Identifying the Neural Bases of Math Competence Based on Structural and Functional Properties of the Human Brain

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Abstract

■ Human populations show large individual differences in math performance and math learning abilities. Early math skill acquisition is critical for providing the foundation for higher quantitative skill acquisition and succeeding in modern society. However, the neural bases underlying individual differences in math competence remain unclear. Modern neuroimaging techniques allow us to not only identify distinct local cortical regions but also investigate large-scale neural networks underlying math competence both structurally and functionally. To gain insights into the neural bases of math competence, this review provides an overview of the structural and functional neural markers for math competence in both typical and atypical populations of children and adults. Although including discussion of arithmetic skills in children, this review primarily focuses on the neural markers associated with complex math skills. Basic number comprehension and number comparison skills are outside the scope of this review. By synthesizing current research findings, we conclude that neural markers related to math competence are not confined to one particular region; rather, they are characterized by a distributed and interconnected network of regions across the brain, primarily focused on frontal and parietal cortices. Given that human brain is a complex network organized to minimize the cost of information processing, an efficient brain is capable of integrating information from different regions and coordinating the activity of various brain regions in a manner that maximizes the overall efficiency of the network to achieve the goal. We end by proposing that frontoparietal network efficiency is critical for math competence, which enables the recruitment of task-relevant neural resources and the engagement of distributed neural circuits in a goal-oriented manner. Thus, it will be important for future studies to not only examine brain activation patterns of discrete regions but also examine distributed network patterns across the brain, both structurally and functionally. ■

INTRODUCTION

Math competence is essential for success in fields that require strong quantitative skills. It involves not only the ability to perform mathematical procedures but also the capacity to comprehend mathematical concepts and apply them in different contexts to solve novel problems. The acquisition of math skills at an early age is important to lay the foundation for the development of high-level quantitative skills and success in modern society (Jordan, Kaplan, Ramineni, & Locuniak, 2009). Despite the importance of math competence, individuals show large differences in math performance and math learning abilities (Artemenko et al., 2019), and the neural bases underlying individual differences in math competence remain unclear. Importantly, early intervention is crucial for individuals with math learning deficits. Studies have shown that remediation is most effective when implemented at an early stage of development (Powell, Fuchs, Fuchs, Cirino, & Fletcher, 2009; Räsänen, Salminen, Wilson, Aunio, & Dehaene, 2009). Therefore, identifying the neural markers associated with math competence is of great importance. This can not only help us to better understand the origins of math learning deficits but also inform the development of more targeted and effective interventions. In addition, neural markers provide objective measures of math competence that can complement behavioral measures, allowing for more accurate tracking of progress during learning and remediation. Thus, understanding the neural mechanisms of math competence is crucial for improving the effectiveness of remediation efforts.

It is well known that the human brain is a complex system that comprises not only individual brain regions but also distributed neural networks. The human brain is efficiently organized by integrating information across various brain regions to minimize the cost of information processing while maximizing the overall efficiency of the brain networks. Modern neuroimaging techniques allow us to identify distinct local cortical regions and investigate large-scale neural networks underlying math competence both structurally and functionally. To gain insights into the neural bases of math competence, this review aims to find answers based on structural and functional properties of the human brain in both typical and atypical populations of children and adults. Specifically, for atypical populations, we will focus on individuals with math learning deficits. Math learning deficits are neurodevelopmental disorders that impair an individual's ability to

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learn and perform math-related tasks. Dyscalculia is a specific type of math learning deficit that affects the development of arithmetical skills and other basic numerical skills (Kuhl, Sobotta, Legascreen Consortium, & Skeide, 2021; Kucian et al., 2014; Rykhlevskaia, Uddin, Kondos, & Menon, 2009). When reviewing findings from atypical population, we will focus on individuals with math learning deficits including those with dyscalculia.

As math competence encompasses many different skills, for studies involving adults, this review will selectively examine the neural bases of relatively complex math skills, such as evaluation of mathematical statements (e.g., "Any equilateral triangle can be divided into two right triangles"; Amalric & Dehaene, 2016, 2019). For studies involving children, we will also include fundamental math abilities such as arithmetic skills that are commensurate with the math skills young children master. However, basic number comprehension and number comparison skills are outside the scope of this review. Moreover, we will consider whether neural markers associated with math competence are unique to math or may be reflective of academic achievement and cognitive abilities more generally.

STRUCTURAL NEURAL MARKERS FOR MATH COMPETENCE

Gray Matter Volume and Math Competence

Brain structural imaging studies have suggested an association between gray matter properties and individuals' math competence. For instance, the "gray matter volume hypothesis" posits that greater gray matter volume (GMV) is associated with higher math competence. In support, Li, Hu, Wang, Weng, and Chen (2013) found that GMV in the sulcus (IPS) positively correlated with arithmetic abilities in children. However, this study was cross-sectional, leaving open the question whether similar relations between GMV and math abilities exist across development. To address this question, Price, Wilkey, Yeo, and Cutting (2016) revealed that GMV in left IPS at the end of first grade correlated with children's math competence a year later at the end of second grade. Similarly, GMV of multiple brain regions such as IPS and prefrontal areas predicts long-term gains in children's math abilities (Evans et al., 2015). Instead of using standardized math assessments (e.g., Woodcock-Johnson Tests of Achievement) as in previous studies, Wilkey, Cutting, and Price (2018) implemented in-school math tests and also found that greater GMV in bilateral hippocampus and right inferior frontal gyrus was associated with higher math achievements in children from third to eighth grade. Correlations between GMV and children's math abilities have also been revealed in other brain regions such as angular gyrus, pFC, and occipito-temporal areas (Evans et al., 2015; Lubin et al., 2013). However, those findings could not differentiate the influence of brain maturation versus math learning experience, which are strongly intertwined at early developmental stages, in explaining observed brain–behavior correlations. In addition, most studies only measured cortical anatomy at one time point and rarely examined the GMV changes in the same sample at different developmental stages. Thus, further studies are needed to investigate the relations between GMV changes and growth in math abilities across development.

A similar relation between GMV and academic skills exists in other domains such as reading (Torre & Eden, 2019; Johns et al., 2018). Interventional studies in reading showed that effective reading training can induce GMV increases (Krafnick, Flowers, Napoliello, & Eden, 2011). However, there is a lack of intervention studies examining the effects of math-related training on GMV, and the relation between training-induced changes in GMV and math learning improvements. More research in this area is needed to fully understand the connections between GMV and math learning outcomes. Moreover, although there is a consistent pattern between GMV and math competence in children, few studies have examined the relations between GMV and math competence in adults.

Reduced GMV in brain regions such as parietal and frontal cortex is an important neural marker associated with math learning deficits. For instance, children with calculation deficits had reduced GMV in the left IPS compared with typically developing children (Isaacs, 2001). Subsequent studies in children with developmental dyscalculia, a severe math learning disability, also found reduced GMV in parietal cortex (including IPS; Cappelletti & Price, 2014; Ranpura et al., 2013; Rykhlevskaia et al., 2009; Rotzer et al., 2008), and frontal areas such as inferior frontal gyrus and middle frontal gyri (Rotzer et al., 2008), within the fronto-parietal system. In addition, GMV reduction has also been observed in parahippocampal gyrus (Rykhlevskaia et al., 2009), occipital-temporal cortex, and insula (Han et al., 2013). Studies in adults with dyscalculia showed reduced GMV in right parietal cortex relative to normal controls (Cappelletti & Price, 2014). However, their findings do not merit drawing causal inferences between abnormal structural properties and math learning deficits because it remains unclear whether the GMV reduction caused math learning deficits or vice versa. Another important issue is that individuals at the lower end of math competence often show higher rates of comorbidity with other cognitive disorders such as dyslexia (Rubinsten & Henik, 2009), a reading learning disorder. Earlier studies have shown that GMV reduction could also evidence dyslexia (Eckert, Berninger, Vaden, Gebregziabher, & Tsu, 2016). Thus, future studies should carefully differentiate structural neural markers for different learning deficits.

To sum up, differences in GMV could reflect individual differences in math competence and other cognitive abilities. Specifically, greater GMV in math-related brain regions (e.g., IPS) is associated with higher math competence. In contrast, reduced GMV may be associated with learning difficulties in general, and reduced GMV, especially in the frontal and parietal regions, may be a neural marker for math learning deficits in particular.

Cortical Thickness and Math Competence

Cortical gray matter is determined by cortical thickness and cortical surface area, and studies suggest that they reflect different neurodevelopmental mechanisms. Specifically, cortical thickness is thought to reflect a neurodevelopmental process of experience-dependent synaptic pruning (Shaw et al., 2006) or myelination (Natu et al., 2019) in response to skill acquisition and skill refining, whereas cortical surface area is thought to reflect genetically determined cortical folding (Panizzon et al., 2009; Kapellou et al., 2006). Although surface area has been speculated to be influenced by experience-dependent synaptic pruning like cortical thickness as well (Lyall et al., 2015; Schnack et al., 2015), there is a lack of studies that have examined the relation between cortical surface area and math abilities specifically, making it difficult to determine the role of surface area in math competence. Thus, the following discussion will mainly focus on the relation between cortical thickness and math competence.

According to the "cortical maturation hypothesis," cortical thinning and increased surface area—both indicators of cortical maturation—are associated with greater math competence. For instance, Schel and Klingberg (2017) found that cortical thinning of right anterior IPS is associated with better math abilities in children older than 12 years, and this region becomes more specialized for mathematics during development. Moreover, they also revealed that thinner cortex in IPS was related to better working memory and reasoning ability. In a longitudinal study following children from kindergarten (5–6 years old) to second grade (7–8 years old), Kuhl et al. (2020) revealed that cortical thinning is associated with better math abilities in the right temporal lobe and left middle occipital gyrus. Lastly, math-gifted adolescents have thinner cortex and larger surface area in the frontoparietal network, which suggested maturation of the neural network for math competence in adolescence (Navas-Sánchez et al., 2016). However, it is important to note that although there are correlations between structural properties and math abilities, the exact role of localized cortical changes for cognitive functioning remains unclear. It is also unknown whether those cortical changes reflect math-specific abilities or support cognitive functioning more generally.

Studies with adults did not reveal correlations between cortical thickness and math competence (Heidekum, Vogel, & Grabner, 2020; Torre, Matejko, & Eden, 2020). For instance, in an MRI study with 89 typically developed adults, Heidekum et al. (2020) investigated the associations between brain structures and math competence. However, they did not find associations between cortical thickness and math competence in math-related brain regions such as IPS. One possible explanation for the contradictory findings between children and adults could be the differences in sample size, or the types and ranges of math skills measured. Another possible explanation is that as cortical thickness changes as a result of learning and practice, adults do not engage in math as frequently as children who are still undergoing formal math instruction, which may lead to less math-related cortical thickness changes in adults (Torre et al., 2020). In addition, human cognition tends to reach a stable state in early adulthood, and the effects of training or learning on cognitive performance are typically limited (Neubauer & Fink, 2009). As a result, training-induced cortical changes, although still possible, may require a large amount of practice and training to achieve. From this perspective, it is possible that cortical thickness may not be directly linked to math competence, but rather to the amount of math practice and training that an individual has had. This could lead to confusion between the two factors. Future research should aim to differentiate the effects of math training and actual math competence on anatomical features.

This discrepancy between children and adults also points to the critical role of cortical plasticity during formal math acquisition. In fact, the importance of cortical plasticity in math is corroborated by intervention studies, which showed that aerobic fitness training could improve children's math learning outcomes via cortical thinning (Chaddock-Heyman et al., 2015), which furthers our understanding of cortical plasticity as a function of training and its importance in math achievement at early developmental stages. However, its role in later development needs more investigation.

In summary, a combination of variation in brain structures such as GMV and cortical thickness could evidence individual differences in math competence. Specifically, greater GMV and cortical thinning merit greater neural resources capacity and neural network efficiency, which further support higher math competence and other superior cognitive abilities. Importantly, the structural neural changes related to math competence are not confined to one particular brain region but cover distributed brain regions, and structural integrity across these regions is critical for high-level math competence and efficient cognitive functions.

White Matter and Math Competence

Individuals who exhibit superior math competence not only rely on the efficient processing in gray matter but also depend on the efficient communication between interconnected white matter structures (Johansen-Berg, 2010). The integrity of the white matter plays a crucial role in fostering and maintaining high-level math competence. Diffusion tensor imaging is a powerful tool to assess structural connectivity within the human brain and investigate the correlation between brain microstructure and cognitive processes (Johansen-Berg, 2010; Ben-Shachar, Dougherty, & Wandell, 2007; Olesen, Nagy, Westerberg,

& Klingberg, 2003). This non-invasive magnetic resonance imaging technique uses the measurement of water diffusion direction and orientation to gain insights into the structural integrity of the white matter fiber tracts in the brain (Jones, 2008). To date, most of the studies exploring the relations between brain microstructure and math competence have focused on children. These studies have identified correlations between children's math abilities and fractional anisotropy, a metric used to quantify the directional orientation of water diffusion in the brain, in various regions including the corpus callosum connecting the left and right hemispheres (Li, Wang, Hu, Liang, & Chen, 2013; Cantlon et al., 2011; Hu et al., 2011), corona radiata connecting the brain stem and the cerebral cortex (Hu et al., 2011; van Eimeren, Niogi, McCandliss, Holloway, & Ansari, 2008), inferior longitudinal fasciculus connecting occipital and temporal cortices (Hu et al., 2011; van Eimeren et al., 2008), and superior longitudinal fasciculus connecting parietal, occipital, and temporal cortices with the frontal cortex (Hu et al., 2011; Tsang, Dougherty, Deutsch, Wandell, & Ben-Shachar, 2009). Specifically, in a study conducted with math-gifted adolescents, Navas-Sánchez et al. (2014) found heightened white matter integrity in the frontoparietal, fronto-striatal, and temporo-parietal tracts compared with age-matched controls. This finding supports the hypothesis that enhanced anatomical connectivity in these regions underlies high-level math competence. Interestingly, a training study has shown that children's behavioral improvement in arithmetic problem solving after 2 months of math tutoring was positively correlated with changes in the fronto-temporal white matter tract (Jolles, Wassermann, et al., 2016). This finding highlights a crucial relation between improvements in math abilities and changes in white matter integrity in children. More importantly, their results also provide novel insights into the plasticity of white matter in childhood as a result of learning, suggesting that the integrity of white matter exhibits dynamic variations in response to learning (Jolles, Wassermann, et al., 2016).

A few studies have also reported similar findings in adults (Matejko, Price, Mazzocco, & Ansari, 2013; van Eimeren et al., 2010). For instance, Matejko et al. (2013) used diffusion tensor imaging to investigate the relation between individual differences in white matter and performance on the math subtest of the Preliminary Scholastic Aptitude Test in adults. They found a positive correlation between fractional anisotropy in the left parietal white matter and math scores, suggesting that the microstructural integrity of white matter in the left parietal cortex is linked to high levels of math competence. This study is also the first to provide evidence for the association between individual differences in white matter and math competence as measured by a nationally administered scholastic aptitude test, which provides important insights into the neural mechanisms underlying math competence in adults.

Reduced fractional anisotropy could evidence math learning deficits. For instance, Rykhlevskaia et al. (2009) found decreased fractional anisotropy in the right temporo-parietal white matter of children with dyscalculia compared with typically developing children. In addition, Kucian et al. (2014) suggested that dyscalculia may be associated with poor white matter connections between regions critical for mathematical processing, such as the parietal, temporal, and frontal regions. However, one caveat is that correlations between brain microstructure and math skills may be specific to a particular disorder or an indirect consequence of neuropathology (see Matejko et al., 2013, for a detailed discussion).

To summarize, these studies indicate a correlation between individual differences in white matter structures and math competence. The integrity of white matter plays a crucial role in supporting high levels of math competence by enabling efficient communication across different brain regions. At the same time, abnormalities in white-matter integrity may evidence math learning deficits. Further investigation is necessary to understand the longitudinal changes in white-matter microstructure in relation to the development of math abilities.

FUNCTIONAL NEURAL MARKERS FOR MATH COMPETENCE

Neural Efficiency and Math Competence

Using advanced neuroimaging techniques such as fMRI, earlier studies have suggested an association between brain functional properties and math competence. For instance, numerous studies have found relations between individual differences in math competence and brain activities across different brain regions. The human brain is organized in an efficient way by integrating and coordinating information and activities across various brain regions to minimize the information processing cost and maximize the overall processing efficiency. According to the *neural efficiency hypothesis*, individuals with superior math performance tend to engage less neural resources, resulting in less brain activity required for task completion, compared with those with low levels of math competence (Haier, 2016; Neubauer & Fink, 2009; Haier, Jung, Yeo, Head, & Alkire, 2004). Support for this hypothesis comes from studies with adults and children. For example, Jeon and Friederici (2017) found that adults with high levels of expertise in math showed less and more confined brain activation in a small number of brain regions in a mathematical hierarchy processing task, whereas adults with low levels of expertise showed greater activation in broadly distributed brain regions. However, because this study lacked variations in task complexity, it is difficult to judge whether these findings would extend to other relatively more complex tasks and how the brain activity patterns change as a function of task complexity. Similar brain activation patterns emerged in adolescents as well such that adolescents with better math competence showed decreased brain activity during arithmetic problems solving in right IPS, likely because of more precise representations of magnitudes, compared with adolescents with lower math competence (Price, Mazzocco, & Ansari, 2013). Greater neural efficiency has also been found to be associated with better performance in other cognitive domains such as working memory and executive control (see Neubauer & Fink, 2009, for a review).

However, there are also studies that suggest the opposite, namely, that individuals with higher math abilities show greater brain activation, instead of reduced activation, in various brain regions compared with those with lower math competence. For instance, Amalric and Dehaene (2016) found that mathematicians showed greater brain activation in the left visual number form area relative to nonmathematicians in response to number stimuli. More importantly, by varying the problem difficulty levels and strategy selection, they suggested a core network consisting of IPS and bilateral inferior temporal regions to be used exclusively for mathematical knowledge representation (Amalric & Dehaene, 2019). However, the role of this core network in explaining other higher-order math abilities remains unclear. Another study, which utilized functional near-infrared spectroscopy in conjunction with EEG, investigated the interaction between math ability and arithmetic complexity. The study revealed that individuals with high levels of math skills exhibited greater brain activation in regions such as the superior temporal gyrus and inferior frontal gyrus, compared with those with low levels of math skills, when solving complex math problems (Artemenko et al., 2019). Similarly, Grabner, Reishofer, Koschutnig, and Ebner (2011) and Grabner et al. (2007) found that individuals with high levels of math competence exhibit greater activation in the left angular gyrus when solving math problems, compared with those with low levels of math competence. Their finding highlights the significance of language-mediated processes in math problem solving and the crucial role of the angular gyrus in math cognition among those with high levels of math competence. Thus, individuals with superior math competence, compared with those with lower math competence, tend to show greater cortical activation and higher usage of task-related neural resources in brain regions such as frontal, parietal, and temporal cortices possibly to strengthen their cognitive processing (see Dehaene, Piazza, Pinel, & Cohen, 2003, for a discussion of parietal region in math cognition; O'Boyle et al., 2005).

One possible explanation for the inconsistency in the findings regarding the neural efficiency hypothesis is that brain activation is modulated by various task demands (Chochon, Cohen, van de Moortele, & Dehaene, 1999). In other words, tasks that are relatively complex or rely less on practice and experience may require greater engagement of task-related brain regions or sophisticated strategies to complete the tasks successfully (Waisman, Brunner, Grabner, Leikin, & Leikin, 2023). This argument is consistent with the finding that when the complexity of the task increases and familiarity with the task decreases, adolescents with higher math abilities showed greater activation in distributed brain regions (e.g., frontal, parietal regions, anterior cingulate gyrus; Desco et al., 2011) compared with average-ability controls. This indicated that individuals with higher math competence will engage more task-relevant neural resources when necessary. However, during relatively simple, familiar math tasks, people with higher math competence may engage a more automatic process that attenuates the dependency on other cognitive resources (e.g., executive control and attention), resulting in less effortful cognitive processing and less brain activation to solve the corresponding tasks. In contrast, individuals with lower math competence may rely more on cognitive resources (e.g., attention, inhibitory control, or working memory) to solve the problems, which leads to stronger activation in brain regions such as frontal areas (Klimesch, Sauseng, & Hanslmayr, 2007).

Several studies support the notion that task difficulty and familiarity modulate the relation between brain activation and math competence. For instance, Zhang, Gan, and Wang (2015b) implemented numerical inductive reasoning tasks with high or low complexity and demonstrated how neural efficiency was modulated by task complexity. Specifically, they found that math-gifted adolescents showed stronger brain activity for the complex task and less brain activity for the easy task in the frontoparietal network, compared with average achieving adolescents. In addition, Amalric and Dehaene (2018) found stronger brain activation in pFC during complex, unfamiliar mathematical statement judgments and reduced frontal activation during simpler, more routinized facts, which suggested the important role of frontal areas in information manipulation when needed.

To sum up, task complexity and familiarity modulate brain activation and neural efficiency related to math ability. Specifically, individuals with high levels of math competence tend to exhibit focused and localized brain activity during relatively simple and familiar tasks, whereas those with low levels of math competence tend to exhibit diffuse and widespread brain activation. Conversely, during relatively complex, less familiar math tasks, people with high levels of math competence tend to activate additional neural resources presumably to achieve efficient neural processing.

Training-induced Brain Activity Changes and Math Competence

Brain activity can also be modulated by the effect of short-term training (Neubauer, Grabner, Freudenthaler, Beckmann, & Guthke, 2004). Studies on complex arithmetic training, specifically complex multiplication training, in adult participants have revealed a decreased activation in the frontal gyri, IPS, and superior parietal lobule, while displaying an increased activation in the angular gyrus (see, e.g., Zamarian, Ischebeck, & Delazer, 2009, for a review). This shift in brain activity indicates a transition from relying on effortful and procedural processes to utilizing memory and retrieval-based strategies (Grabner & De Smedt, 2012; Grabner et al., 2009; Ischebeck, Zamarian, Schocke, & Delazer, 2009; Ischebeck, Zamarian, Egger, Schocke, & Delazer, 2007; Ischebeck et al., 2006; Delazer et al., 2003, 2005). Consistently, developmental imaging studies in the field of arithmetic reasoning also support the notion that the automation of mathematical processes is accompanied by a shift in activation from frontal to parietal regions (Rivera, Reiss, Eckert, & Menon, 2005). Importantly, Wirebring et al. (2015, 2022) conducted a study comparing the effectiveness of two different math training methods—one involving the repeated practice with solutions provided, and the other focusing on fostering creative problem-solving skills. Individuals who underwent training in creative thinking exhibited improved performance in math problem solving, as well as brain activation changes in several regions such as the angular gyrus, which facilitates the engagement of relevant brain regions for the task and optimizes the efficiency of neural resource allocation.

Studies exploring the impact of short-term training on children, although scarce, have demonstrated that, through proper training, children can experience improved neural processing and function as well. For instance, Soltanlou et al. (2018) showed that arithmetic training leads to not only improved math performance in children, but also a reduction in brain activation in the frontoparietal network, as assessed through a combination of functional near-infrared spectroscopy and EEG. Furthermore, prior research has revealed that a decrease in frontoparietal activation is accompanied by increased activation in the hippocampus, and greater connectivity between the hippocampus and frontal regions is correlated with higher math competence in children (Qin et al., 2014; Supekar et al., 2013). It is possible that individuals with superior math abilities have stronger memory and knowledge representation for mathematics, compared with those with low levels of math competence. The heightened activation observed in the hippocampus of such individuals may indicate a more robust memory representation as a result of semantization and/or consolidation, thereby contributing to their superior math competence.

In summary, all these studies suggest that training can induce changes in brain activity and enhance neural efficiency by selectively engaging relevant brain regions to varying degrees, depending on the specific task demands. Specifically, participants may initially engage in effortful processing, relying heavily on cognitive resources such as working memory to process information. However, as they become more skilled in the task, they may develop stronger memory and math knowledge representations, leading to a shift toward more automatic and efficient processing modes that require less cognitive efforts for task completion (Zhang et al., 2015b; Neubauer & Fink, 2009; Neubauer et al., 2004). It is worth noting that the changes in brain activity may vary based on the type of instruction received (Delazer et al., 2005). Hence, future studies, particularly in children, should investigate the effects of different learning environments and instructional methods on brain activity changes to enhance children's math learning outcomes (Grabner & De Smedt, 2012).

Aberrant Neural Responses Mark Math Learning Deficits

Aberrant neural responses may be a neural marker for math learning deficits. For instance, children with math learning deficits showed either hyper-activation or hypo-activation in multiple brain regions, including parietal, occipital-temporal, and prefrontal regions during math problem solving compared with peers with average math abilities (Peters & De Smedt, 2018; Iuculano et al., 2015; Berteletti, Prado, & Booth, 2014; De Smedt, Holloway, & Ansari, 2011; Molko et al., 2003). Moreover, children with math learning deficits showed a lack of task difficulty-related modulation of neural activity. For instance, Ashkenazi, Rosenberg-Lee, Tenison, and Menon (2012) found that typically developing children showed increased brain activity for complex arithmetic problems, whereas children with dyscalculia did not, suggesting that children with dyscalculia do not modulate their brain activity in accordance with task complexity. However, their findings do not allow for causal claims between math learning deficits and brain activity patterns as it is unclear whether dyscalculia caused the lack of task-based brain activity modulation or vice versa. In addition, one should interpret the results with caution because of the comorbidity with other cognitive disorders (e.g., dyslexia, attention-deficit/hyperactivity disorder; Rubinsten & Henik, 2009). For instance, arithmetic skill, especially arithmetic fact retrieval, is associated with reading ability (Chu, vanMarle, & Geary, 2016; De Smedt & Boets, 2010), and such aberrant brain activity patterns have also been found in children with dyslexia. In an fMRI study, Evans, Flowers, Napoliello, Olulade, and Eden (2014) investigated the differences in brain activity between children with and without dyslexia during arithmetic addition and subtraction operations. They found that children without dyslexia showed strong activation in right supramarginal gyrus only for subtraction, whereas dyslexic children engaged this region during both subtraction and addition problems, suggesting a less optimal route for retrieval-based arithmetic problems and a lack of task-based brain activity modulation.

In summary, aberrant brain activity might be because of lower efficiency in engaging task-related brain areas, which results in less optimal routes for problem solving. Moreover, aberrant brain activation may extend beyond the domain that is affected by the particular learning deficit as evidenced by difference in brain activation during math problem solving for children with and without dyslexia. Thus, one challenge for future studies is to address the heterogeneity in children with math learning deficits, which may cause inconsistent finding across different studies (Jolles, Ashkenazi, et al., 2016). To investigate the neural markers that are specific to math learning deficits, subject selection and matching criteria based on other cognitive abilities should be carefully implemented.

Neural Representations and Math Competence

Despite the common activation of broad brain regions associated with math cognition, it is possible that the neural representations within these regions may vary among individuals. In other words, although the general regions of the brain that are activated during mathematical tasks may be similar across individuals, neural representations within these regions may still differ. These differences in neural representations could potentially serve as an alternative neural marker for math competence. For instance, using a multivariate representational similarity method, Ashkenazi et al. (2012) found that children with developmental dyscalculia showed less differentiated neural representations for addition problems at different difficulty levels, compared with typically developing children. However, it is unclear whether a lack of representational differentiation also extends to other numerical operations in children with dyscalculia. Chen et al. (2021) further investigated this question and revealed that children with low math abilities showed less differentiated neural representation patterns between addition and subtraction problems in various brain regions including fusiform gyrus and IPS than children with greater math abilities. These studies highlighted the importance of examining the neural representations within these regions, rather than solely relying on the activation of broad regions, to fully understand the neural underpinnings of math competence. As addition and subtraction problems are only two basic math skills, it would be useful to further implement multivariate approaches to investigate the neural representations for other relatively complex math problems. In summary, based on the evidence reviewed above, individuals with math learning deficits not only exhibit aberrant neural activity but also fail to modulate task-related neural responses and generate distinct neural representations for different math problems.

However, such aberrant neural responses and representations could be altered and normalized to be indistinguishable from those of typically developing peers with effective training (Iuculano et al., 2015). Specifically, after an 8-week, one-on-one cognitive tutoring intervention, aberrant functional brain responses in regions such as frontal and parietal brain areas were normalized to be comparable to typically developing children. In addition, multivariate pattern analyses showed that the brain activity patterns in children with math learning deficits were also altered to be indistinguishable from those of typically developing peers. Thus, their findings suggest that tutoring-induced functional changes, manifested in normalized brain activation and neural representations, could be an effective intervention strategy in children with math learning deficits. Importantly, they used rigorous quantitative approaches to demonstrate the tutoring-induced functional brain plasticity. More experimental studies like these are needed to demonstrate the causal link between math competence and various neural markers associated with math abilities.

Functional Connectivity and Math Competence

Another neural marker of math competence may be functional connectivity, which is based on temporal coupling of neural responses to examine context- and stimulus-dependent interactions across different brain regions (Jirsa & McIntosh, 2007). According to the parieto-frontal integration theory (P-FIT), stronger connectivity and integration between frontal and parietal regions enable efficient communication among regions, which underpins the neural basis for higher intelligence (Jung & Haier, 2007). The important role of the frontoparietal network has been manifested in other cognitive abilities as well such as in cognitive control, working memory, adaptive behavior, and creative problem solving (Barbey, Colom, Paul, & Grafman, 2014; Barbey, Colom, & Grafman, 2013; Barbey et al., 2012; Cole, Yarkoni, Repovš, Anticevic, & Braver, 2012). For instance, Sheffield et al. (2015) found positive correlations between functional integration of the frontoparietal network and overall cognitive ability, which suggested that a greater functional integration of the frontoparietal network is crucial for supporting better overall cognitive functioning.

As math competence tends to be linked to general intelligence and other domain-general cognitive abilities such as working memory and executive functioning (Menon, 2014, 2016; Desco et al., 2011; Mrazik & Dombrowski, 2010), P-FIT may also be applicable to math competence. Specifically, evidence in support of P-FIT comes primarily from studies with children. Mental rotation tasks such as mental rotation of 3-D objects have been suggested as well-suited for assessing math competence as it is a complex visuospatial task that involves creation and manipulation of mental images (Gill, O'Boyle, & Hathaway, 1998), which are two important factors for high-level mathematical thinking and reasoning (O'Boyle, Benbow, & Alexander, 1995). Greater functional connectivity between frontal and parietal regions is required for successful completion of such complicated tasks. For instance, in an fMRI study with a mental rotation task, Prescott, Gavrilescu, Cunnington, O'Boyle, and Egan (2010) found increased frontoparietal connectivity in math-gifted adolescents compared with those with average math ability. Similarly, O'Boyle et al. (2005) revealed that mathematically gifted male adolescents showed higher activation in the frontoparietal network and anterior cingulate during mental rotation tasks. Similar positive associations between frontoparietal connectivity and math abilities have been revealed in other tasks as well. For instance, Emerson and Cantlon (2012) found that greater frontoparietal connectivity during a natural video watching task was associated with greater math abilities in children. The frontoparietal network is also activated during arithmetic problem solving, and the activity of the network is modulated by strategy use, expertise, and training (see Peters & De Smedt, 2018, for a review). Such patterns also exist in resting-state data where increased functional connectivity between number-related areas (e.g., number form area) and frontoparietal network is associated with greater math abilities across development (Nemmi, Schel, & Klingberg, 2018). Moreover, the frontoparietal network has been suggested as a flexible hub to facilitate adaptive and novel task performance (Cole et al., 2013).

Consistent findings regarding the frontoparietal network do not rule out the important roles that other neural connections may play for math competence. In other words, at the subject level, there might be individual differences in strategy selection or engagement of different neural circuits, and only the frontoparietal network might emerge consistently across an entire group of participants. However, other brain regions and their neural connections may also be involved in math competence. For instance, previous studies have suggested that the posterior inferior temporal cortex is an important region in mathematical processing, and it exhibits high functional connectivity with the IPS (Hermes et al., 2017; Daitch et al., 2016). In addition, utilizing intracranial EEG during a mental arithmetic task, Pinheiro-Chagas, Daitch, Parvizi, and Dehaene (2018) demonstrated that the posterior inferior temporal cortex plays a crucial role in the early identification of problem difficulty and mathematical processing. In a meta-analysis, Arsalidou, Pawliw-Levac, Sadeghi, and Pascual-Leone (2018) revealed that regions such as the insula and claustrum may play critical roles in children's math problem solving. The hippocampus has also been suggested as an important brain region for math competence especially for math fact representation, and its connectivity strength to the frontoparietal network could be an indicator of math competence (Qin et al., 2014; Supekar et al., 2013; Cho et al., 2012). However, most studies have mainly focused on relatively strong connections of highly correlated brain regions (e.g., the frontoparietal network) and have held the assumption that "stronger connectivity is always better." Nevertheless, it is crucial to acknowledge that both strong and weak connections play important and different roles in brain functioning (Schwartz et al., 2021; Cole et al., 2012; Gallos, Makse, & Sigman, 2012). More critically, weak connections, which are often overlooked, may largely contribute to individual differences in higher cognitive functioning (Santarnecchi, Galli, Polizzotto, Rossi, & Rossi, 2014). For instance, it is possible that the relatively weaker connections between claustrum and the frontoparietal network could evidence individual differences in math competence. Future studies should explore how connections between different brain regions and connectivity strengths relate to individual differences in math competence.

In summary, functional connectivity could evidence individual differences in math competence, and enhanced functional connectivity is a fundamental component for higher math competence. Specifically, functional connectivity within the frontoparietal network not only plays a critical role in math competence but also supports other cognitive processes more generally. Individuals with high levels of math competence or overall cognitive abilities may rely on the frontoparietal network for effective neural communication and information processing. Importantly, future studies should aim to further explore the important roles of relatively weak neural connections in explaining individual differences in math competence.

Functional Dysconnectivity and Math Learning Deficits

Functional dysconnectivity, such as abnormal functional integration and aberrant connectivity, may be a neural marker for math learning deficits. For instance, hyperconnectivity between IPS and multiple brain regions (e.g., the frontal and parietal regions), along with weaker performance in math problem solving, was observed in children with math learning deficits (Rosenberg-Lee et al., 2015). Jolles, Ashkenazi, et al. (2016) used task-free MRI to investigate the differences in intrinsic functional connectivity of IPS between typically developing children and children with math learning deficits. They found that children with math learning difficulties showed hyperconnectivity of IPS with multiple brain regions including those in the bilateral frontoparietal network. Moreover, a machine learning classification algorithm showed that aberrant IPS connectivity patterns can discriminate children with math learning deficits from typically developing children. Thus, these findings suggested that children with math learning difficulties, instead of showing dysfunction of IPS alone, may show aberration in the connectivity patterns, and aberrant IPS connectivity can be a neural marker for math learning deficits (see Dehaene, Molko, Cohen, & Wilson, 2004, for a discussion).

One possible explanation why math learning deficits are linked to aberrant functional connectivity is that a greater engagement of multiple brain circuits may cause intrusion of irrelevant information, resulting in interference and less optimal routes for problem solving (Rosenberg-Lee et al., 2015). This is supported by behavioral evidence that children with math learning deficits showed poor inhibition of irrelevant information when attempting to retrieve arithmetic facts from long-term memory (Geary, Hoard, & Bailey, 2012). Another possible explanation would be that hyperconnectivity may result in less flexibility and efficiency in engaging and modulating task-relevant brain circuits (Jolles, Ashkenazi, et al., 2016; Uddin et al., 2015). Thus, atypical functional brain circuit dynamics may contribute to math learning deficits. As previous studies mainly focused on the role of IPS connectivity in math competence, future studies should aim to explore the roles of aberrant functional connectivity of other brain regions, besides IPS, in explaining math learning deficits as well as other learning difficulties.

Frontoparietal Network Efficiency Theory

Math competence is not only related to the activation of individual cortical regions (see Menon, 2014, for a review), but also to the interconnection between different brain regions, as indicated by the functional neural markers reviewed above. Individuals with high levels of math competence are expected to exhibit high neural efficiency as well as high functional connectivity across brain regions to accomplish the task successfully. The human brain is known to be organized in complex neural networks that support high efficiency, with the goal of minimizing the cost of information processing while maximizing the capacity for growth and adaptation (Bullmore & Sporns, 2012). In this context, information is processed not only by functionally segregated brain areas but also by functional integration across spatially distributed brain regions through their dynamic interactions for efficient information processing (Sporns, Tononi, & Edelman, 2000; Alexander, O'Boyle, & Benbow, 1996). The functions of individual brain regions might be important during early stages of developing cortical resources for mathematical learning, and then their relations with other higher-order cognitive areas are slowly forged to form an interconnected and dynamic neural network to support high levels of math competence (Alexander et al., 1996).

Thus, to better understand the neural basis of math competence, we propose examining the neural processing at the network level, specifically, by assessing frontoparietal network efficiency. The frontoparietal network is a key network involved in math processing, orchestrating the exchange of information between task-related brain regions, both within the network itself and between the frontoparietal network and other networks, in a way that maximizes efficiency in the overall information processing. Thus, to better understand the neural mechanisms underlying math competence, it is necessary to not only examine the internal efficiency within the frontal–parietal network, but also its interactions with other brain networks. This approach, which we term the frontoparietal network efficiency theory (FP-NET), will provide deeper insights into how different neural networks work together to support math abilities and their relations to individual differences in math competence, offering a more comprehensive understanding of the neural mechanisms underlying math competence beyond what can be explained by the function of individual brain regions alone.

The FP-NET represents a theoretical framework that synthesizes various components of neural efficiency theory and frontoparietal integration theory, with a particular emphasis on overall brain network efficiency. It captures how the brain processes information from a different perspective based on the overall performance of the brain networks, and how it relates to individual differences in math competence. FP-NET embodies two key aspects: (1) the efficiency in engaging the frontoparietal circuit; (2) the efficiency that uses the frontoparietal network as a functional hub to integrate information across networks and enable optimal routes based on task demands.

FP-NET postulates that the frontoparietal network is efficiently engaged and used as a functional hub to integrate information across different brain networks, enabling the formation of optimal routes for rapid information transfer between discrete brain regions based on task demands. Task demand is determined by the extent and type of neural processing required to complete the task, which can depend on factors such as the cognitive demands (e.g., attention, working memory), individual differences (e.g., expertise, prior knowledge), and/or the interplay between them. Different types of tasks require different types of neural processing and pose varying cognitive demands between and within individuals, which will engage the frontoparietal network to different degrees. Thus, FP-NET requires the human brain to flexibly activate and coordinate these brain regions and leverage the functions of different brain networks in response to the current task demands. This flexibility necessitates the dynamic adjustment of the strength and pattern of connectivity between these regions based on task complexity to maximize the overall information processing efficiency.

Put differently, brain networks can be seen as a complex map that consists of streets connecting different locations. For relatively simple, familiar tasks, higher efficiency can be achieved by taking a direct route from one region (e.g., frontal area) to another (e.g., parietal area) for faster information transfer to meet the goal (Figure 1A for F → P pathway). In contrast, for relatively complex, unfamiliar tasks, multiple paths will be engaged, and information will travel to the hub (P), where information will be integrated, from different sources and locations (e.g., F and D in Figure 1B). It is possible that the efficiency for the direct route (F → P) is high, but the global efficiency of integrating the information from different paths (especially D → P) might be low, which will likely increase the information processing cost (Figure 1B). Thus, sacrificing some efficiency of the direct route (F → P) and increasing efficiency of other task-related routes (e.g., D → P) might increase the overall global efficiency for information processing (Figure 1C).

One important aspect of FP-NET is that it does not attempt to supersede previous theories in the field; rather, it proposes a complementary approach to investigate the neural basis of math competence based on network efficiency. FP-NET is consistent with earlier findings that

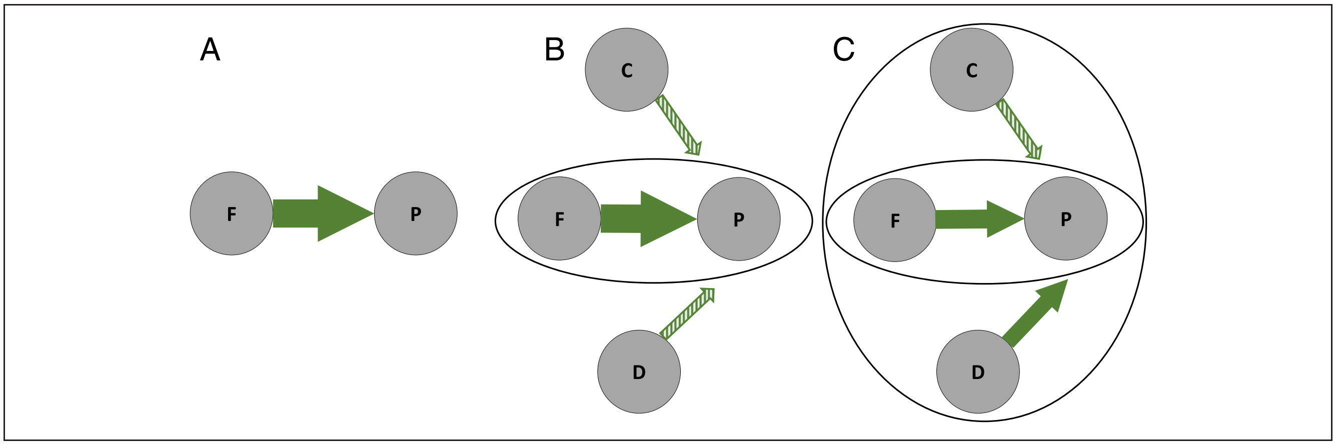

Figure 1. Schematic of the frontoparietal network efficiency theory (FP-NET). (F) represents frontal areas, (P) represents parietal areas, (C) and (D) represent other brain regions relevant for solving a specific, math-related task. Arrows represent information transfer, and the width and patterning of the arrows represents efficiency for information transfer. The wider and more solid the arrow, the higher the efficiency and faster information transfer. (A) illustrates high efficiency in engaging a direct route connecting frontal (F) and parietal (P) areas for relatively simple, familiar tasks. (B) and (C) illustrate what might happen during more complex, unfamiliar tasks when information will travel to the hub (P) from different sources (e.g., F and D). Specifically, (B) illustrates the situation where the efficiency of the direct route (F→P) is high, but the global efficiency is low because efficiency of the other task-relevant route (D→P) is low. (C) illustrates that to achieve higher global efficiency, efficiency of the direct route (F→P) sometimes will need to be sacrificed to enhance the efficiency of another task-relevant route (D→P).

human intelligence is related to how efficiently the brain integrates information from multiple brain regions (van den Heuvel, Stam, Kahn, & Pol, 2009), and that the efficiency in re-organizing brain networks based on current task demands is positively correlated with general intelligence (Schultz & Cole, 2016). Specifically, Zhang, Gan, and Wang (2015a) found that when comparing a resting state to a deductive reasoning task, individuals with higher math competence showed a significant frontoparietal network shift from modular subsystems toward a globally efficient network architecture. In other words, based on different task demands, there is a significant change of the frontoparietal network from being modular and characterized by locally clustered subsystems toward a higher globally efficient network with shorter global connectivity paths and better interconnected brain regions. This shift in functional network architecture promotes task-related functional intercommunication across discrete brain regions in a timely manner. FP-NET aligns well with small-world network theory as well in that brain networks consist not only of dense local connections to reduce wiring cost but also long-distance connections with short paths to support global information processing (Bassett & Bullmore, 2006, 2017; Watts & Strogatz, 1998). FP-NET is also in line with the "flexible hub" theory that the frontoparietal network could rapidly and flexibly update its global connectivity to support adaptive behaviors (Cole, Braver, & Meiran, 2017; Cole et al., 2013).

Overall, FP-NET posits increased speed of information transfer and reduced information processing costs, promoting efficient communication within the frontoparietal system and across different brain networks in a goal-oriented manner. Thus, FP-NET reflects the capacity and flexibility of brain systems in engaging different brain circuits dynamically and efficiently. Importantly, FP-NET provides a different perspective in understanding of the neural mechanisms underlying math competence beyond the function of individual brain regions alone, highlighting the importance of network-level processing and the interactions between brain regions in understanding higher cognitive functions.

Although FP-NET is a promising framework, further investigation is required to fully understand the neural mechanisms underlying math competence, the extent to which network efficiency is a crucial component and its implications. To test FP-NET, future studies should investigate how the frontoparietal network dynamically interacts with other brain regions during different tasks, and how it changes as a function of ability level, experience, age, and so forth. Specifically, systematic task manipulations are required (e.g., task complexity or strategy use) to investigate to what extent different brain networks are recruited, and how they relate to individual differences in math competence. To investigate the interaction and connectivity patterns between specific regions, researchers can use methods such as TMS or transcranial direct current stimulation to temporarily disrupt or enhance the connectivity, and then observe changes in task performance. This approach can help to elucidate the role of a particular brain region in a cognitive process and provide insights into the interactions between different regions. To test the network efficiency, one common method is through graph theoretical analysis of functional connectivity data. These data could be derived from neuroimaging techniques, such as fMRI or EEG, and allows for the characterization of the topology of brain networks and the quantification of their efficiency based on various metrics, such as path length, clustering coefficient, and betweenness centrality. This approach can provide insights into how the frontoparietal network interacts with other brain regions to support mathematical thinking and how these interactions relate to individual differences in math competence. However, it is important to note that the appropriate method for evaluating frontoparietal network efficiency may depend on the specific research question and the type of data available, which requires further investigation.

In summary, empirical testing of FP-NET would require a combination of neuroimaging techniques and experimental manipulations of neural activity and connectivity. By comparing the neural response patterns of individuals performing simple and complex tasks and manipulating connectivity strength, along with novel analytic approaches, researchers can gain a better understanding of how the brain optimizes its processing efficiency, the factors that influence this optimization, and how this process relates to individual differences in math competence. Thus, FP-NET offers a new perspective and a starting point for future research in understanding the neural basis of math competence.

CONCLUSIONS AND FUTURE DIRECTIONS

Understanding the neural bases of math competence based on both structural and functional brain properties is of utmost importance. Previous studies have primarily focused on the important role of IPS in numerical processing (e.g., Schel & Klingberg, 2017; Menon, 2014). However, neural markers related to math competence are not confined to one particular region; rather, they are characterized by a distributed and interconnected neural network across the brain, primarily focused on frontal and parietal cortices. More importantly, the structural integrity and functional efficiency across these regions are critical for higher math competence, which allows for recruiting the most task-relevant neural resources and neural circuits during problem solving. Thus, to gain a comprehensive understanding of the neural underpinnings of math competence, it is essential for future studies to not only investigate the local brain activity patterns and functional connectivity (e.g., Emerson & Cantlon, 2012) but also examine the neural processing efficiency at the network level.

However, many questions remain to be answered. For example, it remains unclear if the structural and functional neural markers are specifically related to math or more domain-general properties that can be found across a broad range of cognitive skills. Future studies should aim to carefully control for or investigate the influence of other cognitive factors (e.g., executive control, working memory) on math competence at the neural level. For instance, one could implement control tasks that are not mathematical in nature but similar in their cognitive demands otherwise, taxing attention, inhibition, and so forth, to examine what differences in brain activities are specific to math and which ones can be found even in control tasks. These studies will also help to explain how much of the differences in math competence between typical and atypical populations can be explained by domain-general factors as compared with domain-specific factors.

In addition, previous studies have most often studied structural and functional neural features separately; however, they are highly related. Brain structural properties can be seen as tools, and their uses are the functions. Although individuals may possess similar tools, they may use the tools differently. For example, a flathead screwdriver could be used to tighten a Phillips screw or replace a chisel, although it will likely not work very well in either case. Thus, it is important to know what tools are at an individual's disposal, and it is also critical to know how individuals use the tools differently. Future studies should examine these two features at the same time to investigate the relations between them across development and their unique roles in explaining individual differences in math competence.

Most of the studies reviewed here do not permit conclusions about the causal relations between structural and functional properties of the brain and math abilities. This is particularly critical for studies on math learning deficits. One possible solution to this problem has been implemented in studies on dyslexia where they matched children with dyslexia not only to age-matched typically developing children, but also to ability-matched children of younger age. In one such study, dyslexic children showed reduced brain activation in parietal and occipitotemporal regions relative to age-matched and ability-matched children, suggesting that the hypo-activation might be the cause of dyslexia (Hoeft et al., 2007). Similar approaches with strict subject selection and matching criteria could be applied in the math domain to further our understanding of the neural markers of math learning deficits.

In addition, how structural and functional neural properties change as a function of age, experience, or intervention, and their relations with math competence, requires further investigation. Longitudinal approaches could be the first step toward this endeavor to track neural changes and examine possible correlations between different neural features and math competence or other cognitive abilities across developmental stages (e.g., Price et al., 2016). More importantly, interventional studies are needed to shed light on how to facilitate math learning, and whether different interventions affect neural markers of math abilities in the same way. Although it is possible that different interventions may yield similar outcomes behaviorally, it stands to reason that interventions that yield brain patterns more similar to those associated with higher math competence may ultimately be superior to interventions that are not associated by normalization in neural markers.

Finally, several methodological approaches merit consideration for future studies. Most studies reviewed here have used MRI techniques, which have limitations in temporal precision. Using more temporally precise techniques such as EEG or near-infrared spectroscopy alone or in conjunction with MRI would allow for a more complete picture of the underlying neural markers associated with math abilities. Lastly, meta-analyses of neuroimaging data are needed as well to synthesize findings in the current literature (see, e.g., Houdé, Rossi, Lubin, & Joliot, 2010, for an example of a neuroimaging meta-analysis on reading and other cognitive functions). Further investigation toward aforenoted directions will undoubtedly help gain more insights into understanding the neural bases of math competence.

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Data Availability Statement

Materials are available upon request.

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Diversity in Citation Practices

Retrospective analysis of the citations in every article published in this journal from 2010 to 2021 reveals a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience* (*JoCN*) during this period were M(an)/M = .407, W(oman)/M = .32, M/W = .115, and W/W = .159, the comparable proportions for the articles that these authorship teams cited were M/M = .549, W/M = .257, M/W = .109, and W/W = .085 (Postle and Fulvio, *JoCN*, 34:1, pp. 1–3). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

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