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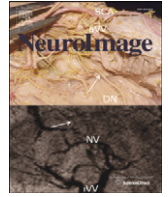
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Neural correlates of numbers and mathematical terms

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ABSTRACT

Numerical processing has been demonstrated to be subserved typically by the brain regions around the bilateral intraparietal sulcus (IPS). The goal of the current study was to investigate whether the processing of mathematical terms shared the same brain regions with numerical processing. Healthy adult participants performed semantic distance judgment tasks on five types of materials, including geometric terms, algebraic terms, linguistic terms, words for tools and other common objects, and Arabic numbers. Brain activation was measured with functional magnetic resonance imaging (fMRI). The results showed that geometric terms had greater activation than algebraic terms, linguistic terms and tool words in the horizontal IPS, but algebraic terms did not have greater activation than linguistic terms and tool words in this region. Arabic numbers showed greater activation than non-number materials (including geometric terms, algebraic terms, linguistic terms and tool words) in the bilateral IPS, right inferior frontal gyrus and bilateral middle frontal gyrus, but the non-number materials showed stronger activation in the left inferior frontal gyrus and left middle temporal gyrus. These results suggest that the brain area for the processing of numbers (the left IPS) seems to be involved in semantic processing of geometric terms, but not that of other mathematical terms such as algebraic terms. Both algebraic and geometric terms share similar brain organization with basic semantic processing in the left temporal and frontal regions.

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Introduction

Several lines of research have shown that numerical processing is subserved by the bilateral intraparietal sulcus (IPS) (e.g., Arsalidou and Taylor, 2011; Butterworth, 1999; Dehaene et al., 1999; Eger et al., 2003; Kadosh et al., 2005, 2007; Piazza et al., 2007; Thioux et al., 2005; see reviews by Brannon, 2006; Dehaene et al., 2003). First, patients with parietal lesions consistently show selective impairments in numerical skills (e.g., Dehaene and Cohen, 1997; Denes and Signorini, 2001; Grafman et al., 1982; Takayama et al., 1994; Warrington, 1982; Zorzi et al., 2002), whereas patients with lesions to other brain regions showed preservation of numerical skills (e.g., Butterworth et al., 2001; Cappelletti et al., 2001, 2002, 2005; Crutch and Warrington, 2002; Diesfeldt, 1993; Jefferies et al., 2004, 2005; Lemer et al., 2003; Zamarian et al., 2006). Second, functional MRI studies have systematically shown that numerical processing elicits greater activation in the parietal lobule than does non-numerical processing (e.g., Ansari et al., 2006; Cappelletti et al., 2010; Eger et al., 2003; Knops et al., 2006; Le Clec'h et al., 2000; Piazza et al., 2004; Thioux et al., 2005; Zago et al., 2008; but see

Göbel et al., 2004; Kadosh et al., 2008; Shuman and Kanwisher, 2004). Third, developmental dyscalculia has also been showed to be associated with structural abnormalities in the IPS regions (e.g., Isaacs et al., 2001; Kucian et al., 2006; Molko et al., 2003, 2004; Rotzer et al., 2008).

Based on the neuropsychological and neuroimaging evidence, Dehaene et al. (2003) proposed a three parietal circuit model for numerical processing: That is, the bilateral intraparietal system is associated with quantity representation, the left angular gyrus with verbal processing of numbers, and the posterior superior parietal lobule with attentional processes. The brain regions around the bilateral intraparietal sulcus are relatively specific to the number-related processes, but the regions for verbal and attentional processes have more general functions. In addition to the parietal cortex, the prefrontal cortex has also been found to be critical for numerical processing (e.g., Arsalidou and Taylor, 2011; Fehr and Herrmann, 2007; Ischebeck et al., 2006; Kong et al., 2005), most likely because it serves the purpose of general information processing, such as the working memory (Arsalidou and Taylor, 2011).

Although the evidence is clear that numbers are specifically processed by the IPS, less is known about the neural substrates for the processing of knowledge about mathematical terms (e.g. “decimal”, “fraction”, “group”, “rectangle”). On the one hand, mathematical terms are verbal materials that are supposed to be processed in the

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language network. On the other hand, they are related to numbers and other aspects of mathematics (e.g., spatial relations in geometry) that are processed by the IPS. To our knowledge, only three neuropsychological studies (Delazer and Benke, 1997; Hittmair-Delazer et al., 1994; Warrington, 1982) and three neuroimaging studies (Andres et al., 2011; Prado et al., 2011; Zhou et al., 2007) have shown limited but relevant results. Warrington (1982) found that lesions in the left parietal cortex led to a loss of memory of arithmetic facts but had no effects on the conceptual knowledge of arithmetic (e.g., operations, commutativity, addition/subtraction inverse principle). These results were confirmed by Hittmair-Delazer et al. (1994). In contrast, Delazer and Benke (1997) found that a patient who suffered from a left parietal glioblastoma completely lost conceptual knowledge of arithmetic, but preserved some arithmetic facts (multiplications, some additions and subtractions). Using fMRI, Zhou et al. (2007) found that addition had more activation in the right superior and inferior parietal lobules than multiplication, whereas the latter had more activation in some of the language-related regions such as the left posterior and anterior superior temporal gyrus. Prado et al. (2011) found a similar disassociation between the analogical and language-based representations of numbers. Andres et al. (2011) used transcranial magnetic stimulation (TMS) to demonstrate that multiplication had greater activation in the bilateral middle and superior temporal gyri than subtraction, though both relied on the horizontal IPS.

These results suggest that the memory of conceptual knowledge of arithmetic may be subserved by the left parietal cortex or the language-related regions such as the left frontal cortex and left temporal cortex. The current fMRI study aimed to examine systematically the processing of two types of mathematical terms—geometric (e.g., “sphere”, “trapezoid”) and algebraic terms (e.g., “even number”, “fraction”). The processing of mathematical terms was compared with that of three types of materials: Arabic numbers, linguistic terms (e.g. “noun”, “poem”), and tool words. The tool words actually included both words for tools (e.g. “scissors”, “rake”) and those for other common objects (e.g., “piano”, “candle”), following the convention of previous studies (e.g., Cappa et al., 1998; Martin et al., 1996). The present study used the semantic distance judgment task (Mummary et al., 1998; Zannino et al., 2006). If mathematical terms involve only verbal processing, we would expect the activation patterns of geometric and algebraic terms to be similar to those of the two types of verbal materials (linguistic terms and tool words). On the other hand, we expected that algebraic terms would activate mental representations of numbers. For example, “odd number” would activate the numbers “1, 3, 5, 7, 9, ...”, “fraction” would activate the numbers “ $\frac{1}{2}$, $\frac{1}{3}$, $\frac{1}{4}$, ...”, and “negative number” would activate the numbers “−1, −2, −3, ...”. Therefore, we expected greater activation in the IPS for the algebraic terms than for linguistic terms and tool words. Similarly, we expected that geometric terms such as “radius”, “arch”, “trapezoid”, and “vertex angle” would activate mental images of the actual geometric shapes, and hence elicit greater activation in the inferior parietal lobule, which has been found to be involved in processing mental images (e.g. Alivisatos and Petrides, 1997; Carpenter et al., 1999; Gauthier et al., 2002; Jordan et al., 2001; Vingerhoets et al., 2001).

Methods

Subjects

Twenty right-handed (10 male; aged 18.8–22.5 years old, and mean age = 20.6 years old) undergraduates were recruited from Beijing Normal University. These subjects reported having no previous history of neurological disorders or head injury. Procedures of the experiment were fully explained to all subjects before they gave informed consent. This study was approved by the Institutional Review Board (IRB) of the Institute of Cognitive Neuroscience and Learning at Beijing Normal University.

Stimuli and materials

Stimulus presentation and recording of behavioral data were programmed using Microsoft Visual Basic 6.0 (Chinese Version) on a Pentium 4 laptop. Stimuli were projected onto a translucent screen placed at the back of the magnet bore. Participants viewed the screen through a mirror mounted on the head coil, at a distance of ~30 cm from the eyes.

Five types of materials were used: algebraic terms, geometric terms, linguistic terms, tool words, and Arabic numbers. They were presented in black against a light gray background (the RGB value was 200, 200, 200). The height of the stimuli was set to ~10°. The width of the Chinese characters and that of the numbers were matched (mean visual angle was ~15°).

Subjects were asked to perform the semantic distance judgment task (Mummary et al., 1998; Zannino et al., 2006) (see below for the specific procedure). For each type of materials, we used 58 terms or numbers (see Appendix A). Subjects were pre-tested to ensure that they knew the exact meaning of every term. For mathematical terms that have alternative meanings (e.g., “ ” [he] means “sum” and “harmony” among others), subjects were told that in this study they should focus on the mathematical meanings in order to perform the semantic judgment task.

Procedure

Before scanning, subjects received a training session to ensure that they understood the instruction of this experiment. The scanning session lasted about half an hour and was organized into three runs, each consisting of five experimental blocks (one 9-trial block for each condition or type of material) and five fixation blocks (with “+” at the center of the screen). The balanced Latin square design (Bradley, 1958) was used to counterbalance the order effect of the 5 types of materials. The five material types (being coded as “1”, “2”, “3”, “4”, “5”, respectively) can be permuted into 10 types of sequences, including 12534, 23145, 34251, 45312, and 51423, and their reversed sequences. The 10 sequences were repeated 6 times to create a total of 60 sequences, which allowed each subject of the 20 subjects to have 3 different sequences.

Each run in the experiment lasted 5 min. Each experimental block lasted for 36 s, and the fixation block for 24 s (see the experimental procedure in Fig. 1). There was a 1–2 min rest after each run.

Subjects were presented triplets of stimuli (one on the top and two at the bottom, see Fig. 1). Their task was to decide which of the two terms or numbers at the bottom were semantically more similar to the term or number above. They responded by pressing either the key on the left response box using the left index finger or the key on the right response box using the right index finger. Both accuracy and speed were emphasized.

fMRI data acquisition

Imaging was performed on a Siemens (Munich, Germany) 3T Trio scanner using a standard eight-channel head coil. After automatic shimming of the magnetic field, three-dimensional (3D) high-resolution T1 anatomical images were acquired for coregistration with the functional images. Next, functional volumes were acquired using a multiple slice T2*-weighted echo planar imaging (EPI) sequence with the following parameters: repetition time = 2000 ms; echo time = 30 ms; flip angle = 90°; matrix dimensions = 64 × 64; field of view = 200 mm; and slice thickness = 4 mm. Thirty-two slices covered the entire brain.

Statistical analysis of the fMRI data

Individual MRI data sets were analyzed using the SPM5 software (Wellcome Department of Imaging Neurosciences, University College

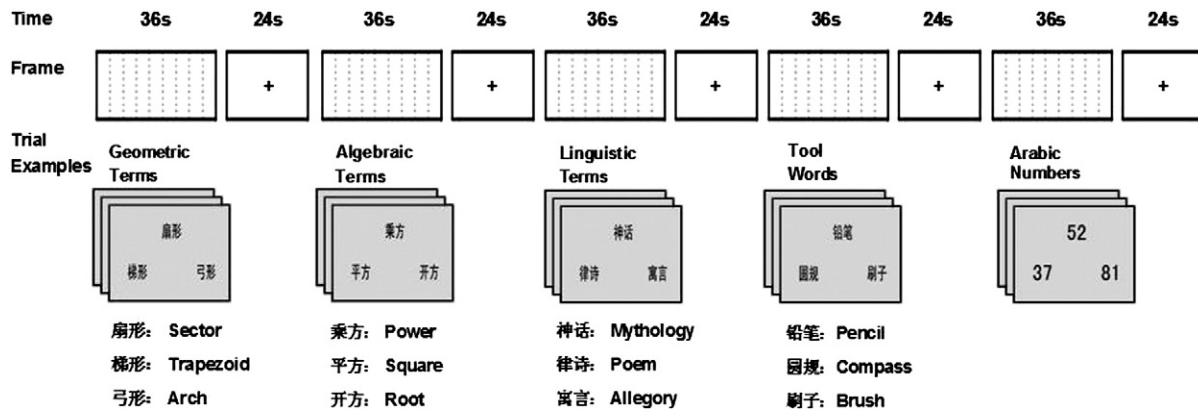


Fig. 1. The experimental procedure of a run and sample trials in the current study. Each run lasted 5 min. It contained five experimental blocks (one block of nine trials for each type of materials) and five blocks of fixation (the baseline task). Each experimental block lasted for 36 s, and each fixation block for 24 s. The order of the blocks was arranged in the Latin square design among the three runs to avoid having the same condition occurring at the same position in different runs.

London, UK, <http://www.fil.ion.ucl.ac.uk/spm>). All volumes were realigned to the first volume and spatially normalized to a common value in order to correct for whole brain differences over time. Images were then smoothed using an isotropic Gaussian kernel of 4 mm and high-pass filtered at a cut-off of 128 s.

We first calculated parameter-estimated images for individual subjects across the whole brain. Then we conducted group analyses with random effects by applying the one-way ANOVA (analysis of variance) in SPM5 on the brain activation maps of all subjects, with material type as the independent variable. We first calculated the brain activation for each type of material relative to fixation. The contrasts among the brain activation for the five types of materials were then conducted. The conjunction analysis on selected contrasts was also conducted. A moderate threshold $p < .001$ (uncorrected) was used in the above analyses except for the contrast analysis among conditions. We used a lenient threshold $p < .008$ (uncorrected) for contrast analysis in order to detect weak differences among conditions.

To examine the role of the parietal cortex, especially the IPS, in the processing of mathematical terms, we then conducted ROI (region of interest) analysis. Two types of independent localizers were used. First, we defined ROIs based on the parietal regions in the widely-cited Dehaene's three parietal circuit model for number processing (Dehaene et al., 2003). The regions include bilateral horizontal segment of the intraparietal sulcus (IPS) for numerical quantity processing, the left angular gyrus (AG) for verbal processing in numerical processing, and the bilateral posterior superior parietal lobule (PSPL) for spatial attention in numerical processing. We defined five ROIs, each as a sphere with a radius of 6 mm, centered on the coordinates for each brain region specified in Dehaene et al.'s model. Second, we defined ROIs based on the differences in brain activation between two types of materials used in the current study: Arabic numbers and tool words. According to a previous study (Thioux et al., 2005), numbers would have greater activation in the parietal cortex and prefrontal cortex. The functional ROIs were defined by the differential activation in the "numbers–tool words" contrast for the following six brain regions: the left inferior parietal lobule (IPL), left superior parietal lobule (SPL), left middle frontal gyrus (MFG), right IPL, right SPL and right MFG. These ROIs were used to compare the brain activation elicited by three types of terms: geometric, algebraic and linguistic terms.

The positive beta values in the ROIs in the con_*.img files were extracted with our in-house software for brain image data processing written in MATLAB 7.1 (Math Works Inc., Natick, MA, USA). The repeated measures ANOVA on the beta values was performed to detect the effect of type of materials. The MRICron software (<http://www.sph.sc.edu/comd/rorden/mricron/>, Rorden et al., 2007) was used to visualize the brain activation.

Brain laterality in the processing of numbers and mathematical terms

To examine hemispheric asymmetries in the processing of numbers and mathematical terms, we selected four Brodmann areas (BA) in the parietal and prefrontal regions according to the study by Arsalidou and Taylor (2011): that is, BA 7 and BA 40 in left and right parietal cortex, BA 9 and BA 46 in left and right middle frontal gyrus. The BAs were created by using the anatomically defined template in WFU PickAtlas toolbox (<http://www.ansir.wfubmc.edu>, Maldjian et al., 2003). Laterality index was calculated as: $LI = (N_L - N_R) / (N_L + N_R)$, where N_L and N_R were defined as the number of voxels above the intensity threshold $p < .001$ (uncorrected) in the left and right BAs (Seghier, 2008). The laterality index was deemed left dominant when $LI > .20$, and right dominant when $LI < -.20$, and values in-between were considered bilateral (Deblaeere et al., 2004; Springer et al., 1999).

Results

Behavioral results

The mean reaction times (RTs) were 1856 ms for Arabic numbers, 1901 ms for geometric terms, 1867 ms for algebraic terms, 1855 ms for linguistic terms and 1866 ms for tool words. The mean error rates were 14.80%, 9.95%, 11.30%, 10.30%, and 10.90%, respectively. RTs and accuracy rates were analyzed with a repeated measures analysis of variance (ANOVA) (five types of materials: algebraic terms, geometric terms, linguistic terms, tool words and Arabic numbers). The main effect of stimulus type was not significant for either RTs, $F(1,19) = .185$, $p = .95$, or the error rates, $F(1,19) = 1.84$, $p = .19$.

Whole-brain analysis

The brain activation data for each type of material relative to fixation, including coordinates, activation volumes, maximum intensities and so on, are displayed in Table S1 in Supplementary Online Materials. The conjunction of the brain activation across the five types of materials is shown in Figure S1 in Supplementary Online Materials. Results showed that the five types of materials were commonly processed in the left inferior and superior parietal lobule, left inferior frontal gyrus, bilateral supplementary motor area, right angular, and left putamen (Table 1).

Details of the differences in brain activation from the direct contrasts are displayed in Table S2 in the Supplementary Online Materials. Arabic numbers elicited greater activation than the word materials (i.e., geometric terms, algebraic terms, linguistic terms and tool words) at the bilateral IPS, bilateral middle frontal gyrus

Table 1

Loci showing significant activations based on the conjunction analysis of the five types of materials (i.e., numbers, geometric terms, algebraic terms, linguistic terms and tool words).

Hem.	Brain region	BA	Coordinates			Vol.	T
			(X, Y, Z)				
L	Superior parietal lobule, PSPL	7	-27	-66	51	3887	10.39
R	(Middle occipital gyrus)	17	27	-96	6		9.29
	(Inferior parietal lobule, IPS)	7	-30	-57	45		9.27
L	Inferior frontal gyrus	44	-45	6	27	791	9.25
L	(Insula)	47	-30	21	3		8.27
L		48	-45	24	27		7.3
L	Supplementary motor area	6	-6	9	54	259	8.07
L		32	-6	21	48		7.05
R		6	9	9	54		5.22
R	Angular	7	27	-63	48	114	6.24
L	Putamen		-21	0	18	95	4.48
L			-21	9	-3		4.36
L	(Thalamus)		-12	-12	3		4.24

Height threshold: $p < .001$, uncorrected. Voxel size: $3 \times 3 \times 3 \text{ mm}^3$. Extent threshold: $k = 50$ voxels. The brain region in the parenthesis refers to the activated region center without maximum peak. IPS: intraparietal sulcus; PSPL: posterior superior parietal lobe. The two brain regions are also specified because they are particularly relevant to numerical processing. Hem., Hemisphere; L, Left; R, Right; BA, Brodmann area; Coordinates (X, Y, Z) are given using the Montreal Neurological Institute (MNI) convention; Vol., volume.

and right inferior frontal gyrus, but the word materials had greater activation typically at the left inferior frontal gyrus and left middle temporal gyrus (See Table 2 and Fig. 2). Geometric terms showed greater activation than the non-mathematical word materials (i.e., linguistic terms and tool words) at the left IPS and the left inferior temporal gyrus (See Table 3 and Fig. 3).

ROI analysis

Based on the ROIs in Dehaene's three parietal circuit model (Dehaene et al., 2003), we found that four ROIs except the left angular gyrus (AG) showed significant differences across the five types of materials: the right IPS, $F(4, 76) = 24.90$, $p < .001$; the left IPS, $F(4, 76) = 7.22$, $p < .001$; the right PSPL, $F(4, 76) = 18.70$, $p < .001$; the left PSPL, and $F(4, 76) = 5.92$, $p < .001$ (Fig. 4). Further multiple comparison tests of activation in these regions showed that Arabic numbers elicited significantly greater activation than other four conditions. Geometric terms showed greater activation in the left IPS than did algebraic terms, linguistic terms, and tool words. Geometric terms also showed greater activation in the left PSPL than did algebraic terms and tool words, but geometric terms only showed greater activation in the right IPS than did algebraic terms.

Using the functional ROIs defined by "Arabic numbers–tool words", we found marginally significant differences among geometric, algebraic, and linguistic terms in the left IPL ROI (MNI coordinates, XYZ: $-48 -39 39$), $F(2, 38) = 2.53$, $.05 < p < .10$, in the right IPL ROI (XYZ: $48-45 51$), $F(2, 38) = 3.00$, $.05 < p < .10$. Further multiple comparison tests of activation in the left IPL ROI showed that geometric terms had greater activation than algebraic terms and linguistic terms, and geometric terms also showed greater activation in the right IPL ROI than did algebraic terms. These results are consistent with ROI analysis presented above based on Dehaene's three parietal circuit model.

No significant effects were found in other ROIs, including the left SPL ROI (XYZ: $-21 -57 54$), right SPL ROI (XYZ: $18-78 54$), left MFG ROI (XYZ: $-27 33 36$) and right MFG ROI (XYZ: $42 36 24$). The brain activation results are displayed in Fig. 5.

Brain laterality of processing of numbers and mathematical terms

Laterality indices are presented in Fig. 6. Arabic numbers showed bilaterality in the parietal cortex (BA 7 and BA 40), but right laterality

Table 2

Loci showing significant activations based on the conjunction analysis of the contrasts of numbers minus word materials (i.e., numbers > geometric terms, numbers > algebraic terms, numbers > linguistic terms, and numbers > tool words) and of the contrasts of word materials minus numbers (i.e., geometric terms > numbers, algebraic terms > numbers, linguistic terms > numbers, and tool words > numbers).

Hem.	Brain region	BA	Coordinates			Vol.	T
			(X, Y, Z)				
I. Greater activations for numbers than for word materials							
R	Inferior parietal lobule, IPS	40	48	-45	51	2769	6.58
R	(Supramarginal gyrus)	40	54	-42	45		5.69
R		40	36	-45	42		5.64
R	(Superior parietal lobule, PSPL)	40	42	-48	60		5.04
L	Middle frontal gyrus	9	-27	30	36	172	5.39
L		9	-33	36	39		4.87
L		45	-42	33	33		2.97
R	Middle frontal gyrus	46	39	36	24	707	6.06
R		45	45	39	30		5.93
R		47	39	51	0		5.09
R	Inferior frontal gyrus	44	57	9	27	69	4.05
R		44	54	9	18		3.97
R	(Precentral gyrus)	44	48	6	30		3.48
R	Precentral gyrus	6	33	-6	54	466	4.75
R	(Superior frontal gyrus)	6	27	0	54		4.49
R		6	27	-9	48		4.38
L	Cerebellum		-42	-48	-42	162	4.56
L		19	-27	-63	-27		4.23
L			-27	-72	-54		4.13
R	Hippocampus		24	-33	9	64	4.49
L	Insula	48	-21	24	12	63	3.79
L		48	-21	15	18		3.61
II. Greater activations for word materials than for numbers							
L	Inferior frontal gyrus	47	-39	36	-12	368	5.27
L		45	-54	24	21		5.23
L		45	-51	36	6		4.88
L	Middle temporal gyrus	21	-63	-51	3	178	4.85
L		21	-54	-48	0		4.18
L		22	-57	-36	3		3.81
L	Inferior temporal gyrus	20	-39	6	-42		2.99
L	Fusiform gyrus	37	-42	-48	-18	58	4.95
L	(Cerebellum)	37	-30	-42	-24		4.54
L	Fusiform gyrus	20	-30	-9	-39	51	4.71
L		20	-36	-15	-36		3.98
L	Inferior occipital gyrus	17	-21	-102	-6	77	4.74
R	Inferior occipital gyrus	17	27	-102	-6	63	5.42
R	Cerebellum		18	-87	-33	160	5.31

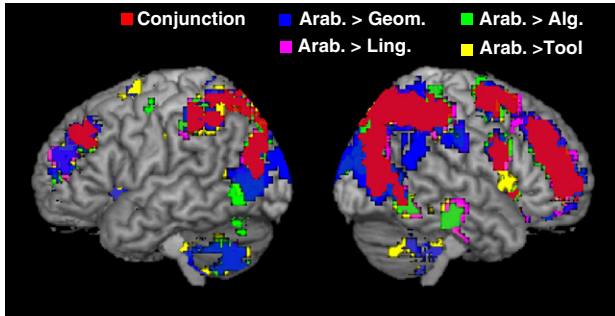
Height threshold: $p < .008$, uncorrected. Extent threshold: $k = 50$ voxels. Voxel size: $3 \times 3 \times 3 \text{ mm}^3$. The brain region in the parenthesis refers to the activated region center without maximum peak. IPS: intraparietal sulcus; PSPL: posterior superior parietal lobe. Hem., Hemisphere; L, Left; R, Right; BA, Brodmann area; Coordinates (X,Y,Z) are given using the Montreal Neurological Institute (MNI) convention; Vol., volume.

in the prefrontal cortex (BA 46). All three types of mathematical terms and tool words consistently showed left laterality in the parietal cortex and prefrontal cortex (BA 7, BA 40, BA 9, and BA 46).

Discussion

The goal of the current study was to investigate the neural correlates of the processing of two types of mathematical terms (geometric and algebraic terms). Control materials were Arabic numbers, linguistic terms, and tool words. The main findings include: (1) Algebraic terms did not elicit greater activation than did linguistic terms and tool words in the horizontal intraparietal sulcus, but geometric terms elicited greater activation than did algebraic terms, linguistic terms and tool words in this brain region; (2) Arabic numbers had significantly greater activation than other four types of materials in the bilateral IPS, the right inferior frontal gyrus, bilateral middle frontal gyrus and right middle temporal gyrus; (3) Non-numerical materials showed stronger activation than Arabic numbers in the left inferior frontal gyrus and the middle temporal gyrus; and (4). Arabic

Greater activation for numbers relative to the word materials:



Greater activations for word materials relative to numbers:

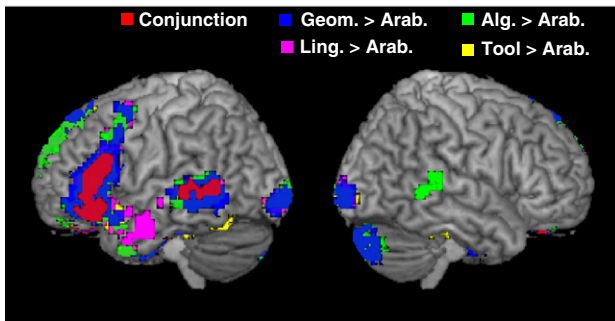


Fig. 2. The contrasts of numbers and word materials (i.e., geometric terms, algebraic terms, linguistic terms and tool words). Height threshold: $p < .008$, uncorrected. Extent threshold: $k = 50$ voxels. Voxel size: $3 \times 3 \times 3 \text{ mm}^3$. Arab: Arabic numbers; Geom: geometric terms; Alg: algebraic terms; and Ling: linguistic terms. The left of picture is the left of brain.

numbers were processed bilaterally, but mathematical terms and tool words showed left dominance. These results suggest that the main brain area for the processing of numbers (the left IPS) seems to be involved in the semantic processing of geometric terms, but not that of other mathematical terms such as algebraic terms. The brain organization for mathematical terms and numbers is discussed in the following sections.

The intraparietal sulcus and the processing of mathematical terms

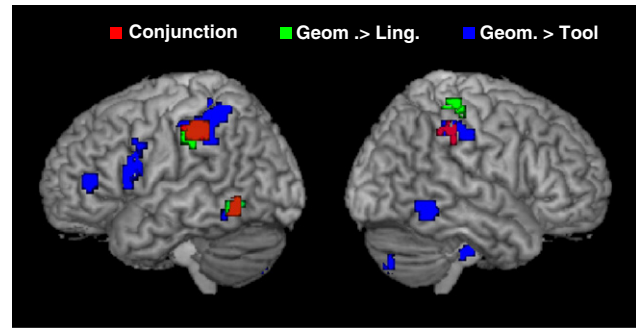
As expected, geometric terms had greater activation than algebraic terms, linguistic terms, and tool words in the left inferior parietal cortex as shown from the two sets of ROI analyses. One explanation of these results lies in the neural basis of mental images of geometric figures. Previous studies have shown that words referring to spatial representations can elicit the processing of spatial figures (e.g., Hayward and Tarr, 1995; Mani and Johnson-Laird, 1982) and that

Table 3
Loci showing significant activation based on conjunction analysis between geometric terms and non-mathematical word materials (i.e., linguistic terms and tool words).

Hem.	Brain region	BA	Coordinates			Vol.	T
			(X, Y, Z)				
L	Intraparietal lobule, IPS	40	-54	-33	42	45	3.63
L		40	-63	-39	42		2.94
R	Supramarginal gyrus	40	66	-33	39	15	3.17
R		40	63	-42	45		2.83
L	Inferior temporal gyrus	37	-54	-60	-9	20	3.74

Height threshold: $p < .008$, uncorrected. Extent threshold: $k = 15$ voxels. Voxel size: $3 \times 3 \times 3 \text{ mm}^3$. The brain region in the parenthesis refers to the activated region center without maximum peak. IPS: intraparietal sulcus. Hem., Hemisphere; L, Left; R, Right; BA, Brodmann area; Coordinates (X,Y,Z) are given using the Montreal Neurological Institute (MNI) convention; Vol., volume.

Greater activation for geometric terms relative to linguistic terms and tool words:



Greater activation for algebraic terms relative to linguistic terms and tool words:

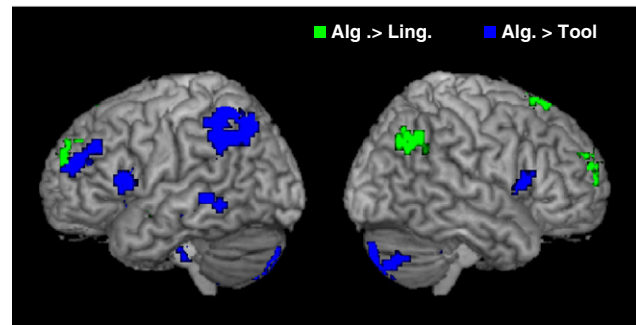


Fig. 3. The contrasts of mathematical terms and non-mathematical word materials (i.e., linguistic terms and tool words). Height threshold: $p < .008$, uncorrected. Extent threshold: $k = 15$ voxels. Voxel size: $3 \times 3 \times 3 \text{ mm}^3$. Arab: Arabic numbers; Geom: geometric terms; Alg: algebraic terms; and Ling: linguistic terms. The left of picture is the left of brain.

spatial processing is subserved by the parietal cortex (e.g., Hilgetag et al., 2001), especially the inferior parietal lobule (e.g., Alivisatos and Petrides, 1997; Carpenter et al., 1999). Geometric terms as well as numbers also had greater activation than algebraic terms and tool words at the posterior superior parietal lobe as shown in the ROI analysis based on Dehaene et al.'s three parietal circuit model. The processing of numbers and geometrical terms seemed to share common neural resources as visuo-spatial processing. The visuo-spatial processing might also extend to the PSPL.

Algebraic terms did not elicit greater activation at the horizontal IPS regions than did linguistic terms and tool words. This result is contrary to our expectation. It is possible that algebraic terms did not activate sufficiently mental representations of numbers. That is, the processing algebraic terms (e.g., "fraction") might not have activated the processing of related numerical exemplars (e.g. " $\frac{1}{2}, \frac{1}{3}, \frac{1}{4}, \dots$ "). This result explains why arithmetic facts and conceptual algebraic knowledge have been found to be dissociated at the IPS (Delazer and Benke, 1997; Hittmair-Delazer et al., 1994; Warrington, 1982).

The language areas and the processing of mathematical terms

Non-numerical words elicited more activations in the left frontal lobe and the temporal lobe than did Arabic numbers. These two brain regions are critical for language processing (e.g., Chee et al., 1999; Petersen et al., 1990; Poldrack et al., 1999; Price et al., 1996; Tan et al., 2000). In terms of the role of the language areas in the processing of mathematical terms, two other issues need to be discussed.

First, a number of the mathematical terms have alternative non-mathematical meanings. For example, " " in Chinese has several meaning, including "sum", "and", "harmony", and "peace". Although

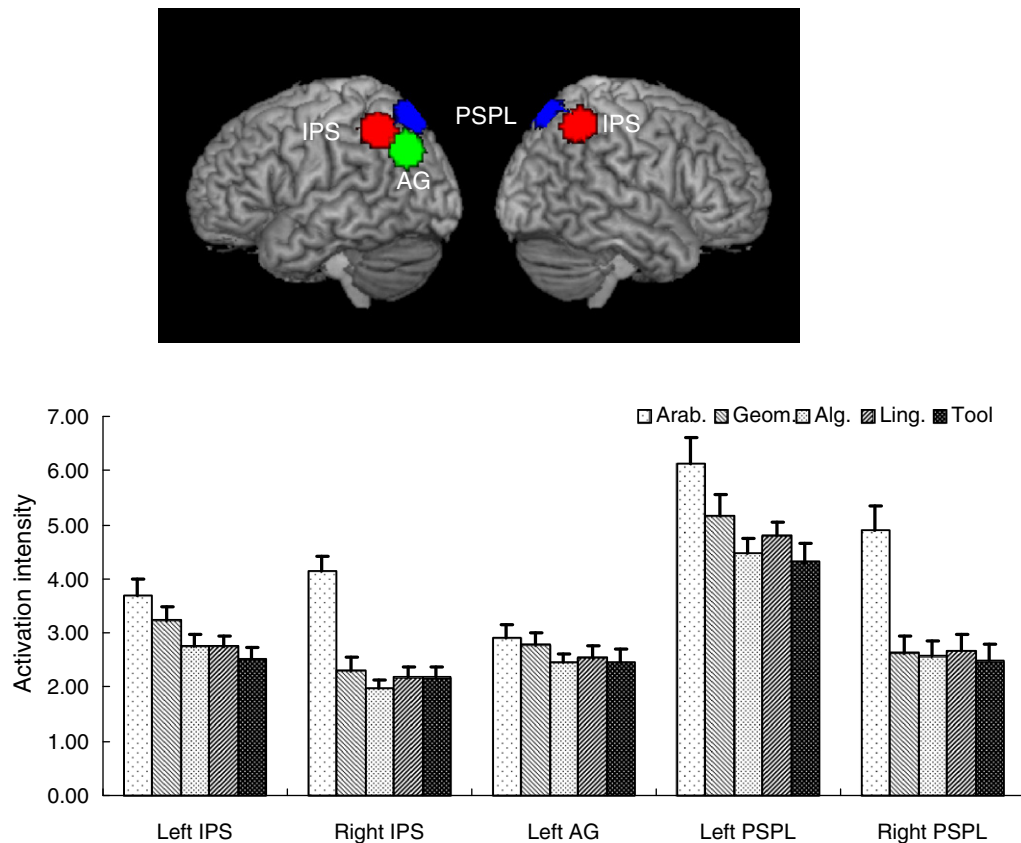


Fig. 4. The ROI analyses showed that Arabic numbers elicited greater activation than geometric terms, algebraic terms, linguistic terms, and tool words in the bilateral horizontal intraparietal sulcus (IPS) and the posterior superior parietal lobe (PSPL), and that geometric terms elicited greater activation than algebraic terms and linguistic terms in the left horizontal intraparietal sulcus. The ROIs as shown in the brain map were defined according to Dehaene's three parietal circuit model of numerical processing (Dehaene et al., 2003). The error bars in bar figure indicate standard error of the mean. Arab.: Arabic numbers; Geom.: geometric terms; Alg.: algebraic terms; Ling.: linguistic terms; AG: angular gyrus. The left of picture is the left of brain.

subjects were instructed to focus on the mathematical meanings of these terms, we could not rule out automatic activation of these words' alternative meanings. Those meanings would activate the language areas. Furthermore, to discriminate among the alternative meanings of a mathematical word in order to judge its semantic proximity with another word would require more cognitive control, which involves, among other regions, the middle temporal and inferior frontal areas (Whitney et al., 2011). Therefore, an alternative explanation of our results regarding algebraic terms may be the involvement of their multiple meanings. Future research needs to specifically test this alternative hypothesis.

Second, Chinese is a logographic script that is much more spatially complicated than alphabetical scripts. In this experiment, all stimuli except for Arabic numerals were written in Chinese. It is plausible that the script differences might offer another confound in the large differences between Arabic numbers and the other materials. However, Wei et al. (2011) recently found that Chinese number words had the same activation at the IPS as Arabic numbers. Therefore, our results did not seem to be driven by differences in scripts. We may then speculate that Western subjects would show a similar pattern of results as ours. Indeed, as reviewed earlier, neuropsychological studies of Westerners have documented a dissociation between mathematical terms and numerical processing (Delazer and Benke, 1997; Hittmair-Delazer et al., 1994; Warrington, 1982).

Dehaene et al.'s three parietal circuit model posits that the angular gyrus supports the verbal representation of numbers (Dehaene et al., 2003). This idea has been supported by some studies (e.g., Chochon et al., 1999; Dehaene et al., 1999; Lee, 2000; Simon et al., 2002), but not others (e.g., Andres et al., 2011; Dehaene et al., 1996; Delazer

and Benke, 1997; Pesenti et al., 2000; Tucha et al., 1997; Van Harskamp et al., 2002; Zhou et al., 2007). For example, several studies have found that injuries to the angular gyrus or even the removal of this brain region did not affect subjects' performance on multiplication (e.g., Delazer and Benke, 1997; Tucha et al., 1997; van Harskamp et al., 2002). Zhou et al. (2007) found that multiplication did not have greater activation than addition in the angular gyrus, only in the superior temporal gyrus, precentral gyrus and supplementary motor area. Andres et al. (2011) also found no activation in the angular gyrus for multiplication relative to subtraction, letter reading or even fixation. This region has also been found to be susceptible to task difficulty, that is, easy arithmetic problems consistently elicit greater activation than difficult arithmetic problems (e.g., Grabner et al., 2009; Jost et al., 2011; Stanesco-Cosson et al., 2000; Zhou et al., 2007).

Brain organization of numerical processing

Previous research has clearly documented the role of the IPS in number processing (e.g. Arsalidou and Taylor, 2011; Dehaene et al., 1999; see a review by Dehaene et al., 2003). Our study extended it to include geometric terms. The IPS's function in processing numbers and spatial information may be one of the same because quantity of numbers has spatial representations as demonstrated by the mental number line (e.g. Zorzi et al., 2002). It seems that geometric terms can activate the IPS because these terms can elicit the mental images of geometric figures.

We also found that numbers also showed greater activations in the frontal gyrus than non-numerical materials. These activations

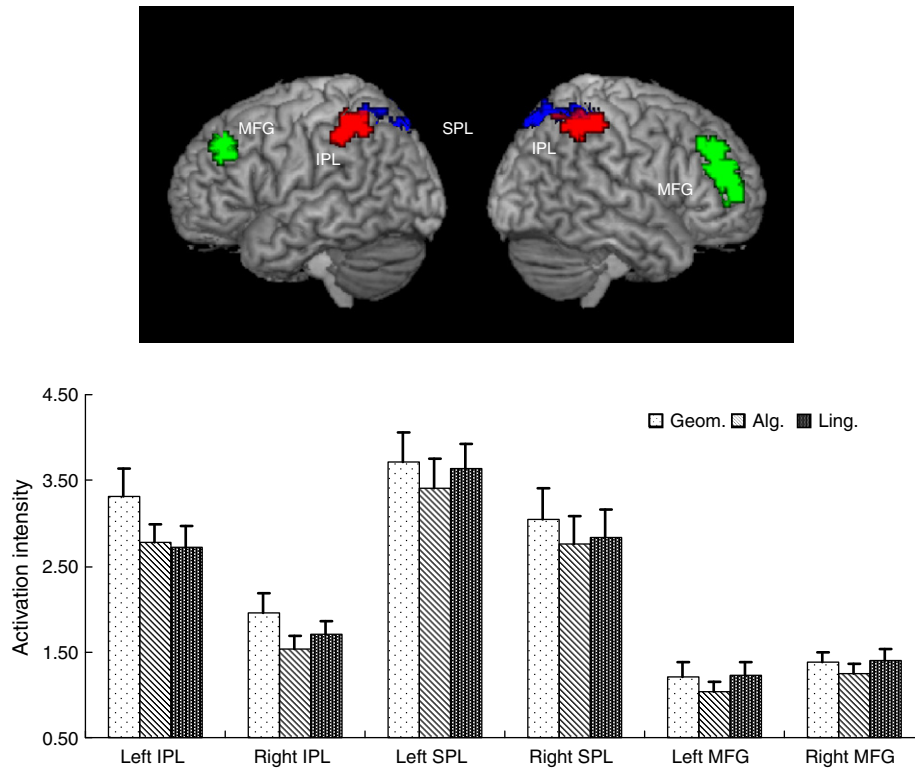


Fig. 5. The ROI analyses showed that geometric terms elicited greater activation than both algebraic terms and linguistic terms in the left inferior parietal lobule. The ROIs as shown in the brain map were defined functionally by the “numbers–tool words” contrast in the following six brain regions: the left inferior parietal lobule (IPL), left superior parietal lobule (SPL), left middle frontal gyrus (MFG), right IPL, right SPL and right MFG. Height threshold: $p < .0001$, uncorrected, extent threshold: $k = 15$ voxels, and voxel size: $3 \times 3 \times 3 \text{ mm}^3$. Error bars indicate standard error of the mean. Geom: geometric terms; Alg: algebraic terms; and Ling: linguistic terms. The left of picture is the left of brain.

may have been due to the differential need for some general-purpose cognitive functions such as working memory (Arsalidou and Taylor, 2011; Christoff and Gabrieli, 2000; Owen et al., 2005). The activation in the middle frontal gyri was attributed to working memory and procedural complexity (Delazer et al., 2003; Fehr and Herrmann, 2007; Kong et al., 2005; Simon et al., 2002; Zhou et al., 2007). Arsalidou and Taylor’s meta-analysis (2011) found that solving calculation tasks elicited ALE (activation likelihood estimation) values in more prefrontal areas than solving number tasks. This difference could also be explained in terms of the working memory load. According to Dehaene and Cohen’s triple-code model, the prefrontal cortex is also responsible for strategy choice and planning (Dehaene and

Cohen, 1997). The greater activation for numerical processing relative to non-numerical materials in the prefrontal cortex is consonant with the greater activation in the IPS, which may reflect the recruitment of working memory on the numerical magnitude information or visuo-spatial codes of numbers.

Brain laterality for numerical processing is a long-standing topic. Arsalidou and Taylor’s (2011) meta-analysis of brain areas for calculations showed that the laterality of numerical processing differed across operations, with addition showing left laterality in the parietal cortex and multiplication right laterality. They thought that lateralization in the parietal cortex (also including BA 46) would be affected by the strategy adopted for solving each operation. That is, addition

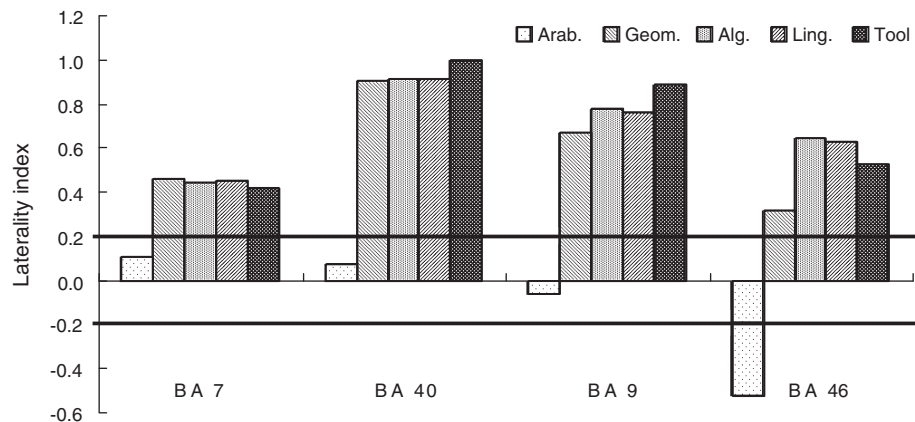


Fig. 6. Laterality indices for regions in the parietal and prefrontal cortex. Black horizontal lines represent the criteria of laterality, whereby $LI > .20$ is deemed left dominant, $LI < -.20$ as right dominant, and values in-between are considered bilateral. Arab: Arabic numbers, Geom: geometric terms; Alg: algebraic terms; and Ling: linguistic terms.

and subtraction with the strategies of counting and transformation (e.g., Imbo and Vandierendonck, 2007) would be more leftward, but automatized multiplication would be more rightward. The current study showed clear bilateralization at the parietal cortex and right lateralization at the prefrontal cortex (BA 46) for numbers, but left lateralization for all materials involving words. According to the differential strategies explanation, numerical processing may involve fewer strategies than the word materials. Alternatively, this pattern of laterality reflects the classic left laterality for language processing and right laterality for numbers and spatial processing, particularly in the prefrontal cortex (Casasanto, 2003; Dehaene et al., 1993; Kuo et al., 2001, 2004; Tan et al., 2000, 2005; Zorzi et al., 2002).

Summary

Our study confirmed that numbers are processed in the bilateral IPS and prefrontal cortex. In addition, we found that geometric

terms elicited more left IPS activations than did algebraic terms and non-mathematical words. Like the non-number words (e.g., linguistic terms and tool words), geometric and algebraic terms are also processed in the general language areas, including the left middle temporal gyrus and the left inferior frontal gyrus. More research is needed to understand how the processing of various aspects of mathematical knowledge (number processing, memory of number facts, knowledge of terms for different areas of mathematics such as geometry and algebra, rules and strategies) is distributed across the brain regions.

Acknowledgments

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Appendix A. Terms, tool words and numbers used in the current study

A.1. Geometric terms.

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
坐标	zuò biāo	Coordinate	平角	píng jiǎo	Straight angle
周角	zhōu jiǎo	Perigon	底面	dǐ miàn	Undersurface
正方形	zhèng fāng xíng	Square	面积	Miàn jī	Area
圆柱(体)	yuán zhù tǐ	Cylinder	半径	bàn jǐng	Radius
圆形	yuán xíng	Circle	点	diǎn	Dot
圆心	yuán xīn	Center of a circle	直径	zhí jìng	Diameter
外接	wài jiē	Circumscribed	内切	nèi qiē	Inscribe
同心圆	tóng xīn yuán	Concentric circles	圆环	yuán huán	Donut
射线	shè xiàn	Radial	直线	zhí xiàn	Straight line
扇形	shàn xíng	Sector	弓形	gōng xíng	Arch
全等	quán děng	Congruent	相似	xiāng sì	Similar
曲线	qū xiàn	Curve	梯形	tī xíng	Trapezoid
曲面	qū miàn	Curved surface	外角	wài jiǎo	Exterior angle
球体	qiú tǐ	Sphere	平面	píng miàn	Plane
平行线	píng xíng xiàn	Parallel	周长	zhōu cháng	Perimeter
内角	nèi jiǎo	Interior angle	垂线	chuí xiàn	Perpendicular
菱形	líng xíng	Rhombus	相交	xiāng jiāo	Intersect
棱	léng	Arris	立方体	lì fāng tǐ	Cube
矩形	jǔ xíng	Rectangle	余角	yú jiǎo	Complementary angle
截面	jié miàn	Section	凸面	tū miàn	Convexity
弧长	hú cháng	Arc length	顶角	dǐng jiǎo	Vertex angle
弧	hú	Arc	体积	tǐ jī	Volume
高	gāo	Height	面	miàn	Face
底	dǐ	Bottom	边长	biān cháng	Side
垂直	chuí zhí	Vertical	相离	xiāng lí	Opening
长方体	cháng fāng tǐ	Cuboid	椭圆	tū yuán	Ellipse
补角	bǔ jiǎo	Supplementary angle	平行	píng xíng	Parallel
凹面	āo miàn	Concave side	方形	fāng xíng	Square
象限	xiàng xiàn	Quadrant	球面	qiú miàn	Sphere

A.2. Algebraic terms.

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
自然数	zì rán shù	Natural number	有理数	yǒu lǐ shù	Rational number
质数	zhì shù	Prime number	实数	shí shù	Real number
指数	zhǐ shù	Exponent	纯小数	chún xiǎo shù	Decimal fraction
正数	zhèng shù	Positive number	除	chú	Divide
整数	zhěng shù	Integer	乘数	chéng shù	Multiplier
真分数	zhēn fēn shù	Proper fraction	众数	zhòng shù	Mode
余数	yú shù	Remainder	减数	jiǎn shù	Subtractor
因数	yīn shù	Factor	分母	fēn mǔ	Denominator
序数	xù shù	Ordinal number	被除数	bèi chú shù	Dividend

(continued on next page)

Appendix A.2 (continued)

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
商	shāng	Quotient	小数	xiǎo	Decimals
幂	mì	Power	等比	děng bǐ	Equal ratio
均数	jūn shù	Mean	平方	píng fāng	Square
绝对值	jué duì zhí	Absolute value	变量	biàn liàng	Variable
假分数	jiǎ fēn shù	Improper fraction	减	jiǎn	Subtract
加数	jiā shù	Addend	乘	chéng	Multiply
积	jī	Product	函数	hán	Function
和	hé	Sum	无理数	wú lǐ	Irrational number
合数	hé shù	Composite number	虚数	xū	Imaginary number
负数	fù shù	Negative number	平方数	píng fāng	Square number
分子	fēn zǐ	Numerator	正整数	zhèng zhèng shù	Positive integer
分数	fēn shù	Fraction	基数	jī shù	Base number
等差	děng chā	Equal difference	偶数	ǒu	Even number
除数	chú shù	Divisor	约数	yuē	Approximate number
乘方	chéng fāng	Power	被减数	bèi jiǎn	Minuend
常量	cháng liàng	Constant	倒数	dào	Reciprocal
差	chā	Difference	等式	děng shì	Equality
比例	bǐ lì	Ratio	开方	kāi fāng	Root
倍数	bèi shù	Multiple	向量	xiàng liàng	Vector
对数	duì shù	Logarithm	奇数	jī shù	Odd number

A.3. Linguistic terms.

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
主语	zhǔ yǔ	Subject	颂	sòng	Eulogy
杂文	zá wén	Essay	会意	huì yì	Knowing
雅	yǎ	Elegant	阙	què	Note
象征	xiàng zhēng	Symbol	律诗	lǜ shī	Eight line poem
象形	xiàng xíng	Representation	议论	yì lùn	Discuss
谓语	wèi yǔ	Predicate	词	cí	Word
唐诗	táng shī	Tang poem	寓言	yù yán	Allegory
宋词	sòng cí	Song poems	书信	shū xìn	Letter
说明	shuō míng	Illustration	对偶	duì ǒu	Antithesis
时态	shí tài	Tense	代词	dài cí	Pronoun
诗	shī	Poem	段落	duàn luò	Paragraph
神话	shén huà	Mythology	同义	tóng yì	Synonymy
日记	rì jì	Diary	副词	fù cí	Adverb
排比	pái bǐ	Parallelism	闽南话	mǐn nán huà	Hokkien
名词	míng cí	Noun	格律诗	gé lǜ shī	Metrical verse
绝句	jué jù	Four line poem	土语	tǔ yǔ	Local expression
句子	jù zǐ	Sentence	反问	fǎn wèn	Rhetorical question
近义	jìn yì	Synonymy	反衬	fǎn chèn	Contrast
介词	jiè cí	Preposition	比拟	bǐ nǐ	Analogy
广东话	guǎng dōng huà	Cantonese	杂剧	zá jù	Poetic drama
古体诗	gǔ tǐ shī	Pre-Tang poetry	汉赋	hàn fù	Han fu
方言	fāng yán	Dialect	序	xù	Preface
反语	fǎn yǔ	Irony	剧本	jù běn	Play
对比	duì bǐ	Contrast	连词	lián cí	Conjunction
动词	dòng cí	Verb	语义	yǔ yì	Semantic
定语	dìng yǔ	Attribute	普通话	pǔ tōng huà	Mandarin
宾语	bīn yǔ	Object	散文诗	sǎn wén shī	Prose poem
比喻	bǐ yù	Metaphor	反复	fǎn fù	Repetition
杂记	zá jì	Notes	状语	zhuàng yǔ	Adverbial

A.4. Tools and other common objects.

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
圆规	yuán guī	Compass	吹风机	chuī fēng jī	Blower
小号	xiǎo hào	Trumpet	喇叭	lǎ bā	Horn
箫	xiāo	Xiao	唢呐	suǒ nà	Zurna
骰子	tóu zi	Dice	铲子	chǎn zi	Shovel
梳子	shū zi	Comb	钳子	qián zi	Pliers
手机	shǒu jī	Cellphone	台灯	tái dēng	Lamp
笙	shēng	Sheng	汤勺	tāng sháo	Ladle
铅笔	qiān bǐ	Pencil	古筝	gǔ zhēng	Koto
耙子	pá zi	Rake	锣	luó	Gong
镊子	niè zi	Tweezers	刀子	dāo zi	Knife
螺丝刀	luó sī dāo	Screwdriver	剪刀	jiǎn dāo	Scissors

Appendix A.4 (continued)

Chinese name	Pronunciation	English	Chinese name	Pronunciation	English
犁	lí	Plough	凿子	záo zi	Chisel
蜡烛	là zhú	Candle	锥子	zhuī zi	Awl
筷子	kuài zi	Chopsticks	电锯	diàn jù	Electric saw
胡琴	hú qín	Huqin	锅铲	guō chǎn	Spatula
鼓	gǔ	drum	订书机	dìng shū jī	Stapler
钢笔	gāng bǐ	Pen	牙刷	yá shuā	Toothbrush
斧子	fǔ zi	ax	起子	qǐ zi	Screwdriver
粉笔	fěn bǐ	Chalk	编钟	biān zhōng	Chime
电钻	diàn zuàn	Electric drill	钢琴	gāng qín	Piano
锉刀	cuò dāo	File	围棋	wéi qí	Go
锤子	chuí zi	Hammer	电熨斗	diàn yùn dòu	Electric iron
菜刀	cài dāo	Kitchen knife	琵琶	pí pa	Chinese lute
裁纸刀	cái zhǐ dāo	Paper cutter	刷子	shuā zi	Brush
杯子	bēi zi	Cup	天平	tiān píng	Balance
扳手	bǎn shǒu	Wrench	琴	qín	Lyre
尺子	chǐ zi	Ruler	绳子	shéng zi	Rope
笛子	dí zi	Flute	拖把	tuō ba	Mop
麻将	mǎ jiàng	Mahjong	黑板擦	hēi bǎn cā	Eraser

Note: Two-digit numbers used in the current study are as follows: 15, 16, 17, 18, 19, 21, 23, 25, 26, 27, 28, 29, 33, 34, 36, 37, 38, 39, 42, 43, 45, 46, 47, 48, 49, 52, 53, 54, 56, 57, 58, 59, 62, 64, 65, 67, 68, 69, 71, 72, 73, 74, 75, 76, 78, 81, 82, 83, 84, 85, 86, 87, 91, 92, 93, 94, 95, 96.

Appendix B. Supplementary data

Supplementary data to this article can be found online at doi:10.1016/j.neuroimage.2011.12.006.

References

- Alivisatos, B., Petrides, M., 1997. Functional activation of the human brain during mental rotation. *Neuropsychologia* 35 (2), 111–118.
- Andres, M., Pelgrims, B., Michaux, N., Olivier, E., Pesenti, M., 2011. Role of distinct parietal areas in arithmetic: an fMRI-guided TMS study. *NeuroImage* 54 (4), 3048–3056.
- Ansari, D., Dhital, B., Siong, S.C., 2006. Parametric effects of numerical distance on the intraparietal sulcus during passive viewing of rapid numerosity changes. *Brain Res.* 1067 (1), 181–188.
- Arsalidou, M., Taylor, M.J., 2011. Is $2 + 2 = 4$? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage* 54 (3), 2382–2393.
- Bradley, J.V., 1958. Complete counterbalancing of immediate sequential effects in a Latin square design. *J. Am. Stat. Assoc.* 53 (282), 525–528.
- Brannon, E.M., 2006. The representation of numerical magnitude. *Curr. Opin. Neurobiol.* 16 (2), 222–229.
- Butterworth, B., 1999. *The Mathematical Brain*. Macmillan.
- Butterworth, B., Cappelletti, M., Kopelman, M., 2001. Category specificity in reading and writing: the case of number words. *Nat. Neurosci.* 4 (8), 784–786.
- Cappa, S., Perani, D., Schnur, T., Tettamanti, M., Fazio, F., 1998. The effects of semantic category and knowledge type on lexical-semantic access: a PET study. *NeuroImage* 8 (4), 350–359.
- Cappelletti, M., Butterworth, B., Kopelman, M., 2001. Spared numerical abilities in a case of semantic dementia. *Neuropsychologia* 39 (11), 1224–1239.
- Cappelletti, M., Kopelman, M., Butterworth, B., 2002. Why semantic dementia drives you to the dogs (but not to the horses): a theoretical account. *Cogn. Neuropsychol.* 19 (6), 483–503.
- Cappelletti, M., Kopelman, M.D., Morton, J., Butterworth, B., 2005. Dissociations in numerical abilities revealed by progressive cognitive decline in a patient with semantic dementia. *Cogn. Neuropsychol.* 22 (7), 771–793.
- Cappelletti, M., Lee, H.L., Freeman, E.D., Price, C.J., 2010. The role of right and left parietal lobes in the conceptual processing of numbers. *J. Cogn. Neurosci.* 22 (2), 331–346.
- Carpenter, P.A., Just, M.A., Keller, T.A., Eddy, W., Thulborn, K., 1999. Graded functional activation in the visuospatial system with the amount of task demand. *J. Cogn. Neurosci.* 11 (1), 9–24.
- Casasanto, D., 2003. Hemispheric specialization in prefrontal cortex: effects of verbalizability, imageability and meaning. *J. Neurolinguist.* 16 (4–5), 361–382.
- Chee, M.W.L., Tan, E.W.L., Thiel, T., 1999. Mandarin and English single word processing studied with functional magnetic resonance imaging. *J. Neurosci.* 19 (8), 3050–3056.
- Chochon, F., Cohen, L., Moortele, P.F., Dehaene, S., 1999. Differential contributions of the left and right inferior parietal lobules to number processing. *J. Cogn. Neurosci.* 11 (6), 617–630.
- Christoff, K., Gabrieli, J.D.E., 2000. The frontopolar cortex and human cognition: evidence for a rostrocaudal hierarchical organization within the human prefrontal cortex. *Psychobiology* 28 (2), 168–186.
- Crutch, S.J., Warrington, E.K., 2002. Preserved calculation skills in a case of semantic dementia. *Cortex* 38 (3), 389–399.
- Deblaere, K., Boon, P., Vandemaele, P., Tieleman, A., Vonck, K., Vingerhoets, G., Achten, E., 2004. MRI language dominance assessment in epilepsy patients at 1.0 T: region of interest analysis and comparison with intracarotid amyltal testing. *Neuroradiology* 46 (6), 413–420.
- 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., Bossini, S., Giraux, P., 1993. The mental representation of parity and number magnitude. *J. Exp. Psychol. Gen.* 122 (3), 371–396.
- Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., Mazoyer, B., 1996. Cerebral activations during number multiplication and comparison: a PET study. *Neuropsychologia* 34 (11), 1097–1106.
- Dehaene, S., Spelke, E., Pinel, P., Stanescu, R., Tsivkin, S., 1999. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science* 284 (5416), 970.
- Dehaene, S., Piazza, M., Pinel, P., Cohen, L., 2003. Three parietal circuits for number processing. *Cogn. Neuropsychol.* 20 (3–6), 487–506.
- Delazer, M., Benke, T., 1997. Arithmetic facts without meaning. *Cortex* 33 (4), 697–710.
- Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., Benke, T., 2003. Learning complex arithmetic—an fMRI study. *Cogn. Brain Res.* 18 (1), 76–88.
- Denes, G., Signorini, M., 2001. Door but not four and 4 a category specific transcoding deficit in a pure acalculic patient. *Cortex* 37 (2), 267–277.
- Diesfeldt, H., 1993. Progressive decline of semantic memory with preservation of number processing and calculation. *Behav. Neurol.* 6 (4), 239–242.
- Eger, E., Sterzer, P., Russ, M.O., Giraud, A.L., Kleinschmidt, A., 2003. A supramodal number representation in human intraparietal cortex. *Neuron* 37 (4), 719–725.
- Fehr, T., Herrmann, M., 2007. Common brain regions underlying different arithmetic operations as revealed by conjunct fMRI-BOLD activation. *Brain Res.* 1172, 93–102.
- Gauthier, I., Hayward, W.G., Tarr, M.J., Anderson, A.W., Skudlarski, P., Gore, J.C., 2002. BOLD activity during mental rotation and viewpoint-dependent object recognition. *Neuron* 34 (1), 161–171.
- Göbel, S.M., Johansen-Berg, H., Behrens, T., Rushworth, M.F.S., 2004. Response-selection-related parietal activation during number comparison. *J. Cogn. Neurosci.* 16 (9), 1536–1551.
- Grabner, R.H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., Neuper, C., 2009. To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. *Neuropsychologia* 47 (2), 604–608.
- Grafman, J., Passafiume, D., Faglioni, P., Boller, F., 1982. Calculation disturbances in adults with focal hemispheric damage. *Cortex* 18 (1), 37–49.
- Hayward, W.G., Tarr, M.J., 1995. Spatial language and spatial representation. *Cognition* 55 (1), 39–84.
- Hilgetag, C.C., Théoret, H., Pascual-Leone, A., 2001. Enhanced visual spatial attention ipsilateral to rTMS-induced ‘virtual lesions’ of human parietal cortex. *Nat. Neurosci.* 4, 953–958.
- Hittmair-Delazer, M., Semenza, C., Denes, G., 1994. Concepts and facts in calculation. *Brain* 117 (4), 715–728.
- Imbo, I., Vandierendondck, A., 2007. The development of strategy use in elementary school children: working memory and individual differences. *J. Exp. Child Psychol.* 96 (4), 284–309.
- Isaacs, E., Edmonds, C., Lucas, A., Gadian, D., 2001. Calculation difficulties in children of very low birthweight. *Brain* 124 (9), 1701–1707.
- Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelst tter, F., Benke, T., Felber, S., Delazer, M., 2006. How specifically do we learn? Imaging the learning of multiplication and subtraction. *NeuroImage* 30 (4), 1365–1375.
- Jefferies, E., Patterson, K., Jones, R., Bateman, D., Lambon Ralph, M., 2004. A category-specific advantage for numbers in verbal short-term memory: evidence from semantic dementia. *Neuropsychologia* 42 (5), 639–660.
- Jefferies, E., Bateman, D., Ralph, M.A.L., 2005. The role of the temporal lobe semantic system in number knowledge: evidence from late-stage semantic dementia. *Neuropsychologia* 43 (6), 887–905.
- Jordan, K., Heinze, H.J., Lutz, K., Kanowski, M., Jancke, L., 2001. Cortical activations during the mental rotation of different visual objects. *NeuroImage* 13 (1), 143–152.
- Jost, K., Khader, P.H., Burke, M., Bien, S., Rösler, F., 2011. Frontal and parietal contributions to arithmetic fact retrieval: a parametric analysis of the problem-size effect. *Hum. Brain Mapp.* 32 (1), 51–59.

- Kadosh, R.C., Henik, A., Rubinsten, O., Mohr, H., Dori, H., van de Ven, V., Zorzi, M., Hendler, T., Goebel, R., Linden, D.E.J., 2005. Are numbers special? The comparison systems of the human brain investigated by fMRI. *Neuropsychologia* 43 (9), 1238–1248.
- Kadosh, R.C., Kadosh, K.C., Kaas, A., Henik, A., Goebel, R., 2007. Notation-dependent and-independent representations of numbers in the parietal lobes. *Neuron* 53 (2), 307–314.
- Kadosh, R.C., Lammertyn, J., Izard, V., 2008. Are numbers special? An overview of chrometric, neuroimaging, developmental and comparative studies of magnitude representation. *Prog. Neurobiol.* 84 (2), 132–147.
- Knops, A., Nuerk, H.C., Fimm, B., Vohn, R., Willmes, K., 2006. A special role for numbers in working memory? An fMRI study. *NeuroImage* 29 (1), 1–14.
- Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., Gollub, R., 2005. The neural substrate of arithmetic operations and procedure complexity. *Cogn. Brain Res.* 22 (3), 397–405.
- Kucian, K., Loenneker, T., Dietrich, T., Dosch, M., Martin, E., Von Aster, M., 2006. Impaired neural networks for approximate calculation in dyscalculic children: a functional MRI study. *Behav. Brain Funct.* 2 (1), 31–47.
- Kuo, W.J., Yeh, T.C., Duann, J.R., Wu, Y.T., Ho, L.T., Hung, D., Tzeng, O.J.L., Hsieh, J.C., 2001. A left-lateralized network for reading Chinese words: a 3 T fMRI study. *Neuroreport* 12 (18), 3997–4001.
- Kuo, W.J., Yeh, T.C., Lee, J.R., Chen, L.F., Lee, P.L., Chen, S.S., Ho, L.T., Hung, D., Tzeng, O.J.L., Hsieh, J.C., 2004. Orthographic and phonological processing of Chinese characters: an fMRI study. *NeuroImage* 21 (4), 1721–1731.
- Le Clec'h, G., Dehaene, S., Cohen, L., Mehler, J., Dupoux, E., Poline, J.B., Lehericy, S., van de Moortele, P.F., Le Bihan, D., 2000. Distinct cortical areas for names of numbers and body parts independent of language and input modality. *NeuroImage* 12 (4), 381–391.
- Lee, K.M., 2000. Cortical areas differentially involved in multiplication and subtraction: a functional magnetic resonance imaging study and correlation with a case of selective acalculia. *Ann. Neurol.* 48 (4), 657–661.
- Lemer, C., Dehaene, S., Spelke, E., Cohen, L., 2003. Approximate quantities and exact number words: dissociable systems. *Neuropsychologia* 41 (14), 1942–1958.
- Maldjian, J.A., Laurienti, P.J., Kraft, R.A., Burdette, J.H., 2003. An automated method for neuroanatomic and cytoarchitectonic atlas-based interrogation of fMRI data sets. *NeuroImage* 19 (3), 1233–1239.
- Mani, K., Johnson-Laird, P.N., 1982. The mental representation of spatial descriptions. *Mem. Cognit.* 10 (2), 181–187.
- Martin, A., Wiggs, C.L., Ungerleider, L.G., Haxby, J.V., 1996. Neural correlates of category-specific knowledge. *Nature* 379 (6566), 649–652.
- Molko, N., Cachia, A., Riviere, D., Mangin, J.F., Bruandet, M., Le Bihan, D., Cohen, L., Dehaene, S., 2003. Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron* 40 (4), 847–858.
- Molko, N., Cachia, A., Riviere, D., Mangin, J., Bruandet, M., LeBihan, D., Cohen, L., Dehaene, S., 2004. Brain anatomy in Turner syndrome: evidence for impaired social and spatial/numerical networks. *Cereb. Cortex* 14 (8), 840–850.
- Mummery, C., Patterson, K., Hodges, J., Price, C., 1998. Functional neuroanatomy of the semantic system: divisible by what? *J. Cogn. Neurosci.* 10 (6), 766–777.
- Owen, A.M., McMillan, K.M., Laird, A.R., Bullmore, E., 2005. N-back working memory paradigm: a meta-analysis of normative functional neuroimaging studies. *Hum. Brain Mapp.* 25 (1), 46–59.
- Pesenti, M., Thioux, M., Seron, X., Volder, A.D., 2000. Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: A PET study. *J. Cogn. Neurosci.* 12 (3), 461–479.
- Petersen, S.E., Fox, P.T., Snyder, A.Z., Raichle, M.E., 1990. Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science* 249 (4972), 1041–1044.
- Piazza, M., Izard, V., Pinel, P., Le Bihan, D., Dehaene, S., 2004. Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44 (3), 547–555.
- Piazza, M., Pinel, P., Le Bihan, D., Dehaene, S., 2007. A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron* 53 (2), 293–305.
- Poldrack, R.A., Wagner, A.D., Prull, M.W., Desmond, J.E., Glover, G.H., Gabrieli, J.D.E., 1999. Functional specialization for semantic and phonological processing in the left inferior prefrontal cortex. *NeuroImage* 10 (1), 15–35.
- Prado, J., Mutreja, R., Zhang, H., Mehta, R., Desroches, A.S., Minas, J.E., Booth, J.R., 2011. Distinct representations of subtraction and multiplication in the neural systems for numerosity and language. *Hum. Brain Mapp.* 32 (11), 1932–1947.
- Price, C.J., Wise, R., Frackowiak, R., 1996. Demonstrating the implicit processing of visually presented words and pseudowords. *Cereb. Cortex* 6 (1), 62–70.
- Rorden, C., Karnath, H.O., Bonilha, L., 2007. Improving lesion-symptom mapping. *J. Cogn. Neurosci.* 19 (7), 1081–1088.
- Rotzer, S., Kucian, K., Martin, E., von Aster, M., Klaver, P., Loenneker, T., 2008. Optimized voxel-based morphometry in children with developmental dyscalculia. *NeuroImage* 39 (1), 417–422.
- Seghier, M.L., 2008. Laterality index in functional MRI: methodological issues. *Magn. Reson. Imaging* 26 (5), 594–601.
- Shuman, M., Kanwisher, N., 2004. Numerical magnitude in the human parietal lobe: tests of representational generality and domain specificity. *Neuron* 44 (3), 557–569.
- Simon, O., Mangin, J.F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. *Neuron* 33 (3), 475–487.
- Springer, J.A., Binder, J.R., Hammeke, T.A., Swanson, S.J., Frost, J.A., Bellgowan, P.S.F., Brewer, C.C., Perry, H.M., Morris, G.L., Mueller, W.M., 1999. Language dominance in neurologically normal and epilepsy subjects. *Brain* 122 (11), 2033–2045.
- Stanescu-Cosson, R., Pinel, P., van de Moortele, P.F., Le Bihan, D., Cohen, L., Dehaene, S., 2000. Understanding dissociations in dyscalculia: a brain imaging study of the impact of number size on the cerebral networks for exact and approximate calculation. *Brain* 123 (11), 2240–2255.
- Takayama, Y., Sugishita, M., Akiguchi, I., Kimura, J., 1994. Isolated acalculia due to left parietal lesion. *Arch. Neurol.* 51 (3), 286–291.
- Tan, L.H., Spinks, J.A., Gao, J.H., Liu, H.L., Perfetti, C.A., Xiong, J.H., Stofer, K.A., Pu, Y.L., Liu, Y.J., Fox, P.T., 2000. Brain activation in the processing of Chinese characters and words: a functional MRI study. *Hum. Brain Mapp.* 10 (1), 16–27.
- Tan, L.H., Laird, A.R., Li, K., Fox, P.T., 2005. Neuroanatomical correlates of phonological processing of Chinese characters and alphabetic words: a meta-analysis. *Hum. Brain Mapp.* 25 (1), 83–91.
- Thioux, M., Pesenti, M., Costes, N., De Volder, A., Seron, X., 2005. Task-independent semantic activation for numbers and animals. *Cogn. Brain Res.* 24 (2), 284–290.
- Tucha, O., Steup, A., Smely, C., Lange, K.W., 1997. Toe agnosia in Gerstmann syndrome. *J. Neurol. Neurosurg. Psychiatry* 63 (3), 399–403.
- van Harskamp, N.J., Rudge, P., Cipolletti, L., 2002. Are multiplication facts implemented by the left supramarginal and angular gyri? *Neuropsychologia* 40 (11), 1786–1793.
- Vingerhoets, G., Santens, P., Van Laere, K., Lahorte, P., Dierckx, R.A., De Reuck, J., 2001. Regional brain activity during different paradigms of mental rotation in healthy volunteers: a positron emission tomography study. *NeuroImage* 13 (2), 381–391.
- Warrington, E., 1982. The fractionation of arithmetical skills: a single case study. *Q. J. Exp. Psychol.* A 34 (1), 31–51.
- Wei, W., Zhang, H., Chen, C.S., Zhou, X.L., 2011. Neural dissociations in quantity processing of quantifiers and numbers. International Conference on the Educational Neuroscience of Mathematical Cognition, Paper Presented at the University of Hong Kong, July 12–13, 2011.
- Whitney, C., Jefferies, E., Kircher, T., 2011. Heterogeneity of the left temporal lobe in semantic representation and control: priming multiple versus single meanings of ambiguous words. *Cereb. Cortex* 21 (4), 831–844.
- Zago, L., Petit, L., Turbelin, M.R., Anderson, F., Vigneau, M., Tzourio-Mazoyer, N., 2008. How verbal and spatial manipulation networks contribute to calculation: an fMRI study. *Neuropsychologia* 46 (9), 2403–2414.
- Zamarian, L., Karner, E., Benke, T., Donnemiller, E., Delazer, M., 2006. Knowing 7 × 8, but not the meaning of 'elephant': evidence for the dissociation between numerical and non-numerical semantic knowledge. *Neuropsychologia* 44 (10), 1708–1723.
- Zannino, G., Perri, R., Pasqualetti, P., Caltagirone, C., Carlesimo, G., 2006. (Category-specific) semantic deficit in Alzheimer's patients: the role of semantic distance. *Neuropsychologia* 44 (1), 52–61.
- Zhou, X., Chen, C., Zang, Y., Dong, Q., Qiao, S., Gong, Q., 2007. Dissociated brain organization for single-digit addition and multiplication. *NeuroImage* 35 (2), 871–880.
- Zorzi, M., Priftis, K., Umiltà, C., 2002. Brain damage – neglect disrupts the mental number line. *Nature* 417 (6885), 138–139.