Brain Research 1643 (2016) 91–102

Contents lists available at ScienceDirect

Brain Research

journal homepage: www.elsevier.com/locate/brainres

Research Report

Non-symbolic and symbolic notations in simple arithmetic differentially involve intraparietal sulcus and angular gyrus activity

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ARTICLE INFO

Article history:
Received 9 September 2015
Received in revised form
19 April 2016
Accepted 22 April 2016
Available online 23 April 2016

Keywords:
Addition
Calculation
Retrieval
Visuospatial working memory
Number format
Mental arithmetic

ABSTRACT

Addition problems can be solved by mentally manipulating quantities for which the bilateral intraparietal sulcus (IPS) is likely recruited, or by retrieving the answer directly from fact memory in which the left angular gyrus (AG) and perisylvian areas may play a role. Mental addition is usually studied with problems presented in the Arabic notation (4+2), and less so with number words (four+two) or dots (:: +·.). In the present study, we investigated how the notation of numbers influences processing during simple mental arithmetic. Twenty-five highly educated participants performed simple arithmetic while their brain activity was recorded with functional magnetic resonance imaging. To reveal the effect of number notation, arithmetic problems were presented in a non-symbolic (*Dots*) or symbolic (*Arabic*; *Words*) notation. Furthermore, we asked whether IPS processing during mental arithmetic is magnitude specific or of a more general, visuospatial nature. To this end, we included perception and manipulation of non-magnitude formats (*Colors*; unfamiliar Japanese *Characters*). Increased IPS activity was observed, suggesting magnitude calculations during addition of *non-symbolic* numbers. In contrast, there was greater activity in the AG and perisylvian areas for *symbolic* compared to non-symbolic addition, suggesting increased verbal fact retrieval. Furthermore, IPS activity was not specific to processing of numerical magnitude but also present for non-magnitude stimuli that required mental visuospatial processing (*Color*-mixing; *Character*-memory measured by a delayed match-to-sample task). Together, our data suggest that simple non-symbolic sums are calculated using visual imagery, whereas answers for simple symbolic sums are retrieved from verbal memory.

1. Introduction

The ability to perform mental arithmetic is a prerequisite for more advanced mathematical skills. Arithmetic proficiency progresses from solving non-symbolic sums (e.g., adding two pieces of fruit) to manipulation of symbols that represent quantities (e.g., "1+1", or "one+one"). With sufficient practice both non-symbolic and symbolic problems can be solved mentally, without needing fingers or pen and paper for visualizing numerosity. Evidence supports that two main processing routes are available for mental arithmetic: answers can be calculated by making use of a fronto-parietal network that includes the magnitude system in bilateral intraparietal sulcus (IPS) and/or answers can be directly retrieved from verbal fact memory with the angular gyrus (AG) as a key brain structure (Dehaene et al., 2003). Behavioral research indicates that the manner in which sums are solved depends on the notation of the numbers within the arithmetic problem. For

Abbreviations: IPS, intraparietal sulcus; AG, angular gyrus; RT, reaction time; fMRI, functional magnetic resonance imaging; ANOVA, analysis of variance; MFG, middle frontal gyrus; IFG, inferior frontal gyrus; ITG, inferior temporal gyrus; Hem., Hemisphere; L, left; R, right; hIP1, human intraparietal area 1; hIP2, human intraparietal area 2; hIP3, human intraparietal area 3; FWE, family wise error corrected; pMTG, posterior middle temporal gyrus; MTG, middle temporal gyrus; HC, hippocampus; pCC, posterior cingulate cortex; aCC, anterior cingulate cortex; medSFG, medial aspect of the superior frontal gyrus; SFG, superior frontal gyrus; TP, temporal pole; ISI, inter-stimulus interval; EPI, echo-planar imaging; TR, repetition time; TE, echo time; FA, flip angle; FOV, field of view; MNI, Montreal Neurological Institute; GLM, general linear model; BOLD, blood-oxygenation-level dependent; HRF, hemodynamic response function; ROI, region of interest

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http://dx.doi.org/10.1016/j.brainres.2016.04.050
0006-8993/

example, university students report to use retrieval more often for simple problems notated in Arabic numbers than for simple problems notated in number words (Campbell and Alberts, 2009). The first aim of the current study was to find neural evidence to support this behavioral finding by assessing whether brain processing used for solving simple addition problems differs according to the format in which the numbers are notated (*non-symbolic*: dots (∷); *symbolic*: Arabic (4), words (four)). Because the IPS has been implicated in operations besides magnitude processing, such as general visuospatial processing (for reviews, see Grefkes and Fink, 2005; Kravitz et al., 2011), the second aim was to explore the nature of observed IPS activity, by investigating the degree to which processing in the IPS is specific to numerical magnitudes.

1.1. Behavioral research on arithmetic and notation

Behaviorally, there is abundant evidence that both calculation and retrieval can be used for solving arithmetical problems (Campbell and Alberts, 2009; Campbell and Fugelsang, 2001; LeFevre et al., 1996). Initially, a calculation strategy - also referred to as a procedural strategy - is employed. Calculation can be thought of as the manipulation of numerical magnitudes, or numerosities. However, with practice, sums and answers can be associated or stored together in memory as facts, such that the use of fact retrieval to solve the sums is employed more often (Shrager and Siegler, 1998). Therefore, the solution method for addition problems can vary depending on familiarity. Simple additions, for example, may especially rely on direct memory retrieval in adults, because these problem-answer combinations have been practiced many times (Ashcraft and Christy, 1995).

Concerning number notation, some have proposed that numerical processing is relatively abstract in nature (Dehaene et al., 2004; McCloskey and Macaruso, 1995), whereas others emphasize the influence of number notation (Campbell and Alberts, 2009; Campbell and Fugelsang, 2001; Campbell et al., 2004). The former idea stems from several number processing phenomena that are not influenced by number notation. One such phenomenon is the *distance effect* which refers to the finding that if one has to judge which of two numerical magnitudes is larger, discrimination is faster if the numbers are farther apart (i.e., participants are faster at discriminating 2 from 9 than 2 from 5). The fact that the distance effect is observed for both non-symbolic (dots: Buckley and Gillman, 1974) and symbolic number notations (Arabic: Moyer and Landauer, 1967; words: Foltz et al., 1984, exp 2) suggests that the cognitive system represents magnitude in an abstract format. On the other hand, Campbell and Fugelsang (2001) observed longer reaction times (RTs) for additions in word notation than for additions in Arabic notation, especially for the larger sums. Moreover, this notation by size effect was replicated in self reported strategy use, with more calculation for number words than for Arabic numbers, especially for the larger sums (cf. Campbell and Alberts, 2009; Campbell et al., 2004). These latter findings emphasize a possible difference in solution method according to the number notation of the problem, even if both notations are symbolic in nature.

In short, behavioral evidence shows that practice in solving arithmetic problems promotes direct retrieval of the answers from fact memory and that, even if the mental representation of magnitude is abstract, notation can have an influence on arithmetic performance. Although metacognitive self-reports provide valuable data, participants are not always aware of which solution methods they use and they may have difficulties in verbalizing them. Furthermore, self-reports are influenced by instruction (Kirk and Ashcraft, 2001; Smith-Chant and LeFevre, 2003), and even though they may be veridical reflections of mental processes, the arithmetic performance itself can be changed by the requirement to self-report (Smith-Chant and LeFevre, 2003). In this regard, the brain activation pattern may provide an objective insight into mental arithmetic and could help to tease apart underlying cognitive processes being discussed in behavioral literature.

1.2. Brain research on arithmetic and notation

1.2.1. IPS for calculation, AG/perisylvian areas for retrieval

Neurally, magnitude calculation and verbal retrieval show specific correlates. Dehaene and colleagues (Dehaene et al., 2003) proposed that the horizontal segment of bilateral IPS is important for calculation, because it is involved in the representation of numerical magnitude. The IPS magnitude system underlies a “sense of number” by holding quantity in an abstract format, such as the “four-ness” that is common among the number notations “∷”, “4”, and “four”. In a functional magnetic resonance imaging (fMRI) paradigm, Piazza and colleagues (Piazza et al., 2004; Piazza et al., 2007) showed that activity of neurons in the IPS decreases when a certain numerical quantity is repeatedly shown (a phenomenon known as “repetition suppression”) but increases again on presentation of another quantity. The IPS activity increase was larger for quantities that were farther away from the adapted numerosity, which is in accordance with the distance effect found at the behavioral level. Similar to the behavioral variant, this neural distance effect has been observed in imaging studies for both non-symbolic (Piazza et al., 2004, 2007) and symbolic numbers (Piazza et al., 2007; Pinel et al., 2001). These results suggest that enculturated symbols map onto abstract internal analogue magnitude representations in the IPS (Verguts and Fias, 2004). In other words, the same IPS magnitude system appears to underlie the representation of numerical magnitude for both non-symbolic and symbolic numbers. Thus, if arithmetic problems are solved via magnitude calculations, the IPS is likely to be involved (Dehaene et al., 2004; for a similar argument, see Venkatraman et al., 2005).

Verbal retrieval of arithmetic facts from memory, on the other hand, appears to be facilitated by the left AG, together with neighboring perisylvian areas including the posterior superior and middle temporal gyrus, and the supramarginal gyrus (Cohen et al., 2000; Dehaene et al., 2004; Dehaene et al., 2003; Prado et al., 2011). Grabner et al. (2009) showed that self-reported arithmetic fact retrieval engages in stronger AG activity than self-reported procedural strategies. However, in contrast to the IPS regions which have been regularly implicated in magnitude calculations, a role for the left AG in arithmetic fact retrieval has been less consistently replicated (e.g., for a non-replication, see Rosenberg-Lee et al., 2011).

1.2.2. (Non-) specificity of IPS activity to numerical processing

A problem with using IPS activity as a reflection of magnitude calculations during mental arithmetic is that it is also observed during other mental processes. Within the numerical domain, the IPS appears to be active during detection of numbers even before the numbers are manipulated (Eger et al., 2003). Therefore, to relate IPS activity to the *mental manipulation* of magnitudes, that is the actual calculation, one has to control for number detection related IPS activity. Venkatraman et al. (2005) set out to investigate whether the addition process in itself (also called “mental addition”) would activate the IPS in a notation independent manner. To overcome ambiguity in interpretation of the results, the authors included numbers in their control condition such that they could dissociate IPS activity due to the addition process from IPS activity related to perceiving numbers. They observed bilateral IPS activity for addition of both dots and Arabic numbers, which led them to conclude that mental addition involves the IPS independent of number notation. However, some

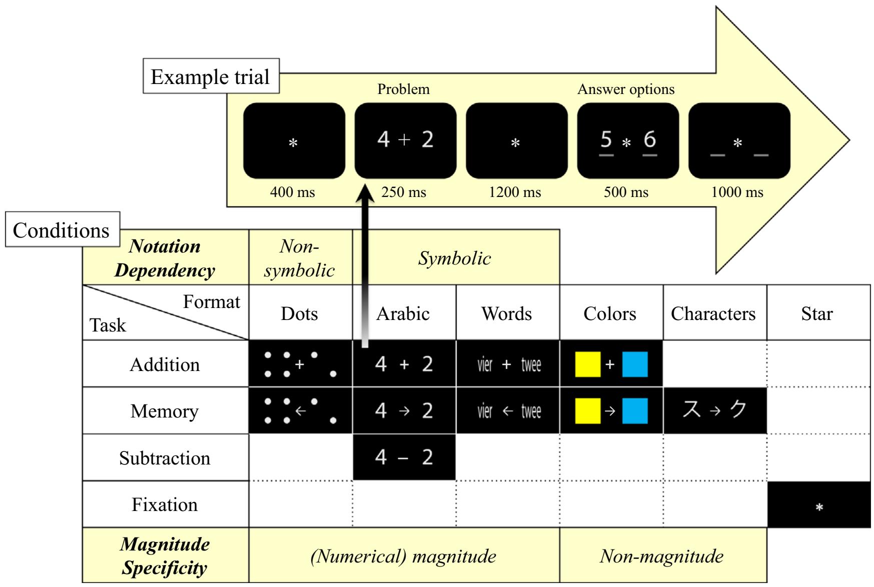

Fig. 1. Conditions & example trial. Example problem for 10 experimental conditions, a low-level baseline fixation condition, and an example trial. For the addition problems, participants were asked to add the two operands and choose the correct solution out of two presented answer options. In case of the color format, the addition task required mixing of paint colors. For the memory task, the participant had to keep in mind the stimulus to which the arrow was pointing, and in the subtraction task the operands had to be subtracted. Answer options were always presented in the same format as the problems. Note about the Dutch number words: vier=four, twee=two.

issues still remain. For each trial, the addition problem was presented with two numbers, whereas the control condition showed only one number. Therefore, the IPS activity increase could partly be attributed to more visual processing in the addition condition (two numbers) as compared to the control condition (one number). Furthermore, inclusion of symbolic numbers as answer options in the non-symbolic condition might have diminished the influence of notation.

Beyond the numerical sphere, there is the issue of how domain specific the IPS is in the processing of (numerical) magnitudes. Some data suggest that there is a part of the IPS that is specifically dedicated to the processing of numerical magnitudes (Dehaene et al., 2003; Simon et al., 2002). Others have proposed that a common magnitude system exists that goes beyond numerosity (for a review, see Cohen et al., 2008). Moreover, the parietal lobe, including the IPS, has been implicated in visuospatial processing (for reviews, see Grefkes and Fink, 2005; Kravitz et al., 2011), which suggests an even more general function of the IPS. Thus, it remains unclear whether mental calculation is performed by number domain specific processing in the IPS, or whether the IPS underlies more general visuospatial processing which may be recruited for mental calculation.

1.3. Present study

To summarize, converging evidence shows that the bilateral IPS is involved in calculation by processing numerical magnitude in a notation independent fashion (Dehaene et al., 2003). The AG and neighboring perisylvian areas have been implicated in retrieving facts from verbal memory (Dehaene et al., 2003; Grabner et al., 2009; Prado et al., 2011). Yet, it is unclear to what degree number notation influences the use of these solution methods when performing simple arithmetic, as reflected by relative differences in IPS and AG processing. Furthermore, although the IPS regions have been evidently implicated in quantity processing, the degree of specialization, from specific processing of numerical magnitude (Dehaene et al., 2003; Simon et al., 2002) to more general visuospatial processing (Grefkes and Fink, 2005; Kravitz et al., 2011), is uncertain.

With a controlled set of stimuli, first, we set out to investigate whether solving single digit addition problems involves differential brain activity, depending on number notation. Second, we addressed the nature of IPS functioning, by investigating whether magnitude related processing recruits the IPS to a different degree than non-magnitude related processing.

As for the first point, if frequency of experience affects the solution method (Shrager and Siegler, 1998) then simple addition problems may be solved differently depending on the format in which the problems are notated. Simple addition problems are often encountered and practiced in the *Arabic* notation and these sums are therefore likely solved via AG retrieval based processing. However, if problems are presented in the less familiar *dot* notation – which is not only less familiar, but also directly displaying quantity – mental arithmetic is more likely to rely on magnitude calculations recruiting the IPS. For written number *words*, the prediction is less clear. In arithmetic problems, written number words are less frequently encountered than Arabic numbers. However, similar to Arabic numbers and contrary to dots, written words are symbols for quantity and therefore show magnitude indirectly, which may lead to less magnitude calculations and a higher reliance on the verbal retrieval route. We expected that addition of non-symbolic numbers (*Dots*) is accompanied by more IPS activity than addition of symbolic numbers (*Arabic*, *Words*). In a similar vein, we expected that simple addition of symbolic (especially Arabic) numbers results in higher activity in the AG/perisylvian areas than addition of non-symbolic numbers.

As for the second point, if a part of the IPS is specifically involved in numerical magnitude processing, we should see a greater activation increase for numerical tasks, whereas if IPS activity is indicative of more generic processing such as visuospatial processing, we may observe elevated IPS responses to tasks with non-magnitude inputs as well. We expected that tasks with numerical stimuli recruit greater IPS activity than tasks with non-magnitude stimuli (*Colors*, *Characters*).

To test the above hypotheses, we recorded brain activity of 25 participants with fMRI, while they performed several tasks (see Fig. 1 for all conditions). To reveal the effect of number notation on activation in the IPS (related to magnitude calculations) and the

AG/perisylvian areas (related to verbal fact retrieval) during simple arithmetic, addition problems were presented in three number formats (*Dots, Arabic numbers, number Words*). We controlled for brain activity unrelated to mental arithmetic – such as detection of the numerical stimuli and answer production – by using memory tasks (delayed matching-to-sample) as baseline conditions for each of the three number notations. Subtraction in Arabic notation, which is thought to rely more on the IPS route than addition, was included to investigate whether there are differences in the involvement of the IPS for simple addition and subtraction. To investigate the magnitude specificity of observed IPS activity, number stimuli were compared with stimuli that do not involve magnitude processing, namely mixing of colors (as a contrast for mental addition with numbers) and Japanese characters (as a contrast for numerical and verbal information processing in the memory task). Colors are similar to numbers in the sense that they are familiar, follow a continuum, and can be added (e.g., “yellow+blue=green”), however colors do not explicitly contain magnitude information. The unfamiliar Japanese katakana-characters were selected as non-magnitude stimuli that would evoke processing in visuospatial memory, without automatic retrieval from verbal memory.

2. Results

In the fMRI scanner, participants were presented with a problem (250 ms) and after a 1200 ms delay, two response options were shown on the screen to which the participants responded with a corresponding button press. The problems consisted of either a mental manipulation condition (addition, subtraction, or mixing for colors) or a memory condition (delayed match-to-sample task). See Fig. 1 for an example trial.

2.1. Behavioral results

For all problems, accuracy of the two alternative forced choice and RT (relative to the onset of the response options) were recorded.

2.1.1. Accuracy

The mean accuracy score was at ceiling level ($M_{\text{proportion correct}}=0.95$) for all conditions ($SD=0.03$, range=0.89–0.99) and all participants ($SD=0.02$, range=0.91–0.98), which indicates that brain activity mainly reflected successful task related processes. Since ceiling level was reached, comparing differences in accuracy rates between conditions would be less informative. Therefore, accuracy differences were not further investigated.

2.1.2. Reaction times

The mean RTs for the correct answers can be found in Table 1. Because the conditions did not constitute a full factorial design, RTs were analyzed in three separate repeated measures analyses of variance (ANOVAs).

The first ANOVA, with Task (*Addition, Memory*) and Format (*Dots, Arabic, Words, Colors*) as factors, revealed a main effect of Task, with faster RTs for memory than for addition ($F(1, 22)=87.98$, $p<.001$, $\eta_p^2=.800$). Also, a main effect of Format was observed ($F(3, 66)=103.26$, $p<.001$, $\eta_p^2=.824$), with the fastest RTs for Arabic, followed by colors, and the slowest RTs for both dots and words (post hoc Bonferroni corrected dependent *t*-tests, all $p\leq.002$, except for *Dots* versus *Words*: $p>.999$). Furthermore, a significant Task × Format interaction effect was observed ($F(3, 66)=20.20$, $p<.001$, $\eta_p^2=.479$): participants were faster for memory tasks than for addition tasks, but for Arabic numbers, there was no difference between the two tasks (post hoc Bonferroni corrected dependent *t*-tests, all $p<.001$, except for *Arabic*: $p>.999$).

A second ANOVA was performed on the factor Task (*Addition, Memory, Subtraction*) for the Arabic format conditions. This analysis revealed that type of task did not significantly influence RTs for the Arabic format ($p=.304$).

The third ANOVA was performed on the factor Format (*Dots, Arabic, Words, Colors, Characters*) in memory task conditions. This revealed that RTs significantly differed over formats ($F(4, 88)=35.01$, $p<.001$, $\eta_p^2=.614$). Participants were fastest for the Arabic and color format, followed by dots. Words and characters took the longest to react (post hoc Bonferroni corrected dependent *t*-tests, all $p\leq.020$, except for *Arabic* versus *Color*, and *Words* versus *Characters*: both $p>.999$).

2.1.3. Distracter distance effect

To identify the involvement of automatic magnitude processing upon detection of numerical information, we investigated a version of the distance effect for all number notations in both the addition and memory task. The distance effect refers to the finding that close numbers are more difficult to compare than distant numbers, which suggests that magnitude is internally represented as quantities along a mental number line. In line with the distance effect, we reasoned that if the internal magnitude system is automatically activated upon the detection of numbers, a distracter (i.e., the incorrect answer option) that is numerically closer to the correct answer will interfere more with selecting the correct answer, resulting in longer RTs. Since the two answer options were always either one or two distance apart, RTs were split out into close (± 1) and far (± 2) distracter answer options (Table 2).

A repeated measures ANOVA on mean RTs for all correctly responded trials with the factors Task (*Addition, Memory*), Format (*Dots, Arabic, Words*) and Distance (incorrect answer: *close, far*) revealed no three-way interaction for Task × Format × Distance ($p=.251$), and no two-way interaction for Task × Distance ($p=.149$). However, the two-way interaction between Distance and Format was significant ($F(2, 44)=5.31$, $p=.009$, $\eta_p^2=.194$), with the pattern showing a decreasing distracter distance effects from dots to Arabic to words. Further investigation with Task × Distance ANOVAs for each format separately, showed that there was a significant distracter Distance effect for dots only (main effect of

Table 1
Mean reaction times (+*SD*) in ms for the correct answers.

Task	Format				
	Dots	Arabic	Words	Colors	Characters
Addition	588 (91)	434 (58)	561 (66)	494 (64)	
Memory	472 (52)	433 (48)	511 (70)	427 (80)	514 (83)
Subtraction		445 (62)			

Note. $N=23$.

Table 2
Mean reaction times (+*SD*) in ms for the correct answers in the memory and addition tasks, split for distance of the incorrect answer.

Task	Format		
	Dots	Arabic	Words
Memory incorrect answer close	486 (56)	433 (50)	506 (80)
Memory incorrect answer far	453 (55)	436 (58)	517 (76)
Addition incorrect answer close	594 (91)	436 (64)	546 (68)
Addition incorrect answer far	578 (101)	432 (64)	583 (87)

Note. Close: incorrect answer option was 1 distance away from the correct answer; Far: incorrect answer option was 2 distances away from the correct answer; $N=23$.

distance: *Dots*: $F(1, 22)=6.33$, $p=.02$, $\eta_p^2=.223$; *Arabic:* $p>.945$; *Words*: $p=.054$), with slower RTs for close distracter trials. For none of the formats was the Task × Distance interaction significant (*Dots*: $p=.194$; *Arabic*: $p=.568$; *Words*: $p=.147$).

The pattern of data suggests that, for non-symbolic numbers there is an automatic processing of numerical magnitude, but not for the symbolic numbers. This implies that the non-symbolic numbers were processed as quantities rather than as symbols. Furthermore, the non-significant interaction between Task and Distance for dots suggests that the amount of magnitude processing for dots was equal for the addition and memory task. Therefore, it is less likely that differential brain activity for mental addition of the non-symbolic numbers is caused by higher magnitude processing for addition compared to memory in the response selection stage.

2.1.4. Questionnaire

Visual strategies, such as the use of mental images (e.g., mental visualization of the two addends on top of each other during addition), were more often reported for the dots, colors, and characters, whereas verbalization appeared to be more often reported for the Arabic numbers and number words. However, because we made use of open questions, the answers were difficult to quantify, and are therefore not reported further.

2.2. Imaging results

We used whole-brain analyses for investigating our hypotheses. Hereafter, the condition names are presented as follows: format (*Dot*; *Arabic*; *Word*; *Color*; *Character*) is combined with task (*add*(*ition*), *memory*; *subtraction*; *fixation*), for example $Arabic_{add}$ for *Arabic Addition*.

2.2.1. IPS regions are significantly more active for non-symbolic simple addition suggesting calculation processing

To reveal brain activity related specifically to the processes of adding and subtracting numbers, relevant images were created for each participant by contrasting each condition with its memory baseline (e.g., $Arabic_{add}$-$Arabic_{memory}$). These difference contrast images were subjected to second-level group analyses for investigation of the influence of number notation (non-symbolic: *Dots*; symbolic: *Arabic*, *Words*).

On the group level, a one-factor full factorial design was created to examine differential activity patterns for non-symbolic and symbolic addition. A conjunction analysis of $[(Dot_{add}\text{-}Dot_{memory})>(Arabic_{add}\text{-}Arabic_{memory})]$ and $[(Dot_{add}\text{-}Dot_{memory})>(Word_{add}\text{-}Word_{memory})]$ showed that, bilaterally, IPS involvement was significantly more pronounced for addition of non-symbolic numbers than for addition of symbolic numbers (Fig. 2 and Table 3). Additionally, activity was observed in frontal regions, such as the middle and inferior frontal gyrus. Further investigation with one-sample *t*-tests revealed that addition of dots (contrast: $Dot_{add}>Dot_{memory}$) was accompanied by activity increase across the entire IPS, bilaterally. However, addition of symbolic numbers (contrasts: $Arabic_{add}>Arabic_{memory}$; $Word_{add}>Word_{memory}$) revealed no suprathreshold cluster activity in the brain; neither did subtraction of Arabic numbers (contrast: $Arabic_{subtraction}>Arabic_{memory}$), nor did a direct contrast between Arabic subtraction and addition (contrast: $Arabic_{subtraction}>Arabic_{add}$). The above suggests that the IPS regions are involved in the mental manipulation of non-symbolic numerical information during simple arithmetic.

2.2.2. AG/perisylvian areas are significantly more active for simple addition of symbolic notations suggesting retrieval processing

Next, we investigated whether specific areas were more active for addition with symbolic number notations (*Arabic* and *Words*) than for addition with a non-symbolic number notation (*Dots*). On whole-brain level, a conjunction analysis of $[(Arabic_{add}\text{-}Arabic_{memory})>(Dot_{add}\text{-}Dot_{memory})]$ and $[(Word_{add}\text{-}Word_{memory})>(Dot_{add}\text{-}Dot_{memory})]$ revealed no suprathreshold clusters in the left AG for symbolic greater than non-symbolic addition. However, one-sample *t*-tests separately for the Arabic and Word relative to the Dot condition did reveal significant activations (contrasts: $[(Arabic_{add}\text{-}Arabic_{memory})>(Dot_{add}\text{-}Dot_{memory})]$; $[(Word_{add}\text{-}Word_{memory})>(Dot_{add}\text{-}Dot_{memory})]$). The left AG and posterior middle temporal gyrus were more active for Arabic addition (Fig. 3 and Table 4), and the left supramarginal and superior temporal gyrus were more active for word addition (Table 5) when contrasted with dot addition. Arabic addition and word addition did not reveal significant differential brain activity (contrasts: $[(Arabic_{add}\text{-}Arabic_{memory})>(Word_{add}\text{-}Word_{memory})]$; $[(Word_{add}\text{-}Word_{memory})>(Arabic_{add}\text{-}Arabic_{memory})]$).

We interpret above AG activity as reflecting more verbal fact retrieval for symbolic than for non-symbolic simple addition. Although the AG is known to be involved in semantic memory retrieval, it is also an area that is often reported to activate during self-generated thought (Andrews-Hanna et al., 2014). Thus an alternative interpretation is that the differences in AG activity between the conditions are driven by differences in mind-wandering (i.e., activation unrelated to the tasks). To exclude this possibility, for the main analyses above, we performed additional analyses with RT-difference values (i.e., shorter RTs reflecting longer mind-wandering opportunity) as a covariate of no interest. Even after controlling for possible activation related to mind-wandering, the patterns for mental addition (*Dots; Arabic; Words; Non-symbolic > Symbolic; Symbolic > Non-symbolic; Dots > Arabic; Dots > Words; Arabic > Dots; Words > Dots*) did not change. This supports our original interpretation, with AG activity reflecting verbal fact retrieval. Fig. 4 illustrates the pattern of activity among

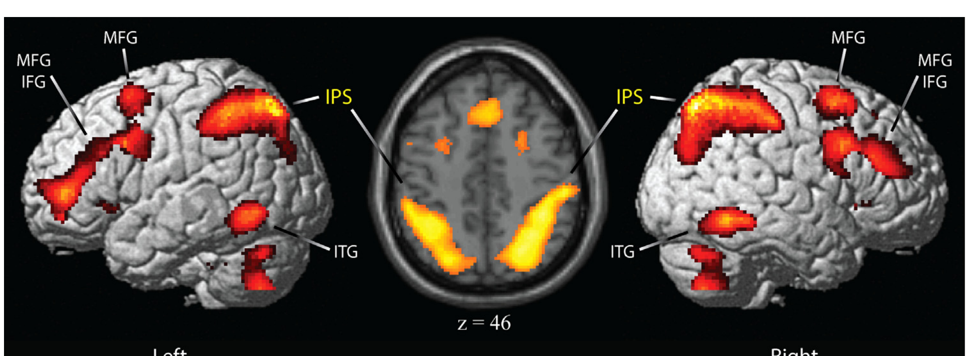

Fig. 2. Non-symbolic addition > symbolic addition. Activity greater for addition of non-symbolic (*Dots*) compared to symbolic numbers (*Arabic, Words*; a conjunction analysis of $[(Dot_{add}\text{-}Dot_{memory})>(Arabic_{add}\text{-}Arabic_{memory})]$ and $[(Dot_{add}\text{-}Dot_{memory})>(Word_{add}\text{-}Word_{memory})]$; $p<.001$, uncorrected, voxel level, for displaying purposes). IPS = intraparietal sulcus; MFG = middle frontal gyrus; IFG = inferior frontal gyrus; ITG = inferior temporal gyrus.

Table 3
MNI coordinates of activation peaks for non-symbolic compared to symbolic addition (conjunction analysis of *[(Dot$_{add}$-Dot$_{memory}$) > (Arabic$_{add}$-Arabic$_{memory}$)]* and *[(Dot$_{add}$-Dot$_{memory}$) > (Word$_{add}$-Word$_{memory}$)]*).

Cluster size	Cluster P_{FWE}	Voxel T value	x	y	z	Hem.	Brain area
7615	< .001	8.32	22	−72	52	R	Superior Parietal Lobule (hIP3)
		7.45	30	−68	34	R	Middle Occipital Gyrus (hIP1)
		7.24	28	−64	38	R	Superior Occipital Gyrus (hIP1)
		7.02	32	−56	44	R	Angular Gyrus (hIP3, hIP1)
		6.75	−14	−72	56	L	Superior Parietal Lobule
		6.74	40	−42	46	R	Inferior Parietal Lobule (hIP2, hIP3, hIP1)
		6.48	−38	−52	52	L	Inferior Parietal Lobule (hIP1, hIP3)
1651	< .001	6.26	−42	48	4	L	Middle Frontal Gyrus
		4.43	−42	36	16	L	Inferior Frontal Gyrus
		4.33	−56	12	36	L	Precentral Gyrus
		3.91	−42	52	−10	L	Middle Orbital Gyrus
1381	< .001	5.22	52	8	30	R	Precentral Gyrus
		4.84	50	34	24	R	Inferior Frontal Gyrus
		4.78	50	32	32	R	Middle Frontal Gyrus
1251	< .001	5.65	−40	−64	−48	L	Cerebellum
		4.72	8	−78	−28	R	Cerebellum
833	< .001	6.01	30	8	56	R	Middle Frontal Gyrus
790	< .001	6.58	40	−68	−50	R	Cerebellum
703	< .001	6.79	54	−54	−12	R	Inferior Temporal Gyrus
608	.001	5.28	−56	−58	−8	L	Inferior Temporal Gyrus
553	.001	5.59	−26	10	62	L	Middle Frontal Gyrus
535	.002	4.91	2	26	48	L	Medial Aspect of the Superior Frontal Gyrus
		4.82	−4	24	50	L	Supplementary motor area
		4.74	4	30	44	R	Medial Aspect of the Superior Frontal Gyrus

Note. Initially thresholded at $p < .001$ on voxel level uncorrected, $p < .05$ family wise error corrected (FWE), cluster level; the representative peak voxel of each brain area is reported; Hem. = Hemisphere; L = left; R = right; hIP = human intraparietal area.

the experimental conditions in the left IPS (upper left), the right IPS (upper right), and the AG (lower left).

2.2.3. *IPS activity does not appear magnitude specific*

For every participant, on the first level, we contrasted number format conditions with non-magnitude format conditions (*Colors*, *Characters*), and we used one-sample *t*-tests on the second level in order to investigate if IPS activity was magnitude (number) specific or not. As mentioned before, all analyses were performed on whole-brain level.

Color stimuli were included to investigate whether IPS activity is specifically related to mental manipulation of numerical magnitude. Similar to addition of dots, addition of colors activated bilateral IPS (contrast: *Color$_{add}$ > Color$_{memory}$*). These IPS areas overlapped with the activity found for mental addition of dots. Numerical addition did not activate the IPS to a greater degree than color addition, no matter what notation the numbers were in (contrasts: *[(Dot$_{add}$-Dot$_{memory}$) > (Color$_{add}$-Color$_{memory}$)]*; *[(Arabic$_{add}$-Arabic$_{memory}$) > (Color$_{add}$-Color$_{memory}$)]*; *[(Word$_{add}$-Word$_{memory}$) > (Color$_{add}$-Color$_{memory}$)]*).

Compared to memory of colors, the number notations generally did not show differential IPS activity (contrasts: *Arabic$_{memory}$ > Color$_{memory}$*; *Word$_{memory}$ > Color$_{memory}$*; *Color$_{memory}$ > Dot$_{memory}$*; *Color$_{memory}$ > Arabic$_{memory}$*; *Color$_{memory}$ > Word$_{memory}$*), but the non-symbolic notation (contrast: *Dot$_{memory}$ > Color$_{memory}$*) revealed greater activity in the right IPS.

Compared to characters in the memory task, none of the number types revealed significantly greater activation in the IPS regions (contrasts: *Dot$_{memory}$ > Character$_{memory}$*; *Arabic$_{memory}$ > Character$_{memory}$*; *Word$_{memory}$ > Character$_{memory}$*). On the contrary, there was significant bilateral IPS activity greater for characters than for symbolic numbers (contrasts: *Character$_{memory}$ > Arabic$_{memory}$*; *Character$_{memory}$ > Word$_{memory}$*). A comparison of characters greater than dots (contrast: *Character$_{memory}$ > Dot$_{memory}$*) did not yield differential activity in the IPS. Overall, it appears that the IPS regions are involved in memory of visually complex stimuli and in the mental visuospatial manipulation of information.

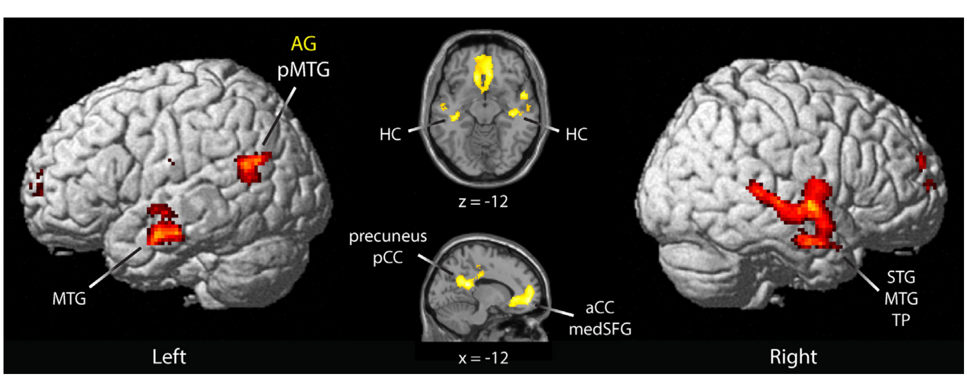

Fig. 3. Symbolic addition > non-symbolic addition. Activity greater for addition of symbolic (*Arabic*) compared to non-symbolic (*Dots*) numbers (*[(Arabic$_{add}$-Arabic$_{memory}$) > (Dot$_{add}$-Dot$_{memory}$)]*; initially thresholded at $p < .001$ on voxel level uncorrected, $p < .05$, FWE, cluster level). AG = angular gyrus; pMTG = posterior middle temporal gyrus; MTG = middle temporal gyrus; HC = hippocampus; pCC = posterior cingulate cortex; aCC = anterior cingulate cortex; medSFG = medial aspect of the superior frontal gyrus; SFG = superior frontal gyrus; TP = temporal pole.

Table 4
MNI coordinates of activation peaks for symbolic (Arabic) compared to non-symbolic addition *([(Arabic$_{add}$-Arabic$_{memory}$) > (Dot$_{add}$-Dot$_{memory}$)]).*

Cluster size	Cluster P_{FWE}	Voxel T value	x	y	z	Hem.	Brain area
3600	<.001	6.34	−8	56	−4	L	Mid Orbital Gyrus
		6.00	−2	24	−18	L	Rectal Gyrus
		5.89	6	58	−6	R	Mid Orbital Gyrus
		5.46	2	60	8	R	Medial Aspect of the Superior Frontal Gyrus
		5.20	−10	58	10	L	Medial Aspect of the Superior Frontal Gyrus
		5.15	−14	48	−2	L	Anterior Cingulate Cortex
		5.12	16	56	6	R	Superior Frontal Gyrus
1298	<.001	5.61	38	−22	−12	R	Hippocampus
		5.36	58	−18	−4	R	Superior Temporal Gyrus
		5.13	52	6	−14	R	Temporal Pole
		5.05	64	−2	6	R	Heschls Gyrus
		5.03	62	2	6	R	Rolandic Operculum
		5.01	40	−16	2	R	Insula
1194	<.001	5.38	−12	−52	24	L	Precuneus
		4.41	−4	−24	46	L	Posterior Cingulate Cortex
847	<.001	4.96	22	−46	10	R	Precuneus
533	.001	5.59	−44	−6	−4	L	Insula
		5.22	−54	−18	−18	L	Middle Temporal Gyrus
		5.03	−38	−26	−12	L	Hippocampus
		4.97	−54	−10	−16	L	Middle Temporal Gyrus
257	.025	4.96	−58	−58	20	L	Middle Temporal Gyrus (PGa)
		4.35	−44	−70	26	L	Angular Gyrus (PGp, PGa)

Note. Initially thresholded at $p < .001$ on voxel level uncorrected, $p < .05$ FWE, cluster level; the representative peak voxel of each brain area is reported; Hem.=Hemisphere; L=left; R=right.

3. Discussion

In reference to the theoretical model of Dehaene et al. (2003), in which IPS activity was suggested to reflect magnitude calculations and AG/perisylvian activity the verbal retrieval of arithmetic facts, we examined the influence of number notation on brain activity during simple arithmetic. As expected, the bilateral IPS was differentially involved, depending on number notation. Only for *non-symbolic* numbers (*Dots*) did IPS activity show an increase for addition compared to the non-addition (memory) baseline task. Conversely, for mental addition of *symbolic* numbers (*Arabic*, *Words*) there was more prominent activity in the AG/perisylvian areas than for non-symbolic numbers (*Dots*).

Furthermore, we investigated whether the observed IPS activity was specific to the magnitude domain (Dehaene et al., 2003) or indicative of more general processing such as visuospatial processing (e.g., Grefkes and Fink, 2005; Kravitz et al., 2011). We did not observe IPS activity specifically for magnitude information: the non-symbolic numbers (*Dots*) showed a similar degree of IPS activation as the non-magnitude operands (*Colors* for mental addition, *Characters* for memory), and for the symbolic numbers, IPS activity was generally smaller than for the non-magnitude operands.

Together, these results indicate that the answers to *non-symbolic* addition problems below 10 are calculated, whereas the answers to *symbolic* arithmetic problems below 10 are retrieved from verbal memory. Furthermore, the IPS seems to be involved in general visuospatial processing.

3.1. *The influence of notation on brain activity during simple arithmetic*

Number notation influenced neural activity during simple mental arithmetic in areas related to magnitude calculations (IPS) and verbal retrieval (AG/perisylvian areas). Simple mental addition of dots activated the entire bilateral IPS, including peak voxels that have been reported in meta-analyses concerning the representation of quantity (Arsalidou and Taylor, 2011; Dehaene et al., 2003). In contrast, simple addition with symbolic numbers activated the AG and perisylvian areas to a higher degree than non-symbolic addition, and these areas have been implicated in verbal retrieval (Cohen et al., 2000; Dehaene et al., 2003; Grabner et al., 2009).

Table 5
MNI coordinates of activation peaks for symbolic (Words) compared to non-symbolic addition *([(Word$_{add}$-Word$_{memory}$) > (Dot$_{add}$-Dot$_{memory}$)]).*

Cluster size	Cluster P_{FWE}	Voxel T value	x	y	z	Hem.	Brain area
898	<.001	5.84	6	56	8	R	Medial Aspect of the Superior Frontal Gyrus
		4.62	−10	50	−2	L	Anterior Cingulate Cortex
		4.43	−6	58	14	L	Medial Aspect of the Superior Frontal Gyrus
678	<.001	4.74	−8	−50	28	L	Posterior Cingulate Cortex
		4.08	−12	−62	30	L	Precuneus
		3.73	2	−52	24	R	Precuneus
594	.001	5.13	−50	−34	22	L	Superior Temporal Gyrus
		4.30	−42	−14	22	L	Rolandic Operculum
		3.99	−44	−28	24	L	Supramarginal Gyrus
		3.95	−36	−14	22	L	Insula Lobe
300	.018	6.26	50	−10	−12	R	Superior Temporal Gyrus
267	.028	5.49	−6	30	−4	L	Olfactory Cortex
		3.75	4	22	−6	R	Olfactory Cortex
		3.74	10	34	−2	R	Anterior Cingulate Cortex

Note. Initially thresholded at $p < .001$ on voxel level uncorrected, $p < .05$ FWE, cluster level; the representative peak voxel of each brain area is reported; Hem.=Hemisphere; L=left; R=right.

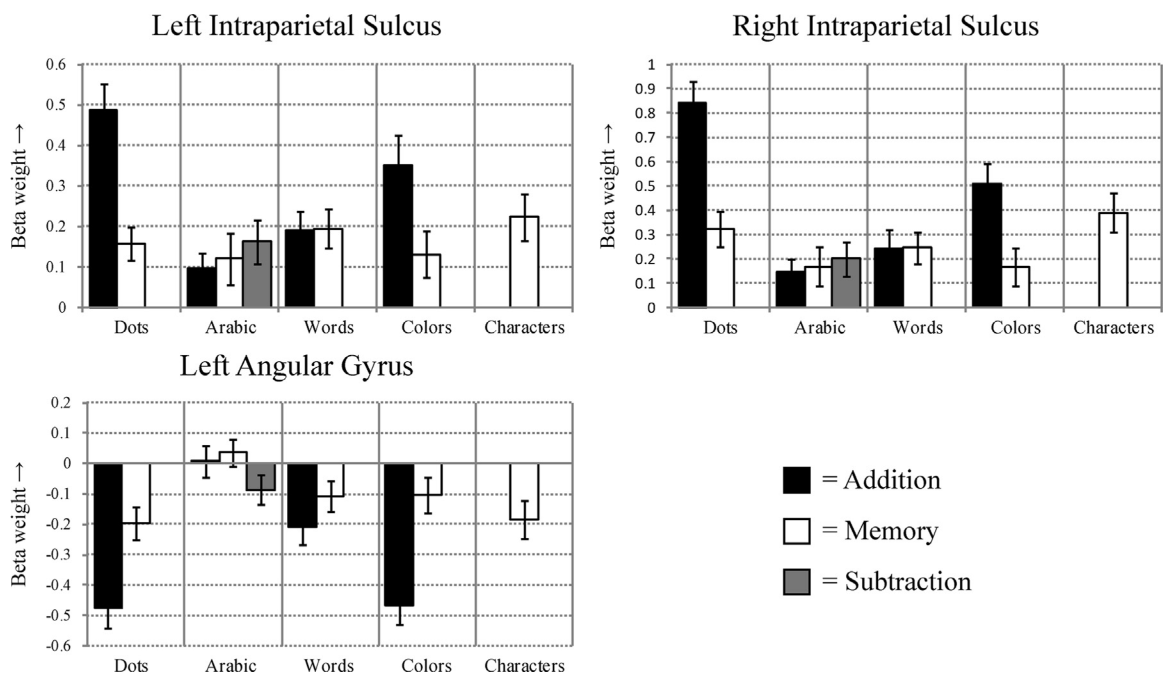

Fig. 4. Beta weights IPS regions & AG for each condition compared to fixation. Mean beta weight (+*SEM*) for each condition contrasted against the fixation baseline, extracted from three predefined ROIs: the left IPS (above left), the right IPS (above right), and the left angular gyrus (AG; below left). These regions of interest were only used to illustrate the pattern of data among the experimental conditions in previously reported areas of interest (Dehaene et al., 2003). We used whole-brain analyses for investigating our hypotheses.

3.1.1. More involvement of the IPS for simple addition of non-symbolic notations

IPS activity during simple mental arithmetic was greater for non-symbolic (*Dots*) than for symbolic number notations (*Arabic, Words*), which suggests a greater use of magnitude calculations for the non-symbolic notation. This finding complements behavioral data that suggest that the route used for solving sums is dependent on number notation (Campbell and Alberts, 2009; Campbell and Fugelsang, 2001; Campbell et al., 2004), but it appears to be in contrast with the fMRI study by Venkatraman et al. (2005). Venkatraman and colleagues stressed their finding on shared IPS activity for non-symbolic and symbolic addition, which could lead to the idea that IPS activity reflecting arithmetic is notation independent. Yet, Venkatraman and colleagues also reported greater bilateral IPS activity for mental addition of dots when contrasted to mental addition of Arabic numbers, which is in line with our finding on notation dependency and the idea that magnitude calculations are more often used for non-symbolic addition.

Contrary to Venkatraman and colleagues, we did not observe an IPS activity increase when the symbolic addition conditions were compared to their corresponding memory baseline. Possibly the IPS activity observed by Venkatraman et al. for Arabic addition is more indicative of general visuospatial processing, because their baseline task was not matched on the number of visual features (two numbers for the experimental versus one number for the control task). They speculate that the tasks were matched concerning visual demands, because no activation differences were observed between the experimental and control condition in the primary visual areas. However, this does not exclude the possibility of differential involvement of the IPS depending on the amount of numerical information. Indeed, Bulthé and colleagues observed that multi-voxel pattern analysis of a single digit was classified as one dot rather than eight dots, suggesting that the IPS response to Arabic numbers may be driven by the number of visual inputs (i.e., the number of digits) rather than the numerosity per se (Bulthé et al., 2015). Recently, Rosenberg-Lee et al. (2011) compared activity for different arithmetic operations performed on Arabic numbers. As in our study, they used single digit addition problems summing to less than 10, with a control task containing numbers, and participants from the university community. They also reported no significant activation increase in the IPS regions for Arabic addition. Note that the education level of our participant pool, which consisted of university students, may have played a role in the use of calculation/retrieval when solving simple arithmetic problems. It is possible that highly educated students have performed symbolic arithmetic relatively often and are therefore more familiar with arithmetic problems than the non-university population. Therefore, the high education level of our participant pool may have led to a relatively high amount of retrieval-based solutions, relying on AG processing, and a relatively low amount of magnitude calculations and IPS processing, especially for the symbolic conditions.

A remaining issue concerns the difference between subtraction and addition. Even though subtraction is thought to rely more on mental manipulations of quantity than addition (Campbell and Xue, 2001), we did not observe significantly increased activity in the IPS for simple subtraction of Arabic numbers, neither for a direct comparison of subtraction with addition. Rosenberg-Lee et al. (2011), who used inverses of the addition problems for subtraction, found that subtraction was accompanied by activations in the left IPS. On the contrary, Kawashima et al. (2004) did not observe significant activity differences anywhere in the adult brain when comparing one digit subtraction with one digit addition in Arabic format. Campbell (2008) suggested that small subtractions (minuend < 10) rely on direct memory retrieval. Our results allude to the idea that subtractions of small numbers, similar to addition of small numbers, are more likely solved via memory retrieval than via magnitude calculations.

3.1.2. More involvement of the AG/perisylvian areas for simple addition of symbolic notations

In favor of the interpretation that simple arithmetic with non-symbolic and symbolic numbers is qualitatively different, separate analyses showed that the AG and neighboring perisylvian areas –

i.e., the superior and middle temporal gyrus, and the supramarginal gyrus – were activated to a higher degree for simple addition of symbolic numbers (*Arabic, Words*) compared to non-symbolic numbers (*Dots*). It has been suggested that the left AG is part of the semantic memory system (Price, 2000) and responsible for retrieval of facts from verbal memory together with neighboring perisylvian areas (Dehaene et al., 2003; Grabner et al., 2009; Prado et al., 2011). Grabner et al. (2009) linked self reported arithmetic strategy with processing in the left AG and found that retrieval strategies showed greater left AG activity than calculation strategies. In line with these studies, our data indicate that simple symbolic arithmetic is solved via verbal retrieval.

The higher level of AG activity for symbolic compared to non-symbolic addition appears to be caused by a larger decrease in activity for addition compared to memory in dot format. In other words, for Arabic numbers and number words, the addition and memory tasks involved processing in the AG to a similar extend, whereas for dots there appears to be a difference between addition and memory. This supports the notion of qualitative differences in arithmetic depending on number notation; with symbolic addition being more closely aligned with memory based processing than non-symbolic addition.

Some of the areas that we observed to be more active for Arabic compared to Dot addition are part of the default mode network which may be active during the generation of inner thoughts or mind-wandering. However, even when activity increases related to shorter RTs (i.e., more opportunity for mind-wandering) were controlled for, the original pattern of activity did not change. Therefore, and since the brain activation pattern for semantic memory retrieval overlaps with regions in the default mode network (Wirth et al., 2011), we tentatively suggest that our activation pattern reflects processes related to the actual task.

Between the two symbolic notations, we did not observe differences in brain activity for mental addition, whereas the self reports in the behavioral study from Campbell and Alberts (2009) suggested more use of retrieval for Arabic than for word addition. It is possible that the two notations in our study differed on retrieval/calculation-based processing in a subset of the addition problems, but that this difference was obscured by retrieval-based processing in the majority of the problems. The brain pattern that we observed for number word addition was more similar to that of Arabic addition than dot addition. Perhaps, both Arabic numbers and number words generate verbal codes on the mental level (internal pronunciation of the problem) and thereby trigger verbal retrieval of the answer.

3.2. Magnitude specificity of the IPS: is calculation visuospatial in nature?

Contrary to our expectations, we did not observe IPS activity that was specific for (the manipulation of) numerical magnitudes. In general, the non-magnitude stimuli (*Characters, Colors*) activated the IPS to the same degree as the non-symbolic numbers (*Dots*) and to a larger degree than the symbolic numbers (*Arabic, Words*). Interesting to note is that for the conditions that evoked the greatest IPS activity, several participants reported the use of mental visual space, such as combining dot arrays in imagery for dot-addition, or placing the colors on top of each other or on the imagined "color wheel" for mixing of the colors. The Japanese characters were reported as being visually more complex, and because these were unfamiliar, participants could not rely on their verbal knowledge during the short retention period.

Together, these results suggest that the IPS regions are not specifically dedicated to numerical magnitude processing, but more generally to visual imagery. Differently put, calculation by manipulation of magnitudes appears visuospatial in nature. Shuman and Kanwisher (2004) also failed to find number specific IPS activity when compared with non-number (color) tasks and they argued against domain specificity of number processing in the IPS. It is well-known that spatial cognition relies on processing in the IPS (Kravitz et al., 2011). These findings can be reconciled by the realization that every magnitude, including numerical quantity, in theory, can be visualized in space. Other researchers have also noted the commonalities between magnitude and space. Hubbard and colleagues (Hubbard et al., 2005) suggested a link between numerical and spatial cognition, as did Fias and Fischer (2004). Walsh (2003) proposed that number, space and time are part of a common magnitude system, sharing neural resources. Future research could focus on how mental arithmetic relates to spatial cognition.

3.3. Beyond the IPS and AG, and limitations

Although the IPS and AG are areas of interest concerning arithmetic processing, other areas have been suggested to play a role (for overviews, see Arsalidou and Taylor, 2011; Menon et al., 2014). Apart from the IPS, we observed several frontal areas, such as the middle and inferior frontal gyrus, that were more active for non-symbolic than for symbolic addition. Activity in these areas could reflect working memory processes during calculation (Arsalidou and Taylor, 2011; Menon et al., 2014) when the answers cannot be directly retrieved from memory. For symbolic addition, the medial aspect of the superior frontal gyrus, the cingulate cortex and the precuneus showed heightened activity as compared to non-symbolic addition, which may reflect increased activation in the memory network (Wirth et al., 2011). For Arabic addition specifically, activity increases were observed in temporal areas, such as the middle temporal gyrus, the medial temporal lobe (hippocampus), and the temporal pole, when compared to non-symbolic addition. Similar to the AG, the left (posterior) middle temporal gyrus may be involved in verbal retrieval of arithmetic facts (Prado et al., 2011). Furthermore, recent evidence points to a role for both the hippocampus (Cho et al., 2011; Qin et al., 2014) and the temporal pole (Julien et al., 2008) in elementary arithmetic.

The dots were arranged in domino pattern to ensure that participants could directly see the amount instead of having to count. Because of the familiar pattern, the non-symbolic numbers might be considered iconic, like the symbolic numbers, and one could wonder if the non-symbolic dots were processed in a symbolic manner. This seems not to be the case, however. We found that, unlike the Arabic and word notation, dots showed a distracter distance effect (closer incorrect answer options resulted in longer RTs), suggesting automatic activation of the mental number line and processing in quantities rather than as symbols for the dot conditions.

In our study, single digit operations were performed by university students, and all stimuli were visual. Future research could investigate notation effects on mental addition of larger numbers, because if sums are not coded as facts in long-term memory, calculation related IPS activation may be also prominent for symbolic addition (cf. Fehr et al., 2007; Kong et al., 2005). In line with this idea, individuals with only rudimentary arithmetic skills, such as young children, are likely to depend on mental calculation, also for symbolic addition of simple sums. Another interesting venue is to use auditory cues to investigate whether IPS activation during simple arithmetic reflects supramodal processing or whether it is specific for visuospatial processing.

3.4. Conclusion

In conclusion, we report that non-symbolic number addition elicited higher levels of activation in the IPS than symbolic number addition, implying that mental quantity manipulation is used for non-symbolic number addition. In contrast, simple symbolic number addition showed a greater recruitment of the AG and perisylvian areas suggesting that answers were retrieved as facts from memory. Furthermore, the stronger activity in the IPS for the color and character conditions relative to the symbolic number conditions challenges the idea that processing in the IPS is magnitude specific. Our findings rather support the idea that magnitude manipulations take the form of mental visuospatial operations with this process reflected as an activity increase in the IPS. In short, for non-symbolic simple addition, magnitudes appear to be manipulated with visual imagery, whereas symbolic simple addition problems are solved via verbal retrieval.

4. Experimental procedure

4.1. Participants

Twenty-five, healthy, right handed, university students participated in the study. All gave written informed consent. Two participants were excluded from the analyses because of incidental findings in the structural scan of the brain. The mean age of the remaining 23 participants (8 males) was 21.04 years (*SD*=2.38). None of the participants reported to have reading problems. All participants had normal or corrected to normal vision without signs of color blindness, and all were native speakers of Dutch who were unfamiliar with Japanese katakana-characters. Participants received 12.50 euro or study credits for participation.

4.2. Tasks

Fig. 1 shows the tasks that participants performed in the MRI scanner. There were two main tasks (*Addition* and *Memory,* the latter acting as baseline condition) with five different formats: one format that represented non-symbolic magnitude (*Dots*), two formats that represented symbolic magnitude (*Arabic* and *Words*), and two other formats that did not represent magnitude (*Colors* and *Characters*). Addition was performed on all, except the characters. For the memory task, all five formats were included. Furthermore, for the Arabic numbers, an extra task was included, namely *Subtraction*. These combinations of tasks and formats resulted in 10 conditions. In case of the color format, the addition task required mixing of paint colors. For the memory task, participants were instructed to remember the number, color or character that the arrow was pointing to during the problem presentation and match that to one of the two answer options.

For all conditions, a trial started with presentation of the problem (250 ms). The problem was presented as two operands of the same format simultaneously, with a sign in between: + for Addition (e.g., 4+2 for *Arabic Addition*), ← or → for Memory (e.g., 4→2 for *Arabic Memory*), and − for Subtraction (e.g., 4−2 for *Arabic Subtraction*). The problem was followed by a fixation star (1200 ms), during which participants could reach the correct solution for the addition/subtraction tasks or keep the appointed stimulus in mind for the memory task. After this short delay, a correct and an incorrect answer were presented (500 ms) in the same format as the problem. Incorrect answers for number trials differed from the correct answers by a magnitude of either 1 or 2. Participants were required to select the correct answer within 1500 ms, by pressing the corresponding button. All participants responded with the left hand (middle finger for left answer, index finger for right answer), to keep motor related activity constant across participants. This choice was made such that the motor related response occurred in the right hemisphere, as to avoid a conflation of motor activity with left hemisphere dominant language activity. When a response was given, the bar beneath the selected answer would turn from grey to green, to let participants know which answer they had chosen. Location of the correct answers was pseudo-randomized such that half of the correct answers appeared on the left side of the screen and half on the right. The total duration of one trial was 2950 ms. Before every trial, a fixation star was presented for 400 ms, serving as inter-stimulus interval (ISI).

Five trials of the same condition composed one block. Every block was preceded by a 2000 ms announcement of the upcoming task (+++ for *Addition*, ←→ for *Memory*, −−− for *Subtraction*). A cycle consisted of 10 experimental blocks, one of each condition, shown in a randomized order. Within each cycle, a random two of these experimental blocks were preceded by a fixation block, with exception of the first experimental block that was always preceded by a fixation block that served as inter-cycle-interval. During fixation blocks, a fixation star was displayed for 17 s There were six cycles in total.

4.3. Materials

The numbers used in problems and answer options were from 1 to 9. They were presented as Arabic numbers, number words (in Dutch), or dot quantities (domino pattern). The dots were arranged in domino pattern to minimize serial counting. For addition and subtraction, 30 unique problems were chosen from 36 available combinations (excluded combinations were: *Addition*: 1+1, 2+2, 3+3, 4+4, 1+2, 2+1; *Subtraction*: 2−1, 3−1, 3−2, 4−1, 4−2, 4−3). The memory problems were created by changing the operator of a subset of the addition and subtraction problems into an arrow that pointed to the left or right. Each addition and memory problem occurred in each number notation. There were no problem repetitions within any of the experimental tasks. For all tasks, incorrect number options were pseudo-randomly selected, such that they fell within the 1–9 range and were either one (53%) or two distances (47%) away from the correct answer option.

Nine Japanese characters (ア, ク, コ, ス, キ, チ, ト, ネ, ヤ, レ) were paired in the same manner as the numbers in the *Memory* task (e.g., with ス instead of 4). The problems with the color stimuli (shown as color filled boxes) were selected such that they were easy to solve (tested in 4 pilot participants not included in this study). These were 30 unique combinations of primary colors, secondary colors, brown, and white (*n*: primary-primary=6; primary-secondary=10; primary-white=6; secondary-white=6; brown-white=2). Stimuli were created with Adobe Illustrator CS4 14.0.0 (Adobe Systems Incorporated) and the paradigm was presented using the software package Presentation (Neurobehavioral Systems, Albany, CA, USA).

A questionnaire was used to ask participants how they solved the problems during the fMRI-task. This questionnaire contained open questions, such as “What strategies did you use?” and “What did you do when you added the colors?”.

4.4. Procedure

Prior to the scanning session, participants underwent a short practice session (one cycle) on the computer outside the scanner, to become acquainted with the tasks. None of the practice trials appeared in the actual experiment. Participants were instructed to fixate on the center of the screen during the entire experiment. Presentation of both problems and answer options was within 10° horizontally in order to reduce eye movements. After the actual experiment, participants completed the questionnaire with open questions about how problems were solved.

4.5. MRI data acquisition

On a Siemens 3-Tesla MRI scanner (Siemens Trio TIM, Erlangen, Germany), equipped with a 32-channel head coil, functional scans were acquired with an echo-planar imaging (EPI) sequence: 35 T2*-weighted axial slices, slice thickness: 3.0 mm, slice gap: .30 mm, repetition time (TR): 2220 ms, echo time (TE): 30 ms, flip angle (FA): 80°, slice matrix: 64×64, field of view (FOV): 212 mm, in-plane resolution: 3.3×3.3 mm. After the task session, high-resolution anatomical images were acquired using a T1-weighted rapid acquisition gradient echo (MP-RAGE) sequence (192 sagittal slices, slice thickness: 1 mm, TR: 2300 ms, TE: 3.03 ms, FA: 8°, slice matrix: 256×256, FOV: 256 mm, voxel resolution: $1 \times 1 \times 1$ mm).

4.6. Data analyses

Data preprocessing and statistical analyses were performed using SPM8 (Statistical Parametric Mapping, Wellcome Department of Cognitive Neurology, London, U.K., http://www.fil.ion.ucl.ac.uk/). The first five EPI volumes of each participant's data set were discarded to allow for T1 equilibration. The remaining functional images were checked for spikes, realigned to the mean, coregistered to the structural image, spatially normalized to SPM8's Montreal Neurological Institute (MNI) T1 template, resampled into $2 \times 2 \times 2$ mm^3 voxels, and spatially smoothed with a Gaussian kernel of 8 mm full-width at half-maximum.

Data were statistically analyzed using general linear models (GLMs) as implemented in SPM8. Eleven explanatory variables were included in the model: 10 experimental conditions and fixation. The expected blood-oxygenation-level dependent (BOLD) response was modeled by convolving the canonical hemodynamic response function (HRF) provided by SPM8 for each block, starting at the "problem" presentation in the first trial, with a duration of 16.7 s. The design matrix also included the six head motion regressors (translations, rotations) to account for movement-related effects. For all participants movement was below 3 mm (from origin in x,y,z), except for two participants who moved 4.8 mm and 5.0 mm. A high pass filter was implemented using a cut-off period of 128 s to remove low-frequency effects from the time series.

Relevant contrast parameter images were generated for each participant and subsequently subjected to a second level analysis, treating participants as a random variable (Penny et al., 2003). Results of the second level analyses were initially thresholded at $p < .001$ (voxel level, uncorrected) followed by a cluster-level threshold of $p < .05$ FWE. For conjunction analysis, voxels that survived the initial threshold of $p < .001$ (voxel level, uncorrected) for all contrasts of interest were considered. The local maxima of significant clusters are reported in MNI-coordinates and the anatomical locations of these clusters were identified using the anatomy toolbox in SPM version 1.7 (Eickhoff et al., 2007; Eickhoff et al., 2005), which identifies three subdivisions of the IPS: the anterior human intraparietal areas 1 and 2 (hIP1 and hIP2; Choi et al., 2006) and the posterior human intraparietal area 3 (hIP3; Scheperjans et al., 2008); and two subdivisions of the AG: one anterior (PGa) and one posterior (PGp) (Caspers et al., 2006). Although the main analyses were all done on the whole brain level, since we were specifically interested in the areas reported to be involved in magnitude calculation (bilateral IPS) and fact retrieval (left AG), we created three regions of interest (ROIs) for displaying the mean beta estimates within these ROIs per condition. The coordinates reported by Dehaene et al. (2003) served as midpoints for 10 mm ROI spheres. Because the coordinates were reported in Talairach space, they were converted to MNI space with the transformation calculation formula provided by Brett and colleagues (Brett et al., 2001; Brett et al., 2002), resulting in MNI coordinates for the left IPS [−48, −44, 44], the right IPS [41, −46, 51], and the left AG [−48, −62, 29]. Although the AG is known to activate during memory retrieval, it also overlaps with the default mode network that shows higher activity during rest/mind-wandering (Greicius et al., 2003; Raichle et al., 2001; Wirth et al., 2011). If an increase in AG activity is due to mind-wandering rather than to task related processing then we would expect trials with short RTs (i.e., longer time to mind-wander) to contribute to an increase in this area. To exclude this possibility, we ran additional analyses for the main arithmetic contrasts controlling for activation that might arise due to short RTs. In practice, we included a regressor with RT-difference values, which reflects the difference in mind-wandering opportunity between the conditions, as a covariate of no interest on the second level. For example, in case of mental addition of Arabic numbers versus dots, the relevant contrast image was created per participant as: (*Arabic Addition-Arabic Memory)-(Dot Addition-Dot Memory);* and the relevant RT-difference value was calculated as: (*RT Arabic Addition-RT Arabic Memory)-(RT Dot Addition-RT Dot Memory)*.

Behavioral data (accuracy and RTs) were analyzed in PASW Statistics 18.0.0 (2009). For all statistical tests, a significance level of .05 was employed. RTs were measured from the onset of the presentation of the answer options until the response. When sphericity was violated, Greenhouse-Geisser estimates of sphericity were used to correct the degrees of freedom.

Acknowledgements

This research was supported by a Grant from National Initiative Brain and Cognition (NIHC; Grant number: 056-35-013).

References

Andrews-Hanna, J.R., Smallwood, J., Spreng, R.N., 2014. The default network and self-generated thought: component processes, dynamic control, and clinical relevance. Ann. N. Y. Acad. Sci. 1316, 29–52. http://dx.doi.org/10.1111/nyas.12360.

Arsalidou, M., Taylor, M.J., 2011. Is 2+2=4? Meta-analyses of brain areas needed for numbers and calculations. Neuroimage 54, 2382–2393. http://dx.doi.org/10.1016/j.neuroimage.2010.10.009.

Ashcraft, M.H., Christy, K.S., 1995. The frequency of arithmetic facts in elementary texts: Addition and multiplication in grades 1–6. J. Res. Math. Educ., 396–421. http://dx.doi.org/10.2307/749430.

Brett, M., Johnsrude, I.S., Owen, A.M., 2002. The problem of functional localization in the human brain. Nat. Rev. Neurosci. 3, 243–249. http://dx.doi.org/10.1038/nrn756.

Brett, M., Christoff, K., Cusack, R., Lancaster, J., 2001. Using the Talairach atlas with the MNI template. Neuroimage 13, 85.

Buckley, P.B., Gillman, C.B., 1974. Comparisons of digits and dot patterns. J. Exp. Psychol. 103, 1131. http://dx.doi.org/10.1037/h0037361.

Bulthé, J., De Smedt, B., Op de Beeck, H.P., 2015. Visual number beats abstract numerical magnitude: format-dependent representation of Arabic digits and dot patterns in the human parietal cortex. J. Cognit. Neurosci. 27, 1376–1387. http://dx.doi.org/10.1162/jocn_a_00787.

Campbell, J.I.D., 2008. Subtraction by addition. Mem. Cogn. 36, 1094–1102. http://dx.doi.org/10.3758/MC.36.6.1094.

Campbell, J.I.D., Xue, Q., 2001. Cognitive arithmetic across cultures. J. Exp. Psychol.: General. 130, 299–315. http://dx.doi.org/10.1037/0096-3445.130.2.299.

Campbell, J.I.D., Fugelsang, J., 2001. Strategy choice for arithmetic verification: effects of numerical surface form. Cognition 80, B21–B30. http://dx.doi.org/10.1016/S0010-0277(01)00115-9.

Campbell, J.I.D., Alberts, N., 2009. Operation-specific effects of numerical surface form on arithmetic strategy. J. Exp. Psychol.: Learn. Mem. Cogn. 35, 999–1011. http://dx.doi.org/10.1037/a0015829.

Campbell, J.I.D., Parker, H.R., Doetzel, N.L., 2004. Interactive effects of numerical surface form and operand parity in cognitive arithmetic. J. Exp. Psychol.: Learn. Mem. Cogn. 30, 51–64. http://dx.doi.org/10.1037/0278-7393.30.1.51.

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., Zilles, K., 2006. The human inferior parietal cortex: cytoarchitectonic parcellation and inter-individual variability. Neuroimage 33, 430–448. http://dx.doi.org/10.1016/j.neuroimage.2006.06.054.

Cho, S., Ryali, S., Geary, D.C., Menon, V., 2011. How does a child solve 7+8? Decoding brain activity patterns associated with counting and retrieval strategies.

Dev. Sci. 14, 989–1001. http://dx.doi.org/10.1111/j.1467-7687.2011.01055.x.
Choi, H.J., Zilles, K., Mohlberg, H., Schleicher, A., Fink, G.R., Armstrong, E., Amunts, K., 2006. Cytoarchitectonic identification and probabilistic mapping of two distinct areas within the anterior ventral bank of the human intraparietal sulcus. J. Comp. Neurol. 495, 53–69. http://dx.doi.org/10.1002/cne.20849.
Cohen, L., Dehaene, S., Chochon, F., Lehericy, S., Naccache, L., 2000. Language and calculation within the parietal lobe: a combined cognitive, anatomical and fMRI study. Neuropsychologia 38, 1426–1440. http://dx.doi.org/10.1016/S0028-3932(00)00038-5.
Cohen Kadosh, R., Lammertyn, J., Izard, V., 2008. Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. Prog. Neurobiol. 84, 132–147. http://dx.doi.org/10.1016/j.pneurobio.2007.11.001.
Dehaene, S., Piazza, M., Pinel, P., Cohen, L., 2003. Three parietal circuits for number processing. Cognit. Neuropsychol. 20, 487–506. http://dx.doi.org/10.1080/02643290244000239.
Dehaene, S., Molko, N., Cohen, L., Wilson, A.J., 2004. Arithmetic and the brain. Curr. Opin. Neurobiol. 14, 218–224. http://dx.doi.org/10.1016/j.conb.2004.03.008.
Eger, E., Sterzer, P., Russ, M.O., Giraud, A.-L., Kleinschmidt, A., 2003. A supramodal number representation in human intraparietal cortex. Neuron 37, 719–726. http://dx.doi.org/10.1016/S0896-6273(03)00036-9.
Eickhoff, S.B., Stephan, K.E., Mohlberg, H., Grefkes, C., Fink, G.R., Amunts, K., Zilles, K., 2005. A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. Neuroimage 25, 1325–1335. http://dx.doi.org/10.1016/j.neuroimage.2004.12.034.
Eickhoff, S.B., Paus, T., Caspers, S., Grosbras, M.-H., Evans, A.C., Zilles, K., Amunts, K., 2007. Assignment of functional activations to probabilistic cytoarchitectonic areas revisited. Neuroimage 36, 511–521. http://dx.doi.org/10.1016/j.neuroimage.2007.03.060.
Fehr, T., Code, C., Herrmann, M., 2007. Common brain regions underlying different arithmetic operations as revealed by conjunct fMRI–BOLD activation. Brain Res. 1172, 93–102. http://dx.doi.org/10.1016/j.brainres.2007.07.043.
Fias, W., Fischer, M.H., 2004. Spatial representation of numbers. In: Campbell, J.I. (Ed.), The Handbook of Mathematical Cognition. Psychology Press, New York, pp. 43–54.
Foltz, G.S., Poltrock, S.E., Potts, G.R., 1984. Mental comparison of size and magnitude: size congruity effects. J. Exp. Psychol.: Learn. Mem. Cogn. 10, 442–453. http://dx.doi.org/10.1037/0278-7393.10.3.442.
Grabner, R.H., Ansari, D., Koschutnig, K., Reishofer, G., Ebner, F., Neuper, C., 2009. To retrieve or to calculate? Left angular gyrus mediates the retrieval of arithmetic facts during problem solving. Neuropsychologia 47, 604–608. http://dx.doi.org/10.1016/j.neuropsychologia.2008.10.013.
Grefkes, C., Fink, G.R., 2005. REVIEW: The functional organization of the intraparietal sulcus in humans and monkeys. J. Anat. 207, 3–17. http://dx.doi.org/10.1111/j.1469-7580.2005.00426.x.
Greicius, M.D., Krasnow, B., Reiss, A.L., Menon, V., 2003. Functional connectivity in the resting brain: a network analysis of the default mode hypothesis. Proc. Natl. Acad. Sci. 100, 253–258. http://dx.doi.org/10.1073/pnas.0135058100.
Hubbard, E.M., Piazza, M., Pinel, P., Dehaene, S., 2005. Interactions between number and space in parietal cortex. Nat. Rev. Neurosci. 6, 435–448. http://dx.doi.org/10.1038/nrn1684.
Julien, C., Thompson, J., Neary, D., Snowden, J., 2008. Arithmetic knowledge in semantic dementia: Is it invariably preserved? Neuropsychologia 46, 2732–2744. http://dx.doi.org/10.1016/j.neuropsychologia.2008.05.010.
Kawashima, R., Taira, M., Okita, K., Inoue, K., Tajima, N., Yoshida, H., Sasaki, T., Sugiura, M., Watanabe, J., Fukuda, H., 2004. A functional MRI study of simple arithmetic—a comparison between children and adults. Cognit. Brain Res. 18, 227–233. http://dx.doi.org/10.1016/j.cogbrainres.2003.10.009.
Kirk, E.P., Ashcraft, M.H., 2001. Telling stories: the perils and promise of using verbal reports to study math strategies. J. Exp. Psychol.: Learn. Mem. Cogn. 27, 157–175. http://dx.doi.org/10.1037/0278-7393.27.1.157.
Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., Gollub, R., 2005. The neural substrate of arithmetic operations and procedure complexity. Cognit. Brain Res. 22, 397–405. http://dx.doi.org/10.1016/j.cogbrainres.2004.09.011.
Kravitz, D.J., Saleem, K.S., Baker, C.I., Mishkin, M., 2011. A new neural framework for visuospatial processing. Nat. Rev. Neurosci. 12, 217–230. http://dx.doi.org/10.1038/nrn3008.
LeFevre, J.-A., Sadesky, G.S., Bisanz, J., 1996. Selection of procedures in mental addition: Reassessing the problem size effect in adults. J. Exp. Psychol.: Learn. Mem. Cogn. 22, 216–230. http://dx.doi.org/10.1037/0278-7393.22.1.216.
McCloskey, M., Macaruso, P., 1995. Representing and using numerical information. Am. Psychol. 50, 351–363. http://dx.doi.org/10.1037/0003-066X.50.5.351.
Menon, V., Cohen Kadosh, R., Dowker, A., 2014. Arithmetic in the Child and Adult Brain. Oxford University Presshttp://dx.doi.org/10.1093/oxfordhb/9780199642342.013.041.
Moyer, R.S., Landauer, T.K., 1967. Time required for judgements of numerical inequality. Nature 215, 1519–1520. http://dx.doi.org/10.1038/2151519a0.
Penny, W.D., Holmes, A., Friston, K., 2003. Random effects analysis. Hum. Brain Funct. 2, 843–850.
Piazza, M., Pinel, P., Le Bihan, D., Dehaene, S., 2007. A magnitude code common to numerosities and number symbols in human intraparietal cortex. Neuron 53, 293–305. http://dx.doi.org/10.1016/j.neuron.2006.11.022.
Piazza, M., Izard, V., Pinel, P., Le Bihan, D., Dehaene, S., 2004. Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron 44, 547–555. http://dx.doi.org/10.1016/j.neuron.2004.10.014.
Pinel, P., Dehaene, S., Riviere, D., LeBihan, D., 2001. Modulation of parietal activation by semantic distance in a number comparison task. Neuroimage 14, 1013–1026. http://dx.doi.org/10.1006/nimg.2001.0913.
Prado, J., Mutreja, R., Zhang, H., Mehta, R., Desroches, A.S., Minas, J.E., Booth, J.R., 2011. Distinct representations of subtraction and multiplication in the neural systems for numerosity and language. Hum. Brain Mapp. 32, 1932–1947. http://dx.doi.org/10.1002/hbm.21159.
Price, C.J., 2000. The anatomy of language: contributions from functional neuroimaging. J. Anat. 197, 335–359. http://dx.doi.org/10.1046/j.1469-7580.2000.19730335.x.
Qin, S., Cho, S., Chen, T., Rosenberg-Lee, M., Geary, D.C., Menon, V., 2014. Hippocampal-neocortical functional reorganization underlies children's cognitive development. Nat. Neurosci. 17, 1263–1269. http://dx.doi.org/10.1038/nn.3788.
Raichle, M.E., MacLeod, A.M., Snyder, A.Z., Powers, W.J., Gusnard, D.A., Shulman, G. L., 2001. A default mode of brain function. Proc. Natl. Acad. Sci. 98, 676–682. http://dx.doi.org/10.1073/pnas.98.2.676.
Rosenberg-Lee, M., Chang, T.T., Young, C.B., Wu, S., Menon, V., 2011. Functional dissociations between four basic arithmetic operations in the human posterior parietal cortex: a cytoarchitectonic mapping study. Neuropsychologia 49, 2592–2608. http://dx.doi.org/10.1016/j.neuropsychologia.2011.04.035.
Scheperjans, F., Hermann, K., Eickhoff, S.B., Amunts, K., Schleicher, A., Zilles, K., 2008. Observer-independent cytoarchitectonic mapping of the human superior parietal cortex. Cereb. Cortex 18, 846–867. http://dx.doi.org/10.1093/cercor/bhm116.
Shrager, J., Siegler, R.S., 1998. SCADS: a model of children's strategy choices and strategy discoveries. Psychol. Sci. 9, 405–410. http://dx.doi.org/10.1111/1467-9280.00076.
Shuman, M., Kanwisher, N., 2004. Numerical magnitude in the human parietal lobe: tests of representational generality and domain specificity. Neuron 44, 557–569. http://dx.doi.org/10.1016/j.neuron.2004.10.008.
Simon, O., Mangin, J.-F., Cohen, L., Le Bihan, D., Dehaene, S., 2002. Topographical layout of hand, eye, calculation, and language-related areas in the human parietal lobe. Neuron 33, 475–487. http://dx.doi.org/10.1016/S0896-6273(02)00575-5.
Smith-Chant, B.L., LeFevre, J.-A., 2003. Doing as they are told and telling it like it is: self-reports in mental arithmetic. Mem. Cogn. 31, 516–528. http://dx.doi.org/10.3758/BF03196093.
Venkatraman, V., Ansari, D., Chee, M.W., 2005. Neural correlates of symbolic and non-symbolic arithmetic. Neuropsychologia 43, 744–753. http://dx.doi.org/10.1016/j.neuropsychologia.2004.08.005.
Verguts, T., Fias, W., 2004. Representation of number in animals and humans: a neural model. J. Cognit. Neurosci. 16, 1493–1504. http://dx.doi.org/10.1162/0898929042568497.
Walsh, V., 2003. A theory of magnitude: common cortical metrics of time, space and quantity. Trends Cognit. Sci. 7, 483–488. http://dx.doi.org/10.1016/j.tics.2003.09.002.
Wirth, M., Jann, K., Dierks, T., Federspiel, A., Wiest, R., Horn, H., 2011. Semantic memory involvement in the default mode network: a functional neuroimaging study using independent component analysis. Neuroimage 54, 3057–3066. http://dx.doi.org/10.1016/j.neuroimage.2010.10.039.