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The neural association between arithmetic and basic numerical processing depends on arithmetic problem size and not chronological age

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A R T I C L E I N F O

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A B S T R A C T

The intraparietal sulcus (IPS) is thought to be an important region for basic number processing (e.g. symbol-quantity associations) and arithmetic (e.g. addition). Evidence for shared circuitry within the IPS is largely based on comparisons across studies, and little research has investigated number processing and arithmetic in the same individuals. It is also unclear how the neural overlap between number processing and arithmetic is influenced by age and arithmetic problem difficulty. This study investigated these unresolved questions by examining basic number processing (symbol-quantity matching) and arithmetic (addition) networks in 26 adults and 42 children. Number processing and arithmetic elicited overlapping activity in the IPS in children and adults, however, the overlap was influenced by arithmetic problem size (i.e. which modulated the need to use procedural strategies). The IPS was recruited for number processing, and for arithmetic problems more likely to be solved using procedural strategies. We also found that the overlap between number processing and small-problem addition in children was comparable to the overlap between number processing and large-problem addition in adults. This finding suggests that the association between number processing and arithmetic in the IPS is related to the cognitive operation being performed rather than age.

1. Introduction

Before children can learn arithmetic they first need to have knowledge of basic numerical concepts. In particular, children need to understand that symbolic numbers refer to a specific quantity (i.e., that the digit 3 can refer to three dots or three apples). A large body of research has investigated how basic numerical competencies relate to arithmetic skills. This research has demonstrated that individual differences in symbolic (Arabic digits) and nonsymbolic (e.g., dots) number processing skills predict arithmetic abilities in children and adults (Bartelet et al., 2014; Bugden and Ansari, 2010; De Smedt et al., 2013; Goffin and Ansari, 2016; Holloway and Ansari, 2009; Lyons et al., 2014; Mundy and Gilmore, 2009; Price and Fuchs, 2016; Sasanguie et al., 2012; Schneider et al., 2016).

Recent research has suggested that the ability to link symbolic numbers (Arabic digits) to their nonsymbolic quantities (e.g., dots) is critical for arithmetic and mathematical skills (Bartelet et al., 2014; Brankaer et al., 2014; Kolkman et al., 2013; Mundy and Gilmore, 2009; Purpura et al., 2013). The ability to map between symbolic and nonsymbolic quantities predicts children's arithmetic performance, even after other basic number processing tasks are taken into account (such as number comparison tasks) (Brankaer et al., 2014). This provides additional evidence in support of the notion that the mapping between symbolic and nonsymbolic representations of number is particularly important for the development of arithmetic skills. Other evidence has also shown that numeral knowledge, such as the ability to identify Arabic digits and associate then with nonsymbolic quantities, mediates the relationship between informal and formal mathematics (Göbel et al., 2014; Purpura et al., 2013). Together, these findings indicate that a fluent understanding of symbolic numbers and symbol-quantity relationships may be particularly important for arithmetic skills.

1.1. Shared networks for number processing and arithmetic

Even though studies have consistently demonstrated relationships between basic number processing skills and arithmetic at the behavioral level, limited research has examined how these abilities may be interrelated at the neural level. There is reason to believe that the brain circuits involved in arithmetic may overlap with those involved in basic number processing. For example, arithmetic problems that require effortful calculation frequently involve the mental manipulation quantities. Therefore, arithmetic may rely on brain regions that are

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associated with basic number processing. Indeed, it has often been assumed that the recruitment of intraparietal sulcus (IPS) during the solution of arithmetic problems is related to the activation of quantity representations within the IPS (Arsalidou and Taylor, 2011; Dehaene et al., 2003). However, surprisingly few studies have examined whether basic number processing tasks and arithmetic have overlapping brain activation in the same sample of participants.

Among the small body of studies that have investigated this question, there exists some indirect evidence that arithmetic and number processing may share common underlying circuitry. In particular, a large body of research has shown that magnitude processing skills and arithmetic both rely on the IPS (Ansari, 2008; Arsalidou and Taylor, 2011). However, this conclusion is derived from studies that have independently investigated either the neural correlates of magnitude processing or arithmetic. A meta-analysis of fMRI studies found that basic number processing and arithmetic had overlapping activity in the superior and inferior parietal lobules, in addition to a number of other cortical regions including visual areas, the insula, fusiform, inferior frontal and cingulate gyri (Arsalidou and Taylor, 2011). Though this provides some evidence for shared neural substrates, meta-analytic methods can only provide indirect evidence because they combine data across multiple studies and are therefore comparing activation profiles for different tasks between-subjects; true overlap of activation patterns can only be established by taking a within-subjects approach.

The association between basic number processing and arithmetic in the IPS has also been indirectly demonstrated using brain-behaviour correlations. Greater activation in the bilateral IPS during arithmetic has been associated with stronger symbolic number processing skills (Matejko and Ansari, 2017), and greater brain activation in the left IPS during symbolic number comparison has been related to higher scores on tests of arithmetic (Bugden et al., 2012). A similar study identified regions involved in number-processing by having children map between symbolic and nonsymbolic quantities (Emerson and Cantlon, 2012). Specifically, children had to identify whether a digit and a set of dots showed the same quantity. Functional connectivity within the network activated by this matching task was found to be related to children's math performance (Emerson and Cantlon, 2012). These studies examining individual differences in brain and behavior suggest that the IPS may be a particularly critical region for the association between basic numerical processing and arithmetic.

The literature discussed above has resulted in claims for common underlying circuitry for arithmetic and basic number processing in light of similar patterns of brain activity across different studies. Few studies have directly examined whether these networks overlap in the same sample of participants. Though no research has examined whether basic number processing and arithmetic have overlapping networks in children, two studies have examined this relationship in the same sample of adults. This research demonstrated that multiplication and number processing tasks (i.e., number comparison tasks) were associated with overlapping activity in the bilateral occipital cortices, left precentral gyrus, and supplementary motor area, but not in the parietal cortex (Dehaene et al., 1996; Rickard et al., 2000). The lack of overlap in the parietal cortex, particularly the IPS, may largely be due to the kinds of strategies used to solve multiplication problems in adults (Matejko and Ansari, 2018). Different strategies are used to solve arithmetic problems and these strategies have been shown to modulate brain activity. Specifically, networks involved in effortful calculation differ from those that are solved by retrieving the solution from memory (Zamarian et al., 2009). Both of the studies that have examined the relationship between basic number processing and arithmetic used single digit multiplication problems, which are predominantly solved using retrieval rather than more effortful calculation strategies (Campbell and Xue, 2001; Imbo and Vandierendonck, 2008; LeFevre et al., 1996). Therefore, these findings could be inconsistent with other literature because the neural association between number processing and arithmetic may be dependent on the kind of strategy that is used to solve the problem.

1.2. How strategies influence the relationship between arithmetic and number processing

Arithmetic problems can be solved using different kinds of strategies. For instance, some problems are solved using more time-intensive strategies such as counting or decomposing the problem into smaller parts (i.e., calculation), whereas other problems are solved by quickly retrieving the solution from memory (i.e., retrieval) (Campbell and Xue, 2001). The difficulty of the problem, and the arithmetic operation (e.g., addition vs subtraction) can influence which strategies are used. Difficult problems with larger operands (sums > 10) are more frequently solved using calculation, whereas easier problems with smaller operands (sums < 10) are more often solved using retrieval (Campbell and Xue, 2001; LeFevre et al., 1996).

Problem size has been used to investigate the different neural networks underlying calculation and retrieval. For instance, a large fronto-parietal network is activated during larger problems, or problems where the participant reports using calculation (Grabner et al., 2009). In contrast, left perisylvian language regions (including the left angular and supramarginal gyri) are frequently activated during small arithmetic problems, or problems where the participant reports using retrieval (Grabner et al., 2009; Kong et al., 2005). These patterns of findings are typically found regardless of the arithmetic operation, and can entirely be attributed to the strategy being performed (Polspoel et al., 2017; Tschentscher and Hauk, 2014). Arithmetic training studies have further demonstrated that there is a shift in activation from the IPS to the angular gyrus as participants become more fluent with arithmetic problems following training (Delazer et al., 2003, 2005; Ischebeck et al., 2006; Zamarian et al., 2009). This is likely indicative of a shift from procedural to retrieval strategies as individuals gain experience with the arithmetic problems. A similar pattern of findings also emerges as children become more experienced with arithmetic. Children increasingly use fewer procedural strategies (Ashcraft, 1982), and there are shifts in brain activation towards greater engagement of the inferior parietal cortex (Rivera et al., 2005).

Problems that are solved using procedural strategies require more quantity manipulations. These problems may have greater overlap with brain regions involved in number processing compared to problems solved using retrieval, which do not rely on quantity manipulations. Therefore, it is not only important to determine how basic number processing and arithmetic networks overlap, but also how the overlap is affected by the kind of strategy used to solve the problem. Though it is often assumed that regions in the parietal cortex subserve both number processing and arithmetic due to the role of quantity manipulations in calculation, this needs to be empirically examined using a within-subjects approach. Investigating the neural networks for arithmetic and basic number processing in the same sample of participants provides a unique opportunity to determine whether they have a shared neural basis in adults and children, and how this relationship changes as a function of the strategy used to solve the problem.

1.3. The present study

In view of the literature discussed above, the aim of the present study was to examine whether arithmetic and number processing recruit common brain regions and how problem size and age influence this relationship. To address this question, we assessed the functional networks for large and small addition problems and examined whether these regions overlapped with those for symbol-quantity matching in both children and adults. Systematically investigating whether there is overlap in the neural circuitry for basic number processing skills and arithmetic may provide unique insights into how these skills are related to one another. It can also help to determine whether this neural overlap persists into adulthood, or whether it changes as arithmetic and basic number processing skills develop. Exploring the relationship between basic number processing and arithmetic in the context of the cognitive operation being performed can also provide a better understanding of age-related differences and similarities. For instance, it is possible that both adults and children will show overlapping activation in the IPS for arithmetic and number processing skills, but only for problems that are solved using calculation and require the manipulation of quantities. Therefore, the relationship between arithmetic and number processing may be more closely tied to the cognitive operation than to age. The present study therefore has the following aims: (a) to determine whether arithmetic and symbol-quantity processing have common underlying neural substrates in adults and children; (b) to examine whether the relationship between number processing and arithmetic is influenced by how demanding the problems are on procedural strategies; and (c) determine whether the association between arithmetic and number processing skills is related to the cognitive operation being performed or to age.

2. Method

2.1. Participants

Twenty-six adults and 59 children were recruited to participate in this study. Two of the children did not complete the MRI session and one child was removed due to an abnormality in their anatomical scan. Eight additional children were removed due to poor accuracy on the fMRI tasks (less than 50% accuracy on either the arithmetic or number matching task), and another 6 children were removed from analyses due to head motion that exceeded 1.5 mm between volumes or more than 3 mm across the whole run. All adults were included in the analyses. The final sample of participants included 26 adults (12 females, all right-handed) and 42 children (20 females, 2 left-handed). Adults were undergraduate and graduate students between 19.5–26.3 years of age (M = 22.2), and children were between 7.5- and 10.4-years of age (M = 9.2). Participants were fluent English speakers, and had normal or corrected to normal vision. All participants (or children's caregivers) gave informed consent and children provided verbal assent. All participants were reimbursed for participating in the study. The Health Sciences Research Ethics Board at the University of Western Ontario approved the methods and procedures for this study.

2.2. Procedure

Participants completed two testing sessions. In the first session, adults and children were given a battery of standardized and experimental cognitive tests. During this session, children also participated in a mock scan where they practiced keeping still while doing a short arithmetic verification task. Participants returned between 1–9 weeks later for the second session where they completed an arithmetic verification task and a symbolic-to-nonsymbolic number matching task in the MRI. Both adults and children were trained on the tasks immediately prior to the scan to ensure they understood the tasks. Children completed an additional 2–3 tasks in the scanner and adults completed an additional 4 tasks that are not discussed here. The task order was counterbalanced using a Latin square design to control for task order effects.

2.3. Experimental tasks & design

2.3.1. Arithmetic task

Participants completed two runs of a single-digit addition task to identify brain regions involved in arithmetic problem solving. The arithmetic task consisted of two experimental conditions and one control condition: Large Problems (experimental), Small Problems (experimental), and Plus 1 Problems (control). Large Problems had solutions greater than 10, Small Problems had solutions less than or equal to 10, and Plus 1 Problems always had a single digit plus 1 (Fig. 1). Tie problems (ie. 3 + 3) and problems containing a 0 were not included. On all problems, two single-digit addends were presented together with a solution, and the participants needed to determine whether the solution was correct or incorrect. The solution was correct in half of the trials, and incorrect in the other half. To make the incorrect solution seem plausible, the incorrect solution was either +1 or +2 above the correct solution (Note: -1 or -2 below the correct solution were not used intentionally to ensure that the presented solution was never the same size or below one of the addends. This could have made it immediately clear to the participant that the solution was incorrect). In the Large and Small Problem conditions, the larger number was presented on the left for half of the trials (4 + 2) and on the right for the other half (3 + 5). If the larger number was presented on the left in run 1, it was presented on the right in run 2 (e.g., Run 1 [5 + 3]; Run 2 [3 + 5]). Each run had 36 addition problems (12 problems per condition), resulting in 72 trials across both runs (for a full list of trials see Supplementary Table 1). All adults and children had above chance performance and good motion on the two arithmetic runs (32/42 children had 2 usable arithmetic runs). If a child did not pass our motion or accuracy criteria on one of the runs, this run was excluded from the analysis and the other run was included. Findings from this arithmetic task have been reported in Matejko and Ansari (2017) in a slightly larger sample of children because motion and accuracy from only one task were considered.

2.3.2. Arithmetic problem solving strategy assessment

Large arithmetic problems are more often solved using procedural strategies (e.g., counting up, decomposition, etc.) whereas smaller problems tend 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 (i.e., all 56 unique trials). Problems 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.

2.3.3. Matching task

We used a number matching task closely adapted from Emerson and Cantlon (2012, 2014) to assess neural networks associated with basic number processing. This task was selected due to the behavioural literature that has found correlations between arithmetic and the ability relate symbolic numbers to their respective quantities (Bartelet et al., 2014; Brankaer et al., 2014; Kolkman et al., 2013; Mundy and Gilmore, 2009). Two conditions were presented in this task: a number matching condition and a shape matching condition. In the number matching condition participants were presented with a single-digit number symbol and a set of dots, and were asked to identify whether they had the same quantity (Fig. 1b). In half the trials the quantities were the same and in the other half of trials the quantities differed. When the trials did not match, the difference between the two number formats was ± 2, 3 or 4. Neither the digits nor the dots ever exceeded the quantity nine. In the shape matching condition (a control condition), two shapes were presented and the participant was asked to determine if they were the same or different shapes. In half the trials the shapes matched and in the other half they did not. One run of the matching

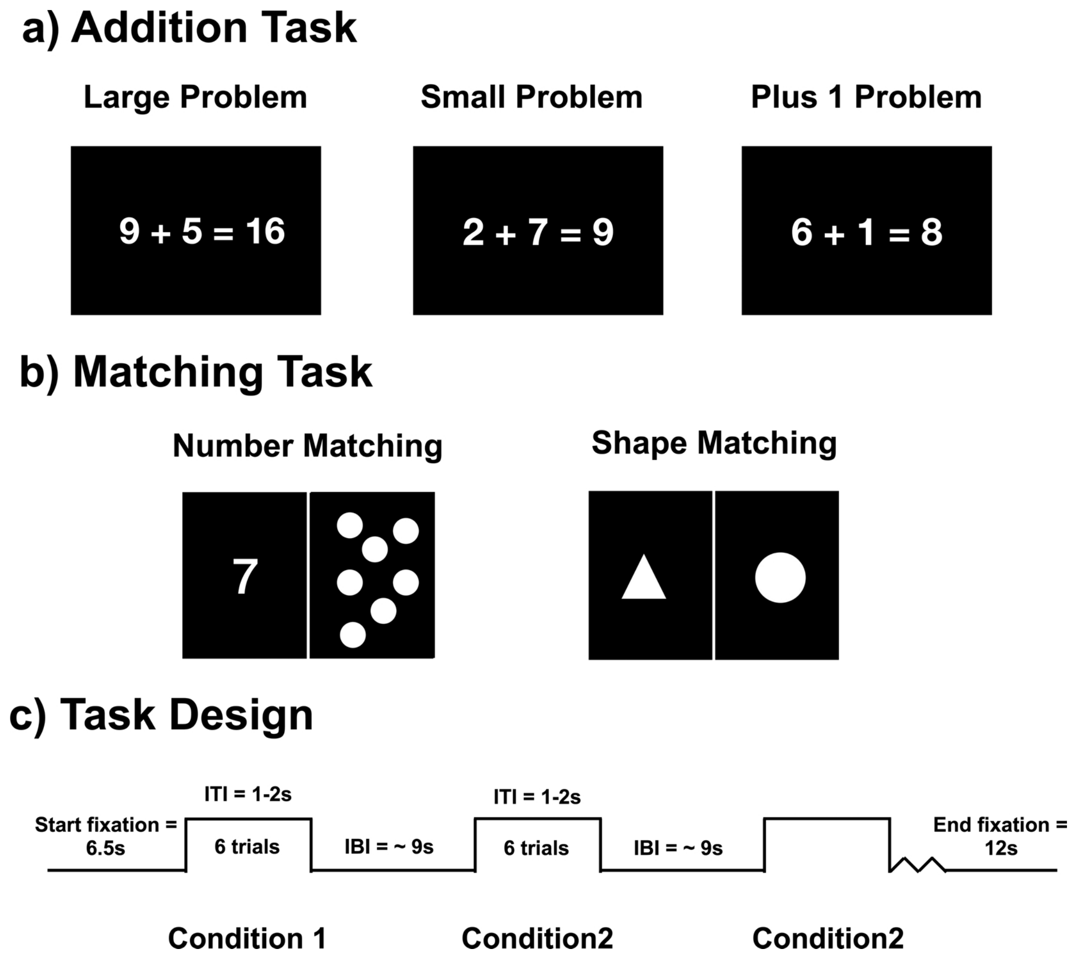

Fig. 1. Tasks performed during the scanning sessions a) Examples of the three conditions in the arithmetic verification task b) Examples of the number matching and shape matching (control) conditions c) Schematic of the timing in the block design for both tasks. Note: ITI = inter-trial interval; IBI = inter-block interval; s = seconds.

task was presented which had a total of 18 trials in the number matching condition and 18 trials in the shape matching trials (36 trials across the entire run).

2.3.4. *Task design*

The addition and number matching tasks were presented using a block design (see Fig. 1c for an illustration of the timing and design of the tasks). Because we were collecting data with a pediatric sample, we implemented a block design (rather than an event-related design) to maximize power to detect activation (Bandettini and Cox, 2000). Both tasks had an initial fixation of 6500 ms and end fixation of 12,000 ms. Each block consisted of 6 trials, with an average inter-trial interval (ITI) of 1500 ms (1000, 1500, and 2000 ms). In the addition task, each trial was presented for 4500 ms and participants could respond while the stimulus was presented or during the ITI screen. In the number matching task the trials were presented for 2000 ms and participants could also respond while the stimulus was presented or during the ITI. Each trial was randomly selected, and the conditions were randomly presented across the run. The inter-block interval (IBI) was an average of 9 s across the runs in both tasks. Due to the nature of the task design, all trials (correct and incorrect) were included in the analysis.

2.4. *MRI acquisition*

Participants were scanned on a 3 T Siemens Prisma Fit whole-body scanner, using a 32-channel receive-only headcoil (Siemens, Erlangen, Germany). High-resolution T1-weighted anatomical scans were collected using an MPRAGE sequence with 192 slices, a voxel resolution of $1 \times 1 \times 1$ mm, and an in-plane resolution of 256×256 pixels (TR = 2300 ms; TE = 2.98 ms; TI = 900 ms; flip angle = 9°). The MPRAGE had a scan duration of 5 min and 21 s. Functional MRI data were acquired during the addition and number matching tasks using a T2* weighted single-shot gradient-echo planar sequence with 35 slices obtained in an interleaved ascending order (TR = 2000 ms, TE = 30 ms, FOV 210×210 mm, matrix size = 70×70, flip angle = 78°). fMRI data had a slice thickness of 3 mm, an in-plane resolution of 3×3 mm, and a 0.75 mm gap. The addition task consisted of 2 runs with 144 volumes each, and the number matching consisted of 1 run with 99 volumes. Padding was used around the head to reduce head motion. The total scan duration was approximately 40 min for children and 1.5 h for adults.

2.5. *Analyses*

2.5.1. *Analyses of behavioural data*

Reaction time (RT) and accuracy data from the arithmetic and matching tasks were separately examined in 2 pairs of mixed-design ANOVAs. These analyses examined the effects of group (adults vs. children), task (arithmetic vs. matching) and condition (experimental condition vs. control condition). The first pair of ANOVAs focused on RT and accuracy data from Large problems and number matching, whereas the second pair of ANOVAs focused on RT and accuracy data from Small problems and number matching. The ANOVAs for RT and accuracy were identical except for the dependent variable. These

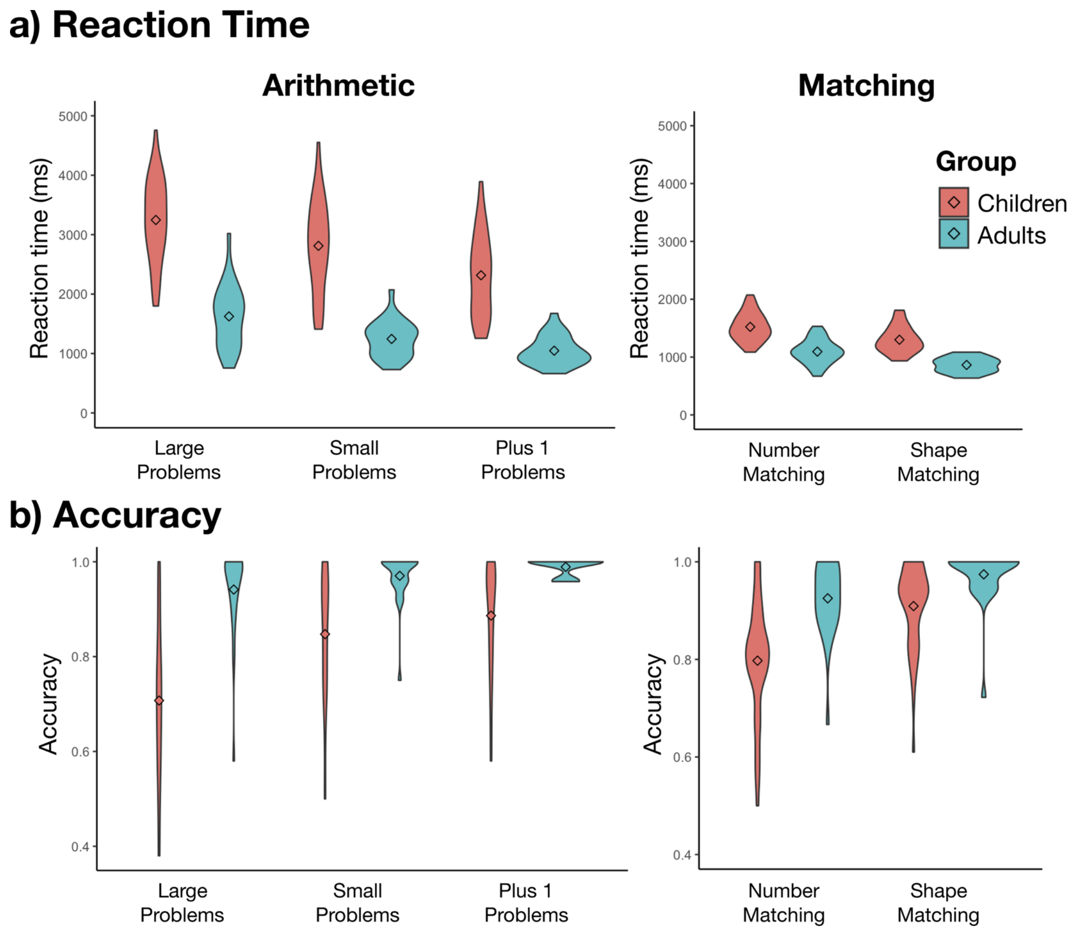

Fig. 2. Violin plots showing reaction time (a) and accuracy (b) data on the arithmetic and number matching tasks in children (in red) and adults (in green). Plots were generated with ggplot in R. Note: ms = milliseconds (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

analyses paralleled the functional neuroimaging analyses in order to better understand how the tasks and conditions compared to one another in each group. All significant interactions were followed with post-hoc tests.

To determine whether adults and children differed in the proportion of calculation strategies used in the arithmetic task, we also conducted a mixed-design ANOVA with condition (Large, Small and Plus 1 problems) as a within subjects factor, and group as a between subjects factor. Any significant interactions were followed with post-hoc tests.

2.5.2. Analyses of fMRI data

Functional images were preprocessed in Brain Voyager QX 2.8.4 (Brain Innovation, Maastricht, Netherlands). The functional data were corrected for differences in slice-time acquisition (cubic spline interpolation), head motion (trilinear/sinc interpolation), linear trends and low-frequency noise (high-pass, GLM-Fourier). Each functional image was coregistered to the subject's T1-weighted anatomical image, transformed into Talairach Space (Talairach and Tournoux, 1988), and then spatially smoothed with a 6 mm FWHM Gaussian smoothing kernel. Using adult-templates to spatially normalize pediatric populations have been found to result in systematic differences in brain anatomy and anatomical variability in children (Burgund et al., 2002). However, such methods have not been found to cause 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, Small problems, and Plus 1 Problems; Number Matching Task: Number Matching and Shape Matching). A random-effects GLM was then performed on the data. The two runs of the arithmetic task were treated as separate sessions. As described above, some children only had one usable run for the arithmetic task (due to poor motion or accuracy) and for these children beta values were only estimated from the single run. Whole-brain contrasts were initially thresholded at an uncorrected *p*-value of .005, then corrected for multiple-comparisons using a Monte-Carlo simulation procedure to determine the minimum cluster threshold size for each analysis (Goebel et al., 2006). Applying this cluster correction threshold resulted in an overall $\alpha < .05$. This cluster thresholding procedure accounts for spatial smoothness and spatial correlations within the data (formulas described in Forman et al., 1995).

We first investigated the arithmetic and number processing networks in children and adults. To determine whether the relationship between the basic number processing and arithmetic was dependent on the problem size (i.e., the type of strategies used to solve arithmetic problems), we separately examined the regions activated for Small and Large problems by contrasting each condition with the Plus 1 control condition [(*Large problems* > *Plus 1 problems*) and (*Small* > *Plus 1*)]. Independently examining Small and Large problems can help determine if the relative differences in the proportion of calculated problems influences whether or not arithmetic networks overlap with those for basic number processing. In the Supplementary Materials we also provide results of the comparison of Large problems > Small problems to determine whether these two conditions show different activation from one another (see Fig. S1 and Table S1).

To isolate regions involved in basic number processing, we contrasted the number matching condition with the shape matching condition (Number Matching > Shape Matching). In order to examine whether the overlap between basic number processing skills and arithmetic is dependent on problem size, we conducted independent conjunction analyses for Small and Large problems with the number matching task [(Large problems > Plus1 problems) ∩ (Number Matching > Shape Matching)] and [(Small problems > Plus1 problems) ∩ (Number Matching > Shape Matching)].

3. Results

3.1. Behavioural performance

3.1.1. Effects of group, task, and condition on reaction time

3.1.1.1. Large problems and number matching task. Adults were significantly faster than children, $F(166) = 124.4$, $p < .001$ and all participants were significantly faster on the matching task than the arithmetic task $F(1, 66) = 236.4$, $p < .001$ (see Fig. 2a). We also found a main effect of condition where participants were slower on the experimental conditions (Large arithmetic problems/number matching problems) compared to the control conditions (Plus 1/shape matching), $F(1, 66) = 194.3$, $p < .001$. We found an interaction between task and group, $F(166) = 81.4$, $p < .001$. Post-hoc tests revealed that children had greater differences in RT between the arithmetic task and matching task than adults ($t(64.9) = 10.3$, $p < .001$). The ANOVA also revealed an interaction between condition and group $F(166) = 6.0$, $p = .017$, where the differences between conditions were greater in children than in adults ($t(66) = 2.5$, $p = .017$). There was also an interaction between task and condition $F(166) = 69.6$, $p < .001$, where differences between conditions were greater in the arithmetic task than in the matching task (t(67) = 8.8, p < .001). Finally, we also observed a Task x Condition x Group interaction, $F(166) = 8.1$, $p = .006$. Post-hoc tests indicated that the magnitude of the difference between conditions in the arithmetic task was greater in children than in adults ($t(65.6) = 3.1$, $p = .003$), but the difference between the conditions in the matching task was the same across groups ($t(66) = -0.19$, $p = .85$).

3.1.1.2. Small problems and number matching task. The ANOVA examining the relationship between Small problems and the number matching task closely resembled the analysis above (see Fig. 2a). Adults had significantly faster reaction times than children, $F(166) = 1166.6$ $p < .001$, and there was a main effect of task where participants were faster on the matching task than the arithmetic task $F(166) = 127.4$, $p < .001$. A main effect of condition indicated that the experimental conditions (Small arithmetic problems/number matching problems) were slower than the control conditions (Plus 1/shape matching), $F(166) = 120.9$, $p < .001$. The ANOVA also revealed an interaction between task and group $F(166) = 71.0$, $p < .001$ where children showed greater differences between the tasks than adults ($t(51.7) = 10.3$, $p < .001$). There was also an interaction between condition and group $F(166) = 7.7$, $p = .007$. Post-hoc tests indicated that differences between conditions were greater in children than in adults ($t(62.6) = 3.2$, $p = .002$). We also found an interaction between task and condition $F(166) = 8.5$, $p = .005$, where the arithmetic task had greater differences between conditions than in the matching task (t(67) = 3.6, $p = .001$). There was also an interaction between Task x Condition x Group $F(166) = 13.6$, $p < .001$. The difference between conditions in the arithmetic task was significantly greater in children than in adults ($t(52.9) = 4.3$, $p < .001$), however, the difference between conditions in the matching task was the same across groups ($t(66) = -0.19$, $p = .85$).

3.1.2. Effects of group, task, and condition on accuracy

3.1.2.1. Large problems and number matching task. To examine the effects of group, task, and condition on accuracy, we conducted identical analyses to those above except with accuracy as the dependent variable (see Fig. 2b). This ANOVA revealed a main effect of group $F(166) = 44.8$, $p < .001$, where adults were more accurate than children. A main effect of condition also revealed that all participants were less accurate on the experimental conditions (Large problem/number matching) than the control conditions (Plus 1 problems/shape matching) $F(166) = 70.9$, $p < .001$. We found no main effect of task $F(166) = 3.23$, $p = .08$. The ANOVA also revealed an interaction between task and group $F(166) = 10.0$, $p = .002$. Children had higher performance on the matching task than the arithmetic task ($t(41) = -3.27$, $p = .002$), but adults performed equally well on both tasks (t(25) = 2.01, $p = .06$). We also found an interaction between condition and group $F(166) = 17.8$, $p = < .001$, where children had greater differences in accuracy between the conditions than adults (t(64.3) = −4.8, $p < .001$). There were no other significant interactions.

3.1.2.2. Small problems and number matching task. Adults had higher accuracy than children on the arithmetic and matching tasks $F(166) = 34.8$, $p < .001$ (see Fig. 2b) We also found a main effect of task $F(166) = 4.14$, $p = .046$ where participants were more accurate on the arithmetic task than the matching task. The ANOVA also showed a main effect of condition $F(166) = 194.3$, $p < .001$, indicating that participants were more accurate on the control conditions (Plus 1 problems/shape matching) than the experimental conditions (Small problems/number matching). We also found an interaction between condition and group $F(166) = 4.35$, $p = .041$, where children had greater differences in accuracy between the conditions than adults (t(56.0) = −2.5, $p = .015$). There was also an interaction between task and condition $F(166) = 7.8$, $p = .007$, where there was a greater difference between conditions in the matching task than the arithmetic task ($t(67) = 3.1$, $p = 002$). No other interactions were significant.

3.1.3. Post-scan strategy reports

To assess how children and adults solved the arithmetic problems, post-scan strategy reports were obtained on each problem in all children and 25/26 adults (Table 1). We conducted a 3 (Large, Small, Plus 1 Problems) x 2 (children, adults) ANOVA to determine whether the proportion of procedural strategies varied across the conditions and groups. Because the assumption of sphericity was violated, a Greenhouse-Geisser correction was applied to all within-subjects effects. A main effect of group revealed that adults used calculation strategies less often than children, $F(164) = 14.2$, $p < .001$. There was also a main effect of condition, $F(1.6, 104.2) = 126.1$, $p < .001$, where Large problems were solved using calculation strategies more often than Small problems ($t(66) = 12.9$, $p < .001$) and Plus 1 problems ($t(66) = 13.1$, $p < .001$). Also, a greater proportion of Small problems were solved using calculation strategies compared to Plus 1 problems ($t(66) = 5.1$, $p < .001$). An interaction between condition and group, $F(1.6, 104.2) = 7.0$, $p = .003$, revealed that strategy use was only significantly different between the groups on the Large (t(65) = 2.9, $p = .006$) and Small problems (t(48.5) = 5.6, $p < .001$), but not the Plus 1 problems (t(65) = .18, $p = .86$). Consequently, the Plus 1 condition was ideally suited as a control condition in the fMRI analyses because children and adults used similar strategies to solve the problems (see Table 1).

Table 1
Proportion of arithmetic problems solved using procedural strategies (counting up, decomposition, etc.) in adults and children (values reported in percentages).

	Large Problems	Small Problems	Plus 1 Problems
Adults (n = 25)	41.0	3.3	3.0
Children (n = 42)	59.2	25.1	3.7

Table 2
Anatomical regions, Talairach coordinates, mean t-scores, and number of voxels for each cluster in each simple contrast.

Anatomical Region	TAL coordinates (x,y,z)			Mean t-score	Number of Voxels
Adults: Large Problems > Plus 1 Problems					
Right MFG	37.59	32.24	29.59	3.56	2651
Right insula	32.93	17.72	7.47	3.66	3104
Bilateral lingual gyri/middle and inferior occipital gyri/cerebellum	−7.13	−71.60	−7.32	3.73	50643
Right intraparietal sulcus	31.00	−51.55	34.88	3.47	3449
Bilateral thalamus	0.54	−15.54	13.71	3.44	1448
Bilateral superior frontal gyrus	−1.42	9.22	47.48	3.78	6059
Left MFG/IFG/insula/SFS/postcentral sulcus	−38.67	13.17	28.72	4.10	24107
Left intraparietal sulcus	−32.29	−51.64	37.41	4.15	14973
Adults: Small Problems > Plus 1 Problems					
Right supramarginal gyrus	52.56	−40.97	21.98	3.34	1118
Right inferior and middle occipital gyri	31.09	−82.24	−1.72	3.40	1712
Right fusiform gyrus	32.03	−59.94	−13.17	3.57	935
Right precuneus	8.28	−73.82	32.00	3.27	1050
Left inferior and middle occipital gyri	−21.74	−91.66	−2.01	3.71	2997
Left IFG	−51.46	11.30	26.96	3.65	1133
Adults: Number Matching > Shape Matching					
Right cerebellum	29.31	−53.63	−26.09	3.39	1874
Right IPS	26.51	−67.51	25.54	3.36	1585
Bilateral lingual gyrus/left superior occipital gyrus	−1.94	−81.04	−1.45	3.67	10555
Brainstem/Pons	−1.79	−23.82	−25.11	3.55	2103
Left IPS/SPL	−19.60	−63.58	36.65	3.49	7499
Left caudate/thalamus	−12.77	−5.05	14.05	3.41	1822
Left MFG/insula	−37.37	21.06	22.71	3.41	5278
Children: Large Problems > Plus 1					
Right middle and inferior temporal gyrus	51.40	−38.30	−8.10	3.70	1627
Right IPS/SPL	30.16	−55.07	43.28	3.95	17211
Right MFG/insula	33.36	21.17	29.72	3.69	11164
Bilateral lingual gyrus/inferior and middle occipital gyri/cerebellum/left inferior temporal gyrus	−4.08	−72.45	−9.93	3.73	39946
Bilateral superior frontal gyrus	−0.69	15.27	44.25	3.86	7404
Left IPS	−32.11	−53.28	42.42	4.15	16371
Left MFG/precentral gyrus/insula	−37.82	14.00	26.36	3.65	7929
Left inferior frontal gyrus	−35.81	50.56	7.45	3.24	1816
Children: Small Problems > Plus 1 Problems					
Bilateral lingual gyrus/inferior occipital gyrus/cerebellum	−7.62	−73.83	−9.46	3.70	39199
Right IPS	24.60	−66.86	47.58	3.32	2340
Right lingual gyrus	14.29	−58.74	4.71	3.34	1223
Left IPS	−24.63	−63.48	44.49	3.78	7525
Left IPS/postcentral sulcus	−40.01	−37.46	44.28	3.42	1232
Left precentral sulcus/inferior frontal sulcus	−42.05	8.13	35.56	3.39	4295
Children: Number Matching > Shape Matching					
Bilateral IPS/superior and middle occipital gyri/lingual gyrus	4.35	−71.76	26.11	3.58	29181
Right insula	30.38	18.22	7.42	3.47	2507
Bilateral superior frontal gyri	3.38	12.87	43.99	3.86	8586
Left cerebellum/inferior occipital gyrus/fusiform gyrus	−31.26	−66.53	−17.56	3.29	2966
Left insula	−32.38	16.92	9.11	3.51	1779

3.2. Brain imaging

3.2.1. Adults

3.2.1.1. Arithmetic and number processing networks. We identified regions involved in arithmetic by using two contrasts, *Large > Plus 1 problems* and *Small > Plus 1 problems*. Regions activated in the first contrast (*Large > Plus 1 problems*) are more likely to be involved in effortful calculation, whereas the second contrast (*Small > Plus 1*) identifies regions that are less likely to be associated with calculation processes. The *Large > Plus 1* contrast revealed a fronto-parietal network of regions that included the bilateral IPS, middle frontal gyri (MFG), insula, superior frontal gyri (SFG) and left inferior frontal gyrus (IFG) (see Table 2 for a full list of regions, and areas in blue in Fig. 3a). The contrast *Small > Plus 1* revealed a different set of regions that included the right supramarginal gyrus (SMG), left IFG, left fusiform gyrus, and several regions in the occipital cortex (see orange regions in Fig. 3a). Finally, to isolate regions involved in number processing, we identified areas that were more active for number matching than shape matching (*Number Matching > Shape Matching)*. This contrast revealed a fronto-parietal network that included the bilateral IPS, left MFG, insula, thalamus, caudate, as well as regions in the occipital cortex (see regions in green in Fig. 3a). All of these networks have been superimposed onto one another in Fig. 3a to better observe regions that are common to each contrast.

3.2.1.2. Conjunction analyses. Two conjunction analyses were conducted to examine whether arithmetic and number processing networks have common underlying substrates, and to determine whether the overlap is related to the cognitive operation being performed on the arithmetic problem. In the first analysis we examined the conjunction between Large problems and number matching relative to their respective control conditions [(*Large problems > Plus1 problems*) ∩ (*Number Matching > Shape Matching*)]. This analysis revealed that the left IPS, left MFG, and bilateral superior occipital and lingual gyri were active for both large arithmetic problems and number matching (see Table 3 and regions in blue in Fig. 4). In contrast, the conjunction between Small problems and number matching [(*Small problems > Plus1 problems*) ∩ (*Number Matching > Shape Matching*)] only showed overlap within the bilateral lingual and superior occipital gyri (regions in orange in

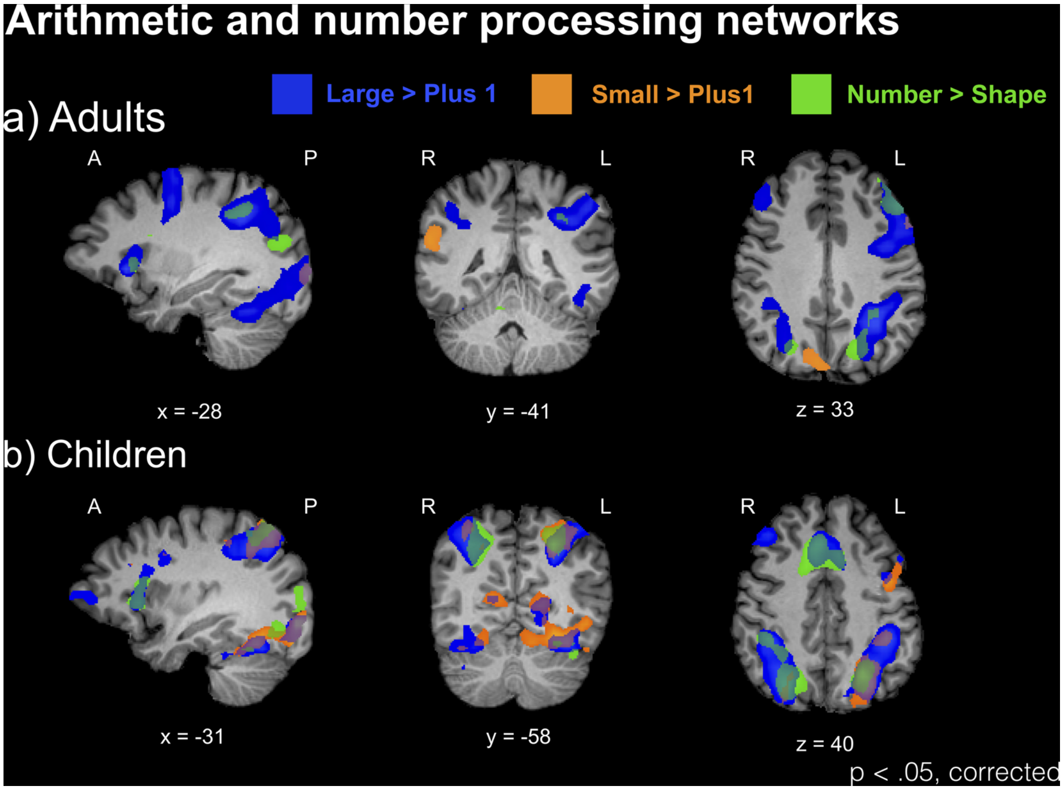

Fig. 3. Statistical maps illustrating regions activated for Large problems, Small problems, and number matching relative to their control tasks in (a) adults and (b) children. Regions that are more active for Large problems than Plus 1 problems are displayed in blue, regions more active for Small problems than Plus 1 problems are shown in orange, and regions more active for number matching than shape matching are shown in green. Note: only significant positive activation (not deactivation) is shown in this figure. Note: A = anterior; P = posterior; R = right; L = left (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Fig. 4). Together, these findings may indicate that the overlap between arithmetic and basic number processing in the IPS may be dependent on task difficulty and the kind of strategies used to solve the arithmetic problems.

3.2.2. Children

3.2.2.1. Arithmetic and number processing networks. We identified networks involved in arithmetic and basic number processing skills in the same way described above for adults. We first identified regions that were more active for Large arithmetic problems than Plus 1 problems (*Large problems > Plus 1 problems*). Similar to adults, this analysis revealed a fronto-parietal network of regions that included the bilateral IPS, right superior parietal lobule (SPL), bilateral SFG, bilateral MFG, bilateral insula, left precentral gyrus, right middle and

Table 3
Anatomical regions, Talairach coordinates, mean t-scores, and number of voxels for each cluster in the conjunction analyses.

Anatomical Region	TAL coordinates (x,y,z)			Mean t-score	Number of Voxels
Adults: Conjunction (Large > Plus 1) ∩ (Number > Shape)					
Bilateral lingual gyrus and superior occipital gyrus	−3.86	−82.88	−0.92	3.43	5137
Left IPS	−25.25	−57.73	34.55	3.34	2231
Left MFG	−40.67	27.56	30.28	3.42	2471
Adults: Conjunction (Small > Plus 1) ∩ (Number > Shape)					
Bilateral lingual gyrus and left superior occipital gyrus	−14.98	−93.67	−2.16	3.48	869
Children: Conjunction (Large > Plus 1) ∩ (Number > Shape)					
Right IPS/SPL	25.82	−58.86	42.70	3.54	6733
Right insula	29.87	19.72	6.18	3.52	1829
Bilateral lingual gyrus/superior occipital gyrus	−5.31	−85.96	−1.66	3.19	3231
Cingulate gyrus/superior frontal gyrus (ventral portion)	−1.29	41.26	3.19	−3.44	4201
Superior frontal gyrus (dorsal portion)	0.53	14.40	44.06	3.77	5432
Superior frontal gyrus	−8.92	52.01	31.02	−3.29	1618
Left IPS	−24.17	−63.44	43.86	3.50	3962
Children: Conjunction (Small > Plus 1) ∩ (Number > Shape)					
Right IPS/SPL	20.98	−69.64	47.66	3.30	1289
Bilateral lingual gyrus/superior occipital gyrus	−2.26	−87.78	0.79	3.21	4392
Left IPS/SPL	−23.60	−62.77	45.38	3.53	4274
Adults (Large > Plus 1) ∩ (Number > Shape) > Children (Small > Plus 1) ∩ (Number > Shape):					
Left MFG	−40.36	31.90	28.39	3.40	2492

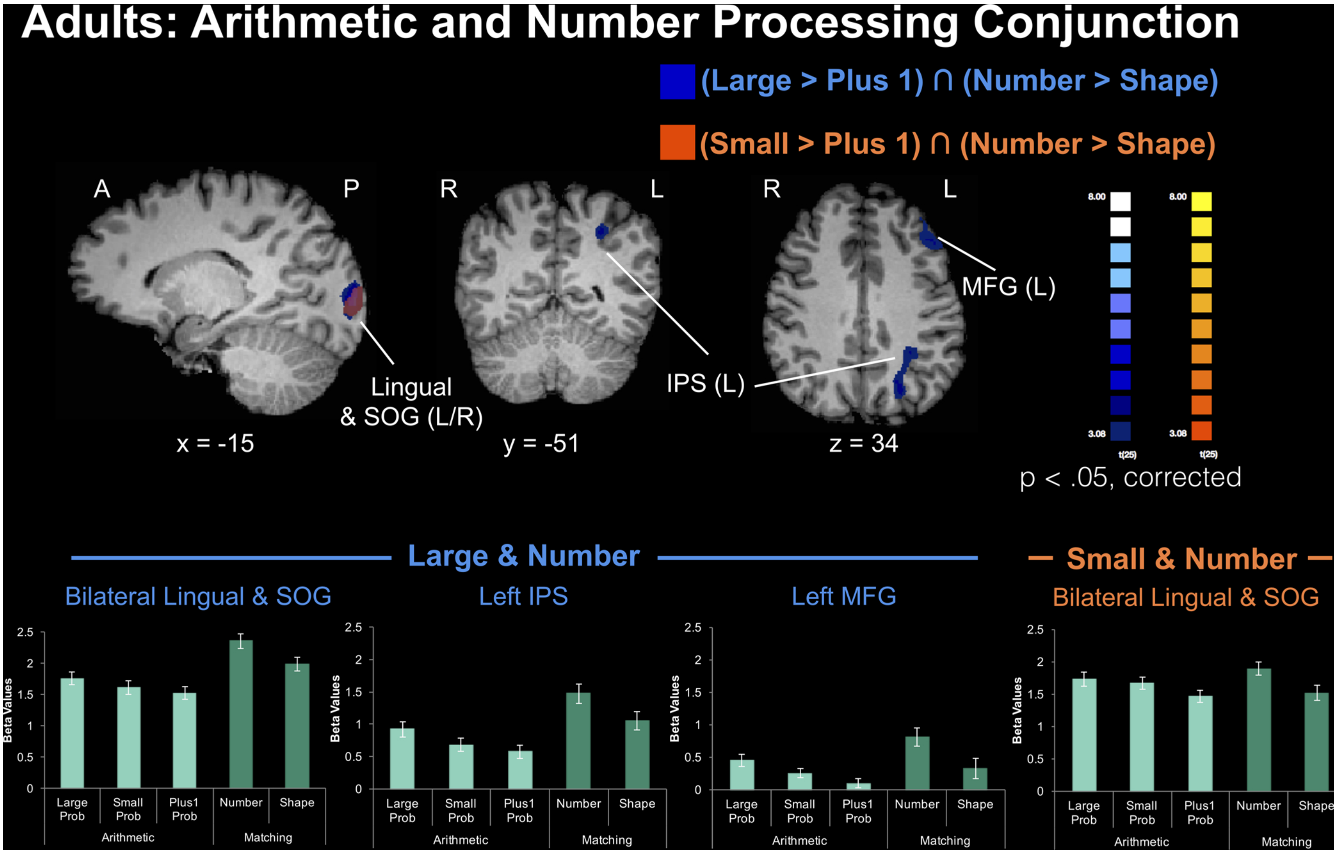

Fig. 4. Statistical map illustrating the conjunction between the arithmetic and matching task in adults. Regions in blue show the conjunction (*Large problems* > *Plus1 problems*) ∩ (*Number Matching* > *Shape Matching*), whereas regions in orange show (*Small problems* > *Plus1 problems*) ∩ (*Number Matching* > *Shape Matching*). Mean beta values are shown for each significantly activated cluster from the conjunction. Note: Only regions that showed significant positive activation (not deactivation) for the conjunction are shown in this figure. See to Table 3 for a full list of regions. Note: A = anterior; P = posterior; R = right; L = left; SOG = superior occipital gyrus; IPS = intraparietal sulcus; MFG = middle frontal gyrus (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

inferior temporal gyri, and several regions within the occipital cortex (see Table 2 and Fig. 3b in blue). The contrast *Small problems* > *Plus 1 problems* revealed a similar set of regions including the bilateral IPS, left precentral sulcus and inferior frontal sulcus, the left postcentral sulcus, as well as bilateral regions of the occipital cortex and cerebellum (see Fig. 3b in orange). Finally, we also examined regions involved in basic number processing (*Number Matching* > *Shape Matching)*. Regions that were more active for number matching than shape matching included the bilateral IPS, bilateral SFG, bilateral insula, and regions throughout the bilateral occipital cortex and cerebellum (see Fig. 3b in green). All networks are superimposed onto each other in Fig. 3b to visualize their overlap.

3.2.2.2. Conjunction analyses. To statistically examine whether arithmetic and basic number processing activated the same brain regions, we conducted two conjunction analyses. Identical to the analyses shown above with the adults, the first conjunction analysis examined regions that were active for both Large problems and number matching relative to their controls [(*Large problems* > *Plus1 problems*) ∩ (*Number Matching* > *Shape Matching*)]. The bilateral IPS, right SPL, right insula, bilateral SFG, and bilateral lingual and superior occipital gyri were active for both Large problems and number matching (see Fig. 5 in blue). The second conjunction analysis examined regions that were active for both Small problems and number matching relative to their control tasks [(*Small problems* > *Plus1 problems*) ∩ (*Number Matching* > *Shape Matching*)]. This analysis revealed several regions including the bilateral IPS and SPL, as well as the bilateral lingual and superior occipital gyri (see Fig. 5 in orange).

3.2.3. Similarities of activation profiles in children and adults

The above conjunction analyses demonstrated some striking similarities between adults and children: the conjunction between Large problems and number matching in adults was similar to the conjunction between Small problems and number matching in children. Both of these conjunction analyses revealed significant activation in the left IPS for number matching and the respective arithmetic conditions in adults and children. This may suggest that adults process large arithmetic problems in a similar way that children process small arithmetic problems. Moreover, this could indicate that adults and children are reliant on basic number processing to the same degree for these conditions.

To test this prediction we conducted several post-hoc analyses to determine whether the conjunction between Small problems and number matching had similar patterns of activation to the conjunction between Large problems and number matching in adults. We first examined whether the RT differences between the Large and Plus 1 conditions in adults were similar to the Small and Plus 1 conditions in children. The independent-samples *t*-test suggested that the magnitude of the difference between these conditions was the same across groups ($t(66) = -0.85$, $p = .40$), suggesting that the relative difficulty of between these two conditions was the same in children and adults (Children: Small vs Plus 1 mean RT difference = 494.9 ms, SD = 417.8; Adults: Large vs Plus 1 mean RT difference = 577.2 ms, SD = 355.0).

To determine whether adults and children recruited the left IPS to the same or differing degrees for these two conjunction analyses, we directly compared them. We first conducted fixed-effects GLM for each subject and subsequently calculated conjunction maps for each individual. The individual conjunction maps were combined into separate

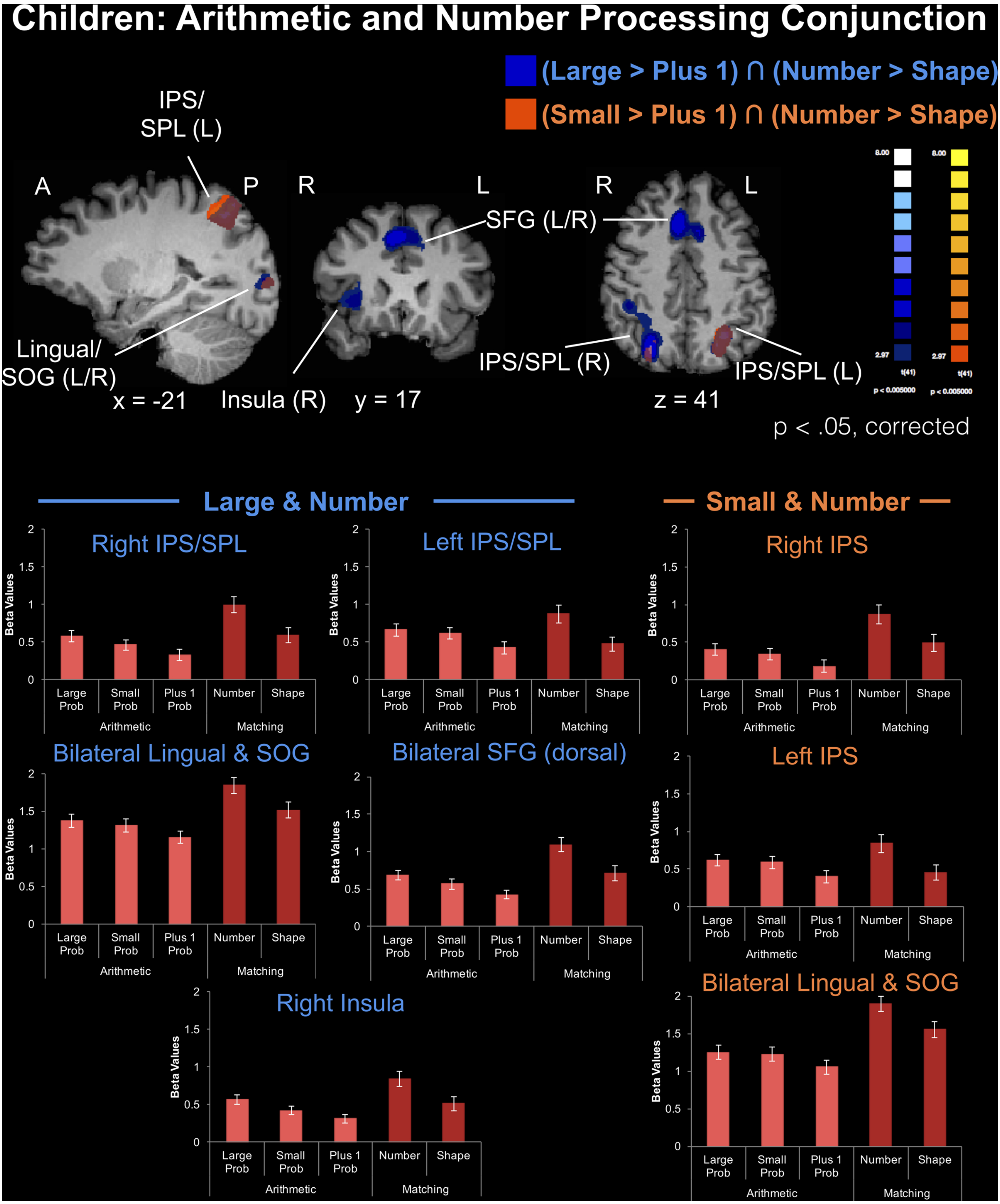

Fig. 5. Statistical map illustrating the conjunction between the arithmetic and matching task in children. Regions in blue show the conjunction (*Large problems > Plus1 problems*) ∩ (*Number Matching > Shape Matching*), whereas regions in orange show (*Small problems > Plus1 problems*) ∩ (*Number Matching > Shape Matching*). Mean beta values are shown for each significantly activated cluster from the conjunction. Note: Only regions that showed significant positive activation (not deactivation) for the conjunction are shown in this figure. Refer to Table 3 for a full list of regions. Note: A = anterior; P = posterior; R = right; L = left; IPS = intraparietal sulcus; SPL = superior parietal lobule; SOG = superior occipital gyrus; SFG = superior frontal gyrus (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

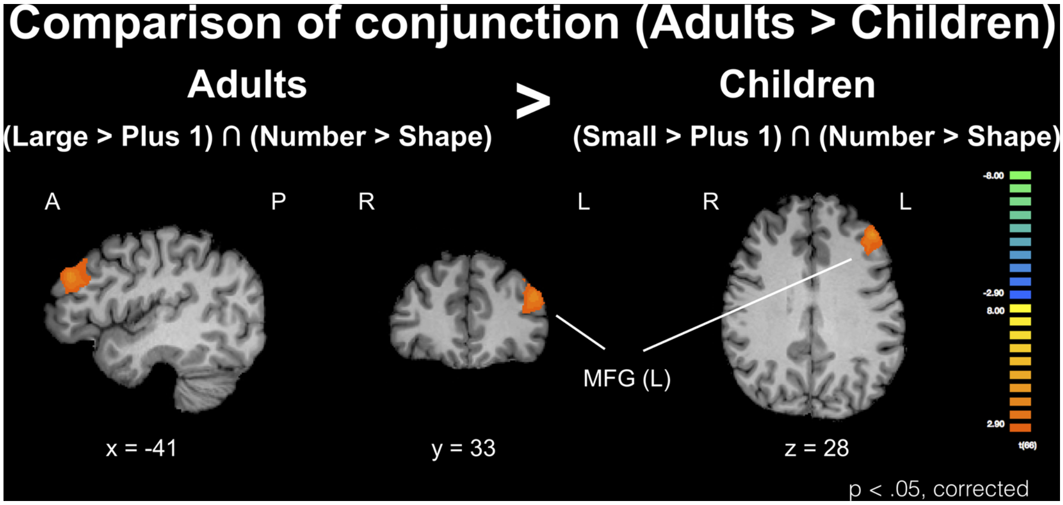

Fig. 6. Statistical maps comparing Large problems and number matching in adults [(*Large* > *Plus 1*) ∩ (*Number* > *Shape*)] to the conjunction between Small problems and number matching in children [(*Small* > *Plus 1*) ∩ (*Number* > *Shape*)]. Regions in orange reflect significantly greater activation for adults. Note: A = anterior; P = posterior; R = right; L = left; MFG = middle frontal gyrus. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

group-average maps for adults and children. We then used a random effects *t*-test to compare the conjunction between Large problems and number matching in adults [(*Large* > *Plus 1*) ∩ (*Number* > *Shape*)] to the conjunction between Small problems and number matching in children [(*Small* > *Plus 1*) ∩ (*Number* > *Shape*)]. This analysis revealed that there were no significant differences in the recruitment of the left IPS for these two conjunction analyses in adults and children. The only region that was found to be significantly different between the two groups was the left MFG which adults recruited more for Large problems and number matching than children did for Small problems and number matching (see Fig. 6). This provides additional evidence that the neural processing of Large problems in adults in the left IPS is similar to the way children process Small problems in the left IPS, and that they could be recruiting basic number skills to the same degree.

3.2.4. Control analyses

It should be acknowledged that differences between adults and children could be attributed to performance differences between the groups. Therefore, we also conducted an analysis that included 26 children who had the highest accuracy on the Small and Large arithmetic problems. We aimed to match performance on the arithmetic task because performance was generally lower on this task than the matching task. Behavioural performance still significantly differed between the two groups, though the higher-performing children were more similar to the adults than the full sample of children. Using this sample of 26 children, we conducted the two conjunction analyses to determine whether task performance was related to the outcome of these analyses. The conjunction analysis between Large problems and number matching (relative to their controls) remained nearly identical in the highest performing children, with the bilateral IPS, SFG and right insula all remaining significant ($p < .05$ corrected). The conjunction between Small problems and number matching was also similar to the full sample and included the left IPS as well as the bilateral SFG ($p < .05$ corrected).

4. Discussion

The recruitment of the IPS during arithmetic has long been assumed to be due to the manipulation of quantities during calculation. However, arithmetic and number processing networks have largely been investigated in isolation of one another and any conclusions about the role of the IPS during calculation has been inferred from comparing across studies or by investigating brain-behaviour correlations. Previous research with adults has failed to find an association between magnitude processing and arithmetic in the parietal cortex (Dehaene et al., 1996; Rickard et al., 2000). However, these studies used multiplication problems to identify regions involved in calculation, which are typically solved using retrieval strategies in adults and therefore require little manipulation of quantities (Imbo and Vandierendonck, 2008). Consequently, the lack of neural overlap between multiplication and magnitude processing may have been related to the type of strategy being used to solve the arithmetic problems. The present study aimed to address these unresolved questions by using a within-subjects approach to determine whether arithmetic and basic numerical processes rely on the IPS in adults and children. We provide the first evidence to suggest that arithmetic and basic number processing have common neural substrates in the IPS in adults and children. Importantly, we found that this relationship differs depending on arithmetic problem size (i.e., proportion of problems that are calculated). Moreover, adults and children recruit the left IPS similarly for number processing and arithmetic when the cognitive demands of the arithmetic task are comparable.

In the present study we found that the IPS plays an important role in the relationship between arithmetic and the processing of the semantic referents of number symbols (i.e., symbol-quantity associations). Indeed, these findings lend support to the idea that procedural arithmetic skills may be scaffolded on an understanding of more basic number processing skills (Matejko and Ansari, 2018). It is possible that individuals with more efficient access to the meanings of number symbols have greater ease in manipulating quantities in the context of calculation. Similar evidence has been shown using brain-behaviour correlations where children who recruited the left IPS more during a symbolic number comparison task also had higher arithmetic scores (Bugden et al., 2012). The present findings, therefore, extend those from Bugden et al. (2012) by indicating that the IPS is particularly important for the relationship between symbol-quantity associations and arithmetic. Behavioural research has also provided compelling evidence that a fluent understanding of symbol-quantity relationships is important for the acquisition of arithmetic skills (Brankaer et al., 2014; Mundy and Gilmore, 2009). Therefore, both behavioural and neuroimaging evidence converge to suggest that a stronger understanding of symbol-quantity associations may play a role in the development of procedural arithmetic.

4.1. Strategy influences the neural overlap between arithmetic and number processing

One particularly novel finding was that the recruitment of the IPS for arithmetic and number matching was also related to the proportion of problems that were calculated. The conjunction analyses revealed that adults exhibit significant overlap in the left IPS for basic number processing and arithmetic, but only for the large addition problems of which 41% of the problems were solved using procedural strategies. In contrast, adults only showed significant activation in the bilateral lingual and superior occipital gyri for the conjunction between Small problems and basic number processing, suggesting that these problems do not rely on quantity-based systems in the IPS. Instead, the regions in the conjunction analysis between Small problems and number matching are likely related to common visual processing demands for both tasks. The lack of overlap within the IPS is consistent with the post-scan strategy reports that showed adults used procedural strategies on only 3% of the small addition problems. Small problems are more often solved using fact-retrieval strategies (Campbell and Xue, 2001; LeFevre et al., 1996), therefore, these problems rely on different neural substrates, which are non-overlapping with those for basic number processing skills. Problems that are solved using retrieval have been found to be associated with activation in the angular and supramarginal gyri (Grabner et al., 2009, 2013; Price et al., 2013). The present data also reveal a similar pattern of findings even when contrasting Small problems with Plus 1 problems, where the right supramarginal gyrus was more active for Small problems than Plus 1 problems.

Related to the notion that the IPS is crucial for problems that require quantity-based strategies, we also found that children recruited the bilateral IPS for both arithmetic and basic number processing, and this was relatively consistent for Small and Large problems. The post-scan strategy reports revealed that this could have been related to children using procedural strategies for both small and large addition. Behavioural research has found that the strength of the relationship between symbolic number processing and arithmetic changes depending on the type of strategy that is implemented. A fluent understanding of symbolic numbers has been shown to be more related to problems that rely on mental calculation versus those that are solved using algorithms (Linsen et al., 2015a, 2015b). Together, these findings indicate a close association between basic number processing and arithmetic at the behavioural and neural levels, however, the relationship changes depending on the type of strategies that are used to solve the arithmetic problem.

The arithmetic training literature provides some additional context to the findings in this study, and shows that brain activity shifts away from the IPS to the angular and supramarginal gyri when individuals become more familiar with arithmetic problems (for a review see Zamarian et al., 2009). Adults initially activate in the IPS for multi-digit arithmetic problems, but after being trained on these problems, there is a shift in activation to the angular gyrus for the same problems (Delazer et al., 2003, 2005; Ischebeck et al., 2006). This has been linked to changes in strategy use from more quantity-based strategies to fact-retrieval (Zamarian et al., 2009). These findings have been corroborated with post-scan strategy reports (Grabner et al., 2009), and in studies investigating individual differences in arithmetic proficiency (Grabner et al., 2007; Price et al., 2013). In the present data, we see a similar pattern of findings in both adults and children where the IPS is recruited for basic number processing and arithmetic when a significant portion of the problems are solved using calculation. However, arithmetic problems that are predominantly solved with retrieval (e.g., Small problems in adults) show no overlap in the IPS.

One of the central findings in this study was that adults and children showed similarities of processing once the cognitive demands of the arithmetic task were similar. These similarities were evident when examining the conjunction between Small problems and number matching in children and the conjunction between Large problems and number matching in adults; in both of these analyses children and adults recruited the left IPS. By directly comparing these conjunction analyses, we found that there were no statistically significant differences between groups in the left IPS. This provides evidence that adults process Large problems in a similar way to the way children process Small problems in the left IPS, and importantly, that the link between arithmetic and symbol-quantity relationships is similar for these conditions in each group. Even though there remained differences in the proportion of problems that reported to be calculated (adults: 41.0% calculated on Large problems; children: 25% calculated on Small problems), the reaction time data indicated that the relative task difficulty of these two conditions was the same across groups. These findings suggest that basic number processing skills are recruited in a similar manner for problems that have similar levels of task difficulty. Therefore, once cognitive demands of the arithmetic problem are matched, adults and children show markedly similar patterns of brain activation within the IPS for number processing and arithmetic. It is possible that the association between number processing and arithmetic is not dependent on age, but rather on the cognitive operation being performed.

4.2. Overlapping activation between arithmetic and number processing outside of the parietal cortex

Though the IPS is a critical brain region for both basic numerical processing and arithmetic, it is notable that we also found overlap in other brain regions in both adults and in children. First, all conjunction analyses in adults and children revealed overlapping activity between number processing and arithmetic in the lingual and superior occipital gyri. This is most likely related to greater engagement of the visual system for the experimental task compared to the control tasks. Adults also demonstrated overlapping activity between number processing and large arithmetic problems in the left MFG. Both children and adults have been shown to activate the MFG for calculation (Arsalidou et al., 2017; Arsalidou and Taylor, 2011). Critically, previous research has found that the MFG is more active for complex (calculated) than simple (retrieved) arithmetic problems (De Smedt et al., 2010; Grabner et al., 2007, 2009; Polspoel et al., 2017). Activity in this region has largely been attributed to processes related to cognitive control, especially working memory processes needed to coordinate complex cognitive tasks (Arsalidou et al., 2017). However, the MFG has also been shown to be active during number processing tasks (Arsalidou and Taylor, 2011), and the lateral prefrontal cortex (which is largely overlapping with the MFG) has been found to be sensitive to numerosities in non-human primates (Nieder, 2005). Therefore, it is unclear whether the overlap between basic numerical processing and arithmetic in the MFG is due to both tasks relying on basic numerical processes, domain-general processes, or a combination of the two.

Children also demonstrated co-activation of brain regions outside of the parietal cortex for large arithmetic problems and number processing, including the right insula and the dorsal superior frontal gyrus. Some researchers have suggested that children may be more reliant on the insular cortices during arithmetic due to their role in motivated, goal-directed processes (Arsalidou et al., 2017). Previous research has also shown that the SFG is activated during both arithmetic and basic numerical processing tasks (Arsalidou et al., 2017; Arsalidou and Taylor, 2011; Houdé et al., 2010; Sokolowski et al., 2017). However, the SFG is also commonly activated during visuo-spatial working memory tasks (for a review see Constantinidis and Klingberg, 2016), therefore the SFG may be recruited for more domain-general visuo-spatial aspects of arithmetic and number processing tasks. It is notable that these prefrontal brain regions only emerged in the conjunction analyses examining overlapping activity between Large arithmetic problems and number matching, rather than Small arithmetic problems and number matching. This lends support to the idea that these regions may be more related to domain-general processes, such as goal-directed behaviour and visuo-spatial working memory, which are likely to play a larger role in large arithmetic problems. Together, these findings illustrate that the IPS does not work in isolation to solve numerical and mathematical tasks, rather, these skills rely on the integration of a number of cortical regions.

4.3. Study limitations

It is also important to consider some of the limitations in the present study. First, we used a block design to assess brain activation for Large problems and Small problems. Therefore, we were not directly able to assess trials solved using calculation or retrieval and could only make inferences about cognitive procedures based on problem size. However, it is likely that the outcome would have been similar if even if we had divided the trials by strategy rather than problem size; though there might be some differences in the extent of brain activity, adults and children are likely to recruit similar brain regions when they are performing the same cognitive operations. Future research will need to empirically examine how the relationship between number processing and arithmetic is modulated by strategy on a trial-by-trial basis.

A second limitation of is that the addition and symbol-quantity matching tasks used in this study may not generalize to all operations and number processing tasks. We used addition because it is an age-appropriate task that most children can solve with a relatively high degree of accuracy. Moreover, addition problems are solved using both procedural and retrieval strategies, particularly in children. Our findings could have differed had we selected an operation such as subtraction, but these differences likely would not have been operation-specific but related to the extent to which the operation demanded procedural or retrieval strategies. Recent research has found that neural differences between operations are related to the proportion of problems that are calculated or retrieved and are not operation-specific (Polspoel et al., 2017; Tschentscher and Hauk, 2014). For example, subtraction problems tend to be solved using more procedural strategies than in addition (Campbell and Xue, 2001). Therefore, using subtraction may have shown greater overlap with number processing skills in the IPS compared to addition, which would further support our findings. We also believe that had we used a different number processing task, we likely would have observed a similar pattern of results to those in this study. Two meta-analyses have shown that the IPS (i.e. superior and inferior parietal lobules), SFG, insula, and MFG are activated across a wide range of number processing tasks in children (Arsalidou et al., 2017) and adults (Arsalidou and Taylor, 2011). Our symbol-quantity matching task revealed brain activity that is consistent with this basic number processing network. Overall, using different tasks will ultimately lead to slightly different results, and future research will be needed to determine the extent to which these findings generalize. However, we believe our main results on the overlap between addition and number matching are likely to hold across a variety of arithmetic and basic number processing tasks based on the prior literature.

Finally, it is also important to note that adults were performing with near perfect accuracy on the arithmetic problems and children had more variable performance. Even though we conducted control analyses examining only the highest performing children, differences in the variability of performance between groups might play a role in some of the qualitative differences in brain activity between the groups (e.g. insula and SFG activity for number processing and arithmetic in children, but not adults). To better control for differences in performance and variability between groups, future research could calibrate problem difficulty for each individual to equate performance between adults and children.

4.4. Conclusions

By using a within-subjects approach to examine arithmetic and number processing, we were able to investigate which brain regions underlie these two skills, and how these relationships change with age. Our findings provide evidence that the IPS is a particularly important region for arithmetic and symbol-quantity associations in both adults and children. However, problem size was found to influence the relationship between these two tasks, which may be related to the proportion of problems being solved by calculation or retrieval. We also provided novel evidence that the IPS was recruited to a similar degree for Small problems in children and Large problems in adults, indicating that these conditions may have similar cognitive demands. Therefore, the association between number processing and arithmetic is related to the cognitive operation being performed rather than age. These findings provide the first evidence to directly test the common underlying relationship between basic number processing and arithmetic and suggest the IPS is recruited during arithmetic due to the importance of manipulating quantities in calculation.

Conflict of interest statement

The authors have no conflicts of interest to declare.

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Appendix A. Supplementary data

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References

Ansari, D., 2008. Effects of development and enculturation on number representation in the brain. Nat. Rev. Neurosci. 9 (4), 278–291. https://doi.org/10.1038/nrn2334.

Arsalidou, M., Taylor, M.J., 2011. Is 2 + 2 = 4? Meta-analyses of brain areas needed for numbers and calculations. NeuroImage 54 (3), 2382–2393. https://doi.org/10.1016/j.neuroimage.2010.10.009.

Arsalidou, M., Pawliw-Levac, M., Sadeghi, M., Pascual-Leone, J., 2017. Brain areas associated with numbers and calculations in children: meta-analyses of fMRI studies. Dev. Cogn. Neurosci. (July), 1–12. https://doi.org/10.1016/j.dcn.2017.08.002.

Ashcraft, M.H., 1982. The development of mental arithmetic: a chronometric approach. Dev. Rev. 2 (3), 213–236. https://doi.org/10.1016/0273-2297(82)90012-0.

Bandettini, P.A., Cox, R.W., 2000. Event-related fMRI contrast when using constant interstimulus interval: theory and experiment. Magn. Reson. Med. 43 (4), 540–548. https://doi.org/10.1002/(SICI)1522-2594(200004)43:4 < 540::AID-MRM8 > 3.0.CO;2-R.

Bartelet, D., Vaessen, A., Blomert, L., Ansari, D., 2014. What basic number processing measures in kindergarten explain unique variability in first-grade arithmetic proficiency? J. Exp. Child Psychol. 117, 12–28. https://doi.org/10.1016/j.jecp.2013.08.010.

Brankaer, C., Ghesquière, P., De Smedt, B., 2014. Children's mapping between non-symbolic and symbolic numerical magnitudes and its association with timed and untimed tests of mathematics achievement. PLoS One 9 (4). https://doi.org/10.1371/journal.pone.0093565.

Bugden, S., Ansari, D., 2010. Individual differences in children's mathematical competence are related to the intentional but not automatic processing of Arabic numerals. Cognition 118 (1), 32–44. https://doi.org/10.1016/j.cognition.2010.09.005.

Bugden, S., Price, G.R., McLean, D.A., Ansari, D., 2012. The role of the left intraparietal sulcus in the relationship between symbolic number processing and children's arithmetic competence. Dev. Cogn. Neurosci. 2 (4), 448–457. https://doi.org/10.1016/j.dcn.2012.04.001.

Burgund, E.D., Kang, H.C., Kelly, J.E., Buckner, R.L., Snyder, A.Z., Petersen, S.E., Schlaggar, B.L., 2002. The feasibility of a common stereotactic space for children and adults in fMRI studies of development. NeuroImage 17 (1), 184–200. https://doi.org/10.1006/nimg.2002.1174.

Campbell, J.I., Xue, Q., 2001. Cognitive arithmetic across cultures. J. Exp. Psychol. Gen. 130 (2), 299–315. https://doi.org/10.1037/0096-3445.130.2.299.

Constantinidis, C., Klingberg, T., 2016. The neuroscience of working memory capacity

and training. Nat. Rev. Neurosci. 17 (7), 438–449. https://doi.org/10.1038/nrn.2016.43.
De Smedt, B., Holloway, I.D., Ansari, D., 2010. Effects of problem size and arithmetic operation on brain activation during calculation in children with varying levels of arithmetical fluency. NeuroImage. https://doi.org/10.1016/j.neuroimage.2010.12.037.
De Smedt, B., Noël, M.-P., Gilmore, C., Ansari, D., 2013. How do symbolic and non-symbolic numerical magnitude processing skills relate to individual differences in children's mathematical skills? A review of evidence from brain and behavior. Trends Neurosci. Educ. 2 (2), 48–55. https://doi.org/10.1016/j.tine.2013.06.001.
Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., Mazoyer, B., 1996. Cerebral activations during number multiplication and comparison: a PET study. Neuropsychologia 34 (11), 1097–1106. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/8904747.
Dehaene, S., Piazza, M., Pinel, P., Cohen, L., 2003. Three parietal circuits for number processing. Cogn. Neuropsychol. 20 (3), 487–506. https://doi.org/10.1080/02643290244000239.
Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., Benke, T., 2003. Learning complex mathematics - a fMRI study. Cogn. Brain Res. 18 (1), 76–88.
Delazer, M., Ischebeck, a, Domahs, F., Zamarian, L., Koppelstaetter, F., Siedentopf, C.M., et al., 2005. Learning by strategies and learning by drill—evidence from an fMRI study. NeuroImage 25 (3), 838–849. https://doi.org/10.1016/j.neuroimage.2004.12.009.
Emerson, R.W., Cantlon, J.F., 2012. Early math achievement and functional connectivity in the fronto-parietal network. Dev. Cogn. Neurosci. 2, S139–S151. https://doi.org/10.1016/j.dcn.2011.11.003.
Emerson, R.W., Cantlon, J.F., 2014. Continuity and change in children's longitudinal neural responses to numbers. Dev. Sci. https://doi.org/10.1111/desc.12215. n/a-n/a.
Forman, S., Cohen, J., Fitzgerald, M., Eddy, W.F., Mintun, M.A., Noll, D., 1995. Improved assessment of significant activation in functional magnetic resonance imaging (fMRI): Use of a cluster-size threshold. Magn. Reson. Med. 5, 636–647.
Göbel, S.M., Watson, S.E., Lervåg, A., Hulme, C., 2014. Children's arithmetic development: it is number knowledge, not the approximate number sense, that counts. Psychol. Sci. 25 (3), 789–798. https://doi.org/10.1177/0956797613516471.
Goebel, R., Esposito, F., Formisano, E., 2006. Analysis of functional image analysis contest (FIAC) data with brainvoyager QX: from single-subject to cortically aligned group general linear model analysis and self-organizing group Independent component analysis. Hum. Brain Mapp. 27 (5), 392–401. https://doi.org/10.1002/hbm.20249.
Goffin, C., Ansari, D., 2016. Beyond magnitude: judging ordinality of symbolic number is unrelated to magnitude comparison and independently relates to individual differences in arithmetic. Cognition 150 (2016), 68–76. https://doi.org/10.1016/j.cognition.2016.01.018.
Grabner, R.H., Ansari, D., Reishofer, G., Stern, E., Ebner, F., Neuper, C., 2007. Individual differences in mathematical competence predict parietal brain activation during mental calculation. NeuroImage 38 (2), 346–356. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/17851092.
Grabner, R.H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., Neuper, C., 2009. To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. Neuropsychologia 47 (2), 604–608. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/19007800.
Grabner, R.H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., 2013. The function of the left angular gyrus in mental arithmetic: evidence from the associative confusion effect. Hum. Brain Mapp. 34 (5), 1013–1024. https://doi.org/10.1002/hbm.21489.
Holloway, I.D., Ansari, D., 2009. Mapping numerical magnitudes onto symbols: the numerical distance effect and individual differences in children's mathematics achievement. J. Exp. Child Psychol. 103 (1), 17–29. https://doi.org/10.1016/j.jecp.2008.04.001.
Houdé, O., Rossi, S., Lubin, A., Joliot, M., 2010. Mapping numerical processing, reading, and executive functions in the developing brain: an fMRI meta-analysis of 52 studies including 842 children. Dev. Sci. 13 (6), 876–885. https://doi.org/10.1111/j.1467-7687.2009.00938.x.
Imbo, I., Vandierendonck, A., 2008. Effects of problem size, operation, and working-memory span on simple-arithmetic strategies: differences between children and adults? Psychol. Res. 72 (3), 331–346. https://doi.org/10.1007/s00426-007-0112-8.
Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstätter, F., Benke, T., Felber, S., Delazer, M., 2006. How specifically do we learn? Imaging the learning of multiplication and subtraction. NeuroImage 30 (4), 1365–1375. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/16413795.
Kolkman, M.E., Kroesbergen, E.H., Leseman, P.P.M., 2013. Early numerical development and the role of non-symbolic and symbolic skills. Learn. Instr. 25, 95–103. https://doi.org/10.1016/j.learninstruc.2012.12.001.
Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., Gollub, R., 2005. The neural substrate of arithmetic operations and procedure complexity. Cogn. Brain Res. 22 (3), 397–405. https://doi.org/10.1016/j.cogbrainres.2004.09.011.
LeFevre, J.-A., Bisanz, J.J., Daley, K.E., Buffone, L., Greenham, S.L.S.L., Sadesky, G.S., 1996. Multiple routes to solution of single-digit multiplication problems. J. Exp. Psychol. Gen. 125 (3), 284–306. https://doi.org/10.1037/0096-3445.125.3.284.
Linsen, S., Verschaffel, L., Reynvoet, B., De Smedt, B., 2015a. The association between numerical magnitude processing and mental versus algorithmic multi-digit subtraction in children. Learn. Instr. 35 (February 2015), 42–50. https://doi.org/10.1016/j.learninstruc.2014.09.003.
Linsen, S., Verschaffel, L., Reynvoet, B., De Smedt, B., 2015b. The association between symbolic and nonsymbolic numerical magnitude processing and mental versus algorithmic subtraction in adults. Acta Psychol. (Amst) 35 (April), 42–50. https://doi.org/10.1016/j.learninstruc.2014.09.003.
Lyons, I.M., Price, G.R., Vaessen, A., Blomert, L., Ansari, D., 2014. Numerical predictors of arithmetic success in grades 1-6. Dev. Sci. 17 (5), 714–726. https://doi.org/10.1111/desc.12152.
Matejko, A.A., Ansari, D., 2017. 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. Hum. Brain Mapp. 38 (8), 3941–3956. https://doi.org/10.1002/hbm.23640.
Matejko, A.A., Ansari, D., 2018. Contributions of functional Magnetic Resonance Imaging (fMRI) to the study of numerical cognition. J. Numer. Cogn. 4 (3), 505–525. https://doi.org/10.5964/jnc.v4i3.136.
Mundy, E., Gilmore, C.K., 2009. Children's mapping between symbolic and nonsymbolic representations of number. J. Exp. Child Psychol. 103 (4), 490–502. https://doi.org/10.1016/j.jecp.2009.02.003.
Nieder, A., 2005. Counting on neurons: the neurobiology of numerical competence. Nat. Rev. Neurosci. 6 (3), 177–190. https://doi.org/10.1038/nrn1626.
Polspoel, B., Peters, L., De Smedt, B., 2017. Strategy over operation: neural activation in subtraction and multiplication during fact retrieval and procedural strategy use in typically developing children. Hum. Brain Mapp. 38 (9), 4657–4670. https://doi.org/10.1002/hbm.23691.
Price, G.R., Fuchs, L.S., 2016. The mediating relation between symbolic and nonsymbolic foundations of math competence. PLoS One 11 (2), e0148981. https://doi.org/10.1371/journal.pone.0148981.
Price, G.R., Mazzocco, M.M.M., Ansari, D., 2013. Why mental arithmetic counts: brain activation during single digit arithmetic predicts high school math scores. J. Neurosci. 33 (1), 156–163. https://doi.org/10.1523/JNEUROSCI.2936-12.2013.
Purpura, D.J., Baroody, A.J., Lonigan, C.J., 2013. The transition from informal to formal mathematical knowledge: mediation by numeral knowledge. J. Educ. Psychol. 105 (2), 453–464. https://doi.org/10.1037/a0031753.
Rickard, T.C., Romero, S.G., Basso, G., Wharton, C., Flitman, S., Grafman, J., 2000. The calculating brain: an fMRI study. Neuropsychologia 38 Elsevier. Retrieved from. http://www.ncbi.nlm.nih.gov/pubmed/10678698.
Rivera, S.M.M., Reiss, A.L.L., Eckert, M.A., Menon, V., 2005. Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. Cereb. Cortex 15 (11), 1779–1790. https://doi.org/10.1093/cercor/bhi055.
Sasanguie, D., De Smedt, B., Defever, E., Reynvoet, B., 2012. Association between basic numerical abilities and mathematics achievement. Br. J. Dev. Psychol. 30 (2), 344–357. https://doi.org/10.1111/j.2044-835X.2011.02048.x.
Schneider, M., Beeres, K., Coban, L., Merz, S., Schmidt, S.S., Stricker, J., De Smedt, B., 2016. Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: a meta-analysis. Dev. Sci. (1), 1–16. https://doi.org/10.1111/desc.12372.
Sokolowski, H.M., Fias, W., Mousa, A., Ansari, D., 2017. Common and distinct brain regions in both parietal and frontal cortex support symbolic and nonsymbolic number processing in humans: a functional neuroimaging meta-analysis. NeuroImage 146 (February 2016), 376–394. https://doi.org/10.1016/j.neuroimage.2016.10.028.
Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain, 1988, vol. 270. Theime, Stuttgart, Germany, pp. 132. https://doi.org/10.1016/0303-8467(89)90128-5.
Tschentscher, N., Hauk, O., 2014. How are things adding up? Neural differences between arithmetic operations are due to general problem solving strategies. NeuroImage 92, 369–380. https://doi.org/10.1016/j.neuroimage.2014.01.061.
Zamarian, L., Ischebeck, A., Delazer, M., 2009. Neuroscience of learning arithmetic—evidence from brain imaging studies. Neurosci. Biobehav. Rev. 33 (6), 909–925. https://doi.org/10.1016/j.neubiorev.2009.03.005.