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The Differential Relationship Between Finger Gnosis, and Addition and Subtraction: An fMRI Study

Firat Soylu*[a], David Raymond[b], Arianna Gutierrez[b], Sharlene D. Newman[b]

[a] The University of Alabama, Tuscaloosa, AL, USA. **[b]** Indiana University, Bloomington, IN, USA.

Abstract

The impact of fingers on numerical cognition has received a great deal of attention recently. One sub-set of these studies focus on the relation between finger gnosis (also called finger sense or finger gnosia), the ability to identify and individuate fingers, and mathematical development. Studies in this subdomain have reported mixed findings so far. While some studies reported that finger gnosis correlates with or predicts mathematics abilities in younger children, others failed to replicate these results. The current study explores the relationship between finger gnosis and two arithmetic operations—addition and subtraction. Twenty-four second to third graders participated in this fMRI study. Finger sense scores were negatively correlated with brain activation measured during both addition and subtraction. Three clusters, in the left fusiform, and left and right precuneus were found to negatively correlate with finger gnosis both during addition and subtraction. Activation in a cluster in the left inferior parietal lobule (IPL) was found to negatively correlate with finger gnosis only for addition, even though this cluster was active both during addition and subtraction. These results suggest that the arithmetic fact retrieval may be linked to finger gnosis at the neural level, both for addition and subtraction, even when behavioral correlations are not observed. However, the nature of this link may be different for addition compared to subtraction, given that left IPL activation correlated with finger gnosis only for addition. Together the results reported appear to support the hypothesis that fingers provide a scaffold for arithmetic competency for both arithmetic operations.

Keywords: finger gnosis, finger sense, arithmetic, fMRI, embodied cognition, numerical cognition, cognitive development

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*Corresponding author at: The University of Alabama, College of Education, Box 870231, Tuscaloosa, AL 35487, USA. Phone: (205) 348 6267. Email: E-mail: fsoylu@ua.edu

Development of mathematical competence begins early and has a neurological basis that is itself linked to the active experiences of children. This study is specifically concerned with the role of children's bodies, specifically their fingers, in grounding and more critically in setting up the neural networks that underlie arithmetic. The construct of finger gnosis (the ability to identify and individuate fingers; also referred to as finger sense or finger gnosia) is not exclusively or originally about number or arithmetic. The ability to localize the stimulation of fingers is, in part, a measure of the preciseness of discriminating regions of sensory stimulation. Due to its relevance to cognition in general, poor finger sense has been used as an indicator of brain dysfunction and learning disability for several decades (Benton, 1979; Critchleey, 1953; Gerstmann, 1940).

In 1924, Josef Gerstmann diagnosed an adult patient who was not able to name her own fingers or point to them on request. Tests on this patient also revealed that she had difficulty differentiating between her right and left hand, or another person's right and left hands. In addition, she performed poorly on calculation tests and had impairments in spontaneous writing. The source of the symptoms was a lesion located in the left angular gyrus (Gerstmann, 1940). It was these studies by Gerstmann in the 1920s that linked neural correlates of fingers to arithmetic for the first time. Since then, a number of studies of patients with parietal lesions have replicated Gerstmann's findings (Mayer et al., 1999). Two transcranial magnetic stimulation studies showed that stimulation of inferior parietal areas, in particular the angular gyrus, leads to disruptions both in number processing and finger gnosis (Roux, Boetto, Sacko, Chollet, & Tremoulet, 2003; Rusconi, Walsh, & Butterworth, 2005). In addition, Reeve and Humberstone (2011) demonstrated that finger gnosis changed between the ages of 5 and 7 and that this change was related to finger use in arithmetic computation, suggesting an important role for finger sense in the development arithmetic skills. It has also been shown that finger gnosis predicts mathematical performance in young children (Fayol, Barrouillet, & Marinthe, 1998; Noël, 2005).

There are some recent studies that show activation of finger related regions during number and arithmetic processing (Berteletti & Booth, 2015; Tschentscher, Hauk, Fischer, & Pulvermuller, 2012). Tschentscher et al. (2012) presented number words to adults and found that the fMRI measured brain activation observed was systematically related to finger counting habits: those who are "left-starters" (start counting on their left hands when asked to count from one to 10 on their fingers), showed increased activation in the right motor cortex while "right-starters" showed more activation in the left motor cortex (no motor response was required). Because finger counting habits have been found to be stable across development (Sato & Lalain, 2008), this finding suggests that while adults may not use their fingers in the service of mathematical calculation very often, those early experiences relating fingers with number (and magnitude) created a lasting neural impression that was activated on seeing a number name even when no motor response was required. Paralleling these results, Newman and Soylu (2014) reported better addition performance both for children and adults (all right handed), who are right-starters, compared to left-starters. They interpreted this as finger-counting habits affecting the lateralization of the network active during addition, due to early finger counting experiences, and left-starters relying more on cross hemispherical communication, reducing the addition performance. Kaufmann et al. (2008) compared brain activation of 7 to 9 year old children in parietal areas, with adults, during a non-symbolic numerical processing task (comparison of numerical information in canonical number gestures). They found comparatively more activation for children in bilateral supramarginal gyrus and lateral portions of the anterior intraparietal sulcus, extending to post and precentral gyrus (areas that were shown to be active with grasping movements). They argued that these results indicate an age-dependent reliance on finger areas for non-symbolic number processing, and a special role of fingers for supporting number magnitude representations in early development.

Finger processing has also been found during arithmetic processing. Berteletti and Booth (2015) found that finger-related motor and somatosensory cortices were active in 8 to 13 year old children during a subtraction task. In comparison, only finger somatosensory areas were active during a multiplication task. They interpreted the differential activation of the motor cortex as use of implicit finger-counting strategies for subtraction, but not for multiplication, due to higher reliance on memory fact retrieval for multiplication, compared to quantity manipulation for subtraction. Krinzinger, Koten, Horoufchin, et al. (2011) found that contribution of finger-related sensorimotor systems was larger for addition than magnitude comparison, and for non-symbolic addition (collection of dots) compared to symbolic (Arabic numerals) addition. They argued that the visually guided finger movement network is active during both the non-symbolic and symbolic addition tasks, and that this reliance does not decrease with age. In a dual-task study with adult participants, Michaux et al. (2013) found differential interference of anatomically ordered finger tapping on addition and subtraction performance, compared to multiplication, implying a larger resource overlap between finger movements, and addition and subtraction. These studies seem to suggest involvement of finger related sensorimotor resources in addition and subtraction, both for children and adults.

There is a growing literature that links fingers to arithmetic processing (see Soylu, Lester, & Newman, in press for a review); however, it is still unclear precisely how fingers contribute. A potential way to explore this relationship is by examining differential involvement of fingers in different arithmetic computations. In the above discussed Berteletti and Booth (2015) study subtraction differentially activated motor cortex suggesting involvement of implicit finger counting strategies for subtraction but not multiplication. Also, Soylu and Newman (2016) explored the relation between addition and finger tapping, and found that one-digit addition is more affected from concurrent anatomically-ordered tapping than two-digit addition, which supports a specific association between addition fact retrieval and anatomically ordered finger movements in adults, possibly due to use of finger counting strategies that deploy anatomically ordered finger movements early in the development. This variance in the involvement of fingers may be related to the differences in the processing required for different arithmetic operations. For example, in older children and adults single digit addition and multiplication problems are typically solved via memory retrieval processes while subtraction and division use calculation strategies. This has also been observed in the differences in brain activation related to these operations (Fehr, Code, & Herrmann, 2007; Rosenberg-Lee, Chang, Young, Wu, & Menon, 2011). For example, Rosenberg-Lee and colleagues found that individual sub-regions of the intraparietal sulcus, superior parietal lobe, and the angular gyrus were differentially involved in the four arithmetic operations. Given that the arithmetic operations rely on different sets of processes (see Arsalidou & Taylor, 2011 for a meta-analysis) it may be expected that fingers play different roles in each.

As suggested in the review above, finger processing may impact arithmetic in a number of ways. First, there is evidence that supports a relationship between fingers and the representation of number magnitude. In a review Di Luca and Pesenti (2011) argued that canonical finger configurations of number are stored in the long-term memory allowing for rapid access to number magnitude, and facilitate the learning of number semantics and symbols. Because producing and automatizing access to canonical finger configurations are linked to the ability to individuate fingers, better finger sense promotes the rapid and efficient acquisition of number knowledge, which impacts arithmetic processing. This leads to the hypothesis that all arithmetic operations will be impacted by finger processing at least at the level of number symbol and magnitude processing. Secondly, finger processing has also an impact on arithmetic processing by way of sequencing or counting. The use and quality of finger counting may vary across arithmetic operations. For example, when learning addition primarily fingers but also other physical objects (e.g., counting rods) are used initially for counting strategies, later to be replaced by retrieval strategies. Children usually start with counting-all strategies, which involve counting each addend, and then count the total. Counting-all eventually is replaced by the more efficient counting-on strategy which involves starting to count from the first number and continuing the second one (e.g., for 3 + 4 the child would count “3” and continue with “4, 5, 6, 7” and answer with “7”). An even more efficient form of the counting-on strategy involves starting from the larger number. The more efficient strategies require developing new competencies. For example, the switch from counting-all to counting-on can only happen when children can spontaneously produce the finger numeral representation for the first addend. For simple addition, the counting strategies are eventually replaced by memorization and retrieval of addition facts (Jordan, Kaplan, Ramineni, & Locuniak, 2008). However, children continue to use counting for complex addition problems (e.g., when the sum is bigger than 10). But, because the number of fingers is limited to 10, the child then uses more advanced strategies, such as chunking fives in the addends and counting what is remaining (e.g., for 7 + 6, “7 is 5 + 2. 6 is 5 + 1. Two 5s is 10, 2 + 1 is 3. 10 … 11, 12, 13. The answer is 13”). Because subtraction is learned later than addition in the first grade, by the time children learn subtraction they already have some mastery of the counting strategies for addition and can spontaneously produce finger configurations for the minuend. There is nothing comparable to counting-all for subtraction. The initial strategies for subtraction include representing the minuend on fingers and removing the subtrahend and reporting the remaining as the answer, or representing first the subtrahend on fingers (or with physical manipulatives) and removing fingers until the minuend is found, and counting how many were removed (Carpenter & Moser, 1984). These differences in finger use and the onset of addition and subtraction may account for differences in the reliance on finger representations.

The primary goal of the current study was to examine the differential relationship between finger gnosis and addition and subtraction in a group of young children. Previous studies have shown both overlapping and non-overlapping neural correlates for subtraction and addition. For example, Rosenberg-Lee and colleagues (2011) found that they equally activated the angular gyrus (the locus of Gerstmann’s syndrome) while subtraction elicits greater activation in posterior superior parietal cortex, a region that has strongly been linked to spatial processing. Based on the previous literature we have developed two major hypotheses. First, finger processing will impact overlapping regions for addition and subtraction in regions linked to number symbol and magnitude. Number symbol processing has been linked to the fusiform gyrus in occipital-temporal cortex (Ischebeck et al., 2006). Magnitude processing is more complicated but has generally been linked to the intraparietal sulcus (IPS) (Cohen Kadosh, Lammertyn, & Izard, 2008; Dehaene, Piazza, Pinel, & Cohen, 2003; Piazza, Pinel, Le Bihan, & Dehaene, 2007). However, the relation between finger configurations and number magnitude is also expected to play a role here, particularly for younger children. This relation might be mediated by the precuneus due to its role in multi-modal processing and links to both spatial and motor imagery (Delazer et al., 2005; Grabner et al., 2009). The second hypothesis is that because of the differential developmental trajectories and neural correlates for addition and subtraction, fingers may be expected to impact these two arithmetic functions in different ways. Since addition involves more fact retrieval than subtraction, and the left inferior parietal lobule (IPL; particularly angular gyrus) has been linked to fact retrieval (Delazer et al., 2003; Grabner, Ansari, Koschutnig, Reishofer, & Ebner, 2013; Kong et al., 2005) and to finger processing (Roux et al., 2003; Rusconi et al., 2005) we hypothesized that the IPL will show a stronger relationship with finger processing for addition than for subtraction.

Methods

Participants

Thirty-six (male = 21) second to third graders (age *M* = 8 years and 3 months, *SD*: ± 4 months) participated in this study. This age group was chosen because they: 1) can understand and perform the finger gnosis task and are on the cusp of having fully developed finger sense (Reeve & Humberstone, 2011); and 2) are still developing arithmetic skills. Six participants were excluded due to excessive motion in the scanner (> 5 mm), three were lost to attrition, and three due to low average accuracy rates (<35%) leaving 24 (male = 12) total participants (age *M* = 8 years and 4 months, *SD*: ± 3 months). Participants were recruited from the Bloomington, Indiana area. Parental consent and child assent were both obtained prior to the experimental sessions, in accordance with the Indiana University Institutional Review Board.

Finger Sense

The finger gnosis test is a standard assessment that dates back to Benton (1955). During the test participants sat with both hands palm down on the table in front of them. They were instructed to close their eyes and to keep them closed during the entire procedure (eyes were checked regularly). There were two phases of the test. During the first phase, the experimenter, with a pointer, touched a single finger of the left hand in a pre-determined order, touching each finger (5 trials). After each finger touch the subject was instructed to indicate which finger was touched, by moving the corresponding finger of the other hand (1 point per trial). During the second phase the experimenter touched a combination of two fingers in succession (5 trials), and the participant was instructed to indicate which two fingers were touched and the order that they were touched, by moving the corresponding fingers of the other hand (2 points per trial; 1 point for the correct fingers and 1 point for the correct order). The score was the total number of points earned divided by the total possible points. There were 15 possible points. The scores were normalized by scaling between 0 and 1.

Arithmetic Task

The scanner task was an arithmetic task that included separate blocks of addition and subtraction. The stimulus set included 24 addition and 24 subtraction problems (see the Appendix for a full list of the addition and subtraction questions). Of the 24 addition problems, 11 of them had sums bigger than 10, in nine the first operand was smaller than the second, in eight the first operand was bigger, and in seven both operands were the same number. For the 24 subtraction questions, the first operand was bigger than the first, except for two questions where both operands were the same number. In half of the trials incorrect responses were shown for validation, and in about half of these the incorrect response matched the parity of the correct response, to avoid problem solving strategies based on odd/even match. There were four problems in each block. The block order was randomized. The duration of the entire scanning session for the arithmetic task was 360 seconds. The trials were self-paced, which was found to be a more reliable alternative to fixed-stimulus designs in numerical tasks with children (Krinzinger, Koten, Hennemann, et al., 2011).

In each trial the participant was first presented with the problem (e.g., “3 + 4 = ” without the answer. Followed by either a button press or 10.5 seconds before the answer appeared (e.g., “3 + 4 = 7”). The participant then pressed a button to indicate whether the answer was correct or incorrect. Each block contained 4 problems, and the blocks were separated by 12 second fixation periods. If the participant did not answer a trial within 10.5 seconds, the program moved to the next trial. Accuracy and reaction time were monitored.

Imaging Parameters

Participants underwent MRI scanning using a 12-channel head coil and a Siemens 3T Tim Trio MRI scanner. The first scan was an anatomical T1-weighted scan used to co-register functional images. An MPRAGE sequence (192 sagittal slices; FOV = 256 mm, matrix = 256x256, TR = 1800 ms, TE = 2.67 ms, TI = 900 ms, flip angle = 9°, slice thickness = 1mm, resulting in 1-mm x 1-mm x 1-mm voxels) was used. The experimental functional scan was a multiband EPI scan (33 axial slices using the following protocol: field of view = 192 mm, matrix = 128 x 128, iPAT factor = 2, TR = 2000 ms, TE = 30 ms, flip angle = 60°, slice thickness = 3.8mm, 0 gap).

Data Analysis

Data was collected using PsychoPy (http://www.psychopy.org). Parsing of logfiles to generate onsets and durations, and for behavioral analysis was done with custom Python scripts. Inferential statistics for behavioral and ROI data were conducted using R (https://www.r-project.org). fMRI data were analyzed with SPM8 (Wellcome Trust Centre for Neuroimaging; http://www.fil.ion.ucl.ac.uk/spm) and custom MATLAB scripts (https://www.mathworks.com/) using SPM8 and MarsBar (http://marsbar.sourceforge.net) functions. Corrections for multiple comparisons were done by using cluster threshold values generated by AFNI 3dFWHMx and 3dClustSim (https://afni.nimh.nih.gov). The results were visualized using the xjView toolbox (http://www.alivelearn.net/xjview) and R.

fMRI data were preprocessed in several steps including slice timing correction, motion correction by realignment, co-registration between functional and anatomical scans, spatial normalization and smoothing. All functional data were resampled to $2mm^3$ isomorphic voxels normalized to the Montreal Neurological Institute (MNI) template. For spatial smoothing an 8mm FWHM Gaussian kernel was applied. On the preprocessed fMRI data of individual subjects, a canonical statistical analysis based on the general linear model (GLM) and Gaussian random field theory was performed (Friston, Frith, Turner, & Frackowiak, 1995). The hemodynamic response for the stimuli blocks were modeled with a canonical HRF, built on the onsets of the question presentation portion of the trial (e.g., “3 + 4”), with the reaction time (time between onset of the question and the response with either of the response buttons, indicating readiness to answer the question) entered as the duration. This is when the bulk of the relevant arithmetic processing is assumed to have taken place. The second portion, when the answer stimulus is shown for validation (e.g., “3 + 4 = 7”), is assumed to include number comparison processing and data from the validation portion was not included in the analysis. Of the 24, eight participants did not click on any buttons to indicate readiness to skip to the validation portion and used the entire 10.5 seconds across all trials.

For each individual data analysis, regressors were built for the problem presentation phase and the fixation periods. Six regressors from the realignment step were also included in the model to remove unexpected effects of noise from head movements. Trials with incorrect responses were excluded from the analysis. A multiple regression analysis was performed within SPM8 with finger gnosis scores entered as a covariate. We used 3dFWHMx in AFNI to estimate noise smoothness values separately for every design specification using the “-acf” (spatial autocorrelation function) option, and using the ResMS (estimated residual variance image) file as the input. The ACF values were used as inputs for 3dClustSim to calculate (using Monte Carlo simulations) the whole brain cluster thresholds that would be appropriate to control for type I errors for an uncorrected $p < .005$, which corresponds to a $p < .05$, corrected for the multiple comparisons in the whole brain volume analysis. The cluster thresholds for masked comparisons were determined in a similar way, but by also including the mask images using the “-mask” option (see Table 1 for cluster thresholds output by 3dClustSim). Approaches that assume constant spatial smoothness in fMRI data was found to lead to an increased rate of type I errors (Eklund, Nichols, & Knutsson, 2016). The approach used here addresses this problem, and is shown to better control for type I errors (Cox, Chen, Glen, Reynolds, & Taylor, 2017).

Table 1

Cluster Threshold Levels for an Uncorrected p < .005, Corresponding to a Corrected p < .05.

	Condition compared to baseline	Correlations with finger gnosis, masked by condition compared to baseline	Correlations with finger sense, masked by add & subtract or fast RT & slow RT overlap
Add	296	143	120
Sub	232	215	122
Fast RT	199	127	104
Slow RT	260	216	122

Data Availability

The raw fMRI data and the affiliated analysis files on which the results are based can be found in the Supplementary Materials.

Results

Behavioral

The average for the normalized finger gnosis scores was .84 (ranged between .53 and 1, *SD* = .14). Participants had relatively high accuracy for the addition and subtraction conditions. For addition the mean percent correct was 86.50 (*SD* = 11.12) and for subtraction 90.74 (*SD* = 7.1). A paired sample t-test showed no significant differences in accuracy between addition and subtraction, *t*(23) = -1.54, *p* = .14, *d* = .31. The mean finger gnosis score was .83 (*SD* = .15) with a range of .53 to 1. Neither the addition, *r*(22) = -.001, *p* = .99, or subtraction, *r*(22) = -.07, *p* = .73, accuracy significantly correlated with finger gnosis scores.

The mean RT (reaction time) was 4.18 sec (*SD* = 3.72) for addition and 4.62 sec (*SD* = 3.85) for subtraction. A paired sample *t*-test showed that the RT differences between addition and subtraction was not significant, *t*(23) = -0.85, *p* = .4, *d* = 0.18. Neither the addition, *r*(22) = .26, *p* = .22, nor subtraction, *r*(22) = .22, *p* = .3, RT was found to be significantly correlated with finger gnosis.

Because the trials were self-paced, with a maximum time limit, the number of problems completed for each operation varied across the participants. On average, participants responded to 14.29 (*SD* = 5.92) addition and 16.54 (*SD* = 4.34) subtraction questions, making the average total (addition and subtraction) number of questions 30.83 (*SD* = 9.82). A paired sample t-test showed that the difference in average number of addition and subtraction questions was significant, *t*(23) = -3.28, *p* = .003, *d* = .68, though the difference (2.25) is relatively small (about 7% of the total number of questions answered), and is unlikely to affect the comparisons between conditions.

fMRI

The comparison of addition and subtraction with the baseline (Figure 1), separately, produced large networks of activation clusters distributed over inferior frontal, superior temporal, and multiple parietal sites, both for addition and subtraction (Table 2).

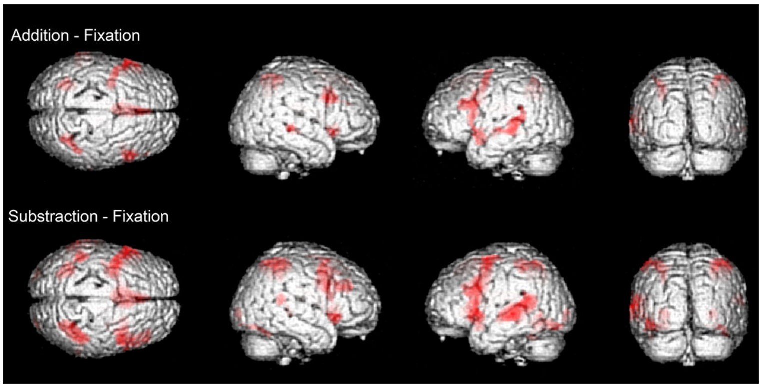

Figure 1. Addition and subtraction compared to baseline.

Table 2

Summary of Activation for Each Condition Compared to Baseline

Region	Cluster Size	Z	MNI,x y z
Addition			
Left/right thalamus	459	4.65	-4 -22 14
Left superior/middle temporal	1085	4.18	-60 -16 -2
Right inferior frontal & insula	442	3.56	44 20 -6
Right middle/superior temporal	353	4.19	48 -28 -4
Right middle frontal gyrus	404	3.92	56 20 38
Left inferior/superior parietal	506	3.63	-28 -52 46
Right inferior/superior parietal	511	3.46	50 -44 56
Left/right supp. motor areas	997	4.19	0 14 50
Subtraction			
Left middle/superior temporal	1688	5.14	-54 -52 16
Right inferior/middle occipital	274	4.08	44 -66 -22
Left frontal	2534	5.30	4 10 56
Left/right thalamus	716	5.03	4 6 8
Right inferior frontal & insula	577	3.97	40 18 -4
Right middle/superior temporal	403	3.95	56 -42 16
Right middle/inferior frontal	1555	4.56	42 8 36
Left inferior/superior parietal	988	3.70	-48 -44 60
Right inferior/superior parietal	1112	4.40	42 -46 62

The regression analysis was performed separately for addition and subtraction. Finger gnosis scores were entered as a covariate in the second level (group) analysis. Neither addition nor subtraction showed activation that positively correlated with finger gnosis. Both operations showed a network of posterior areas including regions in the temporal, occipital, and parietal cortices that were negatively correlated with finger gnosis scores (Figure 2). The regions that were negatively correlated with finger gnosis for both addition and subtraction were identified using the “common regions” function in xjView which selects voxels that are marked as active across both conditions. This procedure produced three clusters common for addition and subtraction (Figure 3, Table 3). One cluster (321 voxels) was in the occipital segment of the left fusiform gyrus, and expanded to the left lingual gyrus. The second cluster (552 voxels) was in the right cingulate gyrus and included parts of the right precuneus. There was a third, smaller, cluster (30 voxels) in the left precuneus.

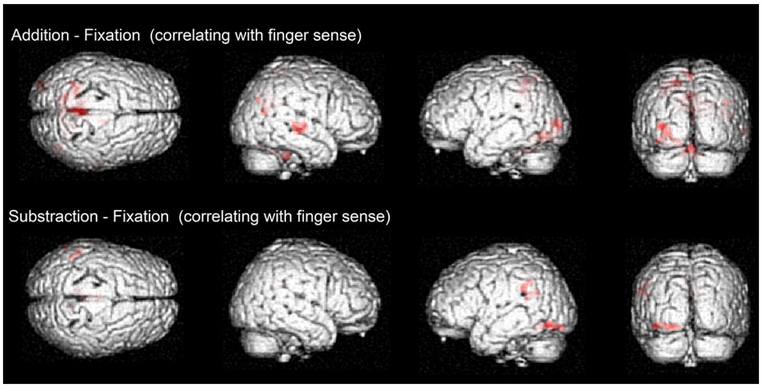

Figure 2. Regions that show activation correlating with finger gnosis scores for addition and subtraction.

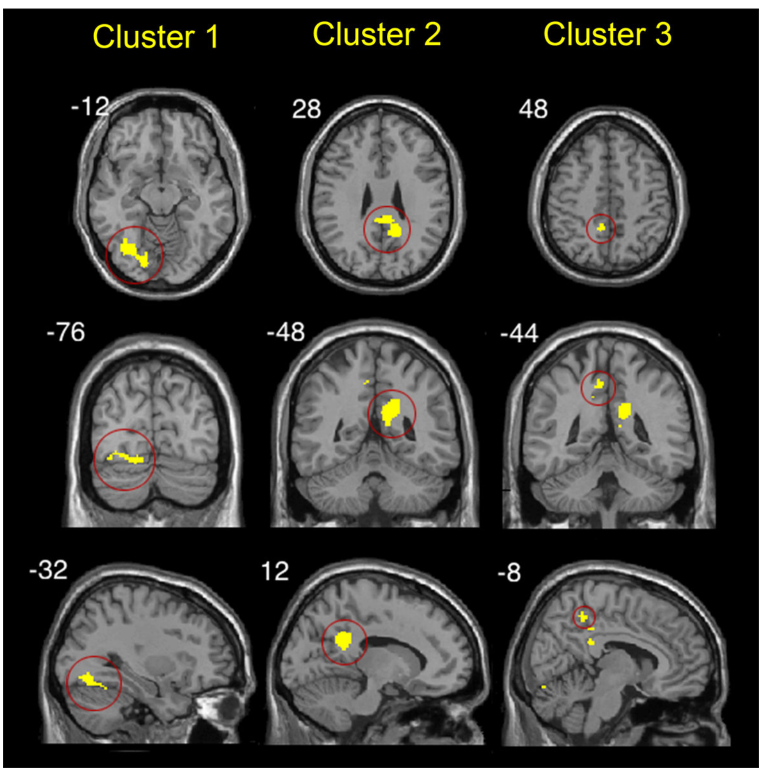

Figure 3. The common regions (three clusters) negatively correlating with finger gnosis, for addition and subtraction. The number next to each transverse, coronal, and sagittal image indicates respective slice numbers from which the images where extracted.

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Table 3

Common Regions for Negatively Correlating With Finger Sense for Addition and Subtraction

Region	Cluster Size	MNI,x,y,z
Left inferior/middle occipital & fusiform	278	-28 -56 -20
Right precuneus & middle cingulum	245	6 -40 6
Left precuneus	30	-8 -46 46

To further unfold how task-related activation for addition and subtraction relate to finger sense skills as well as to explore how finger sense may differentially impact addition and subtraction, we examined correlations with finger gnosis only in areas that were active during addition and subtraction. We first created separate masks based on the contrasts that involve comparison of task conditions (addition and subtraction) with the baseline. We calculated separate cluster thresholds for the masked comparisons by inputting the masks created with the "-mask" option to 3dClustSim (see Table 1 for cluster thresholds generated). No areas were found to be significant, when the areas that negatively correlate with subtraction were masked with the subtraction – baseline comparison. When the addition – baseline mask was applied to areas that negatively correlate with finger gnosis scores during addition, a single inferior parietal cluster (221 voxels, MNI: -26 -46 44) was found to be significant.

To further explore the differential relationship between finger gnosis and activation of the inferior parietal cortex, a third mask based on the common regions activated for the addition – baseline and the subtraction – baseline comparisons was created. The purpose of this third mask was to compare commonly activated areas between addition and subtraction. Even though both addition and subtraction activated the inferior parietal cortex we wanted to ensure that the comparison with finger gnosis was being performed on the same region for both tasks. The masked image again failed to produce significant clusters for subtraction, but for addition the inferior parietal cluster was again found to be significantly correlated with finger gnosis (Figure 4). Based, on the first two masked contrasts (correlations masked with comparison to baseline, separately for addition and subtraction), we inferred that this inferior parietal cluster is active for both addition and subtraction, but is only significantly linked to finger gnosis scores for addition.

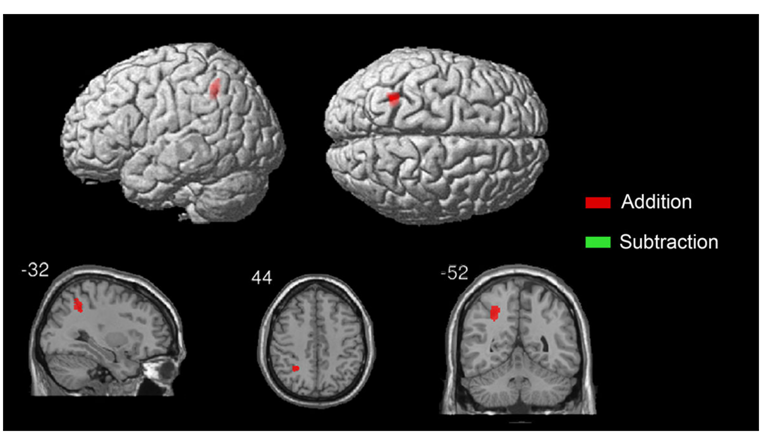

Figure 4. Areas that show activation negatively correlating with finger gnosis for addition and subtraction, masked by common regions for addition – baseline and subtraction – baseline contrasts. Only one inferior parietal cluster, negatively correlating with finger gnosis for addition was significant (141 voxels, MNI: 26 -48 46).

There are at least two explanations for the above results. First, the negative correlation between finger gnosis and activation during addition is due to a deeper and sustained association between finger representations and addition, but not subtraction. The second explanation is that different strategies are used for addition and subtraction. Children in this age group, being more proficient in addition compared to subtraction, may rely more on retrieval based strategies for addition, and calculation strategies for subtraction. Therefore, the difference may in fact be due to differences in the use of finger-related circuitry for retrieval vs. calculation in the inferior parietal lobule, and not essentially due to inherent differences related to addition and subtraction. To test these two alternative explanations we reanalyzed the data by grouping all the addition and subtraction trials at the within-subject level, and creating two conditions, slow RT and fast RT, based on a median-split of reaction time values.

RT median split. The purpose of the RT median split analysis was to determine whether the differential correlation in the inferior parietal cluster was due to differences in the use of retrieval vs. calculation strategies, or due to task-related differences between addition and subtraction. For each participant, the slow RT condition included trials with slower responses than the median, and the fast RT condition included trials with faster responses (equal to or faster than the median). Of the total 660 trials across 24 participants there were 325 trials in the slow RT condition, and 335 trials in the fast RT. On average, there were 13.54 slow RT (*SD* = 4.39) and 14.00 fast RT (*SD* = 5.10) mixed addition and subtraction trials for each participant (a non-significant difference; paired sample t-test, *p* = .29). The addition and subtraction questions were almost evenly distributed across slow RT and fast RT. For slow RT, 44.62% of the trials involved addition, and 55.38% involved subtraction. For fast RT, 45.37% involved addition, and the remaining 54.63% involved subtraction. This is not surprising given that there was no significant RT difference between addition and subtraction. Given the almost equal distribution of addition and subtraction questions between slow RT and fast RT, we assume that the following analysis represents a reliable picture of differences between retrieval and calculation strategies across the two operations.

We followed the same procedures to compare the relation between finger gnosis and slow RT and fast RT conditions, as we did with addition and subtraction. We first examined comparisons with fixation baseline for each condition. Both slow RT and fast RT conditions produced a distributed network of clusters in frontal, temporal, and parietal areas, typically observed in arithmetic tasks. The clusters were larger for fast RT than slow RT (Figure 5; Table 4).

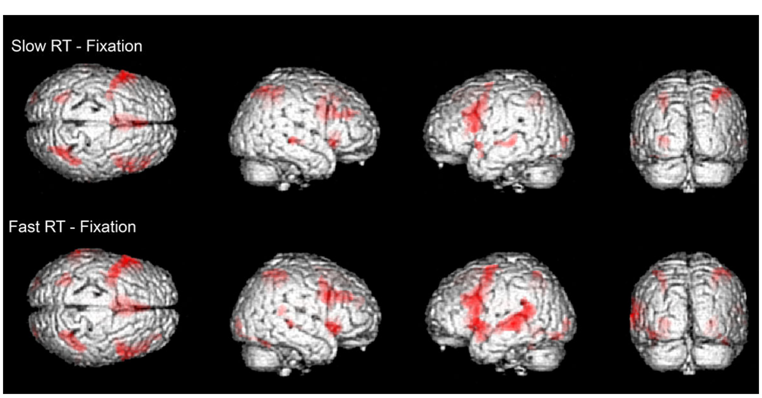

Figure 5. Slow RT and fast RT compared to baseline.

Table 4

Summary of Activation for Each Condition Compared to Baseline

Region	Cluster Size	Z	MNI,x y z
Slow RT			
Left middle/inferior occipital	230	4.15	-28 -96 2
Left inferior frontal gyrus & insula	878	4.21	-60 14 14
Right inferior frontal gyrus & insula	607	3.83	40 20 0
Right middle/superior temporal	325	3.72	52 -28 -2
Left middle/superior temporal	396	3.58	-58 -12 -4
Left/right caudate/thalamus	535	4.13	8 2 16
Right precentral	365	4.54	40 0 32
Left inferior/superior parietal	529	4.15	-28 -66 42
Right inferior/superior parietal	795	4.13	34 -60 52
Left/right supplementary motor	1035	4.74	2 10 54
Fast RT			
Left superior/middle temporal gyrus	3097	4.90	-50 -28 -4
Righ inferior/middle occipital	281	3.98	44 -66 -22
Left/right caudate & thalamus	1286	4.68	-2 4 10
Right inferior frontal & insula	765	4.06	42 18 -4
Right middle/superior temporal	518	3.61	48 -32 -2
Righ middle/inferior frontal	1187	4.33	52 22 34
Left inferior/superior parietal	547	3.33	-26 -66 42
Left inferior/superior parietal	778	3.59	32 -58 50

The masked comparisons did not show any areas that significantly correlated with finger gnosis scores (the comparisons included (1) slow RT masked with slow RT – baseline, (2) fast RT masked with fast RT – baseline, (3) slow RT and fast RT separately masked with the common regions for slow RT – baseline and fast RT – baseline). This result provides support for the first explanation, that the differential correlation in the inferior parietal cluster is related to addition processing, but not subtraction. This relation does not seem to be modulated by strategy differences between addition and subtraction, but more due to task-related processing differences between the two operations.

Discussion

The primary aim of the current study was to examine the differential relationship between finger gnosis and addition and subtraction in second to third grade children. A secondary goal was to determine whether associations between finger gnosis and arithmetic exist at the neural level, even when a behavioral association is not observed.

The findings presented here provide further insight into how finger sense may impact arithmetic performance in young children. First, the addition and subtraction behavioral performance did not significantly correlate with finger gnosis. Second, activation in three regions, left fusiform, and left and right precuneus were found to negatively correlate with finger gnosis both during addition and subtraction. Third, activation in a cluster in the left inferior parietal area was found to negatively correlate with finger gnosis only for addition, even though this cluster was active both during addition and subtraction. And fourth, contrary to our hypothesis, the differential negative correlation between activation in this inferior parietal cluster for addition and finger sense scores was not related to fact retrieval processes. This fourth result is based on the comparison of slow RT and fast RT conditions, where slow RT is assumed to involve calculation and fast RT retrieval. Neither the slow nor fast RT showed a correlation with finger gnosis scores in the left inferior parietal cortex.

There are conflicting findings on the relation between finger gnosis and arithmetic skills in 5 to 8 year old children, some reporting strong associations (Fayol et al., 1998; Noël, 2005), while others showing no behavioral associations (Long et al., 2016; Newman, 2016) for roughly the same age groups. Newman (2016) reported that children 5-8 failed to show a relationship between addition performance and finger gnosis, while children 9-12 did show such a relationship; finger gnosis better predicted performance in older children than younger children. The explanation provided for the discrepancy, between the two age groups on how finger gnosis relates to addition performance, was that both addition and finger sense skills are still developing in the younger group. However, both skills should be developed within the older group (9-12 years old), making the relationship between these two factors more evident (see Fischer, 2017 for a critical commentary on this conclusion). In the current study, like in the previous one, no significant relationship was observed between finger gnosis and behavioral performance. However, the brain activation does provide evidence for the budding relation between finger sense and arithmetic processing systems in younger children, even though the effects of this association is not yet observable at the behavioral level.

Overlapping Regions Correlating With Finger Gnosis

Three regions showed a correlation between finger gnosis and both addition and subtraction – the left fusiform gyrus and the left and right precuneus. There are a number of common processes linked to addition and subtraction, and these regions have been linked to those processes. The occipital segment of the left fusiform and lingual gyri has been reported in previous studies examining arithmetic as well as number/symbol processing. This region is thought to be related to processing of Arabic numerals (Ischebeck et al., 2006). Lee et al. (2007) reported left lingual gyrus activation in an algebraic problem solving study when symbolic problem representations were compared to pictorial representations, paralleling the previously affiliated role of processing Arabic numerals for lingual gyrus. In a study comparing neural correlates of trained and untrained processing of complex (two digit times one digit) multiplication problems, left lingual activity was reported for the untrained vs. trained comparison (Delazer et al., 2003), indicating that reliance on this area is modulated by memory retrieval. Left fusiform and lingual activation was found to increase with the length of the string in the stimulus, both for Arabic numerals (Ischebeck et al., 2006), as well as word strings in reading tasks (Mechelli, Humphreys, Mayall, Olson, & Price, 2000), further supporting the role of these areas for processing of visual symbols. Additionally, Cantlon et al. (2006) reported bilateral fusiform and lingual gyri activation in an approximate numerical processing task with adult participants, when standard stimuli was compared to shape deviants, showing sensitivity to visual features of non-symbolic numerical stimuli in these areas. The negative correlation in this cluster might be due to children with better finger sense skills also being better at linking finger presentations to number representations, which may facilitate linking of Arabic numerals to number representations, during both addition and subtraction.

The precuneus is the other region that showed a negative correlation with finger gnosis for both addition and subtraction. The precuneus has been shown to participate in a range of multimodal, integrated tasks that involve visuo-spatial processing (see Cavanna & Trimble, 2006 for a review), including visuo-spatial imagery, episodic memory retrieval, first-person perspective taking, encoding and retrieval of spatial locations (Frings et al., 2006), and in regeneration of contextual associations (e.g., word-picture associations; Lundstrom et al., 2003). Precuneus activation has also been consistently reported in arithmetic tasks (see Arsalidou & Taylor, 2011 for a review) even when compared across cultures (Tcheang, 2014). For example, Delazer et al. (2005) compared neural correlates of addition and subtraction after receiving two forms of training: 1) learning-by-strategy where participants learned about algorithmic solutions for arithmetic problems, or 2) learning-by-drill where the participants memorized arithmetic facts. While the drill condition showed stronger left angular gyrus activation, the strategy condition activated the precuneus. This difference was interpreted as being due to the use of rote memory retrieval (angular gyrus), which is assumed to be language dependent, for drill problems and to the use of visuospatial strategies (precuneus), particularly visual imagery, for the strategy problems.

Even though there seems to be a consensus regarding the involvement of the precuneus in arithmetic processing being due to use of visuospatial processing, the nature of this visuospatial processing and how it changes across different numerical tasks are not clear. Differences in the involvement of the precuneus across different forms of arithmetic processing has been reported previously. For example, Ischebeck et al. (2006) compared training effects on neural correlates of multiplication and subtraction, and found that while trained vs. untrained problems showed right precuneus activation for subtraction, no precuneus activation was found for the same comparison for multiplication. They argued that, based on the Delazer et al. (2005) findings, this result indicated that trained subtraction relies more on visual imagery than trained multiplication.

One explanation for the negative correlation found in the precuneus is that children with high finger gnosis scores have better visuospatial skills particularly in location encoding and recognition (which precuneus is an important component of; Frings et al., 2006). Spatial processing is a strong predictor of mathematics performance such that performance on spatial tasks like mental rotation is correlated with mathematics achievement in school age children (Alloway & Passolunghi, 2011; Raghubar, Barnes, & Hecht, 2010) and visuospatial working memory is related to number and mathematics problem-solving (Rasmussen & Bisanz, 2005). Since higher skill levels are known to lead to decreased activation in attentional and sensory processing areas in a wide range of tasks, for example driving (Bernardi et al., 2013), music (Meister et al., 2005), and sports (Milton, Solodkin, Hluštík, & Small, 2007), the negative correlation found in the precuneus may be due to both the finger gnosis and arithmetic tasks using an overlapping visuospatial system. Therefore, the casual relation between finger sense and reliance on precuneus during arithmetic processing might be mediated through a non-domain specific visuospatial system.

An alternative explanation is that finger representations, possibly in the form of visual and motor imagery, are involved in both addition and subtraction particularly in young children. Therefore the observed negative correlation is due to better finger sense leading to an earlier symbolic representation of numerosities via canonical finger patterns and a more efficient network for these visuo-spatial and motor representations of number in the service of arithmetic. This explanation is more likely given the accumulating evidence for participation of finger-based representations in mental arithmetic (see Andres & Pesenti, 2015; Berteletti & Booth, 2016; Soylu, Lester, & Newman, in press, for reviews). Addition and subtraction, in particular, rely on finger representations, due to early finger counting experiences. For example, Michaux et al. (2013) found differential interference of anatomically ordered finger tapping on addition and subtraction performance, with adult participants, compared to multiplication, implying a larger resource overlap between the finger sensorimotor system, and addition and subtraction, compared to multiplication. Andres, Michaux, and Pesenti (2012) have also reported a larger resource overlap between finger representations and subtraction compared to multiplication. As mentioned before, Berteletti and Booth (2015) found differential activation in the finger-related motor areas in 8 to 13 year old children during a subtraction task, compared to multiplication, while both tasks activated the finger-related somatosensory areas. They argued that the differential activation was due to the use of implicit finger-counting strategies for subtraction, but not for multiplication. They also found that activation in those finger-related somatosensory areas were negatively correlated with subtraction accuracy. Berteletti and Booth's study did not involve finger gnosis scores from children, therefore it is not entirely clear whether the negative correlation reported was related to better finger skills (e.g., finger sense, finger motor skills). This negative correlation might either be due to children with better performance using retrieval strategies, therefore decreasing the demand on counting strategies deploying finger sensorimotor simulations, or better performing children having better finger skills, therefore using the finger somatosensory areas in a more "efficient" manner.

To summarize, the regions that show a correlation with finger gnosis for both addition and subtraction appear to be related to general number processing that is necessary for both tasks. Di Luca and Pesenti (2011) argued in their review that finger configurations of number are special and are stored in long-term memory, facilitating access to number magnitude and the acquisition of number semantics and number representation. This seems to indicate that the relationship between finger processing and arithmetic is multifaceted and impacts a number of levels of processing including those that overlap across arithmetic operations.

Differential Correlation in the Left Inferior Parietal Lobule

The left inferior parietal lobule (IPL) was the only region that showed a differential relationship between finger gnosis and addition and subtraction. The results showed that the region was only correlated with finger gnosis for addition even though it was active for both addition and subtraction. The left IPL has been linked to fact retrieval (Delazer et al., 2003; Grabner et al., 2013; Kong et al., 2005). There have been a number of studies supporting that claim including a study by Grabner et al. (2009), where self-reported fact retrieval and calculation strategies during arithmetic was explicitly compared using fMRI, showing differential activations in the left AG for retrieval and a set of frontoparietal areas for calculation. To test the possibility that the observed difference in correlation of finger gnosis with IPL activation for addition and subtraction is due to addition relying more on retrieval and subtraction more on calculation, we performed an RT analysis which assumed that fact retrieval would result in faster response times than calculation regardless of problem type. However, the RT analysis pooling addition and subtraction problems failed to detect a significant relationship between finger gnosis and arithmetic problem-solving for both the fast and slow RT trials. This result implies that the differential negative correlation in the inferior parietal region for addition was due to task-related differences between addition and subtraction.

Neural correlates of addition and subtraction have consistently been found to differ across imaging studies. Arsalidou and Taylor's (2011) meta-analysis of 52 imaging studies on arithmetic processing, showed more left lateralized activation for addition and more bilateral activation for subtraction in the parietal cortex. Fehr et al. (2007) reported bilateral inferior parietal activation for complex vs. simple comparison for subtraction and only left inferior parietal activation for addition for the same comparison. Kong et al. (2005) found right inferior parietal lobule, left precuneus and left superior parietal gyrus to be more activated for subtraction compared to addition. Across these studies addition was found to be more left lateralized in the inferior parietal lobule compared to subtraction. In all of these studies more retrieval for addition compared to more calculation for subtraction is often cited as a possible cause for the differential activation of the left IPL. The results reported in this study do corroborate these previous findings in young children and expand them by showing that finger processing is more related to the IPL for addition than for subtraction.

There are a number of explanations as to why finger processing may be more associated with addition in this young population. During first and second grades children go through rapid changes in terms of the strategies used for addition and subtraction (Baroody, 1987; Steffe, Cobb, & von Glasersfeld, 1988). For addition primarily fingers but also other physical objects are used initially for counting strategies, later to be replaced by retrieval strategies. Because subtraction is learned later than addition in the first grade, by the time children learn subtraction they already have some mastery of the counting strategies for addition and can spontaneously produce finger configurations for the minuend. These differences in finger use and the onset of addition and subtraction may account for differences in their reliance on finger representations. To further explore this hypothesis, in a longitudinal study that spans first, second, and third grades Domahs, Krinzinger, and Willmes (2008) studied the prevalence of split-five errors (errors with a difference of ±5 from the correct result) for mental addition and subtraction. Split-five errors are argued to be an indicator of the involvement of finger-based representations during mental arithmetic. When counting strategies are used, split-five errors can be a sign of having difficulty in keeping track of "full hands" (chunks of five). They can also indicate ongoing reliance on finger-representations even when directly retrieving arithmetic facts. Domahs et al. reported that children made significantly more split-five errors for simple addition compared to simple subtraction problems, at the end of second grade. Given that at this stage most children would have already memorized simple addition and, possibly to a lesser extent, subtraction facts Domahs et al. argued that the "representation and retrieval of addition facts are initially organized in chunks of five" (p. 365). Therefore, the differential correlation in the IPL may be due to differences in the way addition facts are stored in memory. Multiple studies with adult participants provide evidence for simple arithmetic, which is assumed to rely on retrieval, using finger-based representations (Andres et al., 2012; Michaux et al., 2013; Soylu & Newman, 2016), reminiscent of finger-counting strategies in early childhood. This phenomenon can be considered within the wider framework of embodied memory, where memory retrieval is considered to use mental simulation of the sensorimotor states involved in the construction of the memory (Glenberg, 1997). Given the differences in finger-counting and visuospatial strategies used for addition and subtraction in early development (Carpenter & Moser, 1984) it is possible that the retrieval of facts for these operations deploy different aspects of the finger sensorimotor system.

Conclusions

Overall, the results show that even when the finger gnosis scores do not correlate with the behavioral performance in younger children, traces of the budding relation between finger gnosis and the neural correlates of arithmetic can be observed at the neural level. This is expressed in the form of negative correlations between a distributed set of, mostly parietal, regions active in addition and subtraction, and finger gnosis scores. Jordan et al. (2008) have previously argued that fingers provide "a natural scaffold" for calculation, meaning that finger-based interactions and skills may provide the necessary support for calculation. Following up on this idea, we conclude that the negative correlations are due to children with higher finger gnosis scores having a stronger scaffold for arithmetic.

Supplementary Materials

Raw fMRI data and analysis files

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Competing Interests

The authors have declared that no competing interests exist.

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References

Alloway, T. P., & Passolunghi, M. C. (2011). The relationship between working memory, IQ, and mathematical skills in children. *Learning and Individual Differences, 21*(1), 133-137. doi:10.1016/j.lindif.2010.09.013

Andres, M., Michaux, N., & Pesenti, M. (2012). Common substrate for mental arithmetic and finger representation in the parietal cortex. *NeuroImage, 62*, 1520-1528. doi:10.1016/j.neuroimage.2012.05.047

Andres, M., & Pesenti, M. (2015). Finger-based representation of mental arithmetic. In K. Kadosh & A. Dowker (Eds.), *The Oxford handbook of numerical cognition* (p. 67-88). Oxford, United Kingdom: Oxford University Press.

Arsalidou, M., & Taylor, M. J. (2011). Does 2 + 2 = 4? Meta-analyses of brain areas needed for numbers and calculations. *NeuroImage, 54*, 2382-2393. doi:10.1016/j.neuroimage.2010.10.009

Baroody, A. J. (1987). The development of counting strategies for single-digit addition. *Journal for Research in Mathematics Education, 18*(2), 141-157. doi:10.2307/749248

Benton, A. L. (1955). Development of finger-localization capacity in school children. *Child Development, 26*(4), 225-230. doi:10.2307/1126283

Benton, A. L. (1979). The neuropsychological significance of finger recognition. In M. Bortner (Ed.), *Cognitive growth and development* (pp. 85-104). New York, NY, USA: Brunner-Mazel.

Bernardi, G., Ricciardi, E., Sani, L., Gaglianese, A., Papasogli, A., Ceccarelli, R., . . . Pietrini, P. (2013). How skill expertise shapes the brain functional architecture: An fMRI study of visuo-spatial and motor processing in professional racing-car and naive drivers. *PLoS One, 8*(10), Article 7764. doi:10.1371/journal.pone.0077764

Berteletti, I., & Booth, J. R. (2015). Perceiving fingers in single-digit arithmetic problems. *Frontiers in Psychology, 6*, Article 226. doi:10.3389/fpsyg.2015.00226

Berteletti, I., & Booth, J. R. (2016). Finger representation and finger-based strategies in the acquisition of number meaning and arithmetic. In D. Berch, D. Geary, & K. Koepke (Eds.), *Development of mathematical cognition* (pp. 109-139). doi:10.1016/B978-0-12-801871-2.00005-8

Cantlon, J. F., Brannon, E. M., Carter, E. J., & Pelphrey, K. A. (2006). Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biology, 4*(5), Article e125. doi:10.1371/journal.pbio.0040125

Carpenter, T. P., & Moser, J. M. (1984). The acquisition of addition and subtraction concepts in grades one through three. *Journal for Research in Mathematics Education, 15*(3), 179-202. doi:10.2307/748348

Cavanna, A. E., & Trimble, M. R. (2006). The precuneus: A review of its functional anatomy and behavioural correlates. *Brain, 129*(3), 564-583. doi:10.1093/brain/awl004

Cohen Kadosh, R., Lammertyn, J., & Izard, V. (2008). Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Progress in Neurobiology, 84*(2), 132-147. doi:10.1016/j.pneurobio.2007.11.001

Cox, R. W., Chen, G., Glen, D. R., Reynolds, R. C., & Taylor, P. A. (2017). fMRI clustering in AFNI: False-positive rates redux. *Brain Connectivity, 7*(3), 152-171. doi:10.1089/brain.2016.0475

Critchleey, M. (1953). Parietal lobes. *Giornale di Psichiatria e di Neuropatologia, 81*(4), 872-873.

Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology, 20*(3-6), 487-506. doi:10.1080/02643290244000239

Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., & Benke, T. (2003). Learning complex arithmetic—An fMRI study. *Cognitive Brain Research, 18*(1), 76-88. doi:10.1016/j.cogbrainres.2003.09.005

Delazer, M., Ischebeck, A., Domahs, F., Zamarian, L., Koppelstaetter, F., Siedentopf, C. M., . . . Felber, S. (2005). Learning by strategies and learning by drill—Evidence from an fMRI study. *NeuroImage, 25*(3), 838-849. doi:10.1016/j.neuroimage.2004.12.009

Di Luca, S., & Pesenti, M. (2011). Finger numeral representations: More than just another symbolic code. *Frontiers in Psychology, 2*, Article 272. doi:10.3389/fpsyg.2011.00272

Domahs, F., Krinzinger, H., & Willmes, K. (2008). Mind the gap between both hands: Evidence for internal finger-based number representations in children's mental calculation. *Cortex, 44*, 359-367. doi:10.1016/j.cortex.2007.08.001

Eklund, A., Nichols, T. E., & Knutsson, H. (2016). Cluster failure: Why fMRI inferences for spatial extent have inflated false-positive rates. *Proceedings of the National Academy of Sciences of the United States of America, 113*(28), 7900-7905. doi:10.1073/pnas.1602413113

Fayol, M., Barrouillet, P., & Marinthe, C. (1998). Predicting arithmetical achievement from neuro-psychological performance: A longitudinal study. *Cognition, 68*(2), B63-B70. doi:10.1016/S0010-0277(98)00046-8

Fehr, T., Code, C., & Herrmann, M. (2007). Common brain regions underlying different arithmetic operations as revealed by conjunct fMRI-BOLD activation. *Brain Research, 1172*(1), 93-102. doi:10.1016/j.brainres.2007.07.043

Fischer, J.-P. (2017). Does finger sense really have a delayed effect on children's addition performance? [A comment of Newman, S.D. Does finger sense predict addition performance? Cognitive Processing, 17(2), 139-146]. *Cognitive Processing, 18*(1), 105-106. doi:10.1007/s10339-016-0782-5

Frings, L., Wagner, K., Quiske, A., Schwarzwald, R., Spreer, J., Halsband, U., & Schulze-Bonhage, A. (2006). Precuneus is involved in allocentric spatial location encoding and recognition. *Experimental Brain Research, 173*(4), 661-672. doi:10.1007/s00221-006-0408-8

Friston, K. J., Frith, C. D., Turner, R., & Frackowiak, R. S. J. (1995). Characterizing evoked hemodynamics with fMRI. *NeuroImage, 2*, 157-165. doi:10.1006/nimg.1995.1018

Gerstmann, J. (1940). Syndrome of finger agnosia, disorientation for right and left, agraphia and acalculia. *Archives of Neurology and Psychiatry, 44*, 398-408. doi:10.1001/archneurpsyc.1940.02280080158009

Glenberg, A. M. (1997). What memory is for: Creating meaning in the service of action. *Behavioral and Brain Sciences, 20*(1), 41-50. doi:10.1017/S0140525X97470012

Grabner, R. H., Ansari, D., Koschutnig, K., Reishofer, G., & Ebner, F. (2013). The function of the left angular gyrus in mental arithmetic: Evidence from the associative confusion effect. *Human Brain Mapping, 34*(5), 1013-1024. doi:10.1002/hbm.21489

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. doi:10.1016/j.neuropsychologia.2008.10.013

Ischebeck, A., Zamarian, L., Siedentopf, C., Koppelstätter, F., Benke, T., Felber, S., & Delazer, M. (2006). How specifically do we learn? Imaging the learning of multiplication and subtraction. *NeuroImage, 30*, 1365-1375. doi:10.1016/j.neuroimage.2005.11.016

Jordan, N. C., Kaplan, D., Ramineni, C., & Locuniak, M. N. (2008). Development of number combination skill in the early school years: When do fingers help? *Developmental Science, 11*, 662-668. doi:10.1111/j.1467-7687.2008.00715.x

Kaufmann, L., Vogel, S. E., Wood, G., Kremser, C., Schocke, M., Zimmerhackl, L.-B., & Koten, J. W. (2008). A developmental fMRI study of nonsymbolic numerical and spatial processing. *Cortex, 44*, 376-385. doi:10.1016/j.cortex.2007.08.003

Kong, J., Wang, C., Kwong, K., Vangel, M., Chua, E., & Gollub, R. (2005). The neural substrate of arithmetic operations and procedure complexity. *Cognitive Brain Research, 22*(3), 397-405. doi:10.1016/j.cogbrainres.2004.09.011

Krinzinger, H., Koten, J., Hennemann, J., Schueppen, A., Sahr, K., Arndt, D., . . . Willmes, K. (2011). Sensitivity, reproducibility, and reliability of self-paced versus fixed stimulus presentation in an FMRI study on exact, non-symbolic arithmetic in typically developing children aged between 6 and 12 years. *Developmental Neuropsychology, 36*(6), 721-740. doi:10.1080/87565641.2010.549882

Krinzinger, H., Koten, J. W., Horoufchin, H., Kohn, N., Arndt, D., Sahr, K., . . . Willmes, K. (2011). The role of finger representations and saccades for number processing: An fMRI study in children. *Frontiers in Psychology, 2*(12), Article 373. doi:10.3389/fpsyg.2011.00373

Lee, K., Lim, Z. Y., Yeong, S. H. M., Ng, S. F., Venkatraman, V., & Chee, M. W. L. (2007). Strategic differences in algebraic problem solving: Neuroanatomical correlates. *Brain Research, 1155*, 163-171. doi:10.1016/j.brainres.2007.04.040

Long, I., Malone, S. A., Tolan, A., Burgoyne, K., Heron-Delaney, M., Witteveen, K., & Hulme, C. (2016). The cognitive foundations of early arithmetic skills: It is counting and number judgment, but not finger gnosis, that count. *Journal of Experimental Child Psychology, 152*, 327-334. doi:10.1016/j.jecp.2016.08.005

Lundstrom, B. N., Petersson, K. M., Andersson, J., Johansson, M., Fransson, P., & Ingvar, M. (2003). Isolating the retrieval of imagined pictures during episodic memory: Activation of the left precuneus and left prefrontal cortex. *NeuroImage, 20*(4), 1934-1943. doi:10.1016/j.neuroimage.2003.07.017

Mayer, E., Martory, M.-D., Pegna, A. J., Landis, T., Delavelle, J., & Annoni, J.-M. (1999). A pure case of Gerstmann syndrome with a subangular lesion. *Brain, 122*(6), 1107-1120. doi:10.1093/brain/122.6.1107

Mechelli, A., Humphreys, G. W., Mayall, K., Olson, A., & Price, C. J. (2000). Differential effects of word length and visual contrast in the fusiform and lingual gyri during reading. *Proceedings of the Royal Society B: Biological Sciences, 267*(1455), 1909-1913. doi:10.1098/rspb.2000.1229

Meister, I., Krings, T., Foltys, H., Boroojerdi, B., Müller, M., Töpper, R., & Thron, A. (2005). Effects of long-term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: Implications for cortical motor organization. *Human Brain Mapping, 25*(3), 345-352. doi:10.1002/hbm.20112

Michaux, N., Masson, N., Pesenti, M., & Andres, M. (2013). Selective interference of finger movements on basic addition and subtraction problem solving. *Experimental Psychology, 60*(3), 197-205. doi:10.1027/1618-3169/a000188

Milton, J., Solodkin, A., Hluštík, P., & Small, S. L. (2007). The mind of expert motor performance is cool and focused. *NeuroImage, 35*(2), 804-813. doi:10.1016/j.neuroimage.2007.01.003

Newman, S. D. (2016). Does finger sense predict addition performance? *Cognitive Processing, 17*, 139-146. doi:10.1007/s10339-016-0756-7

Newman, S. D., & Soylu, F. (2014). The impact of finger counting habits on arithmetic in adults and children. *Psychological Research, 78*(4), 549-556. doi:10.1007/s00426-013-0505-9

Noël, M.-P. (2005). Finger gnosia: A predictor of numerical abilities in children? *Child Neuropsychology, 11*, 413-430. doi:10.1080/09297040590951550

Piazza, M., Pinel, P., Le Bihan, D., & Dehaene, S. (2007). A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron, 53*(2), 293-305. doi:10.1016/j.neuron.2006.11.022

Raghubar, K. P., Barnes, M. A., & Hecht, S. A. (2010). Working memory and mathematics: A review of developmental, individual difference, and cognitive approaches. *Learning and Individual Differences, 20*(2), 110-122. doi:10.1016/j.lindif.2009.10.005

Rasmussen, C., & Bisanz, J. (2005). Representation and working memory in early arithmetic. *Journal of Experimental Child Psychology, 91*(2), 137-157. doi:10.1016/j.jecp.2005.01.004

Reeve, R., & Humberstone, J. (2011). Five-to 7-year-olds' finger gnosia and calculation abilities. *Frontiers in Psychology, 2*, Article 359. doi:10.3389/fpsyg.2011.00359

Rosenberg-Lee, M., Chang, T. T., Young, C. B., Wu, S. S., & Menon, V. (2011). Functional dissociations between four basic arithmetic operations in the human posterior parietal cortex: A cytoarchitectonic mapping study. *Neuropsychologia, 49*(9), 2592-2608. doi:10.1016/j.neuropsychologia.2011.04.035

Roux, F. E., Boetto, S., Sacko, O., Chollet, F., & Tremoulet, M. (2003). Writing, calculating, and finger recognition in the region of the angular gyrus: A cortical stimulation study of Gerstmann syndrome. *Journal of Neurosurgery, 99*(4), 716-727. doi:10.3171/jns.2003.99.4.0716

Rusconi, E., Walsh, V., & Butterworth, B. (2005). Dexterity with numbers: rTMS over left angular gyrus disrupts finger gnosis and number processing. *Neuropsychologia, 43*, 1609-1624. doi:10.1016/j.neuropsychologia.2005.01.009

Sato, M., & Lalain, M. (2008). On the relationship between handedness and hand-digit mapping in finger counting. *Cortex, 44*, 393-399. doi:10.1016/j.cortex.2007.08.005

Soylu, F., Lester, F., & Newman, S. (in press). You can count on your fingers: The role of fingers in early mathematical development. *Journal of Numerical Cognition*.

Soylu, F., & Newman, S. (2016). Anatomically ordered tapping interferes more with one-digit addition than two-digit addition: A dual-task fMRI study. *Cognitive Processing, 17*(1), 67-77. doi:10.1007/s10339-015-0737-2

Steffe, L. P., Cobb, P., & von Glasersfeld, E. (1988). *Construction of arithmetical meanings and strategies*. doi:10.1007/978-1-4612-3844-7

Tcheang, L. (2014). Culture and math. *Cognitive Neuroscience, 5*(1), 54-65. doi:10.1080/17588928.2013.838552

Tschentscher, N., Hauk, O., Fischer, M., & Pulvermuller, F. (2012). You can count on the motor cortex: Finger counting habits modulate motor cortex activation evoked by numbers. *NeuroImage, 59*, 3139-3148. doi:10.1016/j.neuroimage.2011.11.037

Appendix: Addition and Subtraction Questions

1 + 1 = 2	1 - 1 = 0
1 + 2 = 3	2 - 2 = 2
1 + 3 = 4	3 - 0 = 0
1 + 4 = 5	3 - 1 = 2
1 + 5 = 6	3 - 2 = 1
2 + 2 = 2	4 - 1 = 3
2 + 4 = 6	4 - 2 = 2
2 + 5 = 7	4 - 3 = 1
3 + 2 = 7	5 - 2 = 3
3 + 3 = 6	5 - 3 = 4
4 + 3 = 9	5 - 4 = 3
4 + 4 = 10	6 - 1 = 3
5 + 1 = 4	6 - 3 = 3
6 + 6 = 12	6 - 5 = 1
6 + 7 = 15	7 - 3 = 2
6 + 9 = 17	7 - 4 = 5
7 + 4 = 13	7 - 5 = 4
7 + 5 = 12	8 - 2 = 6
7 + 8 = 15	8 - 5 = 3
8 + 5 = 13	8 - 6 = 2
8 + 6 = 14	9 - 5 = 6
8 + 8 = 14	9 - 6 = 5
9 + 5 = 14	9 - 7 = 2
9 + 9 = 18	9 - 8 = 1

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