



## SHORT REPORT

# Neural representational similarity between symbolic and non-symbolic quantities predicts arithmetic skills in childhood but not adolescence

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## Abstract

Mathematical knowledge is constructed hierarchically from basic understanding of quantities and the symbols that denote them. Discrimination of numerical quantity in both symbolic and non-symbolic formats has been linked to mathematical problem-solving abilities. However, little is known of the extent to which overlap in quantity representations between symbolic and non-symbolic formats is related to individual differences in numerical problem solving and whether this relation changes with different stages of development and skill acquisition. Here we investigate the association between neural representational similarity (NRS) across symbolic and non-symbolic quantity discrimination and arithmetic problem-solving skills in early and late developmental stages: elementary school children (ages 7–10 years) and adolescents and young adults (AYA, ages 14–21 years). In children, cross-format NRS in distributed brain regions, including parietal and frontal cortices and the hippocampus, was positively correlated with arithmetic skills. In contrast, no brain region showed a significant association between cross-format NRS and arithmetic skills in the AYA group. Our findings suggest that the relationship between symbolic-non-symbolic NRS and arithmetic skills depends on developmental stage. Taken together, our study provides evidence for both mapping and estrangement hypotheses in the context of numerical problem solving, albeit over different cognitive developmental stages.

## KEYWORDS

arithmetic skills, cognitive development, cross-format, neural representational similarity, number representation, quantity discrimination

## 1 | INTRODUCTION

Foundational mathematical knowledge acquired in childhood is essential for everyday activities, such as counting objects and comparing quantities, and is predictive of later academic achievement and professional success (Butterworth & Walsh, 2011; Geary et al., 2017; Jordan et al., 2009; National Mathematics Advisory Panel, 2008). Mathematical knowledge is thought to be constructed hierarchically, from basic

understanding of *non-symbolic* quantities (e.g., array of three dots) and the *symbols* that denote them (e.g., “3”) to abstract mathematical concepts. Once core numerical skills are acquired, children learn to carry out numerical problem solving such as adding and subtracting to and from numerical quantities (Feigenson et al., 2004). An important step in advancing our knowledge about numerical skill acquisition is elucidating the mechanisms by which individuals learn the meaning of symbols and acquire mathematical competence across development.

To account for the role of symbolic and non-symbolic representations of quantities in numerical problem-solving skill acquisition, two predominant theoretical views have emerged. According to the “mapping account,” the meaning of symbols is acquired by linking them to concrete non-symbolic representations of numerical quantities (Carey, 2004; Lipton & Spelke, 2005). Such mapping is thought to be fundamental for facilitating numerical problem solving (Dehaene, 2011; Szklarek & Brannon, 2017), and early deficits in mapping between the two formats have been associated with long-term difficulties with arithmetic problem solving (De Smedt & Gilmore, 2011; Rousselle & Noel, 2007). A second account, the “estrangement account,” assumes that once individuals acquire an understanding of symbolic numbers by mapping them onto a non-symbolic number system, symbolic numerical representations become estranged over the course of development, and thus show weaker associations with non-symbolic numerical representations (Bulthé et al., 2018; Lyons et al., 2012; Reynvoet & Sasan-guie, 2016; Wilkey & Ansari, 2020). Here we address a critical open question about how the overlap in neural representations between symbolic and non-symbolic number formats relates to numerical problem solving in children, and whether this relationship changes over the course of cognitive development.

In adults, there is growing evidence suggesting that neural representations of symbolic and non-symbolic quantities may be distinct (Bulthe et al., 2014; Bulthe et al., 2015; Lyons & Beilock, 2018; Lyons et al., 2015). For example, classifiers trained to discriminate between non-symbolic magnitudes do not generalize better than chance level to symbolic magnitudes (Bulthe et al., 2014; Bulthe et al., 2015). It has been suggested that weaker overlap between symbolic and non-symbolic numerical representations may be associated with better numerical problem-solving ability in adults (Bulthé et al., 2018). Despite progress in characterizing neural representations of symbolic and non-symbolic quantities in adults, there have been few neuroimaging investigations with children, presenting a significant gap in foundational knowledge of how children acquire mathematical skills. Although behavioral evidence suggests that the ability to link symbolic and non-symbolic quantity representations in early childhood may facilitate acquisition of numerical problem-solving skills (Brankaer et al., 2014; Malone et al., 2019; Mundy & Gilmore, 2009), this hypothesis has not been directly tested at the neural level. It remains an open question whether distinct neural representations between the two formats are associated with better numerical problem solving in children, similar to adults. Conversely, children may need to engage more overlapping representations between formats as symbolic numerical skills are built by links between symbolic and non-symbolic representations of quantities during early stages of development.

Here we test the hypothesis that the association between symbolic and non-symbolic mapping and numerical problem solving changes across development stage. Strong mapping between formats early in development may underlie better mathematical problem solving (Brankaer et al., 2014; Malone et al., 2019; Mundy & Gilmore, 2009), especially during a period when children rely on non-symbolic quantities to understand the relations between symbolic representations of numbers. Over the course of development, however, with greater expe-

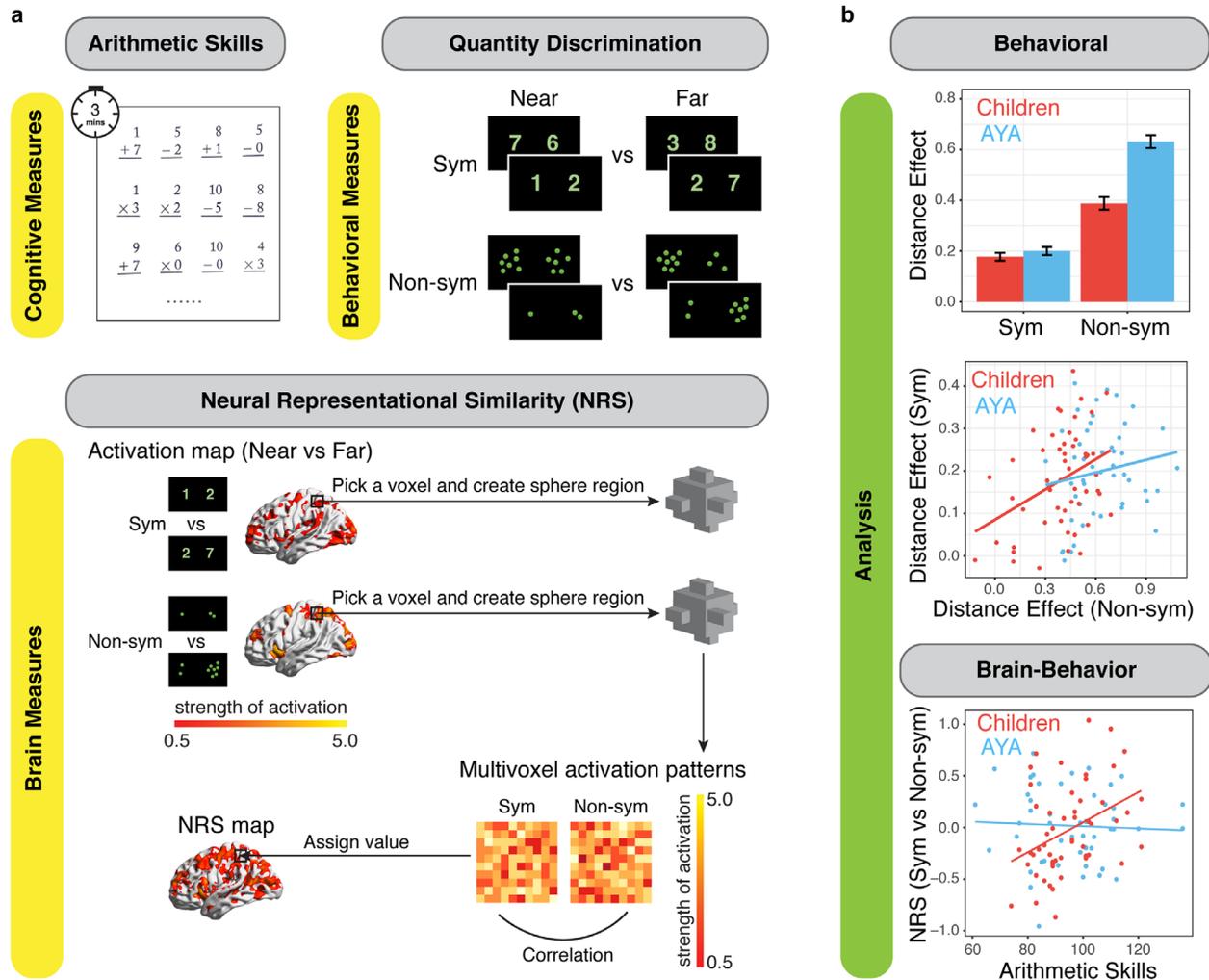
## RESEARCH HIGHLIGHTS

- We examined how neural representational similarity (NRS) between symbolic and non-symbolic quantities relates to numerical problem solving at different stages of development and skill acquisition.
- NRS between symbolic and non-symbolic quantities in distributed brain regions encompassing parietal and frontal cortices, and hippocampus, predicted arithmetic problem-solving skills in children.
- No brain regions showed a significant relation between NRS and arithmetic skills in adolescents and young adults.
- NRS between symbolic and non-symbolic numerical quantities contributes to early numerical problem-solving skill acquisition, but such relationship diminishes later with increased proficiency with symbols.

rience with symbolic numbers, stronger associations between symbolic numbers may overshadow the dependence on links between symbolic and non-symbolic representations of magnitude (Bulthé et al., 2018; Lyons et al., 2012). Thus, it is possible that links between cross-format, symbolic-non-symbolic mapping, and numerical problem solving are stronger earlier in development, consistent with the mapping theory (Brankaer et al., 2014; Mundy & Gilmore, 2009), and weaker, shifting to a dissociation, later in development, consistent with the estrangement theory (Bulthé et al., 2018; Lyons et al., 2012).

To address how the neural representations of symbolic and non-symbolic quantities relate to numerical problem-solving skills at different stages of development, the current study examined this relationship in children and in adolescents and young adults (AYA), corresponding to early and late stages of development, respectively. Our analysis strategy is summarized in Figure 1. We used NRS analysis (Kragel et al., 2018; Kriegeskorte, 2008; Kriegeskorte et al., 2006) to determine the overlap in spatial patterns of brain activity elicited during symbolic and non-symbolic quantity discrimination and examined its relationship to arithmetic problem-solving skills in elementary school children, aged 7–10, and AYA, aged 14–21. We first evaluated voxel-wise NRS between brain responses associated with comparison of small versus large distances between two numbers, reflecting numerical distance effects (Moyer & Landauer, 1967), which allowed us to assess neural representations of quantities while carefully controlling for low-level perceptual features, motor responses, and mental activity associated with resting baseline. The relation between individuals' cross-format NRS and arithmetic problem-solving skills was then compared between children and the AYA group.

We hypothesized that the relationship between cross-format NRS of quantity discrimination and arithmetic skills is different across development: (a) *earlier in development (in children)*: mapping between symbolic and non-symbolic numerical quantities may be associated with arithmetic skill acquisition, and thus a positive relationship



**FIGURE 1** Key steps in data analysis. (a) *Cognitive measures*. Arithmetic skills in children and adolescents and young adults (AYA) were measured by WJ-III Math Fluency subtest. *Behavioral measures*. Behavioral performance related to numerical distance effects (Near efficiency vs. Far efficiency) was computed for the symbolic (Sym) and non-symbolic (Non-sym) quantity discrimination tasks. *Brain measures*. Neural representational similarity (NRS) between brain responses associated with numerical distance effects of symbolic and non-symbolic numerical quantity discrimination tasks was computed at each voxel across the whole brain (see also *Methods*). (b) *Behavioral analysis*. Numerical distance effects for both formats and groups, and correlation between distance effects were examined. *Brain-behavior analysis*. Regression analysis was used to determine brain regions where NRS showed a significant relation with standardized measures of arithmetic problem-solving skills

between cross-format NRS and arithmetic skills may be observed; and (b) *later in development (in AYA)*: arithmetic proficiency may no longer depend on mapping between symbolic and non-symbolic numerical quantities, and thus this relationship may become weaker, or possibly negative as previously shown in adults (Bulthé et al., 2018).

## 2 | METHODS

### 2.1 | Participants

One hundred and twenty-three right-handed participants (66 children and 57 AYA) with no history of neurological or psychiatric disorders were recruited to participate in the study. All study protocols were approved by the Stanford University School of Medicine Institutional

Review Board and informed consent was obtained from participants (18 years old and older) or their parents (under 18 years old). Thirteen children and nine AYA were excluded from data analysis due to poor behavioral performance, poor image quality, excessive head movement, missing data, or technical issues (see details in Supplementary Methods). The final sample consisted of 53 children (age:  $M = 8.2$ ,  $SD = 0.65$ , range = 6.8–10 years; 28 females) and 48 AYA (age:  $M = 18.2$ ,  $SD = 1.56$ , range = 14.3–21.2 years; 26 females).

### 2.2 | Symbolic and non-symbolic number comparison fMRI tasks

In the symbolic number comparison task during fMRI scanning, participants were asked to determine which of two Arabic numerals was

larger. Similarly, in the non-symbolic number comparison task, participants were asked to determine which of two sets of random arrays of dots was larger. We used a 2 (Distance: near, far)  $\times$  2 (Magnitude: big, little) experimental design to control for effects of numerical magnitude at each level of numerical distance. Quantities between one and nine, excluding five, were used in both tasks. Half of the trials had a *near* distance (one unit) between the two quantities (e.g., 7:6), while the remaining trials had a *far* distance (five units) between the two quantities (e.g., 3:8). Numerical magnitude was matched between the two distance conditions with an equal distribution of “big” (sum of pair of quantities  $>10$ ) and “little” (sum of pair of quantities  $<10$ ) conditions. Participants completed symbolic and non-symbolic tasks in two separate runs, with order of runs randomized across participants. Additional details on fMRI tasks are described in Supplementary Methods.

### 2.3 | Behavioral performance on symbolic and non-symbolic tasks

Trials with response times lower than 150 ms were excluded from the analysis. For each task, we computed an efficiency score (efficiency = accuracy/median RT) for near and far conditions separately to account for the speed-accuracy trade-off. Higher scores indicated higher performance efficiency. We first conducted one-sample *t*-tests to examine whether there were behavioral numerical distance effects, assessed by subtracting efficiency scores for far trials from those for near trials, for each task and group. Next, we used Pearson correlations to examine whether distance effects are correlated between symbolic and non-symbolic tasks for each group. Near and far conditions included an equal distribution of trials with large and small magnitude as described above. Both correct and incorrect trials were included in the analysis and post-hoc analysis was performed to confirm that the results hold with only correct trials (Supplementary Results).

### 2.4 | Arithmetic problem-solving skills

Arithmetic problem-solving skills were assessed using the Math Fluency subtest of the Woodcock Johnson-III (Vought & Dean, 2011). Participants were instructed to solve as many problems (up to 160 problems) as they could within 3 min. Problems involved simple addition, subtraction, and multiplication with operands between 0 and 10. Standardized scores based on age norms on WJ-III Math Fluency subtest were used in relevant analyses.

### 2.5 | fMRI data acquisition and preprocessing

Task-based functional data were acquired on a 3T GE scanner using a T2\* weighted gradient echo-spiral in-out pulse sequence. A T1-weighted, high-resolution structural image was acquired to facilitate anatomical co-registration of functional images. Images were preprocessed and analyzed using SPM12 (Ashburner et al., 2020). Additional

details on fMRI data acquisition and preprocessing procedures are described in Supplementary Methods.

## 2.6 | fMRI data analyses

### 2.6.1 | First-level statistical analysis

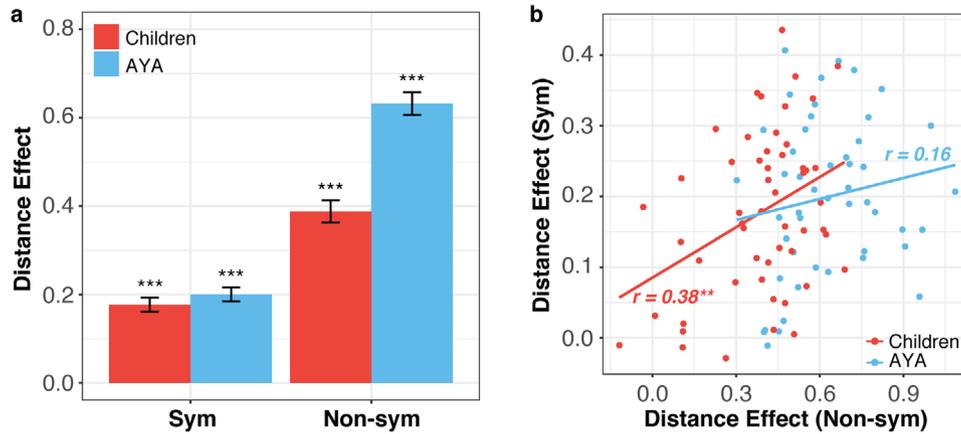
Task-related brain activation was assessed using the general linear model (GLM) implemented in SPM12. At the individual subject level, brain responses representing correct trials for each of 2 (Distance)  $\times$  2 (Magnitude) conditions (i.e., near/big, near/little, far/big, far/little) were modeled using boxcar functions convolved with a canonical hemodynamic response function and a temporal derivative to account for voxel-wise latency differences in hemodynamic response. An error regressor was also included in the model to account for the influence of incorrect trials. Additionally, six head movement parameters generated from the realignment procedure were included to control for the potential influences of head motion. Serial correlations were accounted for by modeling the fMRI time series as a first-degree autoregressive process. The GLM was applied to the symbolic and the non-symbolic tasks separately. Voxel-wise contrast maps were generated for each participant for the symbolic and non-symbolic tasks (Figure 1). The contrast of interest was the near vs far condition corresponding to numerical distance effects (see also Supplementary Methods).

### 2.6.2 | Multivoxel NRS analysis

To assess similarity in the neural representation of the numerical distance effect between formats, multivariate spatial correlation of brain activity patterns between symbolic and non-symbolic numerical distance effects was computed across the whole brain for each individual (Figure 1). This multivoxel NRS analysis approach provides a way to assess whether cognitive processes share similar neural features across different tasks or conditions and to determine which brain areas are most sensitive to overlapping neural representations, in an advance over univariate measures of task-related brain activation levels (Kragel et al., 2018; Kriegeskorte, 2008) (see also Supplementary Methods).

In each individual, voxel-wise brain activation was first computed by contrasting the near and far distance conditions. Voxel-wise NRS was then computed as the spatial correlation between multivoxel activation patterns elicited by symbolic and non-symbolic task conditions, within a 6-mm spherical region centered at each voxel. The resulting spatial correlations were Fisher Z-transformed to generate the NRS, and this value was assigned in the center voxel of the region. This procedure was repeated for all voxels across the whole brain (Kriegeskorte et al., 2006) to create NRS maps in each individual.

The relation between cross-format NRS and arithmetic skills was determined in each group, using standardized WJ-III Math Fluency scores to compare brain-behavior associations between groups (Figure 1). Whole-brain regression analysis was first performed in each



**FIGURE 2** Numerical distance effects in children and AYA. (a) Numerical distance effects were observed in both symbolic (Sym) and non-symbolic (Non-sym) quantity discrimination tasks in children and AYA. (b) Numerical distance effects were correlated between formats in children but not AYA. Distance effects (Near efficiency – Far efficiency) were multiplied by  $-1$  for illustration purposes. Higher scores indicate greater distance effects (less efficient performance on Near trials, compared to Far trials). \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$

group with arithmetic skills as a covariate of interest to identify brain regions that showed a significant relationship between NRS and arithmetic skills. Multiple regression analysis was then performed to examine the interaction between group (children, AYA) and arithmetic skills in each region of interest (ROI; 6-mm spheres centered at peaks or sub-peaks) identified from whole-brain regression analysis. Pearson correlation was used to examine the correlation between NRS and arithmetic skills for each ROI in each group. Additional confirmatory cross-validation analysis procedure is described in Supplementary Methods. Finally, we performed a whole-brain GLM with WJ-III Math Fluency, group, and their interaction as regressors to determine brain regions that show a group difference in the relationship between arithmetic skills and NRS. All statistical maps were masked with a grey matter mask, and significant clusters were identified using a height threshold of  $p < 0.01$ , with whole-brain family-wise error rate correction at  $p < 0.01$  (spatial extent of 128 voxels) based on Monte Carlo simulations.

### 3 | RESULTS

#### 3.1 | Symbolic and non-symbolic quantity discrimination in children and AYA

##### 3.1.1 | Overall behavioral performance

On both symbolic and non-symbolic quantity discrimination tasks, AYA were more accurate and faster than children, assessed by efficiency (accuracy divided by median response times) on these measures (two-sample t-tests: symbolic:  $t(99) = 15.40$ ,  $p < 0.001$ , Cohen's  $d = 3.07$ ; non-symbolic:  $t(99) = 11.86$ ,  $p < 0.001$ , Cohen's  $d = 2.36$ ). These results demonstrate that children are less proficient than AYA in processing symbolic and non-symbolic numbers.

##### 3.1.2 | Numerical distance effects

To address cognitive mechanisms of quantity discrimination, we examined numerical distance effects for each format in children and AYA. We found significant distance effects (i.e., reduced efficiency on near distance trials, compared to far distance trials) for both symbolic and non-symbolic quantity discrimination tasks in children (symbolic:  $t(52) = -11.24$ ,  $p < 0.001$ , Cohen's  $d = 1.54$ ; non-symbolic:  $t(52) = -15.52$ ,  $p < 0.001$ , Cohen's  $d = 2.13$ ) and AYA (symbolic:  $t(47) = -12.60$ ,  $p < .001$ , Cohen's  $d = 1.82$ ; non-symbolic:  $t(47) = -24.35$ ,  $p < 0.001$ , Cohen's  $d = 3.51$ ; Figure 2a). Notably, distance effects were significantly correlated between formats in children ( $r = 0.38$ ,  $p = 0.006$ ) but not AYA ( $r = 0.16$ ,  $p = 0.27$ ) (Figure 2b). These results suggest that children may rely on similar cognitive mechanisms during quantity discrimination in symbolic and non-symbolic formats.

#### 3.2 | NRS between symbolic and non-symbolic quantities correlates with arithmetic problem-solving skills in children but not AYA

##### 3.2.1 | Standardization of numerical problem-solving measures

To determine how the mapping between symbolic and non-symbolic quantity representations relates to individual differences in numerical problem-solving skills at different stages of development, we next assessed whether cross-format NRS relates to arithmetic skills in children and AYA. As expected, AYA ( $M = 113.8$ ;  $SD = 25.3$ ) outperformed children ( $M = 36.7$ ;  $SD = 13.0$ ; two-sample t-test:  $t(99) = 19.53$ ,  $p < 0.001$ , Cohen's  $d = 3.83$ ) on raw WJ-III Math Fluency scores. To allow comparisons between groups in subsequent brain-behavior analyses, we used standardized WJ-III Math Fluency scores, which were not

**TABLE 1** Brain regions showing significant effects of cross-format representational similarity associated with math fluency score

Group	Region	Cluster Size	Peak T-value	MNI coordinates		
				x	y	z
Children	<b>Positive relation</b>					
	R THA	1402	5.32	14	-14	2
	L THA		4.79	-16	-18	0
	L Insula		4.32	-38	-8	-10
	R HIPP		3.36	24	-20	-16
	L HIPP		3.25	-20	-16	-14
	R COper	157	4.78	42	-8	16
	R IPS	170	4.56	30	-52	38
	R IPS/SMG		3.64	42	-44	46
	L MFG/FEF	152	4.15	-34	2	64
	L Premotor		3.82	-16	-6	62
	L PreCG	213	4.05	-2	-24	70
	R PreCG		3.55	4	-22	62
	L IPS/LOC	151	3.54	-22	-62	48
	L IPS/SPL		3.20	-26	-52	48
	L IPS/SPL/SMG		3.04	-36	-48	48
		<b>Negative relation</b>				
	No significant clusters					
AYA	<b>Positive relation</b>					
	No significant clusters					
	<b>Negative relation</b>					
	No significant clusters					

Abbreviations: AYA, Adolescents and Young Adults; COper, Central Operculum; FEF, Frontal Eye Field; HIPP, Hippocampus; IPS, Intraparietal Sulcus; L, Left; LOC, Lateral Occipital Cortex; MFG, Middle Frontal Gyrus; PreCG, Precentral Gyrus; Premotor, Premotor Cortex; R, Right.; SMG, Supramarginal Gyrus; SPL, Superior Parietal Lobule; THA, Thalamus.

significantly different between children ( $M = 94.5$ ;  $SD = 11.6$ ) and AYA ( $M = 95.5$ ;  $SD = 16.1$ ; two-sample  $t$ -test:  $t(99) = 0.36$ ,  $p = 0.72$ ).

### 3.2.2 | Whole-brain analysis in children and AYA

In children, a whole-brain analysis revealed a significant positive correlation between arithmetic skills and cross-format NRS in multiple brain regions, including bilateral intraparietal sulcus (IPS), and hippocampus, left insula, and left middle frontal gyrus/frontal eye field (Table 1; Figures 3a-b). No brain region showed a negative correlation between arithmetic skills and NRS in children. In the AYA group, no significant clusters were identified in the whole-brain analysis.

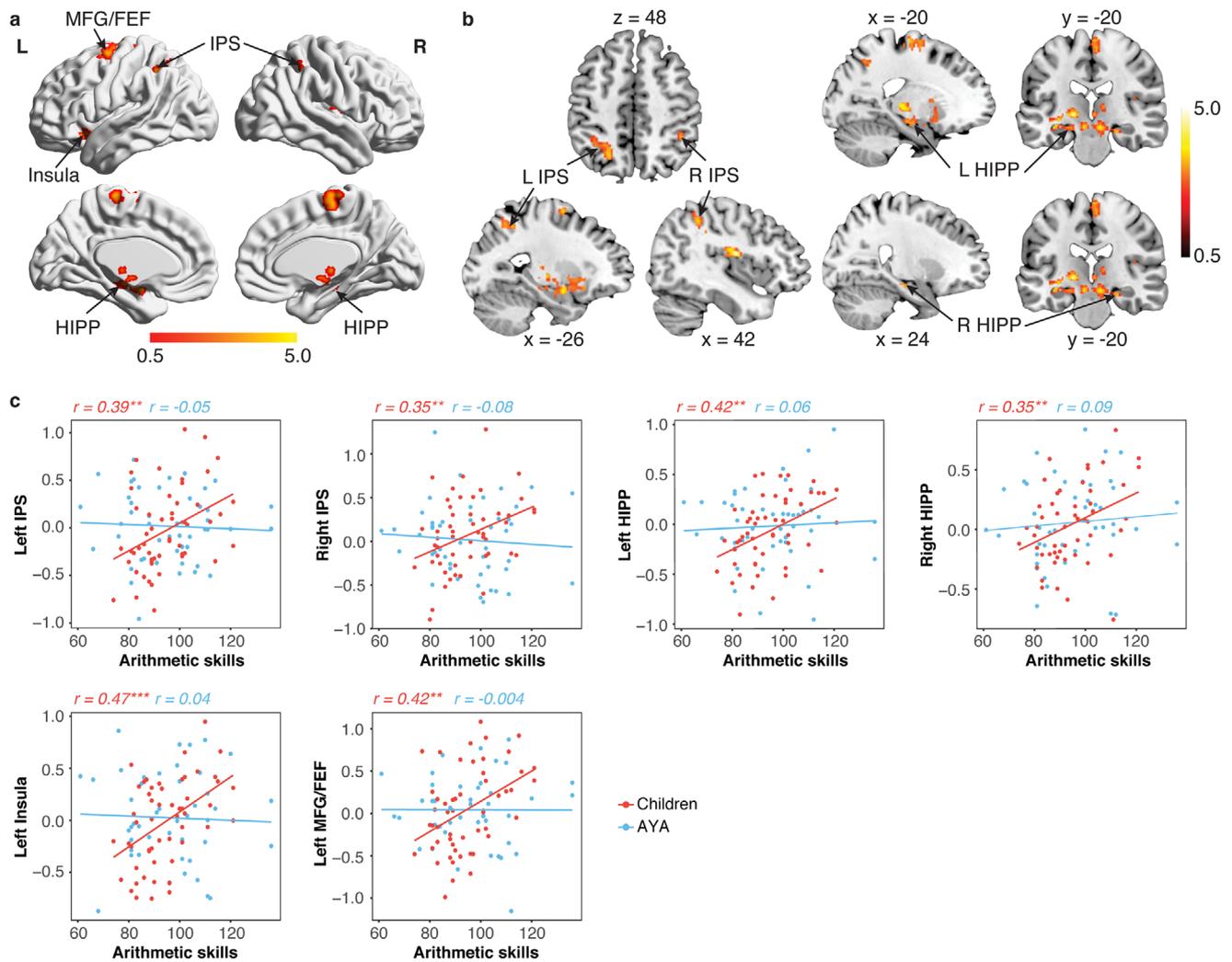
### 3.2.3 | Region-wise group $\times$ skill interaction analysis

A significant group (child, AYA) by arithmetic skill interaction in NRS measures was observed in all brain regions in which children showed an association between NRS and arithmetic skills ( $ps < 0.05$ ),

except the right hippocampus ( $p = 0.098$ ) (Supplementary Table S1). Follow-up analyses of brain-behavior associations in each group revealed a positive correlation between cross-format NRS in all identified brain regions and arithmetic skills in children ( $rs > 0.35$ ,  $ps < = 0.01$ ; Figure 3c; Supplementary Figure S1) and no significant associations between cross-format NRS and arithmetic skills in AYA ( $-0.13 < rs < 0.25$ ,  $ps > = 0.09$ ). Additional analyses addressing potential confounds, including variations in distance effects and response times, showed that the positive association between cross-format NRS and arithmetic skills in children remained significant (Supplementary Results). Finally, a balanced fourfold cross-validation combined with linear regression (Cohen et al., 2010; Supekar et al., 2013) was performed to further validate the robustness of our findings (Supplementary Results; Supplementary Table S2).

### 3.2.4 | Whole-brain interaction analysis

To further examine whether AYA show a relationship between cross-format NRS and arithmetic skills, differently from children in any brain



**FIGURE 3** Cross-format NRS correlates with arithmetic skills in children but not AYA. (a–b) In children, cross-format NRS positively correlates with arithmetic skills in multiple distributed brain areas (see also Table 1), including bilateral intraparietal sulcus (IPS) and hippocampus (HIPP), left insula, and left middle frontal gyrus/frontal eye field (MFG/FEF). No brain areas showed an association between NRS and arithmetic skills in AYA. (c) A significant positive relationship between cross-format NRS and arithmetic skills in bilateral IPS (MNI coordinates:  $[-22, -62, 48]$  and  $[42, -44, 46]$ ), bilateral HIPP (MNI coordinates:  $[-20, -16, -14]$  and  $[24, -20, -16]$ ), left insula (MNI coordinates:  $[-38, -8, -10]$ ), and left MFG/FEF (MNI coordinates:  $[-34, 2, 64]$ ) was observed in children but not AYA. For bilateral IPS ROIs with multiple peaks, those with strongest group  $\times$  arithmetic skill interaction effects are plotted. Similar profiles were observed in other brain regions (see Figure S1). L: left; R: right. \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$

region, we conducted a follow-up whole-brain analysis with group, arithmetic skills, and group  $\times$  arithmetic skill interaction as regressors. This analysis confirmed a significant group by arithmetic skill interaction: NRS between the two formats was positively correlated with arithmetic skills in children, but not in AYA (Supplementary Table S3).

Taken together, these results provide converging evidence that NRS between symbolic and non-symbolic quantity discrimination supports arithmetic problem-solving skills in children but not AYA.

## 4 | DISCUSSION

Our findings reveal that the relationship between neural representations and individual differences in numerical problem-solving skills

changes between two distinct periods of development—childhood and adolescence. Specifically, we found a positive correlation between cross-format NRS and arithmetic skills in multiple brain regions, including parietal and frontal cortices and the hippocampus, in children but not the AYA group. No brain areas showed a negative correlation between cross-format NRS and arithmetic skills in either group. Our findings suggest that neural mapping between symbolic and non-symbolic numerical magnitude representations plays an important role in numerical problem-solving skills in childhood, but once individuals acquire fluency with symbolic quantities, their arithmetic problem-solving skills are no longer reliant on mapping between the two formats. Together, these findings elucidate neural representations of symbolic and non-symbolic quantities across distinct developmental stages and provide a cognitive framework for understanding core



processes underlying the development of numerical problem-solving skills.

Similar to previous observations (Holloway & Ansari, 2009; Lonemann et al., 2011; Moyer & Landauer, 1967; Mundy & Gilmore, 2009), strong numerical distance effects in both symbolic and non-symbolic formats were observed in children and AYA. Critically, children, but not AYA, showed a significant correlation between the symbolic and non-symbolic numerical distance effects. This suggests that children, who are less proficient on numerical processing and problem solving than AYA, may rely on a common underlying mechanism across symbolic and non-symbolic quantities. In support of these results, a significant positive relation was observed between neural representations of symbolic and non-symbolic quantity discrimination and arithmetic problem-solving skills in children, but not AYA.

We found a striking relationship between NRS and arithmetic skills in multiple brain regions in children, including the frontal-parietal cortex and the hippocampus. Crucially, these results suggest that in children, the degree of NRS between symbolic and non-symbolic neural representations of quantity discrimination may be a neural mechanism that supports early acquisition of arithmetic skills, consistent with behavioral findings suggesting that children may rely on the mapping between symbolic and non-symbolic quantities to acquire mathematical competence (Brankaer et al., 2014; Malone et al., 2019; Mundy & Gilmore, 2009).

Our findings shed new light on the contribution of the IPS in building common representations of quantity that support better numerical problem solving in children. The role of the IPS in symbolic and non-symbolic quantity discrimination is well established (Butterworth & Walsh, 2011; Cantlon, 2012; Fias et al., 2003; Nieder, 2016; Piazza et al., 2007) as well as its role in arithmetic problem solving (Arsalidou et al., 2017; Evans et al., 2015; Jolles et al., 2016; Menon, 2015; Rivera et al., 2005; Rosenberg-Lee et al., 2011; Wu et al., 2009). The IPS is thus well placed to anchor a common neurofunctional core system that children may rely on for all three domains, thus contributing to the observed link between symbolic and non-symbolic quantity discrimination and arithmetic skills.

Our results revealed that NRS in the hippocampus is positively correlated with arithmetic skills in children, but not AYA. Recent studies have begun to highlight an important role for the hippocampus in learning and development of arithmetic skills in children (Chang et al., 2019; Cho et al., 2012; De Smedt et al., 2011; Qin et al., 2014; Rosenberg-Lee et al., 2017; Supekar et al., 2013). Multiple lines of research have shown that the hippocampus plays a crucial role in the formation of relational memory (Giovanello et al., 2004; Olsen et al., 2012; Ranganath, 2010; Staresina & Davachi, 2009). Thus, our results suggest that the hippocampus may contribute to problem-solving skills via binding of neural representations across symbolic and non-symbolic formats in children, whereas AYA may be less reliant on such mechanisms.

How might cross-format NRS facilitate arithmetic problem solving in children? We suggest that the IPS and hippocampus facilitate the binding of neural representations of the numerical distance effect across formats, leading to enhanced numerical problem solving during

early stages of skill acquisition. To process numerical quantity, children may rely on a common internal “mental number line” that represents quantity across symbolic and non-symbolic formats (Roggeman et al., 2007; Verguts & Fias, 2004). Symbolic and non-symbolic number inputs are thought to be mapped onto specific locations on the number line. Such mapping to common internal representation of numbers may be one mechanism by which quantity discrimination results in similar behavioral distance effects and brain activation patterns across the two formats in brain regions involved in representing quantities, most notably the IPS, and those involved in binding of neural representations between each format and internal representation of quantity, most notably the hippocampus, in children. In this context, our findings suggest that the ability to engage the common internal representation of numbers contributes to more efficient numerical problem solving in children (see also Supplementary Discussion).

Our whole-brain analysis in children also revealed a significant positive correlation between NRS and arithmetic skills in the insula and middle frontal gyrus/frontal eye field, brain regions thought to be associated with cognitive control during numerical problem solving in children (Arsalidou et al., 2017; Fias et al., 2013; Menon, 2016; Peters & De Smedt, 2017). These results support theoretical models that posit that multiple brain regions contribute to different aspects of numerical problem-solving skill development, including quantity representations, declarative memory, and cognitive control (Menon, 2016). More broadly, these findings provide further evidence that poor numerical skills impact distributed brain areas, including those involved in cognitive control, rather than just the parietal cortex (Fias et al., 2013; Kucian, 2016; Menon et al., 2020; Sokolowski et al., 2017).

In contrast to the positive association between cross-format NRS and arithmetic skills observed in children, the AYA group showed no such relation. This result converges with the estrangement account, which suggests that with extensive exposure and practice with symbolic numbers in formal educational settings, individuals may rely on other mechanisms such as the relation between symbolic numbers, rather than cross-format mapping, for successful numerical problem solving (Lyons et al., 2012). Further studies assessing NRS between individual symbolic numbers may help determine whether arithmetic skills are built upon stronger associations between symbolic number representations in AYA.

Taken together, our results provide support for both mapping and estrangement accounts of symbolic and non-symbolic quantity representations in the context of numerical problem solving, albeit at distinct periods of cognitive development during childhood and adolescence.

## 5 | CONCLUSION

Our study provides novel evidence that overlapping brain representations of symbolic and non-symbolic quantities underlie numerical problem-solving skills in children. Critically, the relationship between cross-format NRS and arithmetic skills changes with developmental stage, from a strong positive association in elementary school children



to a weak, non-significant association in adolescents, and young adults. We suggest that representational overlap between symbolic and non-symbolic numerical quantities in multiple brain regions contributes to early stages of numerical skill development in elementary school, but such relationship diminishes later with increased proficiency with symbols.

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## CONFLICTS OF INTEREST

The authors declare no competing financial interests.

## DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available on request from the corresponding author.

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