How Do Individual Differences in Children's Domain Specific and Domain General Abilities Relate to Brain Activity within the Intraparietal Sulcus During Arithmetic? An fMRI Study

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Abstract: Previous research has demonstrated that children recruit the intraparietal sulcus (IPS) during arithmetic, which has largely been attributed to domain-specific processes such as quantity manipulations. However, the IPS has also been found to be important for domain-general abilities, such as visuo-spatial working memory (VSWM). Based on the current literature it is unclear whether individual differences in domain-specific skills, domain-general skills, or a combination of the two, are related to the recruitment of the IPS during arithmetic. This study examines how individual differences in both domain general and domain specific competencies relate to brain activity in the IPS during arithmetic, and whether the relationships are related to how brain activity is measured. In a sample of 44 school-aged children, we found that VSWM was only weakly related to a neural index of arithmetic complexity (neural problem size effect), whereas symbolic number processing skills (symbolic comparison and ordering) were related to overall arithmetic activity (both small and large problems). By simultaneously examining multiple domain-general and domain specific measures, we were also able to determine that symbolic skills were a stronger predictor of brain activity within the IPS than domain general skills such as VSWM and domain specific skills such as non-symbolic number processing. Together, these findings highlight that neural problem size effect may reflect different cognitive processes than brain activity across both small and large arithmetic problems, and that symbolic number processing skills are a critical predictor of variability in IPS activity during arithmetic. *Hum Brain Mapp* 38:3941–3956, 2017. © 2017 Wiley Periodicals, Inc.

Key words: arithmetic; fMRI; children; domain-general; domain-specific; visuo-spatial working memory; symbolic number processing; individual differences

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INTRODUCTION

Achieving fluency with arithmetic is an important milestone in the development of mathematical skills. It is therefore important to investigate which competencies scaffold the development of arithmetic abilities in children. The cognitive foundations of arithmetic have been studied extensively using behavioral methods. Researchers differentiate between domain specific and domain general predictors of arithmetic abilities. Domain specific skills refer to abilities that are specifically related to mathematical competencies (e.g., understanding the meanings of number symbols), whereas domain general skills are abilities that

are important for information processing across domains (e.g., working memory or attention) [Vanbinst and De Smedt, 2016]. Much research has investigated how domain specific and domain general competencies predict arithmetic skills, but how these competencies relate to the recruitment of different brain regions in the arithmetic network is still unclear. This study aims to better understand these relationships and elucidate the cognitive underpinnings of the neural basis of arithmetic.

Behavioral research has identified several domain specific abilities that correlate with concurrent or future arithmetic skills. This includes skills such as symbolic (e.g., Arabic numerals) and nonsymbolic (e.g., dot arrays) number processing skills, which are often assessed using number comparison tasks [Bartelet et al., 2014; De Smedt et al., 2009; Holloway and Ansari, 2009; Nosworthy et al., 2013; Schneider et al., 2016]. More recently, symbolic ordering abilities (e.g., being able to identify that a series of numbers are in the correct ascending order) have also been found to be related to individual differences in arithmetic [Goffin and Ansari, 2016; Lyons et al., 2014; Lyons and Ansari, 2015; Lyons and Beilock, 2011].

In addition to research showing that a variety of domain specific skills relate to individual differences in arithmetic abilities, several studies have documented the importance of domain general skills [Alloway and Passolunghi, 2011; DeStefano and LeFevre, 2004; Passolunghi and Lanfranchi, 2012; Peng et al., 2015; Raghubar et al., 2010; Swanson and Kim, 2007]. Visuo-spatial working memory (VSWM) may contribute to arithmetic by manipulating numbers and holding intermediate solutions in mind when calculating. Other skills such as verbal and phonological skills may also play a role in the acquisition of arithmetic [De Smedt et al., 2010b; Durand et al., 2005; Passolunghi and Lanfranchi, 2012; Szucs et al., 2014; Vukovic and Lesaux, 2013].

Though some consensus has emerged on how individual differences in domain general and domain specific abilities predict success in arithmetic, much less is known about how individual differences in these skills are related to the neural networks that underlie arithmetic problem solving. Many studies have mapped out the brain regions supporting arithmetic. This body of literature converges to suggest that a fronto-parietal network is engaged during arithmetic in both adults and children [Arsalidou and Taylor, 2011; Davis et al., 2009; De Smedt et al., 2010a; Kucian et al., 2008; Rivera et al., 2005]. The frontal cortex is thought to be more involved in domain general demands of arithmetic, such as cognitive control and working memory. In contrast, the parietal cortex, particularly the intraparietal sulcus (IPS), is believed to be involved in domain specific processes such as magnitude representations [Dehaene et al., 2003; Menon et al., 2000]. However, brain activity in the IPS could be attributed to a number of factors because arithmetic shares common brain regions with other processes such as VSWM [Constantinidis and Klingberg, 2016; Klingberg, 2006; Zago et al., 2008] and basic

magnitude processing [Ansari, 2008; Arsalidou and Taylor, 2011; Vogel et al., 2015]. Thus, the contributions to the recruitment of the IPS during arithmetic are likely multifaceted and could be a product of domain general or domain specific processes, or a combination of the two. Understanding how individual differences in domain general and domain specific abilities contribute to the recruitment of the parietal cortex during arithmetic can provide a better understanding of the neural basis of arithmetic. Moreover, it can provide convergent validity with studies that have examined the overlap between arithmetic, domain general and domain specific skills [e.g., Knops and Willmes, 2014; Zago et al., 2008]. For instance, if the recruitment of the IPS during arithmetic not only overlaps with VSWM and number processing skills, but also correlates with individual differences in these abilities, then this provides additional evidence that brain activity in the IPS partially reflects the engagement of these cognitive processes.

Although some research has employed brain-behavior correlations to better understand the relationship between arithmetic and domain general or domain specific skills, these studies have not simultaneously examined these abilities in the same sample of participants. Therefore, it is still unclear whether some cognitive skills contribute to IPS activity more than others, or whether they contribute equally. Studies that have used brain-behavior relationships to determine how domain general and domain specific abilities are related to arithmetic have provided evidence that the IPS is an important locus in all of these abilities. For instance, Dumontheil and Klingberg [2012] measured brain activity during a VSWM dot-matrix task and found that individual differences in the recruitment of the left IPS were related to arithmetic scores 2 years later, even after accounting for other behavioral measures. Other research has investigated how working memory abilities are related to individual differences in the recruitment of different brain regions during the solution of arithmetic problems [Metcalf et al., 2013]. Children who had higher VSWM scores also showed greater recruitment of the right IPS, left supramarginal gyrus, and several regions within the frontal cortex during arithmetic [Metcalf et al., 2013]. A similar study demonstrated that, among typically developing children, individual differences in VSWM were related to brain activity during arithmetic in fronto-parietal brain regions [Ashkenazi et al., 2013]. However, children with math learning disabilities showed no such relationship between VSWM and individual differences in the recruitment of the arithmetic network [Ashkenazi et al., 2013]. Together, these findings provide evidence that there is a relationship between VSWM and arithmetic and that the IPS seems to be consistently implicated in this association.

The studies discussed above have begun to examine the relationship between brain activation during arithmetic and well-known behavioral correlates of arithmetic

competence. However, no study to date has explored how individual differences in domain specific or basic number processing skills modulate brain activity during arithmetic. Some existing literature has indicated that activity in the IPS during basic number processing is related to individual differences in arithmetic. One study demonstrated that children who exhibit greater modulation of the left IPS during a symbolic number comparison task also performed better on a standardized test of mathematical fluency [Bugden et al., 2012]. Similarly, greater modulation of the right parietal cortex (including the right IPS) during nonsymbolic number comparison has been associated with a standardized measure of math performance [Haist et al., 2014]. Based on this literature, it remains unclear whether individual differences in basic number processing skills are related to the neural correlates of arithmetic.

The behavioral predictors of brain activity in the IPS may also depend on the neural indices that are being used. For example, a common way of isolating brain regions involved in calculation is to examine regions that are more active for large arithmetic problems (e.g., sums > 10) than small problems (e.g., sums < 10), which is also referred to as the neural problem size effect (PSE) [e.g., De Smedt et al., 2010a]. The PSE is marked by more accurate and faster reaction times on small compared with large problems [Campbell and Xue, 2001; LeFevre et al., 1996]. Different brain regions are activated as a function of problem size; large problems recruit the bilateral IPS and several frontal brain regions more than small problems, whereas small problems activate the supramarginal and angular gyri more than large problems [Stanescu-Cosson et al., 2000]. The neural PSE is thought to reflect increasing demands on the neural systems that underpin calculation [De Smedt et al., 2010a; LeFevre et al., 1996], therefore it is possible that this index of brain activity might be more tied to domain general processes such as working memory. In contrast, brain activation for relatively easy (Small problems) and more difficult problems (Large problems) might both be related to basic number processing skills because individual differences in number processing skills are related to performance on both calculated and retrieved problems [Vanbinst et al., 2012]. By only using the PSE as a measure of brain activity underlying arithmetic, it is possible that processes that are common to both small and large problems cannot be assessed. Therefore, it is important to examine how domain general and domain specific competencies relate to multiple indices of arithmetic activity within the IPS as they may be related to different cognitive processes.

The present study aims to examine how children's domain general and domain specific skills are related to individual differences in the recruitment of the bilateral IPS during the solution of arithmetic problems. Based on the literature to date, it is unclear whether domain general skills, domain specific skills, or a combination of the two contribute to the recruitment of the IPS during arithmetic.

To examine this question, we first isolated regions that were more active for large problems than small problems in children between 7 and 10 years of age. This is a particularly important developmental period because children are actively becoming more fluent with arithmetic during this time [Butterworth, 2005; Carr and Alexeev, 2011]. We examined how domain general and domain specific skills predicted the neural PSE and overall brain activity within the IPS, and selected measures that have consistently been associated with arithmetic proficiency in the behavioral literature such as: verbal skills, VSWM, nonsymbolic comparison, symbolic comparison, and symbolic ordering. Simultaneously examining multiple measures allows us to determine whether domain general or domain specific skills contribute more to brain activity in the IPS, or whether they each uniquely predict the recruitment of this brain region.

METHOD

Participants

Fifty-nine children between 7.5 and 10.4 years of age ($M = 9.2$) were recruited to participate in this study. Two children did not complete the MRI, and nine children were removed from analyses because they had accuracy below chance on the arithmetic task in the scanner or on the non-standardized behavioral measures. Three additional children were excluded from analyses due to head motion that exceeded 1.5 mm between volumes or more than 3 mm over the entire scan, and one child was removed due to atypical neurological signs. Therefore, a total of 44 children were included in the final analysis (19 females, 2 left-handed). All children were fluent English speakers and had normal or corrected to normal vision. The Health Sciences Research Ethics Board at the University of Western Ontario approved the methods and procedures in this study. Children's caregivers gave informed consent, and children were reimbursed for their participation in the study.

Procedure

This study consisted of two testing sessions: a behavioral session and an fMRI session. In the behavioral session we assessed performance on three number processing tasks (nonsymbolic and symbolic number comparison, and symbolic ordering), intelligence, standardized measures of math achievement, and visuo-spatial working memory. Children also completed a mock scanning session to familiarize them with the MRI environment and procedures. Children practiced keeping their head still while completing a short arithmetic verification task in the mock scanner. Participants returned to complete the MRI component of the study 1–66 days following the behavioral session ($M = 13$ days). During the MRI session participants

completed the arithmetic verification task, as well as an additional 3–4 tasks in the scanner, which are not discussed here. The order of the tasks was counterbalanced using a Latin square design.

EXPERIMENTAL TASKS AND DESIGN

Behavioral Assessment

Domain specific measures

We included three measures of basic number processing skills: nonsymbolic and symbolic number comparison, and symbolic ordering. Previous research has identified each of these tasks as predictors of arithmetic skills [Bartelet et al., 2014; Goffin and Ansari, 2016; Lyons et al., 2014; Nosworthy et al., 2013; Schneider et al., 2016].

Nonsymbolic and symbolic number comparison. For the nonsymbolic comparison task, participants were presented with two arrays of dots (from 1 to 9 dots), and were instructed to select the array with more dots. On half of the trials the two dot arrays were equated on total surface area and on the other half of trials the arrays were equated on total circumference. In the symbolic comparison task, participants were presented with two Arabic digits (from 1 to 9) and were instructed to select the larger number. On both symbolic and nonsymbolic tasks, the participant was asked to press a button with their right hand if the stimulus on the right side of the screen was bigger, and to press the button with their left hand if the stimulus on the left side of the screen was bigger. The side that had the greater quantity was counterbalanced; half of the trials had the larger quantity on the left side of the screen, and the other half of trials had the larger quantity on the right side of the screen. The stimuli were presented for 850 ms with an inter-trial fixation of 3,000 ms. Participants could respond while the stimulus was presented or on the fixation screen. The task consisted of two blocks with 32 trials (64 trials in total), with a break separating each block. The number pairs were identical in the symbolic and nonsymbolic tasks, and had distances that ranged from 1 to 8. Each task had a set of six practice problems and participants were instructed to respond as quickly and accurately as possible.

Symbolic ordering. Participants were shown 3 Arabic digits that were presented horizontally. On half of the trials the digits were in a numerically increasing order (e.g., 1 2 3 or 4 6 8), and on the other half of trials the digits were not in order (e.g., 3 1 2 or 6 8 4). Participants were instructed to press a button with their right hand if the numbers were in increasing order and a button with their left hand if the numbers were mixed. The digits were separated by a distance of 1, 2, or 3 (e.g., Distance 1 = 2 3 4; Distance 2 = 3 5 7; Distance 3 = 2 5 8). There were 2 blocks of trials that were separated by a break, with 30 trials per block (60 trials in total across both blocks). Of the 15 trials

that were in order in each block, 7 trials had a distance of 1, 5 trials had a distance of 2, and 3 trials had a distance of 3. There were an unequal number of trials per distance because we only used single digits trials, therefore, there are only a limited number of possible sequences. The out-of-order trials were identical to the in-order trials, except they were mixed. The mixed trials in Blocks 1 and 2 had different combinations. Each stimulus was presented for 3,500 ms followed by an inter-trial fixation of 1,500 ms. Participants could respond during the stimulus or fixation screens. The ordering task had a set of 10 practice problems, and participants were asked to respond as quickly and accurately as possible.

Domain general measures

Verbal and nonverbal intelligence. Intelligence was assessed using the Kaufman Brief Intelligence Test-Second Edition (KBIT2) [Kaufman and Kaufman, 2004]. The KBIT2 measures verbal abilities using two subtests: verbal knowledge and riddles. Verbal knowledge assesses receptive language skills, whereas the riddles subtest assesses verbal reasoning skills. We combined the two verbal subtests into one measure of verbal intelligence by averaging children's scores on the verbal knowledge and riddles subtests. Nonverbal intelligence was assessed using the matrices subtest, which requires participants to understand the relationships among visually presented stimuli (both meaningful and abstract visual stimuli). In all analyses we report raw scores for verbal and non-verbal intelligence rather than standard scores because standard scores were negatively correlated with age $r(42) = -0.39$, $P = 0.009$, suggesting that the test norms were not representative of the children in this sample.

Visuo-spatial working memory. We assessed VSWM using the computerized Automated Working Memory Assessment (AWMA) [Alloway et al., 2008]. In the dot matrix task, the participant is presented with a four by four matrix and a dot moves positions through the matrix. The participant is then asked to recall the dot sequence by tapping it on the screen. Even though age was not correlated with the standard scores on the AWMA, we report raw scores to remain consistent with the other standardized measures.

Math achievement

The Math Fluency subtest from the Woodcock Johnson III was administered to each participant. This is a timed measure of arithmetic fluency where children solve single-digit addition, subtraction, and multiplication problems as quickly possible in 3 minutes [Woodcock et al., 2001]. We also administered Numerical Operations and Math Reasoning from the Wechsler Individual Achievement Test (Second Edition: Canadian) [Wechsler, 2005]. However, our analyses and results only discuss the Math Fluency

a) Arithmetic Task

b) Task Design

Figure 1.

(a) Examples of the three conditions in the arithmetic verification task. Participants were asked to identify if the solution was correct or incorrect. (b) Schematic of the timing of the arithmetic task in the scanner.

subtest from the Woodcock Johnson III due to the focus on single digit arithmetic skills. In all analyses we use raw scores because age was negatively correlated with standard scores on the Woodcock Johnson III $r(42) = -0.35$, $P = 0.02$, indicating that the test norms were not representative of the children in this sample.

fMRI Arithmetic Task

To investigate neural processing associated with arithmetic problem solving, participants completed two runs of a single-digit arithmetic verification task that consisted of three conditions: (1) Small problems; (2) Large problems; and (3) Plus 1 problems. For all conditions, an addition problem with two addends was presented along with a solution. Participants were asked to identify if the solution was correct or incorrect. Small problems had a solution less than or equal to 10, Large problems had a solution greater than 10, and Plus 1 problems were always a single digit plus 1 (Fig. 1a). Tie problems (i.e., $3 + 3$) and problems containing a 0 were excluded from the problem list. In half of the trials the solution was incorrect and on the other half of trials the solution was correct. If the solution was incorrect, the presented solution was +1 or +2 above the correct solution. Each run consisted of 36 unique problems (12 problems per condition), resulting in 72 trials across both runs. For the Small and Large problem conditions, half the trials had the larger number presented on the left ($4 + 2$) and in the other half of the trials the larger number was presented on the right ($3 + 5$). If the larger number was presented on the left for a specific problem in run 1, it was presented on the right in the second run

(e.g., Run 1 [$4 + 2$]; Run 2 [$2 + 4$]). Thirty-five of the 44 children passed the motion and accuracy criteria on both arithmetic runs, and only 1 run was used for the other 9 children.

The arithmetic task was presented using a block design with an initial fixation of 6,500 ms and end fixation of 12,000 ms (see Fig. 1b for a schematic of the timing and design). Each problem was presented for a total of 4,500 ms, and the inter-trial interval (ITI) was 1,500 ms on average (duration was 1,000, 1,500, and 2,000 ms). Participants could respond during the presentation of the problem or on the ITI screen. The duration of the inter-block interval (IBI) averaged to 9 seconds in each run. The conditions and trials were randomly presented.

Arithmetic Strategy Assessment

Large arithmetic problems are more often solved using procedural strategies (e.g., counting up, decomposition, etc.) whereas smaller problems tend to be solved by retrieving the solution from memory [Campbell and Xue, 2001]. To verify this in the present sample of participants, we obtained strategy reports immediately after the MRI. Participants were first given three practice trials and were instructed to verbally provide an answer and to explain how they solved the problem. Participants were provided some examples of how they might solve the problem (e.g., Memory: "You might know the answer from memory"; Counting: "You can count to get the answer"; Decomposition: "9 and 1 make 10, and then there are 3 left over so the answer is 13"). Following the three practice trials, participants were asked to verbally provide a solution and

explain how they solved the problem for every trial shown in the scanner. Trials were presented in a pseudo-random order. If participants used a strategy that involved counting or decomposing the problem into smaller parts, we classified this problem as a *procedural* problem. If the participant said they knew the item from memory or just knew the answer we classified this as a *retrieval* problem. We were then able to use these strategy reports to determine the proportion of problems solved using procedural or retrieval strategies in each condition.

MRI Data Acquisition

MRI data were acquired on a 3T Siemens Prisma Fit whole-body scanner, using a 32-channel receive-only head-coil (Siemens, Erlangen Germany). A whole-brain high resolution T1-weighted anatomical scan was collected using an MPRAGE sequence with 192 slices, a resolution of $1 \times 1 \times 1$ mm voxels, and a scan duration of 5 minutes and 21 seconds (TR = 2,300 ms; TE = 2.98 ms; TI = 900 ms; flip angle = 9°). The in-plane resolution was 256×256 pixels. Functional MRI data were acquired during the arithmetic task using a T2* weighted single-shot gradient-echo planar sequence (TR = 2,000 ms, TE = 30 ms, FOV 210×210 mm, matrix size = 70×70 , flip angle = 78°). Thirty-five slices were obtained in an interleaved ascending order with a slice thickness of 3 mm, an in-plane resolution of 3×3 mm, and a 0.75 mm gap. There were 2 runs of the arithmetic task with 144 volumes. Padding was used around the head to reduce head motion. The total scan duration was approximately 40 minutes.

Analyses

Behavioral analyses

In all analyses, raw scores on the standardized measures of intelligence and visuo-spatial memory were used due to the negative correlations between age and standard scores. For each of the domain specific measures we could have used task-specific dependent measures such as distance or reverse distance effects [e.g., Goffin and Ansari, 2016; Turconi et al., 2006]. However, we used dependent measures of overall task performance to make the variables more comparable across tasks. Performance scores were calculated to combine reaction time and accuracy data on the domain specific measures (nonsymbolic and symbolic comparison, and symbolic ordering). Accuracy and reaction time (on correct trials only) were combined to form performance scores based on the formula described in Lyons et al. (2014): $\text{Performance} = \text{RT}(1 + 2\text{ER})$. ER refers to the error rate, or $1 - \text{total accuracy}$ (e.g., 70% accuracy = 0.3 ER). Using this formula, higher values indicate poorer performance.

To examine how domain general and domain specific factors contributed to arithmetic skills, we conducted partial correlations (correcting for age) between Math Fluency

scores from the Woodcock Johnson III and each domain general and domain specific measure. Any measures that were significantly correlated with Math Fluency were then entered into a linear regression to determine which measures predicted unique variance in arithmetic performance.

Brain imaging analyses

Brain imaging data were analyzed using Brain Voyager QX 2.8.4 (Brain Innovation, Maastricht, Netherlands). Functional data were corrected for differences in slice time acquisition, head motion, linear trends, and low frequency noise. Functional images were spatially smoothed with a 6-mm FWHM Gaussian smoothing kernel. The functional images were then coregistered to the T1-weighted anatomical images and transformed into Talairach Space [Talairach and Tournoux, 1988]. Due to the pseudo-jitter in the ITI between each trial, a 2-gamma hemodynamic response function was used to model the expected BOLD signal for each 4,500 ms trial (as opposed to a traditional boxcar function). Large, Small, and Plus 1 trials were modeled as separate conditions. A random-effects GLM was then performed on the data. Whole-brain contrasts were first thresholded at a voxelwise P -value of 0.005, uncorrected and then corrected for multiple-comparisons using Monte-Carlo simulation procedure to determine a minimum cluster threshold [Goebel et al., 2006], resulting in an overall $\alpha < 0.05$. This cluster thresholding method estimates and accounts for spatial smoothness and spatial correlations within the data [estimates of spatial smoothness are based on the formula discussed in Forman et al., 1995].

We isolated regions involved in the neural PSE by contrasting Large problems with Small problems (*Large* > *Small*). To more precisely examine brain activity within the IPS, the neural PSE was selected to isolate brain regions recruited during arithmetic rather than other contrasts such as a comparison of both Small and Large problems with the Plus 1 condition. Comparing both arithmetic conditions to the Plus 1 condition revealed a distributed fronto-parietal network that extended far into the parietal cortex and included brain regions outside of the IPS including the superior and inferior parietal lobules. Both contrasts showed entirely overlapping patterns of brain activity with the parietal cortex except that the brain activity identified by the neural PSE was more restricted to the IPS.

We extracted beta values from the regions in the bilateral IPS, which exhibited a significant neural PSE (after a cluster correction). We separately calculated the neural PSE in the left and right IPS by subtracting the Small beta estimates from the Large beta estimates (*Large* – *Small*). We then conducted a partial correlation (controlling for age) between each of the behavioral measures and the neural PSE in each hemisphere. To examine whether these relationships were specific to the neural PSE, we also examined the average activation to Large and Small problems in the IPS. In order to directly compare the brain-behavior correlations between the neural PSE and

average arithmetic activation in the IPS, we used the same clusters from the analysis above. We averaged the beta estimates for the Large and Small conditions within the left and right IPS ([Large Problems + Small Problems]/2), and subtracted the beta values from the Plus 1 condition from this average (average arithmetic activation – Plus 1 condition). The Plus 1 condition served as a control in order to remove any brain activity associated with response selection and visual features of the stimuli. Moreover, the strategies used in this condition have been found to be very homogenous in previous studies [Metcalf et al., 2013]. We then examined how each of the domain general and domain specific measures were correlated with this measure of average arithmetic activity in the left and right IPS, after controlling for age. If more than one of the domain general or domain specific skills was significantly correlated with the neural measures, we entered these variables into a linear regression to determine which of these measures explained unique variance in brain activation.

To better understand the relative strength of the relationships between measures, we conducted both frequentist and Bayesian statistics on all of the behavioral and brain-behavior analyses. To address the issue of multiple comparisons for the frequentist correlations, we provide both uncorrected and corrected results using the Holm-Bonferroni correction for multiple comparisons (where applicable). Bayesian analyses provide information about the strength of the evidence, and Bayes Factors (BF) can indicate whether the evidence is in favor of the alternative hypothesis (BF_{10}) or the null hypothesis (BF_{01}) [Wagenmakers et al., 2011]. Bayes factors (BF_{10}) above 3 are considered moderate evidence for a relationship between the variables of interest, whereas Bayes factors above 10 are considered strong evidence [Jeffreys, 1961]. A Bayes factor of 10 indicates that the relationship being investigated (i.e., the alternative hypothesis) is 10 times more likely than the null hypothesis. To the best of our knowledge, there are no tools for correcting for Type 1 error rates of Bayes Factors. However, it is important to note that Bayesian statistics do not rely on the same assumptions as frequentists statistics where Type 1 error rates need to be controlled for across multiple tests. Frequentists statistics concerns the probability of data given a theory, whereas Bayesian statistics concerns the probability of a theory given the data [Dienes, 2011]. Therefore, Bayesian statistics quantify the relative evidence for different hypotheses.

Behavioral and neuroimaging analyses were completed on all 44 children except for analyses that included the Dot Matrix task (VSWM) from the Automated Working Memory Assessment. We did not obtain data from 1 child on this task, therefore any analyses that included the Dot Matrix task were conducted on 43 children. All frequentist analyses were conducted in SPSS (Version 24) and Bayesian analyses were conducted in JASP [JASP Team, 2016].

RESULTS

Behavioral Assessment: Domain General and Domain Specific Predictors of Math Achievement

To determine which domain general and domain specific skills were related to math achievement, we first examined whether the measures were correlated with Math Fluency performance (after controlling for age). Higher arithmetic performance on the Math Fluency test was related to better performance on three measures: (1) verbal IQ $r(41) = 0.37$, $P = 0.014$; (2) symbolic number comparison $r(41) = -0.37$, $P = 0.016$; and (3) symbolic ordering $r(41) = -0.49$, $P = 0.001$ (see Table I). The negative correlations between Math Fluency and symbolic comparison and ordering are related to the way those measures were scored (see above), where higher scores indicate poorer performance. None of the other domain general or domain specific measures were significantly correlated with math achievement. In addition to significance testing, we also calculated Bayes Factors for each of the correlations. The results of this analysis indicated that the evidence was in favor of a relationship between arithmetic and verbal IQ ($BF_{10} = 16.18$), symbolic comparison ($BF_{10} = 20.07$) and symbolic ordering ($BF_{10} = 162.96$).

It is important to note that the correlations reported above are uncorrected, and when using a Holm-Bonferroni correction for multiple comparisons only symbolic ordering remains significantly correlated with Math fluency skills. Therefore, the frequentist and Bayesian statistics converge to suggest that symbolic ordering is one of the strongest predictors of arithmetic fluency.

To further examine whether age, verbal IQ, symbolic number comparison, and symbolic ordering predicted unique variance in children's math achievement, we entered each of these measures as predictors in a linear regression. The regression model was significant $F(4,39) = 10.21$, $P < 0.001$, and predicted 51% of the variance in children's arithmetic scores. However, only verbal IQ and symbolic ordering were found to uniquely predict individual differences in arithmetic performance (see Table II). The Bayes factors of inclusion also indicated that there was strong evidence that verbal IQ ($BF_{inclusion} = 119.42$) and symbolic ordering ($BF_{inclusion} = 70.79$) were unique predictors of arithmetic fluency. Together, these findings suggest that verbal skills and symbolic ordering are unique predictors of a child's arithmetic abilities, even after accounting for age and symbolic comparison in the model.

Brain Imaging

Behavioral performance on the in-scanner arithmetic task

A within-subjects ANOVA revealed that accuracy on the three conditions in the arithmetic task significantly

TABLE I. Pearson correlation matrix with Bayes Factors (BF₁₀) shown below in brackets

	1	2	3	4	5	6	7	8	9	10	11
1. Neural PSE Right IPS	–										
2. Neural PSE Left IPS	0.78*** (3.37 × 10 ⁷)	–									
3. Avg. arithmetic Right IPS	0.16 (0.35)	0.29 (1.18)	–								
4. Avg. arithmetic Left IPS	0.13 (0.27)	0.29 (1.18)	0.69*** (8.46 × 10 ⁴)	–							
5. Math Fluency	0.33* (2.40)	0.39* (5.49)	0.37* (4.31)	0.27 (0.97)	–						
6. Verbal IQ	0.26 (.95)	0.11 (0.28)	–0.11 (0.20)	0.01 (0.19)	0.37* (16.18)	–					
7. Nonverbal IQ	0.28 (1.21)	0.16 (0.34)	–0.09 (0.20)	0.07 (0.21)	0.13 (0.36)	0.28 (1.75)	–				
8. VSWM	0.29 (1.39)	0.28 (1.13)	0.02 (0.20)	0.03 (0.20)	0.24 (1.55)	0.04 (0.29)	0.20 (0.64)	–			
9. Nonsymbolic Comparison	0.21 (0.24)	0.28 (0.36)	–0.02 (0.21)	0.04 (0.19)	0.03 (0.32)	0.04 (0.34)	0.08 (0.19)	–0.06 (.51)	–		
10. Symbolic Comparison	–0.03 (0.22)	–0.07 (0.23)	–0.46** (22.39)	–0.32* (1.69)	–0.37* (20.07)	0.09 (0.21)	0.05 (0.19)	–0.48*** (211.77)	0.51*** (4,098.67)	–	
11. Ordering	–0.22 (0.63)	–0.24 (0.71)	–0.42** (12.04)	–0.23 (0.62)	–0.49*** (162.96)	0.15 (0.19)	–0.18 (0.50)	–0.33* (4.51)	0.12 (0.74)	0.57*** (2,673.38)	–

Note. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, all Pearson correlations are corrected for age.

differed from one another $F(2,43) = 30.19$, $P < 0.001$ (Fig. 2a). Children were less accurate on the Large problems than Small problems, $t(43) = -5.81$, $P < 0.001$, and Plus 1 problems, $t(43) = -7.01$, $P < 0.001$. Differences in accuracy between the Small and Plus 1 problem conditions were only marginally significant, $t(43) = -1.87$, $P = 0.068$. A second within-subjects ANOVA indicated that there were significant differences in response times between the three conditions, $F(2,43) = 68.06$, $P < 0.001$ (Fig. 2a). Children had longer reaction times on the Large problems than the Small problems, $t(43) = 5.87$, $P < 0.001$, and Plus 1 problems, $t(43) = 9.64$, $P < 0.001$. Small problems also had significantly longer reaction times than Plus 1 problems $t(43) = 7.57$, $P < 0.001$. Overall accuracy on the arithmetic task in the scanner (average performance on the Small and Large problems) was correlated with performance on the Math Fluency test, $r(42) = 0.65$, $P < 0.001$.

We also conducted a within-subjects ANOVA to compare the proportion of procedural strategies used within each condition, which revealed that the three conditions significantly differed from one another, $F(2,43) = 116.4$, $P < 0.001$ (Fig. 2b). Children used procedural significantly more on Large problems than both Small problems, $t(43) = 10.96$, $P < 0.001$, and Plus 1 problems, $t(43) = 12.37$, $P < 0.001$. Small problems were also solved using significantly more procedural strategies than Plus 1 problems, $t(43) = 6.67$, $P < 0.001$. These findings reveal that even though Large problems are solved using procedural strategies more often than Small problems, a significant portion

of Small problems are still solved using time-intensive calculation strategies.

Neural problem size effect

We first identified regions that were more active for Large problems than Small problems. The bilateral IPS were the only regions that were more active for Large problems than Small problems (orange regions in Fig. 3, Table III). There were additional regions that were more active for Small problems than for Large problems, however, they are not discussed here because they were not the focus of the study. Also shown in Figure 3 are brain regions that were more active for both Small and Large problems compared with the Plus 1 control condition (*Large and Small > Plus 1*). Though we did not use this contrast to select regions of interest, Figure 3 shows that brain activity from the neural PSE is entirely overlapping.

TABLE II. Regression analysis predicting Math Fluency scores

Predictor	β	b	SE	t	BF _{Inclusion}
Age (in months)	–0.029	–0.04	0.18	–0.22	0.26
Verbal IQ	0.46	1.72	0.45	3.79**	119.42
Symbolic Comp	–0.14	–0.01	0.01	–0.95	0.39
Ordering	–0.47	–0.01	0.003	–3.28**	70.79

Note. * < 0.05 and ** < 0.01 .

a) Task Performance

b) Arithmetic Strategies

Figure 2.

(a) Task performance (accuracy and reaction time) on the in-scanner arithmetic task. (b) Proportion of problems solved using procedural strategies within each condition on the in-scanner arithmetic task. Note: ** $P < 0.01$, † denotes a marginally significant difference ($P = 0.07$).

Brain-behavior correlations with the neural PSE

To better understand how individual differences in domain general and domain specific skills related to the neural PSE within the IPS, we extracted the beta values from these regions and conducted partial correlations (controlling for age) to examine these relationships (see Table I). Though no correlations met statistical significance, individual differences in VSWM were marginally correlated with the neural PSE in the right $r(40) = 0.29$, $P = 0.062$, and left IPS $r(40) = 0.28$, $P = 0.072$. Nonverbal IQ was also marginally correlated with the neural PSE in the right IPS, $r(41) = 0.28$, $P = 0.066$. Bayes factors also confirmed that there was relatively weak evidence for the relationship between the neural PSE and VSWM ($BF_{10} (R \text{ IPS}) = 1.39$, $BF_{10} (L \text{ IPS}) = 1.10$), as well as nonverbal IQ ($BF_{10} (R \text{ IPS}) = 1.21$).

Brain-behavior correlations with average arithmetic activation

Because children use calculation strategies for both Small and Large problems (Fig. 2b), it is possible that they are relying on basic number processing skills in both conditions. Consequently, the neural PSE may be removing a large part of the variance associated with number processing skills. To determine whether this may be the case, we examined average activation of Large and Small problems compared with the Plus 1 control condition. These analyses were conducted in the same IPS regions defined above to ensure the findings for the PSE and average arithmetic activation were comparable. We first used a one-sample t -test to determine whether both Small and Large conditions activated the IPS above zero, and both conditions

Figure 3.

Significantly activated brain regions during the arithmetic task. Regions showing a significant neural problem size effect (*Large problems* > *Small problems*) are shown in orange, whereas regions more active for both arithmetic conditions versus their control (*Large & Small* > *Plus 1*) are shown in yellow. The anatomical ROIs of the bilateral IPS are shown in blue. [Color figure can be viewed at wileyonlinelibrary.com]

significantly activated the left and right IPS above zero (all tests $P < 0.001$). Paired-samples t -tests revealed that both Small and Large conditions activated the left and right IPS significantly more than the Plus 1 condition in both regions (all tests $p < .05$). We therefore averaged the beta values from the Large and Small conditions ($\text{Large} + \text{Small}/2$) and subtracted the Plus 1 control condition ($\text{Average arithmetic activation} - \text{Plus 1 condition}$) separately within the left and right IPS.

Compared with the neural PSE, the average activation in the left and right IPS related differently to the domain general and domain specific variables (Table I). In the right IPS, greater overall arithmetic activation was related to better performance on the symbolic comparison ($r(41) = -0.46$, $P = 0.002$) and symbolic ordering tasks ($r(41) = -0.42$, $P = 0.005$). Greater activation for arithmetic in the left IPS was associated with better performance on the symbolic comparison task ($r(41) = -0.32$, $P = 0.034$). Bayes factors revealed a similar pattern of findings, with evidence in favor of a relationship between activity in the right IPS and symbolic comparison ($\text{BF}_{10} = 22.39$) and symbolic ordering ($\text{BF}_{10} = 12.04$). In the left IPS, frequentist statistics suggested a correlation between average arithmetic activity and symbolic comparison, however, the Bayes factor indicated that there was relatively weak evidence for this relationship ($\text{BF}_{10} = 1.69$).

To further examine whether symbolic comparison and symbolic ordering predicted unique variance in arithmetic activity within the right IPS, we conducted a linear regression with average arithmetic activation in the right IPS ($\text{Average arithmetic activation} - \text{Plus 1 condition}$) as the dependent variable. The overall model was significant $F(3,40) = 4.64$, $P = 0.007$ and predicted 26% of the variance in children's brain activity (Table IV), however, neither symbolic comparison nor symbolic ordering were significant unique predictors of brain activity within the right IPS. This likely indicates that both symbolic comparison and ordering account for variance in right IPS activity, however, they do not account for unique variance above and beyond the other predictor.

Another noteworthy finding is that, unlike in some previous studies [Haist et al., 2014; Metcalfe et al., 2013], we did not find any association between VSWM or nonsymbolic performance with average arithmetic activity in the IPS (all P -values > 0.81). However, frequentists statistics with a P -value of > 0.05 cannot provide evidence for the null hypothesis. Therefore, we conducted additional Bayesian analyses on the relationships between overall arithmetic activity in the IPS, VSWM, and nonsymbolic performance to determine whether the evidence did indeed support the null hypothesis (i.e., no significant association between these

TABLE III. Anatomical regions, Talairach coordinates, mean t -scores, and number of voxels for the neural problem size effect (*Large problems* > *Small problems*)

Anatomical region	TAL coordinates (x,y,z)			Mean t -score	Number of voxels
<i>Large Problems > Small Problems</i>					
R Intraparietal Sulcus (IPS)	34.42	−43.02	39.94	3.25	2,369
L Intraparietal Sulcus (IPS)	−36.59	−49.40	39.82	3.23	1,395

TABLE IV. Regression analysis predicting average arithmetic activation in the right IPS

Predictor	β	b	SE	t	$BF_{\text{Inclusion}}$
Age (in months)	-0.11	-2.31×10^{-3}	3.09×10^{-3}	-0.75	0.39
Symbolic Comp	-0.36	-3.50×10^{-4}	1.79×10^{-4}	-1.95 [†]	2.92
Ordering	-0.24	-6.47×10^{-5}	4.6×10^{-5}	-1.41	1.22

Note: [†] $P = 0.058$.

measures). This can be achieved by calculating BF_{01} (evidence for the null hypothesis) rather than BF_{10} (evidence for the alternative hypothesis). Bayes factors indicated that there was no association between VSWM and average arithmetic activation in the left or right IPS, and that the null hypothesis was five times more likely than the alternative hypothesis ($BF_{01\_RIPS} = 4.95$; $BF_{01\_LIPS} = 4.97$). The same was also true for nonsymbolic performance and brain activity in the bilateral IPS, and Bayes factors suggested that the evidence was in favor of the null hypothesis rather than the alternative hypothesis ($BF_{01\_RIPS} = 4.66$; $BF_{01\_LIPS} = 5.32$).

It is important to acknowledge the possibility of Type I error due to the multiple comparisons being made. Following a Holm-Bonferroni sequential correction for family-wise error, only symbolic comparison and ordering were significantly correlated with arithmetic activity in the right IPS. Therefore, the correlation between left IPS arithmetic activity and symbolic comparison should be interpreted with some caution. The results that survived this correction were also those for which the Bayes Factor analyses revealed very strong support for the alternate hypothesis ($BF > 10$). Thus, the Bayes Factor analyses converged with the frequentist analyses by revealing that those correlations which survived the correction for multiple comparison were also those which exhibited the strongest evidence in favor of the alternate hypothesis.

Control Analyses

In order to ensure that the reported correlations were not related to how the ROI was selected, we additionally conducted some control analyses using an anatomical ROI of the IPS (blue regions in Fig. 3). We extracted beta values from anatomical ROIs of the bilateral IPS provided by Brain Voyager (dilated sulci ROIs found in Brain Voyager Brain Tutor) and calculated the neural PSE and overall arithmetic activity in the same way described above. Brain activity was similarly correlated with the behavioral measures using this method. After correcting for age, VSWM was positively correlated with the neural PSE in right IPS $r(40) = 0.33$, $P = 0.036$ ($BF_{10} = 1.56$). Similarly, symbolic comparison and ordering were correlated with overall arithmetic activity in the right IPS $r(41) = -0.40$, $P = 0.009$ ($BF_{10} = 5.16$) and $r(41) = -0.34$, $P = 0.025$ ($BF_{10} = 2.59$), respectively. No other correlations were significant. These control analyses indicate that the patterns of findings are

relatively consistent, regardless of what kind of ROI is used, and provide additional evidence that the index of brain activity matters for brain-behavior correlations.

DISCUSSION

To date, the fMRI literature on the relationship between arithmetic and domain general and domain specific skills has been fragmented. Given that there is great overlap in the neural architecture supporting these abilities [Arsalidou and Taylor, 2011; Zago et al., 2008], particularly in the IPS, there is reason to believe that domain general and domain specific skills may both contribute to individual differences in brain activity within this region. The present study provides the first systematic examination into how individual differences in multiple domain general and domain specific abilities are related to the recruitment of the IPS during arithmetic problem solving. Importantly, we investigated this question in a group of children that are in the early elementary school years (Grades 2–4), and are still becoming fluent with arithmetic [Butterworth, 2005; Carr and Alexeev, 2011]. Variability in skills such as VSWM or basic number processing is likely to play a critical role in children’s arithmetic fluency during this developmental period. In this group of children we replicated previous behavioral literature demonstrating a relationship between arithmetic and children’s verbal and ordinal processing skills [LeFevre et al., 2010; Lyons et al., 2014; Lyons and Ansari, 2015; Vukovic and Lesaux, 2013]. Though we found that symbolic comparison skills were correlated with arithmetic fluency, they did not uniquely predict arithmetic fluency once other abilities were accounted for. We also extended previous research by demonstrating that the relationship between domain general skills, domain specific skills, and IPS activity during arithmetic is dependent on the neural index that is being assessed. In particular, we found that the neural PSE was only weakly related to VSWM abilities, but not domain-specific skills, whereas overall arithmetic activity was more associated with individual differences in symbolic number processing skills (i.e., symbolic comparison and ordering).

The above-reported results replicated previous behavioral literature by demonstrating a relationship between arithmetic and children’s verbal and ordinal processing skills [LeFevre et al., 2010; Lyons et al., 2014; Lyons and Ansari, 2015; Vukovic and Lesaux, 2013]. Though we

found that symbolic comparison abilities were correlated with arithmetic fluency, they did not uniquely predict variance once other abilities were accounted for. We also extended previous research by demonstrating that the index used to measure brain activity is associated with individual differences on different behavioral measures. In the present study we found that the neural PSE was weakly (and only at trend levels) related to domain general abilities such as VSWM, whereas overall arithmetic activity was more closely associated with individual differences in basic numerical competencies. These findings indicate that individual differences in symbolic processing skills play an important role in the variability within the right IPS. Importantly, by examining multiple domain general and domain specific measures within the same sample of children, we were also able to determine that symbolic skills explained more variability than other domain general skills such as VSWM, and domain specific skills such as nonsymbolic processing.

Our findings for the relationship between VSWM and the neural PSE were relatively weak, and were only evident at trend levels in the bilateral IPS or just below threshold in our anatomical ROI of the right IPS. Therefore, it is possible that the association between the neural PSE and VSWM is relatively small or non-existent. The PSE could reflect demands on computational resources because large problems are more computationally demanding than small problems (which is reflected in poorer accuracy and slower reaction times). Consequently, individual differences in domain general variables such as VSWM may modulate the neural PSE more than domain specific measures. However, we found relatively weak evidence for such a relationship. Though little research has specifically investigated the neural PSE and its association with domain general abilities, there has been some evidence that the bilateral IPS are both recruited for VSWM and arithmetic in adults [Zago et al., 2008]. Moreover, other research using brain-behavior correlations has provided evidence that children's VSWM abilities (measured behaviorally) are related to brain activity during arithmetic [Metcalfe et al., 2013]. In this study, the authors contrasted complex ($3 + 4 = 8$) problems with simple arithmetic problems ($3 + 1 = 4$; identical in format to the Plus 1 condition in the present study). In a whole-brain regression, VSWM abilities were related to greater neural activity during complex problems relative to simple Plus 1 problems in the bilateral IPS (in addition to a number of other frontal and inferior parietal brain regions). Other research has also demonstrated that children who recruit the left IPS more for VSWM have higher arithmetic scores 2 years later [Dumontheil and Klingberg, 2012]. Greater recruitment of the left IPS has also been related to larger VSWM capacities [Klingberg et al., 2002], therefore, children with higher VSWM abilities show greater modulation of the IPS which may in turn, be related to arithmetic proficiency. The role of VSWM in the IPS during arithmetic problem solving may be to modulate brain activity according to

cognitive and computational demands of the problem, and individuals with higher VSWM capacities can modulate these regions to a greater degree [Klingberg et al., 2002]. Our findings expand on this literature by providing evidence that the relationship between IPS activity during arithmetic and VSWM is relatively weak in comparison to symbolic number processing skills. Importantly, even though our results point to a weak association between VSWM and brain activity in the IPS during symbolic arithmetic, it does not mean that these brain regions are not engaged in domain general processing and perhaps we would have seen different relationships with other measures of VSWM.

The IPS has also been consistently implicated in basic numerical processing [Ansari, 2008; Franklin and Jonides, 2009; Holloway et al., 2010; Vogel et al., 2015]. We found evidence for a relationship between individual differences in basic number processing skills and overall arithmetic activity in the IPS. However, there was no such association between basic number processing skills and the neural PSE. It is possible that basic number processing skills are related to brain activity on both small and large problems, and any variance associated with basic number processing is therefore subtracted out when contrasting the two conditions in the neural PSE. This may especially be the case in children because they still rely on effortful calculation strategies for both small and large problems. This prediction was supported by the present findings. Specifically, when overall brain activity for both small and large arithmetic problems was considered, we found significant relationships between individual differences in symbolic comparison in the bilateral IPS and symbolic ordering in the right IPS. Therefore, children with better performance on the symbolic number processing tasks recruited the IPS to a greater degree when solving both small and large arithmetic problems. It is also noteworthy that average arithmetic activity for small and large problems was not related to VSWM skills, with Bayes factors suggesting that the null hypothesis was approximately five times more likely than the alternative hypothesis ($BF_{01\_RIPS} = 4.95$; $BF_{01\_LIPS} = 4.97$). Together, these findings indicate that individual differences in VSWM are weakly related to the neural PSE, whereas basic number processing skills explain more variance in IPS activation across all arithmetic problems studied. They also indicate that the neural correlates of arithmetic in the IPS are more strongly predicted by basic number processing than they are by VSWM.

Though no research has directly examined whether basic number processing skills and arithmetic have shared neural substrates in children, some adult literature has suggested that this is likely to be true. For example, one meta-analysis found qualitative similarities between basic number processing and arithmetic networks [Arsalidou and Taylor, 2011] and other work has found similarities in ordinal processing and arithmetic within the right IPS [Knops and Willmes, 2014]. The data presented in this study provides converging evidence to suggest that the

IPS does not just show overlap between basic number processing skills and arithmetic, but the recruitment of this region during arithmetic is also related to individual differences in basic number processing skills. Critically, the evidence for relationship between neural activity during basic arithmetic and basic number processing was strongest for symbolic comparison and ordering. There was no significant correlation between non-symbolic number comparison and arithmetic, and the Bayesian analysis revealed evidence in support of the null hypothesis.

For the first time we demonstrated that individual differences in children's basic numerical competencies are associated with the degree to which the IPS is activated during the solution of arithmetic problems. Greater activity in the bilateral IPS was related to higher symbolic comparison abilities, and the right IPS was additionally related to symbolic ordering abilities. Research with adults has found symbolic ordering and arithmetic have common neural substrates in the right IPS, and that spatial patterns of activation in this region are similar for the two tasks [Knops and Willmes, 2014]. Our findings are consistent with the idea that the right IPS plays an important role in linking ordinal processing and arithmetic. They also extend this literature by demonstrating that individual differences in children's symbolic ordering abilities are associated with brain activity in the right IPS during arithmetic. Our results are also similar to those of Bugden et al. [2012] who found that higher Math Fluency scores were associated with more mature neural signatures of symbolic number processing in the left IPS. Together, these studies indicate that the IPS may play an important role in mediating the relationship between symbolic number processing (comparison and ordering) and arithmetic.

It may be surprising that we did not find any relationship between nonsymbolic abilities and activity in the IPS during arithmetic, given that some literature has found associations between nonsymbolic comparison skills and arithmetic at both behavioral and neural levels of analysis [Chen and Li, 2014; Haist et al., 2014; Schneider et al., 2016]. Indeed, Bayesian analyses indicated that the null hypothesis was 5 times more likely than the alternative hypothesis ($BF_{01\_RIPS} = 4.92$; $BF_{01\_LIPS} = 5.32$). The relationship between arithmetic and symbolic comparison has been shown to be stronger and more consistent than with nonsymbolic comparison [De Smedt et al., 2013; Schneider et al., 2016]. Neuroimaging studies have also found that symbolic and nonsymbolic processing have qualitatively different representations in the IPS by using multivoxel pattern analyses [Bulthé et al., 2014; Lyons et al., 2015]. It is, therefore, possible that we did find not a relationship between arithmetic and nonsymbolic skills at the neural level because they have fewer shared cognitive processes than arithmetic does with symbolic skills. This is particularly notable because even though nearly all of the performance measures on the basic number processing tasks were correlated with one another (Table I), they did not all

predict brain activity similarly, indicating that these measures are likely reflective of different cognitive processes.

Another important consideration is that all of the brain-behavior correlations were positive relationships and illustrated that better behavioral performance was related to greater brain activity within the IPS. This may seem surprising because the opposite pattern of results could also be true; individuals with better number processing and arithmetic skills may rely on the IPS less and use other brain regions in the inferior parietal cortex more [e.g., Price et al., 2013; Zamarian et al., 2009]. However, the children in this study were still becoming fluent in arithmetic, which was demonstrated by the high proportion of procedural strategies on single-digit problems. It is possible that children tend to calculate, and those who have better numeracy skills may be relying on the IPS more effectively than poorer performing children. It is also possible that there may be positive relationships between behavioral performance and brain activity within the IPS in childhood, but this relationship may reverse in adulthood when individuals are relying on more efficient retrieval strategies and are recruiting the IPS less [Price et al., 2013].

It is also worth noting that the behavioral and neuroimaging results reported above are marked by some converging as well as divergent findings. For instance, though symbolic number processing skills were related to both behavioral and neural metrics, verbal abilities were not related to any of the neural indices within the IPS. This is likely related to the brain regions being investigated. The IPS has rarely been implicated in verbal fluency and other regions of the arithmetic network may be more tied to verbal processing. For example, developmental and training studies have provided evidence that as individuals become more familiar with arithmetic problems, they rely more on verbally mediated retrieval strategies (e.g., remembering the solution from memory), and this is associated with a shift in brain activity from the IPS to the angular or supramarginal gyri [Delazer, 2003; Ischebeck et al., 2006; Rivera et al., 2005; Zamarian et al., 2009]. Other work from structural brain imaging has demonstrated that a left inferior parietal white matter tract, the superior longitudinal fasciculus, was related to arithmetic operations that were more reliant on retrieval strategies (addition and multiplication) [van Beek et al., 2013]. This relationship disappeared once the authors controlled for phonological processing abilities, suggesting a close association between left inferior parietal structures, language-related abilities, and arithmetic skills. Therefore, it is not surprising that individual differences in the IPS were unrelated to verbal skills, because the association between verbal abilities and arithmetic is likely mediated by other brain structures.

LIMITATIONS AND FUTURE DIRECTIONS

The data in this study indicate that individual differences in symbolic number processing skills (and possibly

VSWM) relate to the recruitment of the IPS during arithmetic. However, it is important to acknowledge a few limitations. First, it was not possible to ascertain precisely which problems were solved using retrieval or calculation due to the nature of our fMRI design. The present study could not determine whether the relationship between arithmetic and domain general and domain specific abilities is dependent on the strategy that is being used. For instance, it is possible that basic number processing abilities may be more essential for trials that are calculated compared with those that are retrieved. Similarly, individual differences in VSWM capacity may be more related to brain activity on trials that required effortful calculation. Future research will need to examine strategies on a trial-by-trial basis to further disentangle these relationships.

Other research has also demonstrated that the domain specific and domain general predictors of arithmetic change over developmental time [Lyons et al., 2014; McKenzie et al., 2003; Raghubar et al., 2010; Rasmussen et al., 2007]. It is likely that these relationships are highly dynamic, and increase or decrease in strength over time. For example, as children develop fluent arithmetic skills by relying more on retrieval-based strategies, working memory demands may decrease. Individual differences in VSWM may then become less critical for arithmetic fluency and the neural response within the IPS. The same may also be true for basic number processing skills; as children rely on fewer quantity-based strategies the relationship between basic number processing skills and the neural response in the IPS may decline. Future research will need to examine how these relationships with the IPS change and whether they strengthen or weaken over time.

CONCLUSIONS

Previous research has suggested that the IPS may have multiple functions during the solution of arithmetic problems related to both domain general and domain specific processes. This study provides the first evidence to systematically examine how individual differences in multiple domain general and domain specific abilities predict the recruitment of the IPS during arithmetic. The results from the present study indicate that children's symbolic number processing skills are related to brain activity within the IPS, however, the relationships depend on the index of brain activity that is being measured. Symbolic number processing skills (comparison and ordering) were related to overall arithmetic activity regardless of problem size, whereas VSWM may be more related to the neural PSE in the bilateral IPS (albeit weakly so). This study provides evidence that the metric used to assess arithmetic activity can tap into different cognitive abilities. By simultaneously examining both domain general and domain specific measures, we were also able to demonstrate that symbolic number processing skills explain more variability in brain activity during arithmetic than other skills such as VSWM

and nonsymbolic number processing. Together, these findings provide a better understanding of the neural basis of arithmetic in children by exploring the domain general and domain specific predictors of brain activity within the IPS.

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