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How number line estimation skills relate to neural activations in single digit subtraction problems

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Abstract

The Number Line (NL) task requires judging the relative numerical magnitude of a number and estimating its value spatially on a continuous line. Children's skill on this task has been shown to correlate with and predict future mathematical competence. Neurofunctionally, this task has been shown to rely on brain regions involved in numerical processing. However, there is no direct evidence that performance on the NL task is related to brain areas recruited during arithmetical processing and that these areas are domain-specific to numerical processing. In this study, we test whether 8- to 14-year-old's behavioral performance on the NL task is related to fMRI activation during small and large single-digit subtraction problems. Domain-specific areas for numerical processing were independently localized through a numerosity judgment task. Results show a direct relation between NL estimation performance and the amount of the activation in key areas for arithmetical processing. Better NL estimators showed a larger problem size effect than poorer NL estimators in numerical magnitude (i.e., intraparietal sulcus) and visuospatial areas (i.e., posterior superior parietal lobules), marked by less activation for small problems. In addition, the direction of the activation with problem size within the IPS was associated to differences in accuracies for small subtraction problems. This study is the first to show that performance in the NL task, i.e. estimating the spatial position of a number on an interval, correlates with brain activity observed during single-digit subtraction problem in regions thought to be involved numerical magnitude and spatial processes.

Keywords

number line task; single-digit subtraction; arithmetic skill; numerical representation; brain-behavior analysis; fMRI; children; intraparietal sulcus; posterior superior parietal lobule

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1. Introduction

Mathematical skill predicts later academic achievement more strongly than early reading and socio-emotional skills (Duncan et al., 2007; US National Mathematics Advisory Panel, 2008). Therefore understanding individual differences has become a central research question for educational policies. Several studies suggest that differences in arithmetical performance are related to neural activations specific for numerical processing (De Smedt et al., 2013, 2011; Price et al., 2007).

A widely used numerical task that has shown to be predictive of future mathematical skill is the Number Line (NL) task (Booth & Siegler, 2006; Cowan & Powell, 2014; Siegler & Booth, 2004; Siegler & Opfer, 2003). This task requires both numerical magnitude and spatial processing since participants are asked to estimate the position of a given number (e.g., 21) onto a black horizontal line with the left and right ends labeled as 0 and 100 (or 1000), respectively. Younger children who have a less precise representation of numerical values overestimate small numbers and underestimate larger ones. Linearity is initially acquired for smaller ranges and progressively, with age and increasing number knowledge, linearity is extended to larger ranges (Berteletti et al., 2010; Siegler and Booth, 2004; Siegler et al., 2009). Performance on the NL task correlates with other estimation tasks (Booth & Siegler, 2006; Laski & Siegler, 2007), improves following interventions on children's linear and cardinal understanding of the numerical sequence (Ramani and Siegler, 2008; Siegler and Ramani, 2008), and is correlated with and is predictive of arithmetic learning and mathematical achievement (Booth & Siegler, 2008; Link, Nuerk, & Moeller, 2014; Linsen, Verschaffel, Reynvoet, & De Smedt, 2014; Ostergren & Träff, 2013; Sasanguie, Göbel, Moll, Smets, & Reynvoet, 2013; Schneider, Grabner, & Paetsch, 2009). Performance is also impaired or delayed in children with math learning difficulty (Geary et al., 2008; Landerl, 2013). Importantly, improving children's performance on the NL task enhances performance in numerical magnitude processing tasks as well as facilitates learning of multi-digit addition problems (Booth and Siegler, 2008; Kucian et al., 2011). Because the NL task has been shown to be a strong and unique predictor of arithmetical ability in grades 1 and 2 over and above other non-symbolic and symbolic tasks (Lyons et al., 2014), and because the NL tasks were correlated to mental multi-digit subtraction performance (Linsen et al., 2014), it can be argued that the NL task is specifically calling upon numerical processes that are crucial for later acquisition of mathematical competences. Two types of functional processes involved in the number line task might explain the relationship with mathematical performance and in particular with subtraction problems. First in both tasks, the symbolic numbers need to elicit the numerical magnitude representation. This allows for a comparison between the symbolic numbers: in the subtraction task, the two digits need to be compared to determine the result; in the number line task, the number to position has to be compared to the numerical boundaries of the interval to determine it's relative numerical magnitude. Second, both tasks call upon visuo-spatial processes. For the number line task, the symbolic number that has to be estimated has to be translated into a visual segment. To do this, children need to focus first on the entire interval and then move their attention along the line to estimate the position. Subtraction tasks have also been shown to rely on visuo-spatial processes (Dehaene et al., 2003; Knops and Willmes, 2014; Knops et al., 2009; Rotzer et al., 2009), and visuo-spatial proficiency has been shown to predict arithmetic performance in children (De Smedt et al., 2009; Rotzer et al., 2009). This result may be explained by the observation that efficient strategies rely on mechanisms that involve shifts of spatial attention (Knops et al., 2009). Indeed, studies have shown that subtraction and addition problems lead to under- and over-estimation and this Operational Momentum effect has been explained in terms of attentional shifts on a spatially organized mental representation of numbers (Knops et al., 2014, 2013, 2009) as if quantities were represented in the format of an internal mental number line (Hubbard et al., 2005; Rotzer et al., 2009).

From a neurofunctional perspective, processing of numerical magnitudes has been identified in the parietal lobes and more specifically in the bilateral intraparietal sulcus (IPS; Ansari, 2008; Nieder & Dehaene, 2009; Piazza et al., 2004; Piazza, Pinel, Le Bihan, & Dehaene, 2007; see Arsalidou & Taylor, 2011 for a meta-analysis). This area is sensitive to the distance effect in digit comparison tasks both for children and adults (Mussolin et al., 2010; Pinel et al., 2001) as well as being less sensitive in children with mathematical learning disability (Mussolin et al., 2010). The IPS is also found to be more active in calculation tasks compared to reading numerical symbols (Burbaud et al., 1999; Chochon et al., 1999; Pesenti et al., 2000), and more active for larger compared to smaller arithmetical problems (Ashkenazi et al., 2012; De Smedt et al., 2011). Moreover, the IPS shows greater activation during subtraction than multiplication (Chochon et al., 1999; Ischebeck et al., 2006; Prado et al., 2014, 2011) likely due to the fact that subtraction problems rely more on calculation procedures (Fayol and Thevenot, 2012) and quantity processing compared to multiplication problems (Dehaene et al., 2003; Prado et al., 2014, 2011).

Another parietal area often active in tasks requiring numerical manipulation is the posterior superior parietal lobule (PSPL) with mesial extension into the precuneus (PCu; Arsalidou & Taylor, 2011; Dehaene et al., 2003; Kaufmann, Wood, Rubinsten, & Henik, 2011). This area is active during number comparison (Pesenti et al., 2000; Pinel et al., 2001), approximation (Dehaene et al., 1999), subtraction of two digits (Knops et al., 2009; Lee, 2000), and counting (Piazza et al., 2002). Increased activation is found for more complex operations (Menon et al., 2000), and for subtraction problems compared to multiplication problems (Prado et al., 2014, 2011). However, this region also plays a role in several visuospatial tasks such as reaching, grasping, eye and/or attention orienting, mental rotation, and spatial working memory (Hubbard et al., 2005; Knops et al., 2009; Simon et al., 2004, 2002). Knops et al., (2009) investigated the relation between eye movement and arithmetic processing in adults using fMRI. They trained a multivariate classifier on saccade-related activity in the PSPL and were able to predict the type of mental operation (i.e., addition of subtraction), irrespective of notation (i.e., symbolic or non-symbolic). The authors suggest that mental arithmetic recruits parietal areas that are associated to visuospatial processing and that mental calculation may (at least partially) rely on the dynamic interplay between subsystems of the parietal cortex (i.e., IPS and PSPL).

On the one hand, imaging studies indicate that different subsystems in the parietal cortex (i.e., IPS for numerical magnitude and PSPL for visuospatial components of numerical and arithmetical processing) support mental calculation and, on the other hand, performance to the NL task is correlated and predictive of future arithmetic skill. However, to our knowledge, there is no direct evidence that estimating the position of a number on a line is related to functional areas used for calculation. Only two studies investigate the neural bases of the NL task. The first study investigated whether an intervention program using a NL-like game induces neurofunctional changes in areas involved in judging the relative magnitude of digits (Kucian et al., 2011). The game was intended to improve both estimation and arithmetical skills (i.e., numbers, sets of dots and arithmetical results had to be positioned on lines) in 9-year-old children with and without mathematical difficulty. Performance to the NL task was significantly improved for both groups. Using fMRI, children were required to judge whether triplets of digits were in ascending order. Training resulted in decreased activation in left IPS along with frontal areas, suggesting an increased efficiency in performing the task. Although these results support the effectiveness of the intervention, the authors showed improvement in magnitude judgment and not in arithmetical processing. The second study, using fMRI, investigates the brain regions involved during a classical NL task and a brightness estimation line task (i.e., continuous magnitude judgment) using shades of gray (Vogel et al., 2013). Results indicated some overlap in the right posterior part of IPS but, most importantly, the bilateral anterior part of IPS was specifically recruited for estimating symbolic numbers. This study is the first that directly investigates the NL task in an imaging paradigm and shows activations in areas typically involved in numerical magnitude processing. Unfortunately, no direct relation between these activations and arithmetical performance was investigated.

In the present study, we test whether performance on the NL task is related to activation found during simple arithmetical processing and if this relation relies on domain-specific processes. This would bring neuro-functional evidence to the behavioral relation found between performance to the NL task and arithmetic skill. We therefore collected behavioral performance on the NL task and functional (fMRI) data during a single-digit subtraction task in 8- to 14-years-old children. In this age range, arithmetical learning and estimation abilities are still improving (e.g., Holloway & Ansari, 2009; Siegler & Booth, 2004) increasing the chance of observing a relation between the two tasks. We chose single-digit subtraction problems because they have shown to rely more on quantitative manipulation compared to other arithmetical operations (Dehaene, 1992; Dehaene et al., 2003; Fayol and Thevenot, 2012; Prado et al., 2014, 2011). In support of this, the symbolic distance effect, that is the ability to determine which of two digits is numerically larger, was found to be specifically related to subtraction problems in children (Lonnemann et al., 2011). To isolate domain-specific areas involved in numerical processing, participants were also asked to perform a numerosity judgment task in the scanner (i.e., numerical comparison of sets of dots). Parietal areas activated by this task were then used as regions of interest (ROI) to investigate the relation between performance on the NL task and activation to the subtraction task. Indeed, the parietal cortex, and specifically the IPS, has shown modulation of activation specifically to changes in numerical information (Cantlon et al., 2006; Piazza et al., 2004).

Within the numerical processing areas, we expected to find a significant relation of performance on the NL task with bilateral IPS activation. The IPS responds specifically to magnitude information required in both the NL task and the Subtractions task (Piazza et al., 2004). Specifically, we expected children with better NL estimation abilities to show greater activation for larger compared to smaller problems (De Smedt et al., 2011; Stanescu-Cosson et al., 2000) indicating greater quantity manipulation for more effortful and less well learned problems. Because children in our study are still learning, only small problems are likely to be adequately mastered thus showing less activation compared to larger problems (Delazer et al., 2003; Ischebeck et al., 2007, 2006). However, children with lower NL estimation abilities were expected to not show a problem size effect: children with lower arithmetical skill have shown less modulation with problem size or even an atypical reversed modulation (De Smedt et al., 2011). Additionally, because the NL task requires transposing into space a numerical value and moving visuo-spatial attention along the physical line, we expected to find a relation within the bilateral PSPL. The PSPL has been found to support different aspects of spatial processing in numerical tasks (Kaufmann et al., 2011; Knops et al., 2009; Lee, 2000; Pinel et al., 2001). In particular, common activation of bilateral PSPL was found for arithmetic problems and shifts of visuo-spatial attentions (Knops et al., 2009). Increased activity in subtraction problems was found for older compared to younger children (Prado et al., 2014) suggesting an increasing reliance on such processes with greater expertise. Moreover, a modulation of activation was found in the PSPL for more complex problems (Menon et al., 2000). Because spatial processes are engaged more in participants with greater expertise and because larger problems can be seen as more complex for children that are still learning, we expected participants with finer ability in estimating the position on the number line task to show greater reliance on PSPL.

2. Materials and Methods

2.1. Participants

Thirty-nine children (22 females, 17 males) between 8 and 13 years of age (mean age=11: 4, SD=1: 6, range= 8:5-13:7) were chosen based on standardized testing performance and fMRI scan quality. All participants had a full-scale IQ standard score greater than 85 on the Wechsler Abbreviated Scale of Intelligence (WASI; Wechsler, 1999) with a group average of 118 (SD=11.3). To ensure participants had no mathematical difficulty, children had to score 85 or above (mean=105.2, SD=11.4) on the Math Fluency (MF) subtest of the Woodcock-Johnson III (Woodcock, McGrew & Mather, 2001). In this task, participants have three minutes to solve one-digit addition, subtraction, and multiplication problems. A timed task was chosen because it is an index of automaticity of procedural strategies and penalizes children that rely on lengthy and immature back-up strategies (Fayol and Thevenot, 2012; Russell and Ginsburg, 1984). Finally, to be included, accuracy to the fMRI tasks had to be 60% or higher. We do acknowledge that the unequal distribution of our true and false trials introduces a response bias towards false alarms that may not be detected.

2.2. Tasks

Number Line Task—As a behavioral measure of numerical ability, participants performed the NL estimation task on a computer. This task required participants to estimate the position of 22 numbers (i.e., 2, 5, 18, 34, 56, 78, 100, 122, 147, 150, 163, 179, 246, 266, 486, 606, 722, 725, 738, 754, 818 and 938) presented one at a time on a black line that had 0 and 1000 as endpoints. Each number was presented centrally above the line. There was no response time limit and no feedback was given. Participants were allowed to adjust their response before giving final confirmation. The NL estimation error was indexed using the mean percent absolute error (PAE) for each participant. The estimated position was calculated in millimeters and transformed to the nearest whole number then the standard formula from Booth and Siegler (2006) was used where smaller values index greater imprecision:

$$PAE = (\text{estimate} - \text{estimated quantity})/1000$$

fMRI Tasks—Participants also performed a Subtraction and a Numerosity task in the fMRI scanner. Based on the existing literature, we selected 12 small and 12 large problems (Campbell and Xue, 2001; Prado et al., 2011; Seyler et al., 2003; Siegler, 1989). Small problems were characterized by a small difference between the minuend and the subtrahend regardless of the size of the minuend (e.g., 4-3). Large problems were characterized by a large difference between the terms (e.g., 8-3). Participants saw a problem and judged whether the proposed answer was correct. There were 12 small and 12 large problems and each was repeated twice with a true answer and once with a false answer, yielding 72 trials for each problem type (36 small problems and 36 large problems). False answers were generated either by adding 1 or 2 (e.g., 6-2=5), or subtracting 1 (e.g., 6-2=3) from the correct answer to balance between parity match and distance from the correct answer. Indeed, creating only false answers that matched for parity could have facilitated an estimation strategy for rejecting distant answers. Twenty-four null trials were included to control for motor responses. In these trials participants had to respond when a blue fixation square turned red. Problems involving 0 (e.g., 6-0), 1 as the second term (e.g., 7-1), and ties (e.g., 4-4; 4-2) were excluded from the experiment but were used for practice purposes (i.e., twelve true and twelve false problems).

For the Numerosity task, participants were presented with two consecutive sets of dots and had to judge which set was numerically larger ignoring perceptual cues. In half of the trials the first set was numerically larger such that the following ratios were distributed equally among trials (i.e., 24 trials for each ratio): 0.33 (i.e., 12 dots vs 36 dots), 0.5 (i.e., 18 dots vs 36 dots), or 0.66 (i.e., 24 dots vs 36 dots). The stimuli were the same as those used in several previous studies (Berteletti et al., 2014; Demir et al., 2014; Prado et al., 2014, 2011). To ensure that participants based their judgment of differences in numerosity rather than cumulative area, six different dot sizes were used. However, totally equating the cumulative surface area between small and large arrays by entirely biasing the distribution of single dot sizes would have made it possible for the subjects to use single dot sizes as a cue for their judgment. Therefore, we found a trade-off (50% bias) between equating as much as possible (1) the cumulative surface areas and (2) the distributions of single dot sizes in each pair. In addition to the 72 total numerosity trials, participants also responded to 24 null trials. Furthermore, 12 different practice trials were run to familiarize the participants with the task outside the scanner.

2.3. Experimental Protocol

Participants were familiarized with tasks and the fMRI environment during a practice session after giving informed consent and having completed standardized testing. During this session, they learned to minimize head movement in a mock fMRI scanner by means of an infrared-tracking feedback device and practiced all tasks. This session was completed within a week prior to actual fMRI data acquisition. In the fMRI scanner, the Subtraction and the Numerosity tasks were split into two 4-minutes runs. The order of the tasks was counterbalanced across participants and the timing and order of trials within each run were optimized for estimation efficiency using optseq2 (http://surfer.nmr.mgh.harvard.edu/optseq/). Behavioral responses were recorded using an MR-compatible keypad placed in the right hand. Stimuli were generated using E-prime software (Psychology Software Tools, Pittsburgh, PA) and projected onto a translucent screen that was viewed through a mirror attached to the head-coil.

2.4. Stimulus Timing

Stimulus timing was identical for all tasks. The first stimulus was presented for 800 ms before being replaced by a blank screen for 200ms. The second stimulus was also presented for 800 ms, but was followed by a red fixation cross for 200 ms. The red square indicated the need to give a response during a variable interval ranging from 2800 ms to 3600 ms. Moreover, null trials were composed of a blue square that lasted for the same duration as the experimental conditions and participants had to press a button when it turned red. Finally, each run ended with 22 s of passive visual fixation.

2.5. fMRI Data Acquisition

Images were collected using a Siemens 3T TIM Trio MRI scanner (Siemens Healthcare, Erlangen, Germany) at CTI, Northwestern University's Center for Translational Imaging. The fMRI blood oxygenation level dependent (BOLD) signal was measured with a susceptibility weighted single-shot echo planar imaging (EPI) sequence. The following parameters were used: TE = 20 ms, flip angle = 80s, matrix size = 128 × 120, field of view = 220 × 206.25 mm, slice thickness = 3 mm (.48 mm gap), number of slices = 32, TR = 2000 ms. Before functional image acquisition, a high resolution T1 weighted 3D structural image was acquired for each subject (TR = 1570 ms, TE = 3.36 ms, matrix size = 256 × 256, field of view = 240 mm, slice thickness = 1 mm, number of slices = 160).

2.6. fMRI Preprocessing

Data analysis was performed using SPM8 (www.fil.ion.ucl.ac.uk/spm). After discarding the first six images of each run, functional images were corrected for slice acquisition delays, realigned to the first image of the first run and spatially smoothed with a Gaussian filter equal to twice the voxel size ($4 \times 4 \times 8$ mm^3 full width and half maximum). Prior to normalizing images with SPM8, we used ArtRepair (Mazaika, Hoeft, Glover, & Reiss, 2009; http://cibsr.standford.edu/tools/ArtRepair/ArtRepair.htm) to suppress residual fluctuations due to large head motion and to identify volumes with significant artifact and outliers relative to the global mean signal (i.e., 4% from the global mean). Volumes showing rapid scan-to-scan movements of greater than 1.5 mm were excluded via interpolation of the 2 nearest non-repaired volumes. Interpolated volumes were then partially deweighted when first-level models were calculated on the repaired images (Mazaika, Whitfield-Gabrieli, & Reiss, 2007). Finally, functional volumes were co-registered with the segmented anatomical image and normalized to the standard T1 Montreal Neurological Institute (MNI) template volume (normalized voxel size, $2 \times 2 \times 4$ mm^3). Scan quality was determined by the number of replacements in each functional run: up to 5% of replaced scans, but no more than 4 consecutive replacements, were accepted for each run.

2.7. fMRI Processing

Event-related statistical analysis was performed according to the general linear model (Josephs, Turner, & Friston, 1997). Activation was modeled as epochs with onsets time-locked to the presentation of the first stimulus and with a duration matched to the length of the trial (i.e., 2 s). For the Subtraction task, trials were classified for problem type (true, false) and for problem size (small, large). However, only true trials were considered of interest in behavioral and fMRI analyses because, for false trials it is impossible to determine if the answer was rejected by using a calculation procedure or relying on alternative strategies such as parity judgment or estimation (Lemaire and Reder, 1999). Moreover, during false trials, conflict detection and error monitoring processes would be affecting activation patterns (Ferdinand and Kray, 2014; Ullsperger et al., 2014; van Veen and Carter, 2006, 2002). For the Numerosity task, trials were classified for difficulty based on the ratio (i.e., easy, medium and hard). Null trials were further modeled in a separate regressor for each task. All epochs were convolved with a canonical hemodynamic response function. The time series data were high-pass filtered (1/128 Hz), and serial correlations were corrected using an autoregressive AR (1) model.

2.8. Region of Interest (ROI) Analyses

The Numerosity task was used to define the numerical processing network. Indeed, studies using a passive presentation of non-symbolic numerosities showed specific IPS activation only for ratio changes both in adults and children (Piazza et al., 2004; Cantlon, et al., 2006). Following our *a priori* anatomical hypotheses, we confined the ROI to the parietal lobes using the Talairach Daemon Atlas in SPM. For the numerosity task, activation from null trials was subtracted from activation from the test trials in order to exclude motor response activations. An uncorrected height threshold was set at $p<.005$ for the contrast maps and using Monte Carlo simulations (3dClustSim), extent threshold was deemed significant for 50 or more voxels ($p<.05$). Briefly, 3dClustSim (available as part of the AFNI fMRI analysis package, available at http://afni.nimh.nih.gov/afni/download) carries out a user-specified number of Monte Carlo simulations (10000 in this case) of random noise activations at a particular voxel-wise alpha level within a masked brain volume. The number of simulations in which clusters of various sizes appear within each volumetric mask is tallied among these simulations. These data are then used to calculate size thresholds across a range of probability values for that region. Cluster reaching these thresholds were therefore included in the ROI to run voxel-wise regression analyses for the Subtraction task.

2.9. Brain-behavior Analyses

A voxel-wise regression was run within the Numerical Processing ROI to investigate the relation between (a) the modulation of brain activation during the Subtraction task and (b) the quality of the numerical representation as established by performance on the NL task (PAE). Age and Math Fluency standard score were entered as control variables and NL estimation error as variable of interest for the Subtraction Large vs Small contrast. The same regression was also run on the whole brain excluding the Numerical Processing ROI to investigate this relation outside our *a priori* regions. Additionally, these significant clusters for the Subtraction task within the Numerical Processing ROI were used as a mask to investigate the relation between NL estimation error and the activation elicited by the numerosity processing in the Numerosity vs Null contrast. An uncorrected height threshold was set at $p<.005$ for the contrast maps and Monte Carlo simulations (3dClustSim) were used to set the extent threshold at $p<.05$. Statistical results are reported in the Montreal Neurological Institute (MNI) coordinate space. Anatomical localization was performed by transformation of the MNI coordinates into the Talairach stereotactic system of coordinates using the Talairach Client (Lancaster et al., 2000).

3. Results

3.1. Behavioral

For the NL task, the average estimation error (PAE) was 6.1% (SD= 5.7%). Groups were divided for higher and lower estimation error based on the median value: the lower NL estimation error group misjudged the position by 2.9% (SD=.9%, n=19), and the higher NL estimation error group misjudged by 9.4% (SD=6.7%, n=20). The two groups were significantly different after controlling for unequal variances ($t_{(19.6)}=-4.25$, $p<.001$).

For the Subtraction task, overall accuracy was 91% (SD=8 ms) and average RT to correct trials was 1082 ms (SD=361 ms). Separate repeated measures ANOVAS were run for accuracies and reaction times (RTs) with NL estimation error group (higher vs lower) as between-subject variable, problem size (small vs large) as within-subject variable and age as covariate. For accuracies, no effects were found (see Table 1). For RTs there were a main effect of problem size ($F_{(1,36)}=6.5$, $p<.05$) and of age ($F_{(1,36)}=8.9$, $p<.005$) indicating that larger problems were slower and, with increasing age, participants were faster.

For the Numerosity task, separate repeated measures ANOVAs were run on accuracies and RTs with NL estimation error group (higher vs lower) as between-subject variable, ratio as within-subject variable and age as covariate. Only the main effect of age on RTs was significant indicating that RTs decreased with increasing participants' age ($F_{(1,36)}=4.41$, $p<.05$). Overall accuracy was 90% (SD=10%) and average RT to correct trials was 927 ms (SD=280 ms).

Pearson correlations were run for the different tasks with age and Math Fluency separately (Table 1). Because we expected performance to improve with age and Math Fluency, all tests are 1-tailed. There was a significant correlation with NL estimation error when treated as a continuous variable indicating that older participants were more precise at positioning numbers. Furthermore, there was a significant correlation with reaction time (collapsed across problem type) on the Subtraction task. The correlation with accuracy to subtractions fell short of significance (p =.008); older participants were faster and tended to be more accurate. Only a marginal negative correlation was found between age and RTs to the Numerosity task (p=.057). For Math Fluency, only accuracy to the Subtraction task collapsed across problem type remained significant after correcting for multiple comparisons.

After partialling out age, correlations were also calculated between the other variables: RTs to the Subtraction task (collapsed across problem type) and the Numerosity tasks were positively correlated (r=.552 p<.001, 1-tailed). The significant correlation between NL estimation error and accuracy to the Subtraction task did not survive for multiple comparisons (r=-.288, p=.04, 1-tailed). The partial correlations between the NL estimation task and the Numerosity task fell short of significance with accuracy (p=.07) and was not correlated to RTs.

3.2. Numerical Processing ROI Definition

Activation during null trials was subtracted from activation during all numerosity trials to account for motor activation related to hand response. The contrast was then intersected with an anatomical mask of the bilateral parietal lobe to further isolate activations within the numerical processing network following our *a priori* hypotheses thus yielding the Numerical Processing ROI. The ROI encompassed the bilateral IPS and the PSPL (see Figure 1).

3.3. Modulation of Activation with Subtraction Problem Size and Performance on the NL Task

A voxel-wise regression was run within the Numerical Processing ROI (see Figure 1) with NL estimation error as regressor of interest and age and Math Fluency score as control variables for the Subtraction Large vs Small contrast. We found a negative relation with NL estimation error in the left IPL, the left SPL and precuneus (PCu), and the right SPL (see Figure 2 and Table 3). The right SPL region covers the peak from Prado et al.'s (2014) PSPL cluster. In addition, the most posterior bilateral activations appear to be in mirror positions suggesting that the significant relation with NL estimation error was covering the bilateral PSPL. Because the two left most posterior clusters (i.e., PCu and SPL; see Figure 2) were part of a same larger cluster at a more lenient threshold, these two areas are further considered as part of the same functional left PSPL cluster. The left IPL cluster was found deep in the anterior part of the IPS less than 8mm apart from a peak found to be commonly activated by several numerical tasks in a meta-analysis (Arsalidou and Taylor, 2011).

To visualize the activations and understand their relationships to the NL estimation error, betas were extracted from the significant clusters (right and left SPL and left IPL) for large and small problem sizes on the subtraction task. In all clusters, the negative relation indicates that participants with better NL performance showed a more positive modulation of activation compared to poor NL performers (Figure 3).

To further understand the negative relation with NL estimation error, beta values for the three main anatomical clusters were averaged separately for high and low NL estimation error and separately for small and large subtraction problems (Figure 4). Participants with better estimation abilities were showing a positive modulation indicating a reduced activation for small compared to large problems whereas participants with poor estimation abilities showed a tendency towards greater activation for small problems.

3.4. Whole Brain Analysis

Two areas were found significant and adjacent to the regions found in the original Numerical Processing ROI analysis: a cluster in the PCu and a cluster in the IPL. However, there were also activations within the left and right MTG, as well as the left and right caudate and putamen (see Table 4). All clusters showed activation patterns similar to the ones within the Numerical Processing ROI: participants showing higher NL estimation error had greater activation for small compared to large problems and those with lower NL estimation error.

4. Discussion

It has been argued that variances in mathematical skill are to be found in individual differences in number specific processes (Butterworth et al., 2011; Dehaene et al., 2003). Among the various basic numerical tasks, performance to the NL task is considered to be indicative of the quality of a child's numerical representation and has shown to be related with and be predictive of future arithmetical skill (Siegler and Booth, 2004; Siegler and Opfer, 2003). However, no study has investigated brain-behavior relations between performance to the NL task and arithmetic. In this study we tested the hypothesis that the NL task taps into basic number-specific processes relevant to the acquisition of arithmetic. We chose subtraction problems because they have been shown to rely more on quantity manipulation and procedural strategies compared to other operations (Dehaene et al., 2003; Dehaene, 1992; Fayol & Thevenot, 2012; Prado et al., 2011, 2014). Specifically, we tested whether NL estimation performance in children was related to neural activation during single-digit subtraction problems in number-specific areas. To identify number-specific regions we used a numerosity task as an independent localizer of numerical processing. Within this Numerical Processing ROI we ran a regression analysis between behavioral performance to the NL task and the modulation of activation with problem size in the subtraction task. Based on previous literature, we expected to find a relation in the IPS where poor NL estimators would show greater activation for small compared to large problems and in PSPL we expected better NL estimators to show increased reliance on visuo-spatial processes, in particular for larger problems. Finally, to understand the implication of different activation patterns in the different functional areas, we compared participants' accuracies on the subtraction task depending on the direction of their modulation with problem size. This study brings neurofunctional support to the hypothesis that performance to the NL task is related to basic number-specific processes relevant to the acquisition of arithmetic.

4.1. Number Line Estimation and Subtraction Processing

As expected, NL performance improved with age indicating an increased understanding of the numerical range and an improvement in estimation ability. The correlation between NL estimation ability and subtraction skill, independent of age, showed a trend which is in line with previous behavioral studies highlighting a relation between NL estimation and arithmetic skill (Booth and Siegler, 2006; Cowan and Powell, 2014; Siegler and Booth, 2004; Siegler and Opfer, 2003). Possibly, the two tasks failed in being sufficiently challenging to observe a clear age-independent relation.

Functionally, we found a significant negative relation between the modulation of activation with problem size and NL performance after controlling for age and Math Fluency. The relation was found in key parietal areas involved in arithmetical processing. The left IPL activation covered parts of the IPS and the peak was less than 8mm from a peak common to several numerical tasks (Arsalidou and Taylor, 2011). In this area, better NL estimators showed reduced activation for smaller problems whereas poorer NL estimators showed similar activation for both problem sizes. Because the left IPS is considered to be responsible for manipulating numerical information (Ansari, 2008; Kaufmann et al., 2009; Nieder and Dehaene, 2009; Nieder, 2004; Piazza et al., 2007; Pinel et al., 2001) it could be that better NL estimators have a more fine grained numerical representation at this age and are more efficient in processing smaller quantities. In support of this, the study from Kucian et al. (Kucian et al., 2011) showed that training children's numerical representation through NL-like games induced a decrease of activation while judging relative symbolic magnitudes in a cluster virtually identical to the one we found (4 mm distance between peaks).

Other significant clusters, within the numerical processing ROI, showing a relation between NL estimation and problem size were found in an area known as PSPL, commonly activated by all operations (i.e., peak distance between 6 and 16 mm; Arsalidou & Taylor, 2011). In subtraction problems, a grade-related effect in the PSPL was found suggesting a greater involvement with greater expertise (Prado et al., 2014). Moreover, greater arithmetical complexity was shown to increase activation in these areas (Menon et al., 2000). In our study, participants with better NL estimation showed greater activation for larger problems while a reversed tendency was found for poor estimators. The bilateral PSPL does not seem to be uniquely related to numerical processing but is also engaged in attentional visuospatial processes (Dehaene et al., 2003). This area has shown to be involved in both numerical tasks (Dehaene et al., 1999; Lee, 2000; Menon et al., 2000) as well as in visuospatial tasks such as reaching, grasping, eye and/or attention orienting, mental rotation, and spatial working memory (Hubbard et al., 2005; Knops et al., 2009; Simon et al., 2004, 2002). In support of the involvement of the PSPL in visuospatial processing in arithmetic tasks, Knops et al. (2009) found that activation induced by saccades in this area could be used to discriminate between activations of different mental operations. Their result indicates that performing mental operations requires some visuospatial movement on an internal quantity representation. Our results suggest that better estimators showed less engagement of these processes for small compared to large problems. Indeed, children at this age are still learning subtraction problems and in particular larger ones. Conversely, poor NL performers could be more challenged and therefore show robust activation in the PSPL for both problem types.

A possible explanation for the problem size effect in the better NL estimators is that they rely on a verbal strategy to solve smaller problems. Because these problems might be more frequent, the solution could be stored in long-term memory and be retrieved. Although some evidence supports this possibility in adults with higher arithmetical skill (Thevenot et al., 2010), the bulk of the findings indicate that abstract procedures associated with numerical magnitude manipulation are more common strategies in subtraction problems (Barrouillet et al., 2008; Dehaene et al., 2003; Fayol and Thevenot, 2012; Prado et al., 2014, 2011). Additionally, neurofunctional evidence shows an increased reliance on parietal areas subtending procedural processing for subtraction problems (Prado et al., 2014) and that by adulthood, a dissociation is observed between operations that rely on procedures versus those that rely on verbal retrieval such as multiplication (Prado, et al., 2011). Indeed, relying on verbal strategies for small problems should have shown an increase of activation in areas previously found to support verbal retrieval such as the left MTG or left inferior frontal gyrus (Berteletti, Prado, & Booth, 2014; Demir, Prado, & Booth, in press; De Smedt et al., 2011; Prado et al., 2011, 2014). Although a relation was found with activation in the left MTG, it was greater for larger problems further challenging the verbal strategy (see next section). An other possible strategy used by participants was to rely on parity compatibility to solve the task (Lemaire and Reder, 1999), however if this were true, it would be hard to explain why children did not rely on the same strategy across all problem sizes but did so only for smaller problems.

Perhaps a better explanation of the problem size effect for the better NL estimators is that they rely on alternative strategies to solve small subtraction problems. In this study, participants were required to judge if the outcome was correct. It is possible that children with a fine-grained numerical representation privileged an estimation strategy given that small problems had outcomes between one and three. This would explain the lower involvement of both IPS and PSPL areas for smaller problems. In support of this interpretation is an adult study where a relation was found between estimation and multi-digit subtraction problems (Linsen et al., 2014). The authors argue that participants with higher estimation skills quickly estimated the distance between the operands to choose the most efficient strategy.

4.2. NL Estimation Outside the Numerical Processing ROI

Negative relations between the problem size effect in the subtraction task and NL performance were also found outside our *a priori* ROI. Two of them were found in the parietal lobes adjacent to the clusters found within our ROI (i.e., the left IPL and right PCu). The numerical processing ROI was selected using a numerosity task thus excluding areas that might be more involved in symbolic processing. In fact, the study comparing activation elicited by the classical NL task and a brightness line task found that the former activated a larger area bilaterally suggesting that symbolic processing taps into more extensive regions as compared to non-symbolic processing (Vogel et al., 2013).

The problem size effect was also found to be significantly related to NL performance in two other bilateral regions: the MTG as well as the caudate and putamen. The left MTG appears to be related to verbal information such as phonology and retrieval of semantic representations (Booth et al., 2002; Booth, 2010) and it has been repeatedly found active during arithmetic fact retrieval, in particular for multiplication problems (Berteletti et al., 2014; Demir, Prado, & Booth, in press; De Smedt et al., 2011; Prado et al., 2011, 2014). The negative relation in our study suggests that better NL estimators relied on additional verbal processes for larger problems in support to the visuospatial processes whereas poor NL estimators showed little activation overall probably due to less reliance on verbal representations. Activations in the caudate and putamen nuclei have also been reported in many numerical processing and arithmetic studies (Ansari et al., 2005; Arsalidou and Taylor, 2011; Chochon et al., 1999; Cowell et al., 2000; Göbel et al., 2004; Gullick and

Wolford, 2014; Ischebeck et al., 2006; Jost et al., 2009; Zago et al., 2008). Greater activations have been found for more complex calculations involving multi-steps procedures (Dehaene and Cohen, 1995; Grabner et al., 2009; Ischebeck et al., 2007; Menon et al., 2000) as well as in subtraction problems involving borrowing (Kong et al., 2005). Interestingly, in a task comparing numerical estimation strategies, activation in these nuclei was considered to reflect spatial attention and eye movement planning (Gandini et al., 2008) and in other studies, they were found active in calculation as well as in saccade tasks (Simon et al., 2004, 2002). We suggest that activation found in the caudate and putamen in our study might be related to visuospatial mechanisms involved in numerical and arithmetical processing. Indeed, there is growing evidence that calculation relies on visuospatial processes such as shifts of attention along a mental number line in a direction determined by the type of operation (Knops et al., 2014, 2009). The causal relation between space processing and calculation has recently been shown with neglect patients where the inability to attend the left side of space affected performance to large subtraction but not addition problems (Dormal et al., 2014).

4.3. Conclusions

This study is the first to demonstrate a direct relation between performance on the NL task and brain activation found during single-digit subtraction and that this relation relies, at least in part, on domain-specific processes. Specifically, precision in NL estimation was related to the modulation of activation with problem size showing a greater sensitivity in higher estimators. Significant relations outside of the numerical processing ROI indicate that NL estimation performance may also rely on other verbal and spatial processes. These results support intervention strategies using the NL task and the creation of NL task-like training games for classroom use to help children improve their numerical magnitude representations necessary for acquiring arithmetic.

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Highlights

- The Number Line task has been found to correlate with and predict arithmetic skill
- We correlate Number Line performance with single-digit subtraction brain activation
- Correlations were found in areas devoted to processing numerical information
- Better Number Line performers showed more efficient processing in these key areas
- First evidence that the Number Line task is related to brain areas involved in arithmetic

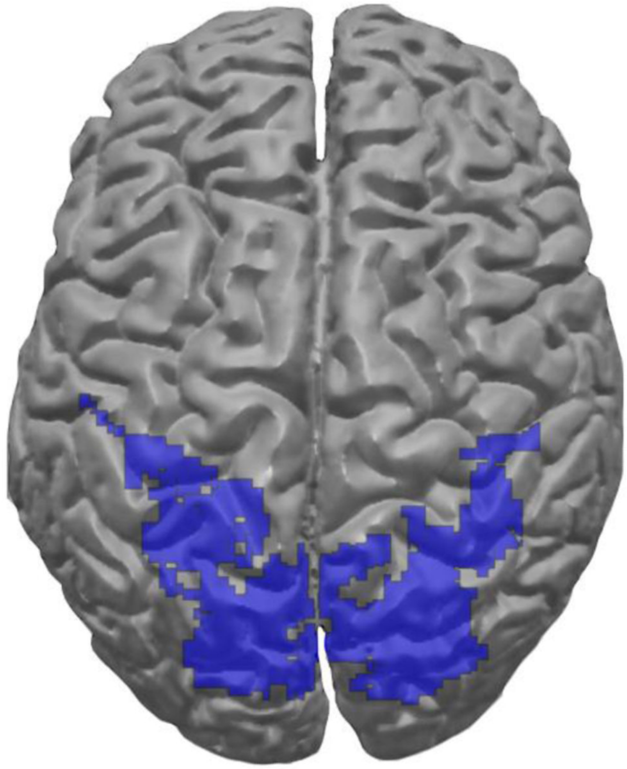

Figure 1.

Significant clusters for the Numerosity vs Nulls contrast within the parietal lobes. The area covered the bilateral IPL and SPL regions including the precuneus. The largest bilateral cluster of 1982 voxels had the peak at [−16, −60, 58] and the other significant cluster included 82 voxels with peak at [12, -74, 22]. Peaks are in MNI coordinates.

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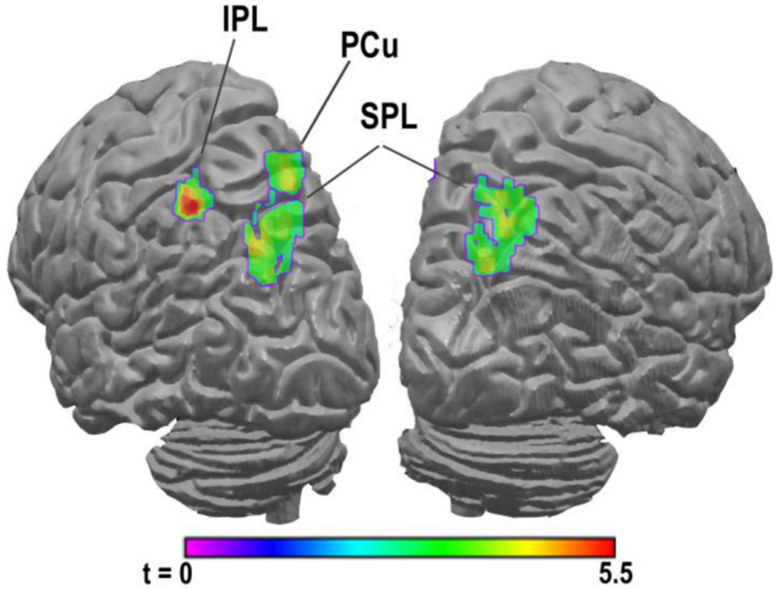

Figure 2.
Clusters showing a significant negative relation with NL estimation error in the Subtraction Large vs Small contrast within the Numerical Processing ROI.

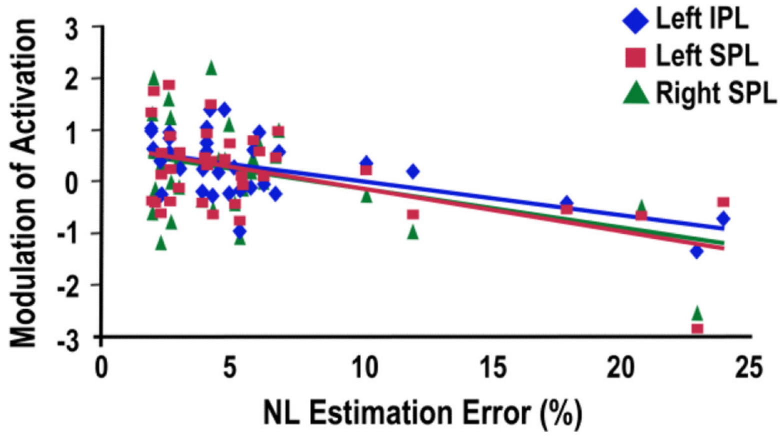

Figure 3.

Modulation of the activation in the subtraction task (Large vs Small contrast) depending on NL estimation error in left IPL, left SPL and right SPL. To visualize the relationship between activation and the NL estimation error, averaged betas for each participant over the entire significant cluster were extracted separately for large and small problems. In all clusters, the negative relation indicates that participants with better NL performance showed a more positive modulation of activation compared to poor NL performers.

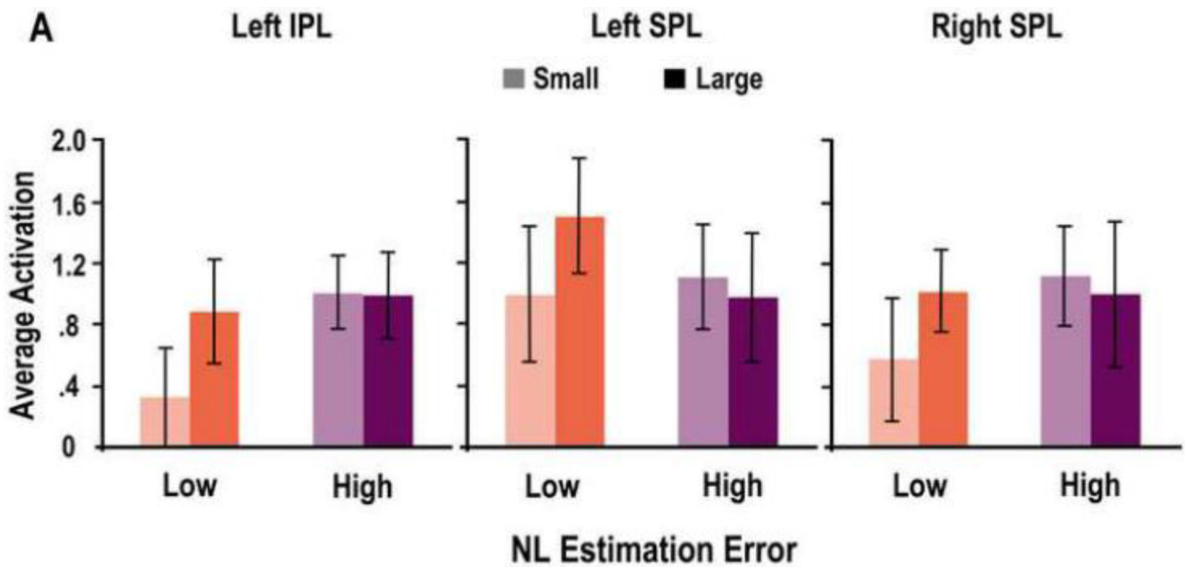

Figure 4.

Activation for large and small subtraction problems depending on NL performance (low vs high error groups) in left IPL (left panel), left SPL (middle panel) and right SPL (right panel). Participants with higher NL estimation abilities show reduced activation for small compared to large subtraction problems.

Table 1

Accuracies and RTs by Subtraction problem size for children with high and low NL estimation error

Subtraction task	Problem size	
	Small	**Large**
Accuracies (%)	93.9 (6.7)	89.6 (10.4)
Higher error group	91.7 (7.3)	86.3 (9.9)
Lower error group	96.3 (5.2)	93.2 (9.8)
Reaction times (ms)	995 (336)	1169 (407)
Higher error group	1051 (329)	1250 (416)
Lower error group	937 (342)	1083 (390)

Note. Standard deviations are in parenthesis.

Table 2

Correlations for age and Math Fluency (MF) with performance to the experimental tasks.

	NL error	Subtraction Task		Numerosity Task	
		Acc	**RT**	**Acc**	**RT**
Age	−.486*	.383§	−.477*	.067	−.257
MF	−.134	.455*	−.283	.153	.082

Note. Correlations are 1-tailed and corrected for multiple comparison (α=.005)

*p<.005

§indicates correlation that fell short of significance for multiple comparisons (*p*=.008).

Table 3

Clusters showing a significant negative relation with NL estimation error in the Subtraction Large vs Small contrast within the Numerical Processing ROI.

Anatomical location (~BA)	MNI coordinates					
	X	Y	Z	voxels	t-value	Sig*
Left Inferior parietal lobule (40)	−36	−44	46	49	5.22	0.006
Left Superior parietal lobule (7)	−28	−68	38	136	3.88	0.0001
Left Precuneus (19)	−8	−60	54	49	3.76	0.006
Right Superior parietal lobule (7)	24	−68	54	142	3.71	0.0001

Note.

~BA: approximate Brodmann Area

*significance is determined by Monte Carlo simulation with 10,000 iterations.

Table 4

Clusters showing significant relations with NL estimation error in the whole brain analysis for the Subtraction Large vs Small contrast

	MNI coordinates					
Anatomical location (~BA)	**X**	**Y**	**Z**	**voxels**	**t-value**	**Sig***
Left Middle temporal gyrus (21)	−56	−56	2	330	5.47	0.0001
Right PCu (7)	4	−66	58	246	5.01	0.0004
Left Caudate and putamen	−20	−16	−6	173	4.77	0.005
Left Inferior parietal lobule (40)	−38	−40	46	377	4.72	0.0001
Right Caudate and putamen	16	14	−2	116	4.45	0.05
Right Middle temporal gyrus (21)	56	−54	6	245	4.16	0.0004

Note.

~BA: approximate Brodmann Area

*significance is determined by Monte Carlo simulation with 10,000 iterations.