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5-1-2021

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### Citation of this paper:

Matejko, Anna A. and Ansari, Daniel, "Shared Neural Circuits for Visuospatial Working Memory and Arithmetic in Children and Adults" (2021). *Brain and Mind Institute Researchers' Publications*. 629. <https://ir.lib.uwo.ca/brainpub/629>



# Shared Neural Circuits for Visuospatial Working Memory and Arithmetic in Children and Adults

Anna A. Matejko<sup>1,2</sup> and Daniel Ansari<sup>2</sup>

## Abstract

■ Visuospatial working memory (VSWM) plays an important role in arithmetic problem solving, and the relationship between these two skills is thought to change over development. Even though neuroimaging studies have demonstrated that VSWM and arithmetic both recruit frontoparietal networks, inferences about common neural substrates have largely been made by comparisons across studies. Little work has examined how brain activation for VSWM and arithmetic converge within the same participants and whether there are age-related changes in the overlap of these neural networks. In this study, we examined how brain activity for VSWM and arithmetic overlap in 38 children

and 26 adults. Although both children and adults recruited the intraparietal sulcus (IPS) for VSWM and arithmetic, children showed more focal activation within the right IPS, whereas adults recruited the bilateral IPS, superior frontal sulcus/middle frontal gyrus, and right insula. A comparison of the two groups revealed that adults recruited a more left-lateralized network of frontoparietal regions for VSWM and arithmetic compared with children. Together, these findings suggest possible neurocognitive mechanisms underlying the strong relationship between VSWM and arithmetic and provide evidence that the association between VSWM and arithmetic networks changes with age. ■

## INTRODUCTION

Arithmetic is a complex skill that requires not only basic number knowledge but also the ability to remember and manipulate information. Working memory (the ability to hold and manipulate task-relevant information for brief periods of time) has been shown to be an important predictor of mathematical skills in both children and adults (for a review, see Menon, 2016; Raghubar, Barnes, & Hecht, 2010). Though working memory is found to correlate with a range of mathematical skills, there has been particular focus on how it relates to arithmetic (Peng, Namkung, Barnes, & Sun, 2016). Individual differences in working memory capacity are correlated with arithmetic proficiency (Dumontheil & Klingberg, 2012; Alloway & Passolunghi, 2011), and longitudinal studies have shown that working memory abilities predict later success in mathematics (Bull, Espy, & Wiebe, 2008). Working memory is thought to contribute to arithmetic by storing and processing intermediate steps involved in finding a solution to a problem (Peng et al., 2016). More difficult arithmetic problems that have multiple intermediary steps are thought to be more demanding of working memory resources (DeStefano & LeFevre, 2004). These problems also tend to be solved using calculation-based strategies as opposed to retrieval-based strategies (where the solution is recalled from memory). It has been argued that demands on working memory may be greater when children are learning new

mathematical skills or when children are doing more complex mathematical problems (Raghubar et al., 2010). Therefore, working memory may be an essential component of learning arithmetic and mathematical concepts at all stages of development.

Working memory is thought to be composed of multiple systems (for a review, see Baddeley, 2003), and many studies make distinctions between working memory for verbal or visuospatial information. Both visuospatial working memory (VSWM) and verbal working memory have been shown to predict mathematical abilities (Peng et al., 2016). However, their relative contributions may depend on the task and the age of the participants. Several studies, for instance, have demonstrated developmental changes in how arithmetic relates to these domains of working memory (Alloway & Passolunghi, 2011; Rasmussen & Bisanz, 2005). Younger children have been found to predominantly rely on VSWM to solve arithmetic problems (McKenzie, Bull, & Gray, 2003; Rasmussen & Bisanz, 2005), whereas older children and adults use both verbal working memory and VSWM (Clearman, Klinger, & Szűcs, 2017; McKenzie et al., 2003). These age-related changes may be related to the kinds of strategies children are using to solve the problems and how familiar they are with the procedures and concepts. The importance of VSWM in the development of arithmetic has also been highlighted in literature examining children with math learning disabilities (developmental dyscalculia). Children with developmental dyscalculia have marked impairments in VSWM and visuospatial short-term memory (Mammarella, Caviola, Giofrè, & Szűcs, 2018; Szucs, Devine, Soltesz, Nobes, & Gabriel, 2013), which

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may be even more significant than their impairments in magnitude processing skills (Szucs et al., 2013). The aforementioned behavioral literature has suggested a strong relationship between VSWM and arithmetic. It is possible that the established behavioral relationship between VSWM and arithmetic could be a product of overlapping neural networks underlying these abilities. Neuroimaging can therefore provide additional evidence to elucidate the neural mechanisms underlying the relationship between VSWM and arithmetic. Little work, however, has detailed the neurocognitive processes by which VSWM and arithmetic interact in adults and children and whether there are age-related changes in the underlying neural networks.

Numerous investigations have examined the neural basis of calculation and have revealed a bilateral frontoparietal network of brain regions that are commonly activated during arithmetic tasks (for a meta-analysis, see Arsalidou & Taylor, 2011). Activation in the frontal cortex, particularly in the bilateral middle and inferior frontal gyri (IFG), as well as in the left superior frontal gyrus (SFG), is thought to reflect more domain-general factors such as working memory (Metcalf, Ashkenazi, Rosenberg-Lee, & Menon, 2013; Arsalidou & Taylor, 2011; Ischebeck et al., 2006; Delazer et al., 2005). Task difficulty has been shown to increase the engagement of the inferior frontal cortex, whereas calculation-specific skills engage the inferior parietal cortex, particularly in the intraparietal sulcus (IPS) and the angular and supramarginal gyri (Kong et al., 2005; Menon, Mackenzie, Rivera, & Reiss, 2002; Gruber, Indefrey, Steinmetz, & Kleinschmidt, 2001; Menon, Rivera, White, Glover, & Reiss, 2000). Like arithmetic, VSWM has also been shown to recruit a remarkably similar frontoparietal network that includes superior frontal regions as well as the IPS (Klingberg, 2006). This network shows increases in activation with age, and activity within the left superior frontal sulcus (SFS) and IPS has been shown to correlate with VSWM capacity (Klingberg, Forssberg, & Westerberg, 2002). Because both arithmetic and VSWM rely on a frontoparietal network of brain regions, there may be considerable overlap in the neural circuitry that underlies these abilities. Yet, VSWM and arithmetic are rarely studied in the same sample of participants; therefore, any inferences about the common neural substrates are largely inferred by comparing across studies. Determining how these networks interact is important for understanding arithmetic development; the development of arithmetic skills are likely a product of interactions within and between large-scale networks subserving multiple cognitive processes (Fias, Menon, & Szucs, 2013; Bressler & Menon, 2010).

Though many studies have separately investigated the brain networks involved in these abilities, little research has simultaneously examined the VSWM and arithmetic networks in the same sample of participants. To our knowledge, only one study to date has directly investigated the distinct and overlapping networks for VSWM and arithmetic. Zago et al. (2008) demonstrated that VSWM and arithmetic were characterized by overlapping activation in the

bilateral IPS, right middle frontal gyrus (MFG)/SFS, left supramarginal gyrus, and right superior parietal lobule in a sample of adults. Because working memory may be particularly important when children are learning arithmetic skills for the first time (and are using time-intensive calculation strategies), using a developmental approach to understand how VSWM and arithmetic neural networks relate to one another could provide additional insights into their relationship. However, to date only indirect evidence has been provided to suggest a relationship between VSWM and arithmetic at the neural level in children; Dumontheil and Klingberg (2012) demonstrated that activation in the left, but not right, IPS for a VSWM task significantly predicted individual differences in future arithmetic performance. Individual differences in activation within frontal and parietal regions during an arithmetic task have also been found to correlate with behavioral measures of VSWM in typically developing children (Demir, Prado, & Booth, 2014; Ashkenazi, Rosenberg-Lee, Metcalfe, Swigart, & Menon, 2013; Metcalfe et al., 2013). These findings suggest that individual differences in children's VSWM capacities can modulate the neural basis of arithmetic. Children with math learning disabilities also seem to recruit VSWM resources differently than typically developing children. In the same regions that typically developing children show correlations between VSWM capacity and brain activity during arithmetic problem solving, children with math learning disabilities fail to show such a relationship (Ashkenazi et al., 2013). Children with dyscalculia also do not engage the right IPS to the same degree as typically developing children during a nonnumerical VSWM task (Rotzer et al., 2009). These findings suggest there is a strong relationship between VSWM and arithmetic and that children with math learning disabilities do not appropriately use VSWM resources. However, such data do not imply that VSWM and arithmetic share an underlying neuronal basis. To ascertain this, one needs to study the neural correlates of VSWM and arithmetic concurrently.

This study aims to expand on the above-mentioned literature by examining whether there are common underlying neural substrates for VSWM and arithmetic in children and adults. Our sample of school-aged children (Grades 2–4) was specifically selected to capture a developmental period where children are learning and becoming more fluent with arithmetic facts (Ashcraft, 1982). We identified VSWM and arithmetic networks in the same sample of participants to identify how they overlap. Given the large body of literature that has independently identified frontoparietal networks for VSWM and arithmetic (e.g., Arsalidou & Taylor, 2011; Klingberg, 2006), we predicted overlap in superior frontal regions and the IPS. Because research has demonstrated that the association between VSWM and arithmetic changes with age, we also examined whether there are age-related changes in the regions subserving arithmetic and VSWM. Given the research that has shown a developmental shift in the role of VSWM to verbal working memory in arithmetic problem solving (Rasmussen & Bisanz, 2005; McKenzie

et al., 2003), it is possible that the networks involved in VSWM and arithmetic may become less associated over time or their anatomical localization could shift. Literature examining the developmental changes in the localization of numerical processing and arithmetic has suggested that there is a shift toward more left-lateralized activation within the parietal cortex (Vogel, Goffin, & Ansari, 2015; Emerson & Cantlon, 2014; Rivera, Reiss, Eckert, & Menon, 2005). On the other hand, the bilateral dorsolateral prefrontal, superior frontal, and parietal cortex show age-related increases for VSWM (Klingberg, 2006; Klingberg et al., 2002; Kwon, Reiss, & Menon, 2002). Therefore, there may be a shift from right or bilateral activation for VSWM and arithmetic in children to greater left-lateralized activation in adults because of the left lateralization of arithmetic and number processing. Characterizing how these networks overlap and change with age will further elucidate the neurocognitive mechanisms by which VSWM and arithmetic interact with one another.

## METHODS

### Participants

Twenty-six adults and 59 typically developing children were recruited to participate in this fMRI experiment. Two of the children did not complete the MRI session, and eight children were removed from analyses because of head motion that exceeded 1.5 mm between volumes or more than 3 mm over the entire scan. Ten additional children were removed because of poor accuracy on the fMRI tasks (less than 50% total accuracy on either of the fMRI tasks), and one was removed because of a neural abnormality. No adults were excluded from the analysis. The final sample of participants included 26 adults (12 women, all right-handed) and 38 children (17 girls, 2 left-handed). Adults were undergraduate and graduate students between ages 19.5 and 26.3 years ( $M = 22.2$  years), and children were between ages 7.7 and 10.4 years ( $M = 9.2$  years). All participants 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 all methods and procedures in this study, and participants were reimbursed for their participation. All participants (or children's caregivers) gave informed consent. The participants included in this study partly overlap with those reported in Matejko and Ansari (2017, 2019) and Matejko, Hutchison, and Ansari (2019); however, these publications had different aims or tasks from this study.

### Procedure

For this study, participants completed two testing sessions. In the first session, a battery of behavioral measures were collected, and children also completed a mock scanning session to familiarize them with the MRI environment (i.e., practice staying still while doing a short arithmetic

task in the mock scanner). Between 1 and 9 weeks after the first session ( $M = 15.3$  days), participants returned for the second session to complete the MRI. During the MRI, participants completed arithmetic and VSWM tasks. Children also completed an additional two to three tasks in the scanner, and adults completed an additional four tasks that are not discussed further here. To control for possible task order effects, the task presentation order was counterbalanced using a Latin square design.

## Experimental Tasks and Design

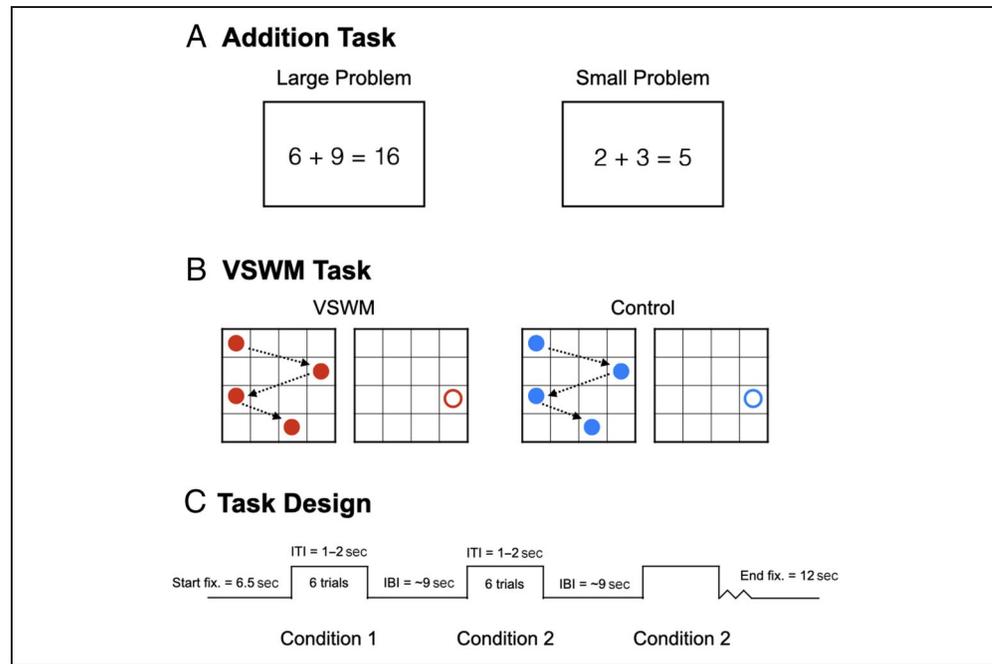
### Arithmetic Task

To isolate brain networks involved in arithmetic, participants completed two runs of a single-digit arithmetic verification task. Participants were presented with an addition problem with two addends and a solution and were asked to determine if the solution was correct or incorrect. The arithmetic task had three conditions: (1) large problems, (2) small problems, and (3) plus 1 problems. For the purposes of this study, only the small and large problem conditions were used (analyses discussed below), and the plus 1 condition is not discussed further. Large problems had a solution that was greater than 10, whereas small problems had a solution that was less than or equal to 10 (Figure 1A). Tie problems (e.g.,  $2 + 2$ ) and problems containing a zero (e.g.,  $3 + 0$ ) were not included in the arithmetic task. In half of the trials, the solution presented was correct, and in the other half of trials, the solution was incorrect. In trials where the solution was incorrect, the solution presented was +1 or +2 above the correct solution. Each run had 36 unique problems (12 problems per condition), resulting in 72 trials across both runs. The larger number was presented on the left side in half of the trials ( $4 + 2$ ) and on the right in the other half of the trials ( $2 + 4$ ); if the larger number was presented on the right in Run 1, it was presented on the left in the second run (e.g., Run 1 [ $2 + 4$ ], Run 2 [ $4 + 2$ ]). All adults and most children had above chance performance and good motion on the two arithmetic runs (30/38 children had two usable arithmetic runs). If a child did not pass our selection criteria for either motion or accuracy on one of the runs, it was excluded from the analysis, and the other run was included.

### Visuospatial Working Memory Task

To isolate networks involved in VSWM, we adapted a dot matrix task from Klingberg et al. (2002).<sup>1</sup> This task was specifically selected because it does not include any symbolic numbers (for an example of a VSWM task that uses symbolic numbers, see Dumontheil & Klingberg, 2012). Therefore, any overlap in the arithmetic and VSWM networks cannot be attributed to the processing of symbolic numbers. The VSWM task consisted of a VSWM condition and a control condition. In the VSWM condition, the participant was instructed to remember which squares the

**Figure 1.** Tasks performed during the scanning session. (A) Examples of the large and small problem conditions in the arithmetic verification task. Participants were asked to identify if the solution was correct or incorrect. (B) Examples of the VSWM condition and the control condition. Participants were instructed to remember the spatial locations in the VSWM condition and identify if the target was in the same spatial location as one of the previous dots. The control condition was identical, except that the participants did not need to remember the spatial locations of the dots and responded to the target stimulus in the same way regardless of where it was located. (C) Schematic of the timing in the block design for both tasks.



red dots passed through in a  $4 \times 4$  grid (Figure 1B). Once the target stimulus was presented (an empty red circle), the participant was asked to identify if this was where one of the previous dots had appeared. On half the trials, the dot was in a correct location that corresponded to one of the dots in the prior sequence, and on the other half of the trials, the dot was in an incorrect location. If the target was presented in an incorrect location, it was presented in a square adjacent to a potentially correct solution. Either two or four dots were presented, with six trials for each load. For all analyses, we collapsed across both loads resulting in 12 trials for the working memory condition. The control condition was identical to the VSWM condition, except that the dots were blue, and participants were instructed to watch the dots and did not need to remember their locations. When the target stimulus appeared (an empty blue circle), the participants always responded with their index finger regardless of where the circle was located. Consequently, the VSWM condition and the control condition were identical in the stimulus presentation, except that participants were instructed to remember the spatial locations in the VSWM condition and to watch the dots and wait for the target in the control condition. The control condition also had two or four dots, which we collapsed across in the analyses, resulting in 12 trials in total for the control condition (six trials for each load).

### Task Design

Both arithmetic and VSWM tasks were presented using a block design with an initial fixation of 6500 msec and an end fixation of 12,000 msec (Figure 1C). Each block consisted of six trials, and the duration of each trial and the number of blocks per run depended on the task. For both

tasks, the intertrial interval was 1500 msec on average (duration: 1000, 1500, and 2000 msec), and the interblock interval was 9 sec on average. Each trial within a block was randomly presented, and the condition order (i.e., block order) was also random.

For the arithmetic task, each problem was presented for 4500 msec, and responses were also recorded during the subsequent intertrial interval. For the working memory task, the duration of the trial depended on the load. Each dot was presented for 500 msec, followed by a blank grid of 500 msec. After all dots had been presented, a wait screen appeared for 1500 msec, followed by the target screen, which appeared for 1500 msec. The trial duration for a two-dot trial was therefore 5000 msec, whereas a four-dot trial was 7000 msec.

### MRI Data Acquisition

MRI data were collected using a 3T Siemens Prisma Fit whole-body scanner, with a 32-channel receive-only head-coil (Siemens). fMRI data were acquired during the arithmetic and VSWM tasks using a T2\* weighted single-shot gradient echo-planar sequence using the following parameters: repetition time = 2000 msec, echo time = 30 msec, field of view =  $210 \times 210$  mm, matrix size =  $70 \times 70$ , flip angle =  $78^\circ$ . Thirty-five slices were obtained in an interleaved ascending order, with an in-plane resolution of  $3 \times 3$  mm, 3 mm slice thickness, and 0.75 mm gap. There were two runs of the arithmetic task with 144 volumes and one run of the VSWM task with 117 volumes. 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 an in-plane resolution of  $256 \times 256$  pixels (repetition time = 2300 msec, echo time =

2.98 msec, inversion time = 900 msec, flip angle = 9°). The MPRAGE scan duration was 5 min 21 sec. Foam padding was used around the head to reduce motion. The total scan duration for all functional and anatomical data was approximately 40 min for children and 1.5 hr for adults. In each scanning session, additional number processing tasks were obtained that are not discussed here; however, task order was counterbalanced across participants to control for possible task order effects. These tasks are discussed in other articles (Matejko & Ansari, 2019; Matejko et al., 2019), and only the VSWM task and arithmetic tasks are analyzed in this study.

## Analyses

Brain Voyager QX 2.8.4 (Brain Innovation) was used to preprocess and analyze the fMRI data. Functional data were corrected for differences in slice-time acquisition, head motion, linear trends, and low-frequency noise. Functional images were coregistered to each participant's T1 weighted anatomical image and normalized to Talairach Space (Talairach & Tournoux, 1988) and then spatially smoothed with a 6-mm FWHM Gaussian smoothing kernel. Though using an adult template to spatially normalize pediatric populations can lead to systematic differences in anatomy and anatomical variability in children, such methods do not result in spurious findings when comparing fMRI data across groups (Burgund et al., 2002). A 2-gamma hemodynamic response function was used to model the expected BOLD signal for each trial in each condition (arithmetic task: large problems and small problem conditions, which are discussed in this study, as well as plus 1 problems, which are not discussed in this study; VSWM task: VSWM condition, control condition). A random-effects general linear model was then performed on the data. Whole-brain analyses were first thresholded at a voxelwise  $p$  value of .005, uncorrected, and then corrected for multiple comparisons using the Monte Carlo simulation procedure to determine a minimum cluster threshold (Goebel, Esposito, & Formisano, 2006), resulting in an overall  $\alpha < .05$ . This method of cluster thresholding estimates and accounts for spatial smoothness and spatial correlations within the data (see Forman et al., 1995, for more details).

First, we separately investigated arithmetic and VSWM networks in adults and children. We isolated regions associated with calculation using the neural problem size effect (Large problems > Small problems). This comparison has been used by numerous studies to identify regions involved in calculation (e.g., De Smedt, Holloway, & Ansari, 2010; Grabner et al., 2007; Stanescu-Cosson et al., 2000). Investigating the problem size effect is particularly important in relation to VSWM because large problems are more likely to rely on VSWM resources (DeStefano & LeFevre, 2004). To identify regions recruited for VSWM, we compared the VSWM condition to its control condition (VSWM > Control), which is a contrast that has commonly been used in previous research (e.g., Dumontheil & Klingberg, 2012;

Klingberg et al., 2002). To investigate regions that are common to both tasks, we conducted a conjunction of random effects analysis between the arithmetic and VSWM tasks [(Large problems > Small problems)  $\cap$  (VSWM > Control)] (Note that Brain Voyager software uses methods recommended by Nichols, Brett, Andersson, Wager, & Poline, 2005, for conjunction analyses). To determine how the overlapping networks for arithmetic and VSWM differ between adults and children, a fixed effects general linear model was conducted for each participant, and individual conjunction maps were calculated. These individual conjunction maps were then combined into two group-average maps, one for adults and one for children. A random-effects  $t$ -test comparison determined differences in the conjunction between the two groups.

## RESULTS

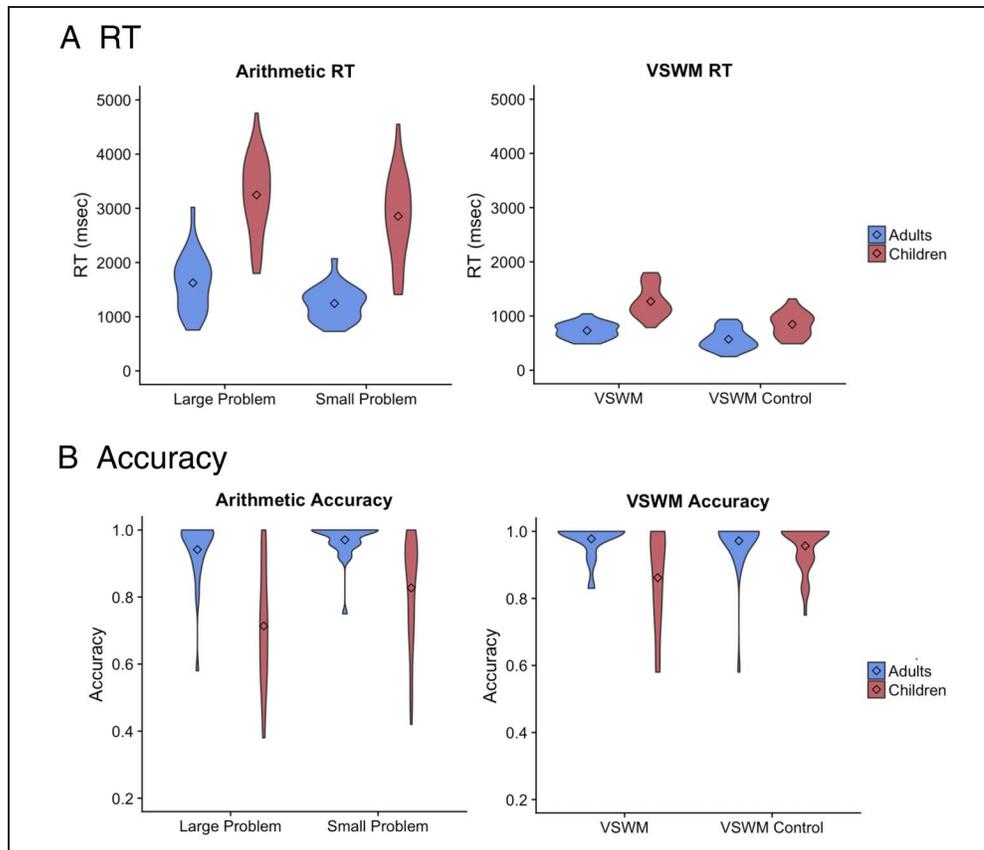
### Behavioral Performance

Two separate mixed-design ANOVAs were conducted on RT and accuracy data, with Task (arithmetic, VSWM) and Condition (large/small problems, VSWM/VSWM control) as within-subject factors and Group (children, adults) as a between-subject factor (see Figure 2 for RT and accuracy data).

The  $2 \times 2 \times 2$  mixed ANOVA with RT as the dependent variable revealed a main effect of Group, where adults were significantly faster than children,  $F(1, 62) = 125.0, p < .001$ , and a main effect of Task, indicating that participants were significantly faster on the VSWM task  $F(1, 62) = 443.8, p < .001$ . This analysis also revealed a main effect of Condition, where participants were slower on the large arithmetic problems and VSWM problems compared with the small arithmetic problems and VSWM control problems,  $F(1, 62) = 155.4, p < .001$ . We found an interaction of Task  $\times$  Group,  $F(1, 62) = 84.2 < .001$ , suggesting that while both adults and children had longer RTs on arithmetic problems compared with VSWM problems, children had greater differences in RT between the arithmetic and VSWM tasks than adults,  $t(60.8) = 10.1, p < .001$ . We also observed an interaction of Condition  $\times$  Group,  $F(1, 62) = 6.43, p = .014$ , where the differences between conditions (large problems vs. small problems, and VSWM vs. VSWM control) were greater in children than in adults,  $t(62) = 2.5, p = .014$ . Finally, the mixed ANOVA also revealed a Task  $\times$  Condition  $\times$  Group interaction,  $F(1, 62) = 4.13, p = .046$ . Post hoc analyses revealed that the magnitude of the difference between the VSWM and control conditions was greater for children than for adults,  $t(62) = 5.3, p < .001$ , but the difference between the large and small arithmetic problems was equivalent across groups,  $t(62) = 0.12, p = .896$ .

The  $2 \times 2 \times 2$  mixed ANOVA with accuracy as the dependent variable revealed a similar pattern of findings. There was a main effect of Group, with adults performing better on the tasks than children,  $F(1, 62) = 8090.1, p < .001$ ; a

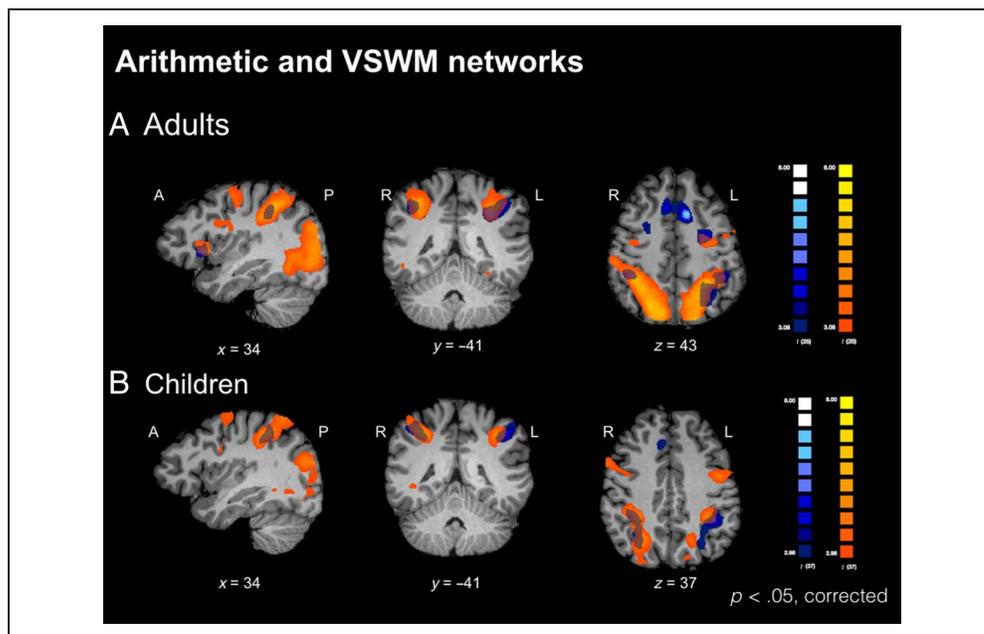
**Figure 2.** (A) RT and (B) accuracy on the arithmetic and VSWM tasks between adults and children.



main effect of Task that showed participants were more accurate on the VSWM task than the arithmetic task,  $F(1, 62) = 26.2, p < .001$ ; and a main effect of Condition, where participants were less accurate on the large arithmetic problems and VSWM problems,  $F(1, 62) = 18.1, p < .001$ . We also found an interaction of Task  $\times$  Group,  $F(1, 62) = 15.2, p < .001$ , where children performed

better on the VSWM task than the arithmetic task,  $t(37) = 6.0, p < .001$ ; however, adults showed no significant differences in performance between the two tasks,  $t(25) = 1.2, p = .24$ . We also observed an interaction of Group  $\times$  Condition,  $F(1, 62) = 11.7, p < .001$ , with post hoc tests revealing that children showed significant differences in the conditions for both tasks,  $t(37) = -5.1, p < .001$ ;

**Figure 3.** Statistical maps illustrating networks for arithmetic and VSWM in (A) adults and (B) children. The arithmetic network (Large > Small problems) is displayed in cold colors, and the VSWM network (VSWM > Control) is shown in hot colors.



**Table 1.** Anatomical Regions, Talairach Coordinates (Center of Gravity Reported), Mean *t* Scores, and Number of Voxels for Each Cluster in Comparisons of Interest

<i>Anatomical Region</i>	<i>TAL Coordinates (x, y, z)</i>			<i>Mean t Score</i>	<i>Number of Voxels</i>
<i>Adults: Large Problems &gt; Small Problems</i>					
R IPS/postcentral sulcus	36.83	-37.52	38.14	3.69	1419
R insula	28.54	21.59	6.52	4.11	2081
R MFG	23.81	-2.82	42.02	3.40	1430
Bilateral SFG	-4.58	14.04	44.12	3.82	3630
Cerebellum	1.18	-68.29	-24.51	3.49	1432
L lingual gyrus	-8.54	-80.11	0.50	3.44	1449
L IPS	-31.06	-48.11	37.16	3.87	7844
L lingual gyrus/cerebellum	-31.28	-58.94	-26.42	3.78	2219
L MFG/IFG	-30.19	-3.19	42.65	3.65	4413
L IFG	-40.45	34.49	20.77	3.56	2781
<i>Adults: VSWM &gt; Control</i>					
Bilateral IPS/SPL/IPL/inferior, superior, middle occipital gyri	0.06	-60.76	21.97	4.21	109562
R IFG	38.99	1.22	25.76	3.31	1485
R MFG/precentral gyrus	26.52	-7.78	54.14	3.92	6536
R insula	29.48	18.08	7.39	3.95	2074
L MFG/precentral gyrus/SFG	-29.57	-6.48	46.74	3.95	11469
<i>Adults: Conjunction [(Large problems &gt; Small problems) ∩ (VSWM &gt; Control)]</i>					
R IPS/superior parietal lobule	36.91	-37.32	38.31	3.62	1292
R insula	30.00	19.64	6.28	3.77	1115
L IPS	-30.47	-45.83	37.93	3.54	4592
L SFS/MFG	-26.98	-6.10	50.42	3.53	1307
<i>Children: Large Problems &gt; Small Problems</i>					
R IPS	32.36	-47.17	41.38	3.20	3104
R insula	27.67	19.84	8.58	3.36	1232
Bilateral SFG	-1.91	19.93	44.11	3.27	1885
L IPS	-39.43	-47.05	41.85	3.28	4252
<i>Children: VSWM &gt; Control</i>					
R IPS/SPL/IPL/superior, middle, inferior occipital gyri	27.85	-60.82	30.94	3.83	35343
R precentral gyrus/IFG	45.73	4.22	30.09	3.42	2920
R SFS/MFG	26.05	-5.50	54.04	3.58	3964
Bilateral lingual gyrus	4.40	-67.06	-17.72	3.21	1880
R thalamus	12.73	-18.06	11.00	3.47	1797

**Table 1.** (continued)

Anatomical Region	TAL Coordinates (x, y, z)			Mean t Score	Number of Voxels
L MFG/precentral gyrus/SFG/SFS	-18.27	-4.71	48.15	3.74	5405
L IPS/SPL/IPL	-22.00	-58.12	43.60	3.75	15454
L thalamus	-18.38	-27.22	9.42	3.62	1217
L middle occipital gyrus	-32.34	-77.54	3.91	3.18	2039
L precentral sulcus/precentral gyrus	-44.96	-3.15	33.42	3.42	2165
L inferior occipital gyrus	-43.92	-62.15	-3.67	3.30	2152
<i>Children: Conjunction [(Large problems &gt; Small problems) ∩ (VSWM &gt; Control)]</i>					
R IPS	31.5	-47.47	41.09	3.20	2722
<i>Age-related changes in the conjunction of arithmetic and VSWM: Adults–Children</i>					
R anterior middle temporal gyrus/supramarginal gyrus	62.54	-31.99	13.31	-3.20	673
R posterior middle temporal gyrus/supramarginal gyrus	49.35	-54.45	18.04	-3.10	602
R inferior occipital gyrus	35.69	-75.86	-5.78	3.27	1666
Cerebellum	0.22	-65.21	-30.23	3.24	914
L anterior IPS	-23.55	-46.30	35.18	3.16	580
L posterior IPS/IPL	-24.83	-69.36	24.01	3.48	1846
L inferior occipital gyrus	-36.70	-76.36	-9.44	3.10	1255
L SFS/MFG	-26.71	-8.02	47.61	3.28	584

Cluster size is reported in  $1 \times 1 \times 1$  mm voxel size resolution. L = left; R = right.

however, adults performed equally well in both conditions,  $t(25) = -0.835$ ,  $p = .44$ . We did not find a Task  $\times$  Condition  $\times$  Group interaction.

## Brain Imaging

### Adults

To isolate regions involved in calculation, we contrasted large problems with small problems (Large problems > Small problems). This revealed a largely frontoparietal network that included regions such as the bilateral IPS, SFG, MFG, left IFG, and right insula (see regions in cold colors in Figure 3A and Table 1). Similarly, a frontoparietal network was also identified when comparing the VSWM task to its control (VSWM > Control; see regions in hot colors in Figure 3A and Table 1). This included regions such as the bilateral IPS, superior and inferior parietal lobules (SPL/IPL), MFG, precentral gyri, right insula, and left SFG. We superimposed these networks in Figure 3A, which illustrates considerable overlap including the bilateral IPS, left MFG, and postcentral gyrus, and left insula.

To statistically examine whether VSWM and arithmetic activate the same brain regions, we conducted a conjunction analysis with the two contrasts used to identify the VSWM and arithmetic networks [(Large problems > Small problems)  $\cap$  (VSWM > Control)]. Adult participants showed activation for both arithmetic and VSWM in the bilateral IPS, right SPL, right insula, left MFG, and SFS (see Figure 4A and Table 1).

### Children

The arithmetic network (identified by the Large problems > Small problems contrast) also consisted of frontoparietal regions in children. This included the bilateral IPS, SFG, and right insula (see cold colors in Figure 3B and Table 1 for a full list of regions). The VSWM task (VSWM > Control) elicited activation in a similar set of regions. This network was composed of regions that included the bilateral IPS, SPL, IPL, MFG, precentral sulci, SFS, right IFG, and regions within the occipital cortex (see hot colors in Figure 3B and Table 1 for a full list of regions).

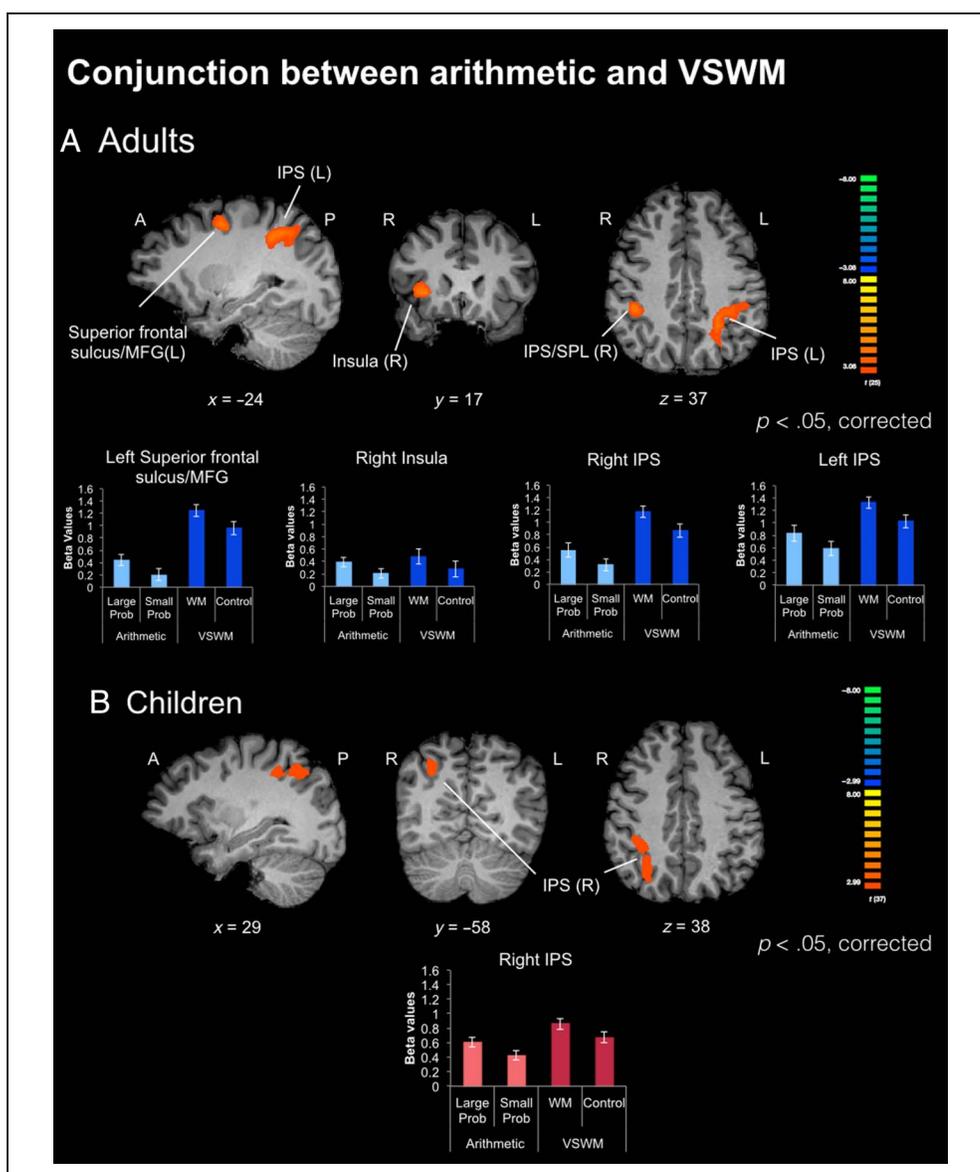
Similar to the adults, children had considerable overlap in their arithmetic and VSWM networks. We also conducted a conjunction analysis to statistically examine whether the VSWM and arithmetic tasks activated the same neuroanatomical regions [(Large problems > Small problems)  $\cap$  (VSWM > Control)]. Only the right IPS was found to be active for both VSWM and arithmetic tasks in children (see Figure 4B and Table 1).

### Age-related Changes

Both arithmetic and VSWM tasks were found to rely on frontoparietal networks in adults and children. However, the conjunction analyses (conducted separately in each group) suggested that there might be relative differences in the regions that children and adults recruit. In adults, for instance, a number of regions were coactivated for

VSWM and arithmetic, whereas children only showed coactivation in the right IPS. To further investigate these age-related changes, we tested whether there were group differences in the conjunction between the arithmetic and VSWM tasks. The group comparison of the conjunctions revealed that adults recruited the left IPS, IPL, MFG, SFS, and bilateral middle occipital gyri for arithmetic and VSWM to a greater degree than children. In contrast, children recruited the right middle temporal and supramarginal gyri more than adults (see Figure 5 and Table 1 for a list of regions and beta values). An examination of the beta values from this region (Figure 5B) revealed that the age-related changes were driven by relatively less deactivation in this region for children. These findings indicate that, though both adults and children recruit similar networks for arithmetic and VSWM, there are age-related changes in the engagement of these regions.

**Figure 4.** Statistical maps illustrating the conjunction between arithmetic and VSWM in (A) adults and (B) children. Also shown are beta values corresponding to each statistically significant cluster of activation where clusters extracted from adults are shown in blue and clusters extracted from children are shown in red.





2011), the literature to date has largely investigated the VSWM and arithmetic networks in isolation of one another. Research has also independently examined how these networks change with age (Rivera et al., 2005; Klingberg et al., 2002). However, the literature is limited in two major ways. First, no research to date has studied how VSWM and arithmetic networks overlap in children. Investigating this relationship in children is critical because VSWM could be particularly important while children are learning arithmetic skills and are using time-intensive calculation strategies that may be more demanding of VSWM (Raghubar et al., 2010). Specifically, it has been thought that VSWM is needed during arithmetic to store and manipulate visual information in the visuospatial sketchpad while generating a solution, and this may be especially important during visually presented arithmetic problems (Raghubar et al., 2010). In contrast, VSWM may be less critical in adults who are more likely to solve arithmetic problems by retrieving the solution from memory (Barrouillet & Fayol, 1998), which does not require the storage and manipulation of numerical or visual information. Second, research has not yet examined whether there are age-related changes in these overlapping networks. This study aimed to address these outstanding questions by examining the VSWM and arithmetic networks in both children and adults. We provide evidence that VSWM and arithmetic are associated with fMRI activation within some of the same regions. Importantly, we also revealed that there are age-related changes in these shared circuits.

We demonstrated that adults recruit a bilateral frontoparietal network for both VSWM and arithmetic that included the bilateral IPS, right SPL, left MFG/SFS, and right insula. This is consistent with previous literature that has shown significant overlap in the IPS, as well as superior parietal and frontal regions for visuospatial tasks and arithmetic problem solving (Hawes, Sokolowski, Ononye, & Ansari, 2019; Zago et al., 2008; Zago & Tzourio-Mazoyer, 2002). As opposed to simply superimposing the VSWM and arithmetic networks, which was the case in many of the previous studies with adults, our analyses provide a more stringent test of the common underlying circuits by using conjunction analyses to identify regions that show significant activation for both VSWM and arithmetic. These findings also suggest that VSWM and arithmetic networks overlap in adults, even though they were solving single-digit addition problems that are likely less demanding of VSWM resources. Despite the fact that adults were given simple arithmetic and VSWM tasks, these findings are consistent with those from Zago et al. (2008), who used significantly more difficult tasks.

We also provide novel evidence that demonstrates how the VSWM and arithmetic networks overlap in children. Though arithmetic and working memory have been found to be correlated in children and adults, working memory may be particularly critical while children are using cognitively demanding strategies to solve arithmetic problems (Raghubar et al., 2010). Consequently, it is important to investigate how these networks relate to one another in

children. Our findings indicate that the only region to demonstrate overlapping activation for the two tasks was the right IPS. This is consistent with other developmental literature that shows individual differences in VSWM performance are correlated with greater activation in the right IPS during the solution of arithmetic problems (Demir et al., 2014; Metcalfe et al., 2013). However, these data go beyond such correlational evidence by showing that children recruit the same brain region for both VSWM and arithmetic. Adults also demonstrated overlap between VSWM and arithmetic in the right IPS, suggesting that the right IPS may exhibit age-invariant activity for both VSWM and arithmetic. The findings in this study are also noteworthy because some of the previous research examining the relationship between VSWM and arithmetic has used a task with symbolic numbers to identify brain regions involved in VSWM (Dumontheil & Klingberg, 2012). It was therefore unclear from this work whether VSWM processes or symbolic number processing within the IPS were related to individual differences in arithmetic. Our results suggest an association between VSWM and arithmetic within the IPS, even though our VSWM task did not include any numerical processing.

Overlapping neural substrates for VSWM and arithmetic in children and adults may be related to the need to store and manipulate visuospatial information when calculating arithmetic problems. Specifically, the IPS is thought to be involved in shifts in spatial attention as well as spatial mental imagery (Hawes et al., 2019; Silk, Bellgrove, Wrafter, Mattingley, & Cunnington, 2010). Thus, overlapping activation within this region could be related to shared demands for these processes during both VSWM and arithmetic tasks. An alternative account is that VSWM and arithmetic may be related to each other through ordinal processing (Attout, Noël, & Majerus, 2014). Ordinal processing skills have not only been found to be related to working memory (Attout, Noël, et al., 2014; Lyons & Beilock, 2009), but also to arithmetic ability (Lyons & Ansari, 2015; Attout, Noël, et al., 2014; Lyons, Price, Vaessen, Blomert, & Ansari, 2014). These processes also rely on similar neural substrates, where ordering tasks have been found to recruit the IPS (Matejko et al., 2019), and the IPS may serve as an important locus for both ordinal processing and short-term memory (Attout, Fias, Salmon, & Majerus, 2014; Majerus et al., 2006). These behavioral and neuroimaging findings indicate that serial ordering abilities (which are likely important in the VSWM task administered in this study) may play an important role in mediating the relationship between VSWM and arithmetic. However, future work will need to explore the precise mechanisms linking VSWM, ordering, and arithmetic skills.

### **Age-related Changes in the Parietal Cortex for VSWM and Arithmetic**

Our findings also demonstrate that there are age-related changes in the brain regions correlated with both VSWM and arithmetic. We found that a number of regions were

more active in adults than in children for the conjunction of VSWM and arithmetic. This included the left IPS, IPL, MFG/precentral sulcus, bilateral inferior occipital gyrus, and cerebellum. Furthermore, children showed greater activation than adults in the right middle temporal and supramarginal gyri for the conjunction between VSWM and arithmetic. These findings indicate that the VSWM and arithmetic undergo developmental changes together and become relatively more left-lateralized in adults.

A particularly notable finding is that the left IPS showed age-related increases in activation for VSWM and arithmetic whereas the right IPS was related to both tasks in adults in children. The left IPS may thus be undergoing more protracted developmental changes compared with the right IPS. Literature examining longitudinal changes in the IPS in response to numbers is consistent with this finding; the right IPS has been shown to have greater continuity, whereas the left IPS shows greater developmental changes during number processing (Emerson & Cantlon, 2014). Other research has also found longitudinal relationships between VSWM activity in the left IPS and arithmetic abilities 2 years later, but brain activity in the right IPS did not predict later arithmetic skills (Dumontheil & Klingberg, 2012). This relationship between activation in the left IPS during VSWM processing and later arithmetic may be related to more “adult-like” VSWM activity in the left IPS for higher achieving children. Our cross-sectional findings converge with the longitudinal evidence above to suggest that the left IPS plays an important role in the developing relationship between VSWM and arithmetic.

Increasingly left-lateralized activation with age has been found in studies of number processing, arithmetic, and VSWM. Specifically, prior research has shown that arithmetic and the processing of numbers becomes left-lateralized over development and that the left parietal cortex becomes increasingly specialized to process symbolic numbers (Vogel et al., 2015; Emerson & Cantlon, 2014; Rivera et al., 2005). Moreover, a large body of literature has also demonstrated that the VSWM network undergoes age-related changes, including the left parietal cortex (Klingberg et al., 2002; Kwon et al., 2002). The data in this study demonstrate, for the first time, that the specialization of the left parietal cortex for symbolic numbers and arithmetic may not necessarily reflect domain-specific change, but rather may reflect other more domain-general constraints on the way information is processed. It is possible that a more general, developmental process of cortical organization is driving the age-related increases in left-lateralized processing of VSWM and arithmetic in the parietal cortex. For instance, the cortex undergoes developmental changes where some aspects of brain structure and function become more asymmetrical and lateralized (for a review, see Duboc, Dufourcq, Blader, & Roussigné, 2015; Toga & Thompson, 2003). Functions such as face or word processing become more lateralized with development, and individuals with more lateralized processing of one function tend to have more lateralized processing of the other function in the opposite hemisphere (Pinel

et al., 2015). Lateralization of function may have cognitive advantages by allowing the brain to process information in parallel (Duboc et al., 2015). Asymmetrical development of brain architecture is also shown in structural brain networks, where the left hemisphere shows greater developmental increases in network efficiencies, while brain architecture in the right hemisphere remains relatively stable from adolescence to adulthood (Zhong, He, Shu, & Gong, 2017). Together, this literature indicates that the brain undergoes large-scale changes in structure and function, with increasing lateralization of function over developmental time. Therefore, the shared developmental specialization of the left IPS for both VSWM and arithmetic may reflect maturational changes in cortical processing that constrain the development of both domains. As a result, the present findings raise doubts about claims that age-related increases in left parietal activation during arithmetic and symbolic number processing are domain specific.

It is also possible that more left-lateralized activation could be related to the development of language and reading skills imposing constraints on the processing of visuospatial information as well as arithmetic. For example, literacy has been shown to impact other networks beyond those directly involved in reading (Dehaene et al., 2010). Moreover, there is indirect evidence to suggest that, as children get older, they increasingly use verbal rehearsal or verbal recoding for visuospatial information (Pickering et al., 2001; Hitch, Halliday, Schaafstal, & Schraagen, 1988). Though speculative, it is possible that both VSWM and arithmetic are relying on more verbally mediated strategies and that language systems may be shaping these networks over development, resulting in more left-lateralized activation for both VSWM and arithmetic.

When investigating age-related changes in the VSWM and arithmetic networks, we also found that children are recruiting the right middle temporal and supramarginal gyri more than adults. Other research has also found overlap between VSWM and arithmetic in adults in the right supramarginal gyrus (Zago & Tzourio-Mazoyer, 2002). The supramarginal gyrus (typically in the left hemisphere) is thought to be involved in verbally mediated strategies, such as fact retrieval during the solution of arithmetic problems (Price, Mazzocco, & Ansari, 2013; Rivera et al., 2005), and becomes increasingly recruited with age (Rivera et al., 2005). However, the right supramarginal gyrus has been found to be active during VSWM tasks (Smith, Jonides, & Koeppel, 1996), and the engagement of this region is positively correlated with age (Scherf, Sweeney, & Luna, 2006; Kwon et al., 2002). An examination of the beta values from these regions indicated that the age-related differences were related to less deactivation in the middle temporal gyrus and supramarginal gyrus. Therefore, it is also possible that group differences could be related to developmental changes in the default mode network, which the middle temporal and supramarginal gyri are part of (Laird et al., 2009). Future research will need to examine the role of the right middle temporal gyrus and supramarginal gyrus to further clarify its role in the development of arithmetic skills.

## Relationships Between Visuospatial Processing and Arithmetic

The numerical cognition literature has traditionally focused on the role of the IPS in the processing of quantities (Ansari, 2008; Dehaene, Piazza, Pinel, & Cohen, 2003). Arithmetic is thought to recruit the IPS because individuals need to manipulate and combine quantities to find a solution. This is particularly true of problems that are solved with more effortful calculation-based strategies (De Smedt et al., 2010; Zamarian, Ischebeck, & Delazer, 2009; Ischebeck et al., 2006; Delazer et al., 2005). Because these types of problems are also more demanding of VSWM, it is possible that IPS activity during calculation is also somewhat attributed to the VSWM demands of the task. In other words, IPS activity during calculation could be a result of manipulating quantities, VSWM demands, or a combination of the two. Indeed, others have argued that activation in the IPS is likely not solely related to processing quantities and that there needs to be a new framework to account for how arithmetic and working memory networks interact (Fias et al., 2013). At the very least, the present findings significantly question the extent to which any developmental changes in IPS activity during arithmetic tasks are domain specific and instead suggest that these reflect changing neuronal mechanisms that underpin both calculation and VSWM.

The overlap of VSWM and arithmetic in the IPS in this study and in others (Zago et al., 2008) also highlights the close relationship between visuospatial processing and numerical processing. Compelling neuropsychological and neuroimaging evidence has been provided to suggest that number and space are closely related to one another (Hubbard, Piazza, Pinel, & Dehaene, 2005) and, more importantly, that visuospatial processing is important for calculation (de Hevia, Vallar, & Girelli, 2008). Memory for visuospatial information has been shown to have retinotopic organization in the IPS (Silver & Kastner, 2009; Konen & Kastner, 2008). Similar brain regions have been hypothesized to be involved in the spatial organization of number in the form of a mental number line (Dehaene et al., 2003; Dehaene & Changeux, 1993). Indeed, it has been proposed that number and space share a frontoparietal network (Hawes et al., 2019; Hubbard et al., 2005). Spatial maps localized in the intraparietal cortex could be utilized for spatial representations of number, which could play a significant role in the relationship between VSWM in arithmetic (Dumontheil & Klingberg, 2012). Our findings provide converging evidence that visuospatial processing and arithmetic likely show a strong relationship because of common underlying networks.

The common underlying neural substrates for VSWM and arithmetic in the right IPS in children also have implications for children with developmental dyscalculia. These children often have poor performance on measures of arithmetic fluency as well as VSWM (Mammarella et al., 2018; Szucs et al., 2013). Neuroimaging studies have demonstrated that

children with dyscalculia have impaired processing in right IPS for both magnitude comparison tasks and VSWM tasks (Rotzer et al., 2009; Price, Holloway, Räsänen, Vesterinen, & Ansari, 2007). Here, we demonstrate, for the first time, that there is colocalization of activity in the right IPS for both VSWM and arithmetic in children. It is therefore possible that impairments in the right parietal circuits could be the cause of both VSWM and arithmetic impairments. This challenges the notion that dyscalculia is caused solely by a domain-specific impairment in the processing of numerical magnitude (Butterworth, Varma, & Laurillard, 2011; Butterworth, 2005, 2010) and instead might suggest that neuronal processes recruited during both mental arithmetic and VSWM are impaired in this learning disorder. It may be that a vulnerability to the shared neural circuitry leads to deficits in both domains. Future research will need to further investigate whether VSWM, numerical magnitude processing, and arithmetic impairments in dyscalculia stem from common neurobiological origins in the right IPS.

## Limitations

It is possible that the age-related differences we observed in this study could be attributed to differences in overall performance between the two groups. To ensure that the same task was used across groups, the tasks needed to be child-friendly. This also resulted in performance differences between the groups where adults had higher accuracy than children on both tasks, and the tasks could consequently be less demanding of arithmetic and VSWM systems in adults. However, in our control analyses, we determined that the findings were relatively consistent even when comparing the adults to a sample of the highest performing children. Furthermore, our adult findings closely resemble those of Zago et al. (2008), who used much more difficult tasks to examine VSWM and arithmetic abilities. This suggests that, even though the tasks used in this study are easier, they are still engaging networks typically associated with arithmetic and VSWM in adults. Another potential explanation for the age-related differences observed in this study is that the group of children may have been composed of a more heterogeneous sample (e.g., greater range of academic ability or socioeconomic status). Therefore, it is possible that we had less statistical power in the group of children to detect shared neural substrates for VSWM and arithmetic. Though we tried to mitigate the frequent issue of less statistical power in child samples by including a greater number of children compared with adults, it is important to acknowledge heterogeneity as a possible explanation for the findings described in this study.

A second limitation is that our arithmetic task consisted of only single-digit addition problems. It is possible that operation-specific (or strategy specific) differences exist in the overlap between VSWM and arithmetic. For instance, subtraction may rely more on working memory resources than addition because of a greater reliance on calculation-based strategies, which could subsequently reveal different

overlapping circuits. Future research will need to examine how arithmetic strategies (calculation vs. fact retrieval) and arithmetic operations affect the relationship with different components of working memory.

Third, demonstrating overlap between VSWM and arithmetic using a conjunction analysis does not necessarily indicate that the tasks are relying on the same underlying processes. Other multivariate methods are needed to help determine whether VSWM and arithmetic have similar representations at the neuronal level. It will also be important for future research examining the similarities between VSWM and arithmetic to use analyses such as representational similarity analyses (Kriegeskorte, Mur, & Bandettini, 2008).

Finally, this study aimed to examine the overlapping rather than the distinct neural circuits involved in VSWM and arithmetic. This focus was motivated by the overwhelming behavioral literature that has demonstrated strong relationships between these two abilities (Peng et al., 2016; Raghobar et al., 2010). How VSWM and arithmetic are interrelated at the neural level has been poorly documented, particularly in children. Therefore, an investigation into which regions are shared among these networks provides additional evidence into their behavioral association. It is evident from the basic contrasts that VSWM and arithmetic also have distinct and nonoverlapping regions of activation that are likely related to different cognitive demands of each task. However, a discussion of these regions and how they develop fell beyond the scope of this study.

## Conclusions

Previous neuroimaging research has largely used brain-behavior correlations to examine how VSWM and arithmetic are related to one another, and no studies have examined whether VSWM and arithmetic have the same neural basis in children. The findings presented within this study expand on this literature by empirically examining whether VSWM and arithmetic recruit the same brain regions within the same sample of children and adults. In this study, we provided novel evidence that VSWM and arithmetic have common underlying neural substrates in both children and adults. We also found that the overlap between VSWM and arithmetic is localized in the right IPS in children but becomes increasingly left-lateralized in adults. These findings provide evidence for the possible neurocognitive mechanisms underlying the strong relationship between VSWM and arithmetic that has been documented in the behavioral literature.

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## Funding Information

Daniel Ansari, Canadian Institutes of Health Research (<http://dx.doi.org/10.13039/501100000024>), Natural

Sciences and Engineering Research Council of Canada (<http://dx.doi.org/10.13039/501100000038>).

## Diversity in Citation Practices

A retrospective analysis of the citations in every article published in this journal from 2010 to 2020 has revealed a persistent pattern of gender imbalance: Although the proportions of authorship teams (categorized by estimated gender identification of first author/last author) publishing in the *Journal of Cognitive Neuroscience (JoCN)* during this period were M(an)/M = .408, W(oman)/M = .335, M/W = .108, and W/W = .149, the comparable proportions for the articles that these authorship teams cited were M/M = .579, W/M = .243, M/W = .102, and W/W = .076 (Fulvio et al., *JoCN*, 33:1, pp. 3–7). Consequently, *JoCN* encourages all authors to consider gender balance explicitly when selecting which articles to cite and gives them the opportunity to report their article's gender citation balance.

## Note

1. It is important to acknowledge that there are terminological inconsistencies for the dot matrix task in the literature. Some studies refer to the dot matrix task as a visuospatial short-term memory, whereas others refer to it as a visuospatial working memory task. To remain consistent with the fMRI literature, we refer to this task as a visuospatial working memory task throughout this paper. Though there are likely to be distinctions between the two, both visuospatial short-term memory and working memory measures load onto the same factor in a factor analysis (Miyake, Friedman, Rettinger, Shah, & Hegarty 2001), and they are both related to individual differences in arithmetic (Szucs, Devine, Soltesz, Nobes, & Gabriel, 2014).

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