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Neural correlates of symbolic and non-symbolic arithmetic

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Abstract

Recent evidence suggests that areas in and around the intraparietal sulcus (IPS) represent magnitude in a stimulus-independent format. However, it has not been established whether the same is true for mental arithmetic or whether activation for higher level numerical processing diverges as a function of stimulus format. We addressed this question in a functional imaging study by presenting participants with simple addition problems using both symbolic (Arabic numerals) and non-symbolic (arrays of dots) stimuli. Conjunction analysis revealed common neural substrates for symbolic and non-symbolic addition in the anterior IPS bilaterally, left posterior IPS, medial frontal gyrus and left precentral gyrus. Right parietal and frontal cortex showed greater activation for non-symbolic addition. Our results demonstrate that mental arithmetic, studied using addition problems, is processed within the IPS independent of stimulus form. Additionally we examined whether exact and approximate addition conditions activated different neural substrates as a function of stimulus format. We did not find any differences between exact and approximate addition using symbolic and non-symbolic stimuli. This could be due to the inability of the participants to suppress exact calculation for single-digit addition problems. In contrast to recent findings, we found no significant activation for exact addition condition in left, language-related areas.

Keywords: Functional MRI; Numerical cognition; Addition; Intraparietal sulcus

1. Introduction

Over the last decade, significant advances have been made in uncovering the neural basis of numerical cognition. Evidence from the study of brain-damaged patients indicates that when the inferior parietal lobes are damaged in adulthood specific deficits in number processing result (Cipolotti, Butterworth, & Denes, 1991; Dehaene & Cohen, 1997; Gerstman, 1957; Mayer et al., 1999). Functional brain imaging studies with healthy individuals show the parietal regions to be consistently activated in numerical tasks (Dehaene & Cohen, 1995; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Pesenti, Thioux, Seron, & De Volder, 2000; Pinel, Dehaene, Riviere, & LeBihan, 2001; Pinel et al., 1999). It has been hypothesised that the intraparietal sulcus (IPS) in particular, represents quantity in an abstract format (Dehaene, Dehaene-Lambertz, & Cohen, 1998). One functional-anatomical model of numerical cognition, the "triple-code model", posits that modality specific codes of numerical information are converted into an abstract and amodal code for number and that these representations are held within the parietal lobes (Dehaene & Cohen, 1995). Furthermore, this model posits that exact arithmetic facts are stored in a verbal format in left-hemispheric perisylvian areas of the brain. Thus, according to the triple code model, there are at least two routes to solving mental arithmetic problems: a direct route involving rote retrieval of arithmetic facts (like simple addition and multiplication) from the language-related frontal regions and an indirect semantic route involving the quantity code in the parietal lobes for solving subtraction and complex addition (Cohen, Dehaene, Chochon, Lehericy, & Naccache, 2000; Dehaene & Cohen, 1995, 1997).Recent evidence has revealed that the IPS is activated when participants made

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both magnitude comparisons between symbolic (digits) and non-symbolic (lines and angles) stimuli (Fias, Lammertyn, Reynvoet, Dupont, & Orban, 2003). Conjunction analysis of all three types of magnitude comparisons revealed a region in the left IPS. In another experiment, participants were presented with numbers, letters and colours in the visual and auditory modalities and were asked to respond to a target item within each of the three categories. Across both modalities, numbers activated a bilateral region in the horizontal IPS to a greater extent than both letters and colours even though participants had not been instructed to attend to number (Eger, Sterzer, Russ, Giraud, & Kleinschmidt, 2003).

The IPS has also been shown to be activated during the processing of mental arithmetic with symbolic stimuli (Menon, Rivera, White, Glover, & Reiss, 2000; Pesenti et al., 2000; Zago et al., 2001). It has been shown that subtraction with Arabic numerals alone activated the IPS among a variety of tasks including pointing, visual saccades, phoneme detection and attention, suggesting a specialized role played by the parietal cortex in the processing of numerical quantity (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). However, it remains to be determined whether mental arithmetic is processed by the IPS in a stimulus-independent manner as has been shown to be the case for simple numerical magnitude processing. To clarify this, we studied healthy adult volunteers as they solved simple addition problems presented in both symbolic (Arabic numerals) and non-symbolic (arrays of dots) stimulus formats.

Additionally, participants were instructed to compute symbolic and non-symbolic arithmetic both exactly as well as approximately. The dissociation between exact and approximate calculation was first proposed by Dehaene et al. (1999), who found greater activation in left frontal areas and the left angular gyrus for exact addition (areas typically involved in language processing) and greater parietal activation for approximate addition using small numbers. In an extension to this study using larger numbers, exact arithmetic was found to increasingly correlate with parietal activation and thus converge with the activation found to underlie approximate calculation (Stanescu-Cosson et al., 2000). More recently, the differences between exact and approximate addition reported by Dehaene et al. (1999) were only partially replicated in an fMRI study using the same paradigm with both normal participants as well as subjects with Turner Syndrome (Molko et al., 2003). In the group of normal participants, approximate addition was found to result in greater activation of IPS. However, this was not found to be true of the group of patients with TS. Most importantly, no significantly greater activation was found for exact versus approximate addition for both the normal and clinical group.

Several neuropsychological and imaging studies have also shown that verbal processes are not obligatory for solving simple exact addition (Dehaene & Cohen, 1997; Pesenti et al., 2000; van Harskamp & Cipolotti, 2001). In their PET study, Pesenti et al. (2000) were unable to detect significant activation in language-related areas of the brain during simple exact addition. Furthermore, Dehaene and Cohen (1997) report data from a patient (BOO) with left frontal subcortical damage whose performance, while being strongly impaired on multiplication, was slow but fairly accurate on addition problems. In another study, van Harskamp and Cipolotti (2001) report data from a patient (FS) who, following damage to the left middle temporal and parietal lobes, exhibited a selective impairment on addition problems with intact subtraction and multiplication performance. Such data suggest that mental addition is also reliant on the quantity representation in the parietal lobes and several strategies other than the retrieval of verbally stored facts may be used by adults for solving these problems (LeFevre, Sadesky, & Bisanz, 1996). With regards to the triple-code model (Dehaene & Cohen, 1995), these findings may suggest that addition problems are typically solved via the indirect semantic route which involves the actual activation of the quantity representations of the operands in a given arithmetic problem and thus primarily involves the parietal lobes. Given the current uncertainty surrounding the role of verbal processes in mental addition, we sought to examine the reliability of the fronto-parietal dissociation between exact and approximate number processing using simple addition as a secondary aim of our study.

2. Methods

2.1. Experimental procedure

Ten healthy right-handed participants (three females) aged between 20 and 25 years gave informed, written consent for this block-design fMRI study. They performed exact and approximate addition on problems presented in two different formats: symbolic (Arabic numerals) and non-symbolic (dots, similar to those on the faces of a dice) in addition to a control number matching task using both numbers and dots. For the addition tasks, they selected an appropriate answer from two alternatives provided subsequently (Fig. 1). They were instructed at the beginning of each run regarding the task to be performed.

The experiment consisted of eight runs with each run comprising of only one of the four experimental tasks and the corresponding control task. Each run started with a 24 s fixation block followed by four experimental and four control blocks of 15 s duration each alternating with fixation of 18 s (Fig. 1). The first four scans from the total of 96 acquisitions in each run were discarded to allow for steady-state magnetization. The order of experimental tasks was carefully counterbalanced across different subjects.

Each experimental block consisted of six events of 2.5 s each (Fig. 1). In each event, an addition problem was flashed for 200 ms. After a 200 ms fixation interval, two numerical choices were presented for another 200 ms at the same location as the operands. Participants then responded by pressing

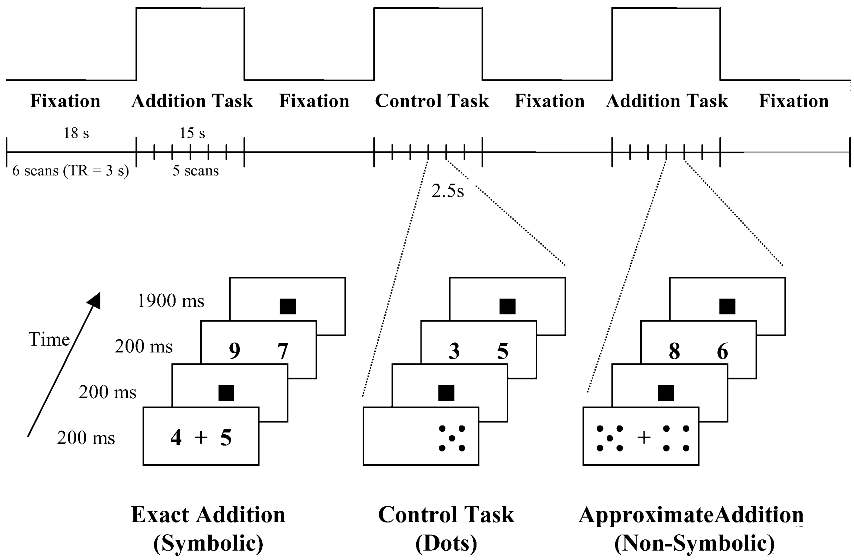

Fig. 1. Schematic showing exemplars of the stimulus display and the timings used in different trial types. This figure provides an illustration of some of the conditions used in this study and does not represent any particular run from the experiment.

a button on a response box. This was again followed by fixation for 1900 ms till the next problem was presented.

The timing and stimuli for the control blocks were similar to the experimental blocks except that subjects were presented with only one operand (a number for symbolic runs and an array of dots for non-symbolic runs) randomly to the left or right of the fixation followed by two choices. Participants were instructed to press the button corresponding to the choice with the same numerical value as the first operand. The control tasks were identical for both exact and approximate runs and were intended to control for surface features and processes related to making directed motor responses. To ensure similar control task performance across the entire experiment, participants performed four blocks of each of the control task outside the scanner. They also performed one block of each of the experimental tasks inside the scanner prior to the actual scanning session to gain familiarity with the experimental paradigm and presentation formats.

2.2. Stimuli

The operands for the symbolic addition tasks were Arabic numerals presented in Times New Roman. The dots for non-symbolic stimuli were arranged like those on the face of a dice. The choices were presented as Arabic numerals for both symbolic and non-symbolic tasks. For all problems, the stimuli ranged from 1 to 5 and problems involving ties (2 + 2) were avoided. For the exact task, the two alternatives proposed were the correct result and a result that was off by two units. In all problems, the two alternatives were of the same parity. For the approximation task, the two alternatives were a number off by at most two units and another number off by at least three units. The choices were always single digit numbers (1–9). The location of the correct response (left or right) was randomly varied and balanced. Each addition problem was repeated at most twice within each experimental task and the same problem was never repeated within the same block.

2.3. Imaging and image analysis

Imaging was performed in a Siemens 3T Allegra system (Siemens Allegra, Erlangen, Germany). Arithmetic addition problems were rear-projected (Epson EMP 7250) onto a silk screen placed at the rear of the magnet bore. Participants viewed the problems via an angled mirror fastened to the head coil. A bite-bar was used to reduce head motion. Thirty-two oblique axial slices were acquired approximately parallel to the AC-PC line using a $T2^*$ weighted gradient-echo EPI sequence (TR = 3000 ms; effective TE = 30 ms; matrix = 64 × 64; FOV = 192 mm × 192 mm; 3.0 mm thickness, 0.3 mm gap). A set of T2 weighted images was acquired in an identical orientation to the functional MR data. High-resolution anatomical reference images were obtained using a three-dimensional MP-RAGE sequence.

The functional images from each subject were preprocessed and analyzed using BrainVoyager 2000 software version 4.9 (Brain Innovation, Maastricht, Holland). Mean intensity normalization was performed for the group analysis. In the spatial domain, data were smoothed with a Gaussian smoothing kernel of 8 mm FWHM for group analysis. A temporal high pass filter of period 100 s was applied following linear trend removal. The functional images were aligned to co-planar high-resolution images and the image stack was then aligned to a high-resolution three-dimensional image of the brain. The resulting realigned data set was transformed into Talairach space (Talairach & Tournoux, 1988).

The expected BOLD signal change was modeled using a gamma function (tau of 2.5 s and a delta of 1.5) convolved with the blocks of cognitive tasks (Boynton, Engel, Glover, & Heeger, 1996). Fixed-effect analysis at the group level was performed using a general linear model (GLM). The threshold for considering a voxel significantly activated was $p < 0.001$ uncorrected. Since each experimental task was performed in separate runs, between task effects were estimated after subtracting the appropriate control tasks. For example, to compare exact addition against approximate addition using symbolic stimuli, we use the contrast (symbolic exact – its control) – (symbolic approximate – its control). A region was considered active only if both exact and approximate addition were more active than their control tasks and the difference between exact addition and its control was significantly greater than the difference between approximate addition and its control. Unless otherwise stated, all results and analyses presented for the experimental tasks followed the subtraction of the appropriate control tasks.

2.4. Post-experimental debriefing

At the end of the fMRI session, a careful debriefing was carried out individually using questionnaires. Participants were asked to assess the relative difficulties of adding symbolic and non-symbolic problems as well as exact and approximate. They were also asked to explain any differences in strategy in solving the different types of problems. Specifically, they were asked if they adopted a two-stage process of computing the result and comparing the solution for approximate calculations.

3. Results

3.1. Behavioral results

Analysis of the reaction time data revealed significant main effects for both stimulus: $F(1, 9) = 33.4$, $p < 0.001$ and calculation: $F(1, 9) = 18.4$, $p < 0.002$. Participants were faster at symbolic than non-symbolic addition and were slower during approximate compared to exact addition. In addition, response times showed a stimulus by calculation interaction: $F(1, 9) = 7.5$, $p < 0.023$. For both symbolic and non-symbolic addition, exact was faster than approximate; this difference being greater for symbolic than non-symbolic addition (Table 1).

Analysis of the accuracy data revealed no significant main effects for both stimulus and calculation. Participants were more accurate when performing approximate relative to exact calculations for non-symbolic addition ($F(1, 9) = 7.4$, $p < 0.024$). There was no difference in accuracy between the two conditions for symbolic addition.

In the control tasks, numbers were processed more quickly ($F(1, 9) = 13.1$, $p < 0.006$) and accurately ($F(1, 9) = 12.8$, $p < 0.006$) compared to dots.

3.2. Introspective reports

Most of the participants (80%) found it more difficult to perform non-symbolic and approximate addition compared to symbolic and exact addition respectively. Eight participants indicated that they found themselves just performing exact addition and then comparing the solutions for approximate addition, with four of them further stating that they found themselves using this strategy only for symbolic problems. For non-symbolic addition, these four subjects indicated that they used a similar strategy of estimating the number of dots, for both exact and approximate addition.

3.3. Functional imaging

Symbolic addition, contrasted with its respective control tasks, activated the bilateral anterior intraparietal sulcus, left posterior intraparietal sulcus, left precentral gyrus and medial frontal gyrus during both exact and approximate calculation. Additionally, approximate addition also activated bilaterally the insular regions. Non-symbolic addition, on the other hand, activated regions along the anterior and posterior intraparietal sulcus, precentral gyrus, dorsolateral prefrontal cortex, insula and fusiform gyrus bilaterally during both exact and approximate calculation. Reported activation for the experimental tasks henceforth refer to voxels significantly activated subsequent to the subtraction of the appropriate control task.

3.3.1. Stimulus-independent activation for addition

The conjunction of activation for all four experimental tasks, exact and approximate addition over both symbolic and non-symbolic stimuli, revealed voxels lying in the bilateral anterior IPS, left posterior IPS, medial frontal gyrus and the left precentral gyrus (Table 3, Fig. 2). Separate conjunctions of symbolic and non-symbolic exact addition yielded results very similar to the conjunction across all four experimental tasks. For approximation, additional activation was observed in the left and right insula.

Table 1
Mean accuracy and response times for each of the experimental and control tasks

Experimental task	Symbolic		Non-symbolic	
	Proportion correct	Reaction time (ms)	Proportion correct	Reaction time (ms)
Exact addition	0.96 (0.036)	357 (85)	0.91 (0.080)	514 (136)
Approximate addition	0.96 (0.010)	457 (113)	0.94 (0.079)	555 (156)
Control (exact addition runs)	0.98 (0.033)	311 (103)	0.97 (0.022)	351 (98)
Control (approximate addition runs)	0.99 (0.010)	317 (106)	0.95 (0.027)	349 (96)

Numbers in parentheses denote S.D.

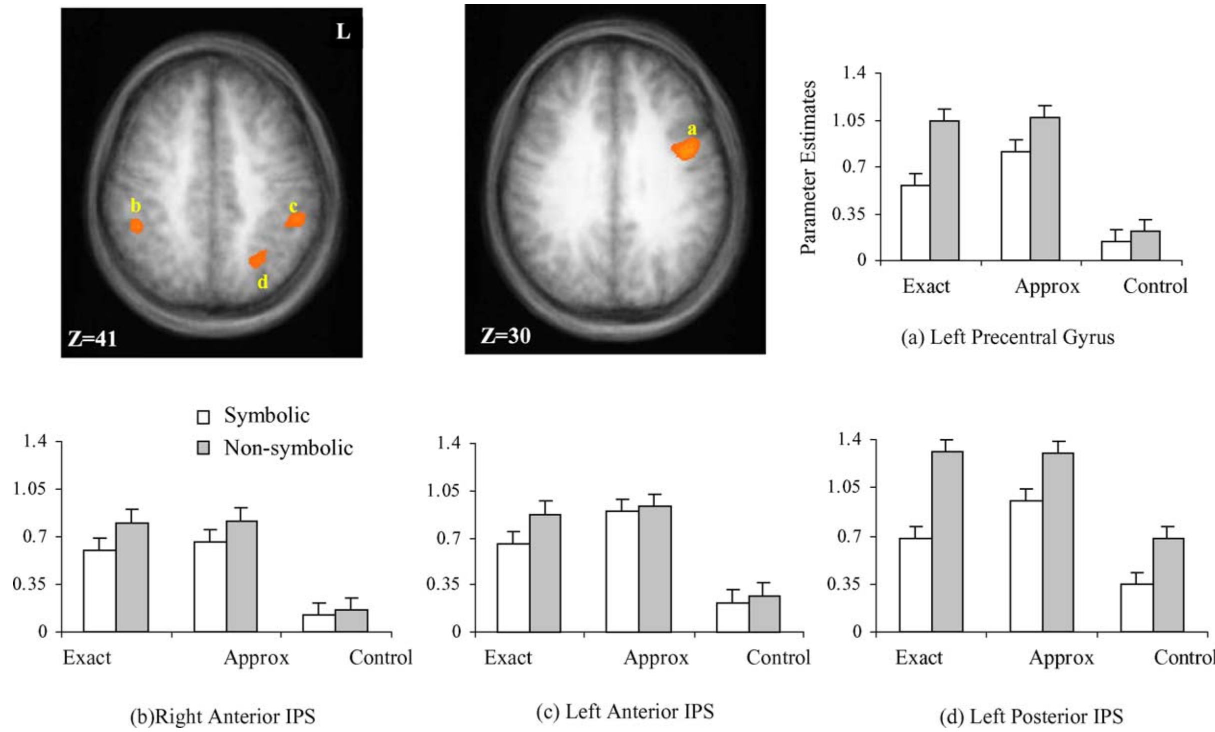

Fig. 2. Axial slices showing areas activated in the conjunction of all four experimental tasks: exact and approximate addition of symbolic and non-symbolic stimuli. The parameter estimates (*z*-scores) for the different tasks (vs. fixation) from the fixed-effect analysis are also provided. The estimates for the control task are averaged across exact and approximate additions. Error bars denote standard error.

3.3.2. Differences between non-symbolic and symbolic addition

Non-symbolic addition resulted in greater BOLD signal change and less asymmetric activation compared to the predominantly left-lateralized symbolic activation associated with addition using symbols (Table 2). To establish specifically, if there were stimulus specific differences in performing addition, we compared non-symbolic versus symbolic addition collapsed across both exact and approximate problems. The contrast revealed significant activation in the right posterior intraparietal sulcus and bilateral dorsolateral prefrontal cortex (DLPFC), precentral gyrus, insula and posterior intraparietal sulcus (Table 3, Fig. 3). Activation was always higher in magnitude for non-symbolic relative to symbolic addition. There were no regions with greater activation for symbolic compared to non-symbolic addition.

3.3.3. Exact versus approximate calculations

For symbolic stimuli, approximate addition activated additional areas in the bilateral insula compared to exact addition (Table 2). The comparison of activation magnitude in Fig. 2 also suggests increased activation for approximate addition in the left anterior IPS although a direct contrast between approximate and exact addition did not reveal any significant activation at the selected threshold. There were no differences in regions activated by approximate and exact addition for non-symbolic stimuli.

Finally, no significant differences in activation were found for exact versus approximate addition contrast using both symbolic and non-symbolic stimuli. Specifically, none of the classical perisylvian frontal language areas were found activated for exact addition using symbolic stimuli. This was even true when the addition was contrasted against fixation.

4. Discussion

Previous brain imaging studies have established the involvement of the parietal lobe in mental arithmetic and identified a region in the parietal lobe involved in supramodal representation of number magnitude (Dehaene et al., 1998; Dehaene, Piazza, Pinel, & Cohen, 2003). The primary aim of this study was to establish whether stimulus-independent regions, similar to those discovered by Fias et al. (2003) for magnitude comparisons, are also involved in performing mental arithmetic. Against the background of recent functional neuroimaging data suggesting that the mere presentation of numerical stimuli leads to magnitude-related activation in the parietal lobes (Eger et al., 2003; Naccache & Dehaene, 2001), we contend that the choice of our control task helps in isolating the experimental conditions of interest (mental arithmetic) from the stimulus-independent magnitude-related activation. We chose to use only one numeral or dot array in our control task to prevent automatic

Table 2
Talairach coordinates of activation peaks for each of the experimental tasks, contrasted with their respective controls, obtained from fixed-effect analysis at $p < 0.001$, uncorrected threshold

Brain region	Talairach coordinates							
	Left Hemisphere				Right Hemisphere			
	x	*y*	*z*	*t*	*x*	*y*	*z*	*t*
Symbolic exact addition								
Medial frontal gyrus	–	–	–		2	6	54	4.10
Precentral gyrus	−43	4	30	**5.22**	–	–	–	
Intraparietal sulcus (anterior)	−49	−38	45	4.50	47	−41	39	**4.98**
Intraparietal sulcus (posterior)	−28	−62	39	4.17	–	–	–	
Symbolic approximate addition								
Medial frontal gyrus	−4	4	53	**5.18**	–		–	
Precentral gyrus	−43	0	30	**4.89**	–		–	
Intraparietal sulcus (anterior)	−49	−38	39	**6.15**	44	−41	45	4.68
Intraparietal sulcus (posterior)	−31	−59	39	**5.29**	–	–	–	
Insula	−34	16	9	**4.90**	27	16	9	4.40
Non-symbolic exact addition								
Medial frontal gyrus	−4	14	45	**7.06**	–	–	–	
Precentral gyrus	−41	1	30	**8.66**	–	–	–	
Intraparietal sulcus (anterior)	−46	−38	48	**6.04**	*	*	*	
Intraparietal sulcus (posterior)	−31	−59	36	**7.62**	29	−56	36	**6.65**
Insula	−34	16	5	**7.51**	29	16	3	**8.08**
Dorsolateral prefrontal cortex	−43	26	24	**6.64**	47	34	26	**6.60**
Fusiform gyrus	−49	−53	−10	**6.12**	50	−44	−12	**6.37**
Non-symbolic approximate addition								
Medial frontal gyrus	−7	6	51	**6.63**	–	–	–	
Precentral gyrus	−43	4	24	**8.30**	35	7	24	**6.11**
Intraparietal sulcus (anterior)	−52	−38	41	**6.96**	47	−35	42	**7.05**
Intraparietal sulcus (posterior)	−28	−62	32	**7.28**	26	−59	30	**7.68**
Insula	−28	17	12	**7.07**	29	19	13	**7.52**
Dorsolateral prefrontal cortex	−37	34	23	**6.32**	41	37	24	**5.47**
Fusiform gyrus	−50	−50	−12	**5.46**	50	−41	−15	**5.27**

The values in bold indicate regions that were significantly active at a threshold of $p < 0.05$, corrected for multiple comparisons across the whole brain.
* The anterior IPS activations for non-symbolic exact addition were not clearly separable from the posterior IPS activation.

Table 3
Talairach coordinates of activation peaks showing common and distinct areas across symbolic and non-symbolic addition obtained from the fixed-effect analysis at $p < 0.001$, uncorrected threshold

Brain region	Talairach coordinates							
	Left Hemisphere				Right Hemisphere			
	x	*y*	*z*	*t*	*x*	*y*	*z*	*t*
Conjunction (symbolic and non-symbolic addition, exact and approximate)								
Medial frontal gyrus	–	–	–		2	7	54	4.22
Precentral gyrus	−43	1	30	**5.13**	–	–	–	
Intraparietal sulcus (anterior)	−49	−38	45	4.50	44	−41	42	4.23
Intraparietal sulcus (posterior)	−28	−62	39	4.17	–	–	–	
Non-symbolic–symbolic (collapsed across exact and approximate addition)								
Medial frontal gyrus	−1	22	42	**4.93**	–	–	–	
Precentral gyrus	−37	−5	33	4.55	32	5	27	4.11
Intraparietal sulcus (anterior)	–	–	–		38	−46	48	4.03
Intraparietal sulcus (posterior)	−31	−62	27	4.67	29	−65	33	**5.04**
Insula	−28	25	11	4.48	31	25	18	**5.80**
Dorsolateral prefrontal cortex	−37	16	27	**5.08**	47	16	33	4.47

The values in bold indicate regions that survived threshold of $p < 0.05$, corrected for multiple comparisons across the whole brain at voxel level.

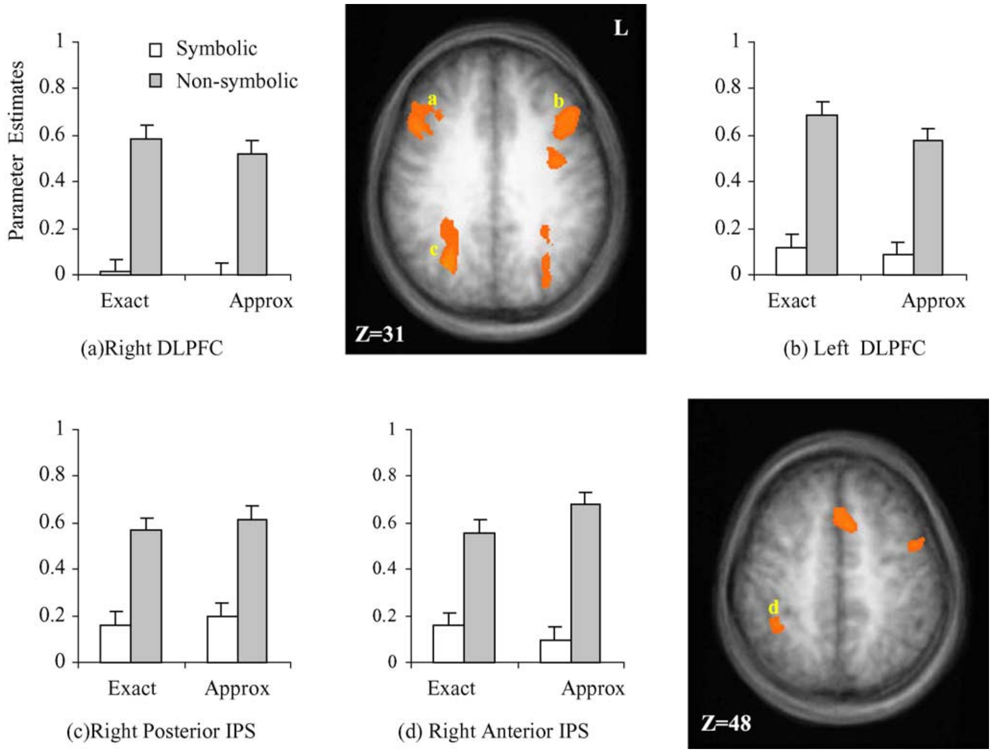

Fig. 3. Axial slices showing increased activation for non-symbolic addition compared to symbolic addition, collapsed across both exact and approximate, using fixed-effect analysis. The parameter estimates (z-scores) for each of the experimental tasks, following the subtraction of control task, from the four ROIs are shown. Error bars indicate standard error.

addition. It could be argued that this did not fully control for the visual demands of the corresponding experimental task. However, we took care to randomize and counterbalance the side on which the number or dot array was presented and did not find any differences in activation in primary visual areas between the control and experimental tasks, indicating that they were well matched with respect to visual demands.

The conjunction of symbolic and non-symbolic exact and approximate addition, following the subtraction of the control task, revealed common activation in the anterior IPS bilaterally, the left posterior IPS and the left precentral gyrus. Only the left posterior IPS among the conjunction sites was found to be activated even in the symbolic and non-symbolic control tasks, indicating that this region may be involved in the stimulus-independent representation of magnitude both when simply accessing number representations and when performing mental arithmetic. This site is in very good accordance with previous studies showing regions for supramodal number representations that are automatically accessed during the presentation of numbers (Eger et al., 2003).

The bilateral anterior IPS and left precentral gyrus were only activated during addition and not during the control tasks, suggesting specifically that they participate in mental arithmetic. The left anterior IPS has been implicated in a number of studies involving mental arithmetic and number comparisons (Dehaene et al., 2003). The present results add to existing knowledge concerning numerical computation by showing that addition activates areas in the left inferior parietal lobe regardless of the surface characteristics of the numerical stimuli.

Activation in the left precentral gyrus has also been reported previously in functional brain imaging experiments using multiplication (Dehaene et al., 1996) and addition tasks (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Pesenti et al., 2000). However, the actual role played by precentral gyrus in numerical tasks is still unclear. It has been suggested that this region together with the left parietal activation constitutes a finger-movement network that may underlie finger counting (Butterworth, 1999a,b; Pesenti et al., 2000). Perhaps finger counting plays a fundamental role in the development of addition skills (Geary, 2000) and therefore areas underlying finger counting, such as the precentral gyrus, come to represent aspects of mental arithmetic over developmental time, leading to their activation during addition task in adulthood.

In addition to the common areas, we also found some differences in activation between symbolic and non-symbolic addition. In general, we found greater activation for non-symbolic addition compared to symbolic addition, attributable to lesser familiarity and greater processing demands for our visuo-spatial dot stimuli. Non-symbolic addition also resulted in more bilateral activation. These observed hemispheric differences in the parietal lobes are consistent with the observation that left and right parietal lobes have slightly different roles in number processing. In general, left parietal activations have been predominantly observed during calculation (Chochon et al., 1999; Pesenti et al., 2000; Zago et al., 2001) while more bilateral activation has been revealed during magnitude comparison (Chochon et al., 1999; Pinel et al., 2001; Pinel et al., 1999). The visuo-spatial nature of the non-symbolic task may require greater processing of magnitude information and thus results in greater involvement of right parietal areas.

In addition, activation of the posterior IPS has previously been associated with serial shifts in attention and eye movements (Culham & Kanwisher, 2001; Wojciulik & Kanwisher, 1999). Even though we used familiar patterns for arrangement of the dots and presented them only for a short interval of 200 ms, subjects could still have tried to scan the display. Right parietal activations similar to those observed in the present study have been found in experiments in which the counting of objects was compared with subitizing (Piazza, Mechelli, Price, & Butterworth, 2002; Sathian et al., 1999). Taken together, these considerations lend support to notion that the slightly greater bilateral parietal activation for our non-symbolic stimuli can be attributed to the characteristics of the stimuli.

The activation in the insula and dorsolateral prefrontal cortices for non-symbolic addition could indicate the use of a counting strategy to estimate the number of dots, before adding them. Piazza, Giacomini, Le Bihan, and Dehaene (2003) recently found similar activations in a study involving counting of squares, and the activation in the dorsolateral prefrontal cortex was attributed to the coordination of spatial tagging process involved in keeping a running total of the count, and the insular activations to the internal recitation of series of number words. We speculate that participants used a mixture of subitizing, counting and addition strategies for solving the non-symbolic problems. For example, problems with one operand less than three could be solved by subitizing or counting serially from the bigger operand whereas larger problems could involve the process of counting to estimate the number of dots in each operand followed by the addition of operands. To verify this hypothesis, we have since split the data into small (at least one operand less than three) and large numbers and analyzed them in an event-related manner (Mechelli, Henson, Price, & Friston, 2003). As expected, we found additional activation in the bilateral dorsolateral prefrontal cortex for large compared to small non-symbolic addition (Venkatraman, Ansari, & Chee, 2004). No differences between large and small numbers were found for symbolic addition.

The secondary aim of this study was to explore the dissociation between exact and approximate calculation proposed by Dehaene et al. (1999). This dissociation has not been systematically replicated (Pesenti et al., 2000; Molko et al., 2003) and it is unclear whether it extends to non-symbolic representations of number. In this study, no significant differences were found between approximate and exact calculation using either non-symbolic or symbolic stimuli. Additionally, we did not find any language-related frontal activations for symbolic exact arithmetic involving simple addition problems. Though these findings contradict those found by Dehaene et al. (1999), they are not surprising against the background of some of the existing literature from both patients as well as neuroimaging studies.

In a recent study with normal as well as patients with Turner Syndrome (TS), no regions were found showing greater activation for exact arithmetic compared to approximate (Molko et al., 2003). One possible interpretation of this finding is that it appears to be difficult for participants to perform mental arithmetic approximately. This is perhaps particularly true for simple arithmetic, where individuals automatically compute the exact answer and have to inhibit this process in order to perform approximate computations. Data from our study lend credence to this interpretation. Using region-of-interest based analysis of activation magnitude (Fig. 2) we observed a trend towards greater activation for approximate compared to exact addition in the left anterior IPS, a finding consistent with Molko et al. (2003). These findings, together with the behavioral data and introspective reports from post-scanning debriefing, indicate that participants could have computed the exact result prior to selecting the closest answer at the decision stage of approximate addition. The bilateral insular activation, seen only for approximations, could be a result of internal speech as volunteers toggled through the two approximate options to assess the more appropriate answer. These considerations lead us to posit that it is likely that the neurocognitive processes underlying exact and approximate conditions in our study were qualitatively similar.

Secondly, our findings and those presented by Pesenti et al. (2000), do not replicate the finding of left frontal activation during exact addition. Although differences in the control task can sometimes explain differences in activation topography, this is unlikely in the present experiment as we did not find activation in the ‘language areas’ even when the addition was contrasted against fixation suggesting that verbal processes are not obligatory to solving simple exact addition. These results are also consistent with findings from a patient with left subcortical lesion whose ability to perform additions using small numbers was still intact while ability to perform multiplications was impaired (Dehaene & Cohen, 1997). In another neuropsychological study, it was found that simple addition is impaired following left parietal damage indicating that rote retrieval may not be the only means of solving simple addition or that retrieval does not inadvertently involve left frontal, language-related, areas (van Harskamp & Cipolotti, 2001; van Harskamp, Rudge, & Cipolotti, 2002). Taken together, these findings suggest that while memory retrieval may be the preferred strategy (Cohen et al., 2000; Dehaene & Cohen, 1995, 1997; Lemer, Dehaene, Spelke, & Cohen, 2003), variety of other strategies are available for performing simple additions such as finger counting and counting on from the larger addend in both adults and children (Geary & Wiley, 1991; LeFevre et al., 1996; Siegler, 1988). It remains for future brain imaging studies to clarify how differences in strategies could modify patterns of neural activation observed while participants engage in mental arithmetic.

Finally, it is important to acknowledge evidence from patient data that strongly suggests the existence of a dissociation between exact and approximate calculation (Dehaene & Cohen, 1995; Lemer et al., 2003). A recent study involving two acalculic patients (LEC and BRI) has demonstrated the existence of two distinct systems of numerical calculations, namely a verbal system of number words in left frontal regions and a non-symbolic representation of approximate quantities in the left parietal lobe (Lemer et al., 2003). However, the conclusions pertaining to the dissociation in these studies are based on a whole battery of multiple arithmetic tasks.

We would also like to reiterate that our conclusions on dissociation between exact and approximate mental arithmetic is based on findings from simple addition problems alone. Future imaging studies should seek to probe the dissociation between approximate and exact calculation using a variety of other mental arithmetic operations, such as multiplication, subtraction and division. These studies will facilitate the examination of operation-specific and operation-general processing of approximate and exact mental arithmetic.

5. Conclusions

The study of the neural processes underlying numerical processing has undergone rapid progress in recent years. It has been found that numerical processing activates areas in the left inferior parietal lobe regardless of the specific characteristics of the stimuli or the modality in which they are presented (Fias et al., 2003; Pinel et al., 1999). Results from our study add to the current literature by revealing that the parietal lobe also participates in mental arithmetic in a stimulus-independent manner. In addition, we found further support for the notion that exact mental addition does not necessarily implicate left-frontal, language-related circuits of the brain. Future studies should assess the precise role of the neural circuits typically involved in language processing in mental arithmetic as a function of strategy use and type of arithmetic operation.

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