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RESEARCH ARTICLE

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Dysfunctions associated with the intraparietal sulcus and a distributed network in individuals with math learning difficulties: An ALE meta-analysis

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Abstract

Math learning difficulty (MLD) is a learning disorder characterized by persistent impairments in the understanding and application of numbers independent of intelligence or schooling. The current study aims to review existing neuroimaging studies to characterize the neurobiological basis in MLD for their quantity and arithmetic dysfunctions. We identified a total of 24 studies with 728 participants through the literature. Using the activation likelihood estimate (ALE) method, we found that the most consistent neurobiological dysfunction in MLD was observed in the right intraparietal sulcus (IPS) with distinct patterns of the anterior and posterior aspects. Meanwhile, neurobiological dysfunctions were also observed in a distributed network including the fusiform gyrus, inferior temporal gyrus, insula, prefrontal cortex, anterior cingulate cortex, and claustrum. Our results suggest a core dysfunction in the right anterior IPS and left fusiform gyrus with atypically upregulated functions in brain regions for attention, working memory, visual processing, and motivation, serving as the neurobiological basis of MLD.

KEYWORDS
ALE, intraparietal sulcus, math learning difficulty, neuro imaging

1 | INTRODUCTION

The ability to process numbers is crucial to individuals' success and well-being (Geary et al., 2012; Harackiewicz et al., 2012; Parsons & Bynner, 2005). Notably, math learning difficulty (MLD) can be detrimental to affected individuals with persistent impairments in basic arithmetic knowledge and skills regardless of intellectual ability or level of education (Fuchs et al., 2005; Geary, 2011; Haberstroh & Schulte-Körne, 2019; Murphy et al., 2007). Despite an estimated 3%–7% rate in children (Haberstroh & Schulte-Körne, 2019; Reigosa-Crespo et al., 2012; Shalev et al., 2000), the neurobiological basis of MLD remains poorly understood (Kaufmann et al., 2011; Peters & De Smedt, 2018). Therefore, the current study aims to employ the activation likelihood estimate (ALE) method to reveal the neurobiological atypicality of MLD compared to the typically developing (TD) peers and the increased or decreased functions in different brain regions with a focus on the intraparietal sulcus (IPS).

The early theory, known as the *core quantity deficit hypothesis*, argues that the quantity processing deficit is the fundamental cause of MLD (Butterworth, 2011; Butterworth et al., 2011; Dehaene & Wilson, 2007; Landerl et al., 2013; Von Aster & Shalev, 2007). Mounting research has shown that processing quantity information in both symbolic (e.g., Arabic numerals) and nonsymbolic (e.g., dot arrays) formats are crucial for the development of math proficiency

Jonathan Tablante and Lani Krossa contributed equally to this study.

(Ansari, 2008; Chen & Li, 2014; De Smedt et al., 2013; Jordan et al., 2010; Schneider et al., 2009, 2017). This ability is also shown to be anchored in the IPS in the lateral parietal lobe (Dehaene et al., 2003; Piazza et al., 2004; Price et al., 2013, 2016; Rosenberg-Lee et al., 2011; Schel & Klingberg, 2016). In comparison, individuals with MLD have been shown to suffer from impairments in processing symbolic quantity information and maybe also in nonsymbolic quantity information (Lyons & Ansari, 2015; Reigosa-Crespo et al., 2012; Salvador et al., 2019; Schwenk et al., 2017; Wong & Chan, 2019). Moreover, neuroimaging studies have revealed that MLD is indeed associated with brain dysfunction or atypical structures in the IPS (Ashkenazi et al., 2012; Isaacs et al., 2001; Jolles et al., 2016; Mussolin et al., 2010; Price et al., 2007; Rotzer et al., 2008).

Recent research further suggests that successful math performance is influenced by working memory (Cowan et al., 2011; Geary et al., 1991; Murphy et al., 2007), attention (Blair & Razza, 2007; Menon, 2014; Wu et al., 2017), visuospatial processing (Ashkenazi et al., 2013; Lambert & Spinath, 2018), language (Cowan et al., 2011; Wu et al., 2017), and affective and motivational factors such as attitude (Chen et al., 2018), motivation (Wang et al., 2015), and anxiety (Ashcraft & Ridley, 2005; Lyons & Beilock, 2012; Ramirez et al., 2013; Supekar et al., 2015; Wu et al., 2012). Accordingly, individuals with MLD were shown to have significantly lower working memory abilities (Mabbott & Bisanz, 2008) and visuospatial skills (Lambert & Spinath, 2018) compared to TD. Ample findings also reported that individuals with MLD had atypical brain activations or aberrant multivoxel representations in distributed regions (Bulthé et al., 2019; Chen et al., 2021; Iuculano et al., 2015; Kucian et al., 2011; Rosenberg-Lee et al., 2015; Rotzer et al., 2008), such as the anterior insula, the dorsolateral and ventrolateral prefrontal cortices (dlPFC and vlPFC), fusiform gyrus along with inferior temporal gyrus (FG/ITG). Therefore, the updated theory, known as the *multifaceted cognitive impairment hypothesis*, proposes that MLD is associated with dysfunctions not only in the IPS for quantity processing but also a distributed brain networks for various domain-general functions (Ashkenazi et al., 2012; Iuculano, 2016; Menon et al., 2020; Peters & De Smedt, 2018; Rapin, 2016; Vogel & De Smedt, 2021).

Currently, neuroimaging studies on MLD are quite limited and with mixed findings, so we need to address critical literature gaps about the neurobiological basis of MLD. First, although existing meta-analyses have revealed the brain regions for math processing in TD (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Hawes et al., 2019; Kaufmann et al., 2011), the consistent neurobiological difference between MLD and TD remains unknown. The only attempt in the literature was more than a decade ago (Kaufmann et al., 2011) with only two studies. As a result, the convergence of the loci of neurobiological atypicality in MLD is entirely unknown. It is critical to show whether a consistent pattern of neurobiological atypicality in the IPS can be observed in MLD compared to TD, and we need to reveal brain regions beyond the IPS that are consistently reported with dysfunctions in MLD. Moreover, due to the inconsistent findings (Ashkenazi et al., 2012; Davis et al., 2009; De Smedt et al., 2011; Devlin & Price, 2007; Iuculano et al., 2015; Rosenberg-Lee et al., 2015; Rykhlevskaia et al., 2009), some researchers argue that individuals with MLD have cognitive deficiencies (Von Aster & Shalev, 2007), whereas other researchers argue that MLD stems from an increased engagement to compensate for their math difficulties (Vogel & De Smedt, 2021). Thus, it is also important to reveal the brain regions that were consistently reported with decreased effects (MLD < TD; *deficiency*) and those with increased effects (MLD > TD; *compensation*). Last, the IPS and adjacent regions have been hypothesized as a critical region for quantity and arithmetic processing (Dehaene & Wilson, 2007; Menon, 2014; Menon et al., 2020; Von Aster & Shalev, 2007), but the spatial convergence of MLD deficits remains unclear. Atypical brain difference between MLD and TD has been found along the IPS from more inferior parts including the IPL, precuneus, and cuneus to more superior and anterior parts along with SPL, but both decreased and increased patterns have been reported (Ashkenazi et al., 2012; Devlin & Price, 2007; Iuculano et al., 2015; Rosenberg-Lee et al., 2015). Therefore, a meta-analysis could potentially reveal the consistently reported foci in subdivisions of the IPS for their roles in MLD.

In sum, we will use the activation likelihood estimate (ALE) meta-analysis (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Hawes et al., 2019; Sokolowski et al., 2017) to reveal the convergence of brain regions associated with MLD, in order to achieve three primary aims. First, we would like to provide a comprehensive review of the neurobiological correlates of MLD compared to TD regardless of the direction of observed effects (i.e., MLD < TD or MLD > TD). This analysis could help us identify whether the IPS is consistently reported in the literature as suggested by the *core quantity deficit hypothesis*, and also help us characterize brain regions beyond the IPS as hypothesized by the *multifaceted cognitive impairments hypothesis*. Second, we plan to conduct a follow-up analysis to reveal how the consistency of the reported brain regions depends on the directional effects, namely, MLD < TD or MLD > TD, in order to reveal brain regions with deficiencies or compensatory roles in MLD. Last, we will examine the foci of subdivisions within the IPS showing the directional effects in MLD.

2 | METHODS

2.1 | Study selection

Following the conventional approach (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Derderian et al., 2021; Jackson, 2021; Müller et al., 2018), we conducted a literature search using PubMed to identify relevant studies that were published or in-press online in English between 2006 and 2020. The following boolean search term was used: (((((mathematical learning difficulties) OR (mathematical learning difficulty)) OR (dyscalculia)) OR (mathematical learning disability)) OR (mathematical learning disabilities) AND (journalarticle [Filter])) AND ((((neuroimaging [Title/Abstract]) OR (fMRI [Title/Abstract])) OR (PET [Title/Abstract])) OR (brain [Title/Abstract]) AND (journalarticle [Filter])) AND (journalarticle [Filter]). Additionally, we conducted an ancestral search based on the references of three review papers (De Smedt

et al., 2013; Kaufmann et al., 2011; Peters & De Smedt, 2018) in order to supplement the PubMed search. Since previous studies were not consistent with the diagnosis criteria and labels for individuals with math difficulties (Geary, 2011; Murphy et al., 2007), we included "dyscalculia," "math learning disability," and "math learning difficulty" as our search terms. As a consequence, the current meta-analysis was conducted with studies of different cut-off criteria (see Supporting Information) and we adopted the term math learning difficulty (MLD) to describe the atypical population for inclusiveness. The search from PubMed returned 393 papers and the citations from three review articles included 289 papers (Figure 1). The two co-first authors went through the titles and abstracts to remove the duplicates and select papers for further examinations, if they: (i) used one of the neuroimaging techniques (MRI, PET, etc.), (ii) had a group of participants classified with dyscalculia, math learning disabilities, or math learning difficulties, and (iii) were not review or meta-analysis articles. As a result, 92 papers were selected for further examinations.

Next, the two co-first authors read these 92 papers in more detail and screened for the following inclusion/exclusion criteria: (i) need to report the sample size of the MLD group, (ii) need to report the peak coordinates in either MNI or Talairach Space, and (iii) need to use the univariate whole-brain analysis approach instead of ROI approaches (Müller et al., 2018). Finally, 24 papers were identified, but two studies reported no group differences between MLD and their TD peers and reported no single-group analysis for MLD. Thus, a total of 22 papers were included in the current meta-analysis. Of these 22 studies, 16 reported univariate functional activations, 2 reported functional connectivity differences, and 4 reported structural differences. Amongst the 22 papers, two studies examined participants of MLD with comorbid conditions of nonverbal learning disability (NVLD; Banker et al., 2021) or Turner syndrome (TS; Molko et al., 2003). All 22 studies reported group differences between MLD and TD, but not every study reported single-group results for MLD or TD

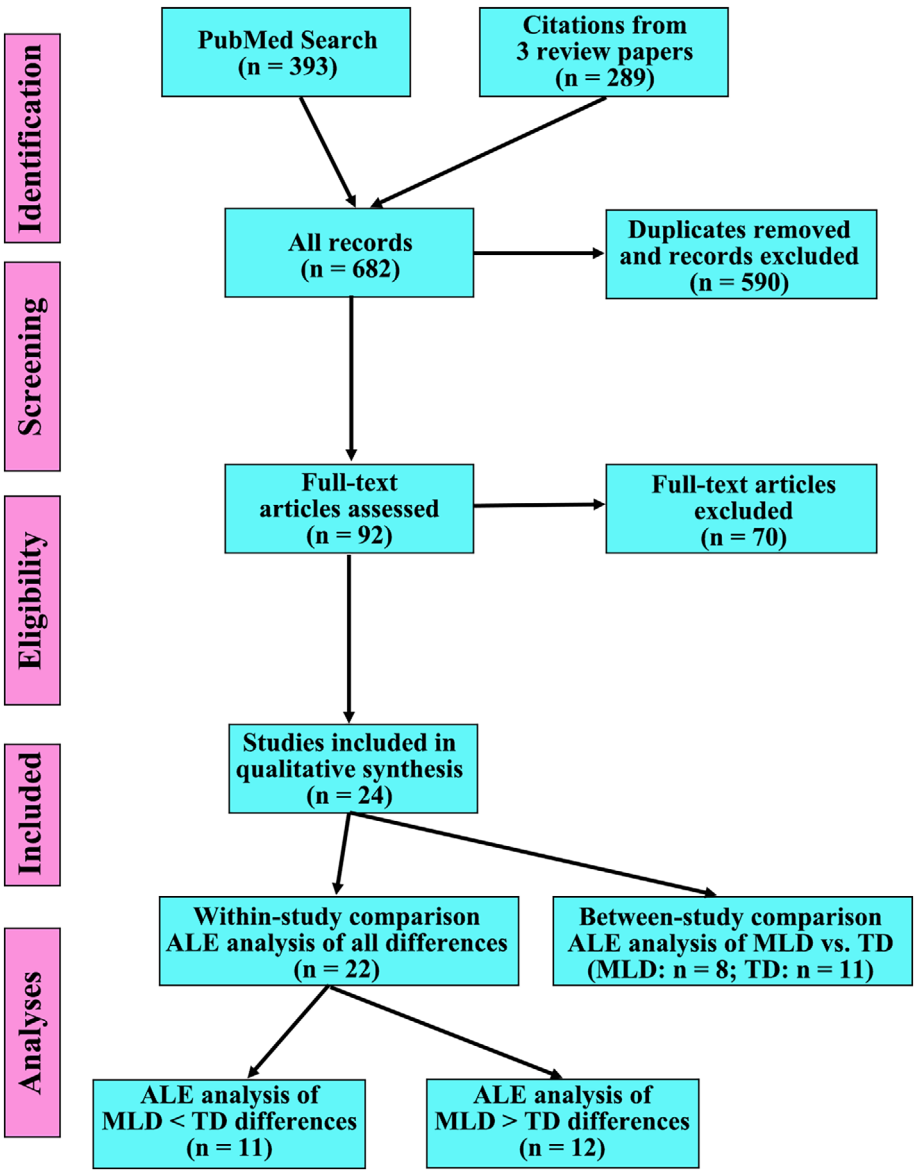


FIGURE 1 Flowchart of literature search, identification of eligible articles and proposed ALE analyses

TABLE 1 Descriptive information of studies included in the within-study and between-study ALE meta-analyses

No.	First author	Year	Major group effects	Voxel-level threshold	Single-group data (TD)	Single-group data (MLD)	Notes
1	Ashkenazi	2012	MLD < TD	$p < .01$, uncorr.	Yes	Yes	
2	Ashkenazi	2013	MLD < TD and MLD > TD	$p < .005$, uncorr.	No	No	
3	Banker	2020	MLD > TD	$p < .001$, uncorr.	No	No	With NVLD comorbidity; functional connectivity
4	Davis	2009	MLD > TD	$p < .001$, uncorr.	Yes	Yes	
5	De Smedt	2011	MLD > TD	$p < .001$, uncorr.	No	No	
6	Iuculano	2015	MLD > TD	$p < .01$, uncorr.	Yes	Yes	Only pretraining data
7	Kaufmann	2009	MLD > TD	$p < .001$, uncorr.	No	No	
8	Kucian	2013	MLD < TD	$p < .001$, uncorr.	No	No	Structural data
9	Kucian	2006	MLD < TD	$p < .001$, uncorr.	Yes	Yes	
10	Kucian	2011	MLD < TD	$p < .01$, uncorr.	Yes	Yes	
11	Kucian	2011	MLD < TD and MLD > TD	$p < .05$, FDR corrected or $p < .01$, uncorr.	Yes	Yes	
12	McCaskey	2017	MLD < TD and MLD > TD	$p < .05$, FWE corrected	Yes	No	
13	McCaskey	2018	MLD < TD	$p < .001$, uncorr.	Yes	Yes	
14	McCaskey	2020	MLD < TD	$p < .05$, FWE corrected	No	No	Structural data
15	Michels	2018	MLD < TD and MLD > TD	$p < .001$, uncorr.	No	No	Only pretraining data; functional connectivity
16	Molko	2003	MLD < TD	$p < .01$, uncorr.	Yes	Yes	With TS comorbidity; structural data
17	Mussolin et al.	2009	MLD < TD and MLD > TD	$p < .05$, FWE corrected	No	No	
18	Price	2007	MLD < TD	$p < .005$, uncorr.	No	No	
19	Rosenberg-Lee	2015	MLD < TD	$p < .001$, uncorr.	No	No	
20	Rotzer	2009	MLD < TD	$p < .001$, uncorr.	Yes	Yes	
21	Rykhlevskaia	2009	MLD < TD	$p < .001$, uncorr.	No	No	Structural data
22	Schwartz	2018	MLD < TD	$p < .05$, FWE corrected	Yes	No	

Note: For the complete reference of studies included, please see the references in Supporting Information. For more detailed information on each study and included data, please see Supporting Information.

Abbreviations: Uncorr., uncorrected; NVLD, nonverbal learning disability; TS, Turner syndrome.

(Table 1). Only the pretraining data from training studies were included in the analysis. We extracted the information about the imaging method type, number of participants in MLD and TD groups, diagnosis criteria, age, and gender of the MLD group, experimental tasks and contrasts used, stimuli type (pictures, words, etc.), coordinate systems and peak coordinates, thresholding criteria, and the direction of the results in between-group comparisons (i.e., MLD > TD or MLD < TD). The complete list of studies, extracted data used in the meta-analysis, and statistical maps are deposited at an open-access site (BOX link: https://app.box.com/s/r1znsd7q255d0x3exbual50h18xpmfoq, for more details; see Supporting Information).

2.2 | ALE meta-analysis procedures

We converted all coordinates to MNI space using Talairach to MNI (SPM) transform for analytic consistency provided by GingerALE (version 3.0.2; Eickhoff et al., 2009, 2012, 2016), and all the reported analyses were conducted in the same version of the GingerALE. The ALE method uses reported coordinates from previous studies to identify loci of brain regions showing consistent findings across studies. Two different ALE meta-analysis procedures were conducted: a within-study comparison and a between-study comparison. The within-study comparison analysis used the peak coordinates reported for group differences between MLD and TD groups, and any significant results

should be interpreted as highly converging evidence for brain regions associated with neurobiological dysfunctions in MLD compared to TD. In contrast, the between-study comparison analysis used the peak coordinates from only the MLD or only the TD groups (i.e., single-dataset analysis). Then, the comparison between MLD and TD came out from both conjunction and contrast analyses at the meta-analytical level. Since the between-study comparison delineated the consistent brain regions for math processing in MLD and TD separately first, the comparison provided us with a direct contrast between MLD and TD. The conjunction analysis revealed brain regions that were consistently reported for both MLD and TD, whereas the contrast analysis revealed brain regions that were reported more consistently in one group (e.g., MLD) compared to the other (e.g., TD).

2.2.1 | Within-study comparison

The major goal of the within-study comparison analysis was to address our first aim to provide a comprehensive understanding of the potential neurobiological basis of the dysfunctions in MLD compared to TD. The next goal was to address the second aim of revealing regions of decreased effects (MLD < TD) or increased effects (MLD > TD). Therefore, we conducted three separate analyses: (i) analysis of neurobiological atypicality in MLD compared to TD using all coordinates regardless of their effect directions, (ii) analysis of decreased functions/structures showing effects of MLD < TD, and (iii) analysis of increased functions/structures showing effects of MLD > TD. The first analysis helped us depict the potential neurobiological dysfunctions in MLD compared to TD overall (Dehghan et al., 2016), whereas the other two directional analyses would provide a more detailed picture of their dysfunctions. For the first non-directional analysis, all coordinates were entered into the analysis, whereas the directional analyses only included coordinates reported with either MLD > TD or MLD < TD effects. Additional results for studies with only functional studies could be found in Supporting Information. For each of the three proposed analyses, we ran the single-dataset analysis with the corresponding coordinates to create the activation maps including the foci and a Gaussian blur with a full width at half maximum (FWHM). The sample size of each study was used to determine the FWHM for the foci, with a larger sample size resulting in a larger and tighter curve around the foci peaks. We first used the cluster-level FWE correction with a p-value of .05 and 1000 permutation to threshold the results, and we also used a less stringent threshold with an uncorrected p-value of .001, and 120 mm^3 volume size. The number of studies and foci entering each analysis could be found in Table 2.

2.2.2 | Between-study comparison

The between-study comparison can address our third aim to examine the converging findings in the IPS and possibly separate loci for MLD < TD and MLD > TD effects within the IPS. The first step was to conduct the single-dataset analysis with reported coordinates from either MLD or TD by cluster-level thresholding with a p-value of .05 and 1000 permutations. Next, we combined the thresholded ALE maps from the single-dataset analyses of MLD and TD to conduct the conjunction and contrast analyses. We set the p-value to .05 with a minimum volume of 50 mm^3 and 10,000 permutations for the conjunction and contrast analyses.

Our analysis in the within-study comparison for MLD < TD and MLD > TD effects and the between-study comparison had a small number of studies (Müller et al., 2018), so we conducted a Jackknife sensitivity analysis (Leroy et al., 2020; Wilson et al., 2018) to show the robustness of our results. We repeated the analysis iteratively by excluding one dataset at a time, and we verified that the observed brain regions in the ALE analysis were reliably found across the iterations (Tables 3, 4, S2, and S3).

3 | RESULTS

Given almost two decades of research in this field (2006–2020), the number of studies was surprisingly low and further stressed the importance of conducting research in this field. In addition, it is still noteworthy that 2 out of 24 (~8%) studies found no group difference between MLD and TD with the fMRI whole-brain analysis and commonly used cut-off criteria for thresholding.

3.1 | Consistent neurobiological dysfunctions in MLD compared to TD across all studies

We included 264 foci from 22 studies with 680 subjects in total for this analysis. With the more stringent thresholding criterion at the cluster-level FWE of $p < .05$, we only found that the right intraparietal sulcus (IPS) along with inferior and superior parietal lobule (IPL/SPL) was consistently reported to show differences between the MLD and TD groups (Figure 2a). With a more relaxed threshold (voxel-level, uncorrected, $p < .001$), consistent reports of differences between MLD and TD were found in multiple brain regions, including the left SPL, right IPL/SPL, right insula, and left inferior temporal gyrus (ITG; Table 3). The results based on only the functional data were comparable (see Table S1).

TABLE 2 Summary of the number of studies and foci included in each ALE meta-analysis

	All	MLD < TD	MLD > TD	Between-MLD	Between-TD
No. of studies	22	11	12	8	11
No. of foci	264	150	114	107	142
No. of participants	680	334	374	276	368

TABLE 3 Brain regions showing consistent neurobiological atypicality in MLD compared to TD from the within-study comparison

Cluster	Hemisphere	Region (Brodmann's area)	Peak center (*x*, *y*, *z*) in MNI space			Cluster size (mm^3)	ALE value
Cluster level threshold: $p < .05$							
1	Right	SPL/IPL (BA 40/7)	48	−50	40	13,000	0.0189
Voxel level threshold: $p < .001$							
1	Left	IPL (BA 40)	−40	−42	50	408	0.0192
2	Right	SPL (BA 40)	48	−50	40	376	0.015
3	Right	IPL (BA 40)	48	−50	40	328	0.0189
4	Right	Insula (BA 22)	48	0	−12	176	0.0178
5	Right	Insula (BA 13)	46	−2	6	168	0.0176
6	Left	ITG (BA 20)	−58	−38	−16	128	0.0162

Abbreviations: ITG, inferior temporal gyrus; SPL/IPL, superior/inferior parietal lobule.

TABLE 4 Brain regions showing consistent neurobiological atypicality in a directional manner (MLD < TD or MLD > TD) from the within-study comparison

Cluster	Hemisphere	Region (Brodmann's area)	Peak center (*x*, *y*, *z*) in MNI space			Cluster size (mm^3)	ALE value	Jackknife sensitivity
MLD < TD								
Cluster level threshold: $p < .05$								
1	Right	SPL (BA 40)	34	−42	52	5464	0.0136	10/11
Voxel level threshold: $p < .001$								
1	Right	SPL (BA 40)	34	−42	52	512	0.0136	10/11
2	Left	ITG (BA 20)	−58	−38	−16	256	0.0162	9/11
3	Left	Insula (BA 13)	−34	−26	16	256	0.0146	9/11
4	Left	Precuneus/IPL (BA 7)	−18	−46	52	256	0.0148	9/11
5	Right	Insula (BA 13)	36	20	6	168	0.012	9/11
6	Left	FG/LG (BA 18)	−20	−82	−4	160	0.0125	9/11
MLD > TD								
Cluster level threshold: $p < .05$								
1	Right	Precuneus/IPL (BA 7)	40	−68	40	8608	0.0142	10/12
2	Right	Insula (BA 13)	46	0	−12	5968	0.0176	10/12
Voxel level threshold: $p < .001$								
1	Left	IPL (BA 40)	−40	−42	50	640	0.0189	12/12
2	Right	Insula (BA 13)	42	14	−10	464	0.0131	10/12
3	Right	Insula (BA 13)	46	0	−12	352	0.0176	10/12
4	Left	IFG (BA 9)	−44	18	20	240	0.0127	10/12
5	Right	FG (BA 37)	58	−52	−18	120	0.0106	10/12

Abbreviations: FG/LG, fusiform gyrus/lingual gyrus; IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; SPL/IPL, superior/inferior parietal lobule.

3.2 | Consistent directional neurobiological dysfunctions in MLD compared to TD

First, we examined brain regions that were consistently reported to show an MLD < TD effect across studies. A total of 150 foci from 11 studies with 334 subjects were included in this analysis (Table 2). At the cluster-level thresholding, the right lateral parietal lobe structures seem to be mostly consistent across studies, centering at the anterior IPS/SPL. At the voxel-level thresholding, decreased patterns in MLD compared to TD were consistently reported beyond the parietal lobe and were found in the left ITG, bilateral insula, the left lingual gyrus and fusiform gyrus (LG/FG), and left precuneus and paracentral lobule (Figure 2b and Table 4).

Next, we analyzed 114 foci from 12 studies with 374 subjects to reveal the brain regions showing consistent effects for MLD > TD (Table 2). Interestingly, we still found consistently increased patterns of MLD > TD at the cluster-level thresholding in the right lateral parietal lobe, including the right precuneus and inferior parietal lobule (IPL) as well as the right insula expanding to the inferior frontal gyrus (IFG). At the voxel-level thresholding, MLD showed consistently

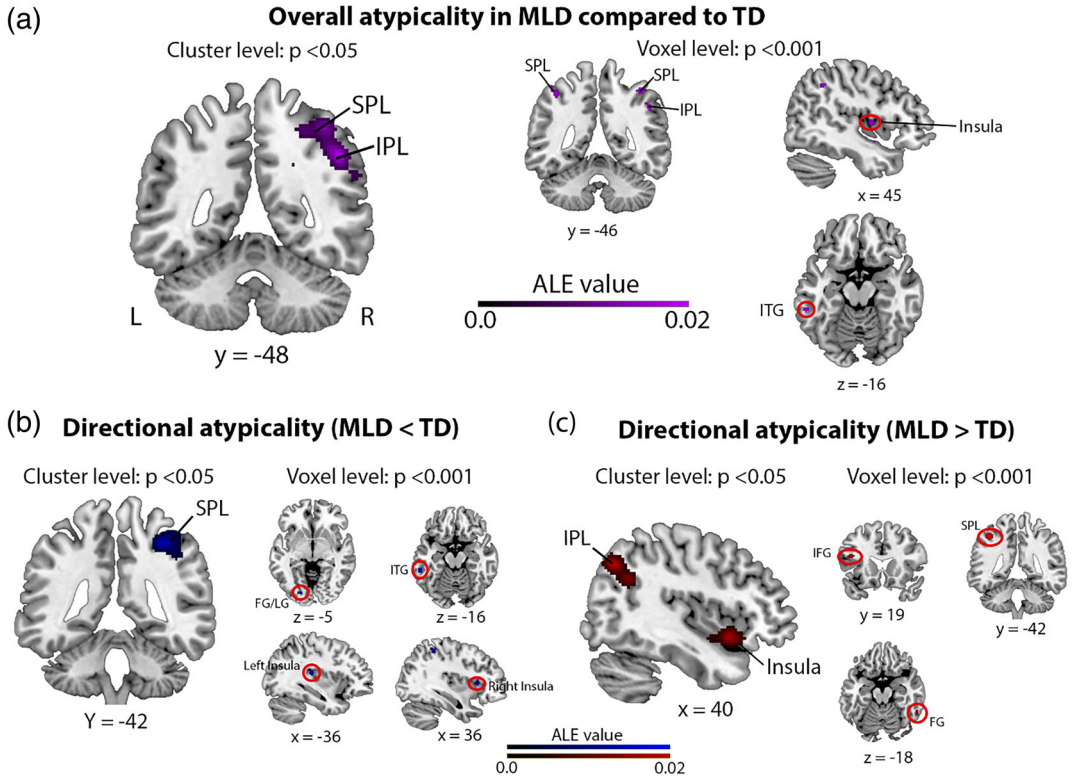


FIGURE 2 Within-study ALE meta-analysis showing overall and directional atypicality in MLD compared to TD. Significant results from a more stringent threshold (cluster-level $p < .05$) and a more relaxed threshold (voxel-level $p < .001$) were reported (for more details, see section 2). FG/LG, fusiform gyrus/lingual gyrus; IFG, inferior frontal gyrus; SPL/IPL, superior/inferior parietal lobule

increased patterns compared to TD in the left and right IPL, right insula, right FG expanding to the cerebellum, and left IFG (Figure 2c and Table 4).

To further compare brain regions of neurobiological dysfunctions in MLD with the brain regions for math processing in TD, we compared our thresholded maps with the association map for the topic "Arithmetic" from Neurosynth (Yarkoni et al., 2011). We found the right insula, bilateral IPS, and left ITG revealed in our meta-analysis also overlapped with the association map from Neurosynth (Figure S1, Supporting Information). This comparison provided convergence on regions of dysfunctions in MLD but also suggested that the neurobiological dysfunctions in MLD may extend beyond the math processing network in TD.

3.3 | Differences in the consistently reported findings in IPS in MLD compared to TD

In the between-study comparison analysis, we have 107 foci from 8 studies with 276 participants for the MLD group and 142 foci from 11 studies with 368 participants for the TD group (Table 2). The conjunction analysis found that there were overlaps in the right IPL/SPL for both MLD and TD groups, but there was still a different locus in the anterior IPS/SPL showing the MLD < TD effect and a different locus in the posterior IPS/IPL showing the MLD > TD effect (Figure 3 and Table 5). This pattern is largely consistent with the observation in the within-study comparison showing the anterior IPS/SPL in the MLD < TD analysis and the posterior IPS/IPL in the MLD > TD analysis (Figure 4).

In addition to the findings in the IPS, we observed differences in the right medial part of the superior frontal gyrus (mPFC), left dorsal anterior cingulate cortex (dACC), right FG extending to the cerebellum, as well as left claustrum for the MLD > TD effect (Figure 3 and Table 5). This is largely consistent with our within-study comparison analysis, suggesting that there is some converging evidence of neurobiological dysfunctions in the right IPS, but increased engagement in a widely distributed network of multiple brain regions.

4 | DISCUSSION

Based on 22 neuroimaging studies, we used the Activation Likelihood Estimate (ALE) analysis to comprehensively characterize the consistent findings on the neurobiological basis of math learning difficulties (MLD). Our analysis has revealed that the most consistent finding of neurobiological atypicality in MLD was found in the right parietal lobe along the intraparietal sulcus (IPS), but also extended into bilateral insula, left SPL, bilateral ITG/FG, left dorsal ACC, bilateral mPFC, and left claustrum through the within-study and between-study analyses. Furthermore, except for the right anterior IPS and left FG/ITG

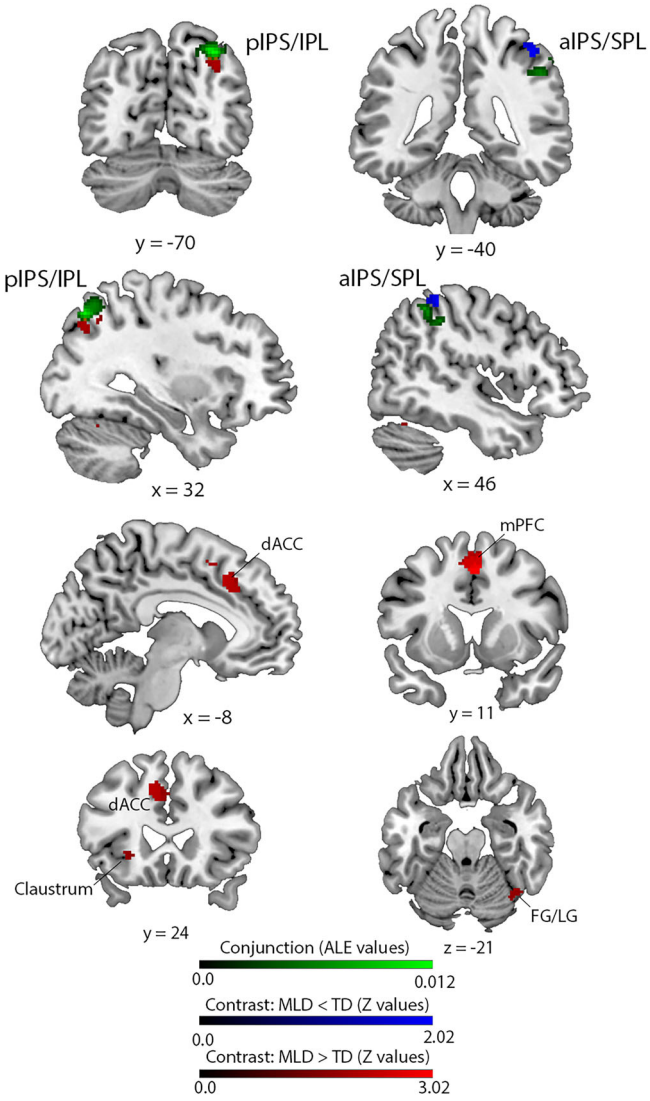


FIGURE 3 Between-study ALE meta-analysis showing overlapping regions (conjunction analysis) related to math processing in both TD and MLD as well differential regions (contrast analysis) related to math processing in MLD compared to TD. aIPS and pIPS, anterior and posterior intraparietal suclus; dACC, dorsal anterior cingulate cortex; FG/LG, fusiform gyrus/lingual gyrus; mPFC, medial prefrontal cortex/medial superior frontal gyrus; SPL/IPL, superior/inferior parietal lobule

showing MLD < TD effects, other brain regions showed increased functions in MLD. Last, the deficiency in MLD was found to be consistently reported for the anterior IPS whereas the increased pattern was consistently reported in the posterior IPS.

4.1 | The central role of the right lateral parietal cortex and the distributed networks in MLD

From our meta-analysis, we found the most consistently reported brain region was the right lateral parietal cortex, centering around the IPS. The IPS serves as a key neurobiological basis for MLD and potentially their deficits in math tasks (Ashkenazi et al., 2012; Bulthé et al., 2019; Menon et al., 2020; Price et al., 2007). The right IPS, along with the adjacent SPL and IPL, are central for math processing across different types of tasks such as quantity comparisons (Chassy & Grodd, 2012; Sokolowski et al., 2017) and exact or approximate calculation tasks (Arsalidou & Taylor, 2011; Ashkenazi et al., 2012; Kucian et al., 2008). Our findings then are consistent with both the *core quantity deficit hypothesis* and *multifaceted cognitive impairment hypothesis*, suggesting that a core deficit in MLD resides in the right IPS for its role in quantity processing (Butterworth et al., 2011; Dehaene & Wilson, 2007; Landerl et al., 2013; Von Aster & Shalev, 2007).

However, as the *multifaceted cognitive impairment hypothesis* suggested, our ALE meta-analysis also revealed a set of brain regions beyond the IPS, showing differences between the TD and MLD groups in the within-study and between-study analyses. The right anterior insula has functional and anatomical connectivity with frontal regions mostly (Cloutman et al., 2012; Supekar & Menon, 2012) with a domain-general role in cognitive control. It has been reported to be activated in number and calculation tasks (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Rosenberg-Lee et al., 2015; Supekar & Menon, 2012), and individuals with MLD showed hyperactivation (Rosenberg-Lee et al., 2015) or undifferentiated neural representations for different arithmetic operations in the right anterior insula (Chen et al., 2021). Another frontal region revealed in our meta-analysis was the left inferior frontal gyrus (IFG, BA 9), which is a domain-general region activated for multiple cognitive tasks, potentially given its role in visual working memory, attention, and selection (Burianova et al., 2010; Corbetta & Shulman, 2002; Jackson, 2021; Thompson Schill et al., 1997). It has been reported for number processing (Berteletti et al., 2014; Rosenberg-Lee et al., 2011; Zhang et al., 2012), mental calculation (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Qin et al., 2014), and meta-cognitive judgments (Bellon et al., 2020). Furthermore, the frontal regions are commonly associated with using laborious strategies to complete math tasks (e.g., counting for calculation; Menon, 2014; Menon et al., 2020; Qin et al., 2014). Our results then suggested that individuals with MLD had dysfunctions in the frontal regions for poorly regulated executive functions to complete math tasks. In addition, we observed the consistently reported differences between MLD and TD in the ventral visual pathway bilaterally, including the ITG and FG extending to the lingual gyrus (LG). These findings suggested potential dysfunctions in MLD for processing high-order visual information (Derderian et al., 2021; Martin & Chao, 2001; Mei et al., 2010), especially the visual forms of numbers (Daitch et al., 2016; Shum et al., 2013).

Our between-study analysis revealed three more brain regions that may underlie the poor math skills in MLD, namely, the left dorsal ACC, bilateral mPFC, and left claustrum. The dorsal ACC, although in the right hemisphere, has been reported to be involved in math tasks (Price et al., 2013; Wilkey et al., 2017), and researchers have argued that it plays an important role in intrinsically motivated behaviors along with insula (Arsalidou et al., 2018). The mPFC has been shown to consistently activate for quantity processing for symbolic or

nonsymbolic numerical materials or even non-numerical materials (Sokolowski et al., 2017), but it is less shown for calculation tasks (Arsalidou et al., 2018; Arsalidou & Taylor, 2011). Last, the function of the claustrum in math processing is less known but some researchers have proposed that the claustrum plays a role in integrating the top-down and bottom-up processes to create percepts of math concepts (Arsalidou et al., 2018; Crick & Koch, 2005; Smith et al., 2020).

4.2 | The deficiency in core number systems but upregulated functions in distributed networks in MLD

Our meta-analysis examined the directional effects of decreased (MLD < TD) and increased (MLD > TD) functions since researchers have proposed different explanations of MLD for both neural deficiency (Von Aster & Shalev, 2007) or compensatory mechanism (Vogel & De Smedt, 2021). The right anterior IPS and left ITG/FG were found to be consistently reported with decreased effects in MLD, suggesting neurocognitive deficiencies for quantity processing (Butterworth et al., 2011; Dehaene & Wilson, 2007; Landerl et al., 2013; Von Aster & Shalev, 2007) and representing visual numeric forms (Chen et al., 2021; Grotheer et al., 2018; Iuculano et al., 2015; Menon et al., 2020; Menon & Chang, 2021).

By contrast, other brain regions such as the right insula and FG, left IFG and IPL, showed increased effects, suggesting that MLD may stem from excessive engagement from these domain-general regions for attention, visual form processing, and working memory resources to compensate their deficits in number systems (Vogel & De Smedt, 2021). However, the increased involvement of these regions could also mark the failure to regulate related but nonessential neural structures during math processing in a form of competition. For example, the right FG was less related to math processing in the healthy population but commonly reported in individuals with MLD (Chen et al., 2021; Iuculano et al., 2015; Menon et al., 2020; Menon & Chang, 2021). A large body of literature has discussed complementary and sometimes even competitive roles between the left and right FG in object processing (Behrmann & Plaut, 2012, 2013; Chen et al., 2017; Dundas et al., 2013; Haxby et al., 2001). Therefore, the increased activation in the right FG could either compensate for the insufficient activation in the left FG (*compensation*) or outperform the left FG undesirably (*competition*) for visual form processing. Future training studies on supporting skills for math would be extremely useful to differentiate these two potential mechanisms in MLD. Specifically, the *competition* hypothesis would predict a reduced engagement in supporting systems such as right FG, whereas the *compensation*

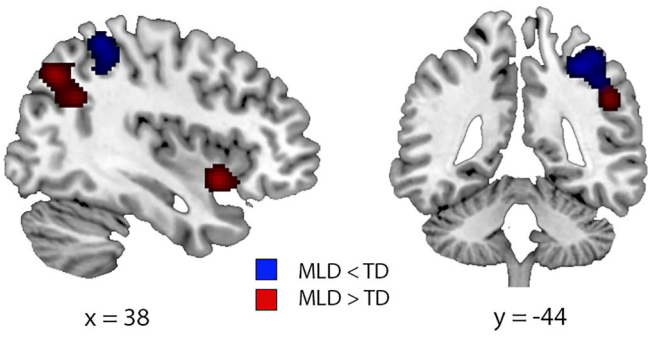


FIGURE 4 The directional atypicality in MLD compared to TD from the within-study ALE analysis show converging results with the between-study ALE analysis, showing MLD < TD effect in aIPS/SPL but MLD > TD effect in pIPS/IPL. The red cluster in the frontal region in the left panel was the anterior insula

TABLE 5 Brain regions showing consistent relationship with math processing in MLD and TD from the between-study comparison

Cluster	Hemisphere	Region (Brodmann's area)	Peak center (*x*, *y*, *z*) in MNI space			Cluster size (mm^3)	ALE value/ *p* value	Jackknife sensitivity
Conjunction analysis								
1	Right	IPL (BA 40)	30	−70	48	4400	0.0113	18/19
Contrast analysis								
MLD < TD								
1	Right	SPL (BA 40)	46	−40	54	424	0.0134	17/19
MLD > TD								
1	Right	mPFC/SFG (BA 6)	1.4	10.9	47.4	2552	0.0012	19/19
2	Left	dACC (BA 32)	−8	20	43	1432	0.0128	18/19
3	Right	FG/LG/cerebellum	39.2	−61	−28.3	728	0.0191	15/19
4	Right	Precuneus/IPL (BA 19)	26	−66	42	552	0.013	19/19
5	Left	Claustrum	−30	24	−2	224	0.0352	11/19

Note: The counts were based on studies that reported corresponding regions in MLD or TD separately.
Abbreviations: dACC, dorsal anterior cingulate cortex; FG/LG, fusiform gyrus/lingual gyrus; IFG, inferior frontal gyrus; mPFC/SFG, medial prefrontal cortex/superior frontal gyrus; SPL/IPL, superior/inferior parietal lobule.

hypothesis would predict a further increased engagement in supporting domain-general systems after the behavioral training.

4.3 | The differential roles of right anterior and posterior IPS in MLD

Some novel insights have emerged from our ALE meta-analysis that the anterior and posterior aspects of IPS may relate to different neurobiological dysfunctions in MLD compared to TD (Figures 3 and 4). The anterior part of right IPS, mostly the subdivision hIP2, has been associated with math processing in previous studies (Ashkenazi et al., 2012; Daitch et al., 2016; Rosenberg-Lee et al., 2015; Schwartz et al., 2018). The cortical thickness (Schel & Klingberg, 2016) or brain matter density (Starke et al., 2013) in the anterior IPS is associated with math abilities in the typically developing population. In addition, studies (Ashkenazi et al., 2012; Chen et al., 2021) have found that weak representations of arithmetic problems in anterior IPS were associated with poor arithmetic abilities as well as being characteristic of MLD compared to TD. Thus, our ALE results further support that dysfunctions in the right anterior IPS could lead to the inability to process quantity information (Dehaene & Wilson, 2007; Devlin & Price, 2007), impaired abilities to represent math concepts (Menon, 2014; Menon et al., 2020; Starke et al., 2013), and even aberrant functional connectivity of IPS to multiple frontoparietal and subcortical regions (e.g., hippocampus) that supports the development of fundamental math knowledge (Abreu-Mendoza et al., 2022; Emerson & Cantlon, 2012; Evans et al., 2015; Jolles et al., 2016; Rosenberg-Lee et al., 2015).

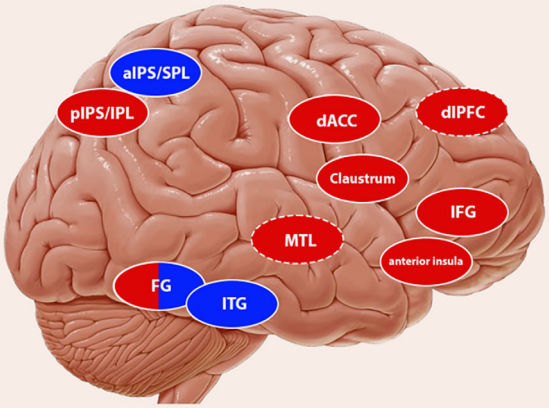
The posterior IPS is mostly connected to the parietal and occipital regions (Chang et al., 2016; Schel & Klingberg, 2016), but the literature was mixed for its function and structure for math skills (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Ashkenazi et al., 2012; Chen et al., 2021; Rosenberg-Lee et al., 2015; Starke et al., 2013). In addition, one previous meta-analysis (Hawes et al., 2019) has suggested that posterior IPS is related to more fundamental cognitive abilities such as mental rotation that could be building blocks for success in math. Presumably, the increased functions in the posterior IPS may suggest a compensatory or competition mechanism in MLD. A similar profile was observed in the left IPS that increased function was consistently reported in the literature. The left IPS is highly related to the successful performance of math tasks in the typically developing population (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Libertus et al., 2009; Sokolowski et al., 2017; Wu et al., 2009). Our results may suggest that the left and right IPS have distinct roles for math processing in MLD and the deficit in the right anterior IPS is more critical to the impairments of MLD. Since the left posterior IPS has been associated with nonverbal reasoning and working memory ability in addition to math (Schel & Klingberg, 2016), the role of the left IPS could be also more supportive and auxiliary just like the right posterior IPS. It is also noteworthy that the different patterns of left and right IPS could be related to factors such as age, grade, and the amount of experience to learn symbolic numbers and arithmetic skills (Chang et al., 2022; Emerson & Cantlon, 2012; Matejko et al., 2013; Rosenberg-Lee et al., 2011).

4.4 | Relations to previous ALE meta-analyses and implications to existing theories of MLD

One leading theory about MLD is their inability to process quantity information anchored in the IPS (Bulthé et al., 2019; Dehaene & Wilson, 2007; Devlin & Price, 2007; Iuculano, 2016; Von Aster & Shalev, 2007). Consistent with this view, namely the *core quantity deficit hypothesis*, our analysis showed the most consistent effect in right IPS and adjacent regions including SPL and IPL in MLD compared to TD. However, our meta-analysis further pinpointed that the deficit is more likely to be in the right anterior IPS, and the posterior IPS may have a different role in MLD. Moreover, our meta-analysis identified the left FG/ITG as another location with insufficient engagement in MLD compared to TD. Studies have shown that a putative number form or a math form area may exist in the ventral visual pathway in the left FG/ITG (Daitch et al., 2016; Grotheer et al., 2018; Shum et al., 2013). Thus, we propose that the core deficit of MLD stems from both right anterior IPS and left FG/ITG (Figure 5) and their connections for integrating symbolic and nonsymbolic quantity information for math processing (Chen et al., 2021; Fias et al., 2013).

Out meta-analysis also characterized the distributed brain networks beyond the IPS and their directional effects observed in MLD, supporting the *multifaceted cognitive impairment hypothesis* (Bulthé et al., 2019; Menon, 2014; Menon et al., 2020). Besides right anterior IPS and left FG/ITG, our meta-analysis also showed consistent findings with previous meta-analyses on math processing in the right anterior insula, mPFC, left IPL/SPL, right FG, dACC, and claustrum (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Hawes et al., 2019; Kaufmann et al., 2011). Advancing previous literature, we further showed that all of these regions showed increased engagements in MLD compared to TD (Figure 5). Therefore, we propose that these brain regions may be involved in more domain-general functions and serve as supporting systems for math processing. Critically, MLD is marked as a combination of core deficits in right anterior IPS and left FG/ITG for math processing and excessive engagement of various brain regions for domain-general cognitive functions.

We should also mention that our meta-analysis failed to reveal consistent findings for two important regions, namely, the dorsolateral prefrontal cortex (dlPFC) and medial temporal lobe (MTL; see Figure 5). Previous literature has shown that dlPFC is important for math processing, especially for its important role in working memory and attention during mental arithmetic (Arsalidou et al., 2018; Arsalidou & Taylor, 2011; Chang et al., 2015; Hawes et al., 2019; Menon, 2014), and other studies have also revealed critical dysfunctions in this region for MLD (Ashkenazi et al., 2012; Chen et al., 2021; Rosenberg-Lee et al., 2015). One possible explanation could be that our meta-analysis is based on studies with various math tasks and with participants of different ages and grades, but the involvement of dlPFC was mostly observed when laborious strategies were used and for individuals at the early stage of math development (Chang et al., 2015; Chen et al., 2021; Menon et al., 2020; Menon & Chang, 2021). A similar reason could also explain why we failed to reveal MTL, especially the hippocampus because the MTL structures



	Brain Systems	Cognitive Functions
MLD < TD (Deficit)	Anterior IPS	Quantity representation
	#FG	Symbolic number representation
	ITG	Associating numerical value to inputs
MLD > TD (Competition or Compensation)	Posterior IPS	Visuospatial processing, Visuospatial WM
	Anterior insula	Cognitive control, attention
	IFG (vlPFC)	Cognitive control and selection
	Dorsal ACC	Motivated behaviors, monitoring
	Claustrum	Integration of percepts
	*dlPFC	Working memory
	*MTL	Associative memory

FIGURE 5 The updated neurocognitive model for math learning difficulties (MLD) based on the current ALE meta-analysis and existing literature. ACC, anterior cingulate cortex; FG, fusiform gyrus; IFG, inferior frontal gyrus; IPS, intraparietal sulcus; ITG, inferior temporal gyrus; dlPFC, dorsolateral prefrontal cortex; MTL, medial temporal lobe; vlPFC, the ventrolateral prefrontal cortex. The blue circles highlight brain regions showing MLD < TD effects whereas the red circles highlight brain regions showing MLD > TD effects. #FG was shown with both effects in the current ALE meta-analysis depending on the hemisphere (left: MLD < TD; right: MLD > TD), and therefore, it was shown with two colors. *dlPFC and *MTL were not directly observed in our meta-analysis but were suggested in previous studies and reviews so they are shown as circles with dashed outlines

are critical for associative memory, so successful retrieval of math facts in children depends on this MTL system (Chang et al., 2022; Chen et al., 2018; Menon et al., 2020; Qin et al., 2014; Supekar et al., 2013). Therefore, we support the existing framework to include both dlPFC and MTL as crucial brain systems for math processing (Menon, 2014; Menon & Chang, 2021), but their roles in MLD over different stages of the development await further investigations.

4.5 | Limitations and future directions

There are key methodological limitations of the current study. Most importantly, our meta-analysis is based on a small set of studies using different tasks (magnitude comparison, calculation, etc.), different formats (nonsymbolic vs. symbolic), different operation types (e.g., addition, subtraction, etc.), different imaging techniques, and participants across different age and grades. This highlights the necessity of more research focused on the neurobiological basis of MLD. Future studies should clarify how the dysfunctions and the direction of dysfunctions (decreased vs. increased) in MLD may depend on various task-relevant factors and subgroups of this population (Lewis & Fisher, 2016; Swanson et al., 2018). In addition, other methods, such as signal differential mapping (SDM; Radua et al., 2012; Ranzini et al., 2022), could potentially provide more robust results for coordinate-based meta-analysis based on a small number of studies. Moreover, longitudinal studies on both TD and MLD groups with neuroimaging techniques are very scarce. Future studies should investigate how factors such as age and grade may moderate brain activation patterns during the typical and atypical development of math skills.

5 | CONCLUSION

In conclusion, our ALE meta-analysis study presents the idea that MLD is related to decreased engagement of the right anterior IPS and left FG/ITG as well as increased engagements of multiple brain regions including the right anterior insula, left IPL/SPL, right FG, dorsal ACC, mPFC, and claustrum. Our results highlight that MLD is marked as a combination of core deficits in the IPS and FG/ITG for quantity and numerical processing as well as atypical increased functions in a wide-distributed brain network for attention, control, visuospatial and magnitude processing, and motivation.

AUTHOR CONTRIBUTIONS

Lang Chen designed the research. Lang Chen, Jonathan Tablante, Lani Krossa, and Lang Chen analyzed the data. Lang Chen, Jonathan Tablante, Lani Krossa, and Tannaz Azimi wrote the manuscript. All authors contributed to editing it.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All the data are shared via open-access data base here: https://app.box.com/s/r1znsd7q255d0x3exbual50h18xpmfoq

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