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Numerical cognition is resilient to dramatic changes in early sensory experience

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ABSTRACT

Humans and non-human animals can approximate large visual quantities without counting. The approximate number representations underlying this ability are noisy, with the amount of noise proportional to the quantity being represented. Numerate humans also have access to a separate system for representing exact quantities using number symbols and words; it is this second, exact system that supports most of formal mathematics. Although numerical approximation abilities and symbolic number abilities are distinct in representational format and in their phylogenetic and ontogenetic histories, they appear to be linked throughout development–individuals who can more precisely discriminate quantities without counting are better at math. The origins of this relationship are debated. On the one hand, symbolic number abilities may be directly linked to, perhaps even rooted in, numerical approximation abilities. On the other hand, the relationship between the two systems may simply reflect their independent relationships with visual abilities. To test this possibility, we asked whether approximate number and symbolic math abilities are linked in congenitally blind individuals who have never experienced visual sets or used visual strategies to learn math. Congenitally blind and blind-folded sighted participants completed an auditory numerical approximation task, as well as a symbolic arithmetic task and non-math control tasks. We found that the precision of approximate number representations was identical across congenitally blind and sighted groups, suggesting that the development of the Approximate Number System (ANS) does not depend on visual experience. Crucially, the relationship between numerical approximation and symbolic math abilities is preserved in congenitally blind individuals. These data support the idea that the Approximate Number System and symbolic number abilities are intrinsically linked, rather than indirectly linked through visual abilities.

1. Introduction

Humans can think about number in two distinct ways. One way uses number symbols (words or digits) to determine the precise numerosity of sets. We can perform exact computations over these number symbols, as when calculating the quotient of a long division problem, or a number's cubed root. This form of numerical thinking is uniquely human and depends on language, emerging slowly over the course of several years as children learn the meanings of number words, and continuing to be modified through mathematical education (Carey, 2009; Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999; Pica, Lemer, Izard, & Dehaene, 2004; Wynn, 1990). Another form of numerical thinking relies on a non-verbal system that allows observers to represent quantities only approximately, such as when estimating the rough number of apples on a tree or birds in a flock. Unlike the exact, symbolic number system, the Approximate Number System (ANS) represents quantity in an inherently imprecise format. As a result, discrimination between approximate quantities is ratio-dependent and obeys Weber's law—quantities become more discriminable as their ratio increases (Whalen, Gallistel, & Gelman, 1999). The Approximate Number System does not require formal schooling or linguistic experience; newborn infants can match approximate numbers of images to approximate numbers of sounds (Izard, Sann, Spelke, & Streri, 2009), and numerical approximation abilities have been identified in various non-human animals including monkeys, birds, rodents, and fish (Agrillo, Dadda, Serena, & Bisazza, 2008; Viswanathan & Nieder, 2013; for review see Brannon & Merritt, 2011).

Despite the differences between the systems for representing symbolic and approximate number, symbolic number reasoning is thought by many to be rooted in the ANS, such that approximate number representations play a role even during symbolic mathematical computation (e.g., Dehaene, Dupoux, & Mehler, 1990). Consistent with this idea, individual differences in the ability to approximate the number of items in an array without counting predicts performance on

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standardized math tests such as the SAT and the Woodcock-Johnson (Bonny & Lourenco, 2013; Halberda, Mazzocco, & Feigenson, 2008; Libertus, Feigenson, & Halberda, 2011; Libertus, Odic, & Halberda, 2012; Lourenco, Bonny, Fernandez, & Rao, 2012; Wang, Halberda, & Feigenson, 2017; for review see Chen & Li, 2014; Feigenson, Libertus, & Halberda, 2013). Furthermore, individual differences in 6-month-old infants' ability to visually discriminate approximate quantities predict symbolic number knowledge at 3.5 years of age (Starr, Libertus, & Brannon, 2013), and improving numerical approximation through specific forms of practice can temporarily boost symbolic math performance (Hyde, Khanum, & Spelke, 2014; Park & Brannon, 2013; Wang, Odic, Halberda, & Feigenson, 2016).

However, the nature of the relationship between the exact and approximate number systems has been a matter of recent debate. One idea is that the link between the ANS and exact symbolic number is specific and reflects shared abstract number content (albeit in different representational formats). An alternative hypothesis is that the apparent relationship between the two systems emerges because each of the systems is independently linked with visual processing (Tibber et al., 2013; Zhou, Wei, Zhang, Cui, & Chen, 2015). For example, individuals who are better at math are also better at sustaining attention in an object tracking task (Anobile, Stievano, & Burr, 2013), have better visual working memory (Bull, Espy, Wiebe, Sheffield, & Nelson, 2011; De Smedt et al., 2009; Le Fevre et al., 2010), and are better at visuo-spatial mental rotation (Reuhkala, 2001), visual movement perception (Sigmundsson, Anholt, & Talcott, 2010), and basic visual perception tasks including discriminating the orientation of lines, comparing objects' shapes, and comparing visual area across arrays (Lourenco et al., 2012; Tibber et al., 2013; Zhou et al., 2015). These findings suggest a link between some aspects of visual perception and symbolic math abilities.

Numerical approximation, too, is linked to various forms of visual perception. People who are more precise at approximating numbers of objects are sometimes reported to be better at estimating the cumulative area of objects in an array (Lourenco et al., 2012; but see Odic, Libertus, Feigenson, & Halberda, 2013). In addition, individuals perform better in numerical approximation tasks when the more numerous array is greater in cumulative area or is visually denser, showing that visual dimensions of a stimulus can affect numerosity perception (Fuhs & McNeil, 2013; Gebuis & Reynvoet, 2012a, 2012b; Gilmore, Attridge, & Inglis, 2011; Halberda & Feigenson, 2008; Rousselle, Palmers, & Noël, 2004; Soltész, Szucs, & Szucs, 2010). Moreover, some researchers have suggested that visual numerical approximation is itself a form of visual perception (Dakin, Tibber, Greenwood, Kingdom, & Morgan, 2011; Morgan, Raphael, Tibber, & Dakin, 2014), pointing to findings that, like other primary visual features including color and contrast, numerosity is susceptible to adaptation. For example, exposure to a large quantity of dots causes a subsequent quantity to be perceived as less numerous; this suggests that numerosity is a visual feature that is extracted early in processing (Burr & Ross, 2008; Ross & Burr, 2010).

Given these findings linking visual perception to both symbolic math and numerical approximation, is there a meaningful relationship between the Approximate Number System and math abilities? Alternatively, is the relationship between these systems a byproduct of individual differences in visual processing abilities that independently predict both numerical approximation and math performance? Evidence from congenitally blind individuals offers a unique opportunity to answer this question. Unlike sighted individuals, congenitally blind individuals have never experienced approximate numerical information through vision—therefore, vision could not "bootstrap" the relationship between the ANS and symbolic number processing during development.

Congenital blindness also offers a window into the role of vision in the development of the ANS itself. For sighted humans, numerosity is a salient visual feature of visual arrays that is processed automatically (Burr & Ross, 2008; Cohen Kadosh, Bien, & Sack, 2012; Ross & Burr, 2010). Indeed, computational modeling shows that hierarchical generative models spontaneously construct representations of numerosity following accumulated experience with simple visual sets (Stoianov & Zorzi, 2012). The neural instantiation of numerical processing is also consistent with the idea that vision, number, and spatial cognition are intimately linked: neural representations of number are localized along the dorsal visual stream in the intraparietal sulcus (Dehaene & Changeux, 1993; Piazza & Eger, 2016; Piazza, Pinel, Le Bihan, & Dehaene, 2007; Roggeman, Santens, Fias, & Verguts, 2011; Uddin et al., 2010), raising the possibility that vision plays a foundational role in the initial development of the ANS.

Furthermore, in some respects, numerical sets are experienced differently through vision compared to audition and touch. Whereas vision permits hundreds of items to be estimated simultaneously within just seconds, humans are limited in the number of tactile and auditory items they can simultaneously individuate in space (Anobile, Cicchini, & Burr, 2014; Dakin et al., 2011). For example, participants can neither accurately enumerate more than 5 simultaneous tactile stimuli on the body nor have been shown to individuate more than 4 simultaneous sounds (Ferrand, Riggs, & Castronovo, 2010; McAdams, 1989; Micheyl & Oxenham, 2010) (although large numbers of tactile and auditory stimuli can be perceived sequentially).

As such, the absence of visual experience with quantities could modify the ANS. Even if vision is not strictly necessary for the formation of an ANS, it could be necessary for optimal ANS tuning. In sighted populations, ANS precision increases markedly over development. For example, whereas sighted infants require a 1:2 or 2:3 ratio between arrays in order to successfully discriminate numerosities (Izard et al., 2009; Lipton & Spelke, 2003; Xu & Spelke, 2000), children and adults can discriminate much finer ratios (Halberda & Feigenson, 2008; Halberda, Ly, Wilmer, Naiman, & Germine, 2012). Improvement is observed even before educational experience and before the emergence of linguistic competence (Halberda & Feigenson, 2008; Libertus & Brannon, 2009, 2010; Lipton & Spelke, 2003; Odic et al., 2013). These developmental increases in ANS precision might be partly driven by visual experience. If so, we would expect blind individuals to perform worse than sighted individuals on numerical estimation tasks.

Alternatively, given that auditory and tactile estimation primarily occur sequentially, whereas visual estimation often occurs simultaneously, blind individuals might substantially outperform sighted individuals on sequential ANS tasks with which they are putatively more practiced. Blind individuals have previously been shown to outperform sighted individuals on some auditory perception tasks (e.g., peripheral sound localization) (Fieger, Röder, Teder-Sälejärvi, Hillyard, & Neville, 2006; Lessard, Paré, Lepore, & Lassonde, 1998; Röder et al., 1999). A parallel finding could be obtained for auditory numerical approximation if the ANS is not, in fact, a unitary cognitive system, but rather comprised of multiple modality-specific or format-specific (i.e., sequential vs. simultaneous) systems. In fact, there is some evidence that sequential and parallel ANS processing depend on partially non-overlapping neural substrates (Dormal, Andres, Dormal, & Pesenti, 2010; Nieder, Diester, & Tudusciuc, 2006). If sequential and simultaneous ANS systems are independent, we might expect blind individuals to exhibit specific improvements in sequential auditory number estimation.

A final possibility is that the ANS is a modality independent, abstract system that does not require input from any one particular modality for proper function. If so, we would expect blind and sighted individuals to perform similarly on sequential auditory ANS tasks.

Two previous studies have compared numerical approximation across blind and sighted participants (Castronovo & Delvenne, 2013; Castronovo & Seron, 2007). Contrary to the proposal that vision is required for ANS development, these studies found that blind individuals actually outperformed the sighted on sequential estimation tasks that involved producing a particular number of actions without counting (e.g., footsteps, key presses) or estimating the number of tones played in

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