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Individual differences in mathematical competence predict parietal brain activation during mental calculation

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Functional neuroimaging studies have revealed that parietal brain circuits subserve arithmetic problem solving and that their recruitment dynamically changes as a function of training and development. The present study investigated whether the brain activation during mental calculation is also modulated by individual differences in mathematical competence. Twenty-five adult students were selected from a larger pool based on their performance on standardized tests of intelligence and arithmetic and divided into groups of individuals with relatively lower and higher mathematical competence. These groups did not differ in their non-numerical intelligence or age. In an fMRI block-design, participants had to verify the correctness of single-digit and multi-digit multiplication problems. Analyses revealed that the individuals with higher mathematical competence displayed stronger activation of the left angular gyrus while solving both types of arithmetic problems. Additional correlational analyses corroborated the association between individual differences in mathematical competence and angular gyrus activation, even when variability in task performance was controlled for. These findings demonstrate that the recruitment of the left angular gyrus during arithmetic problem solving underlies individual differences in mathematical ability and suggests a stronger reliance on automatic, language-mediated processes in more competent individuals.

Keywords: Angular gyrus; Arithmetic; Intelligence; Individual differences; Mathematical competence; Parietal cortex

Introduction

The ability to perform basic arithmetic operations such as addition or multiplication represents a fundamental prerequisite for the acquisition of higher-order numerical competence. The central role played by arithmetic is also reflected in the fact that most psychometric tests of human intelligence comprise arithmetic problems to assess an individual's level of numerical–mathematical ability (Carroll, 1993; Deary, 2001), which, in turn, is predictive of his or her educational and vocational success in life (Neisser et al., 1996; Schmidt and Hunter, 1998). While it is well known that substantial individual differences in arithmetic abilities exist, the source of this variability is poorly understood (Dowker, 2005). In the present study, functional neuroimaging was used to investigate the neural correlates underlying individual differences in mathematical competence.

A large body of data from neuropsychological patients (Gerstmann, 1940; Henschen, 1919) and functional neuroimaging studies point to a critical role for areas of the parietal cortex in mental calculation (Burbaud et al., 1995; Dehaene et al., 1996, 1999, 2003, 2004; Delazer et al., 2003, 2005; Ischebeck et al., 2006, 2007; Menon et al., 2000a,b; Prabhakaran et al., 2001; Roland and Friberg, 1985; Rickard et al., 2000; Rueckert et al., 1996; Venkatraman et al., 2006; Zago and Tzourio-Mazoyer, 2002; Zago et al., 2001).

In the first neuroimaging study on arithmetic thinking, Roland and Friberg measured changes of the regional cerebral blood flow by means of the Xe intracarotid method during the performance of a continuous subtraction task and found significant blood flow increases in prefrontal and parietal cortices. Interestingly, whereas the prefrontal activation was also apparent in verbal and figural–spatial task conditions, bilateral activation in the angular gyrus was found to be exclusively associated with the calculation task. This finding led the authors to conclude that the angular gyrus is involved in the "retrieval of the memory for subtraction and integers"

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(p. 1241). Similarly, Rueckert et al. used fMRI to investigate brain regions involved in mental subtraction and revealed that areas of the (predominantly left) parietal cortex (angular and supramarginal gyri) were involved in arithmetic problem solving. In addition to these parietal areas, also prefrontal cortices were modulated by the subtraction task. A special role for the left parietal cortex in calculation (in particular the angular gyrus) was also uncovered by Dehaene et al. (1999) who found greater activation of the angular gyrus during exact relative to approximate calculation, suggesting a crucial role of the AG in the exact computation of arithmetic facts.

Against the background of these and other findings, Dehaene et al. (2003) proposed a tripartite functional organization of the parietal cortex for the processing and representation of number. In this model, the horizontal segment of the intraparietal sulcus (IPS) bilaterally is regarded as the core quantity system in which numerical quantity is represented in a language-independent format, perhaps analogous to a mental number line. The left angular gyrus, on the other hand, located posterior and inferior to the horizontal segment of the IPS, is thought to engage in linguistically mediated operations in mental calculation inasmuch as some arithmetic operations require verbal coding of numbers or draw on verbally stored knowledge (e.g., multiplication tables). Finally, the posterior superior parietal system is thought to support spatial and non-spatial attentional processes, for instance in the selection of quantities on a mental number line.

Interestingly, recent studies suggest that the engagement of these parietal circuits does not only depend on the cognitive demand or task under investigation, but that furthermore the activation of these regions is also modulated by development and training and that dynamic shifts in the reliance on one of these circuits to another can occur. First, developmental neuroimaging studies point to an increasing functional specialization of inferior parietal brain regions for mental arithmetic with age. Using fMRI, Rivera et al. (2005) administered simple addition and subtraction problems to children and adolescents between 8 and 19 years and observed significant positive correlations between activation and age in the left supramarginal gyrus and IPS (a trend was also observed in the angular gyrus), coupled with negative correlations in several prefrontal brain regions. These results indicate that older children less strongly engage auxiliary cognitive functions such as executive processes and working memory while solving arithmetic problems, and more strongly rely on task-specific parietal brain regions (see also Ansari et al., 2005, 2006).

Second, studies employing short-term training of arithmetic problems in adults have demonstrated training-related changes in parietal regions typically engaged during calculation (Delazer et al., 2003, 2005; Ischebeck et al., 2006, 2007). In a pioneering study, Delazer et al. (2003) trained adult students on a set of 18 complex multiplication problems (e.g., “7 × 12”) over 1 week until they had learned all answers to the 18 problems perfectly. In a subsequent fMRI test session, participants were presented with the trained problems as well as with novel (untrained) problems. Contrasting brain activation between trained and untrained problems revealed higher activation in the left IPS and inferior frontal gyrus for the untrained set. In contrast, activation in the left angular gyrus was found to be stronger for the trained relative to the untrained problems. These results suggest that learning of arithmetic knowledge is accompanied by a shift from more frontal to more parietal regions and, within the parietal lobe, from the IPS to the angular gyrus. Against this background, it has been contended that the stronger activation in the angular gyrus for trained problems might reflect increasing reliance on automatic, verbal fact retrieval as a consequence of training (see also Delazer et al., 2005; Ischebeck et al., 2006, 2007).

Taken together, there is converging evidence that parietal brain circuits are crucially involved in mental calculation. Furthermore, developmental and training studies have demonstrated that the activation of these regions is not static, but changes as a function of training, experience, and development. In this way, they provide important insights into neurophysiological changes accompanying the acquisition of arithmetic skills and mathematical competence. It is unclear, however, whether the observed stronger recruitment of parietal brain regions with increasing mathematical performance is generalizable beyond developmental trends and the short-term training of a small set of arithmetic problems. Therefore, the aim of the present fMRI study was to investigate how the recruitment of parietal brain circuits during mental calculation in adults is modulated by the general level of mathematical competence an individual has achieved. If the successful acquisition of mathematical knowledge indeed is reflected by increasing recruitment of the angular gyrus as suggested by previous training studies, then mathematically more competent individuals should also display a stronger activation of this brain region than their less competent counterparts. By administering single-digit multiplication problems primarily drawing on arithmetic fact retrieval as well as more complex ones (multi-digit problems), it was moreover investigated whether a potential activation difference between more and less competent individuals also depends on the complexity of arithmetic demands or whether mathematical competence affects the neural correlates of simple and complex calculation equally.

To the best of our knowledge, only one study thus far has tackled the issue of the relationship between brain activation and individual differences in arithmetic performance. Menon et al. (2000a) administered arithmetic problems involving addition and subtraction to a sample of 16 participants who were, based on their task performance in the fMRI test session, divided into groups of perfect performers (accuracy of 100%) and imperfect performers (average accuracy of 92%). Region-of-interest (ROI) analyses in three parietal brain areas revealed a significant group effect in the left angular gyrus suggesting that perfect performers displayed lower activation than imperfect performers.

Menon et al.’s study focused on relatively high performers, who were grouped according to their score in an experimental fMRI task, rather than on the basis of external measures of mathematical competence. To ensure that individual differences in activation are generalizable beyond the specific demands of the experimental task, we assessed mathematical competence with standardized psychometric tests of intelligence and arithmetic competence. This procedure additionally allowed us to deliberately select groups of individuals with relatively high (though not gifted) or low mathematical competence but verbal and figural–spatial aptitude within the normal range. Consequently, any observed differences in brain activation between more and less competent individuals could be attributed to their level of mathematical competence but not to other intellectual abilities.

Materials and methods

Participants

In order to obtain groups of participants which differ only in their mathematical competence but not in other intellectual abilities, a large pool of 138 adult students (German speaking; 99 males) was recruited and screened with respect to their intelligence structure, multiplication performance, and personality profile by means of the psychometric tests described in Psychometric tests. From the entire pool, 30 male participants were selected for the fMRI test session as follows: first, only male students of average verbal and figural–spatial intelligence (i.e., within ±1 SD of the standard mean IQ of 100) were considered. Within this subsample, a selection of students with comparably low or high mathematical competence was made based on their mathematical–numerical intelligence test score and their performance in the multiplication test. Finally, two groups were formed that were matched with respect to verbal and figural–spatial intelligence. The appropriateness of the matching procedure was evaluated by means of statistical group comparisons yielding significant differences in mathematical–numerical IQ and multiplication test performance separately (all $ps < .001$) but not in verbal and figural–spatial IQ ($ps > .88$). The rationale for selecting only male participants is based on evidence of sex differences in the relationship between intelligence or performance and brain activation (e.g., Grabner et al., 2004; Haier and Benbow, 1995; Neubauer et al., 2002, 2005; Skrandies et al., 1999) which might confound the evaluation of potential competence-related group differences.

Due to movement artifacts and technical acquisition problems, 5 participants had to be excluded from further analyses. The remaining sample of 25 participants was divided into groups of lower ($n=13$) and higher ($n=12$) mathematical competence (see Table 1). Two-sample t-tests revealed that the group of higher mathematical competence (higher math) displayed significantly higher mathematical–numerical intelligence, $t(23)=-8.62$, $p<.001$, and performance in both the easier, $t(23)=-6.01$, $p<.001$, and the more complex multiplication test condition, $t(18.16)=-7.11$, $p<.001$, than the lower mathematical competence (lower math) group. There were no significant group differences in either verbal or figural–spatial abilities. Furthermore, no differences were found between the groups in chronological age or any scale of the personality questionnaire. Participants' field of study comprised engineering ($n=6$), medicine ($n=3$), and psychology ($n=4$) in the lower math group, and biology ($n=1$), economics ($n=1$), engineering ($n=5$), psychology ($n=1$), sports ($n=1$), and physics ($n=3$) in the higher math group. The participants gave written informed consent approved by the local ethics committee and were paid for their participation in the fMRI test session.

Psychometric tests

The screening test session took place between about 2 and 6 weeks before the fMRI test session and comprised the following tests.

For assessing the intelligence structure of the participants, a short version of the well-established Berlin Intelligence Structure Test (BIS-T; Jäger et al., 1997) was administered. This test draws on three content components of intelligence (i.e., verbal, figural–spatial, and mathematical–numerical) and, within the three content components, on four operational abilities (processing speed, memory, reasoning, and creativity). The applied short version of the BIS-T comprised 21 subscales, yielding a test time of about 1 h. The applied mathematical–numerical subscales, for instance, required participants to continue number series (reasoning), memorize pairs of digits (memory), solve different types of arithmetic problems (formal and text problems; drawing on processing speed, reasoning, and creativity), or to estimate the results of complex calculation problems (reasoning). The individual IQ scores in the three content components of the BIS-T represent the standardized test performance aggregated over all respective subscales.

In addition to the BIS-T, a self-constructed test on multiplication performance consisting of two forms of 32 one-digit times one-digit (with numbers between 2 and 9) and two forms of 25 one-digit times two-digit (between 11 and 19) multiplication problems was administered. The problems were presented with time limits of 30 s for the easier and 60 s for the more difficult problems. The standardized IQ value for the multiplication performance in both tests was calculated as the number of correct solutions relative to the performance of the entire screening ample (138 participants).

Table 1
Descriptive statistics of age and psychometric test data of the lower ($n=13$) and higher ($n=12$) mathematical competence group

	Lower mathematical competence				Higher mathematical competence			
	Min	*M*	SD	Max	Min	*M*	SD	Max
Age in years	22.00	25.38	3.20	32.00	22.00	25.92	3.45	32.00
Intelligence structure[a]								
Verbal intelligence	92.80	102.47	4.46	109.30	89.50	100.83	5.72	108.70
Figural–spatial intelligence	88.90	98.55	6.24	110.20	87.40	98.95	7.43	114.70
Mathematical–numerical intelligence	80.50	88.18	5.03	95.50	100.00	107.15	5.96	118.60
Multiplication performance[a]								
One-digit times one-digit problems	75.29	86.81	9.06	102.63	100.25	112.04	11.86	129.96
One-digit times two-digit problems	80.21	90.65	6.72	104.15	104.15	116.45	10.79	134.07
Personality[b]								
Neuroticism	36.42	44.45	8.46	62.54	28.96	44.19	10.53	63.78
Extraversion	37.98	55.38	8.25	66.25	40.95	53.08	9.00	69.23
Openness to experience	39.31	57.33	9.47	73.90	36.16	52.79	8.88	62.89
Agreeableness	46.47	56.83	6.82	68.91	44.87	54.09	4.54	59.29
Conscientiousness	46.34	54.72	5.65	62.47	32.90	48.36	9.39	66.51

[a] IQ scale ($M=100$, SD=15).
[b] T scale ($M=50$, SD=10).

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Finally, participants' personality profile was measured by means of the NEO-Five-Factor-Inventory by Costa and McCrae (1989; German translation by Borkenau and Ostendorf, 1993). This questionnaire allows a comprehensive and time-efficient personality assessment in accordance with the currently well-established big five model of personality comprising neuroticism, extraversion, openness to experience, agreeableness, and conscientiousness.

The entire screening test session took about 1 h and 45 min including a short break.

Experimental design and procedure

During functional MR imaging, participants were presented with 60 multiplication problems including the correct answer or a distractor, whereupon they had to respond by button press whether the presented solution was correct or not. Half of the items were one-digit times one-digit multiplication problems (e.g., $4 \times 6 = 24$; single-digit condition), and the other half consisted of two-digit times one-digit (15 items) or one-digit times two-digit (15 items) multiplication problems (e.g., $13 \times 7 = 91$ or $7 \times 16 = 112$; multi-digit condition).

In the single-digit task condition, one operand always contained numbers from 2 to 5 and the other one from 2 to 9 in an effort to maximize the probability of participants employing a memory retrieval strategy. Fifteen multiplication problems showed the correct solution, in the other problems operand errors (i.e., numbers belonging to the same table) were presented as distractors. The items in the multi-digit task condition were constructed following the procedure described by Delazer and colleagues (Delazer et al., 2003; Ischebeck et al., 2006). The larger operand contained numbers from 12 to 19 (without 15 in order to increase task difficulty) and the smaller operand numbers from 3 to 8. Problems with solutions divisibly by 10 were excluded. Distractors were either operand errors (correct result plus or minus the smaller operand) or numbers with incorrect decade digit (plus or minus 1). Thus, incorrect solutions could not be rejected with the help of fast strategies such as approximating the solution or checking the unit-digit or the parity only.

An additional control task was administered in which participants were presented equations with three one-digit numbers (e.g., $3 = 3 = 3$) or three two-digit numbers (e.g., $12 = 13 = 12$). The equations in both control conditions contained the same numbers as in the experimental task (e.g., only numbers from 2 to 9 in the single-digit condition). The task of the participants was to indicate by button press whether the three digits are identical (the equation is correct) or not. The deviant number (± 1) within each condition was equally distributed across the three positions.

Both tasks were presented in an fMRI block design. One block consisted of 5 items with each item presented for 5000 ms, followed by fixation cross for 1500 ms. The 24 blocks of both tasks (12 experimental, 12 control; 6 blocks of each condition) were divided into 6 runs. One run started and ended with a 15 s fixation period and comprised 4 blocks with an inter-block interval of 15 s. Within each run, experimental and control condition blocks were presented in alternating sequence. The total experimental time for both tasks was about 20 min. Before MR imaging was performed, the tasks were demonstrated and practiced. Instructions stressed both speed and accuracy.

MRI acquisition

Imaging was performed on a 3.0 T Tim Trio system (Siemens Medical Systems, Erlangen, Germany) using an 8-channel head coil. To minimize head movement, subjects' heads were stabilized with foam cushions. Functional images were obtained with a single shot gradient echo EPI sequence sensitive to blood oxygen level-dependent (BOLD) contrast (TR = 2800 ms, TE = 30 ms, FA = 90°, matrix size = 64×64, pixel size = 3×3 mm). Thirty-six 3.0-mm-thick transverse slices with a distance factor of 25% were acquired parallel to the AC-PC line. In each session, 426 functional volumes were obtained. The first two volumes were discarded to account for T1 saturation effects. Structural images were obtained using a T1-weighted 3D MPRAGE sequence (TR = 1900 ms, TE = 2.2 ms) which provided $1 \times 1 \times 1$ mm isotropic resolution.

Stimulus presentation was accomplished with the Eloquence system (Invivo Corporation, Orlando, FL), containing an LCD display with full XGA solution, visible for the participant through a mirror mounted above the head coil. The paradigm was presented with the software package Presentation (Neurobehavioral Systems, Albany, CA). For responding, two response boxes were placed in the participants' left and right hand, respectively. In case of a correct equation (or a correct solution, respectively), the participant had to press the button of the right response box with his index finger, and in case of incorrect equations, the left-hand button was pressed.

Analysis of MRI data

Structural and functional imaging data analysis was performed using SPM5 software (Wellcome Department of Imaging Neuroscience, London, U.K.). The functional data of each participant were motion-corrected, co-registered with the structural data, and then spatially normalized into the standard MNI space (Montreal Neurological Institute). Finally, the data were smoothed in the spatial domain using a Gaussian kernel of 8 mm FWHM. The statistical analysis was conducted by means of the general linear model. Model time courses for each experimental condition block were generated on the basis of the hemodynamic response function implemented in SPM5. A high-pass filter with a cut-off frequency of 1/256 Hz was employed to remove low frequency drifts. The analysis for the entire group was performed by computing linear t contrasts (experimental conditions vs. fixation period) for each subject individually which were then entered into a random effects full-factorial Analysis of Variance (ANOVA) model.

The ANOVA of the fMRI data comprised the factors ARITHMETIC COMPLEXITY (single-digit vs. multi-digit) and MATH COMPETENCE (higher vs. lower). Since the effect of arithmetic complexity was stronger than the group difference, two different significance thresholds were applied. Arithmetic complexity effects are reported at $p < .01$ corrected for multiple comparisons by means of the conservative FWE (family wise error) procedure, whereas significant activation differences between groups and a potential interaction of both factors are identified at $p < .00001$ uncorrected.[2] Only activation clusters exceeding a spatial extent threshold of 20 voxels ($2 \times 2 \times 2$ mm) are reported.

[2] Since the between-subjects effects were weaker than the within-subjects effects, an uncorrected but relatively conservative threshold was used for the investigation of activation differences related to mathematical competence. However, the higher vs. lower math group effect in the angular gyrus also emerged at $p < .05$ FWE corrected but did not exceed the spatial extent threshold of 20 voxels ($k = 5$, $t = 5.51$; peak activation at $x = -52$, $y = -64$, $z = 28$).

Results

Experimental task performance

An ANOVA with the factors ARITHMETIC COMPLEXITY (single-digit vs. multi-digit) and MATH COMPETENCE (higher vs. lower) on the solution rate (accuracy) in the experimental task revealed significant main effects of ARITHMETIC COMPLEXITY, $F(1,23)=88.82$, $p<.001$, $\eta^2=.79$, and MATH COMPETENCE, $F(1,23)=25.45$, $p<.001$, $\eta^2=.53$, indicating that the more complex multiplication problems (two-digit times one-digit) were more difficult to solve than the easier (one-digit times one-digit) problems (80.91 vs. 96.33%), and that the participants with higher mathematical competence outperformed their less competent counterparts (94.03 vs. 83.21%). In addition, the interaction reached significance, $F(1,23)=23.42$, $p<.001$, $\eta^2=.51$, showing that the group difference in accuracy is stronger in the multi-digit (90.28 vs. 71.54%) than in the single-digit task condition (97.78 vs. 94.87% for the higher vs. lower math group, respectively).

A corresponding result pattern emerged for the response time data. The multi-digit multiplication problems required more time to solve than the single-digit problems (3.46 vs. 1.39 s; $F(1,23)=280.76$, $p<.001$, $\eta^2=.92$). Furthermore, the more competent participants were faster than the less competent ones (2.09 vs. 2.77 s; $F(1,23)=27.15$, $p<.001$, $\eta^2=.54$), with the group effect being larger in the multi-digit (2.97 vs. 3.96 s) than in the single-digit task condition (1.22 vs. 1.57 s, for the higher vs. lower math group, respectively; $F(1,23)=6.51$, $p<.05$, $\eta^2=.22$).

fMRI data

ANOVA results

The detailed results of the ANOVA effects on the fMRI data are presented in Tables 2 and 3.

First, a main effect of ARITHMETIC COMPLEXITY was observed in several frontal regions in the left hemisphere including the inferior and middle frontal gyrus as well as the precentral gyrus (see Fig. 1a). Further frontal activation was observed in the insula and middle cingulate gyrus, bilaterally. Activation in the parietal cortex emerged in the inferior parietal lobule bilaterally which extended to the angular gyrus in the left hemisphere. Finally, significant activation clusters were found in the cerebellum bilaterally, in the right thalamus, and in the vermis. Subsequent *t*-contrasts between the single-digit and multi-digit task conditions (collapsed over both groups of mathematical competence) revealed that practically all of the aforementioned activation clusters significant in the main effect were due to the higher activation in the multi-digit task condition (see Fig. 1a). Three activation clusters located in the left inferior frontal gyrus and left thalamus additionally reached statistical significance in the *t*-contrast. The reverse contrast (single-digit>multi-digit) only revealed one significant activation cluster in the left angular gyrus, indicating that this brain region was more strongly activated in the single-digit as compared with the multi-digit task condition (see Fig. 1a).

Most importantly, also a main effect of MATHEMATICAL COMPETENCE was observed (see Fig. 1b and Table 3). This effect comprised two clusters in the left angular gyrus and middle temporal gyrus. *t*-contrasts between both groups of mathematical competence (collapsed over both complexity conditions) revealed that these brain areas are more strongly activated in the group of higher mathematical competence (see Fig. 1b). Further brain regions with stronger activation in the higher math group (as compared with the lower math group) included the left supplementary motor area and the left medial superior frontal gyrus. In the reverse contrast (lower>higher math group), no significant activation clusters appeared.

Neither at the threshold used for the group comparison ($p<.00001$ uncorrected) nor at the more liberal threshold of $p<.001$

Table 2
Overview of significant activation clusters (voxelwise $p<.01$ corrected) for the main effect ARITHMETIC COMPLEXITY and the subsequent *t*-contrasts between single-digit and multi-digit multiplication problems

Brain area	MNI peak coordinate			Main effect ARITHMETIC COMPLEXITY			Multi-digit>single-digit			Single-digit>multi-digit		
	x	*y*	*z*	*k*	*F*	p_{corr}	*k*	*t*	p_{corr}	*k*	*t*	p_{corr}
R cerebellum	36	−68	−26	240	86.71	<.001	280	9.31	<.001	–	–	n.s.
L insula	−28	26	−4	415	76.36	<.001	494	8.74	<.001	–	–	n.s.
R insula	30	30	−2	356	75.26	<.001	437	8.68	<.001	–	–	n.s.
L inf parietal G	−36	−42	44	488	74.83	<.001	727	8.65	<.001	–	–	n.s.
L inf frontal G, precentral G	−46	8	30	143	66.75	<.001	183	8.17	<.001	–	–	n.s.
L cerebellum	−42	−66	−30	119	65.42	<.001	154	8.09	<.001	–	–	n.s.
Vermis; L cerebellum	0	−74	−24	253	64.26	<.001	394	8.02	<.001	–	–	n.s.
R mid cingulate G	10	26	36	92	63.95	<.001	116	8.00	<.001	–	–	n.s.
L mid frontal G	−26	−2	54	114	59.22	<.001	161	7.70	<.001	–	–	n.s.
L mid cingulate G	−10	16	44	83	55.29	<.001	114	7.44	<.001	–	–	n.s.
L calcarine cortex	0	−70	10	47	53.97	<.001	69	7.35	<.001	–	–	n.s.
R inf parietal G	38	−46	42	49	49.46	.001	85	7.03	<.001	–	–	n.s.
R thalamus	24	−28	6	55	45.33	.002	92	6.73	<.001	–	–	n.s.
L inf frontal G	−48	36	28	–	–	n.s.	27	6.96	.001	–	–	n.s.
L thalamus	−10	−22	12	–	–	n.s.	37	6.64	.001	–	–	n.s.
L angular G	−58	−64	32	–	–	n.s.	–	–	n.s.	24	6.72	.001

Note. Coordinates are reported in MNI space as given by SPM5 and correspond only approximately to Talairach and Tournoux space (Talairach and Tournoux, 1988). Anatomical labels are based on the AAL (automated anatomical labeling) atlas (Tzourio-Mazoyer et al., 2002). The first label represents the location of the peak activation, additional labels denote submaxima if located in a different brain region.
Abbreviations: L=left hemisphere, R=right hemisphere, G=Gyrus, inf=inferior, sup=superior, mid=middle.

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Table 3

Overview of significant activation clusters (voxelwise $p<.00001$ uncorrected) for the main effect MATHEMATICAL COMPETENCE and the subsequent t-contrasts between the groups of higher vs. lower mathematical competence

Brain area	MNI peak coordinate			Main effect MATHEMATICAL COMPETENCE			Higher > lower mathematical competence			Lower > higher mathematical competence		
	x	y	z	k	F	p_{uncorr}	k	t	p_{uncorr}	k	t	p_{uncorr}
L angular G	−52	−64	28	26	30.36	<.0001	45	5.51	<.0001	–	–	n.s.
L mid temporal G	−50	−54	16	35	30.06	<.0001	56	5.48	<.0001	–	–	n.s.
L SMA	−10	18	56	–	–	n.s.	24	5.88	<.0001	–	–	n.s.
L medial sup frontal G	−6	54	34	–	–	n.s.	27	5.54	<.0001	–	–	n.s.

Note. Coordinates are reported in MNI space as given by SPM5 and correspond only approximately to Talairach and Tournoux space (Talairach and Tournoux, 1988). Anatomical labels are based on the AAL (automated anatomical labeling) atlas (Tzourio-Mazoyer et al., 2002). The label represents the location of the peak activation.

Abbreviations: L = left hemisphere, R = right hemisphere, G = Gyrus, SMA = supplementary motor areas; sup = superior, mid = middle.

uncorrected a significant interaction between the factors ARITHMETIC COMPLEXITY and MATH COMPETENCE emerged. This implies that the activation profiles for the two groups differed equally from one another at each of the two levels of task complexity.

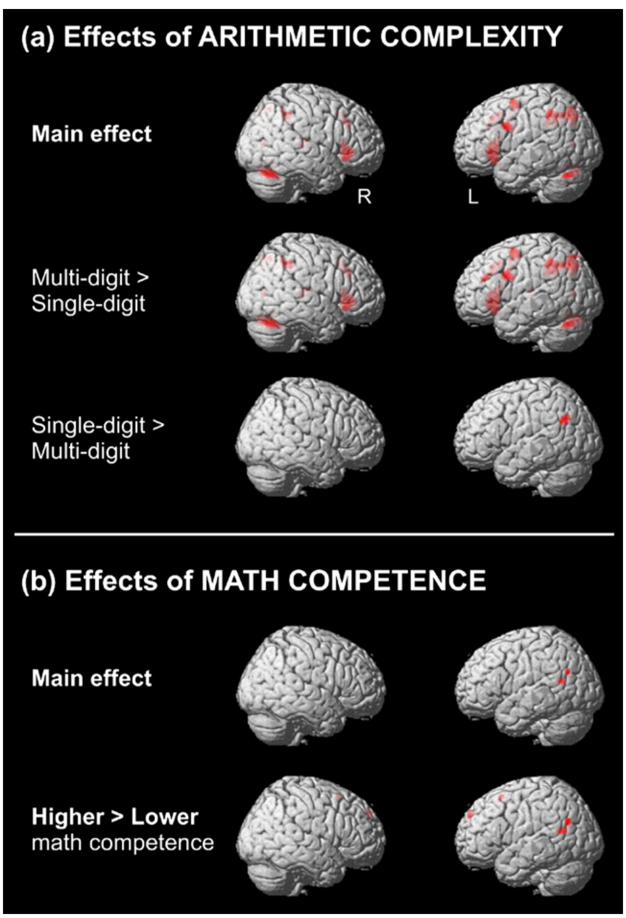

Fig. 1. Significant ANOVA effects of the contrasts experimental conditions against fixation. Activation clusters are depicted on the standard single-subject volume-rendered brain implemented in SPM5 (sagittal views). (a) Main effect of arithmetic complexity (F-test; top), t-contrasts between experimental conditions of higher vs. lower task complexity (second and third row); all effects at voxelwise $p<.01$ corrected for multiple comparisons. (b) Main effect of mathematical competence (F-test, first row), t-contrast between the group of higher vs. lower math competence (second row); all effects at voxelwise $p<.00001$ uncorrected.

Multiple regression analysis

In order to cross-validate the observed group differences and to identify brain regions that are significantly correlated with mathematical competence, we additionally computed a random effects regression analysis on the t-contrast of experimental task vs. fixation (collapsed over both complexity conditions, similar to the ANOVA main effect) with the participants' mathematical–numerical intelligence (IQ) as covariate. It should be noted that – although group selection was also on this variable and the groups do not overlap – the distribution of mathematical–numerical IQ for the entire sample did not significantly differ from normal distribution (Kolmogorov–Smirnov $Z=.47$, $p=.98$) and can therefore be used both in the discrete, group analysis above as well as in a continuous, regression-based approach.

At $p<.001$ uncorrected, an activation cluster in the left angular gyrus was found to display a positive correlation with mathematical–numerical intelligence (see Fig. 2). Notably, the location of this cluster is almost identical to that observed in the group comparison (peak activation at $x=-50$, $y=-64$, $z=28$; $k=82$, $t=3.90$). Convergent with this, a correlation analysis of the individual parameter estimates at the peak coordinate of the regression analysis and mathematical–numerical IQ displayed a significant correlation of $r=.63$ ($p<.001$), suggesting that higher mathematical competence is associated with stronger activation in the left angular gyrus (see scatterplot in Fig. 2). Brain areas showing significant negative correlations with math competence were not found (at $p<.001$ uncorrected).

In order to exclude the possibility that the significant association between left angular gyrus activation and mathematical competence can be accounted for by individual differences in task performance, we computed a partial correlation with task performance as a control variable. A single measure for experimental task performance (accuracy and speed in both levels of task complexity) was obtained by a principal component analysis (PCA) of the accuracy and response times in both experimental conditions (first unrotated factor with an Eigenvalue of 2.28 and accounting for 57% of the variance). Controlling for task performance using a partial correlation did not eliminate the significant correlation between left angular gyrus activation and mathematical competence ($r=.52$, $p=.01$), suggesting that this finding is not due to the potentially confounding effects of task performance.

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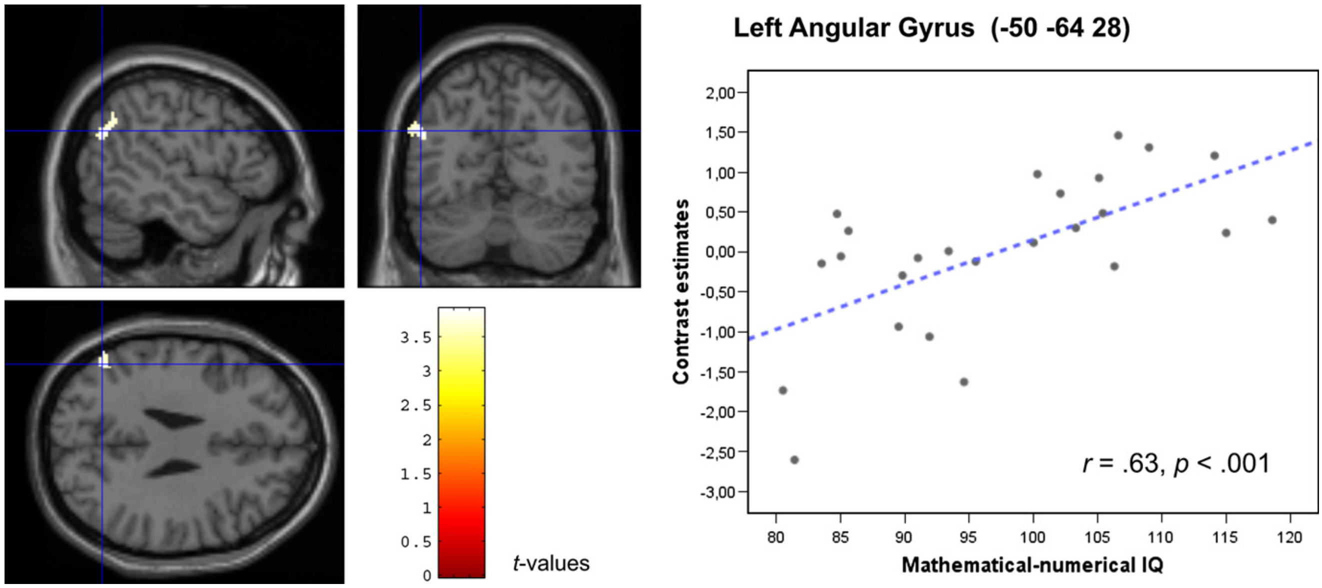

Fig. 2. Significant correlation between peak activation in the left angular gyrus ($x=-50$, $y=-64$, $z=28$) and mathematical–numerical intelligence. In the scatterplot, the individual contrast estimates of experimental condition against fixation collapsed over both complexity conditions are depicted.

Region of interest analysis

In order to evaluate whether the group effect in the left angular gyrus reflects differences in relative activation or deactivation and, furthermore, if there are also activation differences in the control task, a region of interest (ROI) analysis was conducted. To this end, the individual mean beta values for the left angular gyrus (anatomically defined by means of the WFU Pick Atlas; Maldjian et al., 2003) were extracted for regressors of both conditions in the experimental and control task. As illustrated in Fig. 3, mostly negative beta values were observed, indicating that the groups largely differ in relative deactivation in reference to the baseline (fixation) period.

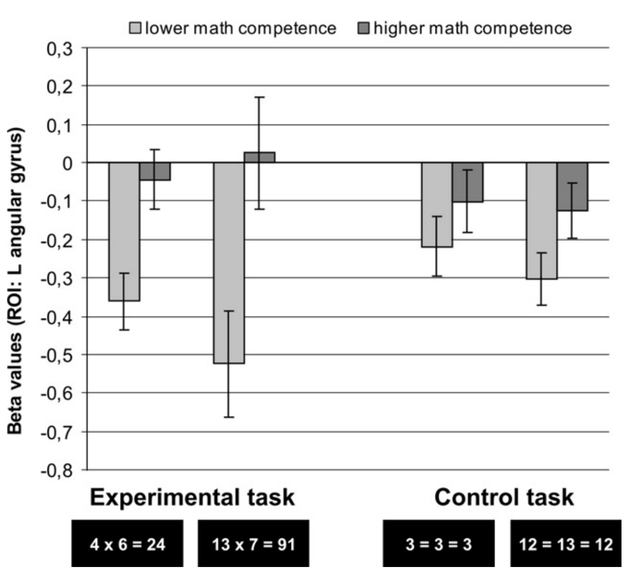

Fig. 3. Mean beta values of both conditions in the experimental and control task averaged over all voxels in the left angular gyrus (anatomically defined by means of the WFU Pick Atlas; Maldjian et al., 2003). Error bars indicate ±1 SE of the mean for the ANOVAs.

An ANOVA with the factors TASK (experimental vs. control), ARITHMETIC COMPLEXITY (single-digit vs. multi-digit), and MATH COMPETENCE on the beta values revealed that the lower math group displayed significantly larger deactivation than the higher math group in both experimental and control task, $F(1,23)=8.85$, $p<.01$, $\eta^2=.28$ (main effect of MATH COMPETENCE). In addition, marginally significant interactions of MATH COMPETENCE with TASK ($F(1,23)=3.58$, $p=.07$, $\eta^2=.14$) as well as with ARITHMETIC COMPLEXITY ($F(1,23)=3.85$, $p=.06$, $\eta^2=.14$) emerged, suggesting somewhat stronger group differences in the experimental task and in the multi-digit problems. The three-way interaction between TASK, ARITHMETIC COMPLEXITY, and MATH COMPETENCE, however, did not reach statistical significance ($p=.36$).

Discussion

In the present fMRI study, multiplication problems of two complexity levels were presented to participants with higher and lower mathematical competence to investigate whether the activation of parietal brain circuits in single- and multi-digit arithmetic problem solving is modulated by individual differences in mathematical competence.

The performance data suggest that the manipulation of task complexity can be considered successful. Expectedly, the two-digit times one-digit multiplication problems displayed a lower solution rate and longer response times than the one-digit times one-digit problems. The different levels of task complexity were also reflected in the fMRI data. Solving the problems with higher (as compared to lower) complexity was accompanied by a stronger and more widespread brain activation primarily comprising a network of frontal and parietal cortices. These regions have been repeatedly found to be involved in mental calculation (Dehaene et al., 1996, 1999; Delazer et al., 2003; Kucian et al., 2006; Pesenti et al., 2000) and to display differential activation depending on the complexity of the arithmetic problems (Menon et al., 2000b; Prabhakaran et al., 2001; Zago et al., 2001).

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There is large consensus that parietal brain circuits subserve arithmetic problem solving (Dehaene et al., 2003, 2004), but the specificity of frontal brain regions for mental calculation has been challenged by studies emphasizing the involvement of general cognitive functions such as executive processes and working memory in mental calculation (Gruber et al., 2001; Rueckert et al., 1996). The necessity to differentiate brain regions supporting scaffolding vs. task-specific processes has been empirically demonstrated in an fMRI study by Menon et al. (2000b). In a factorial design, Menon et al. manipulated the complexity of an arithmetic verification task (by presenting two-operand vs. three-operand equations) as well as the mere task difficulty independent of task-specific complexity (by varying the presentation rate of the equations). It was observed that the presentation rate modulated prefrontal brain regions, whereas the two different arithmetic complexity conditions modulated activation of the angular gyrus and parietal regions adjacent to the IPS bilaterally. Hence, in the present study, the stronger activation in the fronto-parietal network observed in the more complex (as compared with the easier) task condition can most likely be traced to both, stronger recruitment of task-specific (parietal) brain regions and higher demands on attentional, executive, and working memory processes supported by frontal cortices.

In contrast, solving the one-digit times one-digit (vs. the multi-digit) multiplication problems was accompanied by a stronger recruitment of the left angular gyrus. This finding is in line with previous investigations comparing exact and approximate calculation (e.g., Dehaene et al., 1999) and corroborates the role of the angular gyrus in the automatic and efficient retrieval of arithmetic facts (cf. Dehaene et al., 2003). Multiplication tables are typically learned by rote verbal memorization early in school so that solving such problems does not require mental manipulation of quantity or the application of problem solving. Accordingly, the observed activation difference in the left angular gyrus can be interpreted to reflect stronger reliance on automatic fact retrieval in the easy as compared with the more complex task condition. This view is also supported by Delazer et al. (2005) who compared arithmetic drill training (learning solutions to fictitious problems by rote) with strategy training (learning the fast execution of algorithms) and revealed a stronger activation of the angular gyrus for problems learned by drill.

What is novel in the present study, however, is the finding that the activation in the left angular gyrus is also modulated by individual differences in mathematical competence. In particular, we have found that mathematically more (as compared with less) competent individuals displayed stronger activation in the left angular gyrus while solving single-digit and multi-digit multiplication problems. Since both groups of individuals did not differ with respect to verbal and figural–spatial intellectual abilities, this group effect can be exclusively traced back to differences in their mathematical competence. A subsequent regression analysis furthermore revealed that the activation in this brain region did not only differ between groups but is also a linear function of the individual level of mathematical competence. Higher mathematical competence was accompanied by stronger activation in the left angular gyrus, independent of the experimental task performance. Neither the group comparison nor the regression analysis yielded brain regions that were more active in mathematically less competent individuals.

The present finding of a positive association between activation in the left angular gyrus and mathematical competence fits seamlessly into previous evidence from developmental and training studies and suggests that the successful acquisition of arithmetic knowledge is reflected in an increasing reliance on parietal brain circuits, in particular the left angular gyrus (Delazer et al., 2003, 2005; Ischebeck et al., 2006, 2007; Rivera et al., 2005). Dehaene et al. (2003) have proposed that this brain circuit is part of the general language system and not specifically concerned with quantity processing and calculation. Several neuroimaging studies of language production and comprehension support this view (for a review, cf. Gernsbacher and Kaschak, 2003). In the context of arithmetic problem solving, angular gyrus activation has been typically found for highly overlearnt problems (such as multiplication tables) whose solutions can be automatically retrieved from long-term memory (e.g., Dehaene et al., 1999; Stanescu-Cosson et al., 2000). A similar mechanism might also underlie the observed individual differences in mathematical competence. Even though it is unlikely that all solutions to the difficult problems were stored in long-term memory, it appears plausible that the retrieval of problem-relevant arithmetic facts (e.g., intermediate results) was more efficient in the individuals with higher competence level.

Menon et al. (2000a) have also emphasized the relevance of this brain region for skill mastery and long-term practice effects in arithmetic, but they have found a negative association between performance and activation. Perfect performers (with 100% accuracy in arithmetic problems) displayed significantly lower activation in the left angular gyrus than imperfect performers (with an accuracy below 100%). However, in the direct comparison between the present study and that by Menon et al., several methodological differences have to be considered, which may explain differences between the present results and those reported by Menon et al. First, Menon et al. administered three-operand arithmetic problems drawing on addition and subtraction (e.g., “4+2−1=4”), which may involve different cognitive processes and brain circuits (e.g., less automatic fact retrieval and stronger recruitment of the quantity system) than multiplication problems (Dehaene et al., 2004; Duffau et al., 2002; Ischebeck et al., 2006). Second, Menon et al.’s sample only included adult college students with very high levels of performance in the fMRI calculation task. In fact, even the group of imperfect performers had an average accuracy score of 92%. In the present investigation, individuals with comparably high vs. low mathematical competence were compared. Third, and presumably most importantly, mathematical competence is defined by scores in standardized psychometric tests of intelligence and arithmetic competence. In contrast to Menon et al.’s study, the independent measures of mathematical competence also allowed us to deliberately select groups solely differing in mathematical competence but not other intellectual abilities. In future studies multiple arithmetic tasks and group selection criteria should be employed in order to further investigate the dynamic nature by which the angular gyrus is modulated by individual differences in task performance and mathematical competence. In addition, the group selection should also consider potential sex differences in the relationship between mathematical competence and brain activation (Haier and Benbow, 1995; Skrandies et al., 1999).

A central but largely unresolved issue in the interpretation of angular gyrus involvement during mental calculation and its modulation by skill acquisition refers to the frequent finding of deactivations in this brain region relative to a low-level (rest) baseline or a control task (Dehaene et al., 1996; Ischebeck et al., 2006; Rickard et al., 2000; Venkatraman et al., 2006; Zago et al., 2001). Rickard et al., for instance, reported that angular and supramarginal gyri were significantly deactivated in an arithmetic (multiplication) verification task relative to magnitude judgment and control tasks, and interpreted this result as evidence for non-involvement of this brain region in mental calculation. Zago et al., in contrast, argued that calculation induces an inhibition of language-related areas (including the left angular gyrus) which is related to the complexity of the calculation task. Using Positron Emission Tomography (PET), they administered single-digit and two-digit multiplication problems and observed stronger deactivations for the more demanding two-digit than for the single-digit problems. Further evidence for a relationship between deactivation and task difficulty comes from Ischebeck et al. (2006) who found the largest deactivation for untrained (multiplication) problems and the smallest deactivation (even a slight activation) for trained multiplication problems (but see also Venkatraman et al., 2006). In the present investigation, the ROI analysis of the left angular gyrus and the regression analysis have also revealed that individuals with different levels of mathematical competence predominantly differ in relative deactivation (in reference to the baseline, see Fig. 3) and not activation. Hence, the relative amount of deactivation appears to be smaller for simple (as compared with difficult) problems, for trained (vs. untrained) problems, and, as the present study has revealed, for individuals with higher (as compared with lower) mathematical competence.

It appears noteworthy that the angular gyrus activation difference between the groups of higher and lower mathematical competence only emerged in the contrast between experimental task and fixation period but not when directly contrasted against the control task. A possible explanation for this result might lie in similar competence-related effects in the control task that may have diminished group differences in the respective contrast. The results of the ROI analysis, showing a main effect of mathematical competence on beta weights extracted from the angular gyrus in both experimental and control task and only marginal interactions between mathematical competence and both task as well as complexity collapsed across the experimental and control task, support this explanation (see Fig. 3). Looking at the control task performance (response times) additionally reveals a marginally significant interaction between arithmetic complexity (single vs. double digits) and group, $F(1,23)=3.71$, $p=.07$, $\eta^2=.14$, suggesting longer response times in the lower (as compared with higher) math group, especially in the multi-digit control task condition. Therefore, individuals of higher vs. lower mathematical competence already seem to exhibit performance differences in the control task that does not require mental calculation but only simple matching of numbers. Interestingly, even in this rather basic task condition deactivations of the angular gyrus emerged. Against the background of these findings, it could be hypothesized that, in addition to being involved in the automatic retrieval of arithmetic facts, the angular gyrus also mediates the mapping between symbols and numerical magnitudes, which, in the present control task, is engaged to a greater extent in the higher relative to the lower math group. This group difference in the automatic access of the semantic information upon presentation of an Arabic numeral may explain both the marginally significant interaction between arithmetic complexity and group and the absence of a three-way interaction with task. Specifically, since in both the experimental and control task the number of Arabic numerals increases as a function of the complexity level, this may result in increased demand on both arithmetic fact retrieval (experimental task) and the activation of the mapping between Arabic numerals and the numerical magnitudes they represent (experimental and control task). It is therefore plausible that both processes (retrieval and mapping) may be engaged to different extents in the two groups, which, in turn, is reflected in the differential engagement of the angular gyrus.

Besides the left angular gyrus, the voxelwise group comparison also yielded competence-related activation differences in the left middle temporal gyrus, supplementary motor area (SMA), and medial superior frontal region. Tentatively, the stronger activation in these left-hemispheric circuits in more competent participants might also be interpreted to reflect competence-related differences in the reliance on language-mediated processes in mental calculation. Activations in the left SMA and medial superior frontal region have been associated with verbal working memory (for reviews, cf. Baddeley, 2003; Smith and Jonides, 1999), and the left middle temporal gyrus is discussed in the context of phonological and semantic processing (Gernsbacher and Kaschak, 2003). The latter brain region was recently found to be related to the acquisition of arithmetic facts. Ischebeck et al. (2007) repeatedly presented a set of three (complex) multiplication problems to participants while lying in the MR scanner and observed a positive correlation between the number of repetitions (the training progress) and the activation of the left middle temporal gyrus. However, in contrast to the effect in the angular gyrus in the present study, none of the aforementioned brain regions emerged in the subsequent regression analysis assessing the relationship between activation patterns and individual differences in mathematical competence. Therefore, too hasty conclusions on the relevance of these brain regions for individual differences in mathematical competence should be avoided.

A well-known behavioral effect that is also related to the acquisition of arithmetic skills in development is the operand order effect, which is characterized by a performance advantage for multiplication problems with the larger operand in first position (cf. Butterworth et al., 2003). We also investigated this effect as well as its interaction with mathematical competence and indeed found that multi-digit problems with the larger operand in first position were solved with both greater accuracy (87.14% vs. 74.68%, $p<.001$) and shorter response times (3.20 s vs. 3.78 s, $p<.001$) than problems with the larger operand in second position. In addition, the operand order effect in the accuracy was significantly more pronounced in the group of lower as compared with higher mathematical competence ($p<.01$), suggesting a greater susceptibility to this effect in mathematically less competent individuals. Since an fMRI block design was used, the present data do not allow for an investigation of the brain correlates of these effects. Future fMRI studies investigating (individual differences in) arithmetic problem solving by means of event-related designs, however, should address this issue.

In conclusion, the present fMRI study has provided first evidence that the activation of parietal cortices during mental calculation is modulated by individual differences in mathematical competence independent of other intellectual abilities. In particular, it has been shown that individuals with higher mathematical competence more strongly activated the left angular gyrus while solving easy and more difficult multiplication problems. This finding is in strong agreement with previous evidence from developmental and training studies and suggests a stronger reliance on language-mediated processes during arithmetic problem solving in mathematically more competent individuals. Future studies will have to show whether the relation between mathematical competence and angular gyrus activation can also be observed in females and in arithmetic tasks other than multiplication.

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References

Ansari, D., Garcia, N., Lucas, E., Hamon, K., Dhital, B., 2005. Neural correlates of symbolic number processing in children and adults. NeuroReport 16 (16), 1769–1773.

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.

Baddeley, A., 2003. Working memory: looking back and looking forward. Nat. Rev., Neurosci. 4 (10), 829–839.

Borkenau, P., Ostendorf, F., 1993. NEO-Fünf-Faktoren Inventar (NEO-FFI) nach Costa und McCrae [NEO-Five-Factor-Inventory]. Hogrefe, Göttingen.

Burbaud, P., Degreze, P., Lafon, P., Franconi, J.M., Bouligand, B., Bioulac, B., Caille, J.M., Allard, M., 1995. Lateralization of prefrontal activation during internal mental calculation—A functional magnetic-resonance-imaging study. J. Neurophysiol. 74 (5), 2194–2200.

Butterworth, B., Marschesini, N., Girelli, L., 2003. Basic multiplication combinations: passive storage or dynamic reorganization? In: Baroody, A.J., Dowker, A. (Eds.), The Development of Arithmetic Concepts and Skills: Constructing Adaptive Expertise. Erlbaum, Mahwah, NJ, pp. 189–202.

Carroll, J.B., 1993. Human Cognitive Abilities: A Survey of Factor Analytic Studies. Cambridge University Press, Cambridge.

Costa, P.T., McCrae, R.R., 1989. The NEO PI/FFI Manual Supplement. Psychological Assessment Resources, Odessa, FL.

Deary, I.J., 2001. Human intelligence differences: a recent history. Trends Cogn. Sci. 5 (3), 127–130.

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), 970–974.

Dehaene, S., Piazza, M., Pinel, P., Cohen, L., 2003. Three parietal circuits for number processing. Cogn. Neuropsychol. 20 (3–6), 487–506.

Dehaene, S., Molko, N., Cohen, L., Wilson, A.J., 2004. Arithmetic and the brain. Curr. Opin. Neurobiol. 14 (2), 218–224.

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.

Delazer, M., Ischebeck, A., Domahs, F., Zamarian, L., Koppelstaetter, F., Siedentopf, C.M., Kaufmann, L., Benke, T., Felber, S., 2005. Learning by strategies and learning by drill-evidence from an fMRI study. NeuroImage 25 (3), 838–849.

Dowker, A., 2005. Individual Differences in Arithmetic: Implications for Psychology, Neuroscience and Education. Psychology Press, New York, NY.

Duffau, H., Denvil, D., Lopes, M., Gasparini, F., Cohen, L., Capelle, L., Van Effenterre, R., 2002. Intraoperative mapping of the cortical areas involved in multiplication and subtraction: an electrostimulation study in a patient with a left parietal glioma. J. Neurol. Neurosurg. Psychiatry 73 (6), 733–738.

Gernsbacher, M.A., Kaschak, M.P., 2003. Neuroimaging studies of language production and comprehension. Annu. Rev. Psychol. 54, 91–114.

Gerstmann, J., 1940. Syndrome of finger agnosia, disorientation for right and left, agraphia and acalculia—Local diagnostic value. Arch. Neurol. Psychiatry 44 (2), 398–408.

Grabner, R.H., Fink, A., Stipacek, A., Neuper, C., Neubauer, A.C., 2004. Intelligence and working memory systems: evidence of neural efficiency in alpha band ERD. Cogn. Brain Res. 20 (2), 212–225.

Gruber, O., Indefrey, P., Steinmetz, H., Kleinschmidt, A., 2001. Dissociating neural correlates of cognitive components in mental calculation. Cereb. Cortex 11 (4), 350–359.

Haier, R.J., Benbow, C.P., 1995. Sex differences and lateralization in temporal lobe glucose metabolism during mathematical reasoning. Dev. Neuropsychol. 11 (4), 405.

Henschen, S.L., 1919. On language, music and calculation mechanisms and their localisation in the cerebrum. Zeitschrift Für Die Gesamte Neurologie Und Psychiatrie 52, 273–298.

Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstatter, 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.

Ischebeck, A., Zamarian, L., Egger, K., Schocke, M., Delazer, M., 2007. Imaging early practice effects in arithmetic. NeuroImage 36 (3), 993–1003.

Jäger, O.A., Süß, H.M., Beauducel, A., 1997. Berliner Intelligenzstruktur-Test [Berlin Intelligence Structure Test]. Hogrefe, Göttingen.

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.

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.

Menon, V., Rivera, S.M., White, C.D., Eliez, S., Glover, G.H., Reiss, A.L., 2000a. Functional optimization of arithmetic processing in perfect performers. Cogn. Brain Res. 9 (3), 343–345.

Menon, V., Rivera, S.M., White, C.D., Glover, G.H., Reiss, A.L., 2000b. Dissociating prefrontal and parietal cortex activation during arithmetic processing. NeuroImage 12 (4), 357–365.

Neisser, U., Boodoo, G., Bouchard, T.J., Boykin, A.W., Brody, N., Ceci, S.J., Halpern, D.F., Loehlin, J.C., Perloff, R., Sternberg, R.J., et al., 1996. Intelligence: knowns and unknowns. Am. Psychol. 51 (2), 77–101.

Neubauer, A.C., Fink, A., Schrausser, D.G., 2002. Intelligence and neural efficiency: the influence of task content and sex on the brain–IQ relationship. Intelligence 30 (6), 515–536.

Neubauer, A.C., Grabner, R.H., Fink, A., Neuper, C., 2005. Intelligence and neural efficiency: further evidence of the influence of task content and sex on the brain–IQ relationship. Cogn. Brain Res. 25 (1), 217–225.

Pesenti, M., Thioux, M., Seron, X., De Volder, A., 2000. Neuroanatomical substrates of Arabic number processing, numerical comparison, and simple addition: a PET study. J. Cogn. Neurosci. 12 (3), 461–479.

Prabhakaran, V., Rypma, B., Gabrieli, J.D.E., 2001. Neural substrates of mathematical reasoning: a functional magnetic resonance imaging study of neocortical activation during performance of the necessary arithmetic operations test. Neuropsychology 15 (1), 115–127.

Rickard, T.C., Romero, S.G., Basso, G., Wharton, C., Flitman, S., Grafman, J., 2000. The calculating brain: an fMRI study. Neuropsychologia 38 (3), 325–335.

Rivera, S.M., Reiss, A.L., Eckert, M.A., Menon, V., 2005. Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. Cereb. Cortex 15 (11), 1779–1790.

Roland, P.E., Friberg, L., 1985. Localization of cortical areas activated by thinking. J. Neurophysiol. 53 (5), 1219–1243.

Rueckert, L., Lange, N., Partiot, A., Appollonio, I., Litvan, I., Le Bihan, D., Grafman, J., 1996. Visualizing cortical activation during mental calculation with functional MRI. NeuroImage 3 (2), 97–103.

Schmidt, F.L., Hunter, J.E., 1998. The validity and utility of selection methods in personnel psychology: practical and theoretical implications of 85 years of research findings. Psychol. Bull. 124 (2), 262–274.

Skrandies, W., Reik, P., Kunze, C., 1999. Topography of evoked brain activity during mental arithmetic and language tasks: sex differences. Neuropsychologia 37 (4), 421–430.

Smith, E.E., Jonides, J., 1999. Neuroscience—Storage and executive processes in the frontal lobes. Science 283 (5408), 1657–1661.

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, 2240–2255.

Talairach, J., Tournoux, P., 1988. Co-Planar Stereotaxic Atlas of the Human Brain. Thieme Medical, New York, NY.

Tzourio-Mazoyer, N., Landeau, B., Papathanassiou, D., Crivello, F., Etard, O., Delcroix, N., Mazoyer, B., Joliot, M., 2002. Automated anatomical labeling of activations in SPM using a macroscopic anatomical parcellation of the MNI MRI single-subject brain. NeuroImage 15 (1), 273–289.

Venkatraman, V., Siong, S.C., Chee, M.W.L., Ansari, D., 2006. Effect of language switching on arithmetic: a bilingual fMRI study. J. Cogn. Neurosci. 18 (1), 64–74.

Zago, L., Tzourio-Mazoyer, N., 2002. Distinguishing visuospatial working memory and complex mental calculation areas within the parietal lobes. Neurosci. Lett. 331 (1), 45–49.

Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., Tzourio-Mazoyer, N., 2001. Neural correlates of simple and complex mental calculation. NeuroImage 13 (2), 314–327.

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