Normed assessment ≤16%ile	Working memory task (n-back/blank screen)	Visual	Active	Letter sounds, pictures (Norwegian)
Grünling et al. (2004)	fMRI	38	Range: NR Mean: TD = 13.31 AD = 13.92	Dyslexia	NR	Rhyming task (Pseudoword rhyming/letter string matching)	Visual	Active	Pseudowords, letter strings (NR)
Georgiewa et al. (1999)	fMRI	34	Range: 9–17 Mean: 14	Developmental dyslexia	Dx (ICD-10 criteria)	Reading task (Word reading/letter string reading) (Nonword reading/letter string reading)	Visual	Active	Words, nonwords (German)
Hoeft et al. (2007)	fMRI	53	Range: 7–16 Mean: 14.4	Dyslexia	IQ/performance discrepancy	Rhyming task (Word rhyming/passive fixation)	Visual	Active	Words (English)
Hu et al. (2010)	fMRI	37	Range: 12.1–16 Mean: NR	Developmental dyslexia	Dx (English); School performance (Chinese)	Semantic judgment (English/Chinese)	Visual	Active	Words (English, Chinese)
						Oral language task (Picture naming/symbol matching)			Pictures (English, Chinese)
						Reading task (Read words aloud/symbol matching)			Words (English, Chinese)
Kronbichler et al. (2006)	fMRI	28	Range: 14–16 Mean: TD = 15.46 AD = 15.89	Severe reading fluency impairment	Normed assessment <11%ile	Reading task (Sentence plausibility judgment/false font matching)	Visual	Active	Words (German)
Kronschnabel et al. (2013)	fMRI	35	Range: NR Mean: TD = 15.9 AD = 16.1	Dyslexia	Normed assessment <20%ile	Passive lexical task (Viewing words and letters/passive fixation)	Visual	Passive (with attending task)	Words, letters (German)
Kronschnabel et al. (2014)	fMRI	35	Range: NR Mean: TD = 15.8 AD = 16.1	Dyslexia	Normed assessment	Passive lexical task (Viewing letters and listening to letter sounds/passive fixation)	Auditory and visual (uni- and dual modality)	Passive (with attending task)	Letters, letter sounds (German)
Richlan et al. (2010)	fMRI	33	Range: 16–20 Mean: TD = 17.89 AD = 18.09	Dyslexia	Normed assessment <10%ile	Lexical decision task (Word, passive fixation)	Visual	Active	Words, pseudowords (German)
Vasic et al. (2008)	fMRI	25	Range: 16–21 Mean: 18.3	Dyslexia	Childhood history of developmental dyslexia	Cognitive Activation task (Letter detection in sequence/lowercase letter detection)	Visual	Active	Letters (German)
Olumide et al. (2012)	fMRI	15	Range: NR Mean: TD = 20.6 AD = 20.7	Reading disabled	Dx	Rhyming task (Words/line judgment) (Pseudowords/line judgment) Spatial rotation task (Figure rotation/line judgment)	Visual	Active	Words, pseudowords (English)
Nicolson et al. (1999)	PET	12	Range: NR Mean: TD = 21.5 AD = 21.4	Dyslexia	Childhood history of dyslexia	Motor sequence task (Tone sequence/rest undefined)	Auditory	Active	Tones (NR)
Lobier et al. (2014)	fMRI	24	Range: NR Mean: TD = 23.8 AD = 21.6	Developmental dyslexia	Dx (ICD-10 criteria)	Visual processing task (Identify character in multi-element string/identify character in single-element string)	Visual	Active	Letters, digits, (Japanese) Hiragana, pseudo-letters (French)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engage-ment	Stimuli (Language)
Brunswick et al. (1999)	PET	12	Range: NR Mean: TD = 23.2 AD = 23	Developmental dyslexia	Childhood history of reading difficulty	Reading task (Read words, pseudowords aloud/rest with eyes closed)	Visual	Active	Words, pseudowords (English)
Paulesu et al. (1996)	PET	10	Range: NR Mean: TD = 27.2 AD = 25.2	Developmental dyslexia	Childhood history of dyslexia	Rhyming task (Consonant rhyming/shape discrimination) Short-term memory task (Letter/shape)	Visual	Active	Letters (English)
Brambati et al. (2006)	fMRI	24	Range: 13–63 Mean: 33	Developmental dyslexia	Dx (ICD-10 criteria)	Reading task (Words, pseudowords/false font matching)	Visual	Active	Words, pseudowords (Italian)
Steinbrin et al. (2012)	fMRI	33	Range: NR Mean: TD = 18.67 AD = 18.61	Developmental dyslexia	Childhood history of dyslexia; normed assessment <16%ile	Phonological judgment task (Different letter sound trials/same letter sound trials)	Auditory	Active	Letter sounds (German)
Christodoulou et al. (2014)	fMRI	24	Range: 18–35 Mean: NR	Dyslexia	Dx; normed assessment ≤25%ile	Reading task (Sentence plausibility judgment/passive fixation)	Visual	Active	Words (English)
McCrory (2001)	PET	18	Range: NR Mean: TD = 20.3 AD = 20	Dyslexia	Childhood history of dyslexia	Oral language task (Picture naming/nonsense line drawings) Reading task (Word reading/false font string length)	Visual Visual	Active Active	Pictures (English) Words (English)
McCrory et al. (2005)	PET	18	Range: NR Mean: TD = 20.3 AD = 20	Dyslexia	Childhood history of dyslexia	Reading task (Word reading/false fonts) Oral language task (Picture naming/nonsense shapes)	Visual	Active	Words, pictures (English)
Danelli et al. (2017)	fMRI	43	Range: NR Mean: TD = 20.6 AD = 21.2	Dyslexia	Childhood history of developmental dyslexia	Reading task (Pseudoword reading/letter sound rhyming Rhyming task (Letter rhyming/tone matching) Visual motion task (Fixation with Gabor patch moving randomly/fixation with stationary Gabor patch)	Visual/ auditory Auditory Visual	Active Active Passive	Pseudowords, letters (Italian) Letters (Italian) Gabor patch (Italian)
Wimmer et al. (2010)	fMRI	39	Range: 15–34 Mean: TD = 20.87 AD = 20.41	Dyslexia	Normed assessment < 10%ile	Lexical decision tasks (Words/passive fixation); (Pseudohomophones/ passive fixation); (Nonwords/passive fixation); (Pseudohomophones/ words); (Nonwords/pseudohomophones)	Visual	Active	Words, nonwords (German)
Hernandez et al. (2013)	fMRI	31	Range: NR Mean: TD = 21.2 AD = 20.9	Dyslexia	Dx (DSM-4)	Rhyming task (Word rhyming/font matching)	Visual	Active	Words (French)
Gilger and Olulade (2013)	fMRI	14	Range: NR Mean: TD = 20.4 AD = 22.1	Nonverbally gifted developmental reading disability	Dx	Rhyming Task (Word, pseudowords/line judgment) Spatial rotation task (Object orientation/line judgment)	Visual Visual	Active Active	Words, pseudowords (English) Pictures (English)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engagement	Stimuli (Language)
McCrory et al. (2000)	PET	14	Range: NR Mean: TD = 22.8 AD = 23	Dyslexia	Childhood history of dyslexia	Language task (Repeating words, pseudowords/passive rest with eyes closed)	Auditory	Active	Words, pseudowords (English)
Karni et al. (2005)	fMRI	16	Range: 22–25 Mean: 23	Dyslexia	Childhood history of dyslexia	Semantic judgment task (Words/passive fixation)	Visual	Active	Words (Hebrew)
						Rhyming task (Pseudowords rhyming/passive fixation)	Visual	Active	Pseudowords (Hebrew)
						Reading task (Sentence plausibility judgment/passive fixation)	Visual	Active	Words, (Hebrew)
Reilhac et al. (2013)	fMRI	24	Range: NR Mean: TD = 26.2 AD = 24.9	Dyslexia	Childhood history of dyslexia; assessment	Perceptual matching task (Letter string matching/letter string framed determination)	Visual	Active	Letters (French)
Ruff et al. (2003)	fMRI	26	Range: 18–43 Mean: TD = 24 AD = 27	Dyslexia	Dx (ICD-10 criteria)	Phonological task (Phonetically different letter sounds/acoustically different letter sounds)	Auditory	Passive (with attending task)	Letter sounds (French)
Rumsey et al. (1997)	PET	31	Range: 18–40 Mean: TD = 25 AD = 27	Dyslexia	Childhood history of dyslexia; Dx (DSM-4)	Reading task (Read high-frequency words/passive fixation) Reading task (Read irregular words/passive fixation)	Visual	Active	Words (English)
Kast (2011)	fMRI	25	Range: NR Mean: TD = 26.3 AD = 26.1	Dyslexia	Childhood history of dyslexia	Lexical decision task (Words/passive fixation)	Auditory and visual (dual modality)	Active	Words, pseudowords (German)
Weiss et al. (2016)	fMRI	43	Range: 19–33 Mean: TD = 28.03 AD = 26.10	Compensated dyslexics	Childhood history of Dyslexia; Dx	Reading task (Word reading/fixation with oral response)	Visual	Active	Words (Hebrew)
Pekkola et al. (2006)	fMRI	20	Range: 22–34 Mean: TD = 27 AD = 28.1	Dyslexia	Childhood history of dyslexia; normed assessment ≤1 SD	Phonological task (Video of person's face saying letter sounds/person's face)	Auditory and visual (dual modality)	Passive (with attending task)	Face video, letter sounds (Polish)
Dufor et al. (2007)	PET	30	Range: NR Mean: TD = 27.6 AD = 30	Dyslexia	Dx (ICD-10 criteria)	Phonological task (Letter sounds judgment/rest undefined)	Auditory	Active	Speech sounds (French)
Ingvar et al. (2002)	PET	18	Range: 20–28 Mean: NR	Dyslexia	Childhood history of dyslexia	Reading task (Word reading/rest with eyes open)	Visual	Active	Words (Swedish)
Ruff et al. (2002)	fMRI	17	Range: NR Mean: TD = 28 AD = 31	Dyslexia	Dx (ICD-10 criteria); assessment	Phonological task (Non-matching letter sounds/matching letter sounds)	Auditory	Passive (with attending task)	Letter sounds (French)
Temple et al. (2000)	fMRI	18	Range: NR Mean: TD = 32 AD = 28	History of developmental dyslexia	Self-report; assessment	Tone discrimination task (High-pitched tones/low-pitched tones)	Auditory	Active	Tones (English)
Waldie et al. (2013)	fMRI	28	Range: NR Mean: TD = 30 AD = 31	Dyslexia	History of reading difficulty; normed assessment ≤2 SD	Lexical decision task (Words/passive fixation) (Pseudowords/passive fixation)	Visual	Active	Words, pseudowords (English)

(continued)

Table 2. Continued.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category (Task/Baseline)	Modality	Engage-ment	Stimuli (Language)
Conway (2003)	fMRI	22	Range: NR Mean: TD = 34 AD = 35	Developmental dyslexia	Childhood history of learning disability	Tone counting task (Tones/white noise)	Auditory	Active	Tones (English)
Conway et al. (2008)	fMRI	22	Range: NR Mean: TD = 34 AD = 35	Dyslexia	Childhood history of learning disability; IQ-achievement discrepancy	Tone counting task (Tones/white noise) Phonemes counting task (Pseudowords/white noise)	Auditory Auditory	Active Active	Tones (English) Pseudowords (English)
Heim et al. (2013)	fMRI	30	Range: NR Mean: TD = 38.1 AD = 33.8	Dyslexia	Normed assessment ≤40%ile	Reading task (Pseudowords/words); (Low-frequency words/high-frequency words)	Visual	Active	Words, pseudowords (German)
Menghini et al. (2006)	fMRI	28	Range: 28–55 Mean: TD = 37.2 AD = 42.1	Developmental dyslexia	Dx (DSM-4)	Serial reaction time task (Blocks/passive fixation)	Visual	Active	Blocks (NR)
Eden et al. (2004)	fMRI	38	Range: NR Mean: TD = 41.1 AD = 44	Dyslexia	Childhood history of dyslexia; normed assessment	Phonological task (Repeating words with deleted initial phone/repeating word)	Auditory	Active	Words (English)
Temple (2001)	fMRI	39	Range: 8–12 Mean: TD = 10.5 AD = 10.7	Dyslexia	History of reading difficulty; normed assessment	Rhyming task (Letter rhyming/letter matching)	Visual	Active	Letters (English)
		18	Range: NR Mean: TD = 32 AD = 28	History of developmental dyslexia	Childhood history of dyslexia; normed assessment	Tone discrimination task (High-pitched tones/low-pitched tones)	Auditory	Active	Tones (English)
		45	Range: 8–12 Mean: TD = 10.5 AD = 10.8	Dyslexia	History of reading difficulty; normed assessment	Tone discrimination task (High-pitched tones/low-pitched tones)	Auditory	Active	Tones (English)
Agnew (2003)	fMRI	40	Range: 18–55 Mean: 43	Dyslexia	Normed assessment ≤25%ile	Motor response task (Response to flashing annulus/passive fixation)	Visual	Active	Flashing annulus (English)
Castro-Caldas et al. (1998)	PET	12	Range: NR Mean: TD = 65 AD = 63	Illiterate	No schooling	Lexical tasks (Repeat pseudowords/repeat words)	Auditory	Active	Words, pseudowords (Portuguese)
Paulesu et al. (2001)	PET	72	NR (Adult)	Dyslexia	Childhood history of dyslexia; normed assessment ≤10%ile	Reading task (Word reading deep orthographies/word reading shallow orthographies)	Visual	Active	Words, nonwords (English, French, Italian)

Table 3. Significant clusters for reading studies.

Cluster	x	y	z	ALE value	Volume (mm^3)	Hemi-sphere	Brain regions	Age range	Type of fMRI tasks	Contributing studies
Atypical reading										
Under activation (TD > RD)	−46	−58	−16	0.0467	12,888	L	30.2% Fusiform gyrus, 14.8% Inferior parietal lobule, 12.8% Inferior temporal gyrus, 12.6% Culmen, 9% Middle temporal gyrus, 7.5% Declive, 6.2% Middle occipital gyrus, 4.1% Supramarginal gyrus, 2.8% Superior temporal gyrus	5–63	Early literacy, reading, oral language, WM, visual/motion processing, math facts	Beneventi et al. (2010a, 2010b); Blau et al. (2010); Bolger et al. (2008); Brambati et al. (2006); Brunswick et al. (1999); Cao et al. (2008); Cao et al. (2018); Cao et al. (2017); Christodoulou et al. (2014); Cutting et al. (2013); Danelli et al. (2017); Evans et al. (2014); Hancock et al. (2016); Heim et al. (2015); Hoeft et al. (2006); Hu et al. (2010); Kast et al. (2011); Kronbichler et al. (2006); Kronschnabel et al. (2014); Lobier et al. (2014); McCrory (2001); McCrory et al. (2005); Meng et al. (2015); Meyler et al. (2008); Norton et al. (2014); Olumide et al. (2012); Olulade et al. (2015); Paulesu et al. (2001); Raschle et al. (2012); Reilhac et al. (2013); Richlan et al. (2010); Rumsey et al. (1997); Schulz et al. (2008, 2009); Specht et al. (2009); Tanaka et al. (2011); van der Mark et al. (2009); Wimmer et al. (2010); You et al. (2011)
	−44	6	36	0.0356	3,016	L	60.8% Precentral gyrus, 21% Middle frontal gyrus, 18.2% Inferior frontal gyrus	8–38	Early literacy, reading, oral language, motion processing, auditory discrimination, WM	Bach et al. (2010); Beneventi et al. (2010a, 2010b); Bolger et al. (2008); Cao et al. (2018); Cao et al. (2017); Dufor et al. (2007); Hancock et al. (2016); Heim et al. (2010); Heim et al. (2013); Hu et al. (2010); Meng et al. (2015); Norton et al. (2014); Siok et al. (2004); Vasic et al. (2008); Wimmer et al. (2010)
Overactivation (RD > TD)	−44	18	12	0.0261	968	L	85.7% Inferior frontal gyrus, 14.3% Insula	9–31	Early literacy, reading, oral language, WM	Gilger and Olulade (2013); Grande et al. (2011); Grünling et al. (2004); Heim et al. (2013); Kronbichler et al. (2006); Siok et al. (2004); Vasic et al. (2008); Waldie et al. (2013)
	−16	0	10	0.0248	928	L	64.4% Lentiform nucleus, 31.1% Thalamus, 2.2% Caudate	10–34	Early literacy, reading	Dufor et al. (2007); Meyler et al. (2008); Richlan et al. (2010); Ruff et al. (2002); Wimmer et al. (2010)
	36	24	2	0.0251	856	R	84.2% **Insula,** 15.8% **Inferior frontal gyrus**	5–30	Early literacy, reading, WM	Dufor et al. (2007); Kast et al. (2011); Meyler et al. (2008); Wimmer et al. (2010); Yamada et al. (2011)

Note. Bolded regions indicate homologous activation with atypical math; R = Right Hemisphere; L = Left Hemisphere; WM = Working Memory.

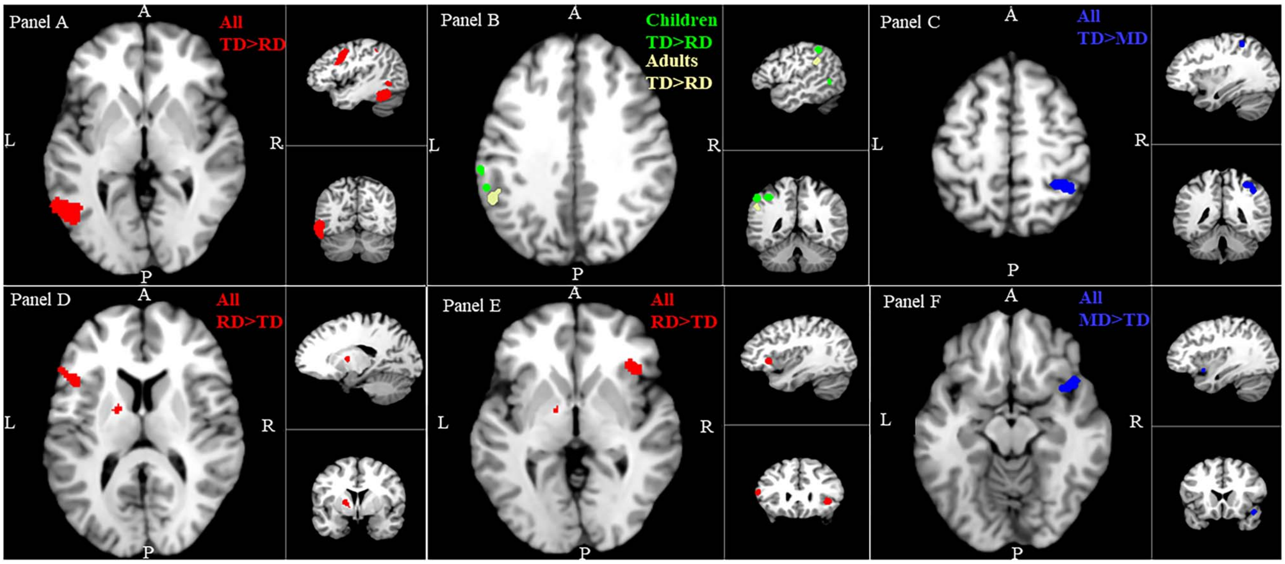

Fig. 3. Activation of atypical individuals compared to TD peers. Under activation of the left (L) fusiform gyrus, inferior parietal lobule, inferior temporal gyrus, culmen, middle temporal gyrus, declive, precentral gyrus, middle frontal gyrus, and inferior frontal gyrus for individuals with RD compared to TD peers is seen in panel A. In panel B, children with RD (in green) exhibited more dispersed under activation than adults (in yellow), compared to TD peers. Though there was under activation in the left (L) inferior parietal lobule, supramarginal gyrus, inferior temporal gyrus, middle temporal gyrus, and middle occipital gyrus for both children and adults, there was no overlap of brain regions. Under activation (in blue) of the right (R) inferior parietal lobule, supramarginal gyrus, superior parietal lobule, and subgyral for individuals with RD compared to TD is seen in panel C. Overactivation (in red) of the L and R inferior frontal gyrus and insula, as well as the L lentiform nucleus, thalamus, and caudate for individuals with RD compared to TD peers in seen in panels D and E. Panel D highlights overactivation in L inferior frontal gyrus for RD and panel E highlights overactivation in R inferior frontal gyrus for RD. Overactivation (in blue) of a single cluster extending to the right R insula, inferior frontal gyrus, claustrum, and extra-nuclear areas for individuals with MD compared to TD peers, is seen in panel D.

Overactivation for RD (RD > TD)

There were 54 studies, representing 453 foci and 1,780 participants, that reported overactivation of RD compared to TD that were entered into the second analysis for reading. This resulted in 3 significant clusters (see Table 3: Fig. 3, Panels D and E). Two of the clusters were in the left hemisphere. The first left cluster (968 mm^3) in the insula and inferior frontal regions was from (−56, 14, 8) to (−42, 28, 18) centered at (−48.3, 20.2, 13.3) with a max value at (−44, 18, 12). Eight studies contributed to this cluster, with participants from 9 to 31 years that completed early literacy, reading, oral language, cognitive activation, or spatial visualization tasks. There were 5 studies that contributed to the next cluster (928 mm^3) that spanned the lentiform nucleus, thalamus, and caudate in the left hemisphere from (−22, −10, −6) to (−10, 2, 12) centered at (−14.6, −3.1, 4.3) with a max value at (−16, 0, 10). Participants aged 10–34 years completed early literacy and reading tasks in this cluster. The final cluster (856 mm^3) was in the right hemisphere of the insula and the inferior frontal gyrus from (32, 20, −4) to (44, 30, 8) centered at (37.2, 24, 1.6) with a max value at (36, 24, 2). There were 5 studies that contributed to this cluster with participants from 5 to 30 years that completed early literacy, reading, or working memory tasks.

Developmental differences for RD

Post-hoc analyses were conducted to examine developmental differences between children (participants < 18 years) and adults (participants ≥ 18 years) with RD compared to TD. There were 30 studies, representing 295 foci, and 777 adult participants; and 52 studies, representing 425 foci, and 1,994 children, that reported under activation of RD compared to TD (TD > RD). Analysis indicated that children exhibited more dispersed under activation than adults, particularly in frontal and parietal regions (Fig. 3, Panel B; Table 4). Although there was under activation in the left inferior parietal lobule, supramarginal gyrus, inferior temporal gyrus, middle temporal gyrus, and middle occipital gyrus for both children and adults, there was no overlap in under activation of brain regions. Because no significant clusters emerged for the overactivation (RD > TD) of children with RD using the standard thresholds, overactivation in children and adults was not compared; however, an analysis examining overactivation for adults was conducted with 21 studies, representing 170 foci, and 483 adult participants. Results are outlined in Table 4.

Non-reading and language tasks for RD

Post-hoc analyses were conducted to examine the activation for RD on tasks that do not include reading, early literary, and oral language. There were 11 studies, representing 63 foci and 287 participants, that reported overactivation for RD (RD > TD) compared to TD that were entered into the first post-hoc analysis. Tasks included working memory, tone counting, visual/movement processing, serial reaction time, and motor sequencing tasks. There were 15 studies, representing 97 foci and 414 participants, that reported under activation for RD compared to TD (TD > RD) that were entered into the second post-hoc analysis. Tasks included working memory, spatial visualization, motion detection, visual processing, serial reaction time, motor sequence task, tone discrimination, and implicit motor learning tasks. There were no significant activation clusters for these post-hoc analyses.

Active and passive tasks for RD

Although there were not enough passive task studies to compare active and passive tasks separately, post-hoc analyses were conducted for TD > RD with only active tasks with 79 studies, representing 700 foci and 2,655 participants. This resulted in 2 significant clusters in the left hemisphere, which overlapped with the significant clusters when all studies were included (see Table 4).

Table 4. Significant clusters for reading studies comparing children to adults.

Cluster	x	y	z	ALE value	Volume (mm^3)	Hemi-sphere	Brain regions	Age range	Type of fMRI task	Contributing studies
Under activation (TD > RD) for atypical reading										
Children	−42	6	30	0.0265	2,448	L	52.2% Precentral gyrus, 27.2% Inferior frontal gyrus, 20.7% Middle frontal gyrus	4–16	Early literacy, reading, oral language, working memory	Beneventi et al. (2010a, 2010b); Bolger et al. (2008); Cao et al. (2017); Cao et al. (2018); Hancock et al. (2016); Hu et al. (2010); Meng et al. (2015); Norton (2014); Siok et al. (2004)
	−56	−56	2	0.0266	1,656	L	53.8% Inferior temporal gyrus, 34.6% Middle temporal gyrus, 11.5% Middle occipital gyrus	5–16	Early literacy, reading, oral language	Cao et al. (2008); Cutting et al. (2013); Heim et al. (2015); Hu et al. (2010); Kronbichler et al. (2006); Maurer et al. (2011); Raschle et al. (2012); You et al. (2011)
	−52	−44	44	0.0261	1,600	L	88.3% Inferior parietal lobule, 11.7% Supramarginal gyrus	4–14	Early literacy, reading	Cao et al. (2008); Cao et al. (2017); Evans et al. (2014); Hoeft et al. (2006); Norton (2014); Schulz et al. (2008); Schulz et al. (2009); Van der Mark et al. (2009)
	−40	−38	46	0.0272	944	L	86.8% Inferior parietal lobule, 13.2% Supramarginal gyrus	7–16	Early literacy, reading, working memory	Beneventi et al. (2010a, 2010b); Hoeft et al. (2006); Kronschnabel et al. (2013); Meyler et al. (2008); Norton et al. (2014); Tanaka et al. (2011)
Adults	−48	−58	−18	0.0293	4,712	L	39.1% Fusiform gyrus, 15.9% Declive, 15% Culmen, 12.4% Inferior temporal gyrus, 9.9% Middle occipital gyrus, 7.3% Middle temporal gyrus	18–40	Early literacy, reading, oral language, visual/motion processing	Danelli et al. (2017); Lobier et al. (2014); McCrory (2001); McCrory et al. (2005); Olumide et al. (2012); Paulesu et al. (2001); Reilhac et al. (2013); Rumsey et al. (1997); Wimmer et al. (2010)
	−52	−46	34	0.0181	1,040	L	66.7% Inferior parietal lobule, 33.3% Supramarginal gyrus	18–40	Early literacy, reading	Dufor et al. (2007); Kast (2011); Olumide et al. (2012); Rumsey et al. (1997)
Active Task	−46	−58	−16	0.0462	12,220	L	29.1% Fusiform gyrus, 16.0% Inferior parietal lobule, 11.4% Inferior temporal gyrus, 10.7% Culmen, 8.7% Middle temporal gyrus, 7.5% Declive, 7.0% Middle occipital gyrus, 5.6% Superior temporal gyrus, 4.1% Supramarginal gyrus	5–63	Early literacy, reading, oral language, working memory, visual processing, motor sequence, math facts	Beneventi et al. (2010a, 2010b); Bolger et al. (2008); Brambati et al. (2006); Brunswick et al. (1999); Cao et al. (2008); Cao et al. (2018); Cao et al. (2017); Christodoulou et al. (2014); Cutting et al. (2013); Danelli et al. (2017); Dufor et al. (2007); Evans et al. (2014); Hancock et al. (2016); Heim et al. (2015); Hoeft et al. (2006); Hu et al. (2010); Karni et al. (2005); Kast et al. (2011); Kronbichler et al. (2006); Langer et al. (2015); Lobier et al. (2014); McCrory (2001); McCrory et al. (2005); Meng et al. (2015); Meyler et al. (2008); Nicolson et al. (1999); Norton et al. (2014); Olumide et al. (2012); Olulade et al. (2015); Paulesu et al. (2001); Raschle et al. (2012); Reilhac et al. (2013); Richlan et al. (2010); Rumsey et al. (1997); Schulz et al. (2008, 2009); Specht et al. (2009); Tanaka et al. (2011); van der Mark et al. (2009); Wimmer et al. (2010); You et al. (2011)
	−44	6	36	0.0356	3,472	L	57.2% Precentral gyrus, 24.5% Middle fFrontal gyrus, 18.2% Inferior frontal gyrus	8–38	Early literacy, reading, oral language, auditory discrimination, working memory	Bach et al. (2010); Beneventi et al. (2010a, 2010b); Bolger et al. (2008); Cao et al. (2018); Cao et al. (2017); Dufor et al. (2007); Hancock et al. (2016); Heim et al. (2010); Heim et al. (2013); Hu et al. (2010); Meng et al. (2015); Norton et al. (2014); Siok et al. (2004); Vasic et al. (2008); Wimmer et al. (2010)
Overactivation (RD > TD) for atypical reading										
Children							No significant clusters			
Adults	38	20	−2	0.0141	816	R	100% Insula	20–34	Early literacy, reading	Dufor et al. (2007); Ingvar et al. (2002); Kast (2011); Pekkola et al. (2006); Rumsey et al. (1997); Waldie et al. (2013)
Active task	−44	18	12	0.0261	1,080	L	84.2.7% Inferior frontal gyrus, 15.8% Insula	9–31	Early literacy, reading, oral language, working memory	Gilger and Olulade (2013); Grande et al. (2011); Grünling et al. (2004); Heim et al. (2013); Kronbichler et al. (2006); Siok et al. (2004); Vasic et al. (2008); Waldie et al. (2013)

Note. L = Left Hemisphere, R = Right Hemisphere.

For RD > TD studies with only active tasks analysis, 49 studies, representing 409 foci and 1,588 participants were included. This resulted in 1 significant cluster in the left hemisphere, which was also observed in the RD > TD comparison when all studies were included; however, 2 clusters that were significant when all studies were included did not reach significance across the studies that included only active tasks (see Table 4).

Math studies

Details of included math studies are in Table 5.

Under activation for MD (TD > MD)

There were 13 studies, representing 75 foci and 387 participants, that were included in the under activation of MD compared to TD analysis. This resulted in one significant cluster (1,304 mm^3) in the right hemisphere of inferior/parietal regions, from (28, −48, 40) to (46, −40, 56) centered at (39, −43.5, 47.7) with a max value at (42, −44, 44; see Table 6; Fig. 3, Panel C). Five contributing studies included participants from 7 to 12 years. Math fact verification, magnitude comparison, ordinality, color comparison, spatial working memory, and reasoning tasks were represented in this cluster.

Overactivation for MD (MD > TD)

There were 13 studies, representing 104 foci and 472 participants, that were included in the overactivation of MD compared to TD analysis. This resulted in 1 significant cluster (496 mm^3) in the insula and inferior frontal gyrus from (32, 8, −14) to (46, 20, −8) centered at (40.1, 13.5, −10.5) with a max value at (42, 14, −10) in the right hemisphere (see Table 6; Fig. 3, Panel F). There were 3 contributing studies that included participants from 7 to 11 years. Tasks represented in this cluster included math fact verification and ordinality.

Developmental differences for MD

Although there were not enough studies with adult participants to examine developmental differences for MD, post-hoc analyses were conducted to explore MD in children. There were 11 studies, representing 66 foci, and 334 children, that reported under activation of MD compared to TD (TD > MD). The significant cluster (1,264 mm^3) in the right hemisphere of the inferior parietal regions, from (28, −48, 40) to (46, −40, 56) centered at (39, −43.6, 47.7) with a max value at (42, −44, 44) overlapped with (see Table 7) the cluster that emerged when the adult and children studies where combined (see Table 6) indicating that the children studies prominently contributed to the MD under activation findings across all studies. There were 11 studies, representing 101 foci, and 319 children, that reported overactivation of MD compared to TD (MD > TD). The significant cluster (528 mm^3) in the right hemisphere of frontal regions, from (32, 8, −14) to (46, 20, −8) centered at (40, 13.4, −10.6) with a max value at (42, 14, −10) overlapped with (see Table 7) the cluster that emerged when the adult and child studies where combined (see Table 6). The number of math studies was insufficient to conduct a post-hoc analysis examining task-related differences in MD.

Similarities and differences in activation for RD and MD

Unique and overlapping activation

Overlap for RD and MD, compared to TD, was examined to determine unique and overlapping areas of activation. Although overactivation was revealed in the right insula and inferior frontal gyrus for both RD and MD compared to TD (see Fig. 4, Panels A and B), conjunction analyses revealed no overlap in these areas (yet underpowered due to limited number of math studies). Notably, this finding was only present when children and adult studies were combined for RD. Compared to TD, RD and MD both displayed under activation in the inferior parietal lobule and the supramarginal gyrus. However, under activation for these regions was in the left hemisphere for RD and in the right hemisphere for MD. There were not enough math studies, when non-math tasks (e.g. working memory) were excluded, to directly compare the math tasks for MD to the reading tasks for RD.

Role of executive function for RD and MD

The NeuroSynth analysis revealed that even though there were no overlapping areas between RD and MD as compared to TD, both RD and MD showed anomalies in areas associated with executive function. Specifically, RD exhibited overactivation in anterior brain regions associated with working memory and inhibition tasks (see Fig. 5, Panel A). Conversely, MD displayed overactivation in anterior brain regions associated with inhibition tasks (see Fig. 5, Panel B) and under activation in posterior brain regions associated with working memory, attention, and shifting tasks (see Fig. 5, Panel C).

Putative visual word form area and intraparietal sulcus

Under activation of the left fusiform gyrus, which includes pVWFA, was corroborated in studies that examined children and adults with RD as they completed reading and early literacy tasks; oral language tasks, such as picture naming; working memory tasks; and other types of tasks including passive visual motion and motion detection. Under activation of the left pVWFA was not present for those with MD (see Fig. 4, Panel C). Additional follow-up analyses revealed that under activation in the left fusiform gyrus remained when passive tasks were removed and for adults with RD. Although under activation emerged in the left inferior/middle temporal region, under activation in the specific ROI derived from Vigneau et al. 2005 ($x = -44$, $y = -58$, $z = -15$) was not present for children with RD. Under activation in the right inferior parietal lobule, which includes the IPS, was demonstrated in studies that examined children with MD in math tasks such as math facts, calculation, magnitude comparison, and other types of tasks including spatial working memory and reasoning tasks. This finding was consistent in additional follow-up analyses. Under activation of the right IPS was not present for those with RD (see Fig. 4, Panel D).

Discussion

The current study extends the literature by exploring the similarities and distinctions of the underlying neurobiological mechanisms of individuals with RD to those with MD when compared to their TD peers across the literature. There were markedly more studies that included individuals with RD than those with MD. Participants included in the studies spanned from elementary to adulthood, yet elementary students represented the majority of the studies in both reading and math. Developmental differences in reading were examined; however, the limited number of studies did not allow for us to compare differences between children and adults in MD and with more granularly in children (e.g. elementary, adolescence) with RD. Future studies should further explore the development of MD and RD to better understand the trajectory of learning difficulties in reading and math.

Table 5. Studies that include individuals with MD organized by mean age.

Study	Technique	Sample size	Age	Atypical sample Description	Dx method	Task Category task/baseline	Modality	Engagement	Stimuli (Language)
Ashkenazi et al. (2012)	fMRI	34	Range: NR Mean: TD = 8.17 AD = 8.12	Developmental dyscalculia	Normed assessment ≤25%ile	Math fact verification task (Two-digit addition/single-digit addition)	Visual	Active	Digits (English)
Davis et al. (2009)	fMRI	48	Range: 8–9 Mean: 8.2	Mathematical calculation difficulties (MD)	Normed assessment ≤25%ile	Math fact verification task (Exact & approximate addition/ Greek letter matching)	Visual	Active	Digits (English)
Cho et al. (2011)	fMRI	103	Range: 7–9.9 Mean: TD = 8.2 AD = 8.6	Counters	Strategy use: Counters (AD) retrievers (TD)	Math fact verification task (Single-digit addition with addends from 2 to 9/Addition with “1” as addend)	Visual	Active	Digits (English)
Rosenberg-Lee et al. (2015)	fMRI	36	Range: 7–9 Mean: AD = 8.34 TD = 8.44	Developmental dyscalculia	Normed assessment ≤25%ile	Math fact and calculation verification task (Subtraction/addition)	Visual	Active	Digits (English)
Iuculano et al. (2015)	fMRI	30	Range: 7–9 Mean: TD = 8.54 AD = 8.65	Severe mathematical learning disabilities (MLD)	Normed assessment ≤16%ile	Math fact verification task (Addition/number matching)	Visual	Active	Digits (English)
McCaskey et al. (2018)	fMRI	28	Range: 8–11 Mean: TD = 9.1 AD = 9.6	Developmental dyscalculia	Normed assessment ≤10%ile	Ordinality task (Number Order/number identification)	Visual	Active	Digits (German)
Kucian, Grond, et al. (2011)	fMRI	32	Range: 8–10 Mean: 9.5	Developmental dyscalculia	Dx	Ordinality task (Number order/number Identification)	Visual	Active	Digits (German)
Michels et al. (2018)	fMRI	31	Range: 7–11 Mean: 9.5	Developmental dyscalculia	Dx normed assessment ≤10%ile (DSM-5)	Ordinality task (Number order/number identification)	Visual	Active	Digits (German)
Kaufmann, et al. (2009)	fMRI	18	Range: NR Mean: TD = 9.7 AD = 9.6	Developmental dyscalculia	1.5 SD IQ/performance discrepancy	Magnitude comparison task (Non-symbolic/spatial orientation)	Visual	Active	Pictures (German)
Kovas et al. (2009)	fMRI	26	Range: 10 Mean: 10	Low math ability	Normed assessment ≤ 1.5 SD	Magnitude comparison task (Non-symbolic/color judgment)	Visual	Active	Pictures (English)
Rotzer et al. (2009)	fMRI	21	Range: 8–10 Mean: AD = 10.4 TD = 10.2	Developmental dyscalculia	Normed assessment ≤1.5 SD	Spatial working memory task (Adapted Corsi Block tapping/color change detection)	Visual	Active	Dots (English)

(continued)

Table 5. Continued.

Study	Tech-nique	Sample size	Age	Atypical sample Description	Dx method	Task Category task/baseline	Modality	Engagement	Stimuli (Language)
Kaufmann, et al. (2009)	fMRI	12	Range: NR Mean: TD = 10.5 AD = 10.5	Developmental dyscalculia	1.5 SD IQ/performance discrepancy	Ordinality task (Number order/passive fixation)	Visual	Active	Digits (German)
						Ordinality task (Size of symbol order/passive fixation);	Visual	Active	Symbols (German)
						Ordinality task (Number order/size of symbol order)	Visual	Active	Digits, symbols (German)
Mussolin et al. (2010)	fMRI	30	Range: 9–11 Mean: AD = 10.5 TD = 10.9	Developmental dyscalculia	Dx	Magnitude comparison task (Symbolic/passive fixation)	Visual	Active	Digits (NR)
						Magnitude comparison task (Symbolic near/symbolic far);	Visual	Active	Digits (NR)
						Color comparison task (Similar colors/different colors)	Visual	Active	Symbols (NR)
Kucian, Loenneker, et al. (2011)	fMRI	30	Range: NR Mean: TD = 10.6 AD = 11.3	Developmental dyscalculia	Dx IQ/performance discrepancy (ICD-10)	Magnitude comparison task (Non-symbolic small ratio/non-symbolic large ratio)	Visual	Active	Pictures (German)
Schwartz et al. (2018)	fMRI	34	Range: 8–12 Mean: TD = 11.10 AD = 11.17	Math learning difficulty	Normed assessment ≤25%ile	Reasoning task (Transitive story questions/non-transitive story questions)	Auditory/visual (dual-modality)	Active	Picture with story read aloud (French)
McCaskey et al. (2017)	fMRI	30	Range: 11–16 Mean: AD = 14.1 TD = 13.8	Developmental dyscalculia	Normed assessment	Magnitude comparison task (Non-symbolic/color judgment)	Visual	Active	Dots (German)
						Spatial magnitude task (Shape/color judgment)	Visual	Active	Pacman (German)
Attout et al. (2015)	fMRI	32	Range: 17–28 Mean: TD = 20.56 AD = 20.44	History of developmental dyscalculia	Self-report childhood difficulties with learning math and current difficulties in daily life	Working memory task (Visuospatial with letters/luminance judgment)	Visual	Active	Letters (French)
Molko et al. (2003)	fMRI	28	Range: NR Mean: TD = 24.3 AD = 24.5	Turner syndrome	Dx	Math fact verification task (Addition/letter matching)	Visual	Active	Digits (NR)
Grabner et al. (2007)	fMRI	25	Range: 22–32 Mean: TD = 25.92 AD = 25.38	Lower mathematical competence	Normed assessment lower performance within sample	Math fact and calculation verification task (Multiplication/digit matching)	Visual	Active	Digits (German)
Cappelletti and Price (2014)	fMRI	112	Range: 24–70 Mean: TD = 42.12 AD = 42.82	Dyscalculic	Normed assessment	Magnitude comparison task (Symbolic or object size/color determination)	Visual	Active	Digits, objects (English)

Note. Dx Method = Diagnosis; NR = Not Reported; TD = Typically Developing; AD = Atypically Developing.

Table 6. Significant clusters for math studies.

Cluster	x	y	z	ALE value	Volume (mm^3)	Hemi-sphere	Brain regions	Age range	Type of fMRI tasks	Contributing studies
Atypical math Under activation (TD > MD)	42	−44	44	0.0161	1,304	R	87.5% Inferior parietal lobule, 6.3% Supramarginal gyrus, 3.1% Superior parietal lobule, 3.1% Sub-gyral	7–12	Math facts, magnitude comparison, ordinality, color comparison, spatial working memory, reasoning	Cho et al. (2011); Kucian, Grond, et al. (2011); Mussolin et al. (2010); Rotzer et al. (2009); Schwartz et al. (2018)
Overactivation (MD > TD)	42	14	−10	0.0131	496	R	58.1% **Insula,** 22.6% **Inferior Frontal Gyrus,** 12.9% Claustrum, 6.5% Extra-nuclear	7–11	Math facts, ordinality	Davis et al. (2009); Iuculano et al. (2015); Michels et al. (2018)

Note. Bolded regions indicate homologous activation with atypical reading; R = Right Hemisphere.

Table 7. Significant clusters for math studies for children.

Cluster	x	y	z	ALE value	Volume (mm^3)	Hemi-sphere	Brain regions	Age range	Type of fMRI tasks	Contributing studies
Under activation (TD > MD) for atypical math										
Children	42	−44	44	0.0160	1,264	R	86.7% Inferior parietal lobule, 6.7% Supramarginal gyrus, 3.3% Superior parietal lobule, 3.3% Sub-gyral	7–12	Math facts, magnitude comparison, ordinality, color comparison, spatial working memory, reasoning	Cho et al. (2011); Kucian, Grond, et al. (2011); Mussolin et al. (2010); Rotzer et al. (2009); Schwartz et al. (2018)
Overactivation (MD > TD) for atypical math										
Children	42	14	−10	0.0131	528	R	54.5% Insula, 21.2% Inferior frontal gyrus, 12.1% Extra-nuclear, 12.1% Claustrum	7–11	Math facts, ordinality	Davis et al. (2009); Iuculano et al. (2015); Michels et al. (2018)

Note. R = Right Hemisphere.

All of the tasks in the math studies were active, while some (~10%) of the reading studies were passive and did not require participants to respond to the stimuli (e.g. listening to letter sounds). The reading studies included tasks presented visually, auditorily, or with dual visual/auditory modality, yet there were no math studies that only presented stimuli in the auditory modality. Although most of the studies included domain-specific tasks (reading or math), there were other tasks such as working memory and tone discrimination included in some RD and MD studies. Similarly, baseline tasks greatly varied across the studies. While all of the math studies had comparison baseline tasks designed to isolate math processing, the baselines in the reading studies varied from rest to tasks that were more aligned with and controlled for the active task. For math studies, the results from post-hoc analyses were consistent with the main analysis. There was some variation in the post-hoc and main analysis findings in the reading studies to which variation in tasks and their baselines may have contributed.

The criteria employed to identify and classify individuals with reading and MD was not consistent across studies. For instance, many of the studies that included children were identified with a current disability/deficit and assessment scores were often reported, though cut-off scores diverged slightly across studies. In contrast, many of the adult studies reported a childhood diagnosis or a history of difficulties. Because many adult studies did not report current abilities, it is unclear if adults' childhood disabilities persisted into adulthood, or if the adults had compensated for their disabilities. These findings highlight the variability in the identification and classification of individuals with learning difficulties in reading and math across studies. Diagnostic inconsistency emphasizes the shortcomings of behavioral measures (differences in criteria and assessments across countries, clinical vs. intervention identification of participants) and the necessity to better understand learning difficulties from a neural perspective. Discrepancies in classification of those with learning difficulties may also be a contributing factor in the variability in results across studies, including the differences in under- and over-activation of specific brain regions. Sample sizes did not allow for the examination of screening and classification criteria as a moderator in the current study; however, future work should investigate the profile differences of learning difficulties and potential neural mechanisms associated with screening and classification criteria.

Reading studies

Under activation for RD (TD > RD)

Children and adults with RD exhibited under activation compared to TD in reading and language areas, centered in the left hemisphere, which, consistent with results of previous meta-analyses (Richlan et al. 2009, 2011). Specifically, we found under activation in frontal and temporal regions that comprise the

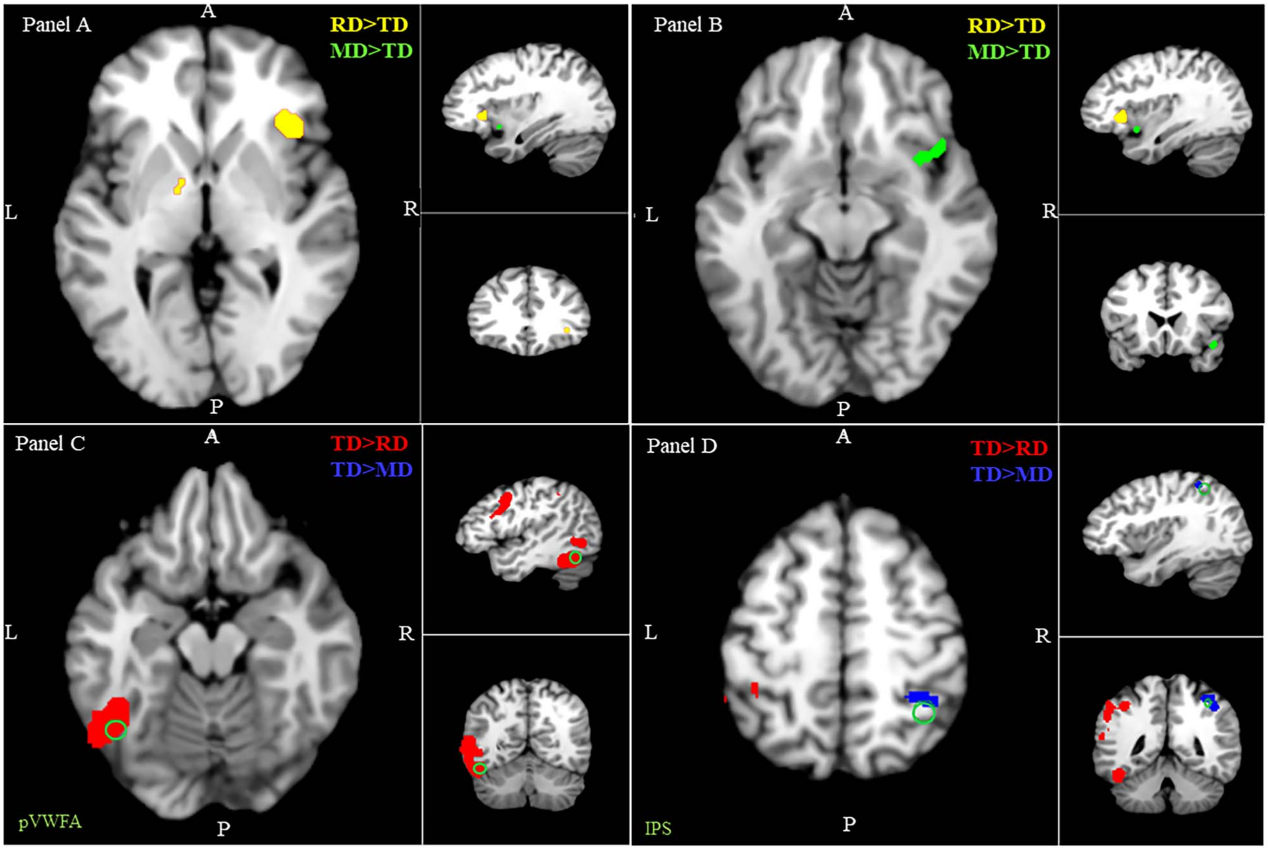

Fig. 4. Panel A highlights overactivation for individuals with RD (in yellow) and panel B highlights overactivation for individuals with MD (in green). Though there was overactivation in the right (R) insula and inferior frontal gyrus for individuals with RD and individuals with MD compared to their TD peers, there was no overlap in these regions. Under activation in the pVWFA (green circle) was present only for individuals with RD (panel C) and under activation in the right IPS (green circle) was present only for individuals with MD (panel D).

reading network (Pugh et al. 2000; Shaywitz and Shaywitz 2003; Schlaggar and McCandliss 2007; Benischek et al. 2020). These areas are generally responsible for the development of literacy skills, including the connection of letters and speech sounds (Pugh et al. 2000; Buchsbaum et al. 2001; Koyama et al. 2017). Children and adults with RD also exhibited under activation temporo-occipital regions, specifically the pVWFA, an established component of the *reading network* which is associated with the visual processing of words during reading (Mechelli et al. 2000; Vigneau et al. 2005). Together these findings substantiate the role of the reading network and correspond with compelling behavioral evidence that suggests phonemic awareness plays a central role in the development of reading skills (Melby-Lervåg et al. 2012). Further, post-hoc analysis showed that these anomalies in RD appear to be specific to active reading and language tasks, suggesting that RD fails to effectively recruit the reading network when needed most—during tasks that require active reading/language engagement.

In line with a prior meta-analysis (Martin et al. 2016), under activation in the “reading network” was consistent in reading across languages. Studies that contributed to the reading network cluster were presented in English, French, Italian, Norwegian, Dutch, German, Japanese, and Chinese. These results indicate that reading areas in the brain are not language-specific. That is, brain areas recruited during reading appear to be relatively consistent regardless of language or script (alphabetic vs. logographic) (Tan et al. 2001). The results also suggest deficits in individuals with RD are similar across modalities. Although most of the tasks of the contributing studies presented the stimuli visually (words, letters), 6 tasks presented the stimuli (words, letter sounds) auditorily, and 3 utilized dual visual–auditory modalities, implying that those with RD may have trouble mapping sounds, regardless of how the stimuli are presented (Facoetti et al. 2010; Kershner 2021).

Post-hoc analyses investigating developmental differences of individuals with RD indicated that children with RD tend to exhibit more dispersed under activation compared to adults with RD. Notably, children with RD tend to exhibit more dispersed under activation in frontal regions, presumably associated with effort. This finding may indicate developmental differences in reading and may reflect that adults with RD have established some semblance of greater automaticity and efficiency during reading than children with RD. Notably, there were differences in the identification of disability criteria in children and adult studies. Studies that included children identified with RD reported either a current diagnosis or underwent some screening criteria to have a current label of RD. In contrast, most, but not all, studies that included adults had past diagnoses or difficulty with reading during childhood (see Table 2, *Dx Method* column). Consequently, it is unclear if discrepancies in children and adults were due to distinctions of reading development from child to adulthood or compensatory mechanisms in adults with RD.

Overactivation for RD (RD > TD)

Individuals with RD exhibited overactivation compared to TD in limited regions of both left and right hemispheres during various tasks in areas associated with early literacy and executive

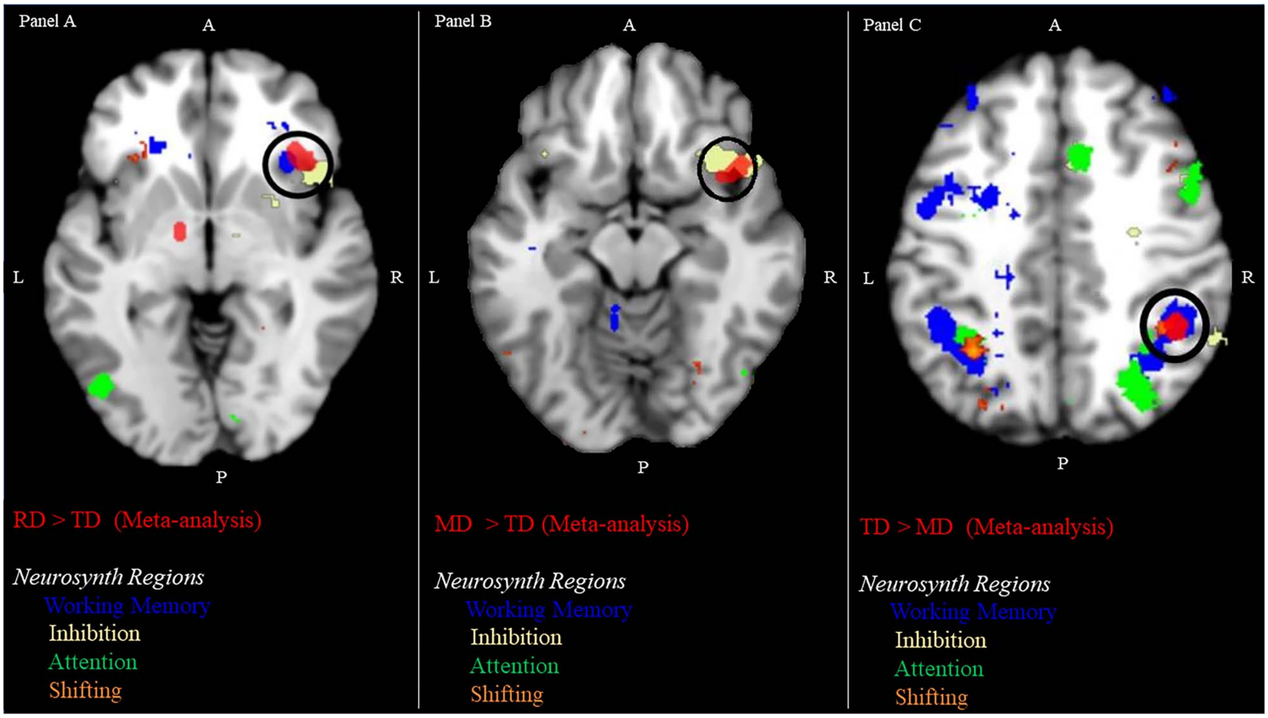

Fig. 5. Overactivation in anterior brain regions associated with working memory (in blue) and inhibition tasks (in yellow) for individuals with RD (in red) compared to TD peers, is seen in panel A. Overactivation in anterior brain regions associated with inhibition tasks (in yellow) for individuals with MD (in red) compared to TD peers, is seen in panel B. Under activation in posterior brain regions associated with working memory (in blue), attention (in green), and shifting tasks (in orange) for individuals with MD (in red) compared to TD peers, is seen in panel C.

functioning. Post-hoc analysis suggests that the anomalies in RD appear to be specific to reading and language tasks. Markedly, we found a bi-hemispheric overactivation in the inferior frontal gyrus for individuals with RD, as they completed early literacy, reading, and oral language tasks. One hypothesis for the bi-hemispheric activation for those with RD may be a compensatory response for inadequate phonological processing in the left hemisphere function (Pugh et al. 2000), with perceptual processing in the right hemisphere (Shaywitz and Shaywitz 2003). This bilateral representation tends to transition into a more specialized left-lateralized process over development, suggesting that with less proficiency in reading more bilateral activation is present in general (Brauer and Friederici 2007). Additionally, proficient readers tend to rely on posterior circuits as opposed to frontal regions (Pugh et al. 2000). Consequently, the overactivation in the inferior frontal gyrus for those with RD may suggest increased reliance on the frontal regions and emphasize increased efforts in articulation for those with RD (Pugh et al. 2000; Costafreda et al. 2006). Notably, the studies that contributed to under activation of the left inferior frontal gyrus differed from the studies that contributed to the overactivation of the left inferior frontal gyrus. Consequently, study-level factors such as task, baseline task, and participants' characteristics may have influenced this finding.

Overactivation was also present in brain regions associated with executive functioning. In addition to linguistic processing, the inferior frontal gyrus is also associated with inhibition and attentional control (Rota et al. 2009; Hampshire et al. 2010). Overactivation of the insula also suggests additional recruitment of attentional resources for RD (Menon and Uddin 2010; Uddin et al. 2017). In addition to working memory, spatial visualization, and cognitive activation, this overactivation was also found during early literacy and reading tasks, highlighting the role of executive functioning in reading skills. Additionally, the overactivation of these executive functioning areas suggests that individuals with RD may recruit executive functioning skills to subsidize their inadequate phonological skills.

Finally, we also observed overactivation in the left thalamus for individuals with RD during early literacy and reading tasks. The thalamus is often thought of as a relay station of sensory information to other cortical areas of the brain, and though somewhat controversial, the thalamus may also be related to language. For instance, the thalamus is thought to act as a monitor for the execution of language functioning, such as selecting one language system over another (Crosson 2013; Klostermann and Ehlen 2013). Thus, overactivation for those with RD may indicate difficulties with selecting an efficient language system due to the broad activation of brain systems utilized.

Findings from task (active vs. passive) and developmental (adults vs. children) post-hoc analyses for overactivation in RD provide additional nuanced indications of the results. Compared to post-hoc findings conducted with TD > RD, the RD > TD post-hoc results were less consistent with the results from the entire sample. First, when passive tasks were removed only 1 significant cluster remained in the left hemisphere, which was also observed when all studies were included. Two clusters that were significant when all studies were included did not reach significance across the studies that included only active tasks. Although the passive tasks conducted in the included studies intend the participants to be engaged (view letters and hear corresponding letter sounds) as indicated by an attending task, there are notable differences from active tasks, such as accuracy and motor response which may add a layer of cognitive processing. Second, when children and adult participants with RD were examined separately, only overactivation in the right insula for adults remained significant. Again, this may be due to developmental differences or compensatory mechanisms used by adults with RD. Tasks and corresponding baseline tasks may also play a role. Younger children who are unable to developmentally complete reading tasks instead completed pre-literacy tasks that may have required less recruitment of executive functions compared to adults who employed attentional resources of the insula. These findings highlight the pronounced variability in participant characteristics (age, classification of RD) and tasks across the reading studies. Although, meta-analyses allow for the summarization of general findings across groups, distinct study characteristics and their impact may be lost as indicated by post-hoc findings.

Math studies

Under activation for MD (TD > MD)

Evidence from the post-hoc analysis that removed adults and only included children revealed that the under activation for MD was seen in children between the ages of 7 and 12. Younger children with MD demonstrated under activation in regions associated with math, specifically in the right inferior parietal lobule region, as labeled by the atlas utilized by GingerAle—an area that likely includes the IPS (Arsalidou and Taylor 2011). In TD individuals, activation in the right IPS is associated with comparison tasks (Price et al. 2007), while the left IPS is related to more language-related multiplication tasks (Chochon et al. 1999). Activation of the right IPS is also demonstrated when participants read word pairs with a number agreement pair violation (Carreiras et al. 2010). Bilateral activation of IPS is linked to calculation tasks, such as subtraction (Chochon et al. 1999). We found under activation of the right IPS during math fact verification, magnitude comparison, ordinality, color comparison, working memory, and reasoning tasks in younger children with MD. This finding is perhaps due to the reliance on similar strategies across math domains in children with MD, rather than more efficient strategies such as retrieval during multiplication (Ashcraft 1982). Although older students and adult studies did not contribute to the under activation of math regions, it is unclear if this is due to developmental differences, or the small number of studies that included older participants with MD.

There is behavioral evidence of executive function deficits, particularly in working memory, for individuals with MD (Peng and Fuchs 2014). This coincides with our findings indicating that younger children with MD exhibited under activation in areas related to executive functioning. Particularly, under activation of the supramarginal gyrus, which is associated with memory retrieval (Russ et al. 2003), and under activation of the superior parietal lobule, which is correlated with visuospatial processing (Stoeckel et al. 2004) are suggestive of more global deficits. The under activation of these areas in children with MD may be due to the ineffective use of executive functioning during math tasks, including math facts, magnitude comparisons, and ordinality. Specifically, children who are not proficient in math operations may be exploiting inefficient strategies to solve math problems and underutilizing memory skills.

Overactivation for MD (MD > TD)

Similar to under activation findings, evidence from the post-hoc analysis that removed adults and only included children revealed that the overactivation for MD was seen in children between the ages of 7 and 11. Younger children with MD exhibited hyperactivity in brain regions associated with emotion, cognitive control, and complex processing. First, younger children with MD displayed overactivation in the right insula. The insula is a heterogenous region related to attention (Eckert et al. 2009), sensory autonomic regulation, as well as emotion (Menon and Uddin 2010). Accordingly, overactivation of the right insula in children with MD may suggest a hyperactive response related to inattention or anxiety due to poor academic performance (de Lijster et al. 2018). Second, overactivation of the inferior frontal gyrus may suggest inefficient regulation of attention and inhibitory responses in complex tasks (Aron et al. 2014; Wilkey and Price 2019) in children with MD. For instance, in children with attention deficit hyperactivity disorder (ADHD), increased activity in the right inferior frontal gyrus is present (Wang et al. 2013), similar to our findings in children with MD in the current study. This could suggest a similar cognitive control deficit in children with MD, that is displayed in children with ADHD. Finally, children with MD displayed hyperactivity in the claustrum, which is related to complex processing and relay (Crick and Koch 2005). As with under activation of brain regions in those with MD, overactivation in these regions was only present for children completing math fact verification and ordinality tasks. Again, this may be due to the limited number of math studies, rather than developmental differences or task specificity. Notably, only 3 studies contributed to these effects, highlighting discrepancies seen across studies and the need for more research with those with MD across the lifespan and math domains (Peters and De Smedt 2018).

Similarities and differences in activation for RD and MD

The third aim of this study was to examine similarities and differences of neural activation in reading and math. There were no overlapping areas for under activation across RD and MD. Instead, hypoactivity was present for domain-specific areas for atypical reading and math. That is, children with MD displayed under activation in math-related areas, while individuals with RD displayed under activation in the reading network. These findings suggest that RD and MD have unique domain-specific deficit profiles. In addition to hypoactivity for domain-specific areas, post-hoc NeuroSynth analyses indicated under activation in posterior brain regions associated with working memory, attention, and shifting tasks for those with MD, suggesting a distinct integration of executive functioning for those with MD compared to RD.

The post-hoc NeuroSynth analyses also revealed that RD exhibited overactivation in anterior brain regions associated with working memory tasks and both RD and MD showed overactivation in right, but not left, insula and inferior frontal gyrus, with the peak coordinates for RD and MD both associated with response inhibition in NeuroSynth (https://neurosynth.org/). Notably, while there was no overlap of the clusters, suggesting that the anomalies associated with RD and MD are neurally distinct, it remains unclear if this is due to true neural distinction between RD and MD or if it is related to the activation distributions generated by GingerALE. The activation distributions are based upon peak coordinates provided in the individual studies, and the use of different software packages and different statistical thresholding could potentially impact how peak coordinates are reported. Further, the distributions generated by GingerALE do not account for the size of the original extents of activation (a small activation volume is input in the same manner as a large activation volume, with weighting based upon subject number rather than extent), such that it is quite possible that these activation estimations, with borders in close proximity, do not capture an area of actual overlap. Nevertheless, findings seem to suggest a common linkage to response inhibition. This finding could indicate that there are some similarities in the types of or the process by which, executive functioning is recruited in those with reading and math deficits. Specifically, RD and MD may each recruit additional executive function resources to compensate for the inadequate use of domain-specific skills. These findings are somewhat paralleled in the behavioral literature showing the complex, yet limited overlap, between MD and RD. Behavioral evidence suggests deficits in working memory (Cirino et al. 2015; Peng et al. 2018; Peng et al. 2016) for both individuals with RD and those with MD. Interestingly, response inhibition is found behaviorally for RD (Schmid et al. 2011), but not for MD (e.g. Censabella and Noël 2007; De Weerdt et al. 2013) during inhibition tasks (e.g. stop-signal task), suggesting that that the deficits in response inhibition may be specific to reading and math tasks for RD and MD, respectively. In sum, RD and MD exhibit both distinct, domain-specific deficits and overactivation in homologous brain regions associated with response inhibition, perhaps providing insight into the similarities and distinctions in how reading and math processes are developed.

Post-hoc analyses examined the functional specificity of the pVWFA and the right IPS in RD and MD, compared to TD. Results indicated that functional under activation of the left pVWFA was specific to those with RD and activation of the right IPS was specific to those with MD. These findings suggest that the functional specificity of the pVWFA and the IPS may be specific to the type of deficits associated with RD and MD, respectively. Notably, only 1 study examined math in individuals with RD (Evans et al. 2014) and there were no studies that examined reading in MD. Conversely, individuals with RD predominantly completed reading and literacy tasks, while those with MD chiefly completed math tasks. Thus, the functional specificity of these brain regions could be task-specific, with the pVWFA and right IPS being associated with the reading and math-related tasks, respectively. Future work is needed to further explore the relation of specificity of the pVWFA and the right IPS to the tasks and deficits in RD and MD, especially for instances of comorbidity.

Limitations and alternative considerations

In the present study, several limitations facilitate and guide future research directions. First, the results are restricted by the demographics of the participants and the number of studies included in the analysis, particularly the limited MD studies. While RD studies spanned across the lifespan, there were very few MD studies that included older students or adults. The number of studies also impacts the power of the analysis. Accordingly, caution should be used with the interpretation and generalizability of these findings, particularly for math. More generally, there were markedly fewer MD studies compared to RD, thus emphasizing the necessity for further research that examines MD, specifically in older individuals.

Second, the current study examines similarities and differences of activation for RD and MD as participants engaged in various types of tasks; however, individuals with RD predominantly partook in tasks related to reading, while individuals with MD typically engaged in math tasks. Behavioral findings indicate that underlying mechanisms related to both reading and math include phonological awareness (Storch and Whitehurst 2002; Slot et al. 2016; Cirino et al. 2018; Child et al. 2019; Amland et al. 2021), working memory (Peng and Fuchs 2014; Peng et al. 2018; Child et al. 2019), and attention (Child et al. 2019). There were not enough studies in the current meta-analysis to examine these factors in RD and MD. As such, additional work is needed to examine RD and MD individuals as they complete tasks that are domain-general, which will further enhance our understanding of the underlying mechanisms for RD and MD. Moreover, under- and over-activation of brain regions are highly dependent on the baseline tasks. These greatly varied across study and may contribute to the inconsistencies in the literature. Notably, while all the math studies utilized a comparable task closely aligned to the active task, this was not the case for some of the reading studies. In particular, some reading studies included rest or passive fixation for their baseline. This methodological difference may have created general activation in brain regions not specific for reading in RD, while math studies highlighted brain regions specific to math for MD. Though lack of power did not allow for follow-up analysis to explore baseline differences, future studies should carefully consider the influence of baseline tasks on their results.

Next, given that the prevalence of comorbid reading and math disabilities is estimated at 7.6% (Dirks et al. 2008), and that additional comorbidities are commonly reported, the inclusion of participants with other/additional comorbid difficulties was expected (DuPaul et al. 2013). Specifically, 2 studies included participants with comorbid RD and ADHD (Langer et al. 2015; Mohl et al. 2015). Though some studies explicitly ruled out comorbidity in their samples (Specht et al. 2009; Lobier et al. 2014), others did not. Consequently, additional comorbidity cases may have been included in some studies. Due to the different cognitive profiles and prognoses of those with comorbid difficulties compared to those with a single deficit (Dirks et al. 2008), the inclusion of comorbidity cases may have altered the findings. Specifically, discrepancies may be more severe and/or broader in individuals with more than 1 disorder, compared to those with a single disability (Dirks et al. 2008). That is, although the current study aimed to compare RD to MD, we may have inadvertently captured similarities of comorbid learning disorders, such as individuals with learning difficulties and ADHD. Interestingly, there were no studies with comorbid RD and MD participants, though 1 study did examine arithmetic in children with RD (Evans et al. 2014). Additional research is needed to explore and understand the underlying complexity of the comorbidity in learning difficulties, and how their neural patterns may differ from single deficits.

Finally, the aim of this study was to examine the functional similarities and distinctions of brain activation between RD and MD. Consequently, the search inclusion criteria eliminated functional connectivity/network analysis and structural analysis. Although examining other types of modalities and analyses were beyond the scope of the current study, examination of these underlying neural components in RD and MD could reveal valuable information to better understand learning difficulties. For instance, findings could reveal similarities or distinctions in the connectivity between domain-specific brain regions (reading, math) and domain-general (executive functions) for RD and MD. Future studies should examine structural as well as brain connectivity in individuals with learning difficulties to further contribute to the understanding of neural mechanisms of RD and MD.

Summary and implications

Despite these limitations, the current findings provide crucial insights into the underlying cognitive mechanisms of RD and MD. Although there has been a recent surge in comorbidity literature, math and reading have primarily been studied separately. Nonetheless, the behavioral literature has uncovered several mechanisms (working memory, phonological processing) related to both reading and math (Slot et al. 2016; Cirino et al. 2018;

Amland et al. 2021). The current study examined similarities and differences in functional neural patterns in RD and MD across studies. In sum, for children and adults with RD, we found under activation in the "reading network" in the left hemisphere, and overactivation of bilateral frontal regions. We also found overactivation in executive functioning and under activation for the pVWFA for those with RD. Together, these RD findings could indicate a compensatory effect for those with RD. Children with MD displayed under activation of math areas, regardless of math domain, and overactivation in executive functioning areas. Though more research is needed for older children and adults with MD, these findings could suggest that deficits in math are similar across different math domains, which may be a result of children utilizing similar compensation strategies.

Together, these findings broaden our understanding of the mechanisms of RD and MD that can facilitate a more reliable and valid approach to the classification and identification of learning difficulties (Fletcher et al. 2019). That is, domain-specific areas seem to play a distinct role for individuals with learning difficulties, as RD demonstrating under activation in the reading network while MD presenting under activation in math regions. Interestingly, the distinction between RD and MD underlines a parallel supposition that those with learning difficulties have reduced efficiency in domain-specific brain regions, regardless of whether their difficulty is in reading or math. Moreover, there was homologous overactivation in executive functioning areas, perhaps highlighting some supplementary similarities in the development and the manifestation of atypical functioning for reading and math. That is, the reduced activation in domain-specific brain regions in RD and MD may lead to the recruitment of executive functions. Notably, the coding of study and participants' characteristics as well as the post-hoc analyses in the current study accentuate that variability in study methodologies may contribute to inconsistencies in the literature and our understanding of learning difficulties. Consequently, future work should elucidate the identification of learning difficulties to progress toward a more consistent and reliable classification of RD and MD.

These findings may also assist educators and researchers in developing effective interventions to help students with learning difficulties. For instance, findings suggest that compensatory brain response for RD may be related to demands of phonological processing during word reading. Thus, reading interventions that promote decoding may help promote more efficient processing (Pugh et al. 2000), and support language and reading. Further, due to hyperactivity in brain regions associated with executive functions, reading interventions should be mindful of the cognitive demands placed on those with RD and integrate strategies to reduce cognitive overload. For children with MD, interventions that promote efficient strategy use may be beneficial to endorse more efficient processing (Cho et al. 2011; Wylie et al. 2012). Similar to RD, when implementing math interventions, educational practitioners should be cognizant of and incorporate cognitive load reducing strategies to diminish the cognitive demands in those with MD.

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Authors' contribution

Amanda Martinez-Lincoln (Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing—original draft, Writing—review & editing), Tess Fotidzis (Conceptualization, Data curation, Writing—review & editing), Laurie Cutting (Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing—review & editing), Gavin Price (Conceptualization, Writing—review & editing), and Laura Barquero (Conceptualization, Data curation, Methodology, Supervision, Visualization, Writing—review & editing)

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(*indicates that the study was included in the meta-analysis.)

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