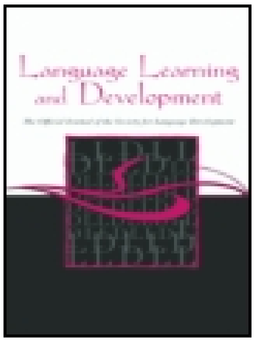

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ABSTRACT

In this article we first review evidence for the approximate number system (ANS), an evolutionarily ancient and developmentally conservative cognitive mechanism for representing number without language. We then critically review five different lines of support for the proposal that symbolic representations of number build upon the ANS, and discuss potential causes of conflicting findings in the literature. Finally, we consider potential mechanisms that could drive a relationship between the ANS and symbolic math. We conclude that while there is considerable evidence the relationship between the ANS and symbolic math is meaningful, we are far from understanding the cognitive and neural mechanisms that underlie this relationship.

Introduction

Although we are not always explicitly aware of our deep dependence on number, mathematics is an integral part of our daily lives. Every time we tell time, determine how many quarters to put in the parking meter, pay our bills, grade a student's exam, or determine the materials needed for a kitchen renovation we are relying on our numerical abilities. Many of these tasks rely on skills honed through years of school-based mathematics education. The concept of natural number, the set of all whole, non-negative numbers, is fundamental to symbolic mathematical thought. A central question in cognitive science is how and from where do natural number concepts arise. To resolve this question, we must come to understand the preverbal cognitive capacities that mathematical education builds upon, discover the evolutionary foundations that support mathematical thinking, and ultimately identify how natural number concepts emerge from these foundations.

While non-human animals and human infants will never prove an algebraic theorem, calculate the tip at a restaurant, or double the proportions to implement a recipe, there is nevertheless extensive evidence that many animals and even the youngest of babies have an intuitive number sense termed here the approximate number system (ANS; Feigenson, Dehaene, & Spelke, 2004). The ANS has two behavioral hallmarks, the distance and size effects. The distance effect refers to the fact that it is easier to discriminate numbers that are further apart in numerical distance (2 vs. 7 is easier than 2 vs. 4), while the size effect refers to the observation that it is easier to discriminate smaller numbers compared to larger numbers at the same distance (2 vs 4 is easier than 22 vs 24). Thus, ANS representations of number follow *Weber's law* such that the difficulty in discriminating any two numbers is dependent on the ratio between them, rather than their absolute difference. In this way the representations supported by the ANS are fundamentally distinct from the exact representations made possible by Arabic numerals. Arabic numerals, for example, allow us to appreciate that the difference between 18 and 19 is exactly the same as the difference between 1,834 and 1,835. The ability to precisely represent number is a necessary prerequisite for humans to perform complex

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calculations and a myriad of other mathematical endeavors. In contrast, the ANS only supports fuzzy magnitude representations that are ratio dependent. Despite these profound differences, there is growing evidence of a link between the ANS and symbolic mathematical ability. In this review, we first summarize properties of the ANS by examining the number sense of infants and non-human primates. We then review the evidence linking symbolic math skill to the ANS, and discuss the potential causes of conflicting findings in the literature. Finally, we discuss implications of this relationship both for the genesis of natural number concepts and educational applications.

Properties of the ANS—evidence from infants and non-human primates

Numerical competence has been observed throughout the animal kingdom, from insects to primates. Numerical representations allow North Island robins to determine successful caching strategies, mosquito and stickleback fish to determine the more numerous social group, and elephants to choose the larger amount of food (Agrillo, Dadda, Serena, & Bisazza, 2008; Garland, Low, & Burns, 2012; Mehlis, Thünken, Bakker, & Frommen, 2015; Perdue, Talbot, Stone, & Beran, 2012). This widespread use of quantity discrimination throughout the animal kingdom is evidence of either the emergence of numerical abilities in a very early common ancestor, or of convergent evolution. Regardless of the evolutionary origin of numerical ability, the ubiquity of these competencies suggests that being able to discriminate the larger of two sets is highly adaptive.

Similarly, infants just moments after birth are sensitive to the numerical attributes of the world around them (Izard, Sann, Spelke, & Streri, 2009). Multiple experimental methods that make use of infants' gaze direction, gaze duration, and brain waves all provide converging evidence that infants rely on the ANS to make numerical discriminations (Hyde & Spelke, 2011; Libertus & Brannon, 2009, 2010; Lipton & Spelke, 2003; Xu & Spelke, 2000). For example, when 6-month-old infants are shown two image streams displaying dot arrays that frequently change in the spacing, location, and size of the dots, infants preferentially attend to the stream that is changing numerically over the stream that is numerically constant (Libertus & Brannon, 2010). Whereas newborns require a 1:3 ratio to detect differences in numerosity (Izard et al., 2009), by 6 months of age babies can handle a 1:2 ratio, and by 9-months a 2:3 ratio (Libertus & Brannon, 2010; Lipton & Spelke, 2003; Xu & Spelke, 2000). This increase in acuity continues throughout childhood (Halberda & Feigenson, 2008), and in a large-scale online study was seen to continue to improve until around 30 years of age (Halberda, Ly, Wilmer, Naiman, & Germine, 2012).

A contentious question in both the comparative and developmental literatures has been whether the putative ability to represent approximate number can be better explained as a sensitivity to continuous variables such as surface area or contours (Clearfield & Mix, 1999, 2001; Cordes & Brannon, 2009; Davis & Pérusse, 1988). For example, Mix and colleagues argued that poor stimulus controls in many infant studies likely resulted in effects that were driven by infants' attending to perimeter or surface area rather than numerosity (Mix, Huttenlocher, & Levine, 2002). A recent series of studies with human infants came to a contrary conclusion using the change detection procedure (Libertus, Starr, & Brannon, 2014; Starr & Brannon, 2015). In one study infants were presented with a screen in which images changed by a 1:3 ratio in area and were constant in numerosity, and a second screen in which the stimuli changed by a 1:3 ratio in numerosity and remained constant in area. Infants overwhelmingly preferred the screen that changed in numerosity. Only when the change in area was increased to a 1:10 ratio did infants look equally long at the two streams. These findings provide strong evidence that when young infants are presented with arrays of discrete items, numerosity is more salient than the cumulative continuous variables of the sets. Cordes and colleagues conducted another series of studies with the visual habituation procedure and came to similar conclusion (Cordes & Brannon, 2008). In those studies, 6-month old infants required a 1:2 ratio change in numerosity to show a reliable novelty effect when tested in the visual habituation paradigm. However, when cumulative surface area of the dot arrays was manipulated, Cordes and colleagues found that 6-month-old infants required a 4-fold change in the cumulative surface area of an array to show a novelty effect. These studies suggest that infants represent both number and continuous variables, but show greater sensitivity to numerical attributes of discrete arrays.

Studies of animal numerical cognition have yielded similar controversies over the relative salience of numerosity and continuous variables of dot arrays. For example, Davis and Pérusse (1988) argued that animals only attend to the numerical attribute of the stimuli when they have had extensive artificial laboratory training to do so, and thus as a "last resort strategy." In contrast, Gallistel (1990) proposed that number, along with time and space, are critical attributes of the world that all organisms represent. Cantlon and colleagues addressed the question of the relative salience of numerosity and other non-numerical attributes in rhesus macaques *(Macaca mulatta)*. Monkeys were trained in a match-to-sample task where the sample and the correct match were the same both in number and in cumulative surface area. Monkeys were then given non-differentially reinforced probe trials where one choice matched the sample in number and not total area, and the other matched in total area and not number. Rhesus monkeys were more likely to match arrays based on numerosity than surface area when the two cues were in conflict (Cantlon & Brannon, 2007). Collectively these studies suggest that although it may seem intuitive that number is more cognitively challenging to represent than continuous variables, this intuition is misleading. Instead, when babies and monkeys are presented with sets of discrete items they are more likely to detect numerosity than they are to form summary statistics of continuous variables.

A powerful aspect of the ANS is that despite its imprecision, it supports arithmetic calculations. For example, rhesus monkeys are capable of performing addition and subtraction operations using ANS representations (Cantlon & Brannon, 2007; Cantlon, Merritt, & Brannon, 2015). In these studies, monkeys were shown addition operations where two sets disappeared behind an occluder, or subtraction operations where after an initial set was occluded a subset of the first array emerged from behind the occluder and left the screen. Monkeys were then given a choice between an array that numerically summed the two addends (or represented the difference in the subtraction problem) and a distractor array. Monkeys were then tested on probe trials with novel numerical values, where they performed above chance expectation indicating acquisition of the arithmetic rules. Training and probe trial performance was dependent on the ratio between the correct answer and the distractor, following *Weber's* law.

The violation of expectancy paradigm suggests that infants also keep track of objects over addition and subtraction events. Karen Wynn pioneered the method demonstrating that infants form expectations about the number of objects that should be behind an occluder when they watch addition and subtraction events (Wynn, 1992). However, in these early experiments it was unclear whether infants relied on the ANS or instead relied on an object-file system that is limited to representing small sets. If infants were relying on the object-file system they would detect incorrect arithmetic solutions by tracking each object, holding these objects in memory, and then noticing the difference between the number of objects stored in memory and the number presented after the arithmetic event. However, McCrink and Wynn (2004, 2009) showed nine-month-old infants animations of arithmetic problems with sets too large to be represented by an object tracking system. When shown events such as 5 + 5 = 5 or 5 + 5 = 10 infants looked significantly longer at the impossible outcomes, presumably because they found them surprising. In other studies, Spelke and colleagues have shown that young children make approximate arithmetic calculations that show systematic ratio dependence (Barth, La Mont, Lipton, & Spelke, 2005; Gilmore, McCarthy, & Spelke, 2010). Moreover, animals and human infants are both adept at approximate ordinal numerical comparisons. Monkeys show ratio dependent number discrimination when trained to choose the larger of two numerical arrays and transfer to novel numerical values (e.g., Brannon & Terrace, 1998) and human infants habituated to a sequence of images that increased (or decreased) in numerosity dishabituated to novel sequences that displayed the reverse ordinal relationship (e.g., Brannon, 2002).

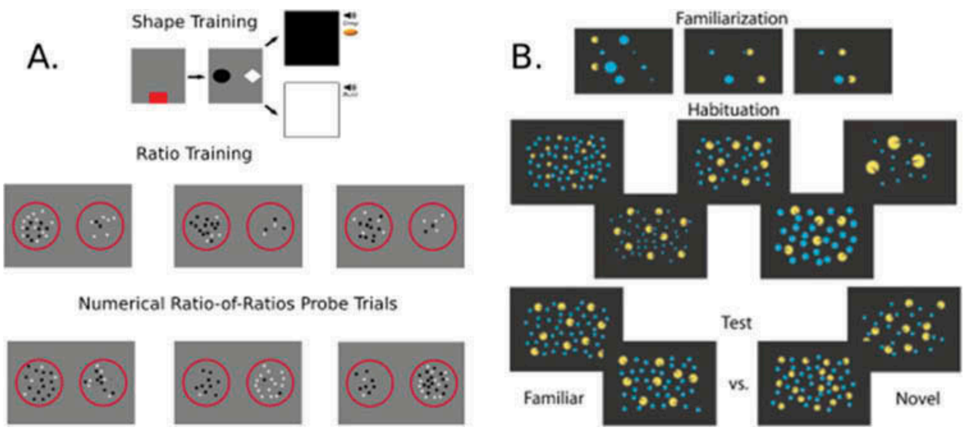

Figure 1. (A) Example stimuli presented to rhesus monkeys in Drucker et al. (2015). In this example the black circle is the positive stimulus and the white diamond is the negative stimulus. The correct answer is on the left. Figure modified from Drucker et al. (2015). (B) Example stimuli presented to 6-month-old infants in McCrink and Wynn (2007). The example habituation ratio shown here is 1:4. Figure modified from McCrink and Wynn (2007).

The ANS also supports the capacity to reason about second order numerical relationships. Drucker, Rossa, and Brannon (2015) presented rhesus monkeys with two arrays that each contained one or more positive items that were associated with reward or negative items that were associated with the absence of reward (see Figure 1A). The monkeys were reinforced for choosing the array that had the more favorable ratio of positive to negative items while ignoring the absolute number of positive or negative items in each array. The monkeys were then tested with novel ratio comparisons. During these unreinforced probe trials the moneys continued to choose the array with a higher ratio of positive to negative items. The monkeys' performance improved as the ratio between ratios increased, following *Weber's* law. This finding demonstrates that monkeys are able to represent the ratio of good to bad items in an array, and compare these two ratios to choose the array that is more favorable.

Human infants also represent the ratio between sets of discrete quantities (McCrink & Wynn, 2007). When infants were habituated to arrays that showed a constant proportion of blue to yellow shapes they selectively dishabituated to new arrays that featured a different proportion of yellow to blue shapes (See Figure 1B). Thus, the ANS not only allows for the approximate representation of numerical values, it supports mental transformations across those representations. These transformations include arithmetic operations, ordinal relationships, and proportional reasoning in human infants and non-human primates.

Is The ANS foundational for symbolic mathematics?

The previous section established the existence of a preverbal number sense present in nonhuman animals and human infants. In this section we explore five lines of evidence that this primitive system is meaningfully related to our uniquely human mathematical mind. The first line of evidence comes from studies that demonstrate a positive correlation between ANS acuity and symbolic math ability. In the first study to show this relationship, Halberda and colleagues demonstrated that *Weber* fraction measured at 14 years of age retroactively predicted standardized math scores at age 5, even after controlling for verbal IQ (Halberda, Mazzocco, & Feigenson, 2008). This positive correlation has since been found in adults (Agrillo, Piffer, & Adriano, 2013; DeWind & Brannon, 2012; Halberda et al., 2012; Libertus, Odic, & Halberda, 2012; Lourenco, Bonny, Fernandez, & Rao, 2012); in school-aged children (Geary, Hoard, Nugent, & Rouder, 2015; Pinheiro-Chagas et al., 2014) ; in children just beginning formal math education (Gilmore et al., 2010; Keller & Libertus, 2015; Mundy &

Gilmore, 2009); and in preschool aged children before they begin formal math education (Chu, vanMarle, & Geary, 2015; Libertus, Feigenson, & Halberda, 2011, 2013; Mazzocco, Feigenson, & Halberda, 2011b; Soto-Calvo, Simmons, Willis, & Adams, 2015; Starr, Libertus, & Brannon, 2013; van Marle, Chu, Li, & Geary, 2014;). Three meta-analyses have concluded there is a significant correlation between ANS and math ability (Chen & Li, 2014; Fazio, Bailey, Thompson, & Siegler, 2014; Schneider et al., 2016). A correlation between ANS acuity and math has, however, failed to emerge in other studies (Holloway & Ansari, 2009; Iuculano, Tang, Hall, & Butterworth, 2008; Lyons, Price, Vaessen, Blomert, & Ansari, 2014; Nosworthy, Bugden, Archibald, Evans, & Ansari, 2013; Sasanguie, Defever, Maertens, & Reynvoet, 2014). We return to these discrepant results and their implications for understanding the role the ANS plays in symbolic math knowledge later in this article.

A second line of evidence comes from longitudinal studies investigating the relationship between numerical acuity and later symbolic math performance. In one study, numerical change detection scores at 6 months of age predicted some of the variance in both ANS acuity and the Test of Early Mathematical Achievement, but not verbal IQ, in 3.5 year-olds. (Starr et al., 2013). Recent longitudinal studies that follow children in the preschool years have revealed a nuanced relationship between the ANS and early symbolic math skills (Purpura & Logan, 2015; Soto-Calvo et al., 2015). Soto-Calvo and colleagues measured preschoolers' ANS ability, a variety of symbolic math skills, phonological awareness, and visual-spatial short term memory at age 4 and then again 14 months later (Soto-Calvo et al., 2015). ANS ability, along with visual-spatial short term memory and phonological awareness, predicted children's accuracy in solving addition and subtraction word problems, but did not predict early counting proficiency. Purpura and Logan (2015) assessed children aged 3–5 at the beginning and end of 1 year of preschool on a battery of cognitive skills including ANS acuity, math language ability, and early symbolic math skills. ANS acuity predicted symbolic math ability only for children in the 25th percentile of the distribution of math scores, while math language ability predicted math scores of the 50–75th percentile of this distribution. These non-linear relationships highlight the fact that different math skills may be important for the acquisition of complex math abilities at different stages of math development. As symbolic math ability develops the connection to ANS acuity may become more complex, but these findings provide evidence for an ongoing link in early childhood.

Evidence that the ANS acuity of young children predicts aspects of math performance suggests a particular directional effect whereby ANS acuity facilitates math performance. However, there is also evidence that the ANS is refined through practice with the symbolic number system (Matejko & Ansari, 2016; for review, Mussolin, Nys, Leybaert, & Content, 2015). Work with the Mundurukú, an indigenous group in Brazil who do not have words for numbers greater than 5, supports this position. Members of this community who have had some formal schooling in math displayed significantly better ANS acuity than members of the community with less formal schooling (Piazza, Pica, Izard, Spelke, & Dehaene, 2013). Mussolin, Nys, Content, and Leybaert (2014) twice assessed the ANS acuity and symbolic math ability of preschool children 7 months apart. Children's performance at time 1 on the full battery of symbolic math assessments and a number word knowledge test predicted accuracy at time 2 on the non-symbolic comparison task. The reverse predictive relationship was not significant. Taken together, the directionality of a potential causal relationship between the ANS and symbolic math is unclear. The possibility of an ongoing bidirectional relationship across development is plausible, and warrants further investigation.

A third and related line of evidence supporting the proposal that the ANS is meaningfully related to symbolic math is that ANS acuity is impaired in at least a subset of children with math specific learning disabilities (Wilson & Dehaene, 2007; Butterworth, Varma, & Laurillard, 2011; Desoete, Ceulemans, De Weerdt, & Pieters, 2012; Mazzocco, Feigenson, & Halberda, 2011a; Piazza et al., 2010; Pinheiro-Chagas et al., 2014). Developmental dyscalculia is a math specific learning disorder diagnosed in children struggling to learn about numbers and arithmetic, but whose performance on tests of vocabulary, IQ, and working memory are within the range of typically developing children

(Butterworth et al., 2011; Landerl, Bevan, & Butterworth, 2004). Researchers have investigated low ANS acuity as one cause of this domain-specific impairment. Piazza et al. (2010) found that school aged dyscalculics (mean age 10.69) have roughly the same ANS acuity of an average typically developing 5-year-old. Mazzocco et al. (2011a) demonstrated that slightly older dyscalculics (mean age 14.83) had significantly lower ANS acuity as compared to low achieving, typically achieving, and high achieving peers. This result persisted after controlling for other domain general abilities that contribute to math ability, such as working memory for spatial locations and lexical retrieval of color and number words. Further, school aged children with math specific difficulties perform poorly on both non-symbolic comparison and non-symbolic addition, two different tasks that both utilize the ANS (Pinheiro-Chagas et al., 2014). It is important to note that developmental dyscalculia is a heterogeneous disorder with evidence supporting multiple causal factors contributing to severe mathematical difficulties (Bugden & Ansari, 2015; Defever, De Smedt, & Reynvoet, 2013; Defever, Reynvoet, & Gebuis, 2013; Fias, Menon, & Szucs, 2013; Geary, 2010). For example, Rousselle & Noël (2007) and Noël & Rousselle (2011) find little evidence of ANS deficits in very young dyscalculic children, and argue that this may reflect the fact that symbolic math sharpens the acuity of ANS representations rather than vice versa. There are likely multiple subtypes of dyscalculia, and one of these subtypes may comprise children with specific impairment in the ANS (Bartelet, Ansari, Vaessen, & Blomert, 2014; Skagerlund & Träff, 2016).

A fourth line of evidence that the ANS is meaningfully related to symbolic math is that overlapping brain structures are recruited when people engage in non-symbolic and symbolic numerical tasks (e.g., Butterworth & Walsh, 2011; Dehaene, Piazza, Pinel, & Cohen, 2003). Using an fMRI adaptation design, Piazza and colleagues showed participants dot patterns and Arabic digits in a sequence. The same numerical magnitude was repeatedly presented as dots or as a digit to create a decrease in BOLD signal. Recovery of the BOLD signal occurred when a new numerical magnitude (i.e., switch from 8 to 16) was presented, but not when a new stimulus format (i.e., switch from dots to digits) was presented. This cross notation adaptation and recovery occurred in the horizontal segment of the intraparietal sulcus (hIPS), suggesting that the hIPS codes numerical quantities and number symbols in the same way (Piazza, Pinel, Le Bihan, & Dehaene, 2007). In an fMRI study that systematically looked at the conjunction in neural activation when completing a symbolic or non-symbolic magnitude comparison task, the right inferior parietal lobule emerged as a region significantly activated by both task formats (Holloway, Price, & Ansari, 2010; see also Libertus, Woldorff, & Brannon, 2007). Similarly, Lussier and Cantlon (2016) had participants perform within format comparisons across dot arrays, number words, and object sizes. The authors found that the right IPS in children and bilateral IPS in adults showed a distance effect for both dot and number word comparisons, but not when comparing object sizes.

In contrast, other functional imagining studies have found evidence against format independent representation of numerical quantities in the IPS using both adaptation designs and comparison tasks (Bulthé, De Smedt, & Beeck, 2014; Bulthé, De Smedt, & Beeck, 2015; Cohen-Kadosh et al., 2011; Lyons, Ansari, & Beilock, 2015). Using an adaptation paradigm, Cohen-Kadosh and colleagues (2011) presented numerals or dots in a sequence where either the magnitude, the format, or the color of the presented stimulus changed as the sequence progressed. Results indicated a recovery of the BOLD signal during a format change in the absence of a change in magnitude of the stimulus, establishing at least some degree of format dependent representation. Damarla and Just (2013) found common neural patterns for different pictorial representations of a given numerosity (i.e., 3 tomatoes and 3 cars), but different neural patterns for pictorial and symbolic representations (e.g., 3 trees and the Arabic numeral 3). However, in a later study Damarla, Cherkassky, and Just (2016) found evidence of shared representation across visual and auditory modalities for small numerical values. The way in which number is defined in the brain is currently far from being fully characterized, and even evidence for co-activation during symbolic and non-symbolic number processing is not necessarily evidence of a shared representation. Future fMRI studies are needed to elucidate the implications of overlapping brain activation, and clarify how approximate and symbolic number are represented in the brain.

The final source of evidence we will review that supports the idea that there is a meaningful relationship between the ANS and math comes from recent studies that have employed training designs in an effort to move beyond correlation and address causality (Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013, 2014). In the first of these studies, Park & Brannon (2013) trained adults to solve approximate arithmetic problems and asked how this affected their ability to perform simple symbolic calculations. On addition trials, participants observed two arrays of dots each disappear behind a centrally located occluder. On subtraction trials, participants observed a single array move behind an occluder and then a subset of items float out from behind the occluder and leave the screen. The participant's task was to estimate the total number of dots behind the occluder to solve the addition or subtraction problem. On some trials, the participant was required to match their mental sum (or difference) to one of two presented arrays. On other trials the participant was shown a single target array and asked to compare their mental sum (or difference) to this new target array to make a greater or less than judgment. Before and after approximate arithmetic training, symbolic math performance was measured by how many two and three-digit addition and subtraction problems a participant could solve within two 5-min blocks. As a control task, a vocabulary test was also administered. For comparison, an age-matched no-contact control group was given the pre and post-tests, but not the ANS training sessions. Results showed that the participants who trained on the approximate arithmetic task improved in symbolic arithmetic performance, but not vocabulary performance. As expected, the no-contact control group did not improve on either measure.

In a second experiment, Park and Brannon (2013) examined the efficacy of approximate arithmetic training in comparison to two different active control groups. One group was trained daily with general world knowledge trivia questions and a second control group was required to make rapid judgments about the order of Arabic numerals. The numerical order judgment condition is particularly interesting in light of evidence suggesting that the ability to access the ordinal relation of numbers could mediate the relationship between the ANS and symbolic math (Lyons & Beilock, 2011). In the numerical order judgment training participants were presented with triads of single digit numbers that moved across the screen rapidly in both horizontal directions. The participant's task was to mouse-click on the triad of digits until all triads moving to the right were in ascending order and all triads moving to the left were in descending order. Although there was clear evidence that the numeral ordering group improved on a post-test assessment of numeral ordering, the group showed no improvement on the timed symbolic arithmetic task. Participants in the approximate arithmetic condition replicated the result from Experiment 1 by demonstrating significant improvement on the symbolic arithmetic test. As expected, the participants in the knowledge training condition did not improve on either measure. The lack of a transfer effect in the symbol-ordering condition argues against the idea that the approximate arithmetic group improved due to a placebo effect (e.g., Dillon, Pires, Hyde, & Spelke, 2015). If participants expected any numerical task to improve their math skills they should have benefited as much or more from numerical ordering.

In a subsequent set of studies Park and Brannon (2014) sought to isolate the components of the approximate arithmetic task that improved math performance. At minimum, approximate arithmetic involves forming representations of approximate numerical magnitudes, holding magnitudes in short-term memory, and combining approximate magnitudes. Would training on only one of these components of approximate arithmetic be sufficient to induce an improvement in symbolic arithmetic? In this study a new cohort of participants trained on approximate arithmetic, a traditional non-symbolic comparison task, a visuo-spatial short-term memory task, or a numeral symbol-ordering task. Results showed that participants who trained in the approximate arithmetic condition showed significantly greater improvement on the symbolic arithmetic test compared to participants in all other training conditions. Training on visuo-spatial short term memory alone was not enough to induce improvement in symbolic arithmetic. Collectively, these training studies suggest that there is a causal relationship between non-symbolic approximate arithmetic and symbolic arithmetic. More research is needed to fully understand the nature of this transfer effect.

Hyde et al. (2014) asked a similar question in children. They gave 6-year-old children a single short session of practice on approximate arithmetic, approximate line length addition, non-symbolic numerical comparison, or approximate brightness comparison, and then tested the same children on a timed symbolic arithmetic test part way through training and immediately after training. Children in both the approximate arithmetic and numerical comparison conditions were faster at completing the symbolic arithmetic test than children in the other two conditions, suggesting increased arithmetic fluency after completing tasks that activated the ANS. Although generally consistent with the Park and Brannon findings, children in the numerosity comparison condition appeared to benefit in symbolic arithmetic, while the same condition had little effect in adults. An interesting possibility for future research is to explore whether this is a true developmental or skill-based difference. In adults with strong symbolic math skills, ANS training might induce improvement in symbolic math ability only when there is a manipulation of mental magnitudes, rather than a simple comparison. It is possible that manipulating arrays of dots for adults is simply a more challenging ANS task that leads to greater motivation to train, whereas both non-symbolic comparison and arithmetic were engaging for young children. Approximate arithmetic training likely utilizes other cognitive abilities to a greater degree than approximate comparison, though as described in Park and Brannon (2014), visuo-spatial short-term memory training alone was not sufficient to induce improvements in symbolic arithmetic. Future work will need to uncover a mechanistic explanation for the approximate arithmetic training effect that includes possible developmental differences in the efficacy of approximate comparison training. We return to possible mechanisms of the relationship between the ANS and arithmetic later in this article.

To further test if approximate arithmetic training improves the early math skills of preschoolers using a pre/posttest design, Park and colleagues trained preschool aged children on an approximate arithmetic or a memory iPad game, and tested their early symbolic math abilities (Park, Bermudez, Roberts, & Brannon, 2016). Children in the approximate arithmetic condition showed significantly greater improvements on the Test of Early Mathematical Achievement (TEMA-3) compared to children in the memory game condition. Future work is exploring how approximate arithmetic training stacks up against commercial applications aimed at teaching numerical symbols (Szkudlarek & Brannon, in prep).

Challenges in describing the relationship between the ANS and symbolic math

As reviewed above, while many studies have reported a correlation between ANS acuity and math performance, a substantial number of studies have failed to find a relationship (e.g., Holloway & Ansari, 2009; Iuculano et al., 2008; Lyons et al., 2014; Nosworthy et al., 2013; Sasanguie et al., 2014). Three meta-analyses found support for a modest but significant positive relation between ANS and math ability ($r = .2$ to $.4$; Chen & Li, 2014; Fazio et al., 2014; Schneider et al., 2016). Fazio et al. (2014) analyzed 19 studies, and found that the relationship between the ANS and math decreased in strength after the onset of formal schooling, though it was still maintained. Chen and Li (2014) analyzed 36 cross sectional studies and found that a positive relationship held even after controlling for general cognitive abilities. ANS acuity also predicted later symbolic math performance, and ANS acuity at a later age was correlated with early symbolic math performance. Schneider et al. (2016) included 45 articles in their analysis, and found evidence of a link between ANS acuity and a wide range of math competencies across all ages. Given the modest effect size described in these meta-analyses, a potentially widespread reason for conflicting findings in the literature is that many studies examining the link between the ANS and math ability are underpowered (Chen & Li, 2014). Nevertheless, these three meta-analyses together lend support for the association between symbolic math and the ANS.

Beyond issues of sample size and power there are additional problematic factors that likely contribute to discrepant findings. One possibility is that the correlation between the ANS and symbolic math is an artifact of the stimulus control protocols employed in ANS tasks. To control for non-numerical stimulus attributes, researchers commonly structure stimuli such that surface area (or sometimes perimeter) is incongruent with numerosity on half of the trials. For example, on a given ordinal comparison trial a stimulus with 10 dots with a total surface area of 100 cm^2 might be presented with another stimulus with 20 dots and a total surface area of 50 cm^2. It has been suggested that inhibitory control demands created by the nature of these incongruent trials drives the observed relationship between ANS acuity and symbolic math (Fuhs & McNeil, 2013; Gilmore et al., 2013; Negen & Sarnecka, 2015; Soltész, Szucs, & Szucs, 2010). To accurately judge numerosity on incongruent trials, participants may need to inhibit a response based on surface area or another stimulus feature typically confounded with numerosity, and focus on the numerosity of the stimulus despite the incongruity. Thus under this proposal the relationship between inhibitory processes and math is masked as a correlation between ANS and math. While this is an interesting possibility, both congruent and incongruent trials have been found to correlate with symbolic math in a number of data sets (e.g., Keller & Libertus, 2015; Libertus et al., 2013; Soto-Calvo et al., 2015).

Many researchers are coming to appreciate that it is not possible to perfectly control for non-numerical attributes of a stimulus array (e.g., DeWind, Adams, Platt, & Brannon, 2015; Leibovich & Ansari, 2016). However, the response to this conundrum has differed. Leibovich and Ansari (2016) suggest that the impossibility of controlling for all stimulus attributes at once is problematic for any attempt to measure ANS acuity. They argue that any observed relationship between ANS acuity and symbolic math cannot be dissociated from potential relationships between other magnitudes and symbolic math abilities. In contrast, DeWind and colleagues (2015) suggest that mathematical modeling can disentangle the contributions of different stimulus attributes (see Figure 2). In their model, all features of the stimulus, both numerical and non-numerical (i.e. total surface area, total perimeter, density, etc.), are expressed as linear combinations of the spacing, size, and numerosity of a dot stimulus. Accuracy on a standard numerical comparison task is analyzed as a function of not only the numerical ratio between the dot arrays that are compared, but also as a function of the *size* ratio and the *spacing* ratio. Using this model Starr, DeWind, and Brannon (in prep) found that young children's numerical acuity, but not their size or spacing acuity, was correlated with symbolic math measures. It will be important to apply this modeling technique to data with animals and human infants.

Another problem for assessing the relationship between ANS acuity and symbolic math is the low reliability of ANS measures. Low ANS reliability has in fact led some researchers to challenge the enterprise of correlating ANS acuity with math ability (Clayton, Gilmore, & Inglis, 2015; Smets, Sasanguie, Szücs, & Reynvoet, 2015). When participants were given the standard numerosity comparison task used to measure ANS acuity with two different stimulus sets that control for non-numerical attributes in different ways, performance was not significantly correlated for the two stimulus sets (Clayton et al., 2015; Smets et al., 2015). However, DeWind and Brannon (2016) re-analyzed the data collected by Clayton et al. (2015) with the model described above, and found that ANS acuity was actually correlated for the two stimulus sets, although the correlation coefficients were not very high. These findings collectively call for a deeper investigation of how stimulus variables (e.g., range of numerosities, range of surface area, and density) influence ANS acuity estimates, and how the choice of stimulus controls influences correlations between the ANS and symbolic math. A gold standard for the assessment of the non-numerical features of a dot stimulus will lead to greater consistency in the literature, and may help resolve whether ANS acuity and symbolic math are fundamentally linked.

Another possible source of conflicting findings is the possibility that the relationship may change over development, or with level of symbolic math skill (Castronovo & Göbel, 2012; Halberda et al., 2012). Indeed, in a number of studies the relationship between ANS acuity and symbolic math is much stronger in children than adults (Fazio et al., 2014; Inglis, Attridge,

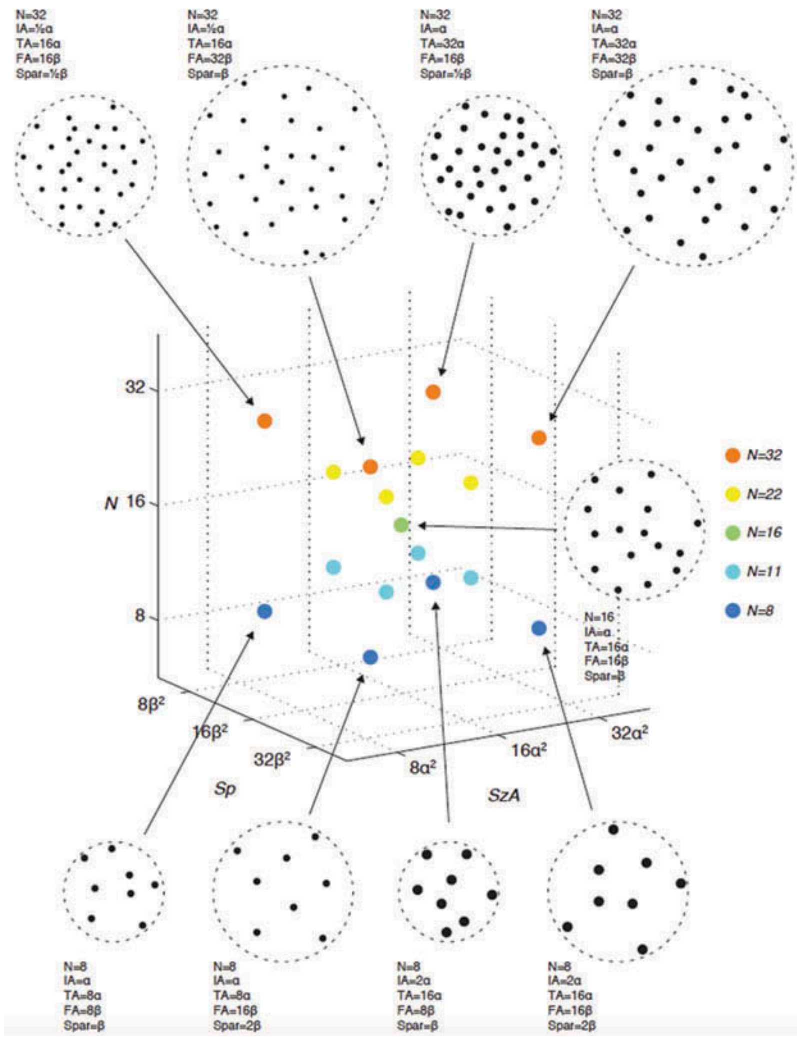

Figure 2. A stimulus space created by plotting the log of size, numerosity, and spacing of dot stimuli along the x, y, and z axes. Any dot stimulus can be represented in this space as a linear combination of the values along these cardinal axes. Figure from (Park, DeWind, Woldorff, & Brannon, 2015).

Batchelor, & Gilmore, 2011). It is also possible that ANS acuity change maps onto periods of rapid symbolic math improvement, such as during late infancy or during the preschool years. For example, Shusterman, Slusser, Halberda, and Odic (2016) found that change in ANS acuity coincided with improved number word knowledge. A greater understanding of the trajectory of ANS acuity change over the course of development could clarify this point. There is also evidence that the relation between ANS acuity and symbolic math may differ as a function of math skill during early schooling. In a longitudinal study, ANS acuity predicted symbolic math ability only for children in the 25th percentile of the distribution of math scores, whereas math language ability predicted math scores of the 50th- 75% percentile of this distribution (Purpura & Logan, 2015). Consistent with that finding, Bonny and Lourenco (2013) tested 3–5 year olds on a dot comparison task and the TEMA-3, a standardized symbolic math test. The authors found that the correlation between performance on these two measures varied with level of symbolic math ability. In children with low math scores there was a stronger correlation between their performance on the dot comparison task and the TEMA-3 than for children who had a high

TEMA-3 score. Interactions between the level of math knowledge a child brings to the experiment and ANS acuity could also be a cause of the some of the differential findings in the literature.

Discrepant findings may also result from the diversity in measurements used to operationally define symbolic math. It is unlikely that all types of symbolic math skills are correlated with ANS acuity. When researchers refer to math, they can be referring to any number of math problem types, and usually these types are presented in combination on a standardized test. On the Test of Early Mathematics −3, a standardized symbolic math test used with young children, ANS acuity is correlated with informal, but not formal mathematics questions (Libertus et al., 2013). Formal math questions involve reading and writing numerals, while informal questions included counting the number of objects on a page, or symbolic number comparison. Using a longitudinal design, Toll, Van Viersen, Kroesbergen, and Van Luit (2015) found that growth in non-symbolic comparison ability was a predictor for math fluency of arithmetic facts in first grade, suggesting ANS ability is foundational for early arithmetic. However, the authors found symbolic comparison skills to be the best predictor of other basic math skills, such as math word problems. These findings highlight the complexity of the interaction between symbolic and non-symbolic math skills during the beginning of formal math training.

To complicate matters further, a correlation between complex math skills and ANS acuity in adults points to the possibility that the ANS continues to support formal math skills as a child progresses through math education. This would indicate that the specific math skills linked to the ANS change over time. In college students ANS acuity is correlated with the mathematical section of the SAT, a college entrance exam that includes many formal math abilities. This result holds even when controlling for performance on the verbal portion of the SAT (Halberda et al., 2012; Libertus et al., 2012). Geary and colleagues (2015) found that ANS acuity is positively correlated with specific algebra skills in 9th grade students. ANS acuity was a significant predictor for accuracy of placing a point in the coordinate plane and for accuracy in evaluating simple algebraic expressions, but not for remembering algebra equations. Similar to the findings with algebra, Lourenco et al. (2012) examined how approximate magnitude representations could be related to specific forms of more advanced math, namely complex calculation and geometry. The authors found that ANS precision was correlated with complex calculation, while performance discriminating the total area of an array of dots was correlated with geometry scores. This result implicates a more complex and longstanding relationship between discrete and continuous magnitude representations and math into adulthood. Often, math skills as a general construct can be too broad of a measure to determine the nature of the relationship between the ANS and symbolic math abilities. By dissecting math skills into different components researchers may be able to ascertain which skills are influenced by ANS acuity.

Mechanisms of the ANS and symbolic math relationship

As the field determines the extent of the relationship between the ANS and symbolic math, we must simultaneously move beyond establishing a correlation to understanding the reason why such a correlation might exist. How is the ability to make fuzzy, inexact numerical judgments related to our ability to calculate the orbital trajectories of planets, or more simply, to learn the meaning of “2”? Does ANS acuity influence only specific aspects of symbolic math performance, such as the understanding of ordinality? Does ANS acuity facilitate the acquisition of early math only as a child, or have input throughout the lifespan? Does ANS acuity influence more complex aspects of symbolic math beyond addition and subtraction?

One prominent mechanistic hypothesis is that sharper ANS acuity facilitates the acquisition of early number word representations in young childhood through understanding of the cardinal principle. The cardinal principle is a major milestone in children’s acquisition of the verbal counting system, and specifies that the number of objects in a set refers to the last number produced when counting the objects in that set. In two recent studies with preschool children the relationship between ANS acuity and early symbolic math achievement was fully mediated by a child's understanding of the cardinal principle (Chu et al., 2015; van Marle et al., 2014). Relatedly, a longitudinal study by Shusterman et al. (2016) found that improved ANS acuity coincided with the understanding of the cardinal principle. Thus, increased ANS acuity may facilitate acquisition of the cardinal principle.

The idea that ANS acuity impacts learning of the cardinal principal is at odds with the proposal that children only come to map approximate number representations onto number words after learning the cardinal principle (Carey, 2009; Le Corre & Carey, 2007). However, there is growing evidence that number words are mapped onto ANS representations *before* children have fully grasped the cardinal principle (Huang, Spelke, & Snedeker, 2010; Odic, Le Corre, & Halberda, 2015; Pinhas, Donohue, Woldorff, & Brannon, 2014; Wagner & Johnson, 2011). Pinhas and colleagues recorded event-related potentials (ERPs) as 3- to 5-year-old children heard the words one, two, three or six and simultaneously looked at pictures of 1, 2, 3, or 6 objects (See Figure 3). On half the trials the auditory number word was incongruent with the number of visual objects, and congruent on the other half. Children with the least number-word knowledge did not show any ERP incongruency effects, whereas those with intermediate and high number-word knowledge showed an enhanced, negative-polarity incongruency response (N_{inc}) over centro-parietal sites from 200–500 ms after the number-word onset. This negativity was followed by an enhanced, positive-polarity incongruency effect (P_{inc}) that emerged bilaterally over parietal sites at about 700 ms. Moreover, children with the most number-word knowledge showed a numerical distance effect in the P_{inc} (larger for greater compared to smaller numerical mismatches). Thus, they showed a larger P_{inc} when the numerical disparity between the auditory number word and the visual object array was greater. Critically, a similar modulation of the P_{inc} from 700–800 ms was found in children with intermediate number-word knowledge. These results suggest that children map number words onto ANS representations before they fully master the verbal count list.

The ERP findings are consistent with behavioral studies that suggest children map number words to ANS magnitude representations before learning the cardinal principle (e.g., Odic et al., 2015). Thus ANS representations may play some role in children's acquisition of the verbal counting system. However, if facilitating number word acquisition were the only function ANS acuity played in symbolic math ability then we might expect the relationship to completely dissipate by late childhood once number words are automatized. While the relationship may get weaker over time, a positive correlation between the ANS and symbolic math skills has been demonstrated in multiple adult samples (e.g., DeWind & Brannon, 2012; Halberda et al., 2012).

Another proposed mechanistic explanation for the relationship between ANS acuity and complex calculation is that the ANS could function as an online form of error detection (Feigenson, Libertus, & Halberda, 2013; Lourenco et al., 2012). As adults or children perform calculations underlying magnitude representations of number could provide an estimate of the correct solution to the problem, allowing the correct rejection of grossly inaccurate results. Adults and children with a more accurate ANS would be able to more adeptly reject incorrect solutions, and therefore would have higher accuracy when solving calculation problems. Similarly, online error detection should be tested as a potential explanation for the mechanism by which approximate arithmetic training enhances symbolic arithmetic in training studies (Park and Brannon, 2013, 2014). This proposal merits further research to establish experimental support.

While there is building evidence that approximate arithmetic training enhances symbolic arithmetic skill, it is less clear whether numerosity comparison training has a similar influence. Park and Brannon (2014) found no evidence for improved symbolic arithmetic after numerosity comparison training with adults, however, Hyde and colleagues (2014) did find evidence that brief exposure to numerosity comparison enhanced arithmetic fluency in young children. If in fact approximate arithmetic training is superior to numerosity comparison for enhancing symbolic arithmetic, a possible mechanism for the transfer is the functional isomorphism between approximate non-symbolic arithmetic and symbolic arithmetic. Young children are capable of solving non-symbolic

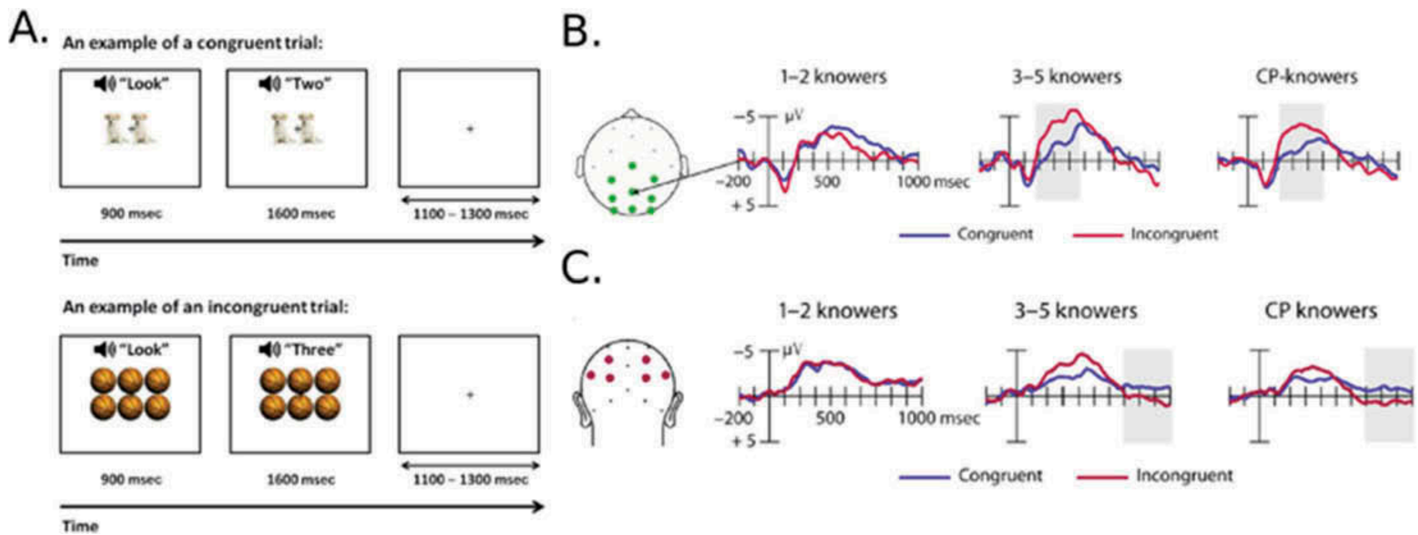

Figure 3. (A) Example stimuli from Pinhas et al. (2014). (B) Differential effects on the N_{inc} by knower level. (C) Differential effects on the P_{inc} by knower level. Figure modified from Pinhas et al. (2014).

approximate addition, subtraction, multiplication, division, and even addend-unknown algebra problems well before they learn how to perform these operations with Arabic numerals (Barth, Baron, Spelke, & Carey, 2009; Barth et al., 2006, 2005; Kibbe & Feigenson, 2015; McCrink & Spelke, 2016; McCrink & Wynn, 2004). When a mathematical operation is performed using only non-symbolic quantities, and without symbols, the meaning of the operation may become more explicit. For example, when solving a non-symbolic approximate arithmetic problem, two arrays are hidden in the same location. Repeated enactment of the operation may thus facilitate a conceptual understanding of addition as the combining of two quantities. Supporting this idea, Pinheiro-Chagas et al. (2014) found that performance on an approximate arithmetic task fully mediated the effects of non-symbolic comparison on a test of symbolic addition, subtraction and multiplication. Thus training approximate arithmetic may allow children, and even adults, to anchor arithmetic and algebra operations conceptually.

There are a host of alternative domain general explanations for both the correlation between ANS acuity and symbolic mathematics and the approximate arithmetic training effect. As Park and Brannon (2013, 2014) discuss, there are notable working memory demands in the approximate arithmetic training task. Although they attempted to control for the possibility that approximate arithmetic benefits symbolic arithmetic by including a working memory control training task and a short-term memory pre- post-test, this possibility remains important given that working memory is known to be an important factor in math performance (e.g., Geary & Brown, 1991). Thus, future work should continue to explore the possibility that approximate arithmetic facilitates symbolic mathematics via domain general mechanisms such as working memory.

Finally, brain-imaging techniques may provide another avenue into understanding the mechanisms that drive the relationship between ANS acuity and symbolic math. Neuroimaging data analysis techniques such as Multi-Voxel Pattern Analysis (MVPA) or Representational Similarity Analysis allow for a nuanced look at how the brain represents number, both symbolically and non-symbolically. If ANS and symbolic number tasks recruit overlapping brain regions, then training on one may result in neural changes that benefit both. Future studies should test this hypothesis by combining cognitive training paradigms with functional brain imaging methods to uncover how the brain changes in response to ANS training (Bugden, DeWind, & Brannon, 2016).

Conclusion and future directions

In this article, we first reviewed properties of the ANS through research that examined the numerical abilities of human infants and non-human primates. We then discussed five lines of evidence that suggest there is a meaningful relation between ANS acuity and symbolic math abilities, and highlighted potential reasons for conflicting findings on the nature of this relationship. Finally, we explored mechanistic explanations for the relation between ANS ability and symbolic math skills. As a field we are only beginning to develop clear testable hypotheses about the mechanisms by which ANS representations could facilitate symbolic numerical operations, but some early ideas have emerged including ANS acuity influencing the acquisition of number words, ANS acuity grounding symbolic arithmetic by facilitating error detection during arithmetic operations, approximate arithmetic working to prime a conceptual understanding of arithmetic, and the possibility that shared neural resources allow training on non-symbolic arithmetic to enhance symbolic arithmetic performance. Many outstanding questions remain.

An important caveat is that even if ANS acuity accounts for unique variance in symbolic math, it is likely that other variables account for equal or greater variance. Parental input (Berkowitz et al., 2015; Casey, Dearing, Dulaney, Heyman, & Springer, 2014; Maloney, Ramirez, Gunderson, Levine, & Beilock, 2015; Ramani, Rowe, Eason, & Leech, 2015) teacher quality (Beilock, Gunderson, Ramirez, & Levine, 2010; Klibanoff, Levine, Huttenlocher, Vasilyeva, & Hedges, 2006), and quantity of math-talk (Gunderson & Levine, 2011; Levine, Suriyakham, Rowe, Huttenlocher, & Gunderson, 2010) have all been shown to influence math readiness in early school years and likely account for a larger percentage of the variance in math performance compared to ANS acuity. Additionally, early symbolic math skills are important predictors of later math success. For example, in a large scale cross sectional study (N = 1391) elementary school students in grades 1–6 were tested on a variety of symbolic and non-symbolic math tasks, and performance on these tasks was used to predict arithmetic skills. The best predictor of arithmetic skills changed by grade level, with numeral ordering increasing in predictive power as children aged, while performance on a number line estimation task predicted more variance in grades one and two. Performance on an ANS dot comparison task did not predict unique arithmetic skill variance at any grade level (Lyons et al., 2014). Thus we do not argue that the ANS is the sole or most important contributor to variability in math, but instead we seek to determine whether ANS acuity accounts for any of the variance in symbolic math ability and to define the mechanisms of this relationship.

Finally, there are important educational implications for this work. If the ANS is indeed foundational for math skills, then finding ways to improve ANS acuity could contribute to a suite of tools to improve math skills. This idea is not new and many early math interventions incorporate number sense training into a larger set of tools (Clements & Sarama, 2011; Kuhn & Holling, 2014). As we learn more about how abstract cognitive skills build upon evolutionarily ancient precursor abilities, we hope that ultimately we can harness these foundational skills to benefit mathematical education (Obersteiner, Reiss, & Ufer, 2013; Räsänen, Salminen, Wilson, Aunio, & Dehaene, 2009; Wilson, Revkin, Cohen, Cohen, & Dehaene, 2006). While efforts to increase ANS acuity alone will be insufficient, this foundational skill could be an important component in building a multifaceted approach to improving math readiness in children at risk for poor math outcomes.

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