Developmental bias for number words in the intraparietal sulcus

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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.

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.

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 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 repre-
sentations 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 larger number of dots in less than 1 second, adults can accurately approximate numerical values and 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
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 (Bulthuis, 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 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

**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).
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 \( t(42) = 0.53, p = .60 \)). Children moved slightly more than adults in the rotational planes (Adult M = 0.004 rad, SD = 0.003; Child M = 0.007 rad, SD = 0.007; \( t(23) = 4.35, p < .0001 \)).

All subjects were native English speakers, right-handed 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 (cm²); average area: 0.25 ratio = 10.46, 0.8 ratio = 10.46; average dot size: 0.25 ratio = 2.42, 0.8 ratio = 0.895), and half were equated for dot size between arrays (cm²); 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 number of phonemes (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 [\( TR = 2530 \text{ ms}, \ TE = 3.44 \text{ ms}, \) flip angle = 7 degrees, \( FOV = 256 \text{ mm}, \) matrix = \( 256 \times 256, \) 160 or 176 (depending on head size), \( 1.3 \times 1 \times 1 \text{ mm sagittal left-to-right slices} \)].

An echo-planar imaging pulse sequence with online motion correction was used for T2* contrast (\( TR = 2000 \text{ ms}, \) \( TE = 30 \text{ ms}, \) flip angle = 90 degrees, \( FOV = 256 \text{ mm}, \) matrix = \( 64 \times 64, \) 30 axial slices, voxel size = \( 4 \times 4 \times 4 \text{ mm} \)). 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) \( \times \) Ratio (0.5, 0.8) 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 \( p < .0001 \)), 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 \( p_\text{s} < .0001 \)) (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: \( t(42) = 9.5, p < .001 \)) and on each condition (Number: 83% vs. 91%, \( t(42) = -2.7, p < .05 \) and responded more slowly on each condition (Number: 1242 ms vs. 930 ms, \( t(42) = -2.7, p < .05 \)). Although

| 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 | 29, 16, 9          | 1650               | 13              |
| Right Insular Region | -31, 16, 15       | 306                | 13              |
| Left Insular Region | 41, 1, 30          | 234                | 6               |
| Right Inferior Frontal Gyrus | n/a               | n/a                | n/a             |
| 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              |

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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: \( t(1, 42) = 8.97, p < .01; \) RT: \( t(1, 42) = 13.3, p < .01 \)).

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

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.
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, $R = −.46$, $t(23) = 3.34$, $p < .005$; 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 (paired $t$-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}

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Slopes = −0.003 to 0.008, all Rs = −0.12 to .21, all ps > .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 Rs = −0.47 to −0.79, all ps < .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 ps > .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,

![Figure 5](image_url)  
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).

| 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 |

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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.
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.

References


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Received: 8 January 2015
Accepted: 22 October 2015

**Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Figure S1.** These panels show the results of the Symbolic task (parallel to Figure 4 of the main article) using child-defined Non-symbolic Task ROIs instead of adult-defined Non-symbolic Task ROIs. A visualization of the child-defined ROIs is shown in Figure 4 of the main article. The table below each figure panel represents p values from t-test comparisons of number words versus object words (top row) and size judgments versus category judgments (bottom row). The general pattern of results is the same as reported in
the main article: the IPS and right IFG show number-selective activation across judgment types whereas other frontal regions show a more domain-general profile of either no number selectivity, or selectivity based on judgment type across numbers and objects. Note that children did not exhibit left IPS non-symbolic number-related activation at the p < .005 voxel-level threshold which explains why the left IPS is omitted from this analysis.

Figure S2. The semantic distance effects for number and object words exhibited the same pattern reported in the main article when computed from the child-defined ROIs (parallel to Figure 5 from the main article). The child-defined ROIs can be visualized in Figure 4. The IPS exhibited semantic distance effects for number words but not object words in children and adults. Note that children did not exhibit left IPS non-symbolic number-related activation which explains why the left IPS is omitted from this analysis. As found with adult-defined ROIs, and in contrast to the IPS, frontal regions tended to exhibit distance effects for both number word and object word judgments in children [ACC: Number R = -.79, Object R = -.61; RINS: Number R = -.74, Object R = -.35; LINS: Number R = -.67, Object R = -.40; RIFG did not show a distance effect for object words: Number R = -.49, Object R = -.10].