

Individual differences in non-verbal number acuity correlate with maths achievement

Justin Halberda¹, Michèle M. M. Mazzocco^{1,2} & Lisa Feigenson¹

Human mathematical competence emerges from two representational systems. Competence in some domains of mathematics, such as calculus, relies on symbolic representations that are unique to humans who have undergone explicit teaching^{1,2}. More basic numerical intuitions are supported by an evolutionarily ancient approximate number system that is shared by adults³⁻⁶, infants⁷ and non-human animals⁸⁻¹³—these groups can all represent the approximate number of items in visual or auditory arrays without verbally counting, and use this capacity to guide everyday behaviour such as foraging. Despite the widespread nature of the approximate number system both across species and across development, it is not known whether some individuals have a more precise non-verbal ‘number sense’ than others. Furthermore, the extent to which this system interfaces with the formal, symbolic maths abilities that humans acquire by explicit instruction remains unknown. Here we show that there are large individual differences in the non-verbal approximation abilities of 14-year-old children, and that these individual differences in the present correlate with children’s past scores on standardized maths achievement tests, extending all the way back to kindergarten. Moreover, this correlation remains significant when controlling for individual differences in other cognitive and performance factors. Our results show that individual differences in achievement in school mathematics are related to individual differences in the acuity of an evolutionarily ancient, unlearned approximate number sense. Further research will determine whether early differences in number sense acuity affect later maths learning, whether maths education enhances number sense acuity, and the extent to which tertiary factors can affect both.

Behavioural, neuropsychological and brain imaging techniques show that a signature of the approximate number system (ANS) is its imprecision²⁻¹³. Unlike exact verbal counting, the ANS produces numerical representations that grow increasingly imprecise as a linear function of the target array, with larger quantities represented less precisely than smaller quantities. This imprecision is expressed as a Weber fraction that indexes the amount of error in the underlying mental representation of any numerosity³⁻⁵. On average, the Weber fraction of adults is approximately 0.11, yielding successful non-verbal discrimination of arrays differing by as little as a 9:10 ratio^{5,14}. Here we address whether there are significant individual differences in ANS acuity, and also whether these differences correlate with individual differences in symbolic maths achievement.

We examined 64 14-yr-old children with normal development whose performance in a variety of mathematical and more general cognitive tasks had been measured longitudinally, starting in kindergarten¹⁵. We tested for correlations between the current ANS acuity of the subjects and their past achievement in symbolic maths, while controlling for a wide range of other variables. Each subject’s ANS

acuity was assessed by psychophysical modelling of performance on a simple more/less judgement task similar to those used previously with infants and non-human animals. On each trial, subjects saw spatially intermixed blue and yellow dots presented on a computer screen too rapidly (200 ms) to serially count (Fig. 1a)¹⁶. Subjects indicated which colour was more numerous by key press and verbal response. The ratio between the two sets varied randomly among 1:2, 3:4, 5:6 and 7:8, with between 5 and 16 dots in each set. The colour of the more numerous set varied randomly, and half of the trials were area-controlled to ensure that responses were on the basis of the

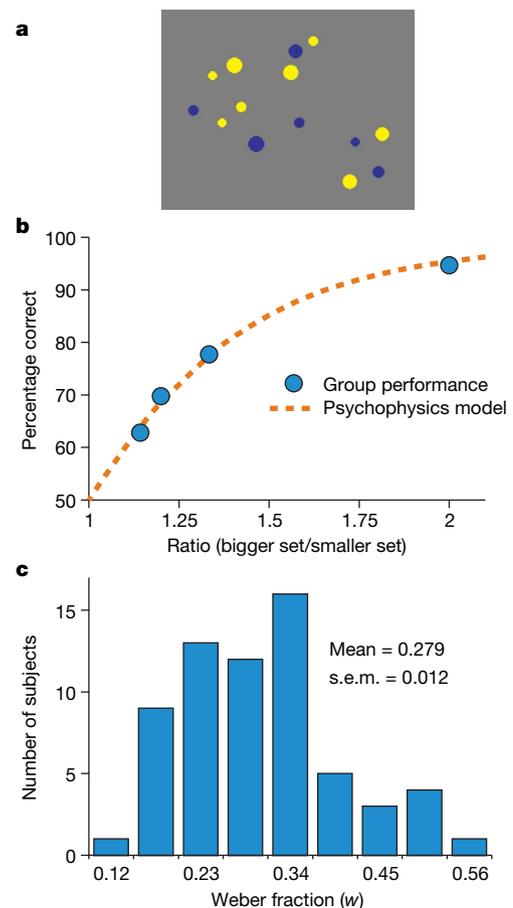


Figure 1 | Method and group performance. **a**, A representation of the trial from the numerical discrimination task. **b**, Group performance and modelled best-fit for all trials in the numerical discrimination task. **c**, Histogram of w , the acuity of the ANS, for the sample ($n = 64$), as determined by the psychophysical model for each subject.

¹Johns Hopkins University, Ames Hall, 3400 North Charles Street, Baltimore, Maryland 21218, USA. ²Kennedy Krieger Institute, 3825 Greenspring Avenue, Painter Building, Top Floor, Baltimore, Maryland 21211, USA.

number of dots and not on the total dot area (see Supplementary Information). Subjects participated in two sessions of 10 practice trials and 40 test trials each, totalling 80 test trials (approximately 10 min of testing per subject).

Collapsing across subjects, numerical discrimination improved as the ratio between the presented numerosities increased, in accord with Weber's law and with previous investigations of the ANS^{3–9} (Fig. 1b). This gradual improvement in performance as a function of ratio was modelled using classical psychophysical tools to determine the group Weber fraction (see Methods and Supplementary Information). This returned a value of 0.265 for the group Weber fraction (w) with an R^2 value of 0.995, suggesting that there is very high agreement between this psychophysical model of the ANS and the behavioural data (Fig. 1b). Next, we used this same method to fit each individual subject's data and thereby determine each subject's Weber fraction. This showed surprisingly large variation in the ANS acuity (w), ranging from 0.119 to 0.567 (Fig. 1c). The Weber fractions of subjects can also be translated into more intuitive whole numbers that show the ratio that would result in 75% correct performance. Using this translation, some subjects could discriminate numerical ratios as fine as 9:10 ($w = 0.11$) whereas others had difficulty with ratios finer than 2:3 ($w = 0.5$; mean subject $w \approx 0.45$).

A question to address is whether these individual differences in ANS acuity (w) predict individual differences in symbolic maths achievement. Each of our subjects was tested annually from kindergarten to sixth grade (ages 5–11) on a battery of standardized and investigator-designed measures. This longitudinal assessment of mathematical, verbal and other cognitive abilities provides a unique opportunity to detect any enduring correlations between ANS acuity and symbolic maths ability while controlling for other factors. Each year (ages 5–11), symbolic maths ability was assessed using the 'test of early mathematical ability, second edition' (TEMA-2)¹⁷ and/or the 'Woodcock–Johnson revised calculation subtest' (WJ-Rcalc)¹⁸, yielding an age-referenced standardized score for each subject. We found that the ANS acuity (w) of subjects correlated with symbolic maths performance in every year tested (from kindergarten to sixth grade) for both of the standardized maths tests, as summarized in Table 1. ANS acuity in ninth grade retrospectively predicted the symbolic maths performance of individual students from as early as kindergarten, a 9-yr time span. The linear correlations of ANS acuity (w) with symbolic maths achievement (TEMA-2 and WJ-Rcalc) for the third grade are shown in Fig. 2a, b.

A further question to address was whether the correlation between ANS acuity and symbolic maths achievement was due to individual differences in more general cognitive or performance factors. In the third grade (when subjects were approximately aged 8) we administered several non-numerical standardized tests including measures of rapid lexical access for colour names (rapid automatic naming, RAN-colour)¹⁹ and full-scale IQ (Wechsler abbreviated scale of intelligence, WASI-full)²⁰. The RAN-colour is an appropriate control

Table 1 | Correlation of ANS acuity (w) with symbolic maths achievement

Grade	TEMA-2 R^2	t d.f. = 62	P	WJ-Rcalc R^2	t d.f. = 62	P
Kindergarten	0.137	3.134	0.003	0.127	2.959	0.004
First	0.140	3.171	0.002	0.326	5.480	8×10^{-7}
Second	0.238	4.399	4×10^{-5}	—	—	—
Third	0.324	5.448	9×10^{-7}	0.282	4.933	6×10^{-6}
Fourth	—	—	—	0.248	4.518	3×10^{-5}
Fifth	—	—	—	0.117	2.866	0.006
Sixth	—	—	—	0.251	4.564	2×10^{-5}

ANS acuity (w) measured in ninth grade retroactively correlated with symbolic maths achievement. R^2 values represent the proportion of the variance in symbolic maths achievement that is explained by ANS acuity. R^2 values >0.25 are considered large in behavioural science and are generally viewed as having large practical significance. t values represent the distance, measured in units of standard error, between the obtained correlation and the null hypothesis of no correlation. P values represent the probability of obtaining the observed correlation in a sample of data by random chance when there is truly no relation in the population.

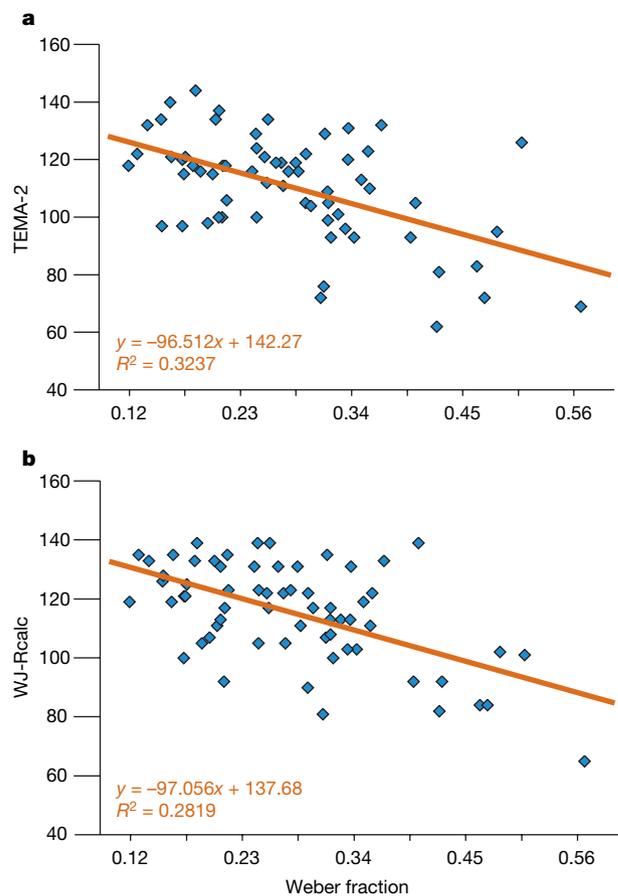


Figure 2 | Regressions. a, b, Linear regression of the standard score for each subject on the TEMA-2 test (a) or on the WJ-Rcalc test (b) of symbolic maths achievement and the acuity of the ANS (w). For TEMA-2 and WJ-Rcalc, higher numbers indicate better performance, whereas for the Weber fraction, lower numbers indicate better performance.

for our task because it measures the reaction time to identify the colours of 50 stimuli quickly; rapid colour naming is precisely the behaviour required by our ANS acuity assessment. The WASI-full IQ test acts as a control for general intelligence. WASI-full and RAN-colour did not correlate with one another in our sample ($P = 0.699$), making them largely orthogonal for purposes of linear regressions with ANS acuity. To examine the relationship of ANS acuity and symbolic maths achievement while controlling for other variables, two separate linear regressions were performed with ANS acuity (w) as the dependent variable and performance on either the TEMA-2 or the WJ-Rcalc test, and WASI-full and RAN-colour as independent variables. These showed that ANS acuity (w) correlated with symbolic maths achievement in the third grade even with rapid lexical access and general intelligence controlled for (Table 2).

To assess the strength of the correlation between ANS acuity (w) and symbolic maths achievement further, we performed extra linear regressions between w (measured at age 14) and an even broader range of standardized test scores obtained when subjects were in the third grade. These 16 measures controlled for the widest possible range of behavioural, cognitive and intelligence factors in our sample including many factors promoted as predictors of mathematical ability (for example, visual-spatial reasoning, working memory)^{21–25}. ANS acuity (w) significantly correlated with symbolic maths achievement (measured in the third grade) for both TEMA-2 and WJ-Rcalc performance, with all 16 measures controlled for ($r_p^2 = 0.167$ and 0.200 , respectively, where p represents partial correlation). In contrast, no other measure correlated with ANS acuity when symbolic maths performance and other variables were controlled for (Table 3). This means that success on tests of symbolic mathematics throughout the school years

Table 2 | Correlations controlled for cognitive and performance factors

Measure (task)	r_p^2	t d.f. = 60	P
With TEMA-2			
Symbolic maths (TEMA-2)	0.146	3.205	0.002
Intelligence (WASI-full)	0.013	0.887	0.379
Task demands (RAN-colour)	0.004	0.492	0.625
With WJ-Rcalc			
Symbolic maths (WJ-Rcalc)	0.155	3.325	0.003
Intelligence (WASI-full)	0.070	2.124	0.038
Task demands (RAN-colour)	0.017	1.023	0.310

ANS acuity (w) measured in ninth grade retroactively correlated with third grade symbolic maths achievement and other measures. r_p^2 values represent the proportion of the variance in ANS acuity accounted for by the listed variable when controlling for the two remaining variables in each analysis (TEMA-2 or WJ-Rcalc). t values represent the distance, measured in units of standard error, between the obtained correlation and the null hypothesis of no correlation. P values represent the probability of obtaining the observed correlation in a sample of data by random chance when there is truly no relation in the population.

can be retrospectively predicted by a subject's ANS acuity in young adulthood, as measured by the simple task of determining which of two quickly flashed arrays has more dots, even with extensive controls for other cognitive and performance factors.

Our results are consistent with at least two interpretations. Given that it is functional in infancy⁷, long before the onset of symbolic mathematics instruction, the ANS may have a causal role in determining individual maths achievement. Indeed, neuropsychological evidence suggests that the ANS is activated during symbolic mathematical reasoning across the lifespan¹³; therefore individual differences in ANS acuity might give rise to individual differences in maths ability.

Table 3 | Correlations controlled for all available factors

Measure (task)	r_p^2	t d.f. = 40	P
With TEMA-2			
Symbolic maths (TEMA-2)	0.167	2.831	0.007
Intelligence (WASI-full)	0.005	0.472	0.640
Task demands (RAN-colour)	0.023	0.981	0.332
Verbal IQ (WASI-verbal)	0.005	0.459	0.649
Performance IQ (WASI-performance)	0.006	0.482	0.632
Executive functions (CNT-B3)	0.021	0.918	0.364
Visual working memory (MemPuzl)	0.067	1.694	0.098
Visual segmentation (DTVPfg)	0.009	0.599	0.552
Object perception (DTVPfc)	0.001	0.172	0.864
Visual reasoning (DTVPvc)	0.025	1.004	0.321
Spatial reasoning (DTVPps)	0.012	0.701	0.488
Visual motor integration (VMI)	0.035	1.213	0.232
Word knowledge (WJ-RIwid)	0.012	0.706	0.484
Reading (WJ-Rwa)	0.001	0.225	0.823
Rapid lexical access (RAN-letter)	0.049	1.435	0.149
Rapid lexical access (RAN-number)	0.012	0.685	0.497
Gender	0.028	1.069	0.291
With WJ-Rcalc			
Symbolic maths (WJ-Rcalc)	0.200	3.149	0.003
Intelligence (WASI-full)	0.013	0.736	0.466
Task demands (RAN-colour)	0.004	0.391	0.698
Verbal IQ (WASI-verbal)	0.009	0.605	0.549
Performance IQ (WASI-perf)	0.013	0.727	0.472
Executive functions (CNT-B3)	0.035	1.208	0.234
Visual working memory (MemPuzl)	0.084	1.916	0.062
Visual segmentation (DTVPfg)	0.032	1.148	0.254
Object perception (DTVPfc)	0.001	0.201	0.842
Visual reasoning (DTVPvc)	0.008	0.578	0.566
Spatial reasoning (DTVPps)	0.018	0.869	0.390
Visual motor integration (VMI)	0.013	0.725	0.473
Word knowledge (WJ-RIwid)	0.014	0.757	0.454
Reading (WJ-Rwa)	0.000	0.014	0.988
Rapid lexical access (RAN-letter)	0.014	0.757	0.454
Rapid lexical access (RAN-number)	0.000	0.037	0.970
Gender	0.012	0.684	0.498

ANS acuity (w) measured in ninth grade retroactively correlated with third grade symbolic maths achievement and other measures. r_p^2 values represent the proportion of the variance in ANS acuity accounted for by the listed variable when controlling for all other variables in the list. t values represent the distance, measured in units of standard error, between the obtained correlation and the null hypothesis of no correlation. P values represent the probability of obtaining the observed correlation in a sample of data by random chance when there is truly no relation in the population.

Alternatively, individual differences in the quantity or quality of engagement in formal mathematics might increase ANS acuity. This latter possibility is hinted at by cross-cultural differences in Weber fractions, with maths-educated adults having better ANS acuity than adults from indigenous cultures lacking maths education^{5,14}. These causal relationships, possible tertiary factors and the trainability of ANS acuity²⁶ remain to be explored. Further evidence will add to the present results, which suggest that our ability to reason over symbolic numbers is deeply entwined with an evolutionarily ancient system for numerical approximation.

METHODS SUMMARY

At age 14 (that is, ninth grade), ANS acuity was assessed for 64 subjects (see Methods). The percentage correct on the ANS task was modelled for each individual subject as $1 - \text{error rate}$, where error rate is defined as:

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

where $\operatorname{erfc}(x)$ is the complementary error function related to the integration of the normalized Gaussian distribution. This model fits percentage correct as a function of the Gaussian approximate number representations for the two sets displayed on a trial (n_1 and n_2 , that is, blue dots and yellow dots) with a single free parameter, the Weber fraction (w ; see Supplementary Information)⁵. Correlations presented were between this estimate of ANS acuity (w), measured at age 14, and scores on standardized cognitive and performance measures, from kindergarten to sixth grade.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 10 February; accepted 4 July 2008.

Published online 7 September 2008.

- Carey, S. Bootstrapping and the origin of concepts. *Daedalus* **133**, 59–68 (2004).
- Feigenson, L., Dehaene, S. & Spelke, E. S. Core systems of number. *Trends Cogn. Sci.* **8**, 307–314 (2004).
- Barth, H., Kanwisher, N. & Spelke, E. S. The construction of large number representations in adults. *Cognition* **86**, 201–221 (2003).
- Cordes, S., Gelman, R. & Gallistel, C. R. Variability signatures distinguish verbal from nonverbal counting for both large and small numbers. *Psychon. Bull. Rev.* **8**, 698–707 (2001).
- Pica, P., Lemer, C., Izard, V. & Dehaene, S. Exact and approximate arithmetic in an Amazonian indigene group. *Science* **306**, 499–503 (2004).
- Gordon, P. Numerical cognition without words: Evidence from Amazonia. *Science* **306**, 496–499 (2004).
- Xu, F. & Spelke, E. S. Large number discrimination in 6-month-old infants. *Cognition* **74**, B1–B11 (2000).
- Nieder, A. & Miller, E. A. Parieto-frontal network for visual numerical information in the monkey. *Proc. Natl Acad. Sci. USA* **101**, 7457–7462 (2004).
- Meck, W. H. & Church, R. M. A mode control model of counting and timing processes. *J. Exp. Psychol. Anim. Behav. Process.* **9**, 320–334 (1983).
- Brannon, E. M. & Terrace, H. S. Ordering of the numerosities 1–9 by monkeys. *Science* **282**, 746–749 (1998).
- Dehaene, S., Dehaene-Lambertz, G. & Cohen, L. Abstract representations of numbers in the animal and human brain. *Trends Neurosci.* **21**, 355–361 (1998).
- Gallistel, C. R. *The Organization of Learning* (MIT Press, 1990).
- Dehaene, S. *The Number Sense: How the Mind Creates Mathematics*. (Oxford Univ. Press, 1997).
- Halberda, J. & Feigenson, L. Developmental change in the acuity of the “Number Sense”: The approximate number system in 3-, 4-, 5-, 6-year-olds and adults. *Dev. Psychol.* (in the press).
- Lachance, J. A. & Mazzocco, M. M. M. A longitudinal analysis of sex differences in math and spatial skills in primary school age children. *Learn. Individ. Differ.* **16**, 195–216 (2006).
- Mandler, G. & Shebo, B. J. Subitizing: an analysis of its component processes. *J. Exp. Psychol. Gen.* **111**, 1–22 (1982).
- Ginsburg, H. & Baroody, A. *Test of Early Mathematics Ability* 2nd edn (Austin, 1990).
- Woodcock, R. W. & Johnson, M. B. *Woodcock-Johnson Psycho-Educational Battery-Revised* (DLM Teaching Resources, Allen, 1989).
- Denckla, M. B. & Rudel, R. G. Rapid automatized naming (R.A.N.): Dyslexia differentiated from other learning disabilities. *Neuropsychologia* **14**, 471–479 (1976).
- Wechsler, D. *Wechsler Abbreviated Scale of Intelligence (WASI)* (Psychological Corporation, 1999).
- Fias, W. & Fischer, M. H. in *Handbook of Mathematical Cognition* (ed. Campbell, J.) 43–54 (Psychology Press, 2005).
- Mazzocco, M. M. M. & Myers, G. F. Complexities in identifying and defining mathematics learning disability in the primary school-age years. *Ann. Dyslexia* **53**, 218–253 (2003).

23. Kurdek, L. A. & Sinclair, R. J. Predicting reading and mathematics achievement in fourth-grade children from kindergarten readiness scores. *J. Educ. Psychol.* **93**, 451–455 (2001).
24. Espy, K. A. *et al.* The contribution of executive functions to emergent mathematic skills in preschool children. *Dev. Neuropsychol.* **26**, 465–486 (2004).
25. Mazzocco, M. M. M. & Kover, S. T. A longitudinal assessment of executive function skills and their association with math performance. *Child Neuropsychol.* **13**, 18–45 (2007).
26. Wilson, A. J., Revkin, S. K., Cohen, D., Cohen, L. & Dehaene, S. An open trial assessment of “The Number Race”, an adaptive computer game for remediation of dyscalculia. *Behav. Brain Funct.* **2**, 19 (2006).

Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements Longitudinal data collection was supported by a National Institutes of Health grant RO1 HD 034061 to M.M. We thank the Baltimore County Public School District and the children and parents who participated in this research, D. Naimen and R. Goodman for help with modelling, and L. Stapleton for help with statistical analyses.

Author Contributions J.H., M.M. and L.F. conceived the experiment; J.H. designed the numerical discrimination procedure; M.M. provided longitudinal data and oversaw data collection; J.H. performed the modelling and data analysis; J.H., L.F. and M.M. wrote the paper.

Author Information Reprints and permissions information is available at www.nature.com/reprints. Correspondence and requests for materials should be addressed to J.H. (halberda@jhu.edu).

METHODS

Subjects. Sixty-four 14-yr-old children participated (32 male; mean age 14 yr 10 months, ranging from 14 yr 3 months to 15 yr 9 months). They were from lower-middle to upper-middle economic backgrounds and were enrolled in normal (that is, non-learning-disabled) public classrooms in a single suburban school district outside of Baltimore, Maryland, USA. Throughout the longitudinal portion of the study, subjects were tested yearly in one, two or three 1-h sessions. The numerical discrimination task was performed during a laboratory visit during the tenth year of the longitudinal study (that is, ninth grade). Further details are given in the Supplementary Information. A total of 80 14-yr-olds were tested during the tenth year assessment but 9 were removed from the final sample owing to high variability in their performance on the ANS acuity assessment (see Modelling and analysis section), and 7 were removed because of missing data for some portion of the standardized tests in grades kindergarden to sixth grade.

Numerical discrimination. Subjects completed this task twice at an interval of approximately 60 min, as the first and last sub-tasks in a larger test battery from the longitudinal study. Each run of the task lasted 5 min. Subjects viewed dot arrays on a computer screen and judged whether there were more blue or more yellow dots. For each trial, pressing the space bar initiated a 250 ms blank-screen delay followed by a 200 ms appearance of an array of intermixed blue and yellow dots. After the array had disappeared, subjects had an unlimited amount of time to indicate their response by pressing a colour-coded keyboard button and saying the name of the more numerous colour aloud. Reaction time averaged approximately 1,100 ms across subjects. Subjects were told that, if they wished to change their choice, they could correct an erroneous key-press response by reporting the intended response to the experimenter, who noted it on a score sheet. Self corrections were reported by only 6 of the 64 subjects and accounted for only 7 out of the 5,120 total trials recorded in the study. The number of dots in each set in the array ranged from 5 to 16. Whether the yellow or blue set was larger was randomized. Each trial was drawn from one of four ratio bins in which the ratio of the smaller to the larger set was 1:2, 3:4, 5:6 or 7:8. For each of two runs of the experiment, subjects received 10 practice trials randomly selected from these ratios followed by 40 randomly ordered test trials (10 trials per ratio). Half of the trials in each ratio were 'dot-size controlled': the size of the average blue dot was equal to the size of the average yellow dot. On these trials, the set with more dots necessarily also had a larger total area on screen. The other half of trials were 'area controlled': the total number of blue pixels equalled the total number of yellow pixels such that the total cumulative area of the two sets was identical. The set with more dots thereby had smaller dots on average. Because the two sets were spatially overlapping and each dot was randomly placed in a shared display window, area-controlled trials also controlled for other continuous variables associated with number such as total dot density, inter-dot distance and the total envelope size of each set. Preliminary analyses showed similar results for dot-size-controlled and area-controlled trials and these data were

therefore combined for each subject. On both dot-size-controlled and area-controlled trials, individual dot size varied randomly by up to $\pm 35\%$ of the set average to discourage the use of individual dot size as a proxy for number. The diameter of a typical dot subtended approximately 1 degree of visual angle from a viewing distance of 50 cm.

Modelling and analysis. Previous investigations have modelled numerical representations either as having linearly increasing means and linearly increasing standard deviation²⁷, or as having logarithmically compressed means with constant standard deviation⁸. Both of these formats capture the performance pattern that is characteristic of the ANS (error that increases linearly with target numerosity). We used a classical psychophysics model that relies on a linear format of the ANS (although a logarithmic model makes the same predictions for our simple numerical acuity task), which provides a psychologically plausible model of performance in numerical discrimination⁵. Percentage correct was modelled as a function of increasing ratio (larger set/smaller set, or n_2/n_1). The numerosity for the blue set and yellow set were represented as Gaussian random variables (that is, X_2 and X_1) with means n_2 and n_1 and standard deviations equal to the Weber fraction $w \times n$. Subtracting the Gaussian for the smaller set from the larger set returned a new Gaussian with a mean of $n_2 - n_1$ and a standard deviation of $w\sqrt{n_1^2 + n_2^2}$ (simply the difference of two Gaussian random variables). Percentage correct was then equal to $1 - \text{error rate}$, in which error rate is defined as the area under the tail of the resulting Gaussian curve, computed as:

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

This model fits percentage correct on the numerical discrimination task as a function of the Gaussian approximate number representations for the two sets (that is, blue and yellow dots) with a single free parameter, the Weber fraction (w). An individual subject's Weber fraction (w) describes the standard deviations for the Gaussian representations of the ANS, thereby describing the amount of overlap between any two Gaussian representations, and thereby predicting percentage correct for any numerical discrimination. Using this model, the best-fit value for the Weber fraction (w) was determined by a program implementing the Levenberg–Marquardt algorithm for nonlinear least-squares fit on the average percentage correct in each ratio bin for each subject. The model attempts to determine the best-fit value for w in 50 iterations, each iteration being an attempt to reduce the sum of squared error. The model did not settle on a value for 9 of the original 80 subjects we tested, owing to high variability in the accuracy of their responses. These subjects were removed from the analysis.

27. Brannon, E. M., Wusthoff, C. J., Gallistel, C. R. & Gibbon, J. Numerical subtraction in the pigeon: evidence for a linear subjective number scale. *Psychol. Sci.* **12**, 238–243 (2001).