Language in calculation: A core mechanism?

Yael Benn [a,*], Ying Zheng [a], Iain D. Wilkinson [b], Michael Siegal [a], Rosemary Varley [c]

[a] *Department of Psychology, University of Sheffield, UK*
[b] *Academic Unit of Academic Radiology, Department of Human Metabolism, University of Sheffield, UK*
[c] *Department of Human Communication Sciences, University of Sheffield, UK*

ARTICLE INFO

ABSTRACT

Although there is evidence that exact calculation recruits left hemisphere perisylvian language systems, recent work has shown that exact calculation can be retained despite severe damage to these networks. In this study, we sought to identify a "core" network for calculation and hence to determine the extent to which left hemisphere language areas are part of this network. We examined performance on addition and subtraction problems in two modalities: one using conventional two-digit problems that can be easily encoded into language; the other using novel shape representations. With regard to numerical problems, our results revealed increased left fronto-temporal activity in addition, and increased parietal activity in subtraction, potentially reflecting retrieval of linguistically encoded information during addition. The shape problems elicited activations of occipital, parietal and dorsal temporal regions, reflecting visual reasoning processes. A core activation common to both calculation types involved the superior parietal lobule bilaterally, right temporal sub-gyral area, and left lateralized activations in inferior parietal (BA 40), frontal (BA 6/8/32) and occipital (BA 18) regions. The large bilateral parietal activation could be attributed to visuo-spatial processing in calculation. The inferior parietal region, and particularly the left angular gyrus, was part of the core calculation network. However, given its activation in both shape and number tasks, its role is unlikely to reflect linguistic processing per se. A possibility is that it serves to integrate right hemisphere visuo-spatial and left hemisphere linguistic and executive processing in calculation.

© 2011 Elsevier Ltd. All rights reserved.

1. Introduction

The cognitive and neural mechanisms involved in calculation are the focus of considerable debate within the cognitive sciences. In particular, the contribution of visuo-spatial mechanisms localized within the bilateral parietal lobes and that of language in the left perisylvian cortex and angular gyrus (AG) is a matter of intensive investigation.

Functional neuroimaging research has consistently identified activation of parietal zones in calculation (Dehaene, Piazza, Pinel, & Cohen, 2003; Gruber, Indefrey, Steinmetz, & Kleinschmidt, 2001; Kawashima et al., 2004; Kazui, Kitagaki, & Mori, 2000; Menon et al., 2000a;Menon, Rivera, White, Glover, & Reiss, 2000b), and dyscalculia can be associated with right hemisphere lesions, including parietal cortex (Dehaene & Cohen, 1997; Granà, Hofer, & Semenza, 2006; Semenza, Miceli, & Girelli, 1997). Recent neuroimaging studies attribute some of these parietal activations to the use of visuo-spatial processing resources during calculation (Dehaene et al., 2003; Zago et al., 2008) suggesting that, at its core, calculation depends upon visuo-spatial processing.

At the same time, there are proposals that language is also involved – or even necessary – for exact calculation (Spelke & Tsivkin, 2001). Many functional brain-imaging studies have reported left perisylvian activity during calculation (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Delazer et al., 2003; Kong et al., 2005; Rickard et al., 2000). In particular, the AG has been implicated in skilled calculation (Menon et al., 2000b) and in retrieval of rehearsed results (Delazer et al., 2003; Grabner et al., 2009a,b; Ischebeck, Zamarian, Egger, Schocke, & Delazer, 2007). The proposal that there is a close relationship between language and calculation is also supported by neuropsychological studies that report an association between dyscalculia and aphasia (Basso, Burgio, & Caporali, 2000; Basso, Caporali, & Faglioni, 2005; Dehaene & Cohen, 1997; Delazer, Girelli, Semenza, & Denes, 1999).

However, the status of language as part of the core of the calculation system is questioned by evidence of retained calculation in the presence of severe aphasia resulting from large left hemisphere lesions encompassing the AG. There have been several demonstrations of a strong dissociation between language and calculation in patients with aphasia (Rossor, Warrington, & Cipolotti, 1995; Varley, Klessinger, Romanowski, & Siegal, 2005). Hence,

* Corresponding author at: Department of Psychology, University of Sheffield, Western Bank, Sheffield, S10 2TP, UK. Tel.: +44 (0) 114 222 6524; fax: +44 (0) 114 276 6515.
E-mail address: y.benn@sheffield.ac.uk (Y. Benn).

rather than part of a core system, language in healthy participants may represent a resource that scaffolds calculation in particular conditions and in the face of specific processing demands. In calculation with numbers, nameable elements of a problem can be rapidly encoded into words and intermediate stages in problem solving can be maintained in verbal working memory prior to responding.

The role of language also varies across different calculation operations. While the neural mechanisms involved in division have been only rarely studied, addition and multiplication appear to show greater language mediation compared to subtraction (Kawashima et al., 2004; Kazui et al., 2000; Kong et al., 2005; Kuo, Yeh, Chen, Liang, & Chen, 2008; Lemer, Dehaene, Spelke, & Cohen, 2003). Using a dual task paradigm, Lee and Kang (2002) report similar results. Whereas verbal shadowing interfered with multiplication, a visuo-spatial secondary task involving the retention of a mental image disrupted performance on subtraction. Findings pointing to greater language mediation of addition and multiplication might reflect training practices that emphasize rote-learning of information and subsequent automatic 'look-up' of results, whereas subtraction and division are believed to involve greater on-line calculation (Dehaene, 1992; Dehaene & Cohen, 1995). In particular, the products of small number calculation (i.e., single digit + single digit) are viewed as likely to involve access to verbally encoded information (Dehaene et al., 1999).

We report an fMRI study exploring brain activations associated with calculation with and without numbers. We sought to account for the variable findings of functional imaging and neuropsychological studies with regard to the involvement of language in exact calculation by examining the extent to which the neural substrates of calculation can be fractionated into 'core' and 'support' systems.

Calculation was explored in two modalities: first with a conventional digit number representation, and second, with abstract shape manipulations. With regard to number calculation tasks, we explored performance on two-digit plus/minus two-digit problems. For the shape task, we adopted Dehaene's (1992, p. 6) definition that calculation represents the ability '. . . to predict by symbolic manipulation the result of a physical regrouping or partitioning act . . .'. Consistent with this definition, participants were presented with complexes of abstract shapes that were not easily nameable. They were required to either add or subtract components from the complex using a set of combinatorial/decompositional rules. Behavioral studies show that spatial transformation and reorientation of objects are highly correlated with success in mathematical problem solving (Hegarty & Kozhevnikov, 1999; Van Garderen & Montague, 2003). Further, studies on the representation of space in the parietal cortex (Husain & Nachev, 2007) or the mental rotation of objects (Kosslyn, DiGirolamo, Thompson, & Alpert, 1998) reveal notable similarities to the parietal activations observed in neuroimaging studies of calculation (Zago et al., 2001).

2. Methods

2.1. Participants

Ethical approval for the study was granted by the local NHS Research Ethics Committee (08/H1308/32). The participants were 11 healthy men. Their ages ranged between 57 and 79 years ($M = 68.75$, SD = 6.63) in order to allow subsequent comparison with the performance of a cohort of patients with severe aphasia. All participants were right-handed and native English speakers who had completed a minimum of 10 years in formal education, including two with a university-level education. Occupational backgrounds varied from manual work (e.g., coal miner, plumber) to professional qualifications (e.g., engineering). Level of mathematics education also varied, but all participants were competent in simple mathematics. Participants had normal, or corrected-to-normal vision, and were screened for neurological and psychiatric illnesses. They gave informed consent to taking part, and received no financial reward for participation. Recruitment took place in various social groups for active healthy retired people, such as golf clubs, University of Third Age, and walking groups. Standard exclusion criteria for MR scanning were applied (e.g., no participants with pacemakers).

Two further participants completed the experiment. However, as their response patterns indicated that they had not complied with task instructions, they were excluded from data analyses (see Section 3 for details).

2.2. Stimuli

Participants completed addition and subtraction problems. In one condition, problems involved a conventional digit symbol set that could be easily encoded into language. In the other, novel shape addition and subtraction tasks were used. These involved complexes of shapes are not readily encodable into language (for example, see Fig. 1 and supplementary material). In each condition, the stimuli for each problem were constructed from four items. Number calculation involved two-digit plus/minus two-digit problems. The same digits were always used across addition and subtraction in order to match problem size across operations (56 + 32; 56 − 32). This procedure also ensured that factors such as the phonological length of digits were matched across addition and subtraction. Stimuli included no ties, i.e., no shared units (25 + 45), shared decades (42 + 43), or both (22 + 44), as the solution for such problems is more likely to be retrieved than calculated. Use of 1 or 9 as units was excluded to avoid round up/down strategies. Participants were presented with the stimulus problem and were required to indicate if a probe item was correct or incorrect by pressing a button. Half the probes were correct and half were incorrect. Probes were either incorrect in units (e.g., 36 − 17 = 17) or decades (36 + 17 = 63), with half of the incorrect probes having wrong units and half wrong decades. The wrong unit probes involved change by two to avoid parity checking strategies during response selection. False decade probes involved change by 10 to make estimation strategies more challenging.

The shape calculation task required participants to add or subtract abstract colored shapes (Fig. 1). For addition, participants were instructed to imagine placing the image on the right of the operator directly on top of the image to the left of the operator. For subtraction, they were instructed to imagine the image on the left without the shape to the right. Participants were again required to classify a probe as either correct or incorrect. Incorrect probes involved changes to the order, orientation, or patterning of shapes. Fig. 1a illustrates two addition problems with correct solutions, and Fig. 1b two addition problems with incorrect probes. Fig. 1c and d show correct and incorrect probes to subtraction problems. In a pilot study with 36 university students, the relative difficulty level of calculation in the two formats was established. There were no significant differences between the shape and number calculations accuracy rates (number calculation: $M = 96.11$, SD = 4.265; shape calculation: $M = 96.10$, SD = 2.79; $F(2,32) = 2.075$, $p = 0.142$).

Control tasks were designed that allowed for subtraction of the visual processing of numbers or shapes, and the motor responses associated with pressing a correct/incorrect key. The number control task involved viewing an array of four digits in horizontal alignment, and then a decision as to whether a probe item was included in the array.

Two shape control tasks were devised: one involved overlapping shapes similar to those of the shape calculation problems, and the other involved discrete shapes. To allow for comparability with the number task where single digits without overlaps were presented, only the results from the discrete shape control task are reported here. The shape control task consisted of a horizontal array of four discrete shapes, drawn from the same shape sets as the calculation task. By pressing a button, participants indicated whether a probe item was identical to one in the stimulus array.

2.3. Procedure and apparatus

To synchronize stimulus presentation with fMRI image acquisition and to facilitate the recording of response time and accuracy, the stimuli were presented via E-Prime (2002) enhanced with Eloquence (2006) IFIS software for paradigm development. Subjects were scanned in an MR system operating at 3T (Achieva, Philips Medical Systems, Best, The Netherlands) with an eight-channel receive-only head coil.

Participants first received 10 min of training outside of the scanner to familiarize them with the experimental tasks. They were first presented with shape addition problems accompanied by the following instruction: "Please add the image on the right (pointing) exactly on top of the image on the left (pointing again). What would it look like?" Participants were then presented with two possible solutions, and asked to select the correct answer. In the training phase, they received feedback on the accuracy of their response and where errors were made, they were shown how their responses violated the combinatorial/decompositional rules. (See supplementary information). Subtraction problems were then trained, and participants were instructed to: "Take away the image on the right (pointing at it) from the image on the left (pointing again). What would it look like?" Again, participants were given feedback on response accuracy, and sources of errors identified. After shape training, participants were shown the format of the familiar number problems and also the control tasks.

In the experiment, stimuli were presented visually on a monitor positioned above the head coil of the scanner, and the participant was instructed to calculate the result. When a participant was ready to answer, he pressed a button (right
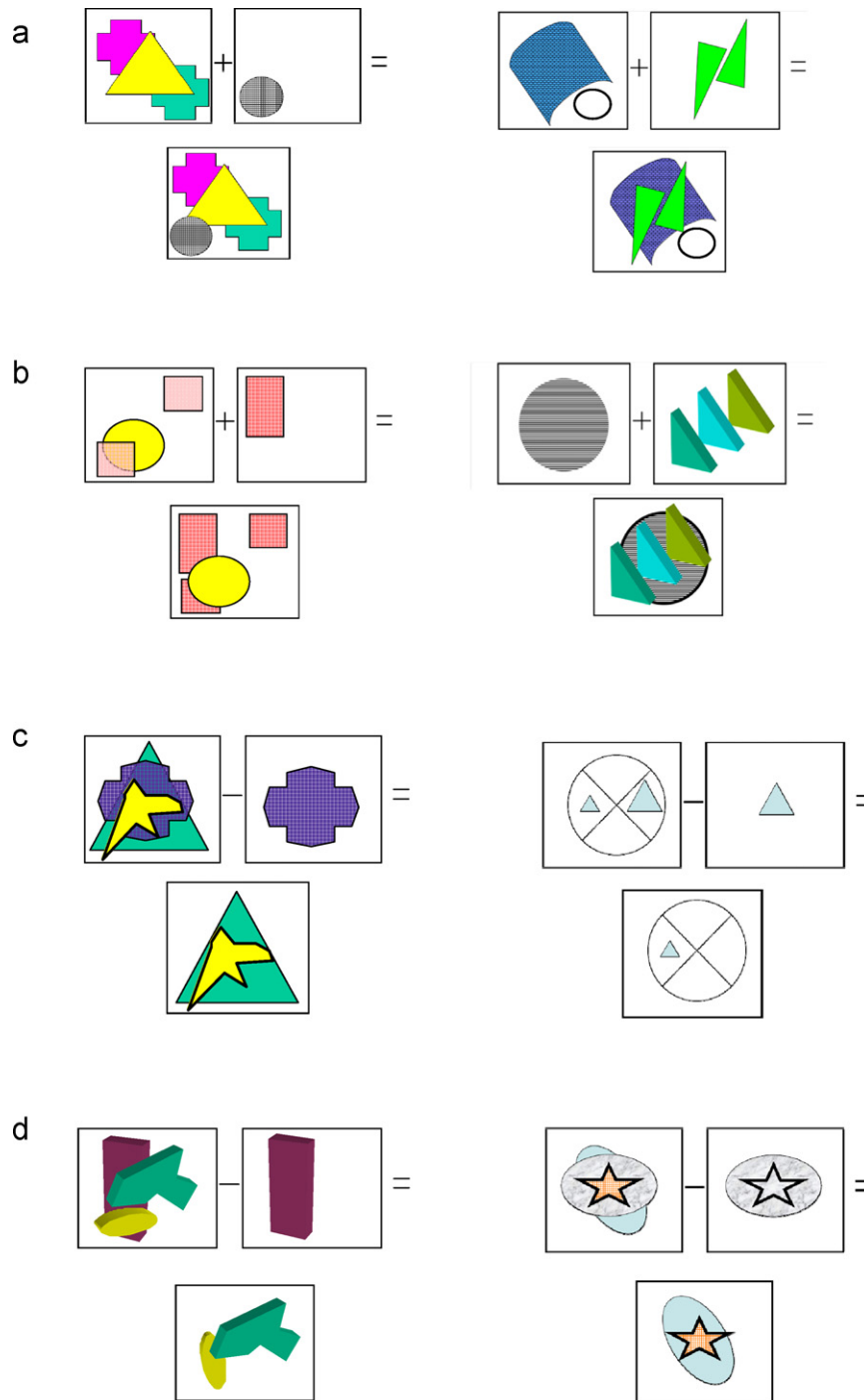
Fig. 1. Examples of shape calculation stimuli and probes. The probes were only visible after participants press a button to indicate they have calculated a solution, and are ready to make a judgment. a. Addition with correct probes. b. Addition with incorrect probes; left: the circle should appear behind the squares; right: the circle should appear with no border. c. Subtraction with correct probes. d. Subtraction with incorrect probes; left: oval is rotated; right: the border around the star should be subtracted.

thumb) on an Eloquence standard 10-button response-box. A probe item was then displayed on the screen below the stimulus slide. The original problem remained visible on the monitor in order to reduce working memory demands. Participants then indicated whether the probe answer was correct by pressing the "correct button" (left index finger) or the "incorrect button" (left middle finger). Button response selection was used rather than verbal responses in order to avoid unnecessary language-related activation and to support a subsequent study with aphasic participants. Response accuracy and timing were recorded in order to enable alignment of the BOLD response to participant behavior.

The time participants took to view the stimulus slide was labeled 'calculation time' (or 'observation time' in the case of the control tasks), whereas the time participants took to make a correct/incorrect judgment on the probe item was labeled 'verification time'.

2.4. Scanning procedure

Response times in the behavioral pilot study were used to determine the best block length. As there were multiple testing conditions, each condition did not appear more than twice in each run. To ensure statistical power, data were acquired over four separate runs so that each task was presented in eight separate periods. The resulting design consisted of four runs of 8 min and 18 s each. Each run was made up of 16 blocks of 30 s, and two instruction blocks of 9 s (Fig. 2).

A 30-s fixation-block began each run and was repeated between the shape and the number tasks. The fixation period was followed by an instruction slide that indicated the nature of the upcoming task (shapes or numbers). The slide was displayed for 9-s and flashed in order to alert the participant to the stimulus set ahead. No indication was given as to the nature of the calculation required (i.e., addition or
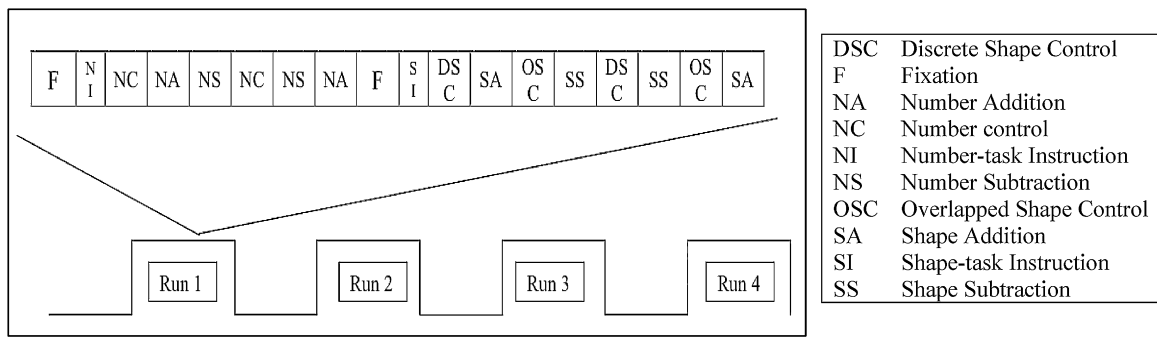
DSC	Discrete Shape Control
F	Fixation
NA	Number Addition
NC	Number control
NI	Number-task Instruction
NS	Number Subtraction
OSC	Overlapped Shape Control
SA	Shape Addition
SI	Shape-task Instruction
SS	Shape Subtraction

Fig. 2. Illustration of the experiment design.

subtraction) or of a change of operation (addition or subtraction) or task type (calculation or control). The first problem of the next condition appeared after the last problem of the previous condition was completed.

Each task was repeated twice in every run. Shape and number tasks were grouped so that all shape tasks appeared consecutively, followed by the blocks of number tasks or vice versa. Items in each block were fully randomized. The order of blocks varied between the runs. Half the runs started with shape blocks and half with number blocks. The number of stimuli in each condition was participant-driven, as the next stimulus appeared on the screen as soon as the participant made a judgment to a given probe.

At the end of the four runs, participants remained in the scanner for an additional 10–15 min. Participants were in the scanner for approximately 45 min in total.

2.5. Data acquisition

Cerebral vascular response to task was recorded using BOLD fMRI. A time series of 175 scans was performed with a repetition time of 3.0 s. At each scan "time point," 35 contiguous, transaxial slices parallel to a line bisecting the AC–PC were acquired using a T2* weighted, gradient-echo, single-shot Echo Planar Imaging (EPI)-based technique (echo time = 35 ms, repetition time = 3000 ms, sensitivity encoding factor = 1.5). Each slice had an in-plane reconstructed size of 1.8 mm × 1.8 mm and a slice thickness of 4 mm.

2.6. Data processing

All image data analysis was performed using Statistical Parametric Mapping software (SPM5, http://www.fil.ion.ucl.ac.uk/spm). Images were time adjusted and realigned to correct for head movements between scans. The realigned scans were then spatially normalized to the size and shape of an EPI template of SPM5. After normalization, images were smoothed using an 8 mm full width half maximum (FWHM) Gaussian filter. To determine brain activation, the following steps were performed. After specifying the design matrix for each of the participants, the hemodynamic responses induced by the different conditions were assessed for each individual using the general linear model and the theory of Gaussian fields (Friston et al., 1995) that formed the contrast images. Second level analysis was carried out using a one-sample t-test for each contrast with the appropriate contrast images from each individual in a random effects model. Activation maps of task vs. control and task vs. task were superimposed onto the mean spatially normalized EPI image to determine the location of activations.

Recruitment of older participants can result in lowered BOLD signal due to reduced cardio-vascular activity (D'Esposito, Deouell, & Gazzaley, 2003). Therefore group level contrasts were analyzed using an uncorrected but conservative p value of 0.0001 (unless otherwise stated) accompanied by a high voxel size threshold (k > 20). Number addition (NA) > control and number subtraction (NS) > control contrasts were compared to results reported from younger participants within the existing literature (Kawashima et al., 2004; Kazui et al., 2000; Kong et al., 2005; Kuo et al., 2008). Activation patterns for both addition and subtraction were checked against a recent meta-analysis of studies based on younger participants (Arsalidou & Taylor, 2011), and revealed comparable patterns to those of our older study participants.

3. Results

Two participants were excluded from the analysis as they produced a response pattern indicating that, rather than engaging in calculation, they had implemented a verification strategy. They had short calculation and long verification times of more than 1.5 SD units from the normative patterns.

3.1. Number calculation

Although overall mean accuracy for number calculation tasks was high (M = 88.47, SD = 6.72), there were significant differences between addition and subtraction. Paired two-tailed t-tests revealed that participants were significantly more accurate on NA than NS, (t(10) = 2.492, p = 0.032). Mean calculation time for NS was also significantly longer than NA (t(10) = −4.345, p = 0.001), but verification times were not significantly different (Table 1).

Brain activation maps of NA minus control and NS minus control are presented in Fig. 3 with the foci of activation shown in Tables 2 and 3. NA evoked activations in the left middle occipital gyrus, left anterior cingulate, medial and superior frontal gyri (BA 6, 24, and 32), left precentral and inferior frontal gyri (Broca's area, BA 44 and 45), bilateral sub-gyral temporal regions, and right frontal-parietal sub-gyral regions. Although activation of the intraparietal sulcus (IPS) was absent from this contrast, strong IPS activation was revealed in the map for NA minus rest and NS minus rest (see supplementary material). This result suggests that the IPS is involved in magnitude processing rather than the performance of calculation routines.

NS evoked a larger network of activation. This included the right inferior and middle frontal gyri, right supramarginal gyrus and inferior parietal lobule, bilateral anterior cingulate and medial frontal gyri. Within the left hemisphere, the inferior, superior, medial and middle frontal gyri, the precentral gyrus (BA 6, 13, 32, 44), the AG supramarginal gyrus, inferior parietal lobule and precuneus (BA 19, 39 and 40) were active, along with a large number of bilateral sub-cortical regions.

Overall, both operations resulted in increased activation in the left hemisphere, while subtraction evoked more activation than addition, and exhibited more inter-hemispheric activation. Furthermore, while addition evoked increased activation around

Table 1
Behavioral patterns of number and shape calculation.

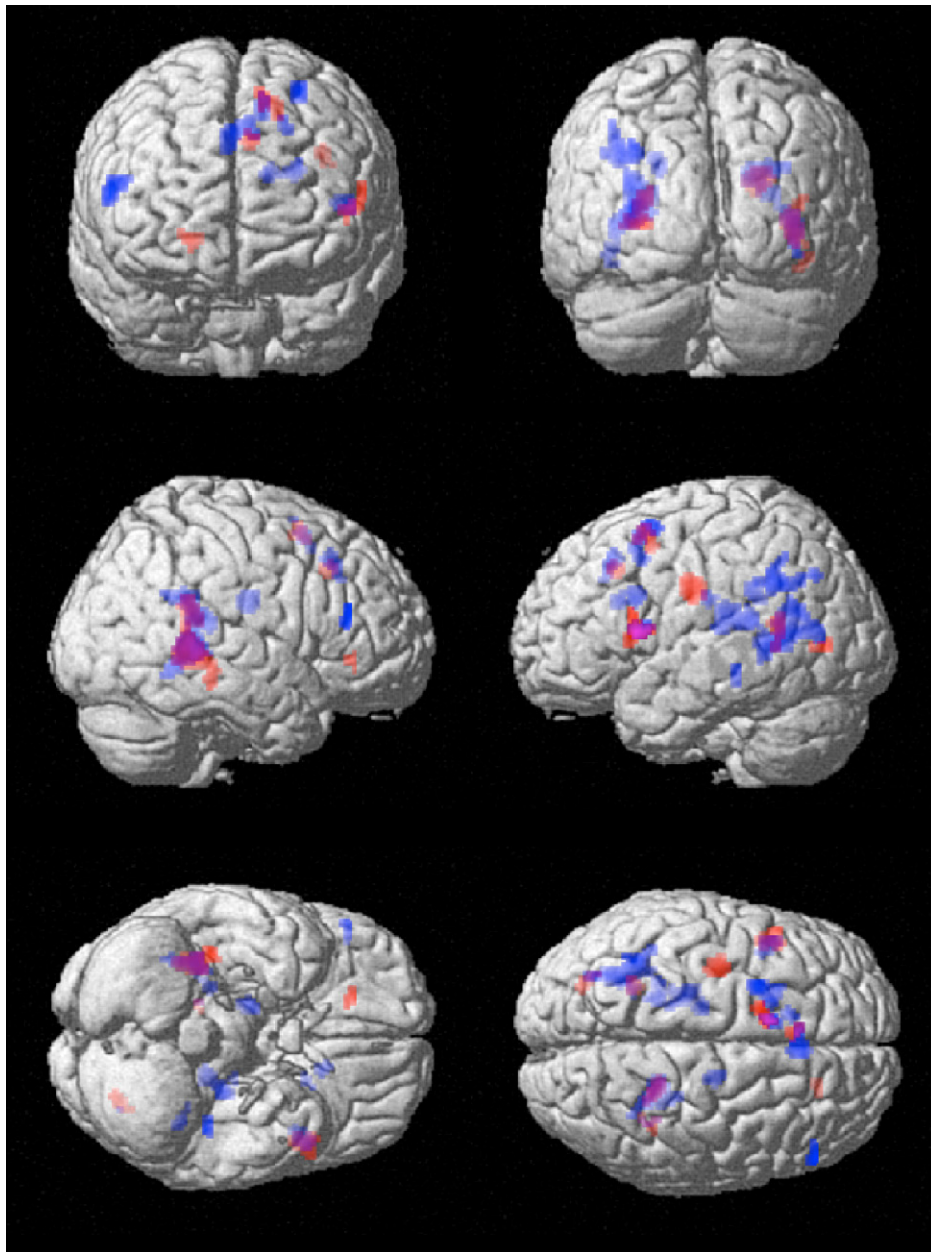|	Calculation time (SD) (MS)	Verification time (SD) (MS)	Accuracy (SD) (%)
Number addition	4061.92 (1297.42)	1655.46 (895.18)	90.97 (4.74)
Number subtraction	4785.47 (1294.51)	1744.44 (1063.22)	85.97 (7.67)
Shape addition	2968.86 (870.95)	2866.34 (993.33)	78.81 (7.51)
Shape subtraction	3143.43 (706.55)	2823.78 (1038.95)	75.08 (11.21)

Fig. 3. Comparison of number operations: number addition > number control (red) vs. number subtraction > number control (blue). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of the article.)

Table 2
Foci of fMRI signal during number addition > number control.

Region		BA	Max coordinates (MNI)			Z score	Cluster size (voxels)
Lobe	Anatomical localization of cluster		x	y	z		
Right							
Frontal lobe	Sub-gyral	–	18	32	−4	4.37	20
Frontal/parietal lobe/Sub-lobar	Extra-nuclear	–	22	−42	24	4.26	85
Temporal lobe	Sub-gyral	36	36	−44	4	5.09	190
Left							
Limbic /Frontal lobe	Anterior cingulate gyrus/Medial frontal gyrus	6.32	−4	22	38	4.03	23
	Anterior cingulate gyrus/Medial and superior frontal gyrus	6/24/32	−16	6	52	4.14	43
Frontal lobe	Precentral gyrus/Inferior frontal gyrus	44/45	−50	12	10	4.66	63
	Precentral gyrus/Sub-gyral	6	−36	−12	30	4.60	89
Temporal lobe	Sub-gyral	–	−28	−52	12	4.20	46
Occipital lobe	Middle occipital gyrus	–	−28	−74	2	4.31	24

Table 3
Foci of fMRI signal during number subtraction > number control.

Region		BA	Max coordinates (MNI)			Z score	Cluster size
Lobe	Anatomical localization of cluster		x	y	z		
Right							
Sub-lobar	Caudate/Cingulate gyrus	–	16	−14	22	4.47	53
Frontal lobe	Inferior frontal gyrus/Middle frontal gyrus	46	54	32	16	4.27	37
Parietal lobe	Supramarginal gyrus/Inferior parietal lobule	40	40	−50	38	4.19	20
Sub-lobar, temporal/Parietal/Frontal lobes	Sub-gyral/Extra-nuclear	19	36	−40	4	5.87	349
Inter-hemispheric							
Frontal lobe (L and R)/Limbic lobe (R)	Anterior cingulate gyrus/Medial frontal gyrus	6/32	4	26	40	4.19	72
Left							
Frontal lobe	Sub-gyral/Extra-nuclear	–	−24	14	26	4.69	37
	Sub-gyral/Superior frontal gyrus	–	−20	10	44	4.11	20
	Middle frontal gyrus	6	−26	4	58	4.44	33
	Superior/Medial-frontal gyrus	6, 32	−10	12	52	4.31	34
	Insula/Precentral gyrus/Inferior frontal gyrus	13, 44	−48	14	10	4.58	50
Limbic/Frontal lobe	Sub-gyral/Anterior cingulate	–	−14	20	26	4.07	20
Frontal/Parietal lobe	Sub-gyral	–	−20	−40	28	4.18	37
Parietal lobe	Sub-gyral/Angular gyrus/Supramarginal gyrus/Inferior parietal lobule/Precuneus	19, 39, 40	−36	−52	32	4.96	128
Temporal lobe	Sub-gyral	–	−42	−32	−8	4.28	24
Temporal lobe/Sub-lobar	Sub-gyral/Middle temporal gyrus/Extra-nuclear	–	−34	−54	4	4.76	320
Sub-lobar	Caudate/Cingulate gyrus/Extra-nuclear	–	−16	−20	26	4.27	25
	Sub-lobar, extra-nuclear	–	−18	−34	14	4.99	204

Broca's area, activation during subtraction extended to the bilateral parietal cortex.

The results of both the NA minus NS, and NS minus NA contrasts (using $p < 0.001$, $K > 20$) are shown in Table 4. While subtraction evoked significantly more activation in the left and right AG, right precuneus and left superior occipital gyrus, addition evoked significantly more activation compared to subtraction in the left middle temporal gyrus, bilateral paracentral lobule, postcentral gyrus and medial frontal gyrus, and right lingual gyrus, inferior parietal lobule and superior temporal and supramarginal gyri. The differential involvement of the bilateral AG (and particularly the LAG) in addition and subtraction suggests that the role of the LAG does not reflect linguistic processing per se, but instead could represent mediation between linguistic and visuo-spatial processes across hemispheres.

3.2. Shape calculation

Behavioral data from shape calculation are shown in Table 1. There were no significant differences between shape addition and subtraction for verification time, error rates and response times.

Activation patterns of shape addition minus control and shape subtraction minus control are presented in Table 5. Both tasks evoked activation around the bilateral parietal region. Shape addition evoked more activation in the right parietal cortex, extending to the right AG, while shape subtraction minus control was localized more around the bilateral superior parietal region. However, these differences in activations were not significant.

3.3. Shape vs. number tasks

Mean accuracy levels were high across all tasks. As would be expected when contrasting a novel with an entrained task, a 2 (content: number vs. shape) × 2 (operation: addition vs. subtraction) repeated measures ANOVA revealed that participants performed significantly better on the number calculation tasks compared to the novel shape problems ($F(2,9) = 38.977$, $p < 0.001$).

Response times were analyzed for correct responses only. A 2 (content: number vs. shape) × 2 (response time: calculation vs.

Table 4
Foci of fMRI signal of number addition (NA) > number subtraction (NS), and of NS > NA ($p < 0.001$, $k > 20$).

Region		BA	Max coordinates (MNI)			Z score	Cluster size
Lobe	Anatomical localization of cluster		x	y	z		
Number addition > number subtraction							
Right							
Occipital	Lingual gyrus/Cuneus	18/19	4	−70	0	3.59	43
Parietal	Inferior parietal lobule	40	58	−28	32	4.81	27
Temporal/Parietal	Superior temporal/Supramarginal gyrus, inferior parietal lobule	13/40	54	−44	24	5.18	74
Inter-hemispheric							
Parietal	Paracentral lobule/Postcentral gyrus	4(R)/5(R,L)	2	−44	68	4.72	54
Frontal	Medial frontal gyrus	6	0	−10	62	4.21	44
Left							
Temporal	Middle temporal gyrus	–	−46	−12	−16	4.21	20
Number subtraction > number addition							
Right							
Temporal/Parietal	Angular gyrus/Precuneus	19/39	34	−78	32	3.69	40
Left							
Occipital/Parietal	Superior occipital gyrus/Angular gyrus	19/39	−38	−82	30	3.57	20

Table 5
Foci of fMRI signal of (shape addition > shape control) and of (shape subtraction > shape control).

Region		BA	Max coordinates (MNI)			Z score	Cluster size (voxels)
Lobe	Anatomical localization of cluster		x	y	z		
Shape addition > control							
Temporal/Occipital parietal (R)	Middle temporal gyrus/Superior occipital gyrus/Angular gyrus	19/39	36	−78	30	4.54	85
Parietal (R)	Superior parietal lobule/Precuneus	7	40	−60	52	4.79	176
			10	−68	58	4.56	34
Parietal (L)	Superior parietal lobule/Precuneus	7/19	−26	−76	40	4.07	62
Shape subtraction > control							
Parietal (R)	Superior parietal lobule/Precuneus	7	26	−74	52	3.94	28
Parietal (L)	Superior/Inferior parietal lobule	7/40	−38	−58	50	4.68	34
	Superior parietal lobule/Precuneus	7/19	−24	−76	46	4.43	77

verification) × 2 (operation: addition vs. subtraction) repeated measures ANOVA revealed a significant main effect for content ($F(2,9) = 19.03$, $p = 0.001$). Furthermore, the response time × content interaction was significant ($F(2,9) = 19.19$, $p = 0.001$). Compared to performance on shape, participants took significantly longer to calculate on the number problems but required significantly less time to verify their answers.

To identify a core area for calculation, we first computed the active regions for each of the shape and number calculation types. For example, in the case of numbers, we computed the following: Core network = {NA − control} + {NS − control}. Number calculation (Table 6) elicited a large bilateral fronto-parietal network of activations. However, shape calculation (Table 7) evoked activation clusters that were bilaterally focused in the occipital–parietal regions.

Differences in activations between shape and number calculations were not significant. Furthermore, common activation between number and shape tasks was identified (Fig. 4 and Table 8). The superior parietal lobule was bilaterally activated in the conjunction of shape and number tasks. Common activation was also observed in the left hemisphere in the precuneus, supramarginal gyrus, AG, inferior parietal lobule, middle and medial frontal gyri, cingulate gyrus, precentral gyrus, and inferior and middle occipital gyri.

4. Discussion

This investigation examined similarities and differences in neural activation between addition and subtraction with numbers and shapes. The objective was to explore whether a common "core" network is apparent in calculation across modalities and hence to determine the extent to which left hemisphere language areas are part of this network.

The findings broadly replicated previous studies in showing differences between number addition and subtraction in both performance and brain activation (Kong et al., 2005; Kuo et al., 2008). Behaviorally, participants took significantly longer to calculate, and made significantly more errors in subtraction. There was some evidence for greater language mediation of addition than subtraction. Activation of Broca's area for addition included a large region of left BA 44 and BA 45, but for subtraction only a small segment of left BA 44. Similarly, the left middle temporal gyrus was significantly more active in addition than subtraction. Conversely, the left and right AG, right precuneus, and left superior occipital gyrus were more

Table 6
Foci of fMRI signal during number (addition + subtraction) > number control.

Region		BA	Max coordinates (MNI)			Z score	Cluster size
Lobe	Anatomical localization of cluster		x	y	z		
Right							
Frontal lobe	Sub-gyral	–	24	36	0	4.43	41
		–	30	8	36	4.29	49
	Sub-gyral/Extra-nuclear	–	30	−10	26	4.56	33
	Inferior frontal gyrus/Middle frontal gyrus	46	44	34	24	4.23	20
Limbic lobe/Sub-lobar	Cingulate gyrus/Caudate	–	14	−14	22	4.05	30
Sub-lobar/Temporal/Parietal/Frontal lobe	Sub-gyral/Extra-nuclear	–	20	−40	24	4.63	243
Temporal lobe	Sub-gyral/Superior temporal gyrus	19	36	−42	4	5.57	174
Inter-hemispheric							
Frontal/Limbic lobe	Cingulate gyrus/Medial frontal gyrus	6 (L,R), 32 (L,R), 8 (L)	−6	24	50	4.01	73
Left							
Frontal lobe	Sub-gyral	–	−26	16	28	4.56	26
	Sub-gyral/Extra-nuclear	–	−28	30	20	4.16	37
	Superior/Medial frontal gyrus	6, 24, 32	−10	12	54	4.26	76
Frontal lobe/Sub-lobar	Insula/Precentral gyrus/Inferior frontal gyrus	44	−50	12	10	4.91	73
	Sub-gyral, insula, precentral gyrus, extra-nuclear	6, 13	−34	−14	34	5.06	194
Sub-lobar	Extra-nuclear	–	−14	−34	14	4.53	62
Sub-lobar/Parietal/Frontal lobe	Sub-gyral/Extra-nuclear	–	−20	−42	28	4.06	23
Sub-lobar/Occipital/Temporal lobe	Sub-gyral/Middle occipital gyrus/Middle temporal gyrus/Extra-nuclear	–	−32	−52	6	4.72	265
Parietal lobe	Sub-gyral/Angular gyrus/Precuneus	19, 39	−32	−66	38	4.11	22
	Precuneus/Supramarginal gyrus	–	−36	−52	32	4.25	31
Temporal/Limbic lobe	Sub-gyral/Parahippocampal gyrus	36	−38	−32	−14	3.99	30

Table 7
Foci of fMRI signal during shape (addition + subtraction) > shape control.

| Region		BA	Max coordinates (MNI)			Z score	Cluster size
Lobe	Anatomical localization of cluster		x	y	z		
Right							
Occipital/Temporal lobe	Sub-gyral/Middle temporal/Superior occipital/Angular gyrus	19, 39	40	−78	22	4.43	42
Parietal lobe	Precuneus/Superior parietal lobule	7	32	−62	58	4.18	122
Inter-hemispheric							
Sub-lobar	Extra-nuclear	–	2	−40	2	4.11	20
Left							
Occipital lobe	Middle occipital gyrus	18, 19	−34	−90	0	4.29	23
Occipital/Temporal lobe	Superior occipital gyrus, angular gyrus	19, 39	−34	−80	28	4.26	24
Parietal lobe	Inferior parietal lobule	40	−40	−58	46	4.38	29
	Precuneus/superior parietal lobule	7, 19	−26	−74	40	4.49	126
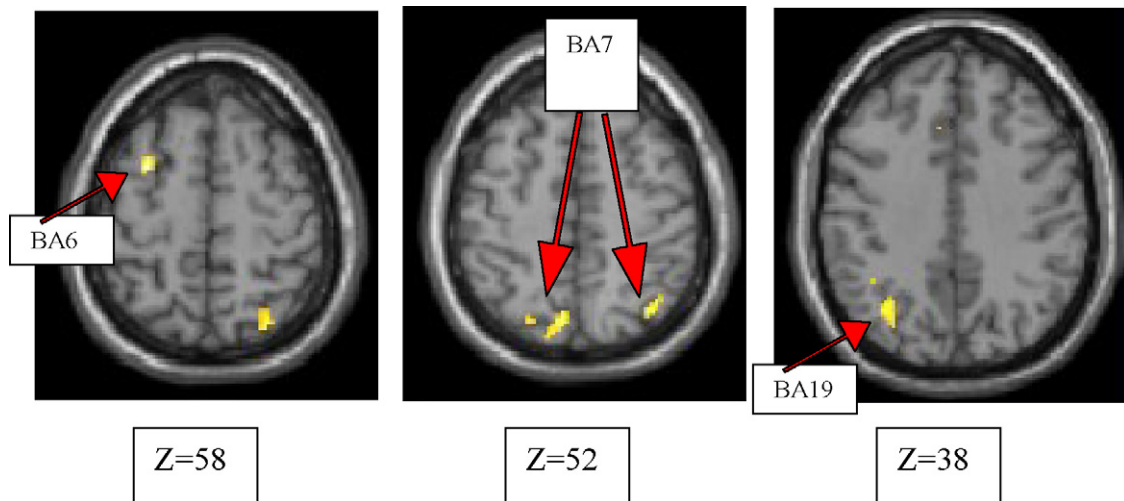
Fig. 4. Conjunction between number and shape calculation in BA6, 7, and 19. {Shape (addition + subtraction) > shape control} + {number (addition + subtraction) > number control}.

active in subtraction than addition. The bias of activity towards the left fronto-temporal areas in number addition, compared to the increased parietal activity observed in subtraction, may represent the effect of retrieval of phonological information during calculation. As addition is considered to rely more on retrieved results (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997; Van Harskamp & Cipolotti, 2001), its dependence on linguistic resources in healthy adults is likely to be more pronounced compared to subtraction. The latter has been shown to rely more on visuo-spatial resources

(Lee & Kang, 2002) that are likely to contribute to increase parietal activity. Although there were differences between number addition and subtraction, there was also large common fronto-parietal, cortical, and sub-cortical activation. Furthermore, activation of these areas was more evident in calculation with numbers rather than shapes.

Despite the importance of the IPS for number and magnitude processing (Dehaene et al., 2003), IPS activation was not evident in number calculation. The nature of the control task influenced

Table 8
Foci of fMRI signal during {shape (addition + subtraction) > shape control} + {number (addition + subtraction) > number control}.

Region		BA	Max coordinates (MNI)			Z score	Cluster size
Lobe	Anatomical localization of cluster		x	y	z		
Right							
Temporal lobe/Sub-lobar	Sub-gyral	–	32	−36	0	4.30	22
Parietal lobe	Superior parietal lobule	7	36	−68	54	4.32	69
Left							
Parietal lobe	Supramarginal gyrus, inferior parietal lobule	40	−36	−54	32	4.06	21
	Precuneus/Superior parietal lobule	7	−6	−70	52	4.56	48
	Precuneus/Sub-gyral/Angular gyrus/Superior parietal lobule	7, 19, 39	−32	−66	38	4.23	115
Frontal lobe	Middle /Superior frontal gyrus	6	−28	6	58	4.81	25
	Cingulate/Medial frontal gyrus	8, 32	−2	24	46	3.91	26
	Sub-gyral/Precentral gyrus/Extra-nuclear	–	−34	−14	28	4.12	30
Occipital lobe	Inferior/Middle occipital gyrus/Sub-gyral	18	−28	−96	−8	4.31	40
Sub-lobar	Extra-nuclear	–	−18	−22	24	4.33	46

the presence of IPS in activation maps. When the control task that involved numbers was partialed out from calculation conditions, IPS activation was absent. It was also absent from previous studies that used digits as a control task (Rickard et al., 2000). By contrast, IPS activation was apparent when the rest condition involving no number forms was subtracted from calculation. This pattern points to a role of the IPS in processing number forms and in number semantics (e.g., via a mental number line) rather than as substrate of calculation per se – a position consistent with the results of a recent meta-analysis of calculation (Arsalidou & Taylor, 2011).

The novel shape task revealed a different pattern of behavioral and imaging results, suggesting that participants may have employed different processes in performing calculations across the shape and number domains. Compared to performance on the shapes, number tasks produced longer calculation and shorter verification times. In the case of numbers, longer calculation times are likely to reflect working memory storage of intermediate results required by multi-digit operations. Further, the availability of number words enables results to be maintained in phonological working memory permitting rapid verification of the offered solution. The use of phonological resources in healthy adults is reflected by the recruitment of left lateralized fronto-temporal perisylvian areas during number calculation.

Whereas number problems triggered calculation routines, shape problems without associated routines elicited a process based on visual reasoning. Outputs from this process could not be encoded and maintained in established forms and the longer verification times likely reflect the need for further manipulation and comparison during the decision phase. The use of purely visual strategies is reflected by activations of the occipital, parietal, and dorsal temporal regions that are often associated with mental visual manipulation tasks such as feature binding (Shafritz, Gore, & Marois, 2002), supporting multi-feature visual working memory (Xu, 2007), and the manipulation of visual information (Champod & Petrides, 2007). In particular, it has been shown that the right parietal region is essential for performance on visual working memory tasks (Berryhill & Olson, 2008).

Nevertheless, despite these differences, both number and shape tasks share properties that are essential for calculation as both require application of combinatorial/decompositional rules that constrain prediction based on physical regrouping or partitioning. In this respect, number and shape tasks revealed a core activation involving the superior parietal lobule (BA 7) bilaterally, right temporal sub-gyral area, and left lateralized activations in inferior parietal (BA 40), frontal (BA 6/8/32) and occipital (BA 18) regions. The right sub-gyral activation, as well as the left occipital and left frontal activations, point to similar general processing demands required by both forms of calculation such as conflict monitoring and executive control in response selection (Nachev, 2006). The large bilateral parietal activation affirms the importance of visuo-spatial processing in calculation (Gruber et al., 2001; Kawashima et al., 2004; Kazui et al., 2000; Menon et al., 2000a,b; Zago et al., 2008).

Because the shape tasks are not intrinsically numeric, a possible objection might be that they do not tap calculation processes. Furthermore, differences in task difficulty, novelty and cognitive strategy utilized in solving the shape problems may limit the attempt to locate a common, core calculation mechanism that is modality independent. However, our aim was to identify the cognitive processes and neural substrates underlying the logical and physical regrouping and partitioning operations necessary for calculation. Through investigating calculation in two formats, we sought to explore these processes independently of surface form, be it number or shape. Although we identified common activations between shape and number calculation, these do not necessarily imply identical neural substrates. For example, owing to limits in

the spatial resolution of fMRI (Grill-Spector & Malach, 2001), the common activation identified here may represent activations of neural zones that are in close proximity, but are functionally and structurally independent.

The age profile of participants in our investigation was atypical for fMRI studies of neurocognitive processing in healthy adults. The older adult sample was selected to obtain normative activation patterns against which performance of aphasic calculators could be compared. Although BOLD signal may be reduced in older adults, the investigation of processing in older cohorts is of particular value in cognitive domains such as calculation. Klessinger, Szczerbinski, and Varley (submitted for publication) have reported faster, more accurate, and more automatized calculation routines in older adults than in university students. These differences are likely to reflect changes across age cohorts in educational practices and tools to support calculation. The fMRI results of the current study are broadly similar to those of other investigations of number calculation. However, comparison of different age groups appears particularly important where behavior is subject to varied cultural practices. This issue requires further investigation.

The inferior parietal region, and particularly the left AG, is part of the core calculation network identified in our study. The left AG has often been implicated in calculation (Dehaene et al., 1999; Delazer et al., 2003; Kuo et al., 2008; Menon et al., 2000b). This region may be recruited in the retrieval of rehearsed results (Delazer et al., 2003; Grabner et al., 2009b; Ischebeck et al., 2007), or may act as a mediator between the perisylvian and parietal regions in facilitating exact calculation (Dehaene et al., 1999). Our results, however, indicate that its role is not confined to the retrieval of learned results as activation of left AG was present in both shape and number tasks. Although many regard the left AG as a classic language region, previous studies reveal activation of this area in tasks that are intrinsically non-linguistic. For example, Girgenrath, Bock, and Seitz (2008) reported an fMRI experiment in which participants were asked to use a joystick to track a target that moved in an unpredictable manner. In this task, activation of the left AG was related to sensori-motor control of the joystick, which involved no linguistic modulation. The anatomical connectivity between the left AG and posterior perisylvian regions (such as Wernicke's area) and the functional connectivity between the left and right AG (Horwitz, Rumsey, & Donohue, 1998) implicate the left AG in the integration of right hemisphere visuo-spatial and left hemisphere linguistic information. Visuo-spatial information such as movement on a "number line" (Hubbard, Piazza, Pinel, & Dehaene, 2005; Knops, Thirion, Hubbard, Michel, & Dehaene, 2009) or re-alignment (Burbaud et al., 2000) is often integrated with verbally encoded information in using pre-learned verbally encoded solutions in calculation. This account is consistent with the observation that AG activation is reduced during number addition compared to subtraction. The availability of verbally encoded information in addition diminishes the need for integration of multiple processing streams. However, the role of the left AG is not restricted to linguistic/visuo-spatial integration as it is also active in non-linguistic tasks such as shape calculation. This pattern of results suggests that the region acts as a processing hub that integrates the attentional/executive, linguistic and visuo-spatial demands required by calculation and other tasks, as observed by Girgenrath et al. (2008).

Although the left AG is active in the calculation of healthy adults, and is part of the core network revealed in this investigation, neuropsychological reports suggest that calculation can be retained despite damage to this region (Varley et al., 2005). In the case of patients with severe aphasia, damage in and around the left AG may lead to a shift of integrative processing to other regions such as right frontal cortex, right AG, or other adjacent parietal regions. This adaptation reflects the inaccessibility of linguistically encoded information and a general reduced reliance on linguistic

processes to mediate performance in a range of cognitive domains (Bek, Blades, Siegal, & Varley, 2010; Varley & Siegal, 2000).

Other networks apparent in number calculation, such as the fronto-temporal perisylvian systems, were not consistently recruited across all conditions. Therefore, we conclude that, despite the support of the language system for calculation in healthy adults, it is not part of core calculation. Instead the large shared parietal network which subserves calculation on both number and shape is representative of a core mechanism that is format-independent and does not rely on retrieved results.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.neuropsychologia.2011.09.045.

References

Arsalidou, M., & Taylor, M. (2011). Is 2+2 = 4? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage*, *54*, 2382–2393.

Basso, A., Burgio, F., & Caporali, A. (2000). Acalculia, aphasia and spatial disorders in left and right brain-damaged patients. *Cortex*, *36*(2), 265–280.

Basso, A., Caporali, A., & Faglioni, P. (2005). Spontaneous recovery from acalculia. *Journal of International Neuropsychological Society*, *11*, 99–107.

Bek, J., Blades, M., Siegal, M., & Varley, R. (2010). Language and spatial reorientation: evidence from severe aphasia. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *36*, 646–658.

Berryhill, M. E., & Olson, I. R. (2008). The right parietal lobe is critical for visual working memory. *Neuropsychologia*, *46*, 1767–1774.

Burbaud, P., Camus, O., Guehl, D., Bioulac, B., Caille, J. M., & Allard, M. (2000). Influence of cognitive strategies on the pattern of cortical activation during mental subtraction. A functional imaging study in human subjects. *Neuroscience Letters*, *287*, 76–80.

Champod, A. S., & Petrides, M. (2007). Dissociable roles of the posterior parietal and the prefrontal cortex in manipulation and monitoring processes. *Proceedings of the National Academy of Sciences*, *104*, 14837–14842.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition*, *44*, 1–42.

Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. *Mathematical Cognition*, *1*, 83–120.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex*, *33*, 219–250.

Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., & Tsivkin, S. (1999). Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science*, *284*, 970–974.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, *20*, 487–506.

Delazer, M., Girelli, L., Semenza, C., & Denes, G. (1999). Numerical skills and aphasia. *Journal of the International Neuropsychological Society*, *5*, 213–221.

Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., et al. (2003). Learning complex arithmetic—an fMRI study. *Cognitive Brain Research*, *18*, 76–88.

D'Esposito, M., Deouell, L. Y., & Gazzaley, A. (2003). Alterations in the BOLD fMRI signal with ageing and disease: a challenge for neuroimaging. *Nature Reviews Neuroscience*, *4*, 863–872.

Eloquence (2006). *Eloquence*. Orlando, FL: Intermagnetics, http://www.igc.com.

E-Prime (2002). *E-Prime psychology software tools*. Pittsburgh, PA, http://www.pstnet.com.

Friston, K., Ashburner, J., Frith, C., Poline, J. B., Heather, J., & Frackowiak, R. (1995). Spatial registration and normalization of images. *Human Brain Mapping*, *2*, 165–189.

Girgenrath, M., Bock, O., & Seitz, R. J. (2008). An fMRI study of brain activation in a visual adaptation task: activation limited to sensory guidance. *Experimental Brain Research*, *184*, 561–569.

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*, 604–608.

Grabner, R. H., Ischebeck, A., Reishofer, G., Koschutnig, K., Delazer, M., Ebner, F., et al. (2009). Fact learning in complex arithmetic and figural-spatial tasks: the role of the angular gyrus and its relation to mathematical competence. *Human Brain Mapping*, *30*, 2936–2952.

Granà, A., Hofer, R., & Semenza, C. (2006). Acalculia from a right hemisphere lesion dealing with "where" in multiplication procedures. *Neuropsychologia*, *44*, 2972–2986.

Grill-Spector, K., & Malach, R. (2001). FMR-adaptation: a tool for studying the functional properties of human cortical neurons. *Acta Psychologica*, *107*, 293–321.

Gruber, O., Indefrey, P., Steinmetz, H., & Kleinschmidt, A. (2001). Dissociating neural correlates of cognitive components in mental calculation. *Cerebral Cortex*, *11*, 350–359.

Hegarty, M., & Kozhevnikov, M. (1999). Types of visual-spatial representations and mathematical problem solving. *Journal of Educational Psychology*, *91*, 684–689.

Horwitz, B., Rumsey, J. M., & Donohue, B. C. (1998). Functional connectivity of the angular gyrus in normal reading and dyslexia. *Proceedings of the National Academy of Sciences*, *95*, 8939–8944.

Hubbard, E. M., Piazza, M., Pinel, P., & Dehaene, S. (2005). Interactions between number and space in parietal cortex. *Nature Reviews Neuroscience*, *6*, 435–448.

Husain, M., & Nachev, P. (2007). Space and the parietal cortex. *Trends in Cognitive Sciences*, *11*, 30–36.

Ischebeck, A., Zamarian, L., Egger, K., Schocke, M., & Delazer, M. (2007). Imaging early practice effects in arithmetic. *NeuroImage*, *36*, 993–1003.

Kawashima, R., Taira, M., Okita, K., Inoue, K., Tajima, N., Yoshida, H., et al. (2004). A functional MRI study of simple arithmetic—a comparison between children and adults. *Cognitive Brain Research*, *18*, 227–233.

Kazui, H., Kitagaki, H., & Mori, E. (2000). Cortical activation during retrieval of arithmetical facts and actual calculation: a functional magnetic resonance imaging study. *Psychiatry and Clinical Neuroscience*, *54*, 479–485.

Klessinger, N., Szczerbinski, M., & Varley, R. The role of number words: the phonological length effect in exact calculation, submitted for publication.

Knops, A., Thirion, B., Hubbard, E. M., Michel, V., & Dehaene, S. (2009). Recruitment of an area involved in eye movements during mental arithmetic. *Science*, *324*, 1583–1585.

Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., & Gollub, R. (2005). The neural substrate of arithmetic operations and procedure complexity. *Cognitive Brain Research*, *22*, 397–405.

Kosslyn, S. M., DiGirolamo, G. J., Thompson, W. L., & Alpert, N. M. (1998). Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. *Psychophysiology*, *35*, 151–161.

Kuo, B. C., Yeh, Y. Y., Chen, D. Y., Liang, K. C., & Chen, J. H. (2008). The capacity constraint in the prefrontal and parietal regions for coordinating dual arithmetic tasks. *Brain Research*, *1199*, 100–110.

Lee, K. M., & Kang, S. Y. (2002). Arithmetic operation and working memory: differential suppression in dual tasks. *Cognition*, *83*, B63–B68.

Lemer, C., Dehaene, S., Spelke, E., & Cohen, L. (2003). Approximate quantities and exact number words: dissociable systems. *Neuropsychologia*, *41*, 1942–1958.

Menon, V., Rivera, S. M., White, C. D., Eliez, S., Glover, G., & Reiss, A. L. (2000). Dissociating prefrontal and parietal cortex activation during arithmetic processing. *NeuroImage*, *12*, 357–365.

Menon, V., Rivera, S. M., White, C. D., Glover, G., & Reiss, A. L. (2000). Functional optimization of arithmetic processing in perfect performers. *Cognitive Brain Research*, *9*, 343–345.

Nachev, P. (2006). Cognition and medial frontal cortex in health and disease. *Current Opinion in Neurobiology*, *19*, 586–592.

Rickard, T. C., Romero, S. G., Basso, G., Wharton, C., Flitman, S., & Grafman, J. (2000). The calculating brain: an fMRI study. *Neuropsychologia*, *38*, 325–335.

Rossor, M. N., Warrington, E., & Cipolotti, L. (1995). The isolation of calculation skills. *Journal of Neurology*, *242*, 78–81.

Semenza, C., Miceli, L., & Girelli, L. (1997). A deficit for arithmetical procedures: lack of knowledge or lack of monitoring? *Cortex*, *33*, 483–498.

Shafritz, K. M., Gore, J. C., & Marois, R. (2002). The role of the parietal cortex in visual feature binding. *Proceedings of the National Academy of Sciences*, *99*, 10917–10922.

Spelke, E. S., & Tsivkin, S. (2001). Language and number: a bilingual training study. *Cognition*, *78*, 45–88.

Van Garderen, D., & Montague, M. (2003). Visual-spatial representation, mathematical problem solving, and students of varying abilities. *Learning Disabilities Research and Practice*, *18*, 246–254.

Van Harskamp, N. J., & Cipolotti, L. (2001). Selective impairments for addition, subtraction and multiplication. Implications for the organization of arithmetical facts. *Cortex*, *37*, 363–388.

Varley, R., & Siegal, M. (2000). Evidence for cognition without grammar from causal reasoning and 'theory of mind' in an agrammatic aphasic patient. *Current Biology*, *10*, 723–726.

Varley, R. A., Klessinger, N. J. C., Romanowski, C. A. J., & Siegal, M. (2005). Agrammatic but numerate. *Proceedings of the National Academy of Sciences*, *102*, 3519–3524.

Xu, Y. (2007). The role of the superior intraparietal sulcus in supporting visual short-term memory for multifeature objects. *Journal of Neuroscience*, *27*, 11676–11686.

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural correlates of simple and complex mental calculation. *NeuroImage*, *13*, 314–327.

Zago, L., Petit, L., Turbelin, M., Andersson, F., Vigneau, M., & Tzourio-Mazoyer, N. (2008). How verbal and spatial manipulation networks contribute to calculation: an fMRI study. *Neuropsychologia*, *46*, 2403–2414.