

Nonsymbolic number and cumulative area representations contribute shared and unique variance to symbolic math competence

Stella F. Lourenco¹, Justin W. Bonny, Edmund P. Fernandez, and Sonia Rao

Department of Psychology, Emory University, Atlanta, GA 30322

Edited by Randy Gallistel, Rutgers University, Piscataway, NJ, and approved September 14, 2012 (received for review May 8, 2012)

Humans and nonhuman animals share the capacity to estimate, without counting, the number of objects in a set by relying on an approximate number system (ANS). Only humans, however, learn the concepts and operations of symbolic mathematics. Despite vast differences between these two systems of quantification, neural and behavioral findings suggest functional connections. Another line of research suggests that the ANS is part of a larger, more general system of magnitude representation. Reports of cognitive interactions and common neural coding for number and other magnitudes such as spatial extent led us to ask whether, and how, nonnumerical magnitude interfaces with mathematical competence. On two magnitude comparison tasks, college students estimated (without counting or explicit calculation) which of two arrays was greater in number or cumulative area. They also completed a battery of standardized math tests. Individual differences in both number and cumulative area precision (measured by accuracy on the magnitude comparison tasks) correlated with interindividual variability in math competence, particularly advanced arithmetic and geometry, even after accounting for general aspects of intelligence. Moreover, analyses revealed that whereas number precision contributed unique variance to advanced arithmetic, cumulative area precision contributed unique variance to geometry. Taken together, these results provide evidence for shared and unique contributions of nonsymbolic number and cumulative area representations to formally taught mathematics. More broadly, they suggest that uniquely human branches of mathematics interface with an evolutionarily primitive general magnitude system, which includes partially overlapping representations of numerical and nonnumerical magnitude.

analog magnitude | Weber's law | estimation |
nonsymbolic magnitude precision | mathematical cognition

How do humans come to understand mathematics? A common view is that the mental capacity for formal math—which includes access to symbolic notations of number, knowledge of quantitative concepts, and the implementation of computational operations—builds on a set of core abilities such as an intuitive, nonverbal sense of numerosity (1–5). Also known as the approximate number system (ANS), this nonsymbolic sense of numerical magnitude is shared with nonhuman animals (6) and is widespread across cultures (7). Unlike the acquisition of symbolic number (e.g., Arabic digits) and formal math concepts, which are learned via explicit instruction and allow for exact quantification, the ANS may be innate (8) and is characteristically “noisy,” with variance increasing linearly as a function of the absolute numerical value (9). This imprecision can be modeled as overlapping Gaussian distributions along an internal continuum (10) and is captured by Weber's law, which holds that subjective differences in intensity are proportional to the objective ratios between values. When people compare numerical values under conditions that prevent counting or that do not allow for explicit calculation, their judgments are systematically approximate, with discriminability becoming more difficult as the ratio approaches 1 (e.g., 10 vs. 5 is easier to discriminate than 10 vs. 9).

Despite vast differences in the nature and developmental trajectories of the ANS and formally taught mathematics (11), accumulating behavioral and neural data suggest that these systems are cognitively and functionally intertwined. Studies using functional (f)MRI, for example, show that activation in and around the intraparietal sulcus (IPS) is similarly modulated by the ratio of Arabic digits and nonsymbolic number arrays (10, 12, 13). Moreover, addition problems solved either exactly with symbolic notation or approximately on nonsymbolic visual displays recruit parietal cortex (14), with impairments for each following injury or temporary deactivation of the IPS (15, 16). Additional evidence for a link between the ANS and symbolic arithmetic comes from individuals with dyscalculia, known as a specific disability in learning school-relevant math (17). Recent studies suggest that dyscalculia is also characterized by deficits in ANS processing such as nonsymbolic number comparison (18), with atypical IPS activation during both symbolic arithmetic (19) and approximate nonsymbolic comparisons (20).

Studies using psychophysical techniques to quantify the coarseness of nonsymbolic number representations point to large individual differences in precision throughout the lifespan (21, 22). Whereas some people have more noise associated with the ANS (i.e., more overlap in the Gaussian curves), others have less noise (i.e., less overlap in the Gaussian curves). Halberda and colleagues (23) reported that individual differences in ANS precision (derived from performance on a nonsymbolic comparison task) at 14 y of age retroactively predicted competence in symbolic arithmetic (measured by standardized tests of calculation ability) during kindergarten through sixth grade. Greater ANS precision was associated with higher standardized math scores. Other studies measuring ANS precision earlier in development (3–6 y) have revealed that children's performance on nonsymbolic number tasks predicts later mastery of number words and knowledge of the school math curriculum, even after controlling for general aspects of intelligence such as verbal competence (24, 25). These studies provide converging behavioral evidence for a functional connection between the ANS and symbolic math, evident before formal instruction and continuing into adulthood.

Here we ask about the nature and specificity of the link between nonsymbolic representations of magnitude and symbolic (formally taught) mathematics. Are the magnitude representations implicated in this network specifically and exclusively numerical? Or does a formal math system interface more broadly with nonnumerical magnitudes that extend across space or time? Such questions follow naturally from debates on the specificity of the

Author contributions: S.F.L., J.W.B., and S.R. designed research; J.W.B., E.P.F., and S.R. performed research; S.F.L., J.W.B., and E.P.F. analyzed data; and S.F.L. and J.W.B. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission.

¹To whom correspondence should be addressed. E-mail: slouren@emory.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1207212109/-DCSupplemental.

ANS. One side of this debate holds that although the ANS is represented in analog format, as are other magnitudes such as spatial extent and duration (5, 9, 26), representations of numerical magnitude are separable, at least functionally, from those of nonnumerical magnitude (27–30). Another side suggests that the ANS may be better conceptualized as part of a larger, more general system of magnitude representation, with shared mechanisms for processing numerical and nonnumerical magnitudes (9, 26, 31–33). Evidence for such a system includes behavioral demonstrations in humans of cognitive interactions between number and spatial extent (e.g., “size congruity effect”) (34, 35), as well as single-cell recordings with rhesus monkeys showing that ~20% of neurons in the horizontal segment of the IPS are tuned to both nonsymbolic number and spatial extent (36) (for evidence in humans of common neural activation, see refs. 13, 37). Although neither side has made explicit claims about whether, and how, nonnumerical magnitude should interface with formal math, there are two predictions that follow. ANS specificity would predict that connections between math and nonsymbolic number should be specific and dissociable from representations of nonnumerical magnitude. In contrast, a general magnitude system with common mechanisms for representing numerical and nonnumerical magnitude would predict that these magnitudes should interface similarly with symbolic mathematics—the caveat being that the amount of representational overlap for numerical and nonnumerical magnitudes may dictate how similarly they interface with a formal math system.

Questions about how broadly uniquely human mathematics interfaces with nonsymbolic magnitude representations shared by humans and nonhuman animals are wide open and in need of empirical investigation. To this end, we examined the extent to which the precision of numerical and nonnumerical magnitudes predicts formal math competence. Participants (college students) were given two magnitude comparison tasks, one in which they estimated number (i.e., “Which array of dots is greater in number?”) and another in which they estimated spatial extent (i.e., “Which array of dots is greater in cumulative area?”). Cumulative area served as the nonnumerical magnitude and the test case of generalization, because, like number for an array of dots, it is a property of visual sets, allowing for a direct comparison of different magnitudes while keeping perceptual features as similar as possible. In both number and area tasks, participants saw spatially intermixed dots of two colors (brown and blue) presented on a computer screen (Fig. 1). Arrays were presented too rapidly (200 ms) to allow for serial counting or explicit computations of cumulative area, such that participants had to rely on an approximate sense of magnitude in both cases. The ratio of brown and blue dots varied widely from 2:1 to 10:9 on each task. Precisions for number and cumulative area representations were computed and compared straightforwardly, using overall accuracy across the tested ratios.

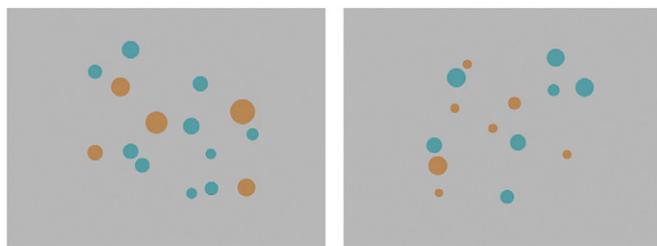


Fig. 1. Sample images from number (Left) and area (Right) tasks. Both images represent a ratio of 2:1, with blue dots greater than brown dots in number or cumulative area (respectively).

Participants were also administered a battery of standardized math tests, including subtests from the Woodcock–Johnson III Tests of Achievement (WJ) (38) and KeyMath 3 Diagnostic Assessment (KM) (39), for an assessment of broad mathematical competence. These tests measure symbolic arithmetic ability, both advanced (WJ-calculation) and elementary (WJ-math fluency), performance on word problems (WJ-applied problems), knowledge of math-related concepts (WJ-quantitative concepts), and geometric understanding (KM-geometry). Existing studies concerned with examining the links between mathematics and nonsymbolic number representations have focused almost exclusively on arithmetic calculations (e.g., refs. 23, 40). Math, however, is not a monolithic domain, and in college students, expertise typically spans multiple branches (e.g., arithmetic, algebra, calculus, and geometry) and can be applied across various contexts, ranging from structured equations with digits and/or variables to less structured word problems, from unlimited time constraints to speeded responses, and from complex calculations to rote recall of facts. Psychometric studies report strong correlations across standardized math tests (38, 39), but the extent to which different types of math may be grounded in nonsymbolic magnitudes has yet to be systematically investigated. Studies using neuroimaging techniques suggest that the neural circuitry recruited for solving different math problems can vary depending on the type of problem; whereas over-rehearsed arithmetic facts have been shown to recruit left angular gyrus (41, 42), word problems activate prefrontal cortex (43, 44). Such differences in brain activation raise the possibility that not all aspects of mathematical competence will interface similarly with nonsymbolic magnitudes, which have been shown to primarily recruit the IPS (13, 37). By including multiple measures of educationally relevant mathematics and by examining the predictive value of both number and cumulative area precision for different types of math, the present study seeks to extend recent research and to provide a direct investigation of the nonsymbolic correlates of uniquely human, highly abstract cognition.

Results and Discussion

Statistical analyses were conducted on 65 participants (*Methods*). Participants completed both magnitude comparison tasks (number and area), followed by a battery of standardized math tests and two tests of verbal competence [WJ-picture vocabulary and WJ-reading vocabulary (38); see *SI Text* for description of tests]. Verbal competence served as the nonmath control because it is a well-known component of general intelligence (45, 46) and because, like mathematical competence, it is affected by formal education, making it both appropriately comparable and contrastive.

Performance on Magnitude Comparison Tasks. As expected, analyses of mean accuracy at each ratio revealed that performance improved as ratio increased on both number, $F(5, 320) = 112.690$, $P < 0.001$, and area, $F(5, 320) = 92.559$, $P < 0.001$, tasks (see *SI Text* for additional analyses). Improvement was also observed for median reaction time (RT) (correct trials only), with faster responses for larger ratios on both tasks: number, $F(5, 320) = 14.055$, $P < 0.001$, and area, $F(5, 320) = 23.785$, $P < 0.001$ (*SI Text*). Effects of accuracy and RT are consistent with Weber’s law and confirm that participants’ estimates were based on representations of approximate magnitude, not explicit strategies of enumeration or exact calculations.

Analyses comparing individual differences in overall accuracy (i.e., mean accuracy across all ratios) revealed that performance on number ($M = 71.0\%$, $SD = 6.2\%$) and area ($M = 71.1\%$, $SD = 6.3\%$) tasks did not differ significantly from each other, $t(64) = -0.100$, $P = 0.921$ (see *SI Text* for distribution of scores), suggesting equivalent levels of precision for nonsymbolic number and cumulative area, at least for the stimulus types and ratios tested here. Moreover, overall accuracy for number and

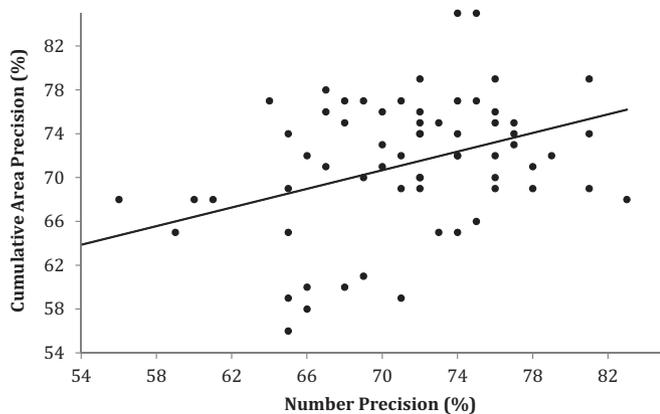


Fig. 2. Scatterplot relating performance on number and area tasks. Precision for nonsymbolic number and cumulative area representations were positively correlated, $r(63) = 0.427$, $P < 0.001$ (zero-order correlation).

area tasks were positively correlated (Fig. 2), a correlation that remained statistically significant when controlling for verbal competence, $r_p(61) = 0.409$, $P < 0.01$, or for performance across all standardized (math and nonmath) tests, $r_p(56) = 0.331$, $P = 0.011$. Participants with better estimates of number displayed better estimates of cumulative area, suggesting at least partially overlapping representations of numerical and nonnumerical magnitude and adding to a growing body of evidence in support of a general magnitude system. A possibility not addressed here is the extent to which basic perceptual parameters such as visual acuity or attentional factors may account for the correlation between number and cumulative area precision, rather than shared representational content for these magnitudes. This is an important issue for future research.

What Is the Relation Between Magnitude Precision and Mathematical Competence? To answer this question, we conducted correlation analyses between overall accuracy on each of the magnitude comparison tasks and performance across the standardized math tests, while controlling for nonmath (verbal) competence (WJ-picture vocabulary and WJ-reading vocabulary; see *SI Text* for age-referenced scores on standardized tests). Both number and cumulative area precision were significantly correlated with WJ-calculation [number task, $r_p(61) = 0.310$, $P = 0.013$; area task, $r_p(61) = 0.260$, $P = 0.040$] and KM-geometry [number task, $r_p(61) = 0.302$, $P = 0.016$; area task, $r_p(61) = 0.360$, $P = 0.004$] (see Fig. 3 for zero-order correlations). These findings build on recent research by showing that individual differences in both nonsymbolic number and cumulative area precision correlate with individual differences in both advanced arithmetic and geometry. As magnitude precision increases (whether numerical or nonnumerical), so, too, does performance on standardized tests of mathematical competence, even when accounting for general aspects of intelligence. No other partial correlations, however, reached statistical significance (all P s > 0.05). That is, neither number nor cumulative area precision systematically related to scores on WJ-math fluency, WJ-quantitative concepts, or WJ-applied problems. The lack of correlations for these math tests suggests that although the link between numerical magnitude and math competence extends to nonnumerical magnitude and beyond advanced arithmetic to geometry, there are clear limits on the grounding of symbolic math in nonsymbolic magnitude representations (*General Discussion*).

In subsequent analyses we focused on advanced arithmetic and geometry, both of which correlated with number and cumulative area precision. Separate multiple-regression analyses were used to examine the relative contributions of number and cumulative

area precision to performance on WJ-calculation and KM-geometry. These analyses revealed that overall accuracy on the number task predicted WJ-calculation scores above and beyond that accounted for by performance on the area task, $\Delta R^2 = 0.053$, $F(1, 62) = 3.748$, $P = 0.057$. Although this particular effect is statistically marginal, the fact that cumulative area precision did not uniquely predict WJ-calculation scores, $\Delta R^2 = 0.019$, $F(1, 62) = 1.329$, $P = 0.253$, suggests that the link between nonsymbolic number and advanced arithmetic is not due to their respective connections to representations of cumulative area (see Fig. 4 for partial correlations). In contrast, overall accuracy on the area task was a unique predictor of KM-geometry scores, $\Delta R^2 = 0.088$, $F(1, 62) = 6.826$, $P = 0.011$, whereas nonsymbolic number showed no unique contribution to KM-geometry, $\Delta R^2 = 0.030$, $F(1, 62) = 2.324$, $P = 0.132$. This suggests that the link between cumulative area representations and geometry is not due to their respective connections to nonsymbolic number (Fig. 4). Because some of the items on KM-geometry require arithmetic computations, one could ask whether the association between geometry and nonsymbolic magnitude is driven exclusively by calculation-like items, similar to those on the WJ-calculation test. Although KM-geometry and WJ-calculation were significantly correlated, $r(63) = 0.563$, $P < 0.001$, regression analyses controlling for WJ-calculation scores revealed that cumulative area precision remained a significant predictor of KM-geometry scores, $\beta = 0.283$, $t(62) = 2.757$, $P = 0.008$ [number precision: $\beta = 0.169$, $t(62) = 1.559$, $P = 0.124$]. These analyses suggest that numerical and nonnumerical magnitudes interface, to some extent, uniquely with advanced arithmetic and geometry, respectively. Importantly,

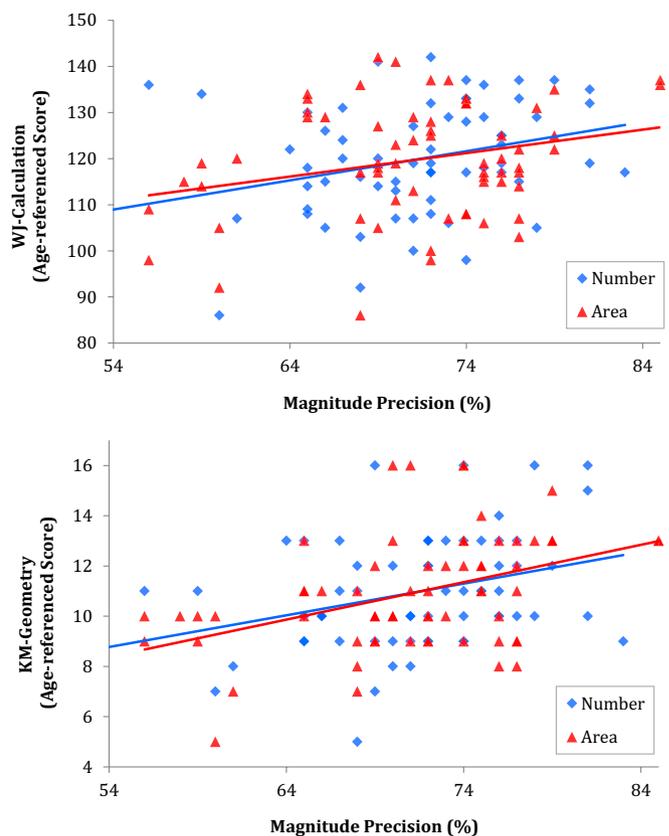


Fig. 3. Scatterplots of zero-order correlations between magnitude precision (number and cumulative area) and mathematical competence on WJ-calculation [Upper: number task, $r(63) = 0.320$, $P = 0.009$; area task, $r(63) = 0.261$, $P = 0.036$] and KM-geometry [Lower: number task, $r(63) = 0.332$, $P = 0.001$; area task, $r(63) = 0.410$, $P = 0.001$].

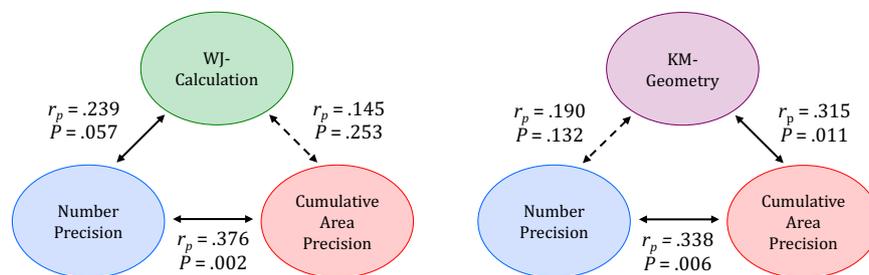


Fig. 4. Diagrams of partial correlations depicting associations between two variables while controlling for a third. (*Left*) Whereas performance on WJ-calculation was positively correlated with number precision when controlling for cumulative area precision, it was no longer significantly correlated with cumulative area precision when controlling for number precision, suggesting a unique connection between numerical magnitude and advanced arithmetic. (*Right*) In contrast, performance on KM-geometry was positively correlated with cumulative area precision when controlling for number precision, but it was no longer significantly correlated with number precision when controlling for cumulative area precision, suggesting a unique connection between nonnumerical magnitude and geometry. (*Left and Right*) Notably, number and cumulative area precision remained positively correlated when controlling for performance on WJ-calculation or KM-geometry, which, as suggested in the main text, may reflect partially shared mechanisms for representing numerical and nonnumerical magnitudes.

they also suggest that the correlations between cumulative area precision and WJ-calculation as well as between number precision and KM-geometry (Fig. 3) reflect shared variance contributed by number and cumulative area precision.

General Discussion

Long-standing theoretical interest in the mental primitives of abstract human cognition (47, 48) sets the stage for fundamental questions about the nonsymbolic basis of mathematics, with proposals that formal math builds on core abilities, including representations of analog magnitude (e.g., refs. 1, 3, 4). Focusing specifically on numerical magnitude (the ANS), recent experiments demonstrate that the precision of nonsymbolic number representations predicts performance on standardized tests of arithmetic (e.g., ref. 23). Building on accumulating evidence that numerical magnitude may not fully dissociate from other magnitudes, the focus of the present study was the potentially broader connections between representations of nonsymbolic magnitude and mathematical competence (see also refs. 49, 50). Our findings point to an interface between symbolic math and nonsymbolic magnitude that includes representations of cumulative area, and, in the case of geometry, that goes beyond numerical magnitude. Altogether, we extend recent experiments by (*i*) demonstrating that both number and cumulative area precision correlate with advanced arithmetic and geometry, even when controlling for general aspects of intelligence, and by (*ii*) providing empirical support for unique contributions of number and cumulative area precision to competence with advanced arithmetic and geometry, respectively.

The combination of shared and unique connections between magnitude representations and formal math in the present study suggests that the nonsymbolic basis of advanced arithmetic and geometry may reside in a general magnitude system with overlapping, but also separable, properties of numerical and non-numerical magnitude. Empirical support for partial (not full) overlap comes from both humans and nonhuman animals. Recent research with human infants using a habituation/dishabituation paradigm suggests that although 9-mo-olds transfer learning of color/pattern mappings across nonsymbolic number and spatial extent, they do not treat these magnitudes interchangeably (32), as would be predicted by a “one-bit” system with no differentiation among magnitudes (31). Moreover, single-cell recordings with monkeys suggest a combination of common and distinct neural codes for number and spatial extent, with some neurons tuned to both magnitudes, but others responding exclusively to each (36). Because single neurons cannot account for complex behaviors across a broad range of stimuli, a challenge for future

research will be to determine how populations of neuronal firing support aspects of shared and distinct processing for numerical and nonnumerical magnitudes. One class of models in vision suggests that shared representations emerge via relative outputs from spatial filters tuned to high vs. low frequencies (51, 52), whereas another class of models, which emphasizes distinct representations, suggests that summation processes invoke additional mechanisms that normalize computations across irrelevant cues (53–55). Although extant models have typically considered shared and distinct representations separately, findings such as those from the present study point to the need for integrative neuro-computational models that simulate how shared and distinct representations might coexist as part of a general magnitude system.

Among the oldest branches of mathematics are geometry and arithmetic (56). Cross-cultural research with indigenous populations and studies using visual attention paradigms with infants suggest that they are also among the most psychologically intuitive. Knowledge of core geometric concepts (e.g., points and lines) and the ability to perform basic (nonsymbolic) arithmetic computations (e.g., addition and subtraction) have been documented in cultures without access to formal math instruction (2, 7) and even in preverbal infants (57, 58). Such intuitions, it is believed, rest on perceptual properties of the visual system and universal spatial experiences. That geometry is highly visual and perhaps grounded in navigation abilities (59) and that arithmetic of small sets of objects recruits parallel individuation processes (60) may provide some basis for protomathematical intuitions. The present findings suggest a further basis for such intuitions by showing that even formally taught mathematics performed by college students may be rooted in analog representations of number and cumulative area, with nonsymbolic magnitude precision predicting individual differences in advanced arithmetic and school-relevant geometry.

Although we can only speculate about the functional significance of the connections between nonsymbolic magnitude and mathematics, existing research suggests two possible benefits. One benefit might occur early in human ontogeny when children begin learning symbolic number notation and formal math computations (11, 61). It has been suggested that numerical symbols (e.g., number words and Arabic digits) acquire meaning when they are mapped to preexisting representations of numerical magnitude such as the ANS (1, 5, 62). Our findings suggest that such mappings may extend more broadly to nonnumerical magnitudes such as cumulative area. In the case of geometry, symbolic manipulations and exact calculations of spatial properties such as the volume of 3D shapes and the relative positions of figures may be grounded in an approximate sense of spatial

extent. This possibility dovetails with “redeployment” (63) and “recycling” (64) theories, which propose that neural assemblies in posterior parietal cortex, having evolved for the sensorimotor coordination of basic actions (65), are co-opted for symbolic mathematics. Another possible benefit might come in the form of online error detection. That traces of nonsymbolic number and cumulative area are evident in the math abilities of college students suggests functional consequences beyond early development. Access to approximate magnitude representations when computing answers to complex arithmetic and geometry problems could serve as an automatic and robust process of identifying calculation errors. Knowing that an answer to a math problem cannot possibly be correct because it falls outside the range of probable outcomes will improve overall accuracy; accordingly, the more precise one’s underlying representations of nonsymbolic magnitude, the more arithmetic and/or geometric errors will be caught. Whereas the benefit to learning symbolic mathematics presumes that nonsymbolic representations of magnitude causally precede math competence, the benefit to error detection highlights the potential for the reverse causal pattern, namely that exposure to symbolic math may affect nonsymbolic magnitude representations. Cross-cultural research showing that adults from indigenous cultures without formal math instruction have less precise representations of numerical magnitude compared with adults in math-educated cultures (7) hints at a causal role for educationally relevant experiences in sharpening the precision of nonsymbolic magnitudes (62).

Not all standardized math tests included in the present study, however, showed systematic connections to nonsymbolic magnitude precision. Despite strong correlations across the math tests themselves (*SI Text*), performance on elementary (and speeded) arithmetic problems (WJ-math fluency), knowledge of math-related concepts (WJ-quantitative concepts), and competence with word problems (WJ-applied problems) were not reliably related to number or cumulative area precision, suggesting that nonsymbolic magnitude representations may not interact evenly across different types of symbolic math and that individual differences in other cognitive abilities may contribute additional variance to performance on these tests. A wealth of studies using behavioral and neuroimaging techniques suggest that people sample from an assortment of strategies when solving math problems, with different strategies recruiting at least partially distinct neural circuits (42, 66). For example, highly routinized arithmetic problems, as in WJ-math fluency, show greater reliance on rote visuo-verbal memory than explicit computations of magnitude (41, 42). Because simple arithmetic problems can be memorized rather than explicitly computed, nonsymbolic magnitudes may contribute minimally (if at all) to their maintenance in memory or their speeded recall. Among the cognitive abilities that are well-known contributors of mathematical competence are semantic memory and metacognitive processes (66, 67), which may affect performance on tests such as WJ-quantitative concepts and WJ-applied problems (see *SI Text* for additional discussion). Separately or in combination, such abilities may play a greater (or more direct) role than magnitude precision in accounting for interindividual variability on these math tests, either by modulating connections to a general magnitude system or by bypassing it altogether (cf. ref. 40).

A recent study with dyscalculic individuals suggests that the mere presence of Arabic digits affects temporal processing, with numerical deficits transferring to estimates of duration (50). Current theories of dyscalculia include specific deficits of the ANS, that is, imprecise representations of nonsymbolic number (18), or specific deficits in mapping symbols to nonsymbolic number representations (68). These and other theories (17) have been silent about how nonsymbolic magnitudes other than number are represented in the brains of children and adults, and by extension, how a system of general magnitude representation, which includes nonnumerical magnitudes such as spatial extent and

duration (69–71), might interface with learning and competence across different types of mathematical problem solving. Dyscalculia and other math-related disorders such as acalculia are heterogeneous in their symptomatology (15, 72). Our findings of shared and unique contributions of nonsymbolic number and cumulative area to symbolic arithmetic calculations and geometry suggest additional complexities that may contribute to heterogeneous phenotypes. We hope that future studies will adopt the methodological approach used here. By using multiple measures of symbolic math competence and comparing precision underlying both numerical and nonnumerical magnitudes, future research may be better able to offer specific predictions about the interactions between symbolic and nonsymbolic systems of quantification under normative conditions and in cases of deficiency.

Methods

Participants completed two magnitude comparisons tasks, one in which the relevant dimension was number (number task) and another in which it was cumulative area (area task). Participants also completed a battery of standardized math tests drawn from the WJ (38) and KM (39). As contrastive nonmath controls, participants completed two additional tests of verbal competence from the WJ (*SI Text*). Participants were tested individually in a single session, lasting ~90 min.

Magnitude Comparison Tasks. Number and area tasks were programmed using E-Prime 2.0 (PST) and presented on a computer screen (48 or 43 cm, diagonal). Participants sat at a distance of ~50 cm from the screen. On each trial, they saw an array ($x = 24.8^\circ, y = 19.9^\circ$ or $x = 19.6^\circ, y = 18.0^\circ$) of spatially intermixed brown and blue dots, matched for luminance (Fig. 1). Participants were instructed to judge which set of dots (brown or blue) was more numerous (number task) or greater in cumulative area (area task). Weber ratios were systematically varied during the test trials; that is, each array varied in the relevant dimension (number or cumulative area) along one of six ratios (2:1, 3:2, 4:3, 5:4, 7:6, and 10:9), allowing discrimination to be quantified parametrically. In the number task, the absolute number of dots for each set ranged from 5 to 14; in the area task, absolute cumulative area ranged from 9.0 to 29.8 cm². In each task, participants received 10 practice trials and 144 test trials (24 per ratio). Practice trials were identical to test trials, except that only one (easier) ratio was used (3:1) to familiarize participants with the task. Instructions emphasized both speed and accuracy. No corrective feedback was provided during practice or test.

Each trial began with a fixation point presented centrally for 1,000 ms. An array of brown and blue dots presented for 200 ms followed. Participants were then prompted (with a question mark) to respond by pressing either “Q” or “P” on a computer keyboard (e.g., “if the brown set of dots is more numerous, press Q; if the blue set is more numerous, press P”). Test trials were grouped into two blocks: one in which Q corresponded to brown sets and P to blue sets and another with the reverse assignment (order counterbalanced). Within block, the color associated with greater magnitude was randomized across trials.

On both tasks, brown and blue sets of dots were created by randomly selecting individual element sizes until constraints for each trial were met. In the number task, three types of controls were implemented to ensure that participants relied on differences in numerical value, rather than spatially related cues, when responding. Similar to previous studies (23, 73), arrays of each ratio were matched either for cumulative area (one-third of trials) or average dot size (one-third of trials). On the former type, brown and blue sets of dots on a given trial were equal in cumulative area ($M = 22.1$ cm², range = 9.6–30.3 cm²); on the latter type, average dot size was equal ($M = 2.3$ cm², range = 1.1–2.8 cm²). On the remaining trials, nonnumerical parameters (i.e., cumulative area and average dot size) were varied randomly (as in ref. 73). Mean difference in cumulative area between arrays was 4.9 cm² (range = 0.1–22.7 cm²) and mean difference in dot size between arrays was 1.9 cm² (range = 0.9–4.1 cm²). In the area task, the numbers of dots in each set (7, 9, or 13) were matched within trial and varied across trials, such that judgments of greater cumulative area could not be based on number.

Participants completed both number and area tasks (order counterbalanced) before taking the battery of standardized tests, which were administered in a fixed order: (i) WJ-calculation, (ii) WJ-math fluency, (iii) WJ-applied problems, (iv) WJ-quantitative concepts, (v) WJ-picture vocabulary, (vi) WJ-reading vocabulary, and (vii) KM-geometry. Participants were tested on the standardized tests by an experienced experimenter who adhered to standard protocols for the WJ and KM.

Participants. Seventy-seven college students (47 female) between 17 and 21 y of age participated. Of these, 12 were excluded from data analyses for failing to follow instructions in one or both of the magnitude comparison tasks. Participants had normal or corrected-to-normal vision. All received course credit or monetary compensation for their participation, and all provided

informed consent. Procedures were approved by the Institutional Review Board at Emory University.

ACKNOWLEDGMENTS. This research was supported by a Scholars Award from the John Merck Fund (to S.F.L.).

- Gallistel CR, Gelman R (1992) Preverbal and verbal counting and computation. *Cognition* 44(1–2):43–74.
- Dehaene S, Izard V, Pica P, Spelke E (2006) Core knowledge of geometry in an Amazonian indigene group. *Science* 311(5759):381–384.
- Leslie AM, Gelman R, Gallistel CR (2008) The generative basis of natural number concepts. *Trends Cogn Sci* 12(6):213–218.
- Carey S (2009) *The Origin of Concepts* (Oxford Univ Press, New York).
- Nieder A, Dehaene S (2009) Representation of number in the brain. *Annu Rev Neurosci* 32:185–208.
- Nieder A (2005) Counting on neurons: The neurobiology of numerical competence. *Nat Rev Neurosci* 6(3):177–190.
- Pica P, Lemer C, Izard V, Dehaene S (2004) Exact and approximate arithmetic in an Amazonian indigene group. *Science* 306(5695):499–503.
- Izard V, Sann C, Spelke ES, Streri A (2009) Newborn infants perceive abstract numbers. *Proc Natl Acad Sci USA* 106(25):10382–10385.
- Gallistel CR, Gelman R (2000) Non-verbal numerical cognition: From reals to integers. *Trends Cogn Sci* 4(2):59–65.
- Piazza M, Izard V, Pinel P, Le Bihan D, Dehaene S (2004) Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44(3):547–555.
- Ansari D (2008) Effects of development and enculturation on number representation in the brain. *Nat Rev Neurosci* 9(4):278–291.
- Eger E, Sterzer P, Russ MO, Giraud AL, Kleinschmidt A (2003) A supramodal number representation in human intraparietal cortex. *Neuron* 37(4):719–725.
- Pinel P, Piazza M, Le Bihan D, Dehaene S (2004) Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron* 41(6):983–993.
- Venkatraman V, Ansari D, Chee MWL (2005) Neural correlates of symbolic and non-symbolic arithmetic. *Neuropsychologia* 43(5):744–753.
- Lemer C, Dehaene S, Spelke E, Cohen L (2003) Approximate quantities and exact number words: Dissociable systems. *Neuropsychologia* 41(14):1942–1958.
- Andres M, Pelgrims B, Michaux N, Olivier E, Pesenti M (2011) Role of distinct parietal areas in arithmetic: An fMRI-guided TMS study. *Neuroimage* 54(4):3048–3056.
- Butterworth B (2010) Foundational numerical capacities and the origins of dyscalculia. *Trends Cogn Sci* 14(12):534–541.
- Piazza M, et al. (2010) Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition* 116(1):33–41.
- Molko N, et al. (2003) Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron* 40(4):847–858.
- Price GR, Holloway I, Räsänen P, Vesterinen M, Ansari D (2007) Impaired parietal magnitude processing in developmental dyscalculia. *Curr Biol* 17(24):R1042–R1043.
- Halberda J, Feigenson L (2008) Developmental change in the acuity of the “Number Sense”: The Approximate Number System in 3-, 4-, 5-, and 6-year-olds and adults. *Dev Psychol* 44(5):1457–1465.
- Halberda J, Ly R, Wilmer JB, Naiman DQ, Germine L (2012) Number sense across the lifespan as revealed by a massive Internet-based sample. *Proc Natl Acad Sci USA* 109(28):11116–11120.
- Halberda J, Mazocco MMM, Feigenson L (2008) Individual differences in non-verbal number acuity correlate with maths achievement. *Nature* 455(7213):665–668.
- Gilmore CK, McCarthy SE, Spelke ES (2010) Non-symbolic arithmetic abilities and mathematics achievement in the first year of formal schooling. *Cognition* 115(3):394–406.
- Mazzocco MMM, Feigenson L, Halberda J (2011) Preschoolers’ precision of the approximate number system predicts later school mathematics performance. *PLoS ONE* 6(9):e23749.
- Meck WH, Church RM (1983) A mode control model of counting and timing processes. *J Exp Psychol Anim Behav Process* 9(3):320–334.
- Hauser MD, Spelke ES (2004) *The Cognitive Neurosciences*, ed Gazzaniga MS (MIT Press, Cambridge, MA), pp 853–864.
- Castelli F, Glaser DE, Butterworth B (2006) Discrete and analogue quantity processing in the parietal lobe: A functional MRI study. *Proc Natl Acad Sci USA* 103(12):4693–4698.
- Burr D, Ross J (2008) A visual sense of number. *Curr Biol* 18(6):425–428.
- Odic D, Libertus ME, Feigenson L, Halberda J (2012) Developmental change in the acuity of approximate number and area representations. *Dev Psychol*, in press.
- Walsh V (2003) A theory of magnitude: Common cortical metrics of time, space and quantity. *Trends Cogn Sci* 7(11):483–488.
- Lourenco SF, Longo MR (2010) General magnitude representation in human infants. *Psychol Sci* 21(6):873–881.
- Cappelletti M, Freeman ED, Cipolletti L (2011) Numbers and time doubly dissociate. *Neuropsychologia* 49(11):3078–3092.
- Henik A, Tzelgov J (1982) Is three greater than five: The relation between physical and semantic size in comparison tasks. *Mem Cognit* 10(4):389–395.
- Hurewitz F, Gelman R, Schnitzer B (2006) Sometimes area counts more than number. *Proc Natl Acad Sci USA* 103(51):19599–19604.
- Tudusciuc O, Nieder A (2007) Neuronal population coding of continuous and discrete quantity in the primate posterior parietal cortex. *Proc Natl Acad Sci USA* 104(36):14513–14518.
- Fias W, Lammertyn J, Reynvoet B, Dupont P, Orban GA (2003) Parietal representation of symbolic and nonsymbolic magnitude. *J Cogn Neurosci* 15(1):47–56.
- Woodcock RW, McGrew KS, Schrank FA, Mather N (2001/2007) *Woodcock-Johnson III Normative Update* (Riverside Publishing, Rolling Meadows, IL).
- Connolly AJ (2007) *Keymath-3 Diagnostic Assessment: Manual Forms A and B* (SAGE Publications, Minneapolis, MN).
- Lyons IM, Beilock SL (2011) Numerical ordering ability mediates the relation between number-sense and arithmetic competence. *Cognition* 121(2):256–261.
- Dehaene S, Cohen L (1997) Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex* 33(2):219–250.
- Delazer M, et al. (2005) Learning by strategies and learning by drill—Evidence from an fMRI study. *Neuroimage* 25(3):838–849.
- Luria AR (1980) *Higher Cortical Functions in Man* (Basic Books, New York).
- Prabhakaran V, Rypma B, Gabrieli JDE (2001) Neural substrates of mathematical reasoning: A functional magnetic resonance imaging study of neocortical activation during performance of the necessary arithmetic operations test. *Neuropsychology* 15(1):115–127.
- Spearman C (1904) “General intelligence,” objectively determined and measured. *Am J Psychol* 15(2):201–292.
- Jensen AR (1998) *The g Factor: The Science of Mental Ability* (Praeger, Westport, CT).
- Descartes R (2001) *Discourse on Method, Optics, Geometry and Meteorology* (Hackett Publishing, Indianapolis).
- Kant I (2003) *Critique of Pure Reason* (Mineola, Dover, DE).
- Luculano T, Tang J, Hall CWB, Butterworth B (2008) Core information processing deficits in developmental dyscalculia and low numeracy. *Dev Sci* 11(5):669–680.
- Cappelletti M, Freeman ED, Butterworth BL (2011) Time processing in dyscalculia. *Front Psychol* 2:1–10.
- Dakin SC, Tibber MS, Greenwood JA, Kingdom FA, Morgan MJ (2011) A common visual metric for approximate number and density. *Proc Natl Acad Sci USA* 108(49):19552–19557.
- Tibber MS, Greenwood JA, Dakin SC (2012) Number and density discrimination rely on a common metric: Similar psychophysical effects of size, contrast, and divided attention. *J Vis* 12(6):8.
- Dehaene S, Changeux JP (1993) Development of elementary numerical abilities: A neural model. *J Cogn Neurosci* 5:390–407.
- Chong SC, Treisman A (2003) Representation of statistical properties. *Vision Res* 43(4):393–404.
- Stoianov I, Zorzi M (2012) Emergence of a ‘visual number sense’ in hierarchical generative models. *Nat Neurosci* 15(2):194–196.
- Merzbach UC, Boyer CB (2010) *A History of Mathematics* (Wiley, Hoboken, NJ).
- Lourenco SF, Huttenlocher J (2008) The representation of geometric cues in infancy. *Infancy* 13:103–127.
- Wynn K (1992) Addition and subtraction by human infants. *Nature* 358(6389):749–750.
- Spelke EE, Lee SA, Izard V (2010) Beyond core knowledge: Natural geometry. *Cogn Sci* 34(5):863–884.
- Feigenson L, Dehaene S, Spelke E (2004) Core systems of number. *Trends Cogn Sci* 8(7):307–314.
- Libertus ME, Feigenson L, Halberda J (2011) Preschool acuity of the approximate number system correlates with school math ability. *Dev Sci* 14(6):1292–1300.
- Verguts T, Fias W (2004) Representation of number in animals and humans: A neural model. *J Cogn Neurosci* 16(9):1493–1504.
- Anderson ML (2007) Evolution of cognitive function via redeployment of brain areas. *Neuroscientist* 13(1):13–21.
- Dehaene S, Cohen L (2007) Cultural recycling of cortical maps. *Neuron* 56(2):384–398.
- Buetti D, Walsh V (2009) The parietal cortex and the representation of time, space, number and other magnitudes. *Philos Trans R Soc Lond B Biol Sci* 364(1525):1831–1840.
- Dehaene S (1992) Varieties of numerical abilities. *Cognition* 44(1–2):1–42.
- McCloskey M (1992) Cognitive mechanisms in numerical processing: Evidence from acquired dyscalculia. *Cognition* 44(1–2):107–157.
- Noel M-P, Rousselle L (2011) Developmental changes in the profiles of dyscalculia: An explanation based on a double exact-and-approximate number representation model. *Front Hum Neurosci* 5:1–4.
- Cohen Kadosh R, Lammertyn J, Izard V (2008) Are numbers special? An overview of chronometric, neuroimaging, developmental and comparative studies of magnitude representation. *Prog Neurobiol* 84(2):132–147.
- Cantlon JF, Platt ML, Brannon EM (2009) Beyond the number domain. *Trends Cogn Sci* 13(2):83–91.
- Lourenco SF, Longo MR (2011) *Space, Time and Number in the Brain: Searching for the Foundations of Mathematical Thought*, eds Dehaene S, Brannon E (Academic, London), pp 225–244.
- Rubinsten O, Henik A (2009) Developmental dyscalculia: Heterogeneity might not mean different mechanisms. *Trends Cogn Sci* 13(2):92–99.
- Holloway ID, Ansari D (2009) Mapping numerical magnitudes onto symbols: The numerical distance effect and individual differences in children’s mathematics achievement. *J Exp Child Psychol* 103(1):17–29.