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Phonology and arithmetic in the language–calculation network

Josefine Andin [a,*], Peter Fransson [b], Jerker Rönnberg [a], Mary Rudner [a]

[a] Linnaeus Centre HEAD, Swedish Institute for Disability Research, Department of Behavioural Sciences and Learning, Linköping University, SE-581 83 Linköping, Sweden
[b] Department of Clinical Neuroscience, Karolinska Institute, SE-171 77 Stockholm, Sweden

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ABSTRACT

Arithmetic and language processing involve similar neural networks, but the relative engagement remains unclear. In the present study we used fMRI to compare activation for phonological, multiplication and subtraction tasks, keeping the stimulus material constant, within a predefined language–calculation network including left inferior frontal gyrus and angular gyrus (AG) as well as superior parietal lobule and the intraparietal sulcus bilaterally. Results revealed a generally left lateralized activation pattern within the language–calculation network for phonology and a bilateral activation pattern for arithmetic, and suggested regional differences between tasks. In particular, we found a more prominent role for phonology than arithmetic in pars opercularis of the left inferior frontal gyrus but domain generality in pars triangularis. Parietal activation patterns demonstrated greater engagement of the visual and quantity systems for calculation than language. This set of findings supports the notion of a common, but regionally differentiated, language–calculation network.

1. Introduction

A connection between language and arithmetic has been suggested in both behavioral (De Smedt, Taylor, Archibald, & Ansari, 2010; Dehaene, Piazza, Pinel, & Cohen, 2003; Lee & Kang, 2002) and imaging studies (Benn, Zheng, Wilkinson, Siegal, & Varley, 2012; Venkatraman, Siong, Chee, & Ansari, 2006), in line with recent models of complex mental processing (Fehr, 2013). Language processing has been suggested to follow two main neural streams which constitute the perisylvian language network; a ventral stream for speech comprehension and a dorsal stream for sensory–motor integration (Hickok & Poeppel, 2007; Rauschecker & Scott, 2009). Neural representations of phonological processing have been found in a left lateralized fronto-temporo-parietal network encompassing the posterior part, pars opercularis, and the anterior part, pars triangularis, of the left inferior frontal gyrus (lIFG), as well as the left angular gyrus (lAG) and the left supramarginal gyrus (lSMG). During rhyme judgement, a prototypical test of phonological processing, lIFG has been shown to be engaged in sensory–motor integration, decoding and covert articulation (Burton, LoCasto, Krebs-Noble, & Gullapalli, 2005), and several studies have dissociated phonological processing in pars opercularis from semantic processing in pars triangularis (McDermott, Petersen, Watson, & Ojemann, 2003; Poldrack et al., 1999; Vigneau et al., 2006). The lAG has been shown to be involved in mapping between phonological and orthographic representations (Booth et al., 2004) while the role of the lSMG seems to be mainly sensory–motor integration (Hickok & Poeppel, 2007; McDermott et al., 2003; Rauschecker & Scott, 2009). Further, the left superior parietal lobule (SPL) has been implicated in phonological processing (Shivde & Thompson-Schill, 2004), as well as the processing of linguistic structures (Monti, Parsons, & Osherson, 2012) and linguistic inference (Monti, Parsons, & Osherson, 2009), extending the perisylvian language network posteriorly.

According to one of the most influential models of numerical cognition, the triple code model (Dehaene, 1992; Dehaene & Cohen, 1995), three different representational systems are recruited in number processing: Numbers are encoded as strings of Arabic numerals within a *visual system*, these numerals are represented verbally within the *verbal system* and the magnitude of the numbers is represented in the *quantity system*. Recent work has suggested that the visual system also extends to include the SPL bilaterally which has been shown to be engaged during orientation of spatial attention (Dehaene et al., 2003) and may be involved in e.g. number comparisons (Pinel, Dehaene, Rivière, & LeBihan, 2001), approximation (Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999) and counting (Piazza, Mechelli, Butterworth, & Price, 2002).

The verbal system is suggested to be located in lAG (Dehaene et al., 2003). This system is thought to be concerned with the

* Corresponding author.
E-mail addresses: josefine.andin@liu.se (J. Andin), peter.fransson@ki.se (P. Fransson), jerker.ronnberg@liu.se (J. Rönnberg), mary.rudner@liu.se (M. Rudner).

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verbal coding of numbers and it has been shown that the more calculation tasks require verbal processes, such as arithmetic fact retrieval, the more the system is activated. For example, more activation has been found for exact calculation compared to approximate calculation (Dehaene et al., 1999) and for multiplication compared to subtraction (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Lee, 2000).

The horizontal portion of the intraparietal sulcus bilaterally, has been associated with the quantity system, and suggested as a candidate region for number specificity (Dehaene et al., 2003). It is also thought to be involved in magnitude manipulation using a mental analogue number line (Piazza et al., 2002). Activation in this region has been reported for non-verbal representations (Dehaene et al., 2003; Piazza et al., 2002) and it responds more for number words compared to non-number words (Dehaene & Cohen, 1995). Further, it has been shown to be activated more for subtraction compared to multiplication (Chochon et al., 1999; Lee, 2000) and for approximate compared to exact calculation (Dehaene et al., 1999),

Behaviorally, it has been shown that language switching interferes with exact but not approximate calculation (Dehaene et al., 1999) and that simultaneous processing of a phonological task interferes with multiplication but not with subtraction (Lee & Kang, 2002), supporting the notion that the verbal system is recruited more for calculation tasks that put greater demands on verbal processing. Several imaging studies have also shown that calculation tasks in general and multiplication tasks in particular activate language related brain regions (Benn et al., 2012; Prado et al., 2011; Rickard et al., 2000; Zhou et al., 2007). Together these findings support the notion of a common language–calculation network with greater similarity between phonological processing and arithmetic when arithmetic fact retrieval is required, i.e. greater similarity between phonological processing and multiplication than between phonological processing and subtraction. However, although the same network has been reported for both phonological and arithmetical tasks, there is evidence of regional differences. In a study by Fedorenko, Duncan, and Kanwisher (2012), functional specificity of Broca's area was identified, showing that arithmetic is processed in the domain-general periphery rather than the language-specific core. Hitherto, the link between language and calculation has largely been examined implicitly by investigating brain activity elicited by calculation in areas that are generally known to be engaged in language processing (e.g. Benn et al., 2012; Delazer et al., 2003) or as defined by a phonological processing (Prado et al., 2011) or a sentence reading task (Fedorenko et al., 2012).

In the present study, we adopted a different approach by directly contrasting multiplication, subtraction and phonological processing in order to investigate differential engagement of a predefined language–calculation network. Importantly, we used the same stimulus material for all three experimental tasks as well as a visual control task and two cognitive control tasks, ensuring similar visual activation across tasks. This was achieved by presenting visual arrays of six characters, arranged in three digit-letter pairs (see Fig. 1). The arithmetic tasks involved determining whether a multiplication or subtraction problem could be constructed from the digits while the phonological task involved identifying a digit/letter pair whose lexical labels rhymed. The visual control task involved identifying whether there were two dots over any of the letters. Subtracting activation generated by this task allowed us to identify task-specific phonological and arithmetic activation not related to visual perception. The cognitive control task for the arithmetic tasks involved determining whether the digits in the array were in numerical order and the cognitive control task for the phonological task involved determining whether the letters in the array were in alphabetical order. Subtracting activation generated by these tasks allowed us to identify task-specific phonological and arithmetic activation not related to alphabetic and numeric ordering.

The language–calculation network was predefined by a mask including the seven regions of interest central to language and calculation: lIFG (BA44/45), lAG (BA39), bilateral SPL (BA7) and hIP. We predicted largely similar patterns of activation for all three tasks versus visual control throughout the language–calculation network, reflecting process similarities. In particular, we predicted a general activation for all three tasks versus visual control in lIFG,

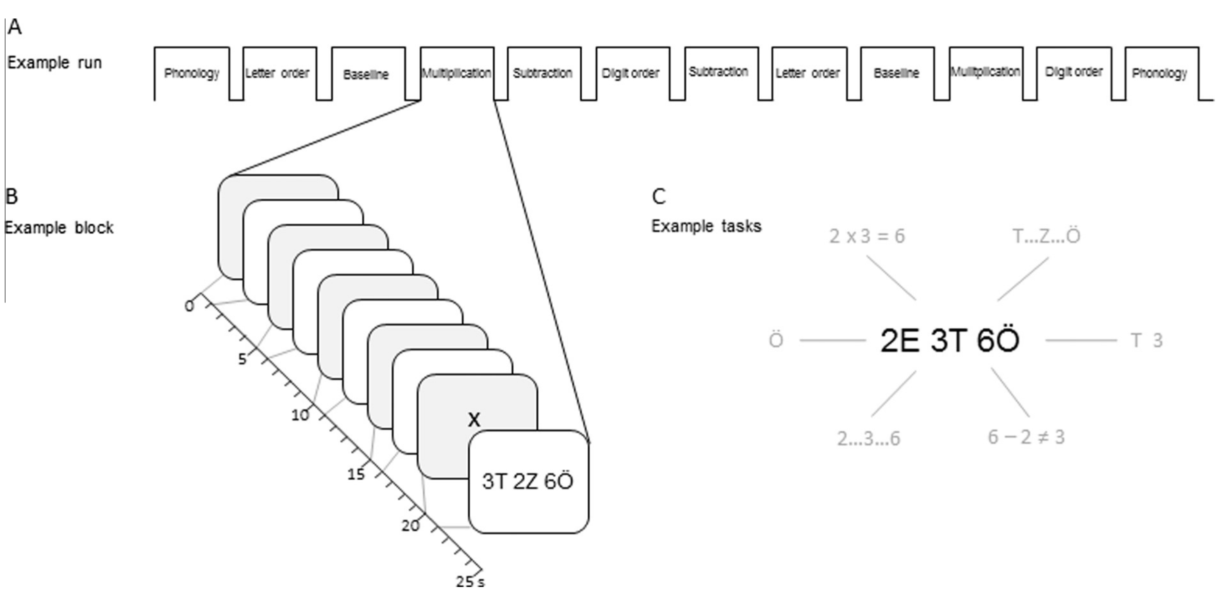

Fig. 1. Schematic representation of (A) a scanning run, (B) an example of stimulus display and timing within a block and (C) an overview of the different tasks: the multiplication task involved determining whether the product of any two of the digits equaled the third (i.e. $2 \times 3 = 6$) and subtraction whether the difference between any two of the digits equaled the third (no solution in the present example). In the phonology task the participants determined if the lexical labels of any of the three digit/letter pairs rhymed (i.e. 3T). The visual control task required identification of two dots over any of the letters (i.e. Ö). The cognitive controls (digit order and letter order) involved determining if the digits and letters are in order (i.e. 236 and ETÖ). Only characters in black are visible upon presentation.

reflecting verbal coding of numbers and letters and left hemisphere parietal regions, reflecting engagement of the verbal system during calculation, and phonological processing in the phonological task. With the cognitive control, we expected to find more specific patterns of activation. In particular, we predicted activation for the phonology and multiplication tasks in the pars opercularis of lIFG and in lAG, along with more activation for these two tasks than for subtraction. Further, we predicted activation for all three experimental tasks in the domain general pars triangularis of lIFG. We predicted that subtraction, which uniquely relies on magnitude manipulation, would activate hIP in the right hemisphere. Further, we predicted significantly more activation for subtraction than both phonology and multiplication in SPL and hIP, supporting the notion that while multiplication is reliant on the verbal system, subtraction is reliant on the visual and quantity system.

2. Methods

2.1. Participants

Seventeen healthy adults (mean age 28.6 years, SD = 4.85, range 22–37; 5 men) were recruited among students and employees of Linköping university and via advertisements. All participants were native Swedish speaking, right-handed as determined by the Edinburgh handedness inventory and had normal or corrected-to-normal vision. They had all completed 9 years of mandatory schooling and 3 years of high school education. Six of these participants had a university degree. Exclusion criteria were self-reported hearing problems, neurological or psychiatric disorders, claustrophobia, being pregnant, on medication or having metal in the body that was not compatible with MRI scanning. The study was approved by and carried out in accordance with the guidelines of the regional ethical review board in Linköping, Sweden (Dnr 190/05). Written informed consent was given by all participants.

2.2. Stimuli and tasks

Forty different but equivalent visual stimuli were created, each consisting of three digit/letter pairs. The digits were selected from the complete set of digits 0–9 and the letters were capitals selected from the Swedish alphabet: B, D, E, G, H, K, L, M, O, P, Q, T, U, V, X, Z, Å and Ö. Each of the forty stimuli could be presented in any of the tasks, see Fig. 1. The tasks were to determine if (1) the three digits in the stimuli were in numerical order ('cognitive control – arithmetic'); (2) the three letters were in alphabetical order ('cognitive control – phonology'); (3) one of the digits multiplied by one of the other equals the third ('multiplication'); (4) one of the digits subtracted from another equals the third ('subtraction'); (5) one of the three digit/letter pairs rhymed ('phonological task') or (6) the array contained a letter with dots over it (Ö, 'visual control').

2.3. Procedure

In the scanning experiment, stimuli were back projected onto a screen positioned at the feet of the participant, using Presentation software (Presentation version 10.2, Neurobehavioral systems Inc., Albany, CA), and viewed by the participants through an angled mirror positioned on top of the head coil. A blocked design was used in which the forty stimuli were randomly assigned to eight blocks of five trials. During each trial the stimulus was displayed for 4000 ms and was preceded by a cue, displayed for 1000 ms, indicating which task to perform (Fig. 1). There were eight blocks per condition distributed over four runs, i.e. the same 40 stimuli were used for each of the six conditions and it was ensured that the proportion of correct and incorrect trials remained constant across blocks and conditions. Each run began with a blank screen for 10 s. Then the first cue of the first block appeared. Each block lasted for 25 s and between blocks there was a 5 s pause when a ¤ symbol was present. During the pause, participants were instructed to relax and keep still. Each of the four runs lasted for 366 s.

The order of conditions was pseudorandomized within runs and order of runs was balanced across participants. The participants responded yes and no using thumb and index finger on a button box. They were instructed to respond as accurately and quickly as possible within the 4000 ms window. Participants were naïve to the hypothesis and expected results.

At least one month before the fMRI scanning, all participants were enrolled in a behavioral testing session to ensure task familiarization and compliance during scanning. In this session participants performed the experimental tasks using half of the stimulus material balanced over participants. There were no performance differences during the fMRI session between new stimuli and stimuli presented during the behavioral testing session ($F(1,15) = .139, p = .715$).

Immediately before the fMRI scanning started, all participants were reminded about the tasks and went through a practice run, consisting of one block of each condition with stimuli that were not repeated in the scanner. The participants were allowed to repeat the practice run as many times as they wanted until they were familiar with the tasks.

2.4. fMRI acquisition

In each of the four runs, 144 whole-brain functional T2*-weighted axial echo planar images (EPI), with anterior commissure-posterior commissure alignment, were acquired using ascending sampling on a 1.5 T GE Instruments scanner (General Electric Company, Fairfield, CT, USA) equipped with a standard eight element head coil, at the Karolinska Institute. The following parameters were used: repetition time (TR) = 2500 ms, echo time (TE) = 40 ms, field of view (FOV) = 220 × 220 mm, flip angle = 90 deg, in-plane resolution of 3.5 × 3.5 mm, slice thickness of 4.5 mm, slice gap of 0.5 mm. The first four volumes of each run were discarded to allow for T1-equilibrium processes. Whole-brain 3D T1-weighted fast spoiled gradient echo anatomical sequence was acquired for each participant at the end of the session (voxel size 0.8 × 0.8 × 1.5 mm, TR = 24 ms, TE = 6 ms, axial slices).

2.5. Data analysis

Analysis of behavioral in-scanner data was performed using SPSS statistics 22 (IBM, SPSS Statistics, version 22, IBM Corporation, New York, USA). Response time and accuracy were analyzed using separate repeated measures analysis of variance followed by post hoc tests using Bonferroni correction for multiple comparisons. Due to technical errors response time measures are based on 15 participants. P-values < 0.05 were considered statistically significant.

Pre-processing and data analysis were performed using statistical parametric mapping packages (SPM8; Wellcome Trust Centre for Neuroimaging, London, UK) running under MatLab 7.10 (Math-works Inc., Natick, MA, USA). Before preprocessing, the quality of each image time series was examined using TSDiffAna (Freiburg Brain Imaging, version updated 2013-05-23). Pre-processing was performed following SPM8 standard procedures. First, images were realigned to the first image in the time series, to correct for head motion, and slice time corrected, to remove differences in the acquisition time between slices. The realigned images were then co-registration to the individual structural images which were then spatially normalized into the Montreal Neurological Institute template (SPM8's MNI Avg152, T1). Finally the images were spatially smoothed using a 10 mm FWHM Gaussian kernel applied to minimize noise and differences in intersubject localization. Further, data was high pass filtered with a cut-off frequency of 1/360 Hz. For one participant the first run was removed from further analyses due to a movement of 5 mm in *y* translation between the start of the first run and second run. All other participants moved less than 3 mm in all directions.

Only blocks with at least four (out of five) correct answers were included in the data analysis; one subtraction and one phonology block from two different participants were removed from the analysis. The whole dataset from one participant were removed due to artifacts probably caused by metallic hair dye. Hence, in total data from 16 participants were included in the analyses. From 14 of the participants data is based on all 48 blocks and from the two remaining participants 47 blocks are analyzed. At the single-subject level a general linear model (GLM) was specified using one regressor for each of the six conditions as well as for each of six motion parameters (derived from the realignment of the images) and response time. For every regressor blocks were modelled as a boxcar of 25 s, convolved with SPM's canonical hemodynamic response function. Contrast images consisting of condition versus visual control and condition versus cognitive control, defined individually for each participant, were first investigated separately and then entered into single sample *t*-tests where multiplication versus controls, subtraction versus controls and phonology versus controls were contrasted separately with each other, in order to address our specific predictions. Because the same stimuli were presented over all conditions, equating visual input, between-task contrasts were conservative and reflected only the differences in cognitive demands between experimental tasks and between experimental tasks and visual or cognitive control. MNI coordinate space was used and anatomical locations were determined using the cytoarchitectonic probability map from the SPM anatomy toolbox version 1.8 (Eickhoff et al., 2005).

Because we had specific predictions regarding activation of the language–calculation network encompassing lIFG, lAG, bilateral hIP and bilateral SPL, small volume correction was performed using a mask including all six areas based on the probabilistic cytoarchitectonic maps from SPM anatomy toolbox version 1.8. This procedure decreased the number of multiple comparisons performed, which made the analysis more sensitive. Further, in the between task contrasts a mask based on each task-minus-visual or task-minus-cognitive control activation was applied to ensure that between task activations are related to activity in one contrast rather than deactivation in the other contrast. Significance was determined using family wise error correction (FWE) for multiple comparisons at $p < .05$ at voxel level for peak values within the specific regions. Images were prepared using SPM8 and MRIcron software (ver. 6/2013, McCausland Center for brain imaging, Columbia, USA).

To locate activation along the *y* axis within lIFG and lAG the three tasks versus visual control contrasts were examined individually by lowering the threshold until a cluster of at least five voxels appeared (Dahlström, Rönnberg, & Rudner, 2011). The location was taken as an indication of peak activity and the *y* coordinates were brought into a paired two-tailed *t*-test where each of the arithmetic tasks was compared to the phonological task. Bonferroni correction for multiple comparisons was used. Cohen's *r* was used as a measure of effect size. *P*-values < 0.05 were considered statistically significant.

3. Results

3.1. Behavioral results

In-scanner behavioral data are shown in Table 1. Analysis of variance showed main effects of task for both accuracy, $F(2,28) = 4.59, p = .019$, and response time, $F(2,28) = 31.7, p < .001$. Post hoc tests showed that the multiplication task was performed faster, $p < .001$, and more accurately, $p = .028$, than the phonological task. Subtraction was performed more slowly than multiplication, $p = .008$, but faster than phonology, $p = .001$, while accuracy on the subtraction task did not differ significantly from either multiplication or phonology.

3.2. Imaging results

3.2.1. Experimental tasks versus visual control

All three experimental tasks versus visual control generated significant activation within the language–calculation network represented by the predefined mask including left pars opercularis, pars triangularis, lAG, bilateral SPL and hIP, in line with our prediction (Table 2 and Fig. 2). Whole brain results are provided for comparison purposes in Table A1.

Specifically, all tasks versus visual control showed significant activation in lAG and lSPL, as predicted. However, in the other regions of the mask, the three tasks patterned differently. For multiplication versus visual control, there was significant activation in pars triangularis, as predicted, as well as in rSPL which was not predicted.

Subtraction versus visual contrast, elicited significant activation in lhIP and rSPL, as predicted, but not in right hIP. There was also a tendency towards the predicted significant activation in pars triangularis, $p_{fwe} = .093$. For the phonological task versus visual control, there was significant activation in pars opercularis, and lhIP as predicted, and a tendency towards the predicted significant activation in pars triangularis, $p_{fwe} = .078$.

Between task contrasts revealed significantly stronger activation for phonology compared to both multiplication and subtraction in pars opercularis but there were no significant activation differences between the three experimental tasks within pars triangularis or in any of the parietal regions investigated.

Further, the value of the *y* coordinate of the peak activation in pars triangularis for multiplication versus visual control, was found to be significantly greater than that for the phonological task versus visual control, $t(15) = 2.28, p = .038, r = .506$ (Fig. 3), indicating that within this region, the activation for multiplication was anterior to that for phonology. The *y* coordinate for subtraction versus visual control was located between that of phonology and multiplication but there was no significant difference between *y* coordinates for subtraction and phonology, $t(15) = 1.04, p = .314, r = .260$. Similarly, despite the absence of significant differences in activation between the three experimental tasks within lAG, both multiplication and subtraction versus visual control elicited significant activation in the anterior (PGa) as well as posterior (PGp) portions of lAG, whereas the phonological task versus visual control only showed significant activation in PGa. Here, the value of the *y* coordinate of the corresponding peak activation for multiplication, $t(15) = 2.92, p = .011, r = .602$, but not subtraction, $t(15) = 1.78, p = .096, r = .417$, was found to be significantly more negative than that for the phonological task, indicating that activation for multiplication was posterior to that for phonology.

Table 1
Behavioral in-scanner data.

	Response time (ms)		Accuracy (% correct)	
	M	SD	*M*	SD
Multiplication	1885	391	96.2	4.10
Subtraction	2038	369	94.0	4.41
Phonology	2424	281	90.2	7.41

Table 2
Activation foci for contrasts within each region. All significant peaks ($p_{FWE} < 0.05$) are listed. In areas where no significant peak was identified the highest uncorrected peak ($p < .001$) is listed. Small volume correction was performed within a mask defined by left pars opercularis (BA44), pars triangularis (BA45), angular gyrus (BA39) and bilateral horizontal portion of the intraparietal sulcus and superior parietal lobule (BA7). For between task contrasts a mask based on each task minus-visual control activation was applied. All contrasts are versus control (visual control in the left panel and cognitive control in the right panel).

	Compared to visual control						Compared to cognitive control					
	Peak level			MNI peak coordinates			Peak level			MNI peak coordinates		
Contrast and brain region	*T*	p_{fwe}	Cluster size	*x*	*y*	*z*	*T*	p_{fwe}	Cluster size	*x*	*y*	*z*
Left pars opercularis (BA44)												
Multiplication	4.10	.389	9	−51	9	39	5.01	.337	37	−47	16	34
Subtraction	4.56	.167	19	−54	16	29	6.36	.009	42	−44	16	29
Phonology	7.77	<.001	46	−58	9	9	7.10	.003	31	−51	9	14
Phonology > multiplication	8.07	<.001	49	−54	9	14	4.76	.225	1	−51	13	9
Phonology > subtraction	9.69	<.001	44	−58	9	9						
Multiplication > phonology												
Subtraction > phonology												
Left pars triangularis (BA45)												
Multiplication	5.34	.039	16	−51	30	24	5.43	.044	35	−47	23	19
Subtraction	4.87	.093	20	−47	30	24	7.02	.003	32	−47	27	24
Phonology	4.97	.078	26	−47	27	29	5.37	.048	1	−47	27	14
Phonology > multiplication	4.90	.110	6	−47	20	14						
Phonology > subtraction												
Multiplication > phonology												
Subtraction > phonology							5.22	.108	6	−51	27	29
Left angular gyrus (BA39)												
Multiplication	5.32	.041	13	−40	−58	54	4.90	.109	11	−30	−68	44
Subtraction	7.58	<.001	19	−33	−68	49	7.08	.003	24	−37	−61	49
	6.07	.011		−44	−54	54						
Phonology	9.11	<.001	14	−40	−58	54	4.14	.365	1	−44	−58	54
	6.28	.008		−37	−61	49						
	5.99	.012		−30	−65	44						
Phonology > multiplication												
Phonology > subtraction												
Multiplication > phonology	4.46	.296	6	−54	−65	24						
Subtraction > phonology							6.43	.018	13	−30	−68	44
Left horizontal portion of the intraparietal sulcus												
Multiplication	4.79	.108	25	−30	−61	49	4.82	.125	36	−33	−61	44
Subtraction	5.79	.018	56	−44	−51	49	7.82	.001	63	−37	−54	44
	5.42	.034		−33	−61	44						
	5.31	.042		−51	−44	44						
Phonology	7.15	.002	34	−40	−58	49						
Phonology > multiplication												
Phonology > subtraction												
Multiplication > phonology							4.11	.443	1	−40	−58	44
Subtraction > phonology							7.10	.008	35	−40	−54	44
Left superior parietal lobule (BA7)												
Multiplication	6.06	.011	34	−30	−68	54	4.26	.203	10	−33	−65	49
	5.76	.019		−16	−72	54						
Subtraction	7.69	<.001	48	−30	−68	54	6.95	.004	25	−33	−65	49
	7.42	.001		−33	−65	49	6.67	.006	27	−19	−72	49
	6.33	.007		−16	−72	54						
	6.13	.010		−37	−58	59						
Phonology	8.34	<.001	51	−37	−58	54	6.17	.013	3	−37	−58	59
	7.26	.002		−19	−72	54						
Phonology > multiplication												
Phonology > subtraction												
Multiplication > phonology												
Subtraction > phonology							6.33	.021	25	−19	−75	44
Right horizontal portion of the intraparietal sulcus												
Multiplication	3.82	.528	1	30	−54	49						
Subtraction	4.06	.333	2	27	−61	49	4.90	.110	7	34	−61	49
Phonology												
Phonology > multiplication												
Phonology > subtraction												
Multiplication > phonology							7.23	.006	20	37	−51	39
Subtraction > phonology	4.54	.208	1	41	−33	39	9.64	<.001	41	37	−47	39
Right superior parietal lobule (BA7)												
Multiplication	5.36	.038	5	16	−72	54						
Subtraction	7.64	<.001	23	20	−72	54						
	7.39	.001		27	−68	54						
Phonology												
Phonology > multiplication												
Phonology > subtraction												
Multiplication > phonology												
Subtraction > phonology							8.29	.002	46	9	−68	49

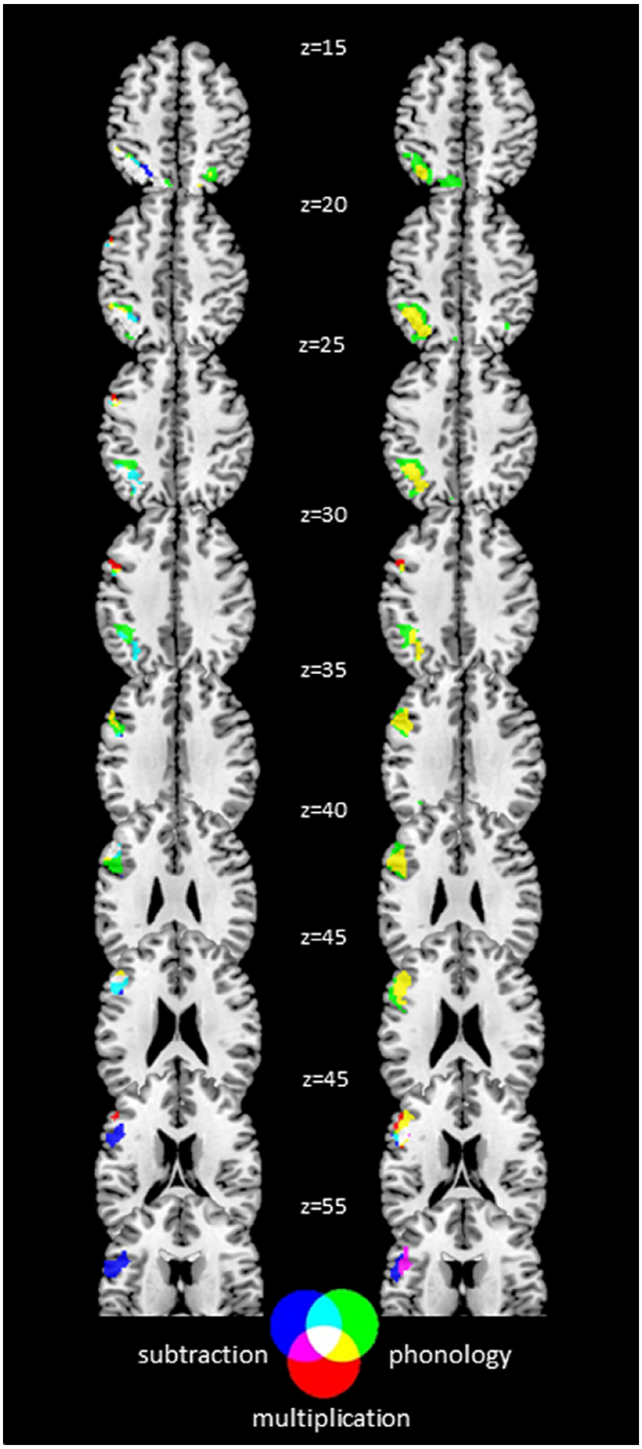

Fig. 2. The figure shows significant activation for task versus visual control (to the left) and task versus cognitive control (to the right) within the mask defined by lIFG, lAG, bilateral hIP and SPL probabilistic cytoarchitectonic maps from SPM anatomy toolbox. fMRI data are superimposed on a normalized canonical image (ch2better template) using the MRIcron software. Red multiplication; green subtraction; blue phonology.

3.2.2. Experimental tasks versus cognitive control

All three experimental tasks versus cognitive control generated significant activation within the predefined language–calculation network, in line with our prediction (Table 2 and Fig. 2). Whole brain results are provided for comparison purposes in Table A2.

Specifically, all tasks versus cognitive control showed significant activation in the domain general pars triangularis, as predicted, while in the other regions of the mask, the three tasks patterned differently. For multiplication versus cognitive control, we did not find the predicted activation in pars opercularis and there was no activation for this contrast in any of the parietal regions included in the mask, although multiplication versus cognitive control did activate rhIP significantly more than phonology versus cognitive control. Subtraction versus cognitive control, on the other hand showed activation in all left hemisphere regions of the mask. This included lhIP and lSPL as predicted, but not the homologous right hemisphere regions, and additionally pars opercularis and lAG. The same contrast showed significantly more activation than phonology versus cognitive control in all parietal regions of the mask, including right hemisphere; we had predicted this for hIP and SPL but not AG. However, subtraction versus cognitive control did not elicit more activation than multiplication versus cognitive control in any region, despite similar predictions. Finally, phonology versus cognitive control activated pars opercularis as predicted, as well lSPL, but not lAG, which we had predicted. Phonology versus cognitive control did not activate any region more than the arithmetic tasks versus cognitive control.

4. Discussion

In the present study we used identical visual stimuli for multiplication, subtraction and phonological tasks. In line with our prediction, we found that all three tasks generated significant activation within the pre-defined language–calculation network. We predicted activation for all three tasks versus visual control in lIFG, reflecting verbal coding of numbers and letters, and in left hemisphere parietal regions, reflecting engagement of the verbal system during calculation as well as phonological processing in the phonological task. With the cognitive control, we expected to find more specific patterns of activation, revealing shared left-lateralized mechanisms for multiplication and phonology, tapping into the verbal system, contrasting with specific bilateral or right-lateralized mechanisms for subtraction, tapping into the visual and quantity systems.

Results provided broad support for predictions showing activation of the language–calculation network for all tasks. In lIFG significant activation was identified for all three experimental

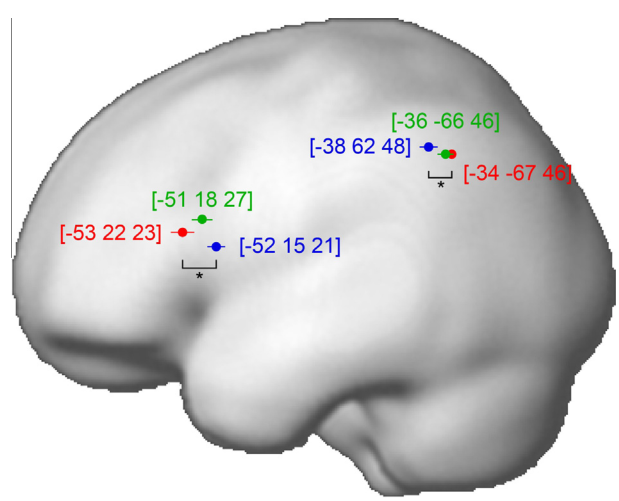

Fig. 3. Within BA44/45 the mean peak of activation for multiplication is located significantly anterior to that for phonology and within BA39 the opposite is true. Dots represent mean coordinates and error bars shows standard error. In brackets mean coordinates are shown. fMRI data are mapped onto a reference brain (smoothed average). Red multiplication; green subtraction, blue phonology. *$p < .05$.

tasks but with different patterns in the more anterior pars triangularis and the more posterior pars opercularis. While activation was general across tasks in pars triangularis, there was specific activation for the phonological task in the pars opercularis. We found pars opercularis to be significantly activated by the phonological task irrespective of which control was applied. There was no significant activation in this region for multiplication with either control. We also found significantly more activation for the phonological compared to the two arithmetic tasks when the visual control was applied, suggesting a less prominent role for pars opercularis in arithmetic compared to phonological processing. Hence, the present data corroborate previous studies that have found lIFG to be activated for both multiplication and phonology (e.g. Prado et al., 2011; Rickard et al., 2000; Vigneau et al., 2006). Here, we also present evidence of a regional differentiation between phonology and multiplication based on direct comparisons between tasks, such that activation of multiplication is primarily located to pars triangularis and that of phonology to pars opercularis as previously established (e.g. Poldrack et al., 1999). Because visual stimulation was kept under tight control, we suggest that this differentiation is related to the different cognitive processes called upon in relation to the specific tasks. Behavioral data indicate that the phonological task was harder than the multiplication task. However, we found no significant activation relating to the contrast between these two tasks in load-related areas such as anterior cingulate, dorsolateral prefrontal cortex or superior parietal cortex (see Table A1, Ma, Husain, & Bays, 2014). Thus, the pattern of effects seems to relate to the processes of interest. Future work should investigate this further.

One interpretation of differential activation within lIFG is that while both the phonological and multiplication tasks require manipulation of representations stored in long term memory, they tap into different kinds of representations and processes. This is in line with Fedorenko et al. (2012) who showed that math is processed in domain-general rather than language-specific parts of lIFG. The phonological task requires subvocalization of letters and digits and comparison of the resulting phonological representations while they are held in working memory to identify rhyme. This induces verbal working memory rehearsal processes, which activate the posterior part of lIFG, i.e. pars opercularis (Fletcher & Henson, 2001). The lack of activation for multiplication within this region and the specific activation of pars triangularis for this task, indicates semantic processing (McDermott et al., 2003; Poldrack et al., 1999), leading us to suggest that during the multiplication task used in the present study, the arithmetic facts may have been retrieved as semantic knowledge rather than phonological code (Fias, Reynvoet, & Brysbaert, 2001). Further work is needed to investigate this notion.

Subtraction versus visual control did not reach significance in either pars triangularis or pars opercularis, but subtraction versus cognitive control reached significance in both regions. This pattern of findings suggests that the subtraction task relies on neurocognitive mechanisms organized in this region that are not tapped by the numerical ordering represented by the cognitive control task, and that the cognitive control task may even suppress these mechanisms. Although subtraction is well-practiced, it is not rote-learned to the same extent as multiplication and thus it is reliant both on phonological processing and on retrieval of semantic knowledge.

Evidence of this dual reliance is provided by examination of the relative positioning of the *y* coordinates of peak activation for the three experimental tasks versus visual control. The value of this coordinate for multiplication in pars triangularis was significantly higher than the corresponding value for phonology, indicating that the area of activation for multiplication was anterior to that of phonology (Fig. 3). Importantly, the corresponding value for subtraction indicated that activation relating to this task was located in between that of multiplication and phonology. This suggests that the multiplication task required a more anteriorly organized higher level selection process than the phonological task (Badre, Poldrack, Paré-Blagoev, Insler, & Wagner, 2005; Badre & Wagner, 2007), possibly due to the demands on attending to and organizing the presented digits in a logical order. Further studies are needed to investigate if this anterior/posterior organization is specific to the relation between arithmetic and phonology or if it reflects a difference in general cognitive processing, where arithmetic is just one example of a domain-general process.

All tasks versus visual control showed significant activation in lAG, revealing engagement of the verbal system during calculation, and phonological processing in the phonological task. LAG has previously been shown to be activated more for multiplication than subtraction (Chochon et al., 1999; Lee, 2000) and has been suggested to be an area that supports arithmetic fact retrieval (Dehaene et al., 2003). Here, we failed to find a difference in activation between multiplication and subtraction, which possibly reflects the simplicity of the subtraction problems used here. It is likely that examples of subtraction of one single-digit number from another are stored in long-term memory and accessed through arithmetic fact retrieval. In other words, easy subtraction can be represented at least partly verbally, without the need for online manipulation of the mental number line, in much the same way that multiplication table knowledge is represented verbally. The finding that all three tasks used in the present study significantly activated lAG is in line with the findings of Simon, Mangin, Cohen, Le Bihan, & Dehaene (2002) who showed that the neural mechanism supporting a simple subtraction task was co-localized with the mechanism supporting a phonological task in lAG. However, with the cognitive control, only subtraction showed significant activation in lAG, and significantly more than for phonology. This pattern suggests that for phonology and multiplication, involvement of lAG does not go beyond the low-level ordering processes engendered by the cognitive control. Interestingly, for subtraction it seems that lAG supports processes that are not tapped by the numerical ordering represented by the cognitive control and may even be suppressed by numerical ordering, just as we argued for lIFG. Göbel, Walsh, and Rushworth (2001) proposed that lAG normally mediates a spatial representation of number. Such a representation may be part and parcel of the subtraction task in the present study, and may be more abstract than the numerical ordering required by the cognitive control. Greater activation of lAG for subtraction versus cognitive control than for phonology versus cognitive control also strongly suggests that the role of lAG in subtraction is not simply linguistic. One novel finding of the present study is that lAG is activated more by subtraction than phonology when cognitive controls are applied, strongly suggesting the engagement of an abstract process, unique to subtraction which we suggest may be spatial representation of number (c.f. Göbel et al., 2001).

Interestingly, the relative anterior–posterior localization of the activation peaks for multiplication and phonology versus visual control in lIFG was reversed in lAG (Fig. 3); the activation peak for multiplication located in the posterior portion of AG (PGp), whereas the activation peak for phonology was to be found in the anterior portion (PGa). This pattern of findings is not surprising considering that the PGa borders on supramarginal gyrus and superior temporal gyrus, two brain regions that are associated with language processing in general, and specifically phonological processing (Hickok, 2009; Hickok & Poeppel, 2007), whereas PGp borders on brain regions associated with spatial cognition (Dehaene et al., 2003). Further, a corresponding topographical pattern was reported in Xiang, Fonteijn, Norris, & Hagoort (2010), showing functional connectivity between pars opercularis and anterior parts of the inferior parietal lobule and between pars triangularis and posterior part of the inferior parietal lobule. Together, evidence suggests functional differences between left lateralized regions of the language–calculation network such that phonological processing engages pars opercularis and PGa while multiplication engages pars triangularis and PGp. However, to firmly establish such functional differences, further studies are needed.

The observed activation of lSPL for both the arithmetic and phonological tasks versus visual control is consistent with findings extending the involvement of this area from number cognition (Dehaene et al., 2003; Fehr, Code, & Herrmann, 2007; Knops, Thirion, Hubbard, Michel, & Dehaene, 2009) to general involvement in manipulation and rearrangement of information into independent entities (Friedrich & Friederici, 2013; Koenigs, Barbey, Postle, & Grafman, 2009). Interestingly, however, lSPL was not significantly activated by multiplication versus cognitive control, although it was activated for both subtraction and phonology versus cognitive control and more so for subtraction than phonology. A similar pattern was found in lhIP. These findings are partially in line with our prediction of greater activation of the visual and quantity systems for arithmetic than phonology. This pattern of activation seen across tasks versus visual control could either stem from two different processes where both language and numerical tasks are co-localized but not intertwined or reflect a more general working memory process (Koenigs et al., 2009). Remembering the relatively complicated task at hand, for all three tasks, while at the same time performing the material manipulation required to solve the task, loads on simultaneous storage and processing capacity conceptualized as working memory. Thus, it is possible that the SPL activation we found here reflects a working memory process (Ma et al., 2014). The latter interpretation is supported by the pattern of results applying the cognitive control: behavioral results show that the multiplication task was the easiest of the three and therefore was less likely to load on working memory mechanisms.

As predicted, subtraction versus visual control showed significant activation in the right hemisphere but only in SPL, and we failed to find the predicted significant activation for subtraction versus visual control in right hIP. Surprisingly we found the left hIP to be activated in all three tasks. Bilateral hIP has been found to be activated in numerical tasks that primarily involve manipulation of the number line (Dehaene et al., 2003), a notion that is supported by the finding that subtraction shows stronger activation than multiplication in this region (Chochon et al., 1999; Lee & Kang, 2002). However, a recent study (Monti et al., 2012) also found hIP activation in an algebraic task that did not contain numbers and magnitudes, suggesting that this region deals with domain-general ordering. hIP activation for letter ordering has also been reported (Fias, Lammertyn, Caessens, & Orban, 2007). The phonological task in the present study did not call for any ordering procedures per se, but there is a spatial component in the set up, which requires the participant to make decisions on the three digit-letter pairs, possibly calling on spatial processing. Likewise, because we find activation that we relate to arithmetic fact retrieval for both multiplication and subtraction in lAG and no evidence of magnitude manipulation in right hIP when applying the visual control, it is possible that the activation found in left hIP for the subtraction and multiplication tasks versus visual control is not related to magnitude processes but instead arises from the reordering of the three digits needed to find an appropriate combination (e.g. $594 \rightarrow 9-5=4$). It is noteworthy that when we subtracted order processing using the cognitive control, rhIP was activated more for both arithmetic tasks than for phonology. This pattern of findings demonstrates the key role in arithmetic of right hemisphere regions supporting the visual and quantity systems. In particular, it shows that the role of the visual and quantity systems in arithmetic is above and beyond low-level numeric ordering. Together with the pattern of findings for left hemisphere parietal regions, the pattern for right hemisphere parietal regions shows that while both multiplication and subtraction are reliant on the verbal system, they are also uniquely reliant on the visual and quantity systems.

5. Conclusions

In the present study we used the same visual stimulus material to investigate differences in phonological and arithmetic processing in a pre-defined language–calculation network. We found that while the pars triangularis of the lIFG showed domain generality, pars opercularis played a less prominent role in arithmetic compared to phonology. All parietal regions in the pre-defined language–calculation network were activated more for subtraction than phonology and rhIPS was also activated more for multiplication than phonology when ordering was controlled for, demonstrating the greater engagement of the visual and quantity systems for calculation than language. Finally, we found no firm evidence that subtraction and multiplication tasks engage different neural systems, suggesting that simple arithmetic problems are stored as unified representations in LTM. This set of findings supports the notion of a common language–calculation network with regional differences between phonology and arithmetic.

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Contributions

JA, PF, JR and MR designed the study. JA conducted the experiment and analyzed the data. JA and MR wrote the manuscript with input from all authors.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.bandl.2015.02.004.

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