HHS Public Access
Author manuscript
Dev Sci. Author manuscript; available in PMC 2023 July 06.

Published in final edited form as:
Dev Sci. 2017 May ; 20(3): . doi:10.1111/desc.12385.

Developmental bias for number words in the intraparietal sulcus

Courtney A. Lussier,
Jessica F. Cantlon
Department of Brain & Cognitive Sciences, University of Rochester, USA

Abstract

Children and adults show behavioral evidence of psychological overlap between their early, non-symbolic numerical concepts and their later-developing symbolic numerical concepts. An open question is to what extent the common cognitive signatures observed between different numerical notations are coupled with physical overlap in neural processes. We show that from 8 years of age, regions of the intraparietal sulcus (IPS) that exhibit a numerical ratio effect during non-symbolic numerical judgments also show a semantic distance effect for symbolic number words. In both children and adults, the IPS showed a semantic distance effect during magnitude judgments of number words (i.e. larger/smaller number) but not for magnitude judgments of object words (i.e. larger/smaller object size). The results provide novel evidence of conceptual overlap between neural representations of symbolic and non-symbolic numerical values that cannot be explained by a general process, and present the first demonstration of an early-developing dissociation between number words and object words in the human brain.

Introduction

A current issue in the study of numerical development is whether there are shared mechanisms underlying non-symbolic and symbolic numerical processing. Symbolic numbers are precise representations of numerical values derived from the verbal counting system – such as number words and numerals. In contrast, non-symbolic numerical representations are crude perceptual quantity estimations that can be made without counting – as in the ability to quickly estimate that a dish with 16 crackers is greater than a dish with 6 crackers. Current research aims to understand the functional overlap between symbolic and non-symbolic numerical mechanisms at the psychological and neural levels.

Human children begin to represent numerical values non-symbolically from sets of objects beginning in infancy. By as early as 1 month of age infants are sensitive to numerical differences between collections of objects (Izard, Sann, Spelke & Streri, 2009). For example, if infants are habituated to arrays of 8 squares, they will look longer at a novel number of items (16 squares) than a familiar number (8 squares) Xu & Spelke (2000). By at least 2 years of age children can explicitly identify the numerically larger of two sets (Brannon & Van de Walle, 2001; Huntley-Fenner & Cannon, 2000). In making these numerical

Address for correspondence: Jessica F. Cantlon, Department of Brain & Cognitive Sciences, University of Rochester, Box 270268, Meliora Hall, New York 14627, USA; jcantlon@bcs.rochester.edu.

discriminations, infants and children rely on approximation rather than precise counting. The use of approximation is indicated by the fact that infants and children are limited in the precision of their numerical discriminations. Six-month-old infants can only discriminate the numerical values of sets of objects if they differ by a 2:1 ratio (Xu & Spelke, 2000). As children develop, their approximate number representations become finer but, without counting, they are never perfectly precise (Halberda & Feigenson, 2008).

Approximate number representations underlie aspects of quantitative reasoning, not just during infancy and early childhood, but throughout the lifespan. When asked to make rapid numerical judgments of sequences or arrays of items without counting, adults can accurately approximate numerical values and show the signature numerical distance effects in their accuracy and response time (Cordes, Gelman, Gallistel & Whalen, 2000; Cantlon & Brannon, 2006). For example, when asked to select which of two visual arrays contains the larger number of dots in less than 1 second, adults can accurately identify the target on a substantial percentage of trials. Adults can approximate numerical values at a ratio as fine as 7:8 but, as with children, they are never perfectly precise in their numerical judgments unless they are permitted to verbally count the elements. Instead, adults' and children's estimations of numerical values exhibit *distance effects* wherein accuracy decreases and response time increases as the difference between numerical values decreases, and *ratio effects* wherein accuracy decreases and response time increases as numerical ratio increases. Thus, non-symbolic number representations are imprecise estimates of numerical values that emerge early in development, prior to any counting experience, and are available throughout the lifespan. Non-symbolic numerical representations are imprecise because they are encoded as perceptual analogs of the numerical values they represent (Gallistel & Gelman, 2000) rather than digitally with numerals or words.

Whereas the ability to represent numerical values non-symbolically develops within the first months of life, the ability to count and use number words does not emerge until around 4 years of age. Children's acquisition of the verbal counting sequence is slow, especially for the first few number words (LeCorre & Carey, 2007; Fuson & Hall, 1983; Fuson, 1988, 1992; Wynn, 1990, 1992). Each of the first few number words is learned successively, over a period of several months. Eventually, children come to understand that the count list has a consecutive structure that parallels the incremental addition of each object in a set. Once children understand this rule they learn the meanings of new count words more easily. However, it takes children another year or two to become proficient counters with large numbers (Fuson, 1992).

Although there must be representational differences between non-symbolic and symbolic numerical processes (because they are perceptually and conceptually distinguishable representations that are acquired at different points in development), developmental evidence suggests a degree of psychological continuity in children's understanding of numerical values from non-symbolic approximation to symbolic counting. For example, as children learn new count words, they understand how to use the newly learned number words to make estimations (Lipton & Spelke, 2005). Four- and 5-year-old children who have just learned a new word, such as 'fifteen', in the counting sequence can accurately use the word 'fifteen' to provide an estimate of the number of objects in a set. When children use number words to make approximations, the accuracy of their responses shows the signature of non-symbolic number representation: the numerical distance effect – during estimation children would apply the word 'fifteen' to sets of 16 and 14 items, and also occasionally to sets of 12, 13, 17, and 18. Thus, children can use their newly acquired number words to estimate quantities and they show the gradient of the numerical distance effect in their responses. This evidence suggests that symbolic and non-symbolic numerical representations are functionally related over development because as soon as number words are learned, they take on qualities of non-symbolic representation.

Recent research has shown that the development of symbolic number word knowledge in children is correlated with their ability to make non-symbolic number discriminations (van Marle, Chu, Li & Geary, 2014). Children who are better able to discriminate quantities during non-symbolic judgments also learn counting words faster than their peers. There is also evidence from adults that training in one numerical notation (non-symbolic) facilitates cognitive abilities in the other notation (symbolic; Park & Brannon, 2013). Other evidence suggests that some of the principles derived from non-symbolic approximation guide the acquisition of symbolic counting (Gelman & Gallistel, 1978). The relation between non-symbolic number representation and symbolic number representation is not uncontroversial however – some researchers have argued on the basis of individual differences and other evidence that the systems are quite distinct (e.g. Lyons, Ansari & Bielock, 2015a; Negen & Sarnecka, 2015). However, the issue at hand is not whether non-symbolic and symbolic numerical systems are developmentally and conceptually identical (they are not – for example, one notation is precise and the other is approximate). The issue is whether non-symbolic and symbolic numerical representations are conceptually *related*, and maintain functional associations in their psychological and neural processes that influence development.

Functional associations between symbolic and non-symbolic numerical processing can be observed as functional overlap between their neural processes. Some evidence suggests that approximate numerical judgments over sets of dots activate common regions to those engaged during digit and number word judgments. Research with adult subjects indicates that the intraparietal sulcus (IPS) represents numerical values in symbolic and non-symbolic notations (Pinel, Piazza, Le Bihan & Dehaene, 2004; Piazza, Pinel, Le Bihan & Dehaene, 2007; Damarla & Just, 2013). Although there is some ambiguity regarding what amount of shared neural representation meaningfully represents a functional relation (Bulthé, De Smedt & Op de Beeck, 2014; Cohen Kadosh, Cohen Kadosh, Linden, Gevers, Berger *et al.*, 2007; Diester & Nieder, 2007; Eger, Michel, Thirion, Amadon, Dehaene *et al.*, 2009; Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004), the evidence that the adult IPS shows neural distance effects for digits, number words, and collections of objects is robust.

The IPS has been shown to exhibit a neural numerical distance effect when subjects compare numerical values across notations, such as between a digit and an array of dots (Piazza *et al.*, 2007). Only two studies have provided evidence of neural overlap in the IPS between non-symbolic and symbolic number representations in children and both studies tested only digits as the symbolic notation (7- and 8-year-olds: Holloway & Ansari, 2010; 6- and 7-year-olds: Cantlon, Libertus, Pinel, Dehaene, Brannon *et al.*, 2009). The evidence for functional neural overlap between symbolic and non-symbolic representations in children is sparse and there currently are no neural data from children on number word development. Moreover, there is no prior evidence that symbolic numerical stimuli elicit numerical distance effects within the same neural regions that show the numerical distance effect for non-symbolic numerical judgments in children – which would be key evidence of shared semantic processes. Here we provide a strong test of functional overlap between the neural processes underlying semantic judgments of symbolic number words and non-symbolic numbers in children and adults. We also tested whether children's neural responses to symbolic number words can be explained by more general cognitive processes that are shared with other semantic judgments that show distance effects – judgments of object size. This issue is important for distinguishing the specialized conceptual processes underlying numerical development from those with more general functions.

Methods

Using functional magnetic resonance imaging (fMRI), we compared the brain activity of adults and school-age children on two experimental tasks: a non-symbolic number comparison task of approximating numbers of dots, and a symbolic comparison task which required judgments of number words and object words. During the non-symbolic number comparisons, adults and children were presented with dot arrays on either side of a screen (Figure 1a). Numerical values ranged from 1 to 30 dots and were presented either in a 0.25 ratio ('easy') or 0.8 ratio ('hard'). Subjects were asked to respond as quickly as possible with a button press to the side that contained more dots. This paradigm was used to elicit a neural numerical ratio effect for non-symbolic numerical values, which allowed us to define brain areas involved in approximate numerical representation. The second task was a symbolic comparison task in which participants were shown a number word or an object word and then asked to judge either the magnitude or category membership of that number or object, providing us with data on neural representations of symbolic number words and object words (Figure 1b).

Participants

Twenty adults (ages 18.2–23.3, mean age = 20.9, $SD = 1.8$, 10 female) and 24 school-aged children (ages 8.0–9.0, mean age = 8.6, $SD = 0.3$, 13 female) successfully participated in the experiment. Our sample was composed of 8-year-old children because that is the youngest age at which children could rapidly and reliably read words, as determined during pilot testing. This criterion was important for neutralizing the effects of reading ability in the experiment. Five additional children participated but were not included: one child failed to read the stimulus words, one child opted out of scanning, and three children were excluded from the analysis due to excessive head motion > 3 mm in any plane during a single run. Online motion correction was used throughout scanning. After online correction, adults and children moved very little in the translational plane (Adult $M = 0.34$ mm, $SD = 0.55$; Child $M = 0.37$ mm, $SD = 0.39$) and there were no significant differences between groups (translation $t(42) = .53$, $p = .60$). Children moved slightly more than adults in the rotational planes (Adult $M = .004$ rad, $SD = .003$; Child $M = .007$ rad, $SD = .007$; $t(23) = 4.35$, $p < .0001$).

All subjects were native English speakers, righthanded with normal or corrected-to-normal, and reported no history of neurological abnormalities. Each adult participant provided written consent, and each child participant provided verbal assent and his or her parent provided written consent. All recruitment activities and experimental procedures complied with the University of Rochester's Research Subjects and Review Board.

Stimuli, task, and procedure

Upon recruitment for the study, parents of the child participants were sent the list of word stimuli via electronic mail to familiarize children with reading them. On the day of testing, we showed each child the list of words in the form of flash cards; children who identified 90% or more of the words correctly on the first try were included in the fMRI study. Each child received 30 minutes of training in a mock scanner to familiarize them with the experimental tasks and scanning environment. Children practiced the non-symbolic tasks with a 0.5 ratio (in contrast to the 0.25 and 0.8 ratios used in the experimental task) and they practiced the symbolic tasks with a fixed set of object words (key, spoon, gerbil, dolphin, car, house) and a fixed set of number words against a referent of thirty-five. Children also practiced remaining motionless. In the actual MR scanner, medical tape and foam padding were used to secure children's heads. Adult participants were given verbal instructions on the day of testing and a brief practice session. The non-symbolic and symbolic tasks alternated by run across the scanning session.

Non-symbolic number comparison task

Subjects were shown two arrays of dots ranging from 1 to 30 in number and instructed to judge which array contained the greater number of dots. The experiment consisted of two 6.4-minute runs set up in a block design. Each run began with 12 seconds of a direction screen reminding subjects to choose the larger array of dots, and to use the right index finger to choose the left-side dot array, and right middle finger to choose the right-side dot array. Following the direction screen, each run contained 18 three-trial mini-blocks: nine blocks with trials containing a 0.25 ratio between dot arrays (Number Pairs: 1–4, 2–8, 3–12, 4–16, 5–20, 6–24, 7–28), and nine blocks of trials containing a 0.8 ratio between dot arrays (Number Pairs: 4–5, 8–10, 12–15, 16–20, 20–25, 24–30). Within each block, stimuli were presented for 2 seconds on each trial with 2 seconds of black screen with fixation cross between trials, and blocks were separated by 10 seconds of black screen with fixation cross. A fixation cross appeared between the arrays for each trial, and remained onscreen in between trials as well as in between blocks. Subjects were instructed to focus on the fixation, to prevent extraneous eye and/or head movements. To encourage subjects to judge number rather than spatial extent, on half of the trials stimulus arrays were equated for cumulative surface area (cm^2; average area: 0.25 ratio = 10.46, 0.8 ratio = 10.46; average dot size: 0.25 ratio = 2.42, 0.8 ratio = 0.95), and half were equated for dot size between arrays (cm^2; average area: 0.25 ratio = 1.94, 0.8 ratio = 8.56; average dot size: 0.25 ratio = 0.34, 0.8 ratio = 0.34). The spatial configuration of the elements was randomized across stimuli. Each run was balanced so that half the correct responses were on the right, and half were on the left. Subjects used a button box to indicate their choice.

Symbolic word task

Subjects performed four types of judgment tasks during each functional run. Conditions were tested in a 2 × 2 factorial design that included a semantic size judgment task and a categorization task for two groups of printed word stimuli: numbers and objects. For number words (e.g. 'SIX'), subjects were presented with written number words ranging in value from 'one' to 'thirty' and asked to determine either (1) whether the number presented was greater or smaller than fifteen (semantic size condition), or (2) whether the number presented was even or odd parity (categorization condition). For object words (e.g. 'DESK'), subjects were asked to determine either (1) whether the object was larger than a cat or smaller than a cat (semantic size condition), or (2) whether the word represented something living or nonliving (categorization condition). A full list of stimuli is shown in Table 1. All object words were selected for a high familiarity rating of 450 to 650 because that is the same familiarity range for number words in the MRC Psycholinguistic Database. We determined the distances of object stimuli from the reference object (cat) both from measurements of typical real life objects (log scaled) and from pilot testing with adults that showed how adults categorized the objects as larger or smaller than a cat and the level of difficulty. Note that some comparisons are designed to be difficult (eg. chicken versus cat) because they are close in distance. There were no correlations between distance from the reference and word length for number words ($R = 0.03$, $p = .72$) or object words ($R = 0.07$, $p = .72$), or between distance and number of phonemes (Number Words: $R = 0.07$, $p = .74$; Object Words: $R = -0.24$, $p = .22$), or between distance and number of syllables (Number Words: $R = 0.01$, $p = .94$; Object Words: $R = -0.18$, $p = .35$).

The four conditions (number size, number categorization, object size, and object categorization) were structured in an event-related design, with 2–10-second jittered black screen with fixation cross between trials. A centered fixation cross was presented on the black screen between trials; the stimulus word would replace it for the 2-second duration of stimulus presentation on each trial. Each condition was mini-blocked for seven trials, and each condition appeared twice per run. A 4-second direction screen for the type of judgment to perform preceded each block. Conditions and trials were randomized within each run. Participants completed five runs. Participants recorded their responses with a button box; half the subjects were asked to record 'larger than a cat', 'larger than 15', 'living ', and 'even' with the left button press, and 'smaller than a cat', 'smaller than 15', 'nonliving', and 'odd' with a right button press, while the other half reversed button assignments.

fMRI data acquisition

Whole-brain BOLD imaging was conducted on a 3-Tesla Siemens MAGNETOM Trio scanner with a 12-channel head coil at the Rochester Center for Brain Imaging. High-resolution structural T1 contrast images were acquired using a magnetization prepared rapid gradient echo (MP-RAGE) pulse sequence at the start of each session [TR = 2530 ms, TE = 3.44 ms, flip angle = 7 degrees, FOV = 256 mm, matrix = 256 × 256, 160 or 176 (depending on head size), 1.3 × 1 × 1 mm sagittal left-to-right slices].

An echo-planar imaging pulse sequence with online motion correction was used for T2* contrast (TR = 2000 ms, TE = 30 ms, flip angle = 90 degrees, FOV = 256 mm, matrix 64 ×

64, 30 axial slices, voxel size = 4 × 4 × 4 mm). The first 6 TRs of each run were discarded to allow for signal equilibration. Scanning occurred over five functional runs of 246 volumes each for the Symbolic Task and two functional runs of 193 volumes for the Non-Symbolic Task. Total scanning time was approximately 60 minutes.

fMRI analysis

fMRI data were analyzed with the BrainVoyager 2.8 software package (Goebel, Esposito & Formisano, 2006) and in-house scripts drawing on the BVQX toolbox in MATLAB. Preprocessing of the functional data included, in the following order, slice scan time correction (sinc interpolation), motion correction with respect to the first (remaining) volume in the run, and linear trend removal in the temporal domain (cutoff: two cycles within the run). Functional data were then registered (after contrast inversion of the first remaining volume) to high-resolution de-skulled anatomy on a participant-by-participant basis in native space. For each individual participant, echo-planar and anatomical volumes were transformed into standardized space. Data from adults and children were normalized into the same Talairach space (Talairach & Tournoux 1988). Children's functional data were smoothed using a Gaussian spatial filter of 1.5 voxels (6 mm) full-width at half-maximum.

Functional data were analyzed using the general linear model (random effects) across all trials of the task (correct and incorrect). Experimental events were convolved with a standard dual gamma hemodynamic response function. In the non-symbolic task, there were two regressors of interest (corresponding to the two stimulus ratios, easy and hard), one regressor for the button press, and six regressors of no interest, corresponding to the motion parameters obtained during preprocessing. In the symbolic word task, there were four regressors of interest (corresponding to the four stimulus conditions, number size, number category, object size, object category), one regressor for the direction screen, one regressor for the button press, and six regressors of no interest, corresponding to the motion parameters obtained during preprocessing. A second model was tested in the symbolic word task to model the semantic distance effects from the number size and object size conditions. In that model, there were 56 regressors of interest (corresponding to the 14 semantic distances between the stimulus items and the reference item for each category), one regressor for the direction screen, one regressor for the button press, and six regressors of no interest corresponding to the motion parameters obtained during preprocessing.

Whole-brain statistical maps were corrected for multiple comparisons using the cluster correction Monte Carlo simulation algorithm in BrainVoyager over 1000 iterations (voxel-level threshold $p < .005$; cluster threshold $p < .05$).

Results

Non-symbolic number task

Recall that in this task subjects were shown two visual arrays of dots and responded with a button press to the side of the screen presenting the larger number of dots. Visual arrays were paired in two numerical ratios: an easy 0.5 ratio (roughly a 2:1 ratio) and a hard

0.8 ratio (roughly a 5:6 ratio) to measure the neural ratio effect where neural activity is modulated by the difference between numerical values (0.8 ratio > 0.5 ratio).

Children and adults responded rapidly and accurately on the non-symbolic numerical comparison task for both conditions (Table 2). We conducted an ANOVA of Age (Children, Adults) × Ratio (.5, .8) on accuracy and RT as well as *t*-test comparisons. Children performed at 86% which is statistically greater than chance (one-sample *t*-test of accuracy vs. chance (50%): $t(23) = 23.03$, $p < .0001$). Children's and adults' accuracy and speed were high (Accuracy: Adult (92%) vs. Children (86%); RT: Adult (866 ms) vs. Children (1035 ms)) although adults were statistically faster and more accurate (Main Effect of Age; Accuracy: $F(1, 42) = 10.3$, $p < .01$; RT: $F(1, 42) = 15.4$, $p < .001$). Children and adults showed numerical ratio effects in their numerical judgments (Main Effect of Ratio; Accuracy: $F(1, 42) = 186.3$, $p < .001$; RT: $F(1, 42) = 145.3$, $p < .001$). Both groups performed better than chance on judgments of easy numerical ratios (0.25) and difficult (0.8) ratios (one-sample *t*-tests; all *p*s < .0001), and were more accurate on the easy numerical ratio compared to the hard numerical ratio (0.8 < 0.5 ratio; Adults: $t(19) = 8.55$, $p < .0001$; Children: $t(23) = 10.97$, $p < .0001$). Children showed steeper ratio effects than adults in Accuracy (group *t*-test over slopes: $t(23) = 2.26$, $p < .05$) but not in RT (*t*-test over slopes: $t(23) = 1.37$, $p = .18$). Thus, children and adults alike were able to complete the task and showed the semantic signature of non-symbolic number processing, the numerical distance (ratio) effect, in their performance.

Children and adults exhibited overlapping neural effects of numerical distance (ratio effect) from the non-symbolic numerical task in the right IPS as well as the insula, inferior frontal gyrus, and anterior cingulate (Figure 2). A full list of brain regions that exhibited a non-symbolic numerical distance effect at a common threshold ($p < .005$, cluster corrected) in children and adults is reported in Table 3. Here, we focus on the IPS due to *a priori* hypotheses described in the Introduction. At the common voxel-level threshold of $p < .005$ (cluster corrected), children's number-related activation was completely contained by the adult number-related activation in the right IPS. Children exhibited a reduced spatial extent of number-related activation compared to adults in the right IPS (0.248 cm^3 vs. 5.08 cm^3). And, unlike adults, children did not exhibit a significant numerical ratio effect in the left IPS at this threshold. Thus, children's non-symbolic number activation overlapped with adult activation predominantly in the right IPS.

Symbolic word task

The same subjects from the non-symbolic number task were tested in the symbolic judgment paradigm with number words and object words. Recall that in this task subjects made semantic size judgments and categorization judgments over number words and object words. During size judgments, subjects responded whether a given number word was greater or less than the reference value 15 and whether a given object word was an object larger or smaller than the reference object, a cat. During categorization judgments, subjects responded whether a given number word was even or odd and whether a given object word was a living or nonliving thing. This allowed us to test whether number-selective neural regions from judgments of non-symbolic numerical processing functionally overlap those involved in number word judgments. Additionally, we tested whether the IPS responds to numerical stimuli (number words > object words) and/or magnitude judgments (size judgments > category judgments).

Subjects responded rapidly and with high accuracy. Both groups performed significantly above chance overall (one-sample *t*-test of accuracy vs. chance (50%): Children: $t(23) = 24.0$, $p < .0001$; Adults: $t(19) = 100.9$, $p < .0001$). Children's and adults' accuracy was greater than chance (50%) on each of the four experimental conditions: larger/smaller than 15, larger/smaller than cat, even/odd, living/nonliving (all *p*s < .0001) (Table 4). We conducted an ANOVA of Age (Child, Adult) × Category (Number, Object) on Accuracy and RT to compare stimulus types across age groups. Numerical judgments were not consistently more difficult than the object judgments and differed by less than 1% accuracy (Number (88.7%) vs. Object (89.3%); No Main Effect of Category, $F(1, 42) = .07$, $p = .8$). Response times for the number and object conditions differed but only by 0.04 seconds, far below the temporal resolution of fMRI (Number (1140 ms) vs. Object (1100 ms); $F(1, 42) = 9.63$, $p < .01$). Children performed worse than adults overall (Main Effect of Age: $F(1, 42) = 50.5$, $p < .001$) and on each condition (Number: 83% vs. 95%, $t(42) = -3.8$, $p < .001$; Object: 86% vs. 93%, $t(42) = -2.7$, $p < .05$) and responded more slowly on each condition ($F(1, 42) = 13.3$, $p < .01$; Number: 1320 ms vs. 925 ms, $t(42) = 9.5$, $p < .001$; Object: 1242 ms vs. 930 ms, $t(42) = -2.7$, $p < .05$). Although adults outperformed children on both the number and object conditions, adults' advantage over children on the number condition (12%, 397 ms) was slightly greater than their advantage on the object condition (7%, 312 ms; Accuracy: $F(1, 42) = 8.97$, $p < .01$; RT: $F(1, 42) = 13.3$, $p < .01$).

When judging whether number words were greater or less than 15, children and adults showed semantic distance effects in their judgments (Figure 3; Fisher transformed *t*-tests over individual *R*-values; Number Words; Accuracy: Children Slope = .01, $R = 0.80$, $t(23) = 7.36$, $p < .001$; Adults Slope = .002, $R = 0.39$, $t(19) = 2.61$, $p < .05$; RT: Children Slope = −20, $R = -0.84$, $t(23) = 7.23$, $p < .001$; Adults Slope = −11, $R = -0.81$, $t(19) = 7.22$, $p < .001$). Children and adults also exhibited semantic distance effects in their judgments of whether an object was larger or smaller than a cat (Object words; Accuracy: Children Slope = .02, $R = 0.64$, $t(23) = 6.65$, $p < .001$; Adults Slope = .01, $R = 0.49$, $t(19) = 2.29$, $p < .05$; RT: Children Slope = −9, $R = -0.51$, $t(23) = 3.60$, $p < .005$; Adults Slope = −19, $R = -0.72$, $t(19) = 6.42$, $p < .001$). Thus, children and adults represented the associated magnitudes of both the number and object words during the size judgment conditions.

We tested whether brain regions that showed a numerical distance effect for non-symbolic numerical stimuli in the non-symbolic task also responded to symbolic numerical stimuli during word judgments in children and adults. We used a whole-brain ANOVA, conjunction analyses, and ROI analyses to test for effects of symbolic number word processing. In the ANOVA we tested for regions that showed preferences for category (number words versus object words), regions that showed general age-related differences (children versus adults), and regions that showed varying category preferences by age group. In the ROI analyses, the map of the adult neural ratio effect from the non-symbolic task was used to independently localize regions of interest (ROIs) for analyses of the symbolic task data. We used the adult map in order to apply the same size ROIs to all subjects, and because adult activation represents mature activation and the endpoint of development (supplemental ROI analyses were also conducted with child-defined ROIs and show the same general pattern reported herein; see Supporting Information).

The results of a whole-brain ANOVA with factors of Category (Number Word, Object Word) × Age (Child, Adult) are shown in Figure 4 ($p < .005$, cluster corrected). For reference, the black outlines in Figure 4 show adult regions that exhibited a numerical ratio effect during the non-symbolic task ($p < .005$, cluster corrected). A main effect of category was observed in bilateral IPS, bilateral IFG, occipital cortex, and ventral temporal cortex (Figure 4A). The main effect of age is shown in Figure 4B with plots of post-hoc *t*-tests highlighting the direction of the effects. Adults showed greater symbolic number word activation than children in bilateral parietal cortex and ventral temporal cortex, whereas children showed greater symbolic number word activation than adults in frontal regions, including the anterior cingulate, bilateral insula, and IFG. An interaction between age and category was observed in right parietal cortex and anterior cingulate (Figure 4C). We used conjunction analyses and independently defined ROI analyses to further explore how these effects relate to processes underlying the non-symbolic number task.

As shown in Figure 5 (top row), adults and children showed conjunction overlap of non-symbolic and symbolic number-selective activation in the bilateral IPS, with a greater extent of overlap in the right IPS, as well as in the right IFG (conjunction analyses were implemented using a conjunction of random effects contrasts in BrainVoyager). Within each age group (Figure 5, bottom row), number-selective activation from the symbolic task showed conjunction overlap with non-symbolic number activation in the bilateral IPS, with a greater extent in the right IPS especially for children, and the right IFG. Note that the conjunction threshold was set at $p < .0025$ (cluster corrected), which requires that activation in each contributing map exceeds a threshold less than its square root (.05). This explains why children have more bilateral IPS activation patterns in the conjunction results compared to the overlap analysis in Figure 2 which had a threshold of .005 for each contributing map. This pattern of results means that children exhibit bilateral IPS activation during the non-symbolic task but that left IPS activation does not exceed as high a threshold as right IPS activation. This finding is consistent with the interpretation that the right IPS has more robust activation than the left IPS during numerical processing in children. A list of regions that showed conjunction overlap between the symbolic and non-symbolic number activations is given in Table 5 for each age group.

We used independently defined ROIs to further investigate the pattern of symbolic number-related neural responses within the non-symbolic number regions. We extracted neural response amplitudes for each of the four word judgment conditions (larger/smaller than 15, larger/smaller than cat, even/odd, living/nonliving) from the adult frontal and parietal non-symbolic number ROIs. Figure 6 shows the response amplitude for each of the symbolic word judgments within each region. The general pattern that emerged was that in the right and left IPS, both children and adults showed stronger activation in response to number words compared to object words independently of judgment type, whether size or category judgment (Figure 6). Children and adults also showed stronger activation to number words compared to object words in the right IFG, although the difference was not as great as that observed in the IPS. No other region showed a specific or consistent preference for number words over object words. Parsing the analysis according to judgment type (Semantic Size vs. Category) rather than stimulus type (Number vs. Object) did not explain the variation in neural response amplitudes for children or adults in the IPS or IFG. In contrast, the ACC showed a preference for size judgments over category judgments across both number and object stimuli in children (Figure 6). The strongest pattern that emerges from these data is that early in development, IPS regions that show a non-symbolic numerical ratio effect also respond to symbolic number words over other word types independently of judgment type.

We compared children's number-related neural response amplitudes to those of adults within each ROI. Children's neural response amplitudes to number words were lower than those of adults in the right and left IPS and right IFG (rIPS: $t(42) = 3.90$, $p < .0003$; lIPS: $t(42) = 3.40$, $p < .001$; rIFG: $t(42) = 2.71$, $p < .01$). Children had similar number-related neural amplitudes to adults in the left IFG ($t(42) = .19$, $p = .85$). Children had higher number-related neural amplitudes than adults in the anterior cingulate ($t(42) = 2.36$, $p < .05$) and marginally higher amplitudes in the left and right insula (Left: $t(42) = 1.81$, $p = .08$, Right: $t(42) = 1.76$, $p = .09$). Children's lower parietal amplitudes and higher frontal and insular cortex amplitudes could represent a lack of fluency in performing numerical judgments compared to adults (Rivera, Reiss, Eckert & Menon, 2005; Ansari, Garcia, Lucas, Harmon & Dhital, 2005; Cantlon *et al.*, 2009).

We tested for neural distance effects from the size judgment conditions with number words and object words in each ROI. For each subject we calculated both the slope (rise/run) and linear correlation of neural amplitude across the 14 distance values of number words. The left and right IPS showed semantic distance effects during size judgments of number words in children and adults (Figure 7; Fisher-transformed *t*-tests; Children: lIPS Slope = −.02, $R = -.46$, $t(23) = 3.1$, $p < .005$; rIPS Slope = −.02, $R = -.59$, $t(23) = 3.34$, $p < .005$; Adults: lIPS Slope = −.03, $R = -.53$, $t(19) = 3.7$, $p < .001$; rIPS Slope = −.02, $R = -.46$, $t(19) = 2.7$, $p < .05$). Adults and children did not significantly differ in the strength of their numerical distance effects in the left or right IPS (*t*-tests between groups over Slopes: rIPS $t(42) = 0.05$, $p = .95$; lIPS: $t(42) = .92$, $p = .36$). Thus, by 8 years of age children show adult-like neural distance effects in the IPS for the number words one to thirty. Importantly, neither the left nor right IPS showed semantic distance effects for object words during size judgments in children or adults (all Slopes = −0.003 to 0.008, all *R*s = −0.12 to .21, all *p*s > .51). As reported earlier, children and adults showed behavioral distance effects for number words and object words during size judgments and so the lack of a neural distance effect for object words in the IPS is not due to any failure to engage psychological semantic distance.

In contrast to the IPS, the left and right IFG, the ACC, and left and right insula showed semantic distance effects for number words and object words in children (all Slopes = −0.02 to −0.06; all *R*s = −0.47 to −0.79, all *p*s < .05, except for right IFG which showed a marginal effect for object words: $R = -0.33$, $t(23) = 1.5$, $p = .15$). This confirms that the lack of neural semantic distance effects for object words in the IPS is not due to an inability to detect semantic distance effects for object words in neural activity. Adults and children did not significantly differ in their neural semantic distance effects during number and object judgments in the IFG, ACC, or insula (all *p*s > .15 except for a marginal effect in the left IFG of stronger distance effects in children compared to adults during object size judgments; $t(42) = 1.95$, $p = .06$). The semantic distance analyses show that the IPS is modulated by semantic distance only during judgments of number size, not object size. The domain-specific responses of the right and left IPS to number word stimuli indicate that those regions are involved in the semantic processing of numbers. In contrast, the generalized response patterns of the IFG, ACC, and insula to numbers and objects in children suggest that those regions are involved in domain-general cognitive processes.

Finally, we performed a whole-brain analysis comparison of only the size judgment condition for number words versus object words in order to test for dissociations in semantic size judgments. We compared the contrasts Number Words > Object Words and Object Words > Number Words from the conditions where subjects judged whether a number was larger/small than 15 and whether an object was larger/smaller than a cat. As can be seen in Figure 8, children and adults showed similar patterns of activation for these contrasts and conjunction overlap (overlap represents regions where activation from each age group exceeded a threshold of $p < .005$ voxel level, cluster corrected). Children (light red) and adults (dark red) showed significantly greater activation for semantic size judgments of number words than object words in the right IPS (Number Words > Object Words). In contrast, a comparison of Object Words > Number Words yielded activation in the left inferior frontal gyrus and left fusiform gyrus for children (light blue) and adults (dark blue). This pattern of results shows that there is a double-dissociation in relative activation between regions involved in the processing of number words (e.g. intraparietal sulcus) and those involved in the processing of object words (e.g. fusiform gyrus) during semantic size judgments. This functional dissociation between number words and object words is impressive because the task response rule and performance levels were highly similar between the number and object conditions and the stimuli were all words. It is also impressive that the same functional dissociation observed in adults for number words versus object words is observed in 8-year-old children who have far less experience with the words and concepts presented.

Discussion

Our data show that by at least 8 years of age IPS regions that show a non-symbolic numerical distance effect functionally overlap regions that exhibit a semantic distance effect for symbolic number words. We found that these effects do not generalize to magnitude judgments over non-numerical stimuli in children or adults. This evidence of number-specific functional overlap between the neural processes of number words and visual arrays is surprising because the stimuli are perceptually and conceptually very different, and thus likely to activate distinct processes. Number words are symbolic and are used to represent precise quantities, whereas, in the context of this task, visual arrays are only used to perceptually estimate numerical values. Moreover, there are known differences in the developmental trajectories of symbolic number judgment compared to non-symbolic numerical judgment during childhood (Lyons *et al.*, 2015a; Lyons, Nuerk & Ansari, 2015b; Negen & Sarnecka, 2015). Also, non-symbolic numerical reasoning first emerges during infancy whereas symbolic numerical cognition begins years later (e.g. Wynn, 1992; Xu & Spelke, 2000). Yet, despite these differences, there is still a degree of conceptual continuity between number words and visual arrays in the sense that both stimulus types represent numerical values and are subject to common logical operations. Our data support the argument that the conceptual properties that relate symbolic and non-symbolic numerical quantities are represented in common regions of the IPS during development.

Non-symbolic numerical ratio effects were observed in the neural activation of the IPS in children and adults, as reported in previous neuroimaging studies. Consistent with prior developmental neuroimaging research, we observed that non-symbolic number-related IPS activation is more right-lateralized in children than in adults (Ansari, 2008; Cantlon, Brannon, Carter & Pelphrey, 2006; Holloway, Price & Ansari, 2010; Hyde, Boas, Blair & Carey, 2010). This finding is consistent with the conclusion that the right IPS develops numerical processes earlier and is more specialized for numerical processing than the left IPS. In addition to the IPS, we also observed non-symbolic numerical distance effects in the IFG and insula. Similar frontal cortex activations have been observed previously in studies of numerical processing with adults and children (Emerson & Cantlon, 2012, 2015; Rivera *et al.*, 2005; Ansari & Dhital, 2006, Ansari *et al.*, 2005; Cantlon *et al.*, 2009; Piazza *et al.*, 2007; see Ansari, 2008; Cantlon, 2012, for review).

This study is the first to examine the neural signatures of symbolic number word representations in children. We observed a selective response to number words compared to object words within neural regions that showed a numerical ratio effect in the non-symbolic number task. Those IPS regions showed semantic distance effects in their neural responses only for number words, not object words. Compared to the non-symbolic task, which elicited right-dominant IPS activation, children exhibited more bilateral number-related activation to number words, suggesting that the left IPS plays a greater role in symbolic numerical judgments than non-symbolic judgments in children (Cantlon & Li, 2013; Emerson & Cantlon, 2015; Vogel, Goffin & Ansari, 2015). In contrast to the IPS, which showed specialization for number words, the IFG, ACC, and insular cortex responded similarly during judgments of number words and object words and showed semantic distance effects for magnitude judgments of both numbers and objects in children. This is evidence that the role of frontal regions in numerical processing is functionally distinct from the role of the IPS. The insula, ACC, and IFG have a more domain-general neural profile than the IPS, possibly reflecting cognitive control or response selection processes associated with semantic judgments (e.g. Bunge & Crone, 2009).

Children showed reduced number-related IPS activation compared to adults and elevated frontal activation during the symbolic word task. This finding is consistent with prior research that reported a developmental fronto-parietal shift in numerical processing (Ansari *et al.*, 2005; Ansari & Dhital, 2006; Cantlon *et al.*, 2009; Nieder, 2009; Rivera *et al.*, 2005). The fronto-parietal shift is thought to represent children’s developing fluency with numerical operations. Eight-year-old children have only 1–2 years of experience reading written number words and thus may be less fluent with the task of transcoding and mentally comparing the values of written number words. In our study, the fronto-parietal differences between child and adult number-related activation could represent children’s relatively immature associations between written number words and their semantic values in memory or it could represent children’s developing fluency with the task operations. Future work comparing children's fronto-parietal activation patterns during judgments of spoken number words, which are more familiar to 8-year-olds than written number words, could help to disentangle these explanations. If the fronto-parietal shift is related to associations between symbolic words and their remembered values then numerical notations that are more familiar (spoken words) should show an earlier fronto-parietal shift than notations that are less familiar (written words). Future research will test this developmental question.

The whole-brain analysis comparing size judgments of number words and object words revealed that the right IPS shows robust activation during number size judgments compared to judgments of object size in children and adults. Recall that in children, the right IPS also showed a more robust neural response than the left IPS during non-symbolic numerical judgments. Thus, the right IPS is unique among regions in its notation-independent selectivity for numerical magnitude judgments in both children and adults. This finding is consistent with the conclusion described earlier that the right IPS is the neural origin of numerical concepts across notations in children (Ansari, 2008; Cantlon, 2012; Cantlon *et al.*, 2006; Hyde *et al.*, 2010; Libertus *et al.*, 2009; Piazza *et al.*, 2007). However, recall that although left IPS activation was overall weaker in children compared to the right IPS in both number tasks, we observed greater activation in the left IPS during the symbolic number word task compared to the non-symbolic number task in children. This observation suggests that the left IPS plays a greater role in symbolic numerical processing compared to non-symbolic numerical processing during development (Cantlon & Li, 2013; Emerson & Cantlon, 2015; Vogel *et al.*, 2015).

Although the IPS has been identified as a neural region important for the semantic processing of numerical values (see Dehaene, Piazza, Pinel & Cohen, 2003, for review), some researchers have raised the possibility that the patterns of IPS activation observed from numerical distance and ratio effects can be explained by task-general cognitive operations (Jiang & Kanwisher, 2003; Göbel, Johansen-Berg, Behrens & Rushworth, 2004). For example, Göbel *et al.* (2004) presented evidence that Arabic numeral distance effects in the IPS disappear when a control task for general difficulty is subtracted. Our data are not consistent with a task-general interpretation of IPS activation because they indicate that among word stimuli, numerical content drives neural responses in the IPS. Numerical judgments elicited elevated response amplitudes and neural distance effects in the IPS, in adults and children alike. Object words did not elicit elevated response amplitudes in the IPS, nor did they elicit a neural distance effect despite the fact that there was a clear behavioral distance effect for those judgments. These results argue against claims that number-related IPS activation patterns reflect domain-general neural processes related to difficulty. Instead, the results show that regions of the IPS that exhibit a numerical distance effect for non-symbolic stimuli show selective neural responses for number words.

Another explanation of number-related IPS activity is that it represents generalized magnitude processing. Prior research has shown that judgments of physical size, brightness, angle, duration, and length engage neural activity in the IPS (Bonn & Cantlon, 2012; Cantlon, Platt & Brannon, 2009; Fias, Lammertyn, Reynvoet, Dupont & Orban, 2003; Pinel *et al.*, 2004; Walsh, 2003). Our data show that a pattern of generalized magnitude-related activation in the IPS does not extend to judgments of object size from semantic memory.

This implicates a novel functional dissociation in the IPS for representing magnitudes: the IPS processes a variety of physical magnitude judgments including number, size, length, and angle but, as shown in the current study, not various types of symbolic magnitude judgments from semantic memory.

This study supports the conclusion that children's semantic representations of number words engage representations in parietal cortex and dissociate from their semantic representations of object words in ventral temporal cortex, along the fusiform gyrus. Why are number words processed so differently by the brain than other types of words? We argue that the reason is that judgments of symbolic number words recruit neural regions that are more involved in judging physical size and intensity (parietal cortex) as opposed to semantic memory (ventral temporal cortex) because numerical processing has an evolutionarily and developmentally primitive neural origin rooted in physical magnitude representation (Dehaene & Cohen, 2007; Cantlon, Platt, & Brannon, 2009). The development of number word meanings in children is unique compared to other words because it relies on functional connections with the primitive physical perception substrates of parietal cortex.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

References

Ansari D (2008). Effects of development and enculturation on number representation in the brain. Nature Reviews Neuroscience, 9, 278–291. [PubMed: 18334999]

Ansari D, & Dhital B (2006). Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. Journal of Cognitive Neuroscience, 18 (11), 1820–1828. [PubMed: 17069473]

Ansari D, Garcia N, Lucas E, Harmon K, & Dhital B (2005). Neural correlates of symbolic number processing in children and adults. NeuroReport, 16 (16), 1769–1773. [PubMed: 16237324]

Bonn CD, & Cantlon JF (2012). The origins and structure of quantitative concepts. Cognitive Neuropsychology, 29 (0), 149–173. [PubMed: 22966853]

Brannon EM, & Van de Walle GA (2001). The development of ordinal numerical competence in young children. Cognitive Psychology, 43 (1), 53–81. [PubMed: 11487294]

Bulthé J, De Smedt B, & Op de Beeck H (2014). Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. NeuroImage, 87, 311–322. [PubMed: 24201011]

Bunge SA, & Crone EA (2009). Neural correlates of the development of cognitive control. In Ramsey JM & Ernst M (Eds.), Neuroimaging in developmental clinical neuroscience (pp. 22–37). New York: Cambridge University Press.

Cantlon JF (2012). Math, monkeys, and the developing brain. Proceedings of the National Academy of Sciences, USA, 109 (1), 10725–10732.

Cantlon JF, & Brannon EM (2006). Shared system for ordering small and large numbers in monkeys and humans. Psychological Science, 17 (5), 401–406. [PubMed: 16683927]

Cantlon JF, Brannon EM, Carter EJ, & Pelphrey KA (2006). Functional imaging of numerical processing in adults and 4-y-old children. PLoS Biology, 4 (5), e125. [PubMed: 16594732]

Cantlon JF, & Li R (2013). Neural activity during natural viewing of Sesame Street statistically predicts test scores in early childhood. PLoS Biology, 11 (1), e1001462. [PubMed: 23300385]

Cantlon JF, Libertus ME, Pinel P, Dehaene S, Brannon EM et al. (2009). The neural development of an abstract concept of number. Journal of Cognitive Neuroscience, 21 (11), 2217–2229. [PubMed: 19016605]

Cantlon JF, Platt ML, & Brannon EM (2009). Beyond the number domain. Trends in Cognitive Sciences, 13 (2), 83–91. [PubMed: 19131268]

Cohen Kadosh R, Cohen Kadosh K, Linden DEJ, Gevers W, Berger A et al. (2007). The brain locus of interaction between number and size: a combined functional magnetic resonance imaging and event-related potential study. Journal of Cognitive Neuroscience, 19 (6), 957–970. [PubMed: 17536966]

Cordes S, Gelman R, Gallistel CR, & Whalen J (2001). Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. Psychonomic Bulletin & Review, 8 (4), 698–707. [PubMed: 11848588]

Damarla SR, & Just MA (2013). Decoding the representation of numerical values from brain activation patterns. Human Brain Mapping, 34 (10), 2624–2634. [PubMed: 22505340]

Dehaene S, & Cohen L (2007). Cultural recycling of cortical maps. Neuron, 56 (2), 384–398. [PubMed: 17964253]

Dehaene S, Piazza M, Pinel P, & Cohen L (2003). Three parietal circuits for number processing. Cognitive Neuropsychology, 20 (3/4/5/6), 487–506. [PubMed: 20957581]

Diester I, & Nieder A (2007). Semantic associations between signs and numerical categories in the prefrontal cortex. PLoS Biology, 5 (11), e294. [PubMed: 17973578]

Eger E, Michel V, Thirion B, Amadon A, Dehaene S et al. (2009). Deciphering cortical number coding from human brain activity patterns. Current Biology, 19 (19), 1608–1615. [PubMed: 19781939]

Emerson RW, & Cantlon JF (2012). Early math achievement and functional connectivity in the fronto-parietal network. Developmental Cognitive Neuroscience, 2 (S1), S139–S151. [PubMed: 22682903]

Emerson RW, & Cantlon JF (2015). Continuity and change in children’s longitudinal neural response to numbers. Developmental Science, 18 (2), 314–326. [PubMed: 25051893]

Fias W, Lammertyn J, Reynvoet B, Dupont P, & Orban GA (2003). Parietal representation of symbolic and non-symbolic magnitude. Journal of Cognitive Neuroscience, 15 (1), 47–56. [PubMed: 12590842]

Fuson KC (1988). Children’s counting and concept of number. New York: Springer-Verlag.

Fuson KC (1992). Relationships between counting and cardinality from age 2 to age 8. In Bideaud J, Meljac C & Fischer J-P (Eds.), Pathways to number: Children’s developing numerical abilities (pp. 127–149). Hillsdale, NJ: Lawrence Erlbaum Associates.

Fuson KC, & Hall JW (1983). The acquisition of early number word meanings: a conceptual analysis and review. In Ginsburg HP (Ed.), The development of mathematical thinking (pp. 49–107). New York: Academic Press.

Gallistel CR, & Gelman R (2000). Non-verbal numerical cognition: from reals to integers. Trends in Cognitive Sciences, 4 (2), 59–65. [PubMed: 10652523]

Gelman R, & Gallistel CR (1978). The child’s understanding of number. Cambridge, MA: Harvard University Press.

Göbel SM, Johansen-Berg H, Behrens T, & Rushworth MFS (2004). Response-selection-related parietal activation during number comparison. Journal of Cognitive Neuroscience, 16 (9), 1536–1551. [PubMed: 15601517]

Goebel R, Esposito F, & Formisano E (2006). Analysis of functional image analysis contest (FIAC) data with Brainvoyager QX: from single-subject to cortically aligned group general linear model analysis and self-organizing group independent component analysis. Human Brain Mapping, 27, 392–401. [PubMed: 16596654]

Halberda J, & Feigenson L (2008). Developmental change in the acuity of the ‘number sense’: the approximate number system in 3-, 4-, 5-, and 6-year-olds and adults. Developmental Psychology, 44 (5), 1457–1465. [PubMed: 18793076]

Holloway ID, & Ansari D (2010). Developmental specialization in the right intraparietal sulcus for the abstract representation of numerical magnitude. Journal of Cognitive Neuroscience, 22 (11), 2627–2637. [PubMed: 19929327]

Holloway ID, Price GR, & Ansari D (2010). Common and segregated neural pathways for the processing of symbolic and nonsymbolic numerical magnitude: an fMRI study. NeuroImage, 49 (1), 1006–1017. [PubMed: 19666127]

Huntly-Fenner G, & Cannon E (2000). Preschoolers' magnitude comparisons are mediated by a preverbal analog mechanism. Psychological Science, 11 (2), 147–152. [PubMed: 11273422]

Hyde DC, Boas DA, Blair C, & Carey S (2010). Near-infrared spectroscopy shows right parietal specialization for number in pre-verbal infants. NeuroImage, 53 (2), 647–652. [PubMed: 20561591]

Izard V, Sann C, Spelke E, & Streri A (2009). Newborn infants perceive abstract numbers. Proceedings of the National Academy of Sciences, USA, 106 (25), 10382–10385.

Jiang Y, & Kanwisher N (2003). Common neural substrates for response selection across modalities and mapping paradigms. Journal of Cognitive Neuroscience, 15 (8), 1080–1094. [PubMed: 14709228]

LeCorre M, & Carey S (2007). One, two, three, four, nothing more: an investigation of the conceptual sources of the verbal counting principles. Cognition, 105 (2), 395–438. [PubMed: 17208214]

Libertus ME, Pruitt LB, Woldorff MG, & Brannon EM (2009). Induced alpha-band oscillations reflect ratio-dependent number discrimination in the infant brain. Journal of Cognitive Neuroscience, 21 (12), 2398–2406. [PubMed: 19016603]

Lipton JS, & Spelke ES (2005). Preschool children's mapping of number words to nonsymbolic numerosities. Child Development, 76 (5), 978–988. [PubMed: 16149996]

Lyons IM, Ansari D, & Beilock SL (2015a). Qualitatively different coding of symbolic and nonsymbolic numbers in the human brain. Human Brain Mapping, 26, 475–488.

Lyons IM, Nuerk HC, & Ansari D (2015b). Rethinking the implications of numerical ratio effects for understanding the development of representational precision and numerical processing across formats. Journal of Experimental Psychology: General, 144 (5), 1021–1035. [PubMed: 26168037]

Negen J, & Sarnecka BW (2015). Is there really a link between exact-number knowledge and approximate number system acuity in young children? British Journal of Developmental Psychology, 33 (1), 92–105. [PubMed: 25403910]

Nieder A (2009). Prefrontal cortex and the evolution of symbolic reference. Current Opinion in Neurobiology, 19 (1), 99–108. [PubMed: 19447604]

Park J, & Brannon EM (2013). Training the approximate number system improves math proficiency. Psychological Science, 24 (10), 2013–2019. [PubMed: 23921769]

Piazza M, Izard V, Pinel P, Le Bihan D, & Dehaene S (2004). Tuning curves for approximate numerosity in the human intraparietal sulcus. Neuron, 44 (3), 547–555. [PubMed: 15504333]

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. [PubMed: 17224409]

Pinel P, Piazza M, Le Bihan D, & Dehaene S (2004). Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. Neuron, 41 (6), 983–993. [PubMed: 15046729]

Rivera SM, Reiss AL, Eckert MA, & Menon V (2005). Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. Cerebral Cortex, 15 (11), 1779–1790. [PubMed: 15716474]

Talairach J, & Tournoux P (1988). Co-planar steotaxic atlas of the human brain. New York: Thieme Medical.

van Marle K, Chu FW, Li Y, & Geary DC (2014). Acuity of the approximate number system and preschoolers' quantitative development. Developmental Science, 17 (4), 492–505. [PubMed: 24498980]

Vogel SE, Goffin C, & Ansari D (2015). Developmental specialization of the left parietal cortex for the semantic representation of Arabic numerals: an fMR-adaptation study. Developmental Cognitive Neuroscience, 12, 61–73. [PubMed: 25555264]

Walsh V (2003). A theory of magnitude: common cortical metrics of time, space and quantity. Trends in Cognitive Neuroscience, 7 (11), 483–488.

Wynn K (1990). Children's understanding of counting. Cognition, 36 (2), 155–193. [PubMed: 2225756]

Wynn K (1992). Children's acquisition of the number words and the counting system. Cognitive Psychology, 24, 220–251.

Xu F, & Spelke ES (2000). Large number discrimination in 6-month-old infants. Cognition, 74 (1), B1–B11. [PubMed: 10594312]

Research highlights

- The study uses fMRI to show functional overlap between children's representations of symbolic and non-symbolic number representations in the IPS.
- The data show that neural relations between children's representations of symbolic and non-symbolic number are content-specific as opposed to domain-general.
- The data provide novel evidence of a functional dissociation between number words and non-numerical words in the developing brain.

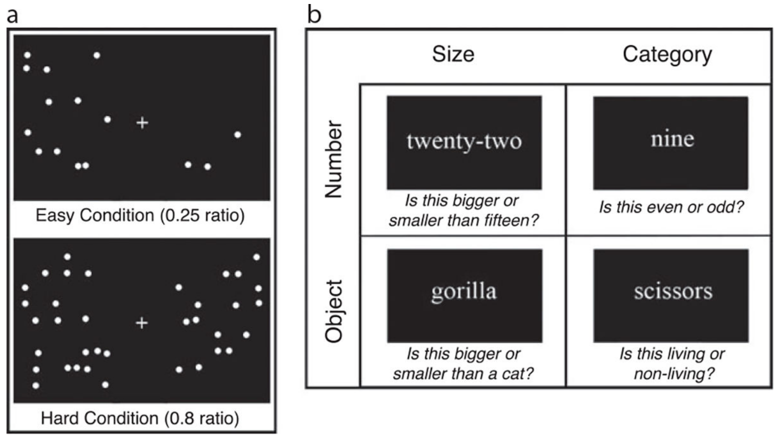

Figure 1.

Stimuli for Experiments 1 and 2. (a) Subjects were shown dot arrays paired in easy (0.25) and hard (0.8) ratios and asked to determine which side had the greater number of dots. (b) In a block design, subjects were presented with written words and judged whether a given number was larger/smaller than a cat (Size Judgment) or even/odd (Category Judgment). In other blocks subjects were presented with object words and judged whether the object was larger/smaller than a cat (Size Judgment) or living/nonliving (Category Judgment).

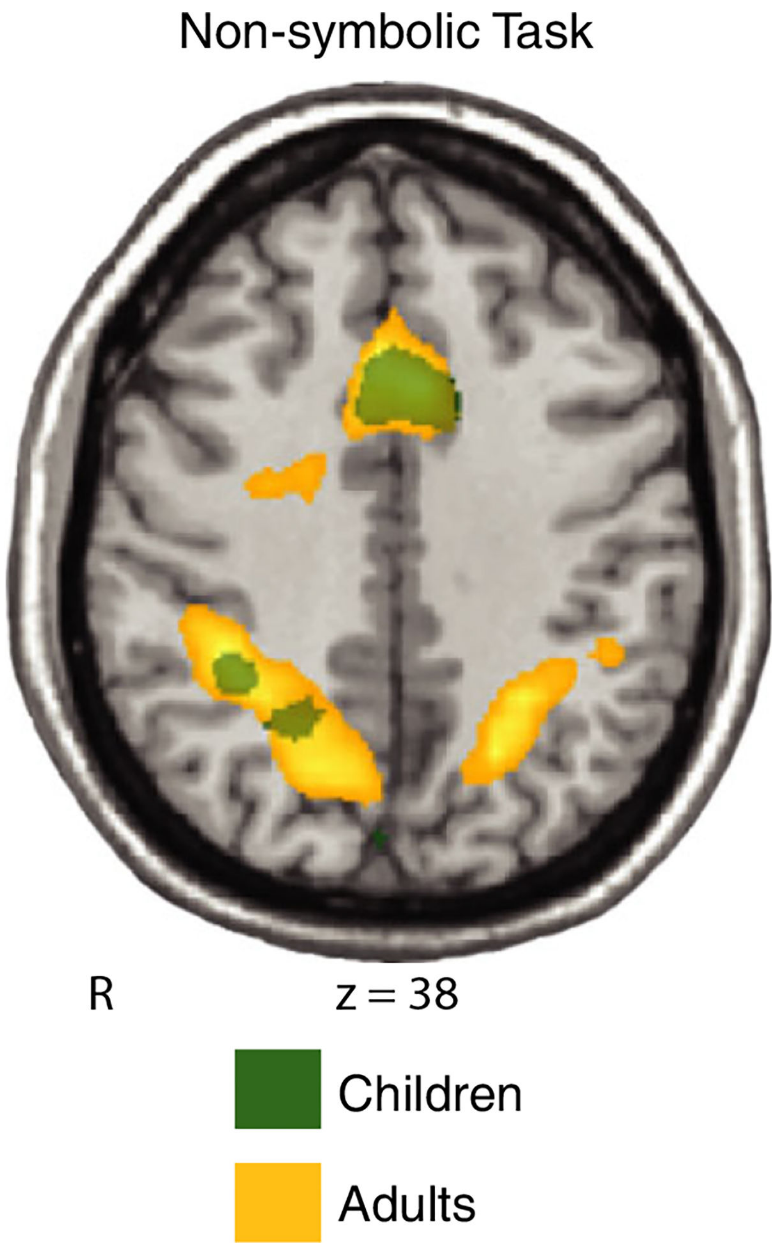

Figure 2.
Regions that showed a numerical ratio effect during the non-symbolic number task. Regions that showed a greater neural response to 0.8 numerical ratio trials compared to 0.5 numerical ratio trials in children and adults ($p < .005$, voxel-level, cluster corrected $p < .05$). Table 3 reports regions with spatial coordinates.

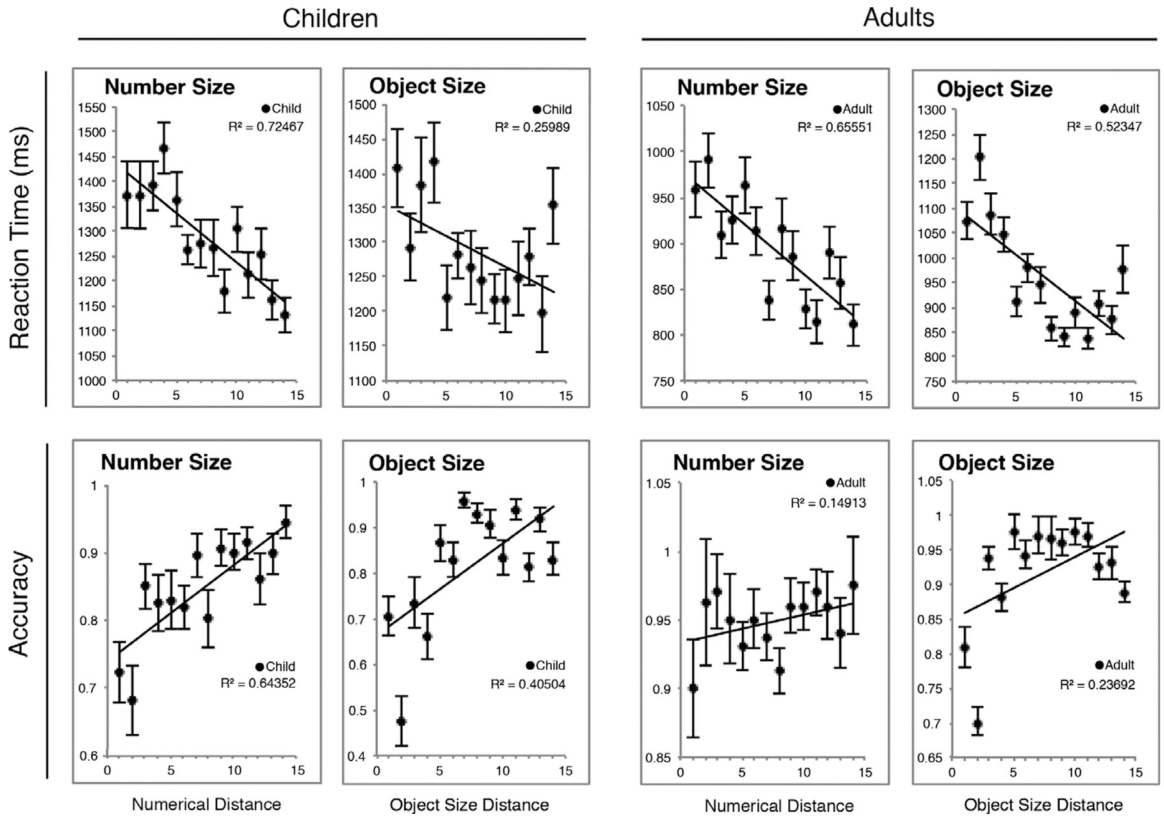

Figure 3.

Behavioral distance effects for number and object stimuli during size judgments in the symbolic task. Children (left panels) and adults (right panels) exhibited behavioral distance effects in RT (top row) and Accuracy (bottom row) for magnitude judgments of number words and magnitude judgments of remembered object size from word stimuli.

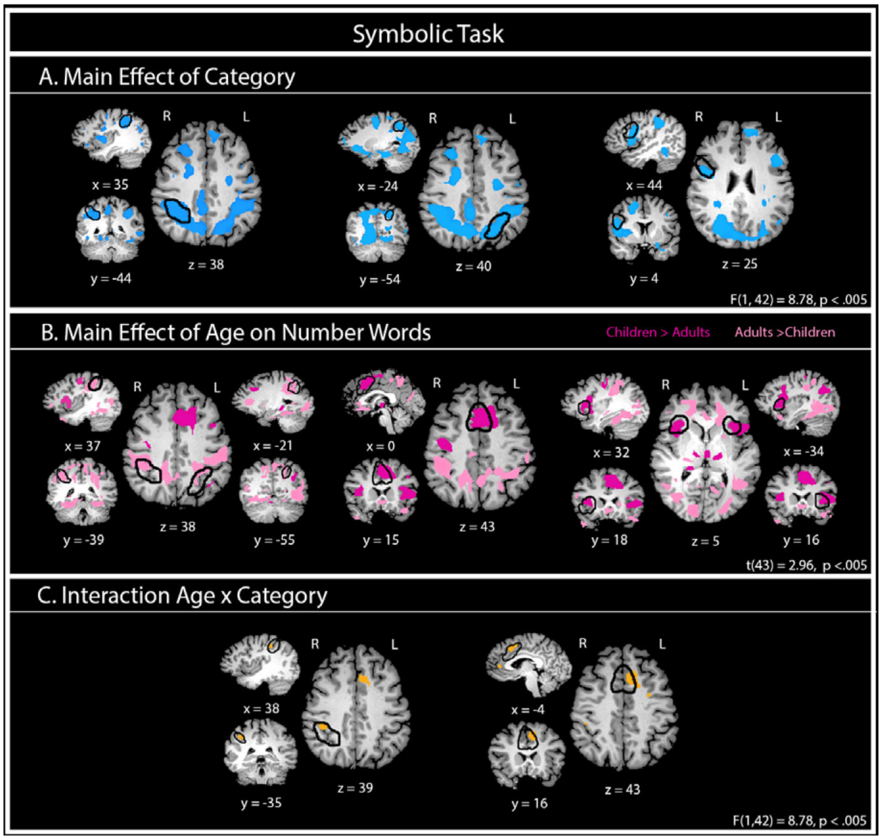

Figure 4.

Whole-brain ANOVA of Category (Number Word, Object Word) × Age (Child, Adult) from the symbolic task. The top row (A) shows the main effect of category, the middle row (B) shows the effect of age on number word activation with a t-test overlaid that shows the direction of the age effects, and the bottom panel (C) displays the interaction of age × category with only a small effect in parietal cortex. The black outlines show regions that exhibited a numerical ratio effect in the non-symbolic task.

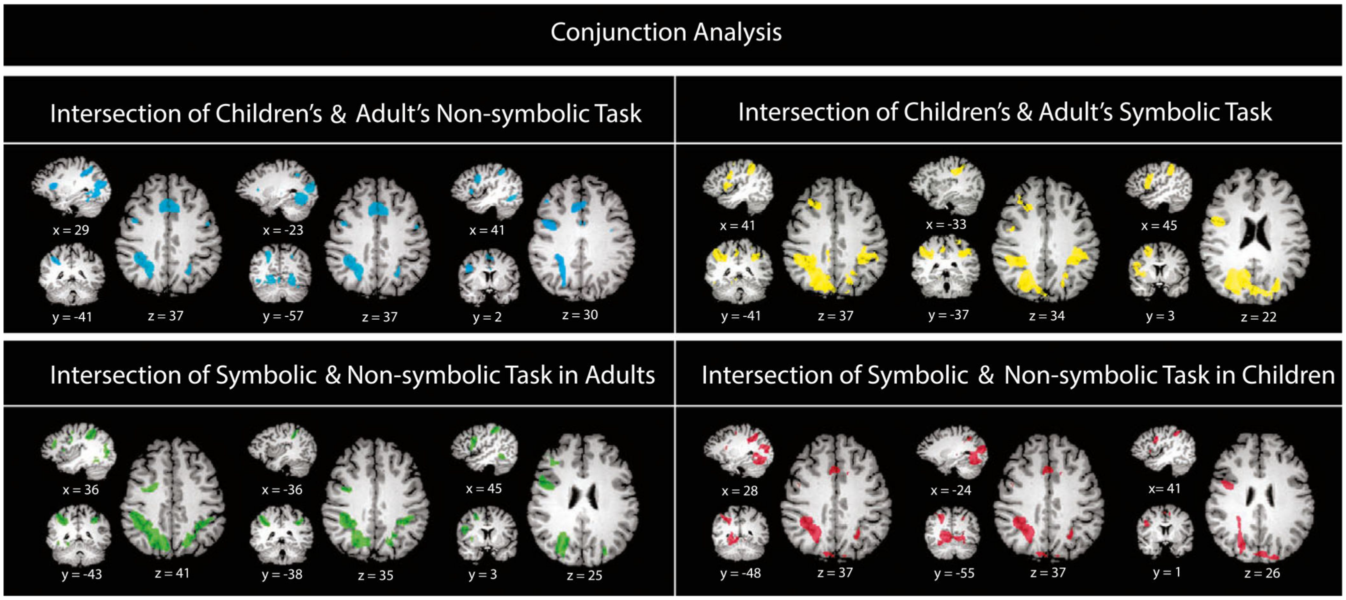

Figure 5.

Conjunction analyses of child ∩ adult activations and activations from the non-symbolic task ∩ symbolic task. The top row shows the intersection of child and adult activation on the non-symbolic task (left) and child and adult activation on the symbolic task (right). The bottom row shows the intersection of symbolic and non-symbolic activation from adults (left) and children (right).

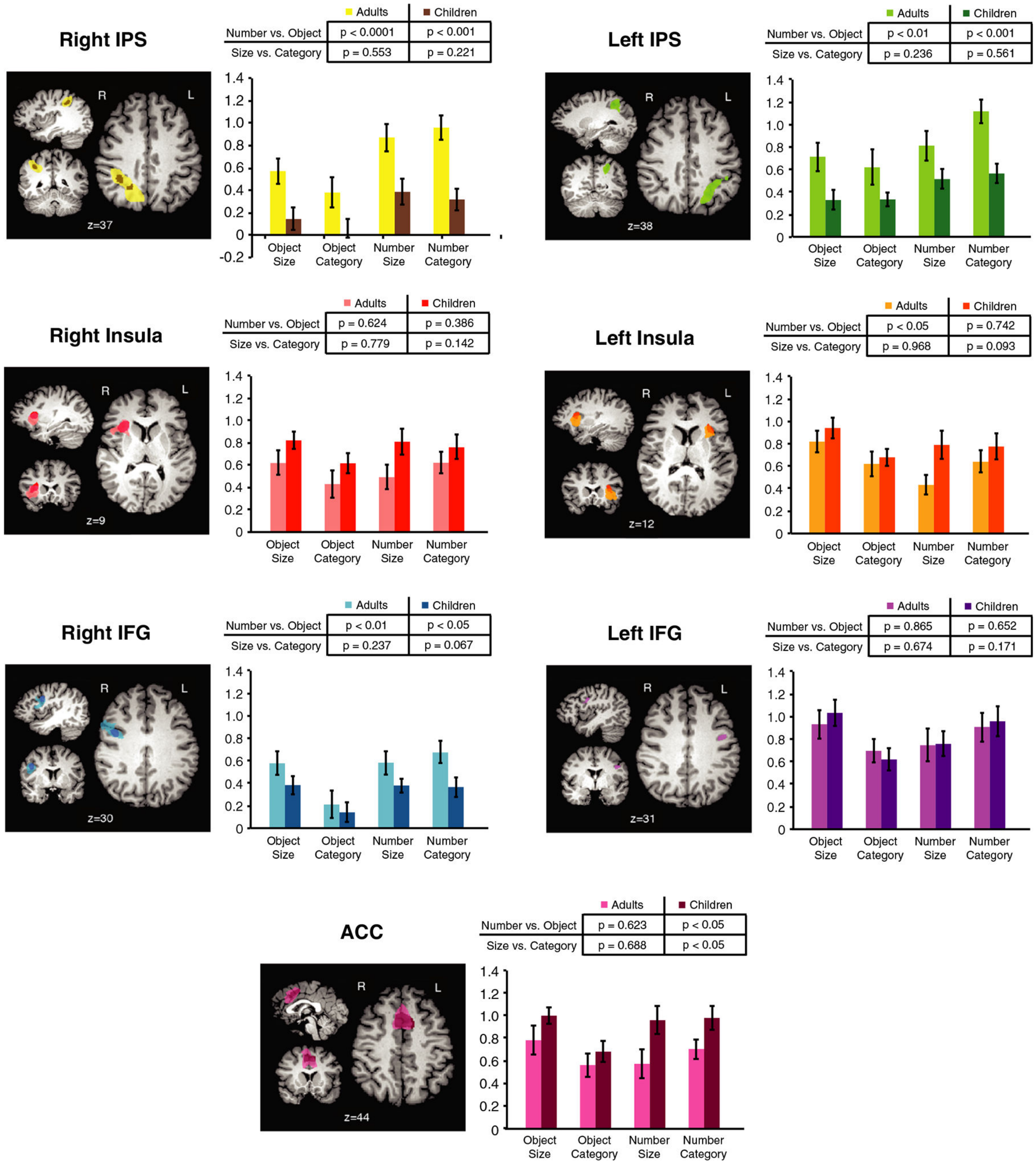

Figure 6.

Neural responses to number words and object words, for size and category judgments in non-symbolic number task ROIs. The left and right IPS showed greater neural responses to number words than object words, independently of judgment type (Size or Category Judgment) in children and adults. The right IFG also showed a number-selective neural response in adults and children. The ACC showed a general preference for size judgments across number and object stimuli as well as an overall preference for number stimuli over object stimuli in children. No other pattern emerged for stimulus type or judgment type in the remaining regions. Children tended to show greater frontal number-related activation and reduced IPS number-related activation compared to adults.

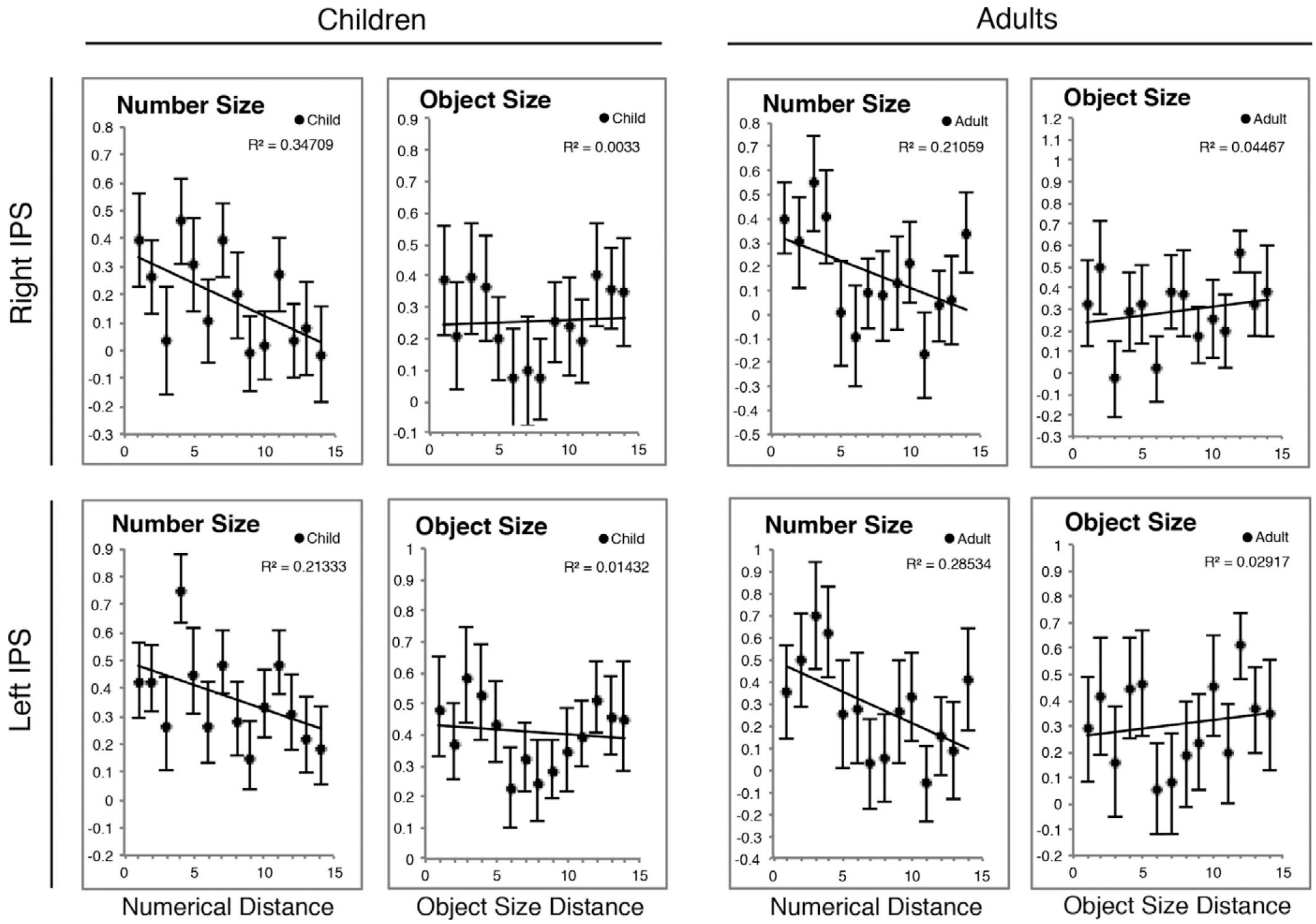

Figure 7.

Neural distance effects from symbolic number word judgments in the non-symbolic task IPS ROIs. The left and right IPS that showed neural effects of numerical distance during the non-symbolic numerical task also showed neural effects of semantic distance during size judgments of number words but not size judgments of objects in adults and children.

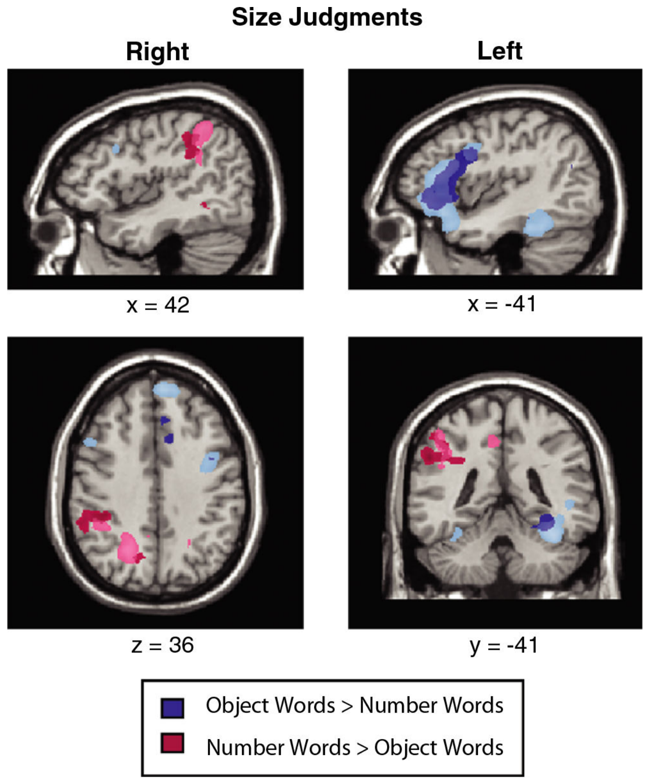

Figure 8.
Whole-brain analysis of semantic size judgments from symbolic task. Regions that showed greater activity during number word judgments compared to object words are shown in red. Regions that showed greater activity during object words compared to number words are shown in blue. Children are shown in light shades, adults are in dark shades ($p < .005$, cluster corrected $p < .05$). The right IPS showed selectivity for number words. The left fusiform and left IFG showed selectivity for object words.

Table 1

Stimuli words for symbolic word task

Number words	Object words
one	bee
two	ring
three	nail
four	shrimp
five	mouse
six	pen
seven	hamster
eight	knife
nine	scissors
ten	rat
eleven	plate
twelve	ball
thirteen	chicken
fourteen	duck
sixteen	wolf
seventeen	stove
eighteen	desk
nineteen	table
twenty	gorilla
twenty-one	booth
twenty-two	cow
twenty-three	bear
twenty-four	horse
twenty-five	shark
twenty-six	whale
twenty-seven	yacht
twenty-eight	plane
twenty-nine	island

Table 2

Non-symbolic number behavioral task

	Mean RT	RT St. Dev	Mean accuracy	Accuracy St. Dev	*t*-test vs. chance
Children					
Easy ratio (0.25)	915	98	0.958	0.065	<.0001
Hard ratio (0.8)	1160	180	0.756	0.107	<.0001
Adults					
Easy ratio (0.25)	715	127	0.990	0.023	<.0001
Hard ratio (0.8)	1020	217	0.844	0.073	<.0001

Table 3

Non-symbolic number regions

	Activation center (Tal x, y, z)	Cluster size (voxels)	Broadmann area
Child			
Right Intraparietal Sulcus	35, −44, 36	248	40
Left Intraparietal Sulcus	n/a	n/a	n/a
Right Insular Region	29, 16, 9	1650	13
Left Insular Region	−31, 16, 15	306	13
Right Inferior Frontal Gyrus	41, 1, 30	234	6
Left Inferior Frontal Gyrus	n/a	n/a	n/a
Anterior Cingular Cortex	6, 14, 46	2964	32
Adult			
Right Intraparietal Sulcus	29, −47, 36	5081	40
Left Intraparietal Sulcus	−25, −50, 42	3610	7
Right Insular Region	29, 22, 6	4248	45
Left Insular Region	−28, 22, 6	3485	45
Right Inferior Frontal Gyrus	44, 1, 27	3479	6
Left Inferior Frontal Gyrus	−39, −5, 33	164	6
Anterior Cingular Cortex	−3, 17, 40	10886	32

Table 4

Symbolic size/category behavioral task

	Mean RT	RT St. Dev	Mean accuracy	Accuracy St. Dev	*t*-test vs. chance
Children					
Object size	1290	143	0.812	0.096	<.0001
Number size	1290	151	0.850	0.099	<.0001
Object category	1200	220	0.910	0.060	<.0001
Number category	1360	161	0.818	0.117	<.0001
Adults					
Object size	959	146	0.939	0.040	<.0001
Number size	892	134	0.974	0.022	<.0001
Object category	903	141	0.968	0.032	<.0001
Number category	957	150	0.977	0.024	<.0001

Table 5

Conjunction of symbolic and non-symbolic tasks for children and adults

Region	Activation center (Tal x, y, z)	Cluster size (voxels)	Broadmann area
Intersection of symbolic and non-symbolic task in adults			
Right Intraparietal Sulcus	39, −40, 40	23775	40
Left Intraparietal Sulcus	−18, −61, 43	4459	40
Right Insular Region	45, 8, 14	1198	13
Right Inferior Frontal Gyrus	48, 8, 22	2718	6
Anterior Cingulate Cortex	−3, 0, 46	73	24
Intersection of symbolic and non-symbolic task in children			
Right Intraparietal Sulcus	35, 44, 36	5997	40
Left Intraparietal Sulcus	−24, −55, 43	278	7
Right Insular Region	30, 14, 10	649	13
Right Inferior Frontal Gyrus	42, 2, 31	1192	6
Anterior Cingulate Cortex	3, 2, 46	3679	6