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Using cognitive training studies to unravel the mechanisms by which the approximate number system supports symbolic math ability

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Abstract

A picture is emerging that preverbal nonsymbolic numerical representations derived from the approximate number system (ANS) play an important role in mathematical development and sustained mathematical thinking. Functional imaging studies are revealing developmental trends in how the brain represents number. We propose that combining behavioral and neuroimaging techniques with cognitive training approaches will help identify the fundamental relationship between the ANS and symbolic mathematics. Understanding this relationship should ultimately benefit educators by providing ways to harness the ANS and hopefully improve math readiness in young children.

Introduction

The human mathematical mind is unique in its ability to accomplish feats such as calculating the trajectory of a rocket to mars, proving the Pythagorean Theorem, or counting the precise number of butterflies in a picture book. Mathematical ability is complex and multifaceted and relies on many component skills including but not limited to working-memory [1], executive function [2], and language [3]. The approximate number system (ANS) may serve as another critical foundation for mathematics [4,5]. The ANS supports our ability to roughly estimate the number of objects in a set (e.g. nonsymbolic quantity representation) without relying on verbal counting [5]. Here, we review both behavioral and neuroimaging data that examine the relationship between the ANS and symbolic mathematical abilities and argue that primitive numerical abilities scaffold symbolic math representations. We propose that the tools of cognitive neuroscience and educational psychology may together uncover the mechanisms by which this scaffolding takes place.

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Conflicts of interest

Nothing declared.

A foundational building block for mathematics: the approximate number system

The ANS is present in a wide variety of animal species [5]; it emerges early in human development [6], and it continues to function throughout adulthood [7]. ANS representations are much like representations of other fundamental perceptual continua such as brightness or size in that they follow *Weber's* law whereby reaction time and error rates decrease as the ratio or distance between to-be-compared quantities increases [8]. Although nonhuman animal and human infant numerical abilities are limited to imprecise enumeration supported by the ANS, adult educated humans are capable of representing exact symbolic numbers (e.g. '16' or 'sixteen'), and this forms the basis of mathematical operations. There is debate over the nature of the initial preverbal representations that ground children's first number words. One proposal is that the ANS scaffolds the acquisition of exact symbolic numerals and subsequent math skills over development and remains tied to symbolic math faculties into adulthood [4]. However, alternative hypotheses suggest that ANS representations are only mapped onto number words later in development and are not involved in symbol grounding [9].

The association between the ANS and math achievement

A key source of evidence that the ANS scaffolds symbolic math is that ANS acuity and symbolic math achievement are correlated across the life span [e.g. 7,10–12]. Individuals with greater precision in discriminating between approximate numerical magnitudes tend to have higher scores on standardized measures of math achievement (see [13] for a meta-analysis). In fact, the association between ANS and symbolic math may be strongest in preschool aged children [14,15*,16]. ANS acuity measured before children enter formal school predicts later math abilities [17,18] suggesting that strengthening the ANS might improve children's readiness to learn math upon school entry. ANS acuity is also lower in children with dyscalculia (severe math difficulties) [19,20], see also [21]. Although these findings suggest a relationship between ANS and symbolic math, recent meta-analyses have shown this relationship to be relatively weak [13,15*,22] and a substantial number of studies have failed to find this correlation [e.g. 23–26]. There are a number of possible explanations for these conflicting results such as diverse dependent measures in both nonsymbolic comparison tasks and standardized tests of math achievement, poor reliability for measures of ANS acuity [27,28, but see 29], true age-dependent differences in the relationship between ANS and math, or the involvement of perceptual processes and inhibitory control related to nonsymbolic discrimination [25,26,30,31] (see [32–35] for detailed reviews of the correlational research). A recent study that failed to find a behavioral correlation between ANS acuity and math performance nevertheless found that individual differences in the size of the neural ratio effect in the bilateral IPS during nonsymbolic comparison correlated with standardized scores of math achievement [36**]. This finding suggests that the relationship between ANS and math may be better revealed by neuroimaging than behavioral indices.

Causal relationship between the ANS and math achievement

Cognitive training studies provide an avenue to move beyond correlations and address the potential causal relationship between ANS acuity and symbolic math ability. Park and Brannon (2013) first demonstrated that computerized approximate arithmetic training enhanced symbolic arithmetic skills. In their study, adults were trained to approximately add and subtract sets of dots over the course of 10 days (e.g. $30 + 16$ dots is 46 dots or 60 dots — see Figure 1a). Following this approximate arithmetic training, participants showed specific improvements in performing complex symbolic arithmetic problems, whereas no improvements were observed for a group of participants in a no-contact control condition or a fact training condition [37]. In a follow-up study, Park and Brannon replicated these results and further demonstrated that training approximate arithmetic resulted in greater gains in symbolic arithmetic skills in comparison to training visuo-spatial short-term memory, approximate number comparison, and symbolic ordering [38**] (see Figure 1b). The fact that participants in the symbol ordering and numerical comparison conditions did not show improvements on symbolic addition and subtraction argues against the idea that the effect was driven by expectations that number related exercises would improve performance [39] see also [40**]. Together these findings suggest that the manipulation of approximate quantities required by arithmetic is driving the transfer effect. One study in young children suggests that training approximate arithmetic may be effective early in development [41**]. Although more studies are necessary to explore the efficacy of training approximate arithmetic in pre-school aged children and children with mathematical difficulties using pre and post-test designs, if successful this approach could have important educational implications. Given that approximate arithmetic games do not require recognition of Arabic numerals or mastery of the verbal counting system this type of training has the potential to improve math readiness in preschool children at risk for math difficulties.

The relationship between the ANS and symbolic number in the brain

Dehaene proposed that the construction of the uniquely human mathematical mind through culture and education is made possible by co-opting brain systems that evolved to represent nonsymbolic quantity [42,43]. This hypothesis rests partly on the finding from functional magnetic resonance imaging (fMRI) studies that the bilateral intra-parietal sulcus (IPS) is a key neural substrate of both nonsymbolic and symbolic quantity processing [42,44–47]. For example, when adults compare the numerical magnitude of Arabic numerals, activity within the bilateral IPS is modulated by distance [47] consistent with behavioral ratio effects. Similar distance related changes in activity have been found in the bilateral IPS when participants are presented with a deviant stimulus that differs in numerosity following adaptation to a steady stream of nonsymbolic quantities (arrays of dots) [45]. These findings have been taken as indirect evidence that there is a common neural code within the bilateral IPS for representing symbolic and nonsymbolic quantities (but see [48] for an alternative view).

There is also evidence that the left IPS becomes specialized for symbolic number. Symbolic and nonsymbolic quantities activate overlapping parietal regions partially lateralized to the right IPS [49,50]. By contrast, there is greater association of the left parietal cortex for exact

symbolic compared to approximate nonsymbolic tasks [44,50]. Specifically, using cross format fMRI adaptation, Piazza and colleagues found evidence that the left IPS contained sharper neural tuning curves for symbolic numerals compared to the right IPS. Consistent with these findings, Holloway *et al.* (2010) found that the right IPS was activated for both symbolic and nonsymbolic number comparison, but found specific activity in the left angular gyrus for symbolic comparison.

Developmental studies are uniquely suited to investigate the emergence of symbolic representations. Indeed, the neural signatures of the ANS are evident in the right IPS in infants [51*,52] and young children [53]. Number representation becomes more lateralized to left IPS over the course of development and may be driven by acquisition of the symbolic number system [54] (see Figure 2a). In direct support of this idea, Emerson and Cantlon found that activation in the right IPS during a dot to numeral matching task was stable in children between four and nine years of age across two fMRI sessions; however, numeral matching acuity was positively correlated with longitudinal increases in left IPS activity [55**]. Comparably, Vogel and colleagues (2015) found age related changes in ratio dependent neural recovery following adaptation to symbolic numerals in the left IPS; however, activity in the right IPS was invariant across all ages (age 6–14 years) [56**]. Furthermore, children with a stronger neural ratio effect in the left IPS during symbolic number processing exhibited higher arithmetic scores [57*].

Another proposed developmental trend in the neural bases of numerical representation is a fronto-parietal developmental shift. When children and adults perform nonsymbolic and symbolic number comparison, neural distance effects are found in both the IPS and the prefrontal cortex. Adults, however, show larger neural distance effects in the IPS in comparison to children [58–60]. Relatedly, Rivera and colleagues (2005) found age was positively correlated with activity in the left parietal cortex, such as the left supramarginal gyrus, left IPS, as well as the left lateral occipital temporal cortex during addition and subtraction. By contrast, young children exhibited greater activity in the prefrontal cortex including bilateral superior and middle frontal gyri, left inferior frontal gyrus, and the left hippocampus [61] (see Figure 2b).

Thus, the emerging picture is that the right IPS processes nonsymbolic magnitudes at birth and remains stable over development supporting the acquisition of symbolic representations in the left IPS. Changes in the left IPS reflect experience-dependent refinement of symbolic representations as a consequence of increasing fluency with numbers [55**,56**]. As symbolic numbers are introduced they activate the IPS with preferentially encoding in the left hemisphere (see Figure 2a). The fronto-parietal shift may thus reflect the fact that children initially recruit prefrontal areas associated with working memory and attention resources when attempting to solve arithmetic problems and learn symbolic numerals. Subsequently, as they develop stronger more automatic associations between symbols and the quantities they represent, activation shifts to the left IPS [54]. Under this scenario, the prefrontal cortex might play a key role in learning semantic associations, but the associations themselves are instantiated in IPS. After the associations are fully automatized the IPS is recruited by both symbolic and nonsymbolic number and prefrontal activity decreases (see Figure 2b) [62].

Overlapping neural activity for symbolic and nonsymbolic numerical processing tasks has been taken as evidence that the ANS scaffolds symbolic mathematical development [44,63]. However, neural overlap between symbolic and approximate numerical representations does not necessitate that the two are causally related [64]. In fact, recent studies using multi-voxel pattern analyses in adults have in some cases uncovered dissimilar patterns of activity in the bilateral IPS for approximate and symbolic number processing [65,66*]. These results show that despite overlapping activation in the IPS for symbolic and approximate numerical processing, the underlying representational structure is highly format dependent. Thus, an alternative possibility is that distinct symbolic representations in the IPS (left IPS) are constructed independent of the ANS [9,54,67]. It will be important to conduct similar fMRI studies with young children because one possibility is that numerical representations are format independent early in development and diverge with numerical experience into adulthood.

Future directions: using training studies to uncover how the human mathematical mind develops

As discussed above, longitudinal studies using fMRI and other non-invasive neuroimaging tools are revealing developmental trends in brain development that coincide with changes in numerical cognition. However, it is difficult to know which brain changes are related to math development and which are related to other concurrent cognitive development. We propose that brain imaging before and after cognitive training is a promising tool that can help differentiate the specific developmental brain changes that underlie a child's acquisition of the symbolic number system and map the emergence of the mathematical mind. FMRI training studies as cartooned in Figure 3, should provide fundamental insights into the relationship between the approximate arithmetic and symbolic math, which can be used as a model to evaluate behavioral and neural changes as a function of different types of ANS training programs.

Indeed, pre-test and post-test functional neuroimaging studies have already begun to uncover important neural changes associated with math interventions in participants with dyscalculia [68*,69], math anxiety [70*], and Turner syndrome (a genetic condition associated with deficits in math skills) [71*]. For example, Iuculano and colleagues found that children with DD exhibited aberrant widespread neural activity in prefrontal cortex, the bilateral IPS, regions in the ventral temporal-occipital cortex, and right hippocampus when performing an addition verification task in comparison to typically developing controls. Following an eight week one-on-one tutoring program that focused on building procedural and conceptual knowledge of basic arithmetic, children with DD showed normalization of brain activity. Specifically, regions that showed atypical activation before receiving tutoring, no longer differentiated children with DD and typically developing children at post-test. Furthermore, training induced functional plasticity, characterized by individual change in neural activity between pre and post-test scans, predicted gains in arithmetic performance following tutoring with greater sensitivity than behavioral measures. These results reveal that a network of brain regions associated with visuo-spatial processing, attention, working memory and basic numerical processes were remediated by the one-on-one tutoring program

[68]. Furthermore, children with Turner Syndrome, who received general number sense and executive function training showed significantly increased activity in the parietal cortex and decreased activity in regions located in the prefrontal cortex, hippocampus, and amygdala during complex arithmetic problems following training [71]. These preliminary findings reveal neural changes in the fronto-parietal network associated with improvements for complex arithmetic and suggest that the fronto-parietal shift may be a significant indicator of math fluency and remediation efficacy; however, the specificity of these findings needs to be further examined with relevant control groups.

Cognitive training studies, such as those conducted by Park and Brannon [37,38], lay the foundation for exploring multiple neural mechanistic hypotheses for the relationship between approximate arithmetic training and symbolic mathematics. First, approximate arithmetic training may increase the association between symbolic representations of numbers and the quantities they represent. If approximate arithmetic training indeed increases the precision of the ANS, and processing symbolic numerals involves accessing their corresponding ANS representations, then increasing ANS precision may facilitate symbolic numeral processing. One potential brain corollary of this change might be increased lateralization of symbolic representations to the left IPS similar to the changes observed over development [55,56], or increased functional connectivity between right and left IPS. Alternatively, approximate arithmetic may benefit symbolic arithmetic due to the shared cognitive operations of addition and subtraction rather than any associated increase in ANS precision. If this is the case we might expect changes in a broader network of prefrontal and parietal areas as a function of approximate arithmetic training (see Box 1 for open empirical questions for future research). Relatedly, some research has suggested that the relationship between ANS acuity and symbolic math is driven by inhibitory control mechanisms necessary to suppress information from visual perceptual cues to make discriminative judgments based on quantity [25,26,31]. For example, a recent training study with low income preschool children has shown that ANS acuity training using nonsymbolic comparison reduces the effect of irrelevant visual perceptual cues on performance during comparison tasks at post-test [72]. Thus, one possibility is that approximate arithmetic training improves inhibitory control comparable to nonsymbolic discrimination training and thus may result in changes in neural networks in prefrontal cortex associated with executive function. Another brain area that may play a special role in arithmetic is the hippocampus, where decreasing activation correlates with improving arithmetic skills [61,73]. Increases in functional connectivity between the hippocampus and bilateral dorsolateral prefrontal cortex and the left IPS has been found to be associated with longitudinal improvements in fact retrieval fluency [73]. One intriguing possibility is that approximate arithmetic affects hippocampal activity by improving the conceptual understanding of basic arithmetic that might facilitate automatic coding of arithmetic facts. Neuroimaging tools in combination with pre-test and post-test behavioral training designs in both adults and children should yield answers to these exciting questions, and provide an important bridge between neuroscience, cognitive science, and education. However, there are many open empirical questions pertaining to the role of the ANS (or approximate arithmetic) in developing symbolic numerical representations and subsequent math skills (see Box 1) that warrant further investigation before this work can be directly translated to the classroom.

Furthermore, by combining different analytical tools to study how individual differences in sensitivity to training are linked with brain changes we may ultimately come to a better understanding of how to tailor interventions to students.

Box 1

Open empirical questions

- Does training approximate numerical abilities have enduring effects on symbolic math performance? Are the effects dose-dependent?
- At what age or mathematical skill level would approximate arithmetic training provide the greatest benefit for mathematical improvement? Can approximate arithmetic training be useful to increase math readiness in preschool children?
- What cognitive and neural mechanistic processes subserve positive transfer effects to symbolic arithmetic skills? Can studying how the brain changes as a function of training provide insight into the mechanism of transfer?
- Does approximate arithmetic training induce structural or functional changes in the bilateral IPS?

Conclusions

There remain many unanswered questions about the precise nature of the relationship between the ANS and symbolic mathematical abilities. Behavioral training studies provide strong support for the proposal that the uniquely human mathematical mind builds upon the evolutionarily ancient ANS. Developmental cognitive neuroscience is uncovering trends in brain development associated with the emergence of the uniquely human mathematical abilities. By combining functional brain imaging methods with cognitive training designs, we will be able to identify the neural networks that change as children become symbolic processors. Ultimately, we hope this endeavor will uncover the true nature of the relationship between the ANS and symbolic math and allow the development and design of interactive and engaging training tools for improving math skills in both typically and atypically developing children at home or in the classroom.

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References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:

- of special interest
- of outstanding interest

1. Raghubar KP, Barnes MA, Hecht SA. Working memory and mathematics: a review of developmental, individual difference, and cognitive approaches. *Learn Individ Differ*. 2010; 20:110–122.
2. Bull R, Lee K. Executive functioning and mathematics achievement. *Child Dev Perspect*. 2014; 8:36–41.
3. Hecht SA, Torgesen JK, Wagner RK, Rashotte CA. The relations between phonological processing abilities and emerging individual differences in mathematical computation skills: a longitudinal study from second to fifth grades. *J Exp Child Psychol*. 2001; 79:192–227. [PubMed: 11343408]
4. Dehaene, S. *The Number Sense: How the Mind Creates Mathematics*. Oxford University Press; 1997.
5. Feigenson L, Dehaene S, Spelke E. Core systems of number. *Trends Cogn Sci*. 2004; 8:307–314. [PubMed: 15242690]
6. Izard V, Sann C, Spelke ES, Streri A. Newborn infants perceive abstract numbers. *Proc Natl Acad Sci U S A*. 2009; 106:10382–10385. [PubMed: 19520833]
7. Halberda J, Ly R, Wilmer JB, Naiman DQ, Germine L. Number sense across the lifespan as revealed by a massive Internet-based sample. *Proc Natl Acad Sci U S A*. 2012; 109:11116–11120. [PubMed: 22733748]
8. Dehaene, S. Symbols and quantities in parietal cortex: elements of a mathematical theory of number representation and manipulation. In: Haggard, P., Rossetti, Y., editors. *Sensorimotor Foundations of Higher Cognition (Attention and Performance)*. Oxford; 2008. p. 527-574.
9. Carey, S. *The Origins of Concepts*, (Oxford Series in Cognitive Development). Oxford University Press; 2009.
10. Halberda J, Mazocco MMM, Feigenson L. Individual differences in non-verbal number acuity correlate with maths achievement. *Nature*. 2008; 455:665–668. [PubMed: 18776888]
11. DeWind NK, Brannon EM. Malleability of the approximate number system: effects of feedback and training. *Front Hum Neurosci*. 2012; 6:1–10. [PubMed: 22279433]
12. Lyons IM, Beilock SL. Numerical ordering ability mediates the relation between number-sense and arithmetic competence. *Cognition*. 2011; 121:256–261. [PubMed: 21855058]
13. Chen Q, Li J. Association between individual differences in non-symbolic number acuity and math performance: a meta-analysis. *Acta Psychol (Amst)*. 2014; 148:163–172. [PubMed: 24583622]
14. Bonny JW, Lourenco SF. The approximate number system and its relation to early math achievement: evidence from the preschool years. *J Exp Child Psychol*. 2012; 114:375–388. [PubMed: 23201156]
15. Fazio LK, Bailey DH, Thompson CA, Siegler RS. Relations of different types of numerical magnitude representations to each other and to mathematics achievement. *J Exp Child Psychol*. 2014; 123:53–72. Found that symbolic and nonsymbolic numerical tasks accounted for unique variance in predicting math achievement. The symbolic comparison and number line estimation tasks accounted for greater unique variance. In a meta-analysis, the relationship between ANS and math was stronger before children enter formal schooling. [PubMed: 24699178]
16. Libertus ME, Feigenson L, Halberda J. Numerical approximation abilities correlate with and predict informal but not formal mathematics abilities. *J Exp Child Psychol*. 2013; 116:829–838. [PubMed: 24076381]
17. Mazocco MMM, Feigenson L, Halberda J. Preschoolers' precision of the approximate number system predicts later school mathematics performance. *PLoS One*. 2011; 6:e23749. [PubMed: 21935362]
18. Starr A, Libertus ME, Brannon EM. Number sense in infancy predicts mathematical abilities in childhood. *Proc Natl Acad Sci U S A*. 2013; 110:18116–18120. [PubMed: 24145427]
19. Mussolin C, Mejias S, Noël M. Symbolic and nonsymbolic number comparison in children with and without dyscalculia. *Cognition*. 2010; 115:10–25. [PubMed: 20149355]
20. Mazocco MMM, Feigenson L, Halberda J. Impaired acuity of the approximate number system underlies mathematical learning disability (dyscalculia). *Child Dev*. 2011; 82:1224–1237. [PubMed: 21679173]

21. Bugden, S., Ansari, D. Probing the nature of deficits in the “Approximate Number System” in children with persistent Developmental Dyscalculia. *Dev Sci.* 2015. <http://dx.doi.org/10.1111/desc.12324>
22. Schneider M, Beeres K, Coban L, Merz S, Schmidt SS, Stricker J, De Smedt B. Associations of non-symbolic and symbolic numerical magnitude processing with mathematical competence: a meta-analysis. *Dev Sci.* 2016; doi: 10.1111/desc.12372
23. Holloway ID, Ansari D. Journal of Experimental Child Mapping numerical magnitudes onto symbols: the numerical distance effect and individual differences in children’s mathematics achievement. *J Exp Child Psychol.* 2009; 103:17–29. [PubMed: 18513738]
24. Sasanguie D, Defever E, Maertens B, Reynvoet B. The approximate number system is not predictive for symbolic number processing in kindergarteners. *Q J Exp Psychol.* 2014; 67:271–280.
25. Gilmore C, Attridge N, Clayton S, Cragg L, Johnson S, Marlow N, Simms V, Inglis M. Individual differences in inhibitory control, not non-verbal number acuity, correlate with mathematics achievement. *PLoS One.* 2013; 8:e67374. [PubMed: 23785521]
26. Fuhs MW, McNeil NM. ANS acuity and mathematics ability in preschoolers from low-income homes: contributions of inhibitory control. *Dev Sci.* 2013; 16:136–148. [PubMed: 23278935]
27. Clayton S, Gilmore C, Inglis M. Dot comparison stimuli are not all alike: the effect of different visual controls on ANS measurement. *Acta Psychol (Amst).* 2015; 161:177–184. [PubMed: 26408864]
28. Dietrich JF, Huber S, Nuerk H-C. Methodological aspects to be considered when measuring the approximate number system (ANS): a research review. *Front Psychol.* 2015; 6:1–14. [PubMed: 25688217]
29. DeWind NK, Brannon EM. Significant inter-test reliability across approximate number system assessments. *Front Psychol.* 2016
30. Szűcs D, Nobes A, Devine A, Gabriel FC, Gebuis T. Visual stimulus parameters seriously compromise the measurement of approximate number system acuity and comparative effects between adults and children. *Front Psychol.* 2013; 4:444. [PubMed: 23882245]
31. Leibovich T, Ansari D. The symbol-grounding problem in numerical cognition: a review of theory, evidence, and outstanding questions. *Can J Exp Psychol.* 2016; 70:12–23. [PubMed: 26913782]
32. De Smedt B, Noël M-P, Gilmore C, Ansari D. How do symbolic and non-symbolic numerical magnitude processing skills relate to individual differences in children’s mathematical skills? A review of evidence from brain and behavior. *Trends Neurosci Educ.* 2013; 2:48–55.
33. Mussolin, C., Nys, J., Leybaert, J., Content, A. How approximate and exact number skills are related to each other across development: a review. *Dev Rev.* 2015. <http://dx.doi.org/10.1016/j.dr.2014.11.001>
34. Lyons, IM., Ansari, D. *Foundations of Children’s Numerical and Mathematical Skills: The Roles of Symbolic and Nonsymbolic Representations of Numerical Magnitude.* Elsevier Inc; 2015.
35. Feigenson L, Libertus ME, Halberda J. Links between the intuitive sense of number and formal mathematics ability. *Child Dev.* 2013; 7:74–79.
- 36••. Haist F, Wazny JH, Toomarian E, Adamo M. Development of brain systems for nonsymbolic numerosity and the relationship to formal math academic achievement. *Hum Brain Mapp.* 2015; 36:804–826. Despite not finding a relationship between behavioral measures of ANS acuity, a non-symbolic neural ratio effect in the bilateral IPS predicted individual differences in symbolic mathematical abilities in children. [PubMed: 25327879]
37. Park J, Brannon EM. Training the approximate number system improves math proficiency. *Psychol Sci.* 2013; 24:2013–2019. [PubMed: 23921769]
- 38••. Park J, Brannon EM. Improving arithmetic performance with number sense training: an investigation of underlying mechanism. *Cognition.* 2014; 133:188–200. Adult participants showed specific gains in complex symbolic improvement following approximate arithmetic compared to participants who received short term spatial memory training, symbolic ordering and approximate number comparison training. Performance gains in symbolic arithmetic were specific to mental manipulation of non-symbolic quantities, given that no improvements were

found when participants completed a memory based non-symbolic matching and comparison training. [PubMed: 25044247]

39. Dillon MR, Pires AC, Hyde DC, Spelke ES. Children's expectations about training the approximate number system. *Br J Dev Psychol.* 2015; 33:411–418. [PubMed: 26399713]
- 40••. Cappelletti M, Gessaroli E, Hithersay R, Mitolo M, Didino D, Kanai R, Cohen Kadosh R, Walsh V. Transfer of cognitive training across magnitude dimensions achieved with concurrent brain stimulation of the parietal lobe. *J Neurosci.* 2013; 33:14899–14907. Using transcranial random noise stimulation (TRNS) study, where electrical stimulation was applied to bilateral IPS during training of an approximate number comparison task, the authors found that improvements in ANS acuity did not lead to enhanced symbolic arithmetic gains. [PubMed: 24027289]
- 41••. Hyde DC, Khanum S, Spelke ES. Brief non-symbolic, approximate number practice enhances subsequent exact symbolic arithmetic in children. *Cognition.* 2014; 131:92–107. First grade children who practiced either approximate arithmetic or approximate number comparison were faster and more accurate at solving exact arithmetic problems in comparison to children who practiced brightness comparison and line length addition. Benefits of ANS training were specific to math performance given that children were not significantly better than the control groups during a reading task. [PubMed: 24462713]
42. Dehaene S, Piazza M, Pinel P, Cohen L. Three parietal circuits for number processing. *Cogn Neuropsychol.* 2003; 20:487–506. [PubMed: 20957581]
43. Dehaene S, Cohen L. Cultural recycling of cortical maps. *Neuron.* 2007; 56:384–398. [PubMed: 17964253]
44. Piazza M, Pinel P, Le Bihan D, Dehaene S. A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron.* 2007; 53:293–305. [PubMed: 17224409]
45. Piazza M, Izard V, Pinel P, Le Bihan D, Dehaene S. Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron.* 2004; 44:547–555. [PubMed: 15504333]
46. Pinel P, Dehaene S, Rivière D, LeBihan D. Modulation of parietal activation by semantic distance in a number comparison task. *Neuroimage.* 2001; 14:1013–1026. [PubMed: 11697933]
47. Pinel P, Piazza M, Le Bihan D, Dehaene S. Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron.* 2004; 41:983–993. [PubMed: 15046729]
48. Cohen Kadosh R, Bahrami B, Walsh V, Butterworth B, Popescu T, Price CJ. Specialization in the human brain: the case of numbers. *Front Hum Neurosci.* 2011; 5:62. [PubMed: 21808615]
49. Dehaene S. Sources of mathematical thinking: behavioral and brain-imaging evidence. *Science.* 1999; 284:970–974. [PubMed: 10320379]
50. Holloway ID, Price GR, Ansari D. Common and segregated neural pathways for the processing of symbolic and nonsymbolic numerical magnitude: an fMRI study. *Neuroimage.* 2010; 49:1006–1017. [PubMed: 19666127]
- 51•. Edwards, LA., Wagner, JB., Simon, CE., Hyde, DC. Functional brain organization for number processing in pre-verbal infants. *Dev Sci.* 2015. <http://dx.doi.org/10.1111/desc.12333> Functional near infrared spectroscopy with six month old infants showed neural activity in the right IPS during numerical change trials, compared to audio visual clips and non-change trials. These findings suggest that the right IPS comes online and shows specialization for numerosity processing before formal education and language development
52. Hyde DC, Boas DA, Blair C, Carey S. Near-infrared spectroscopy shows right parietal specialization for number in pre-verbal infants. *Neuroimage.* 2010; 53:647–652. [PubMed: 20561591]
53. Cantlon JF, Brannon EM, Carter EJ, Pelphrey KA. Functional imaging of numerical processing in adults and 4-y-old children. *PLoS Biol.* 2006; 4:e125. [PubMed: 16594732]
54. Ansari D. Effects of development and enculturation on number representation in the brain. *Nat Rev Neurosci.* 2008; 9:278–291. [PubMed: 18334999]
- 55••. Emerson, RW., Cantlon, JF. Continuity and change in children's longitudinal neural responses to numbers. *Dev Sci.* 2014. <http://dx.doi.org/10.1111/desc.12215> Neural activity in the right IPS showed stable brain responses during a symbol to dot matching task in children between 4.5 and 9 years of age and a group of adults over a one to two year period. However, changes in neural

activity in the left IPS predicted individual differences in behavioral performance on the task, whereas the right IPS did not

- 56••. Vogel SE, Goffin C, Ansari D. Developmental specialization of the left parietal cortex for the semantic representation of Arabic numerals: an fMR-Adaptation study. *Dev Cogn Neurosci*. 2015; 12:61–73. Ratio dependent recovery of brain activity in the right IPS in an fMRI adaptation paradigm that used numerical symbols was found to be developmentally stable across ages 6–14 years. However, ratio dependent modulation of the neural signal changed as a function of age in the left IPS, suggesting that the left IPS becomes more specialized across development for processing symbols. [PubMed: 25555264]
- 57•. Bugden S, Price GR, McLean DA, Ansari D. The role of the left intraparietal sulcus in the relationship between symbolic number processing and children's arithmetic competence. *Dev Cogn Neurosci*. 2012; 2:448–457. Ratio dependent modulation in the left IPS during a symbolic number comparison task predicted individual differences in arithmetic fluency in 8–9 year old children. A larger neural ratio effect was associated more precise symbolic numerical representations and greater arithmetic fluency performance. [PubMed: 22591861]
58. Ansari D, Dhital B. Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. *J Cogn Neurosci*. 2006; 18:1820–1828. [PubMed: 17069473]
59. Ansari D, Garcia N, Lucas E, Hamon K, Dhital B. Neural correlates of symbolic number processing in children and adults. *Neuroreport*. 2005; 16:1769–1773. [PubMed: 16237324]
60. Cantlon JF, Libertus ME, Pinel P, Dehaene S, Brannon EM, Pelphrey KA. The neural development of an abstract concept of number. *J Cognitive Neurosci*. 2009; 21:2217–2229.
61. Rivera SM, Reiss AL, Eckert MA, Menon V. Developmental changes in mental arithmetic: evidence for increased functional specialization in the left inferior parietal cortex. *Cereb Cortex*. 2005; 15:1779–1790. [PubMed: 15716474]
62. Nieder A. Prefrontal cortex and the evolution of symbolic reference. *Curr Opin Neurobiol*. 2009; 19:99–108. [PubMed: 19447604]
63. Fias W, Lammertyn J, Reynvoet B, Dupont P, Orban GA. Parietal representation of symbolic and nonsymbolic magnitude. *J Cogn Neurosci*. 2003; 15:47–56. [PubMed: 12590842]
64. Poldrack RA. Can cognitive processes be inferred from neuroimaging data? *Trends Cogn Sci*. 2006; 10:59–63. [PubMed: 16406760]
65. Lyons IM, Ansari D, Beilock SL. Qualitatively different coding of symbolic and nonsymbolic numbers in the human brain. *Hum Brain Mapp*. 2015; 36:475–488. [PubMed: 25238646]
- 66•. Bulthé J, De Smedt B, Op de Beeck HP. Format-dependent representations of symbolic and non-symbolic numbers in the human cortex as revealed by multi-voxel pattern analyses. *Neuroimage*. 2014; 87:311–322. Using multi-voxel pattern analyses, they found different patterns of neural activity for both symbolic and nonsymbolic number comparison across the parietal cortex. [PubMed: 24201011]
67. Ansari, D. Number symbols in the brain. In: Berch, DB, Geary, DC., Koepke, KM., editors. *Development of Mathematical Cognition: Neural Substrates and Genetic Influences*. Elsevier; 2016. p. 27-50.
- 68•. Iuculano T, Rosenberg-Lee M, Richardson J, Tenison C, Fuchs L, Supekar K, Menon V. Cognitive tutoring induces widespread neuroplasticity and remediates brain function in children with mathematical learning disabilities. *Nat Commun*. 2015; 6:8453. Found that an 8 week one-on-one math tutoring program remediated atypical brain activity during arithmetic performance in children with math learning disabilities (MLD) before tutoring, children with MLD showed higher activity during arithmetic in brain regions located in the prefrontal cortex, inferior and superior parietal cortices, ventral temporal-occipital cortex as well as subcortical areas including the left hippocampus. Following tutoring, brain activation in these identified regions no longer differentiated children with MLD from typically developing children. These findings are consistent with the notion that atypical neural activity during arithmetic in children with MLD was normalized following participating in a math tutoring program. [PubMed: 26419418]
69. Kucian K, Grond U, Rotzer S, Henzi B, Schönmann C, Plangger F, Gälli M, Martin E, von Aster M. Mental number line training in children with developmental dyscalculia. *Neuroimage*. 2011; 57:782–795. [PubMed: 21295145]

- 70•. Supekar K, Iuculano T, Chen L, Menon V. Remediation of childhood math anxiety and associated neural circuits through cognitive tutoring. *J Neurosci*. 2015; 35:12574–12583. Math anxiety was significantly reduced in high math anxious children following a one-on-one math tutoring program. Math anxious individuals showed normalization of brain activity following tutoring in regions in the prefrontal and parietal cortices, as well as the amygdala. Before training, high math anxious children showed greater effective connectivity between the right and left amygdala compared to low math anxious individuals. After training, no differences were found. [PubMed: 26354922]
- 71•. Kesler SR, Sheau K, Koovakkattu D, Reiss AL. Changes in frontal-parietal activation and math skills performance following adaptive number sense training: preliminary results from a pilot study. *Neuropsychol Rehabil*. 2011; 21:433–454. Participants with Turner syndrome between the ages 7 and 14 completed a number sense training program where exercises included practice in quantity comparisons, estimations, mental calculation and executive function tasks. Reduced activity was found in the prefrontal cortex, and increased activity was found in the parietal cortex following the intervention. [PubMed: 21714745]
72. Fuhs MW, McNeil NM, Kelley K, O’Rear C, Villano M. The role of non-numerical stimulus features in approximate number system training in preschoolers from low-income homes. *J Cogn Dev*. in press.
73. Qin S, Cho S, Chen T, Rosenberg-Lee M, Geary DC, Menon V. Hippocampal–neocortical functional reorganization underlies children’s cognitive development. *Nat Neurosci*. 2014; 17:1263–1269. [PubMed: 25129076]

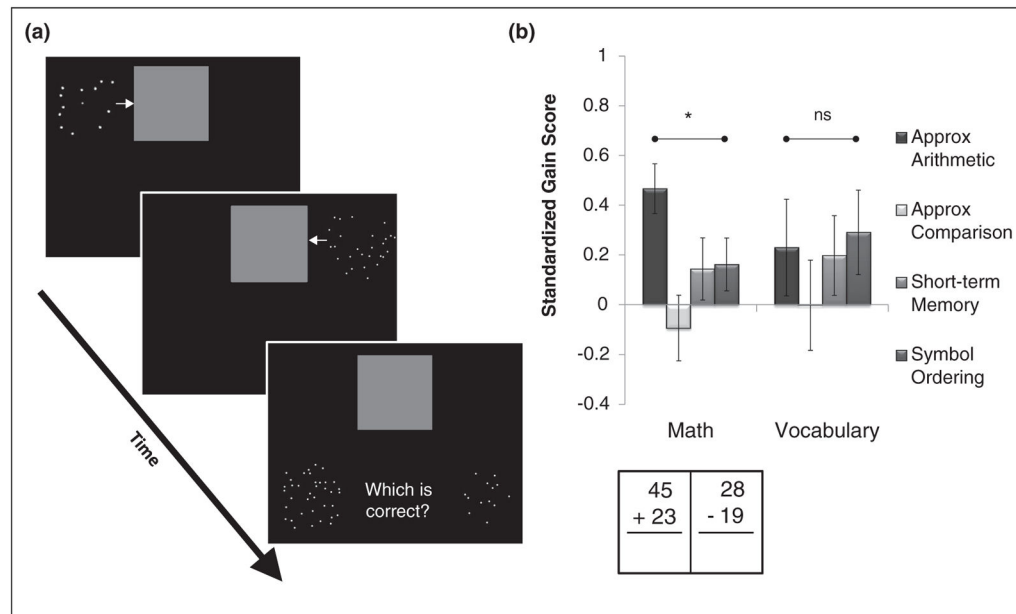


Figure 1.

(a) During an addition trial of the approximate arithmetic training task, an array of dots moves behind a screen followed by a subsequent array of dots. Participants are then asked to select the dot array that matches the sum. On other trials participants had to make a greater-or-less-than comparison between the sum and a single array. **(b)** The approximate arithmetic training was shown to improve performance on complex addition and subtraction compared to a vocabulary task to a greater extent than approximate number comparison, short-term memory, and symbolic ordering training. A portion of the data replotted from [38].

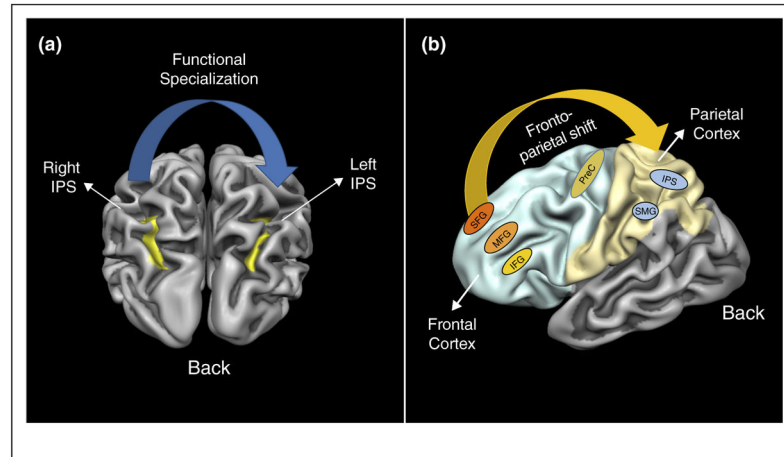


Figure 2.

An illustration of the developmental changes in brain activity for numerical and arithmetic tasks. **(a)** A cartoon depiction of the developmental specialization of the left IPS. **(b)** Fronto-parietal shift over the course of development. IPS: intraparietal sulcus, SFG: superior frontal gyrus, MFG: middle frontal gyrus, IFG: inferior frontal gyrus, PreC: precentral gyrus, SMG: supramarginal gyrus.

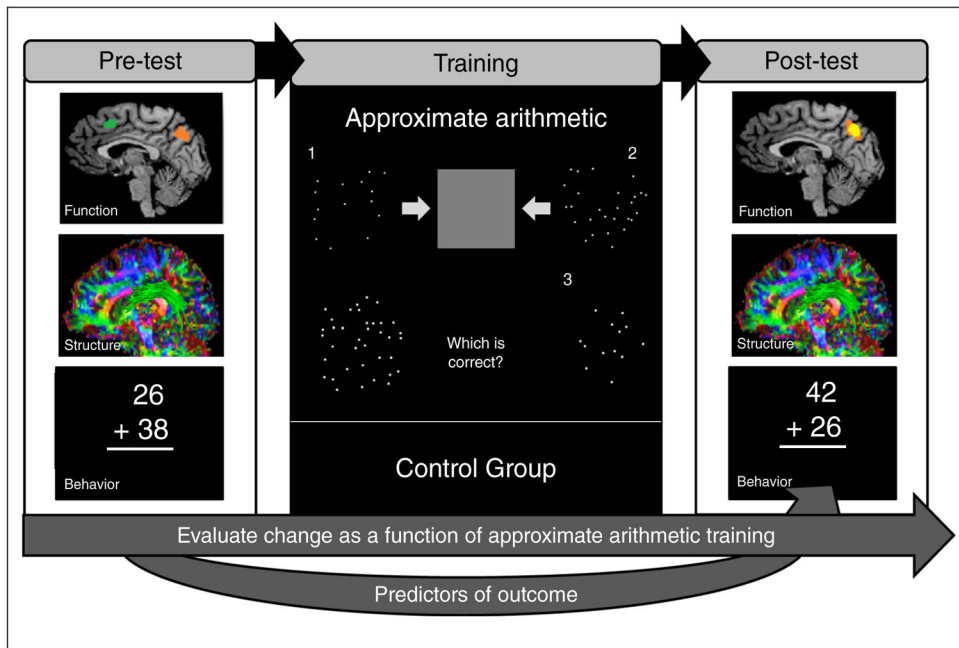


Figure 3.

A schematic illustration of a neuroimaging pre-test and post-test training design. Neural analytical tools can be used to identify both functional and structural neuro-markers, as well as behavioral performance can be used to either predict individual differences in training gains and/or uncover the relationship between approximate arithmetic and symbolic math. The schematic of the approximate arithmetic represents one trial, however, in the true task, the dot arrays are not displayed simultaneously as depicted.