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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 a sequence (Castronovo & Delvenne, 2013; Castronovo & Seron, 2007). One possible concern with these findings, however, is that participants in these studies may not have relied exclusively on the ANS to perform the task. Although participants were instructed not to count, their near-perfect accuracy with very large target quantities suggests that they likely engaged resources beyond the ANS. For instance, blind individuals potentially were better able to rapidly verbally count numbers of items in these tasks relative to sighted individuals. Indeed, blind individuals outperform sighted on some verbal tasks (e.g., verbal working memory), suggesting the possibility that their performance may not reflect ANS precision but rather effective alternative strategies (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Raz, Striem, Pundak, Orlov, & Zohary, 2007).

The current study therefore had two aims. The first was to ask whether congenitally blind participants show similar ANS precision to sighted participants when counting is rigorously prevented. The second aim was to ask whether individual differences in ANS precision correlate with math performance among blind individuals who have never experienced number visually. To this end, a group of congenitally blind participants and a group of sighted participants completed an auditory numerical approximation task and a timed symbolic math task using spoken numerals. In the ANS task, participants judged which of two tone-sequences was more numerous. In the symbolic math task, participants completed as many subtraction problems as they could in four minutes and as many division problems as they could in another four minutes. We then correlated ANS performance and symbolic math performance across participants.

To determine the specificity of any observed relationship between ANS precision and symbolic math performance, we also tested participants on a series of control tasks. We administered a standardized test of math concepts that tests participants' knowledge of math facts. Previous work suggests that ANS precision does not relate to rote memory for mathematical information (for review see Chen & Li, 2014). We therefore predicted that knowledge of math facts would not correlate with ANS precision (Dehaene, Piazza, Pinel, & Cohen, 2003). We also tested participants' working memory, reading, and verbal knowledge; this allowed us to partial out the effect of these skills from the relationship between ANS precision and symbolic math performance.

2. Participants

Twenty-four congenitally blind and fifteen sighted participants contributed data. Sighted and blind groups were matched on average age and education (see Table 1). All blind participants had, at most, minimal light perception and reported never having seen shapes, color or motion. One additional blind participant was excluded after testing because further screening revealed non-congenital blindness. Three additional participants were tested but excluded from the final sample due to performance on the ANS task. One sighted participant was excluded because their performance on the ANS task was two standard deviations away from the sighted mean and was unusually poor relative to published samples of ANS performance in sighted participants (Halberda et al., 2012). Two blind participants were excluded because their ANS performance was poorly fit by the psychophysical model ($R^2 \leq 0$; two blind participants).

Working memory data from one blind participant were not included because the participant confused the sounds of letter stimuli in the letter span task. One blind participant did not complete the analogies subtest of the oral vocabulary task. This participant's vocabulary score consisted of the mean of their synonym and antonym scores.

Table 1
Participant demographic information.

Participant	Age	Education	Cause of vision loss
CB_01	23	Some College	LCA
CB_02	48	JD	LCA
CB_03	44	BA	ONH
CB_04	34	BA	ONH
CB_05	33	Some College	ROP
CB_06	29	MA	ROP
CB_07	43	Some College	ONH
CB_08	26	Some College	LON
CB_09	57	MA	CG
CB_10	26	BA	LCA
CB_11	30	Middle School	Unknown
CB_12	28	BA	AN
CB_13	43	High School	RB
CB_14	29	Some College	ONH
CB_15	32	BA	PCA
CB_16	39	BA	AN
CB_17	44	MA	SOD
CB_18	27	Some College	Aniridia
CB_19	42	BA	LCA
CB_20	27	PhD	MO
CB_21	44	JD	Unknown
CB_22	33	BA	ROP
CB_23	40	PhD	ROP
CB_24	25	MA	LCA
Group average	Age	Years of education	
Congenitally Blind	35	16.94	–
Sighted	37	17.60	–

AN = Anopthalmia; CG = Congenital Glaucoma; LCA = Liebers Congenital Amaurosis; MO = micro-opthalmia; ONH = Optic Nerve Hypoplasia; RB = Retinal Blastoma; ROP = Retinopathy of Prematurity; SOD = Septo-optic Dysphasia; BA = Bachelor of Arts; JD = Juris Doctor; MA = Master of Arts; PhD = Doctor of Philosophy.

3. Methods

3.1. Auditory approximate number discrimination task

Blind and blind-folded sighted participants heard pairs of auditory tone sequences over headphones and indicated which sequence was more numerous by pressing one of two buttons on a response pad (blind) or computer keyboard (sighted controls). The second test sequence was smaller than the first on half of the trials (small test) and larger on the other half (large test). The number of tones in the first and second sequence differed by one of 5 ratios: 1.08, 1.15, 1.2, 1.44 or 2 (e.g., 20 vs. 40 is a ratio of 2, where ratio is the larger numerosity divided by smaller numerosity). Each of the 5 ratios was presented 16 times over the course of the experiment and was instantiated as 8 unique numerosity pairs, each of which occurred twice (all pairs shown in Table 2).

To prevent participants from relying on duration to make their responses, we controlled the total duration of sound presented within a given pair of tone sequences (i.e., the sums of individual tone durations). This is analogous to visual experiments that control the total area of presented dots. On half the trials the total duration of sound was congruent with respect to the ratio between the two numerosities (i.e., the more numerous sequence was longer) and on half the trials it was incongruent (i.e., the more numerous sequence was shorter). Thus relying on total sound duration to judge number would systematically yield the incorrect answer on half the trials.

Frequency was also not a reliable cue to numerosity, as inter-tone interval was randomly selected from geometric distribution (mean

Table 2
Numerosity pairs in the auditory approximate number discrimination task.

Ratio	Sample	Small test	Large test
1.08	14	13	15
	16	15	17
	18	17	18
	20	19	22
1.15	14	12	16
	16	14	18
	18	16	20
	20	18	23
1.2	14	11	17
	16	13	19
	18	15	22
	20	17	24
1.44	14	9	20
	16	11	23
	18	13	26
	20	14	29
2	14	7	28
	16	8	32
	18	9	36
	20	10	40

ISI = 158.83 ms, min = 100 ms, max = 806 ms). Thus, participants could not use frequency (ISI) as a reliable cue to numerosity because they were not correlated. Note that controlling for total sound duration and ISI duration precluded us from also controlling for total sequence duration (i.e., total sound duration + total ISI duration). However, subsequent analyses showed that participants were reliably above chance at judging numerosity, even when numerosity was incongruent with total sequence duration (see Results).

While the average duration of tones and ISIs was controlled, the durations of individual tones and ISIs were jittered to preclude participants from counting. Both individual tone duration and the interval between tones varied randomly within and across trials. This procedure has been shown to effectively preclude participants from counting (see Cordes, Gallistel, Gelman, & Latham, 2007).

To further prevent counting, on each trial, participants verbally repeated a different two-letter sequence (e.g., "D-F") during the presentation of the stimulus sequences. Previous work has found that similar verbal loads were successful in preventing participants from counting (Cordes, Gelman, Gallistel, & Whalen, 2001).

To ensure that the two tone sequences were separately perceived, the first tone sequence always consisted of 400 Hz tones to the left ear and the second sequence always consisted of 500 Hz to the right ear. Each individual tone ramped up in volume, reached a plateau and then ramped down. Immediately after their response on every trial, participants heard auditory feedback to indicate whether their response was correct ("ding" sound) or incorrect (buzzer sound).

Participants pressed the space bar on a keyboard to begin each trial. Each trial began with a unique pair of spoken letters for participants to begin repeating (0.87–1.55 sec), followed by the first tone sequence (see above), a delay interval (2 sec), the second tone sequence (see above), a response period (3 sec), and a feedback tone (0.41–0.5 sec). Participants then waited the remainder of the 3-second response period before starting the next trial.

Trials on which a participant's response time was more than two standard deviations away from their own mean (across all ratios) were dropped from all analyses (blind: M = 3.46 trials dropped, SD = 1.47; sighted: M = 4 trials dropped; SD = 2).

3.2. Psychophysical modeling of performance on auditory ANS task

We assessed individual differences in the precision of participants' approximate number representations in terms of Weber fractions. The Weber fraction (w) is a number greater than 0 that indexes the amount of noise in ANS representations for a given individual. Each participant's Weber fraction was determined using a least squares method to fit their accuracy (percent correct across trials) for each ratio with a curve generated by the model shown below (Halberda et al., 2008; Libertus et al., 2012; Odic et al., 2013; Pica et al., 2004).

$$\frac{1}{2} erfc\left(\frac{n_1 - n_2}{\sqrt{2w}\sqrt{n_1^2 + n_2^2}}\right) \times 100$$

The model assumes that for a given trial, the numerosity of each of two stimulus arrays is represented by a Gaussian distribution (with means n_1 and n_2), and that comparing the two quantities involves a Gaussian subtraction of these two distributions in order to determine the magnitude of their difference. The probability of responding correctly following this subtraction is predicted by the complementary error function.

The Weber fraction, w, is the only free parameter in this model. The Weber fraction quantifies the variance in the Gaussian representation of each numerosity (the standard deviation for a distribution representing the numerosity n will be $w * n$). Thus, a larger Weber fraction corresponds to larger variance in the numerical representation. Larger Weber fractions are worse because wider distributions exhibit more overlap, which makes numerosities less discriminable.

Goodness of fit of the Weber function was determined using the following formula: 1.0-($SS_{Regression}/SS_{Mean}$), where $SS_{Regression}$ is sum of squared distances between each data point and its predicted value based on the psychophysical model, and SS_{Mean} is the sum of squared distances between each data point and the mean of the data points. This formula produces a positive value (with 1 indicating a perfect fit) if the Weber function predicted a participant's accuracy better than a horizontal line through their mean accuracies. Negative values indicate that that the Weber function fit the participant's data worse than a horizontal line through the participant's mean accuracies.

3.3. Auditory symbolic math task

Previous research suggests that ANS precision is linked with only a subset of symbolic math abilities, suggesting that the link between the ANS and math reflects reliance of particular mathematical computations on magnitude representations, rather than reflecting the contribution of meta-cognitive or emotional factors, such as self confidence in math, or math anxiety. We tested participants on timed subtraction and division tasks and examined the correlation between ANS precision and performance on these two arithmetic operations separately. We chose to test participants on subtraction and division because they require active quantity manipulation more than addition and multiplication, which can often be solved by rote memorization (Dehaene & Cohen, 1997; Dehaene et al., 2003; Lee & Kang, 2002). Subtraction performance (tested independently and intermixed with addition problems) has been shown to correlate with ANS precision (Price, Palmer, Battista, & Ansari, 2012; Wei et al., 2012). Subtraction also activates the IPS more than multiplication (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Lee, 2000). However, to our knowledge, division has not previously been shown to correlate with ANS precision (Chen & Li, 2014; Gebuis & van der Smagt, 2011; Lindskog, Winman, Juslin, & Poom, 2013).

Participants mentally solved as many subtraction or division problems as possible within two four-minute blocks. Participants heard the math problems over headphones, spoke their answers aloud, and pressed a button to advance to the next problem. Participants could use as much time as they needed for any problem (within the allotted four minutes), and could skip problems but could not return to skipped problems. There were 29 subtraction problems and 32 division problems, taken from the Kit of Factor-Referenced Cognitive Test (Ekstrom, French, Harman, & Dermen, 1976). Minuends in the subtraction task

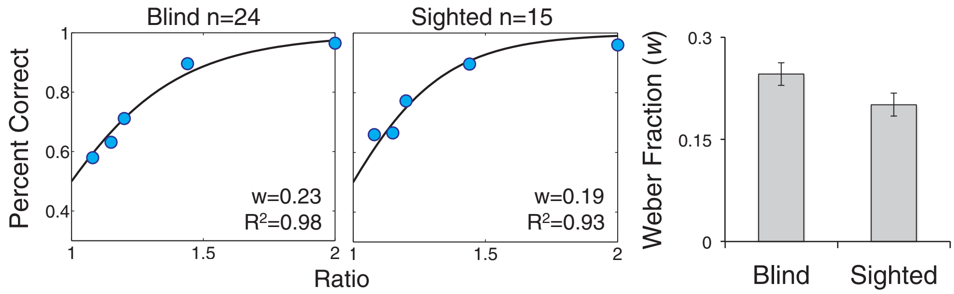

Fig. 1. Two left graphs: Percent of correct trials across participants for each ratio; best fitting curve for group accuracy from psychophysical model shown with black line and group Weber fraction shown on bottom right of each graph. Right graph: Average Weber fraction across participants in blind and sighted groups (right bar). Error bars represent standard error of the mean.

ranged from 18 to 98, subtrahends ranged from 11 to 65, and answers ranged from 4 to 70. Divisors in the division task ranged from 2 to 9, dividends ranged from 42 to 792, and answers ranged from 7 to 99. Participants did not receive any feedback on this task.

3.4. Working memory task

Forward and backward letter-span tasks were adapted from the Third Edition of the Wechsler Adult Intelligence Scale (WAIS-III) digit-span task. Digits 1–9 were assigned letters A-I. Participants heard strings of letters over headphones. In the forward span task, they repeated the letters back in the same order as they were presented, and in the backward span task they repeated the letters in the reverse order in which they were presented. Letter strings began with 2 letters and increased by one letter every two trials, with a maximum of 10 letters for the forward span and 8 letters for the backward span task. The task stopped when participants recited two letter strings of the same length incorrectly or when participants reached the maximum number of trials (max 16 and 14 trials for forward and backward letter span, respectively). Letters within a string were separated by a one second delay. All participants completed the forward and then the backward span task. Participants' forward and backward letter span scores were averaged to obtain a working memory score for each participant.

3.5. Woodcock-Johnson III quantitative concepts, reading, and vocabulary knowledge tasks

Portions of the Third Edition of the Woodcock Johnson III Standardized Test (WJ-III) were administered to blind participants in Grade II Braille (using the WJ-III Braille Adaptation) and to sighted participants in visual print (Jaffe, 2009; Jaffe, Henderson, Evans, McClurg, & Etter, 2009).

To measure participants' general math knowledge (e.g., how many square feet are in a square yard), we administered the last 26 questions of the WJ-III Quantitative Concepts test. The experimenter asked the participants questions verbally and participants answered verbally. Some questions required tactile (for blind) or visual (for sighted) graphics.

To measure participants' reading ability, we administered the WJ-III Letter/Word Identification and Word Attack tests in Braille for blind participants and in print for sighted participants. On the Letter/Word Identification test, participants read 60 words aloud (e.g., "scientist"; "bounties") and on the Word-Attack test, participants read 33 non-words aloud (e.g., "lindify"; "knoink"). Scores from these two reading sections were averaged to obtain a reading score for each participant.

To measure participants' vocabulary knowledge, we administered the WJ-III Oral Vocabulary test which consisted of Synonym, Antonym and Analogies subtests. On the Synonym and Antonym tests, participants verbally provided synonyms and antonyms for 24 different words (12 synonyms, 12 antonyms; e.g., provide synonyms for "assist" and "obvious"; provide antonyms for "attract" and "demure"). On the analogies test, participants completed 12 analogies (e.g., run is to fast as walk is to __). Scores across the three subtests were averaged to obtain one vocabulary score per participant.

Items in each section of the WJ-III were presented in increasing difficulty. On all subtests, participants were allowed to take as much time as needed and did not receive any feedback. Each section was scored by dividing the number of items participants completed correctly by the total number of items tested from that section.

4. Results

4.1. Precision on auditory approximate number task

We first asked whether there was a difference between the numerical approximation abilities of the congenitally blind versus sighted participants. In overall accuracy, congenitally blind and sighted participants performed similarly: the blind participants averaged 75.41% correct (SD = 6.76%) and the sighted participants averaged 79.08% correct (SD = 4.80%; unpaired *t*-test: $t(37) = -1.83$, $p = 0.08$). Even on trials on which numerosity was incongruent with total sequence duration, both blind and sighted participants successfully identified the more numerous sequence (blind accuracy = 63.99%, SD = 17.85; sighted accuracy = 62.32%, SD = 11.55). Furthermore, performance was ratio-dependent on these total duration incongruent trials (blind $w = 0.33$, $R^2 = 0.83$; sighted $w = 0.52$, $R^2 = 0.80$).

Both blind and sighted participants' data was well fit by the psychophysical model. On average, the model accounted for 71.19% (SD = 18.15, Min = 37.35, Max = 95.45) of the variation in the accuracy across ratios of blind participants, and 66.37% (SD = 24.79, Min = 11.63, Max = 96.61) of the variation in the accuracy across ratios of the sighted participants (unpaired *t*-test: $t(37) = 0.7$, $p = 0.49$).

The Weber fractions, or *w*'s, of the blind participants averaged 0.25 (SD = 0.08) and of the sighted participants averaged 0.20 (SD = 0.07; unpaired *t*-test: $t(37) = 1.81$, $p = 0.08$) (Figs. 1 and 2). Note that the marginal difference in ANS performance between blind and sighted groups disappeared when ROP participants were excluded from analysis (see below).

4.2. Relationship of ANS and symbolic math performance

Our next question concerned symbolic math performance and its link with ANS precision. We found similar performance across blind and sighted participants on the symbolic subtraction and division tasks. On the subtraction task, blind participants correctly answered 67.39% (SD = 25.96) of problems and sighted participants correctly answered 59.77% (SD = 24.72) of problems (unpaired *t*-test: $t(37) = 0.91$, $p = 0.37$; Table 3). On the division task, blind participants correctly answered 30.21% (SD = 15.63) of problems and sighted participants correctly answered 33.33% (SD = 15.96) of problems (unpaired *t*-test: $t(37) = -0.60$, $p = 0.55$; Table 3).

A key question was whether ANS precision on a numerosity discrimination task is linked to symbolic math ability in both sighted

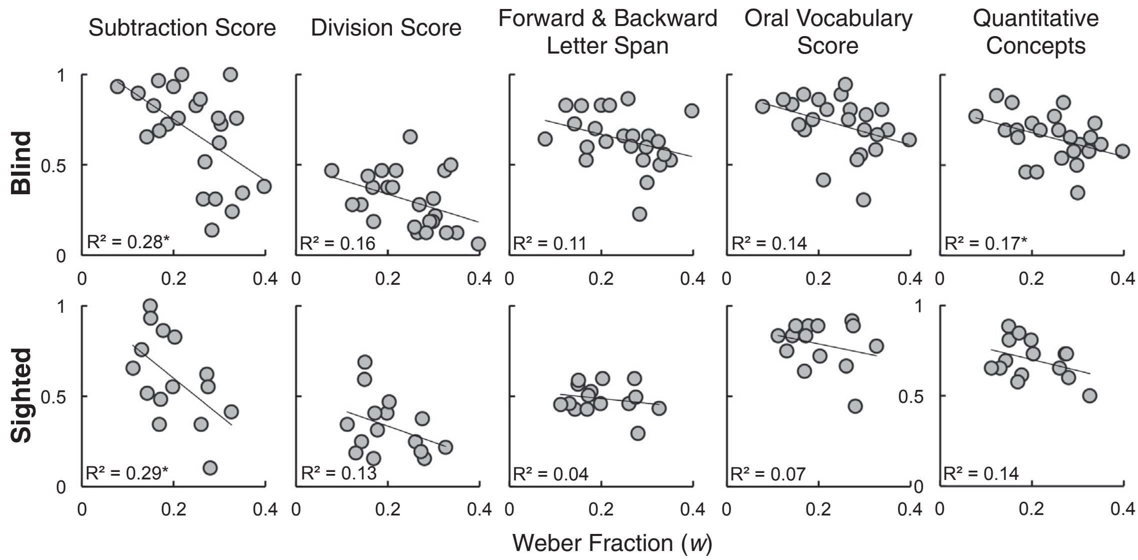

Fig. 2. Correlation between individual subjects' Weber fractions and scores for subtraction, division, working memory, oral vocabulary, and quantitative concepts tasks (from left to right). Significant correlations marked with asterisk ($p < 0.05$).

participants (as has been observed in many previous studies) and congenitally blind participants. We found that ANS precision (Weber fraction, *w*) was negatively correlated with subtraction performance in both the sighted group ($R^2 = 0.29$, $p = 0.04$) and the blind group ($R^2 = 0.28$, $p < 0.01$; Fig. 2). This correlation did not differ across groups (Fisher z transform test for difference among independent sample correlation coefficients, $z = 0.06$, $p = 0.95$; Fisher, 1921). The correlation between ANS precision and division performance was marginally significant in the blind group ($R^2 = 0.16$, $p = 0.051$) but was not present in the sighted group ($R^2 = 0.14$, $p = 0.18$) (Fig. 2).

To characterize the specificity of the relationship between ANS precision and symbolic math performance, we examined the correlation between ANS precision and performance on the non-math WJ-III tests. Blind and sighted participants performed similarly on control WJ-III subtests, as summarized in Table 3. We found that ANS precision was not significantly correlated with the ability to read words and nonwords (mean of WJ-III letter/word identification and word attack scores; blind: $R^2 = 0.09$, $p = 0.16$; sighted: $R^2 = 0.05$, $p = 0.41$). ANS performance and vocabulary knowledge were marginally correlated in the blind group (mean of WJ-III synonym, antonym and analogy scores; $R^2 = 0.14$, $p = 0.07$) but were not correlated in the sighted group ($R^2 = 0.07$, $p = 0.34$). Similarly, ANS precision was correlated with knowledge of math concepts in the blind group ($R^2 = 0.17$, $p = 0.05$) but not in the sighted group ($R^2 = 0.14$, $p = 0.17$).

Finally, we asked whether the relationship between ANS precision and math performance was mediated by general working memory abilities. Consistent with previous studies, blind participants performed significantly better then sighted participants on the working memory task (blind: 63.99%, SD = 15.50; sighted: 48.66%, SD = 8.17; unpaired *t*-test: $t(36) = 3.51$, $p = 0.001$) (Amedi et al., 2003; Crollen, Mahe, Collignon, & Seron, 2011; Dormal, Crollen, Baumans, Lepore, & Collignon, 2016; Occelli, Lacey, Stephens, Sathian, &, Rehabilitation, 2016; Raz et al., 2007). Working memory was correlated with subtraction performance in both the blind ($R^2 = 0.34$, $p = 0.003$) and sighted groups ($R^2 = 0.66$, $p < 0.001$), to the same extent (Fisher r to z transformation, $z = -1.31$, $p = 0.19$; Fisher, 1921). The correlation between ANS precision and subtraction performance when controlling for working memory held in the both sighted group (sighted: $R^2 = 0.43$, $p = 0.01$) and was marginally significant in the blind group (blind: $R^2 = 0.14$, $p = 0.09$).

Blind participants with retinopathy of prematurity (ROP, n = 5) performed slightly worse than non-ROP blind participants despite comparable age and education (ROP mean accuracy on ANS task = 69.70%, SD = 4.56, mean w = 0.31, SD = 0.05; non-ROP mean accuracy on ANS task = 76.91%, SD = 6.50; mean w = 0.23, SD = 0.08). After excluding blind participants with ROP, ANS precision was similar across blind and sighted (unpaired t-tests; accuracy: $t(32) = -1.08$, $p = 0.29$; Weber fraction: $t(32) = 1.09$, $p = 0.28$). Among blind participants without ROP, ANS precision (*w*) was still correlated with subtraction and division performance (subtraction:

Table 3
Summary of results.

Task	Blind			Sighted		
	Mean (SD)	Min	Max	Mean (SD)	Min	Max
ANS Task (percent correct)	75.41 (6.76)	63.45	92	79.08 (4.8)	71.49	84.82
ANS Task (Weber fraction)	0.25 (0.08)	0.08	0.4	0.20 (0.07)	0.11	0.33
Subtraction Task	67.39 (25.96)	13.79	100	59.77 (24.72)	10.35	100
Division Task	30.21 (15.63)	6.25	65.63	33.33 (15.96)	15.63	68.75
Forward Letter Span Task	68.97 (15.55)	31.25	93.75	55.42 (9.41)	37.50	75.00
Backward Letter Span Task	59.01 (16.99)	14.29	85.71	41.90 (11.09)	21.43	57.14
Reading Words	89.10 (13.98)	36.67	100	93.11 (6.48)	75.00	100
Reading Non-words	83.15 (19.23)	20.00	100	88.28 (11.78)	54.55	96.97
Math Concepts	64.90 (13.14)	34.62	88.46	69.90 (10.70)	50.00	88.46
Verbal Task: Synonyms	81.60 (16.30)	50.00	100	83.33 (13.73)	50.00	100
Verbal Task: Antonyms	74.65 (17.11)	25.00	100	77.78 (13.61)	41.67	91.67
Verbal Task: Analogies	59.29 (21.48)	16.67	91.67	75.56 (17.10)	41.67	100

$R^2 = 0.38$, $p = 0.005$; division: $R^2 = 0.29$, $p = 0.02$), even when controlling for working memory (subtraction: $R^2 = 0.28$, $p = 0.03$; division: $R^2 = 0.21$, $p = 0.07$). In this group, ANS precision (w) remained uncorrelated with reading ability ($R^2 = 0.06$, $p = 0.31$) and with vocabulary knowledge ($R^2 = 0.16$, $p = 0.09$) and remained correlated with knowledge of math concepts ($R^2 = 0.23$, $p = 0.04$).

5. Discussion

5.1. Preserved ANS precision in congenital blindness

If visual experience with sets of objects is necessary for the normal development of precision, then congenitally blind individuals should exhibit impaired performance on a numerical approximation task. Contrary to this hypothesis, congenitally blind and sighted individuals demonstrated equal precision when estimating the numerosity of auditory tone sequences. For both groups, performance was well described by the same psychophysical function. These results suggest that vision is not required for typical development.

We also found no evidence for the idea that blind individuals show superior ANS precision on auditory sequential estimation tasks. Thus, blindness does not render the ANS more “auditory” or “sequential,” consistent with the idea that the ANS is a modality-independent system. By contrast, two previous studies reported that blind individuals are more precise on numerical estimation tasks that involve producing sequences of a particular numerical quantity (e.g., produce 35 footsteps or 20 key presses) (Castronovo & Delvenne, 2013; Castronovo & Seron, 2007). There are a number of reasons why our results might differ from these prior investigations. First, our numerical approximation task did not require overt production. Participants listened to two sequences of tones and judged which was more numerous. Unlike production tasks, which are inherently subject-paced, the tones in our current experiment occurred rapidly and were spaced at variable intervals. Furthermore, we required participants to perform a concurrent verbal shadowing task that has previously been shown to prevent counting (Cordes et al., 2001). We adopted these measures because pilot testing revealed that blind participants were better able to count the auditory stimuli than sighted participants, producing nearly perfect performance, independent of numerical ratio. Thus, it is possible that some of the previously reported advantages in numerical estimation among blind individuals result not from changes in ANS precision itself but from differences between blind and sighted groups' ability to rapidly count.

It is worth nothing that one prior study reported slightly better performance among blind individuals in a non-production task, specifically when estimating the numerosity of sequences containing more than 40 auditory tones (Castronovo & Seron, 2007). In the current study we did not test any numerosities above 40. Therefore, it remains possible that blind individuals have increased precision for estimating the numerosity of larger auditory sequences. It is unclear why changes to ANS precision would affect performance with large but not small numbers. One possibility is that performance on larger number sequences is more dependent on working memory abilities, which are enhanced in individuals who are blind (Amedi et al., 2003; Dormal et al., 2016; Occelli et al., 2016; Raz et al., 2007). The available data are thus most consistent with the hypothesis that the ANS is neither specialized for a particular modality nor for a particular input format (sequential versus simultaneous).

If not vision, what kinds of experiences are relevant to ANS development? It may be that experiences estimating numerosities in any modality or format are equivalently suited to drive improvements in ANS precision. According to some theories, numerical processing shares a common mechanism with other magnitude systems (e.g., estimation of temporal duration (Allman, Pelphrey, & Meck, 2012; Bueti & Walsh, 2009; Meck & Church, 1983; Walsh, 2003). If so, numerical estimation could plausibly even be improved by judging these other magnitudes (Allman et al., 2012; Bueti & Walsh, 2009; Walsh, 2003; but see Odic et al., 2013 for an alternative view). Furthermore, some evidence suggests that educational and cultural experiences can hone the precision of approximate number representations. Members of the indigenous Amazonian Munduruku group have an extremely limited numerical lexicon, little or no mathematical experience, and relatively poor ANS precision. However, members of this group who completed at least three years of education and therefore learned number words and simple arithmetic had significantly better ANS precision than those with less exposure to math, even when controlling for age (Piazza, Pica, Izard, Spelke, & Dehaene, 2013). This suggests that math education—whether primarily visual or auditory in nature – may sharpen ANS representations (Piazza et al., 2013). Alternatively, the majority of age-related improvement in the precision of the ANS could be intrinsically driven and result from maturation rather than learning. The evidence we present here is most consistent with the hypotheses that ANS precision changes regardless of experience, or that experience tunes the ANS, but equally so regardless of the sensory modality and format in which it occurs.

5.2. Preserved relationship between ANS and symbolic number abilities in congenital blindness

Our second key finding is that individual differences in performance on a numerical approximation task predict performance on a symbolic math task in both sighted and congenitally blind individuals. Thus the relationship between the ANS and symbolic numerical reasoning is preserved even in those who have never experienced number visually, and who arguably are less likely to experience number spatially because of the unique capacity of the visual system to perceive large numbers of objects in parallel (Anobile et al., 2014; Dakin et al., 2011). These results suggest that the link between ANS precision and symbolic math abilities is not mediated by visual abilities. Note however that our results do not rule out the possibility that there is an independent relationship between spatial and mathematical abilities. Whether spatial abilities among blind individuals independently predict mathematical performance is an important question to explore in future research. Furthermore, since the current study is, to our knowledge, the first to look at this relationship between ANS precision and mathematics in blindness, it will be important to replicate our findings in future work.

The precise nature of the relationship between the ANS and math remains an open question. According to one hypothesis, children with better ANS precision may quickly learn to map number words to discrete numerical quantities, whereas those with noisier ANS representations may have more trouble forming this mapping (Libertus et al., 2011). Such an advantage in early math education may cause those with better ANS precision to pursue and practice math. Consistent with this idea, in the current experiment we find some evidence that ANS precision is correlated with the knowledge of math facts. Another possibility is that higher ANS precision allows individuals to better evaluate their answers when performing math (Gilmore, McCarthy, & Spelke, 2007; Libertus et al., 2012; Lyons & Beilock, 2011). For example, an individual with poor ANS precision may be less likely or slower to realize that $34–19 = 25$ is implausible. A third possibility is that more experience with math, or better symbolic math abilities, hones the precision of the ANS (Piazza et al., 2013; Shusterman, Slusser, Halberda, & Odic, 2016). Of course, some combination of these influences is also possible.

5.3. Relationship between numerical and working memory abilities

Consistent with prior studies, we also found that symbolic math performance correlated with working memory. However, the relationship between the ANS and symbolic math persisted even when working memory performance was factored out. In addition, we replicated previous findings that congenitally blind individuals have superior verbal working memory, relative to sighted individuals, as measured by participants' forward and backward letter spans (Amedi et al., 2003; Dormal et al., 2016; Occelli et al., 2016; Raz et al., 2007). Working memory advantages associated with blindness can be traced back to childhood: blind children between the ages of 7 and 13 are better at remembering lists of pseudo-words than sighted children (Crollen et al., 2011).

There is some evidence that blind children spontaneously rely on working memory-demanding strategies to complete some numerical tasks, such as counting the number of times that particular syllables appear in a series of other syllables (Crollen et al., 2011). Whereas sighted children use their fingers to keep track of syllable numbers, blind children were more likely to count mentally (Crollen et al., 2011). However, we found no evidence for the idea that blind adults were more likely than the sighted to rely on working memory to solve approximate number tasks or solve simple arithmetic equations, as correlations between arithmetic performance, ANS precision, and working memory were equivalent across blind and sighted groups. Finally, although blind subjects had substantially better working memory, their performance on the arithmetic task was equivalent to the sighted.

One possibility is that the particular aspect of working memory that is improved in blindness is not the same component of working memory that is most relevant to solving symbolic math equations—at least not the types of equations we tested here. Blind individuals consistently show enhanced verbal working memory and serial or sequential memory (Amedi et al., 2003; Crollen et al., 2011; Dormal et al., 2016; Occelli et al., 2016; Raz et al., 2007). However, it is unclear whether other aspects of working memory, such as spatial working memory, are improved in blindness. At least one study directly compared verbal and spatial working memory abilities in blind and sighted individuals and found specific improvements in verbal working memory but not spatial working memory in blindness (Occelli et al., 2016). Thus, it is possible that blind individuals experience improvements in specific aspects of working memory that do not necessarily translate to enhancements in subtraction and division problem solving. By contrast, blind individuals do outperform sighted individuals on multiplication tasks that rely more heavily on verbal memory for arithmetic facts (Dehaene & Cohen, 1997; Dormal et al., 2016).

6. Conclusions

In summary, the present findings suggest that the cognitive building blocks of numerical cognition develop independently of visual experience. First, the precision of approximate number representations is indistinguishable across blind and sighted individuals. Second, blind and sighted individuals performed similarly on a simple timed arithmetic task. Finally, ANS precision was correlated with symbolic number reasoning in both blind and sighted individuals. Thus, despite the strong links between numerical processing and visual abilities, we find that key signatures of numerical cognition are preserved in the total absence of vision.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.cognition.2018.06.004.

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