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PAPER

The relationship between non-verbal systems of number and counting development: a neural signatures approach

Daniel C. Hyde, Charline E. Simon, Ilaria Berteletti* and Yi Mou*

Department of Psychology, University of Illinois at Urbana-Champaign, USA

Abstract

Two non-verbal cognitive systems, an approximate number system (ANS) for extracting the numerosity of a set and a parallel individuation (PI) system for distinguishing between individual items, are hypothesized to be foundational to symbolic number and mathematics abilities. However, the exact role of each remains unclear and highly debated. Here we used an individual differences approach to test for a relationship between the spontaneously evoked brain signatures (using event-related potentials) of PI and the ANS and initial development of symbolic number concepts in preschool children as displayed by counting. We observed that individual differences in the neural signatures of the PI system, but not the ANS, explained a unique portion of variance in counting proficiency after extensively controlling for general cognitive factors. These results suggest that differences in early attentional processing of objects between children are related to higher-level symbolic number concept development.

Research highlights

- Individual differences in neural signatures of parallel individuation and approximate number correlate with conceptual understanding of counting in preschool-aged children.
- Relationship between parallel individuation and counting holds after controlling for general cognitive and linguistic abilities.
- Quantitative and qualitative differences in the spontaneous neural response to number between developing and proficient counters.

Introduction

Two non-verbal cognitive systems allow for numerical abilities before educational instruction (see Feigenson, Dehaene & Spelke, 2004, for review). One, the approximate number system (ANS), allows us to mentally represent, compare, and compute over sets of items on the basis of their approximate numerical magnitude (e.g. Dehaene, 1997). The other, the parallel individuation system (PI), draws on attention and working memory resources to differentiate, track, and remember a limited number of individual items simultaneously (~3 or 4) (e.g. Carey, 2009; Trick & Pylyshyn, 1994). Both systems are present from infancy, are shared with a wide variety of non-human animals, arise from distinct cortical regions, and are characterized by distinct brain and behavioral signatures (Feigenson *et al*., 2004; Hyde, 2011). It is widely hypothesized that these two core systems form a basis for symbolic numerical and mathematics abilities (Carey, 2009; Dehaene, 1997; Gallistel & Gelman, 1992; Spelke, 2011). There is, however, substantial debate as to whether and/or to what extent each system is actually involved, and behavioral evidence to date has been largely inconclusive (see Carey, 2009, for review). Here we investigate the role of these systems in early symbolic number development by measuring the relationship between individual differences in the spontaneous brain signatures associated with each core system and the acquisition of the symbolic number system in preschool-aged children.

Address for correspondence: Daniel C. Hyde, Department of Psychology, University of Illinois at Urbana-Champaign, 621 Psychology Building, 603 East Daniel Street, Champaign, IL 61820, USA; e-mail: dchyde@illinois.edu
*These authors made equal contributions to the study.

Some hypothesize that the ANS forms a conceptual foundation for symbolic number and mathematics understanding (Dehaene, 1997; Gallistel & Gelman, 1992). Under this view, acquiring a symbolic number system involves mapping symbolic numbers onto the pre-existing concepts of number inherent in the ANS (Gallistel & Gelman, 1992; Gallistel, 2007). The main empirical evidence put forth to support this hypothesis is that individual differences in ANS acuity, or the precision with which an individual can compare two arrays of items on the basis of numerosity, are correlated with mathematics achievement scores (Gilmore, McCarthy & Spelke, 2010; Halberda, Mazzocco & Feigenson, 2008). Unfortunately, a vast majority of these studies to date analyze the relationship between the ANS and mathematics achievement, leaving open the question of whether the ANS is related to the initial acquisition of a symbolic number system (Libertus, Feigenson & Halberda, 2013). One case where the ANS has been associated with early symbolic number understanding (e.g. Wagner & Johnson, 2011) has been questioned on methodological grounds (Negen & Sarnecka, 2015) and is challenged by other evidence showing that the association between the two is formed only after critical conceptual development occurs (e.g. Le Corre & Carey, 2007).

Others hypothesize that the PI system combined with features of natural language are involved in initial symbolic number concept development (Carey, 2009; Le Corre & Carey, 2007). Under this view, the PI system allows children to remember, uniquely identify, and ultimately associate linguistic terms to sets of small numbers of items within its capacity. Then, after acquiring meaning of the first few number words in a piecemeal manner, children are able to make a generalization to figure out how counting represents larger numbers (Carey, 2009). Major proponents of this view also explicitly argue that the ANS is not involved in initial symbolic number learning (see Carey, 2009, for a review). The main evidence to date for such a role of the PI system in initial conceptual development of the symbolic number system is entirely qualitative: learning symbolic number concepts first involves learning the numbers that fall within the capacity limit of the PI system, one, two, three, in a piecemeal fashion (e.g. Le Corre & Carey, 2007; Wynn, 1992).

Finally, some propose a hybrid view that the PI system and ANS are both involved in development, possibly at distant times or in unique ways (e.g. Huang, Spelke & Snedeker, 2010). Under this view, each core system contains part but not all of the conceptual information needed to understand how counting represents number. The PI system allows children to make associations between the first few number words and the exact quantities they represent, while the ANS allows children to understand that larger sets can have cardinal values that are different from one another. It is proposed that numerical language, including the count list and quantifiers, allows children to bring the non-verbal numerical information inherent in these two core systems together to understand how counting represents number (Spelke, 2011; Spelke & Tsivkin, 2001). The main evidence put forth to support this view is that the early qualitative pattern of counting development mentioned above, combined with later behavioral patterns more consistent with ANS, suggest that both systems play a role in symbolic number system acquisition (Huang *et al.*, 2010).

Despite substantial theorizing and debate, no studies to date have empirically compared these alternatives. The majority of previous work has exclusively focused on the relationship between individual differences in the ANS and symbolic number development. To our knowledge, no published studies have directly investigated whether and how individual differences in the PI system are related to early symbolic number development nor compared the relative contribution of PI and the ANS to early numerical development. Here we used event-related potentials (ERPs) to obtain spontaneous neural measures of both core systems (PI and ANS) hypothesized to contribute to symbolic number development within each participant and analyzed their relationship to early counting ability. Recent work in cognitive neuroscience has identified distinct neural markers of PI and ANS engagement: these markers can be engaged spontaneously and they dissociate in functional pattern, timing, and neuroanatomical source (Hyde, 2011; Hyde & Spelke, 2009, 2011, 2012; Hyde & Wood, 2011). Obtaining spontaneous neural measures of both systems in preschoolers allowed us to avoid the strong executive, performance, comprehension, and/or motoric demands recently raised as problematic to interpreting correlations between core, non-verbal and symbolic numerical abilities (e.g. Gilmore, Attridge, Clayton, Cragg, Johnson *et al.*, 2013), while testing a broader range of hypotheses regarding their relationships to symbolic number development. We reasoned that if one or both of the core, non-verbal numerical systems are related to the initial development of the symbolic number system, then individual differences in the spontaneous brain signatures of these core systems should correlate with individual differences in symbolic counting proficiency in preschoolers. Furthermore, these relationships should hold after controlling for general cognitive and linguistic factors.

Method

Participants

Participants were part of a larger, longitudinal intervention study of mathematical development. Although an a priori power analysis to estimate sample size was not appropriate given that no published study to date has investigated the link between neural processing of number and counting in preschoolers, an evaluation of the effect sizes found in purely behavioral studies of the relationship between ANS and early mathematics achievement (Libertus *et al.*, 2013; Starr, Libertus & Brannon, 2013) revealed that a sample size of between 42 and 110 (depending on the exact dependent measure of the ANS used) would be needed to achieve statistical power of .80 or above. We took the first 100 participants to participate in the tasks of interest for this particular study on their first visit to the lab for the longitudinal study as our stop rule. All children resided in the Urbana-Champaign, IL region and ranged in age from 3 years 7 months and 18 days to 4 years 3 months and 16 days (*M* age = 3y. 10 m. 22 d.; *SD* age = 52 days). Written informed consent of a parent or guardian and verbal assent of the child participant was obtained prior to initiating the experiment. The study was conducted under the approval of the University of Illinois Institutional Review Board for the Protection of Human Subjects.

Procedure

Children completed a battery of behavioral and brain (ERPs) tasks used to assess non-verbal numerical, verbal numerical, linguistic, and general cognitive abilities in the laboratory over the course of 2–3 hours. Children were given breaks approximately every 45 minutes to an hour or upon request. Only those tasks reported below were analyzed for the research question of this study.

Counting assessments

Two established counting tasks were administered to assess children's conceptual understanding of the symbolic number system. The average of the two scores was taken as our measure of counting proficiency.

Give A Number (GAN). This task was a computerized version of the 'give me a number' counting assessment (Wynn, 1992). Children were shown a line of 10 identical items (i.e. butterflies, fish, or apples) at the top of the screen. They were instructed that the computer program would ask for a certain number of items (1–8), and that they were to produce that same number of items by pressing the SPACE BAR on the computer. Each SPACE BAR press brought one item from the top (all items in a line) to the center of the screen. Participants were further instructed to press the ENTER button when they had the correct number of items in the center of the screen. Given that this was the first computer task, the first trial asked for 'one' and corrective feedback was given to make sure the child understood how the SPACE BAR and ENTER buttons worked. Besides the first trial, the numbers 'one' through 'eight' were requested in random order within three different contexts (butterflies, fish, birds). In total, 24 test trials were presented and no feedback was given on any of the trials except the first. Children were allowed to complete the task independently without substantial intervention from the experimenter. In occasional cases where the child forgot to press ENTER but was clearly finished (as indicated by a discontinuation in pressing the button and/or a long pause), the experimenter prompted that, if finished, the child should press the ENTER button. In cases where the child explicitly indicated that he/she had brought down too many items but had not yet pressed the ENTER button to end the trial, the experimenter reset the trial (all the items were reset to the top of the screen and the number was requested by the program again). A total proportion correct (out of 24) was derived to score the test.

What's On This Card? (WOC). This task was a computerized version of the 'what's on this card?' counting assessment (Gelman, 1993; Wynn, 1992). Children were shown a set of animals/items and asked 'How many X (where X equaled the type of item, e.g. fish, apples, etc.)? Can you count them?' The first trial started with 1 item, with corrective feedback. After the first trial, children were tested with 1–8 items in a random order in three different contexts (apples, butterflies, fish) with no feedback, for a total of 25 trials. The items were visible until the experimenter entered the verbal response of the child into the computer. A total proportion correct (out of 25) was derived to score the test.

Executive functions assessments

Three tasks were administered to assess different aspects of executive functions. The tasks were modified versions of classic executive functions tasks for use with preschoolers (see Willoughby, Blair, Wirth & Greenberg, 2010, for preschool modifications).

Working Memory (n-back). This task assessed visual working memory for pictures of objects using an *n*-back memory task (e.g. Kirchner, 1958). To do this, children saw a stream of object images sequentially presented on a white background and had to indicate when the same object was repeated anytime during the task. Actual repeated images occurred either immediately after (1-back) or separated by 1 image (2-back) from the initial image presentation. Images were presented for 2 seconds and separated by 500 ms of blank white screen. Children were asked to press a button with a sticker on it ('k') on the computer when they saw a repeated image. Detection of the first repeat was completed together with the experimenter; all other trials were completed under the supervision, but without the assistance, of the experimenter. Feedback was given by positive (higher pitched) chime following correctly identified repeated images. Twelve total test trials were presented among 60 total images. The task was scored as the proportion of repeated images detected (out of 12).

Inhibition (Go/No-go). This task is a modified version of the classic go/no-go task adapted to test response inhibition in young children (e.g. Durston, Thomas, Yang, Uluğ, Zimmerman *et al.*, 2002). In this task, children were told that they would see pictures of cartoon animals (e.g. cow, lion, etc.) on the screen. They were asked to press a button when they saw an animal (i.e. go trials) that was not a snake. When they saw the image of the snake, participants were asked to not press the button (i.e. no-go trials). No-go trials were separated by 1, 3, or 5 go trials. Images were presented for 2 seconds and separated by a 250 ms blank screen. Participants saw 15 no-go images embedded within 60 total images. Feedback was given by positive (higher pitched) and negative (lower pitched) chimes following correct and incorrect responses. The task was scored as the proportion of no-go images correctly inhibited (out of 15).

Spatial conflict processing (arrows). This is a modified version of the Simon task used to assess inhibitory and conflict processing (Gerardi-Caulton, 2000). Children were presented with an arrow on the screen and were instructed to press the button that corresponded to the direction of the arrow presented. The arrow stayed on the screen until a response was given. The task was presented in three phases. In the first phase, arrows were presented in the middle of the screen (8 trials). In the second phase, arrows were presented laterally and were consistent with the direction in which the arrow was pointing (e.g. left arrows were presented on the left side, 14 trials). In the final phase, arrows were again presented laterally, but were also randomly presented in a spatially incongruent or congruent manner (20 trials). Feedback was given by positive (higher pitched) and negative (lower pitched) chimes following correct and incorrect responses. The task was scored as the proportion of correct responses during the final phase (out of 20 trials).

Linguistic abilities assessment

Peabody Picture Vocabulary Test IV (PPVT-IV). This is a standardized picture-based assessment of receptive vocabulary (Dunn & Dunn, 2007). In this task, children heard a word and were asked to choose the picture corresponding to that word (out of four possible choices). Children completed standardized vocabulary lists (of 12 items) that progressed in difficulty. The task started with the list that corresponded to their age and progressed until the child made errors on 8 or more items in a given list (of 12 items). The raw PPVT score, calculated as the total number of correctly answered items,[1] was taken as the score for this task.

Neural signatures of non-verbal numerical abilities

In addition to behavioral testing, we measured event-related potentials (ERPs) from the scalp as a measure of spontaneous neural processing of number in two tasks: an approximate number change task and an individual object processing task (Hyde & Spelke, 2009; Libertus, Brannon & Woldorff, 2011). Both tasks were passive-viewing tasks, where children were simply told to pay attention to the images with no mention of the numerical aspect of interest. Ongoing electrophysiological recordings were taken from the scalp during each task.

Approximate numerical change processing. This task modified the approximate number alternation paradigm from previous behavioral and ERP work on numerical processing in infants to measure spontaneous processing of large, approximate numerosity changes (e.g. Hyde & Spelke, 2011; Libertus & Brannon, 2010; Libertus *et al.*, 2011; Temple & Posner, 1998). During the task, children were asked to watch streams of sequentially presented novel dot arrays (white on a black background). Previous work with infants, children, and adults has shown that a mid-latency positivity over posterior scalp (P2p) is sensitive to the ratio of approximate numerical change between successive non-symbolic item arrays, and, as such, is taken to be a neural marker of ANS engagement (Hyde & Spelke, 2009, 2011, Hyde & Wood, 2011;

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[1] The raw score included the number of items on lists for younger children not administered. Given the narrow range of ages in our study, there were only two starting lists: one list for 3-year-olds and the subsequent list for 4-year-olds.

Temple & Posner, 1998). To measure spontaneous sensitivity of the ANS to numerical change in our sample, we manipulated ratio of change between blocks by presenting sequences of dot arrays that alternated by three ratios: 1:1, 1:2, or 1:4 (no change, small change, and large change) using 8, 16, and 32 dots (in the following combinations: 8:8, 8:16, 8:32, 32:8, 32:16, 32:32). In total, children were presented six blocks of 40 images each. However, as we were only interested in neural sensitivity to numerical change, no-change blocks were not included in our analysis. Each numerical image appeared for 500 ms and was separated by an inter-stimulus interval of 500 ms. Children were instructed to sit quietly and watch the images. To maintain attention, short cartoon clips would appear between blocks.

Non-numerical aspects of the displays varied pseudo-randomly in individual item size, inter-item spacing, total occupied area, and total luminance such that these parameters were not systematically related to number over the experiment. Since all these parameters cannot be controlled at once, the set of images for the experiment were created such that half of the arrays over the entire set were equated on intensive parameters (individual item size and inter-item spacing) and the other half of arrays varied along a continuum, but were on average equated for the extensive parameters (total occupied area and total luminance). A novel random ordering of the images (with equal numbers of extensively and intensively controlled images) was presented for each participant to ensure that number was not systematically related to these non-numerical parameters within a given participant or over the course of the study. A similar logic of controlling for non-numerical parameters is routinely used in behavioral number comparison tasks with adults and children (e.g. Barth, LaMont, Lipton & Spelke, 2005; Dehaene, Izard, Spelke & Pica, 2008; Piazza, Izard, Pinel, Le Bihan & Dehaene, 2004) as well as behavioral looking studies with infants (e.g. Libertus & Brannon, 2010; Starr *et al.*, 2013). Furthermore, the same method and design has been used in a recent ERP study of numerical change processing in infants (Hyde & Spelke, 2011).

Early attentional processing of individual items. This task measured visual attentional processing of small numbers of objects within the capacity limit (i.e., 4) of the PI system. Previous work has shown that early visual-attentional processing (N1) over posterior scalp sites is sensitive to the total number of objects presented up to the capacity of the PI system and, as such, is taken to be a neural marker of PI engagement (Hyde & Spelke, 2009; Hyde, 2011). To measure spontaneous engagement of the PI system in our sample, we presented arrays of 1 to 4 white dots on a black background. The same controls for non-numerical intensive and extensive stimulus parameters as used in the approximate numerical processing task were used in this task. Arrays were presented for 350 ms and were separated by an inter-stimulus interval that varied randomly in duration between 550 and 950 ms. Longer inter-stimulus intervals than in the approximate numerical processing task were used to encourage isolated responses to a given numerical image (rather than processing of relationship between images) and shorter image presentation times were used to discourage serial counting of small numbers of items. Four blocks containing 12 of each of the 4 cardinal values (total 48 images of each cardinal value) were presented to each participant in a random order with the constraint that each cardinal value (1–4) was presented before order re-randomization occurred. To maintain attention, children were told to fixate and to wait quietly until a cartoon image appeared on the screen. The image appeared after each of the four blocks. When the cartoon image appeared, children were told to press a button.

ERP data acquisition and pre-processing

Standard procedures of electrode cap preparation, fitting, placement, and quality assurance (e.g. Hyde & Spelke, 2009) were employed using a 128 channel HydroCel Geodesic Sensor Net (HGSN 128, EGI, Eugene, OR). Impedances below 50 kΩ were obtained in a majority of channels before recordings began. Data were recorded at 250 samples per second and digitally filtered online at 0.1–100 Hz, referenced online to the vertex. Offline, continuous data were high-pass filtered at .1 Hz, low-pass filtered at 20 Hz, and then segmented into epochs from −100 ms before to 800 ms after stimulus onset for each trial of each experiment for each subject. Epochs containing eye blinks (max-min > 200 μV over 20 ms moving average within vertical eye blink channels), eye movements (max-min > 200 μV, over 20 ms moving average within horizontal eye movement channels), or more than 10 bad channels (max-min > 200 μV over entire segment over any channel) were automatically eliminated from further analysis. Bad channels in epochs containing less than 10 total bad channels were corrected using spherical spline interpolation from surrounding sites. Remaining artifact-free epochs were averaged for each condition for task for each participant, re-referenced to the average reference, and baseline-corrected from −100 ms to stimulus onset.

Participants who retained at least 10 artifact free trials per condition for a given task were considered to have useable data. Of the 100 participants, six did not produce any useable data for either ERP task and were eliminated from all further analyses. Three participants produced useable data for the large number change processing (ANS), but not the small number processing (PI) task, and thus were excluded from analyses of the neural signatures of PI. No differences were observed in the number of trials retained after artifact detection between approximate number change conditions (medium change: M = 50 trials, SD = 13 trials; large change: M = 50 trials, SD = 14 trials; $F(1, 93) = 0.02$, $p = .878$) or between individual object processing conditions (1: M = 30 trials, SD = 7 trials; 2: M = 30 trials, SD = 7 trials; 3: M = 31 trials, SD = 7 trials; 4: M = 30 trials, SD = 7 trials; $F(3, 270) = 0.76$, $p = .520$).

Analysis

Defining brain signatures in individual subjects

We focused our analysis on brain electrophysiology during time windows characterizing the two components hypothesized a priori to show signatures of the PI and ANS system: N1 for parallel individuation and P2p for approximate number processing. It should be noted that the neural signatures of PI and ANS that we target in our investigation have been shown in previous work to dissociate in functional pattern, timing, and neuroanatomical source, providing strong evidence that they mark distinct cognitive systems (Hyde, 2011; Hyde & Spelke, 2009, 2011, 2012; Hyde & Wood, 2011). Exact time windows were chosen to characterize the grand average (all conditions averaged together) of the N1 (235–275 ms) and the P2p (350–450 ms) response, so as to not bias time window selection towards a particular pattern of modulation. The observed latencies for these components in preschool-aged children are compatible with previous work, as they are slightly slower than those latencies seen for the N1 and P2p in adults, yet earlier than those latencies observed in equivalent infant components (e.g. Hyde & Spelke, 2009, 2011). Mean amplitudes over the time windows of interest were extracted for each experimental condition for each task from each subject for further computation and analysis.

Studies of the approximate number system show behavioral and brain sensitivity to the numerical ratio between numbers being compared both in cases of implicit numerosity processing and explicit comparison tasks (Hyde & Spelke, 2009; Libertus, Woldorff & Brannon, 2007; Temple & Posner, 1998). To characterize spontaneous sensitivity of the ANS to numerical change for each participant in our data, we computed a difference score between our two numerical change conditions by subtracting the response to the small ratio change blocks (1:2 ratio) from the response to large ratio change blocks (1:4 ratio) (see Pinhas, Donohue, Woldorff & Brannon, 2014, for similar logic) during the time frame of the P2p, an established component shown to be sensitive to numerical change (e.g. Hyde & Spelke, 2009; Libertus *et al.*, 2007; Temple & Posner, 1998).

Studies of parallel individuation show brain and behavioral sensitivity to the total number of objects being individuated and tracked (Feigenson *et al.*, 2004; Hyde & Spelke, 2009; Trick & Pylyshyn, 1994). To characterize spontaneous sensitivity of the PI system to the total number of individual objects presented, we subtracted the response to 2 items, the lower bound of multiple-object processing, from the response to 4 items, the presumed capacity limit for simultaneous object processing, during the time frame of the N1. N1 is broadly related to visual-attentional processing of objects (see Luck, 2005, for a review) and specifically sensitive to the total number of objects represented within the capacity of the PI system (e.g. Hyde & Spelke, 2009; Hyde & Wood, 2011). The decision to use a difference score (between processing 4 and 2 items) as our measure of PI sensitivity in individual participants was based largely on the rationale for and success of such an approach in the adult ERP working memory literature in finding brain–behavior correlations (e.g. Drew & Vogel, 2008; Vogel & Machizawa, 2004).

Identifying brain and behavioral correlations

We used a data-driven approach to identify spatially clustered regions where the brain signatures of the two systems correlated with behavior. More specifically, we extracted the computed signature sensitivities of PI and the ANS at each of 128 electrode sites for each subject over the time windows defined above. After eliminating the data channels surrounding the eyes (16 total channels eliminated), we ran a correlational analysis between counting proficiency and the signature neural response at each channel (i.e. over the 112 remaining active channels) for all participants to determine the relationship, if any, between behavior and the brain response over the entire dataset at each channel. Next, we used an effect-matched spatial clustering algorithm, similar to algorithms for effect-matched spatial filtering (e.g. Schurger, Marti & Dehaene, 2013), to identify spatially contiguous electrical activity that was correlated with behavior. More specifically, we identified clusters of electrodes (2 or more spatially adjacent electrodes) showing a significant ($p < .05$, uncorrected) correlation with behavior across the entire dataset. We then ran 10,000 permutations of the data (randomly assigning individual subject brain data–behavioral data correspondences with each permutation) with the same cluster thresholds to determine the distribution maximum cluster sizes if brain and behavioral data associations were random. Finally, we compared the observed max cluster sizes obtained from the random permutations with the cluster sizes observed in the actual data to determine the likelihood of obtaining such clusters by chance (p = number of permutations with max cluster size larger than the actual observed cluster size/total number of permutations) (see Cohen, 2014). This analysis was carried out using a combination of in-house and open-source Matlab (Mathworks, Inc., Natick, MA) code for EEG/ERP analysis (EEGLAB: Delorme & Makeig, 2004; Massive Univariate ERP Toolbox: Groppe, Urbach, & Kutas, 2011).

Further testing of correlations between brain and behavior

We employed a leave-one-subject-out (LOO) procedure to identify clusters and extract data independently from our spatial cluster identification algorithm for further analysis (Esterman, Tamber-Rosenau, Chiu & Yantis, 2010). Essentially, this procedure calculated the spatial cluster(s) of electrodes showing a significant correlation with behavior in all but one subject (subject left out) and used that defined spatial cluster to extract the defined neural signature from the subject that was left out. In this way, the actual data extracted were independent from the data used to define the electrodes of interest. These data were entered into correlational analyses with counting proficiency, partial correlation analyses controlling for general cognitive and linguistics factors, and into a multiple linear regression analyses to further determine the extent of contributions of PI and ANS to early conceptual development of symbolic numerical abilities.

Further analysis of functional brain signatures on conceptual development

To gain further purchase on the relationship between brain signatures of non-verbal numerical cognitive system and conceptual development, we divided participants into two groups based on their counting performance: developing counters (i.e. children who only know the meanings of number words from one up to four) and proficient counters (i.e. children who know the meanings of number words larger than four). This division decision was based on previous literature showing qualitative differences in conceptual understanding between children who understand the meaning of numbers 4 or below and those that understand the meaning of numbers larger than four (Carey, 2009; Le Corre & Carey, 2007; Wynn, 1992). A child was taken to know the meaning of a number word if she or he performed perfectly on that number and all previous numbers in the give-a-number task, with the allowance of one error in the sequence. We then employed a repeated-measures ANOVA to analyze the within-subjects effect of approximate numerical change (small change vs. large change) on P2p and the within-subjects effect of number of objects (1, 2, 3, or 4 items) on N1 by the between-subjects factor of counting stage (developing or proficient) using the ERP data from clusters identified as significant through the spatial clustering algorithm (outlined above).

Results

Identifying correlations between neural signatures and counting ability

An effect-matched spatial clustering algorithm combined with cluster-size permutation testing (10,000 permutations) identified several distinct electrode clusters characterizing spontaneous numerical processing of the PI and ANS that correlated with counting ability in preschoolers (see Figures 1 & 2). Spontaneous neural sensitivity to the total number of objects presented during the N1 time frame, an established signature of parallel individuation, correlated with counting proficiency at two distinct clusters: negatively with a right posterior electrode cluster (N1, 9 electrodes, p = .008, electrodes 96, 97, 98, 99, 100, 101, 102, 103, and 108) and positively with a central scalp electrode cluster (P2c, 15 electrodes, p = .002, electrodes 6, 7, 13, 29, 30, 31, 35, 37, 53, 54, 55, 61, 62, 106, and 129, see Figure 1).[2] Spontaneous neural sensitivity to approximate numerical change during the P2p time frame, an established signature of the ANS, positively correlated with counting proficiency over a single, large, right-lateralized posterior electrode cluster (P2p, 23 electrodes, p = 0; electrodes 55, 77, 79, 83, 84, 85, 86, 87, 88, 89, 90, 91 92, 93, 95, 96, 97, 98, 100, 101, 102, 107, and 108, see Figure 2). Locations identified by the data driven effect-matched spatial clustering algorithm are consistent with previous literature identifying N1 and P2p for numerical processing (e.g. Dehaene, 1996; Hyde & Spelke, 2009; Libertus *et al.*, 2007; Temple & Posner, 1998).

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[2] We did not impose directionality or spatial constraints on our data-driven search algorithm. The search did turn up the anticipated negativity over posterior sites, N1. Our data-driven approach also turned up this positive central component during the N1 time window. For lack of a better term, we called it P2c (as it was positive, occurred after the P1, and was central).

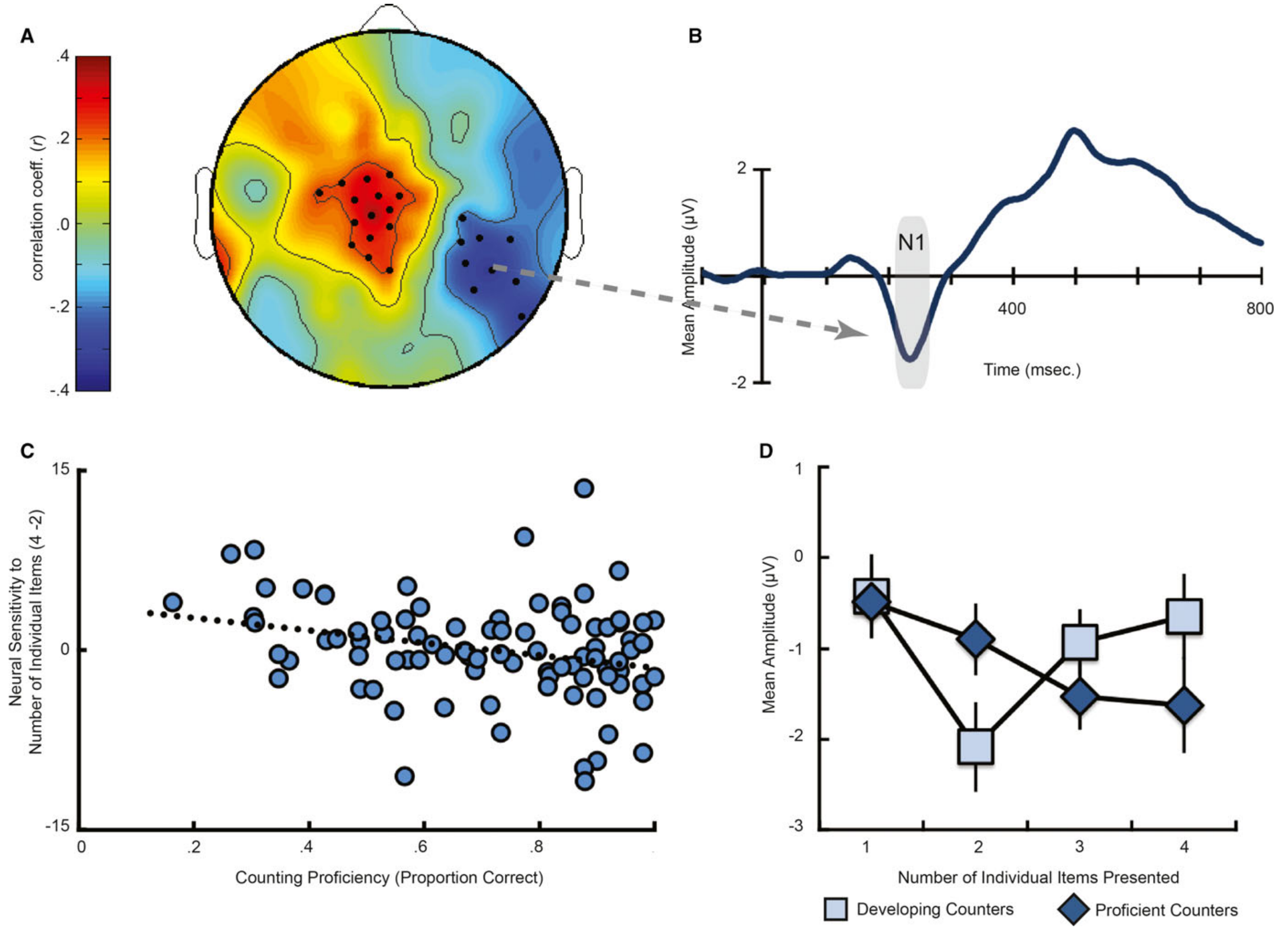

Figure 1 *Spontaneous engagement of parallel individuation and counting proficiency. (A) Topographical scalp map of correlations between counting proficiency and spontaneous N1 sensitivity to number (response to 4 items minus the response to 2 items). Black dots represent the scalp positions of electrodes identified through permutation testing to be of significant size to warrant further investigation. (B) Grand average waveform from temporal-parietal cluster of interest. (C) Scatter plot showing relationship between counting proficiency and spontaneous neural sensitivity to number derived from the leave-one-subject-out procedure. (D) N1 mean amplitudes in response to each set size presented between developing (square) and proficient (diamond) counters.*

Counting, core number, and general cognitive abilities

Using data derived from our leave-one-subject-out procedure as an independent estimate of correlation coefficients, we observed a significant correlation between the spontaneous signature of the PI system with counting proficiency on the N1 (r (89) = -0.27, $p = .009$, but not on the P2c (r (89) = 0.20, $p = .053$, see Figure 1c) and between the spontaneous neural signature of the ANS with counting proficiency(r (92) = 0.27, $p = .008$, see Figure 2c). However, only correlations between N1 and counting proficiency held after entering them into a partial correlations analysis controlling for non-numerical cognitive abilities including vocabulary (PPVT), inhibitory control, conflict processing, and working memory (N1: r (85) = $-.22$, $p = .042$; P2c: r (85) = .11, $p > .250$; P2p: r (87) = .18, $p = .091$) (see Figures 1 & 2).

To directly compare the potential contribution of each core number system and other hypothesized non-numerical cognitive and linguistic abilities, as well as to determine what combination of these factors explained the most variance in counting ability, we entered both neural measures of core systems (N1 for PI and P2p for ANS) and behavioral measures of general cognitive (inhibition, conflict processing, and working memory) and linguistic factors (PPVT) into a stepwise multiple linear regression (Table 1). The model explaining the most variance ($F(4, 86) = 11.78$, $p < .001$, $R^2 = .35$) included the neural measure of the PI system (N1), inhibition, vocabulary, and working memory score, but

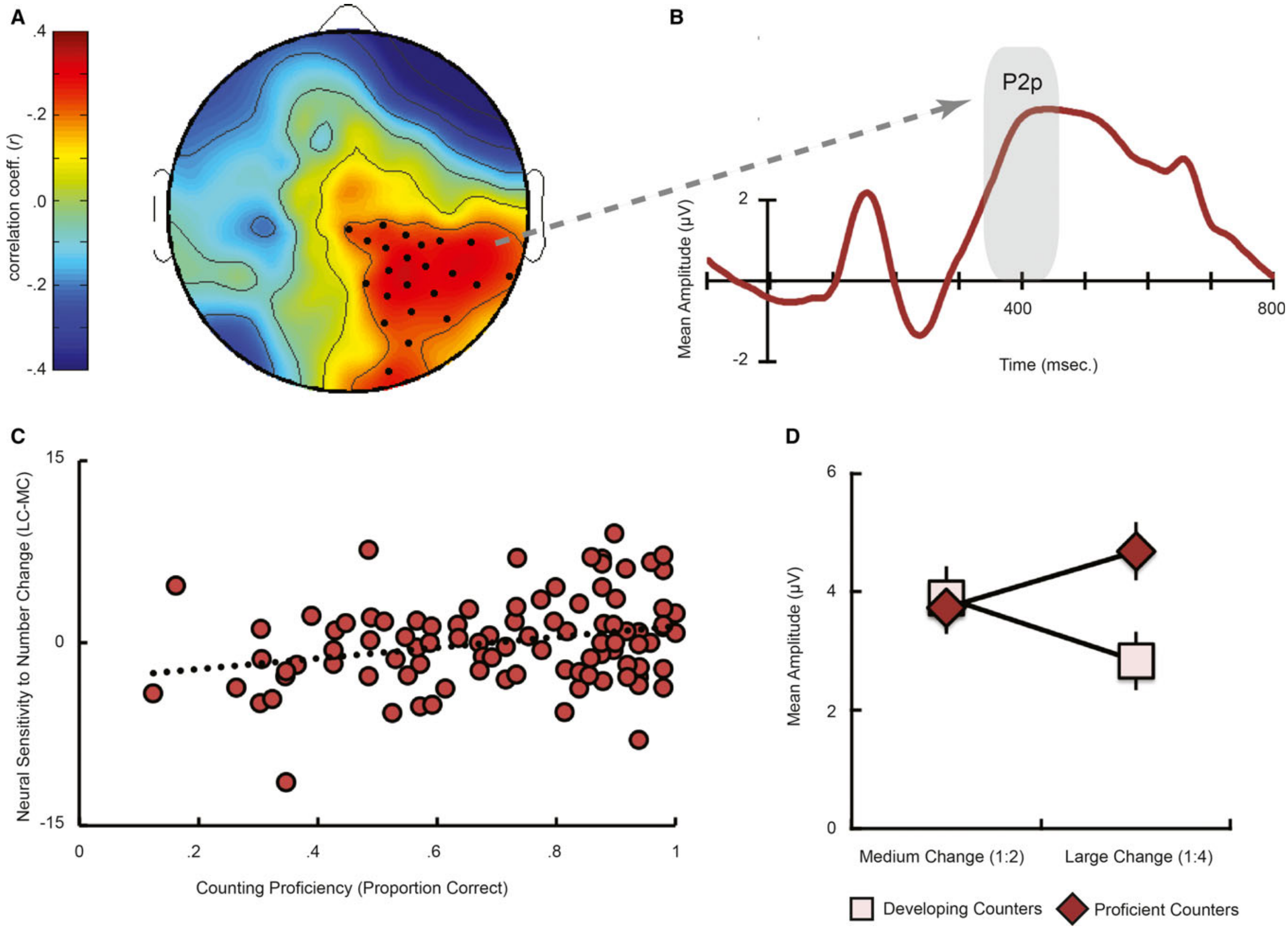

Figure 2 *Spontaneous engagement of approximate number system and counting ability. (A) Topographical scalp map of correlations between counting proficiency and spontaneous P2p sensitivity to approximate number change (response to large change minus response to medium change). Black dots represent the scalp positions of electrodes identified through permutation testing to be of significant size to warrant further investigation. (B) Grand average waveform from posterior parietal cluster of interest. (C) Scatter plot showing relationship between counting proficiency and spontaneous neural sensitivity to approximate number change derived from leave-one-subject-out procedure. (D) P2p mean amplitudes in response to each number change condition between developing (square) and proficient (diamond) counters.*

Table 1 *Best model from stepwise linear regression analysis*

	Stand. Coeff. (β)	*t*	Sig. (*p*)
Parallel Individuation (N1)	−.192	−2.18	.032
Vocabulary (PPVT)	.298	3.12	.003
Working Memory (N-back)	.252	2.67	.009
Inhibition (Go/No-go)	.225	2.58	.012

did not include spatial conflict processing or the neural measure of the ANS.

Together these results from correlational and regression analyses suggest that individual differences in the spontaneous engagement of the PI system hold a significant relationship with individual differences in counting ability that cannot be accounted for by individual differences in general cognitive or linguistic ability.

Functional brain signatures and conceptual development

Using the spatial clusters of electrodes identified by our effect-matched spatial clustering algorithm, we extracted ERP waveform data to further investigate the effects of conceptual development on the functional brain response. More specifically, we divided our sample into two groups, developing counters (n = 48) and proficient counters (n = 52), based on their conceptual understanding of symbolic number words (LeCorre & Carey, 2007) and compared the two groups on their ERP signatures of the ANS and PI. The two groups did not differ in age ($t(98) = -1.45$, $p = .148$; developing counters: 3 years 10 months 18 days vs. proficient counters: 3 years 11 months 4 days).

Analysis of PI system engagement, or sensitivity to the number of individual items presented on the N1, revealed a main effect of Number ($F(3, 267) = 2.70$, $p = .046$, $\eta^2_p = .029$) and a significant interaction between Number and Counting Stage ($F(3, 267) = 3.07$, $p = .028$, $\eta^2_p = .033$; no main effect of Stage $F(1, 89) = 0.08$, $p > .250$, $\eta^2_p = .001$). Post-hoc linear contrast analysis of each group separately revealed that N1 modulated linearly with the number of individuals from 1 to 4 for proficient counters only (Developing Counters: Number $F(1, 42) = 0.10$, $p > .250$, $\eta^2_p = .002$; Proficient Counters: Number $F(1,47) = 4.85$, $p = .033$, $\eta^2_p = .094$, see Figure 1d). Further post-hoc exploratory investigation of data from the developing counters revealed that N1 was only modulated by number from 1 to 2 items (1 vs. 2 items ($F(1, 42) = 7.03$, $p = .011$, $\eta^2_p = .143$) and then tapered off with 3 or more items (see Figure 1d). A further breakdown into performance levels revealed this pattern of scaling, up to 2 items and then tapering off, was not clearly related to the level of number knowledge within the developing counter group (1-knowers, $n = 9$; 2-knowers, $n = 10$; 3-knowers, $n = 16$; 4-knowers, $n = 8$).

An analysis of ANS engagement, or sensitivity to approximate numerical change on the P2p, revealed an interaction between Ratio Change and Counting Stage (Ratio by Stage: $F(1, 92) = 10.35$, $p = .002$, $\eta^2_p = .101$; No main effects of Ratio: $F(1, 92) = 0.03$, $p > .250$, $\eta^2_p < .001$ or Stage: $F(1, 92) = 1.84$, $p = .178$, $\eta^2_p = .020$). Post-hoc analysis of each developmental stage separately revealed a linear decrease in P2p amplitude with an increase in ratio for developing counters (Number $F(1, 45) = 6.62$, $p = .013$, $\eta^2_p = .128$) and an increase in P2p amplitude with an increase in ratio for proficient counters ($F(1, 47) = 4.15$, $p = .047$, $\eta^2_p = .081$). That is, P2p was modulated linearly for both proficient and developing counters, but the direction of the ratio effect on the P2p was opposite between groups (see Figure 2d).

Discussion

Humans are born with at least two cognitive systems for non-verbal numerical cognition (see Feigenson *et al.*, 2004). It is widely proposed that these non-verbal numerical abilities form a basis for symbolic number system acquisition (e.g. Carey, 2009; Dehaene, 1997; Gallistel & Gelman, 1992; Spelke, 2011). However, there is substantial disagreement as to whether or to what extent each system is actually involved (see Carey, 2009, for a review) and empirical evidence from behavioral studies to date has been largely inconclusive. Here we used brain measures to obtain spontaneous neural signatures of PI sensitivity to the number of items being simultaneously attended, and ANS sensitivity to approximate numerical change between successively presented large number arrays in individual participants (Hyde, 2011; Hyde & Spelke, 2009, 2011, 2012; Hyde & Wood, 2011). We observed significant correlations between individual differences in the spontaneous neural signatures of the ANS and the PI with individual differences in counting ability in preschool children, suggesting a relationship between core numerical cognition and early symbolic number concept development. While relationships between individual differences in the PI system and counting proficiency held after controlling for general cognitive and linguistic factors, relationships between the ANS and counting did not.

Others have shown that individual differences in approximate numerical comparison ability correlate with and even predict future performance in mathematics achievement (Libertus *et al.*, 2013; Starr, Libertus & Brannon, 2013; Wagner & Johnson, 2011). Although we replicate a simple correlation between the ANS and counting proficiency, the full results of our study do not provide strong support for this relationship. Here we outline at least three possibilities as to why this might be the case in our data. First, it is possible that previous studies showing a relationship have not sufficiently controlled for non-numerical cognitive and linguistic abilities, thereby revealing a relationship actually driven by other non-numerical cognitive or linguistic factors (e.g. Wagner & Johnson, 2011). It may be the case that after employing a spontaneous neural measure and accounting for general cognitive and linguistic factors in our study, the relationship between the ANS and counting was truly eliminated. Second, it is possible that the ANS does contribute to later developing symbolic number and mathematics abilities (Carey, 2009), but does not contribute to early symbolic number system acquisition tested here. Since the most relevant published studies to date have only examined the relationship between the ANS and preschool mathematics achievement broadly (Libertus *et al.*, 2013; but see van Marle, Chu, Li & Geary, 2014), it is possible that our data dot not conflict with previous work because we focus on an earlier and more specific aspect of numerical development (but see Wagner & Johnson, 2011). Third, it is possible that the spontaneous neural signature of the ANS we report here captures an aspect of the ANS that is different from active numerical comparison measures shown to correlate with symbolic number and mathematics achievement in other studies (e.g. Wagner & Johnson, 2011). Specifically, our neural measure may have captured qualitative changes resulting from the conceptual development of a symbolic number system, rather than individual differences in ANS precision (Halberda *et al.*, 2008). Actual relationships between the ANS and symbolic number and mathematics ability may then exist, but were not observed in our study because we were not measuring the most relevant aspect of the ANS to counting (Gilmore, Attridge, De Smedt & Inglis, 2014).

Interestingly, the direction of the P2p ratio effect is qualitatively different between developing and proficient counters. Developing counters showed a decrease in amplitude with an increase in numerical ratio between arrays, a pattern observed on the P2p during passive or spontaneous numerical processing tasks with infants and adults (e.g. Hyde & Spelke, 2009, 2011) and in some active numerical comparison tasks (e.g. Dehaene, 1996; Libertus *et al.*, 2007). Conversely, proficient counters showed an increase in P2p amplitude as the numerical ratio between arrays increased, a pattern observed in other studies involving explicit numerical comparison (e.g. Temple & Posner, 1998; Heine, Tamm, Wissmann & Jacobs, 2011; Heine, Wissmann, Tamm, De Smedt, Schneider *et al.*, 2013; Paulsen & Neville, 2008), and also in non-numerical ordinal processing (e.g. Zhao, Chen, Zhang, Zhou, Mei *et al.*, 2012).[3] Although speculative, the difference in the direction of the P2p ratio effect could be due to differences in the degree to which participants recognize the numerical difference between numbers in ordinal terms (increasing vs. decreasing or larger vs. smaller), with proficient counters more likely to explicitly detect ordinal relationships between numerical arrays than developing counters. However, this speculation would need to be verified through experiments directly aimed at this issue before any firm interpretation can be made.

What appears to be very clear from our study is that individual differences in PI are related to individual differences in symbolic number development. Thus, our results uphold views of numerical cognition that propose a role for the PI system in early symbolic number system acquisition (Carey, 2009; Huang *et al.*, 2010). Until now, the role of the PI system in early symbolic number concept development has been hypothesized based solely on the reliable, yet merely qualitative, stages seen in typical counting development (Le Corre & Carey, 2007; Wynn, 1992). We observed greater spontaneous sensitivity of the N1 to the number of individual items (greater response to 4 compared to 2 items) to be associated with greater counting proficiency, beyond general cognitive and linguistic factors. The N1 ERP component has been classically associated with early visual-attentional processing (Hyde, 2011; Luck, 2005). Further, dividing children into groups based on this conceptual tipping point revealed an interaction whereby N1 amplitude scaled with number of items from 1 to 2 and then fell off in developing counters, while N1 scaled linearly with number from 1 to 4 items for proficient counters. Such asymptotic processing differences on the N1 mirror those seen in the ERP literature of individual differences in working memory (e.g. Drew & Vogel, 2008), suggesting the possibility that these groups may differ in attentional processing capacity of the PI. Given the correlational nature of our data, however, it is unclear whether these differences are a cause or a consequence of cognitive development.

Analyzed together with general cognitive and linguistic factors, our results suggest that the individual differences in counting, the earliest symbolic number development, are reliably related to individual differences in general working memory, executive function, verbal abilities, and parallel individuation. It is uncontroversial to propose that individual differences in numerical development can be explained by individual differences in general cognitive or linguistic capacities. More intriguing, however, is the suggestion from our results that individual differences in the PI system might underlie early numerical cognition, as the mental representations of PI are not inherently numerical (Carey, 2009). How, then, might the ability to select, track, and remember individual items be related to high-level conceptual understanding of number, a property of sets (Gallistel, 2007)? It has been shown that PI allows for numerical comparisons using one-to-one correspondence to determine the exact equality of small sets containing the same types of items (Feigenson *et al.*, 2004; Izard, Streri & Spelke, 2014). For example, 12–14-month-olds infants can use parallel individuation to keep track of small numbers of food items hidden sequentially in two distinct cache locations and use that information to selectively retrieve from the more

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[3] The matter is complicated by the fact that explicit numerical comparison tasks have elicited distance/ratio effects in both directions and the directionality of the distance effect has been shown to interact with numerical notation and numerical range in some contexts (e.g. symbolic versus non-symbolic: Temple & Posner, 1998; smaller versus larger numbers: Heine *et al.*, 2011; Libertus *et al.*, 2007). Further, directionality of the ratio/distance effect in explicit comparison tasks often depends on which part of the second posterior positivity is being analyzed (earlier half of the rising positivity typically associated with greater positivity for closer distance comparisons; later half of the falling positivity typically associated with greater positivity for grater ratio distance, see Dehaene, 1996; Turconi, Jemel, Rossion & Seron, 2004). This may be due to spatial and temporal overlap in the earlier, smaller P2p and the later, larger P3b component, with such overlap being worse in developmental populations compared to adults. Focused experiments manipulating implicit versus explicit, ordinal versus magnitude, and numerical versus non-numerical are needed to sort out the nature of directionality in these distance effects before firm conclusions regarding their meaning can be derived.

numerous food cache (see Feigenson *et al.*, 2004, for a review). Similarly, 2½-year-old children who have yet to mastered counting can nonetheless use one-to-one correspondence to judge the exact equality of even larger sets of items as long as those items are of the same type (Izard *et al.*, 2014). Both of these examples show young children making a comparison of number without using a mental representation of the cardinal value of the set. Although speculative, it is possible that being better at distinguishing the exact equality of small sets of objects (on the basis of one-to-one correspondence) would provide an advantage in learning the association between the cardinal value of a set and the corresponding number word and how counting represents number. Of course, given the correlational nature of our data, it is also possible that learning the exact meanings of number words enables better parallel individuation of objects. Future work using longitudinal methods may distinguish between these possibilities. Nevertheless, the results reported here legitimize the possibility that a foundation for high-level, uniquely human mental abilities such as numerical or mathematics could have roots in more basic non-verbal abilities to select and process individual objects.

Author contributions

DCH designed the experiment. CES, IB, and YM collected the data. DCH and CES conducted the statistical analyses. DCH wrote the manuscript with input and approval from all other authors.

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