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Core systems of number

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What representations underlie the ability to think and reason about number? Whereas certain numerical concepts, such as the real numbers, are only ever represented by a subset of human adults, other numerical abilities are widespread and can be observed in adults, infants and other animal species. We review recent behavioral and neuropsychological evidence that these ontogenetically and phylogenetically shared abilities rest on two core systems for representing number. Performance signatures common across development and across species implicate one system for representing large, approximate numerical magnitudes, and a second system for the precise representation of small numbers of individual objects. These systems account for our basic numerical intuitions, and serve as the foundation for the more sophisticated numerical concepts that are uniquely human.

> 'The knowledge of mathematical things is almost innate in us… This is the easiest of sciences, a fact which is obvious in that no one's brain rejects it; for laymen and people who are utterly illiterate know how to count and reckon.'
>
> Roger Bacon (c. 1219–1294)

> 'Mathematics may be defined as the subject in which we never know what we are talking about, nor whether what we are saying is true.'
>
> Bertrand Russell (1872–1970)

How is it possible simultaneously to view mathematics as a system of transparent truths and as a tangle of relations between opaque entities? Why is it that small children demonstrate some degree of mathematical understanding, yet many adults view mathematics as a domain best left to only the wisest of academics? In short, why is mathematics both so easy and so hard?

Combined efforts from developmental psychology, psychophysics, comparative cognition and neuroscience have begun to paint a picture of both continuity and change in the domain of numerical thinking. Here, we review evidence that two distinct core systems of numerical representations are present in human infants and in other animal species, and therefore do not emerge through individual learning or cultural transmission. These two systems are automatically deployed, are tuned only to specific types of information, and continue to function throughout the lifespan.

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The two core systems are limited in their representational power. Neither system supports concepts of fractions, square roots, negative numbers, or even exact integers. The construction of natural, rational and real numbers depends on arduous processes that are probably accessible only to educated humans in a subset of cultures, but which nevertheless are rooted in the two systems that are our current focus and that account for humans' basic 'number sense' [1].

Core system 1: Approximate representations of numerical magnitude

Core system 1 in infants

Even in infancy, children exhibit numerical knowledge. Xu and Spelke tested 6-month-old infants' discrimination of the numerosities 8 vs. 16 using a habituation paradigm [2]. Infants first saw repeated presentations of either 8 or 16 dots (Figure 1a). Careful controls for non-numerical dimensions ensured that infants responded to numerosity only (see Box 1). When tested with alternating arrays of 8 and 16 dots, infants looked longer at the numerically novel test arrays regardless of whether they had been habituated to 8 or 16, showing that they successfully responded to number.

Further experiments have revealed important limits on infants' representations of number. First, infants' numerical discriminations are imprecise and subject to a ratio limit: 6-month-old infants successfully discriminate 8 vs. 16 and 16 vs. 32 dots, but fail with 8 vs. 12 and 16 vs. 24 under the same conditions as those described above [2]. Second, numerical discrimination increases in precision over development: 6-month-olds can discriminate numerosities with a 1:2 but not a 2:3 ratio, whereas 10-month-old infants also succeed with the latter (Xu and Arriaga, unpublished), and adults can discriminate ratios as small as 7:8 [3,4]. Third, numerical discrimination fails when infants are tested with very small numerosities in tasks controlled for continuous variables: infants fail to discriminate arrays of 1 vs. 2, 2 vs. 4, and 2 vs. 3 dots, even though these differ by the same ratios at which infants succeed with larger numerosities [5].

Infants' approximate number representations are not limited to visual arrays. When tested with sequences of temporally distinct events such as sounds, 6- and 9-month-old infants show the same pattern of success and failure as with dot arrays [6,7]. In particular, infants discriminate numerosities controlled for continuous variables, their

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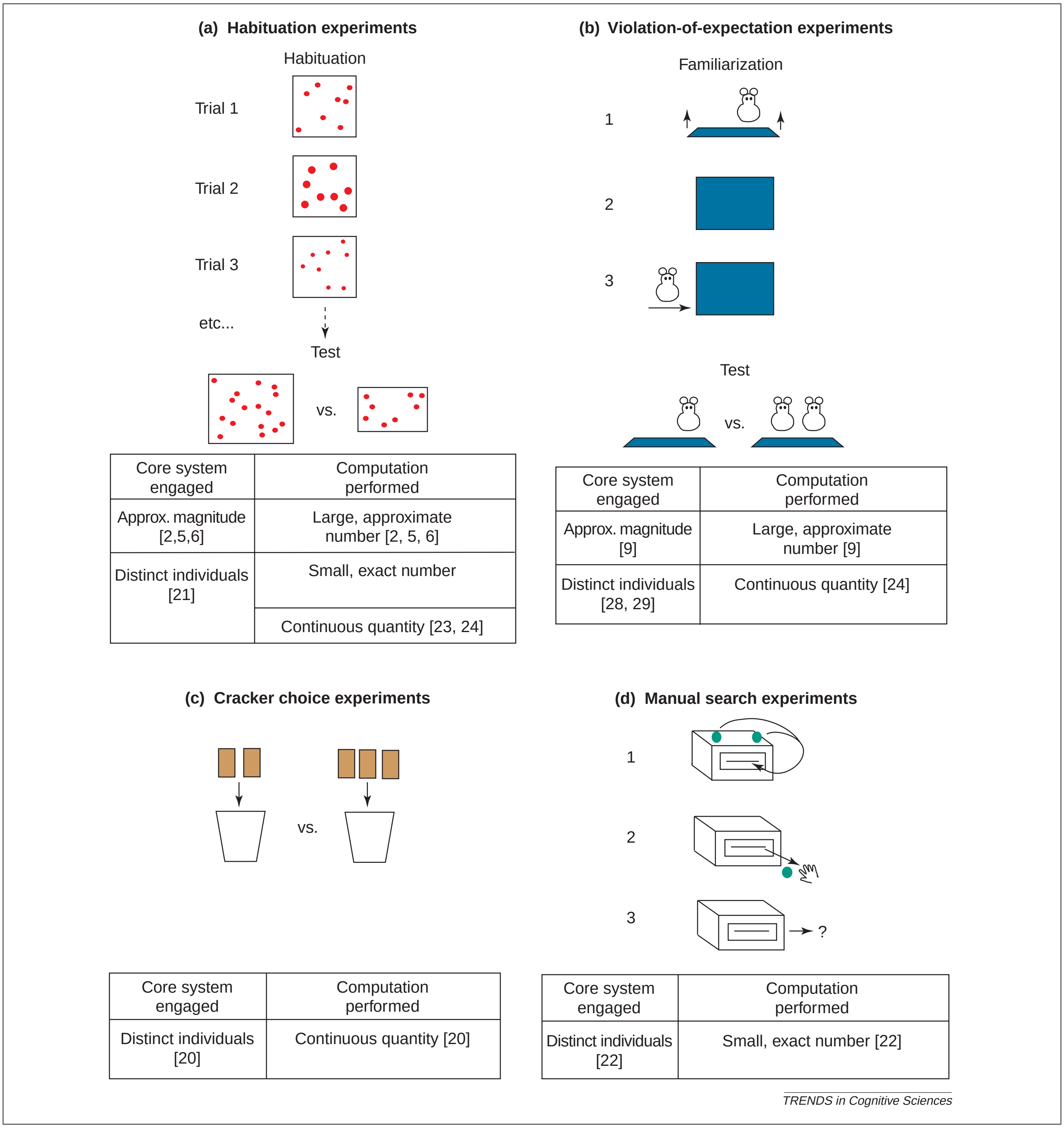

(a)

Core system engaged	Computation performed
Approx. magnitude [2,5,6]	Large, approximate number [2, 5, 6]
Distinct individuals [21]	Small, exact number
	Continuous quantity [23, 24]

(b)

Core system engaged	Computation performed
Approx. magnitude [9]	Large, approximate number [9]
Distinct individuals [28, 29]	Continuous quantity [24]

(c)

Core system engaged	Computation performed
Distinct individuals [20]	Continuous quantity [20]

(d)

Core system engaged	Computation performed
Distinct individuals [22]	Small, exact number [22]

Figure 1. **(a–d)** Four types of tasks used to test infants' quantity representations. The tables below each task list evidence that has been obtained for the engagement of either of the two core systems, and for which computations are performed over the representations generated by the systems. 'Approximate magnitude' is the representation generated by the first core system. 'Distinct individuals' is the representation generated by the second core system. Parenthetic references cite experiments yielding conclusive evidence for the engagement of either of the two core systems. Other experiments on infants' quantitative abilities remain indeterminate as to which system is contacted (e.g. [67]).

discrimination is subject to a ratio limit of 1:2 at 6 months and of 2:3 at 9 months, and they successfully discriminate only numerosities of four and above. The convergence of findings across these disparate types of entities suggests that infants' discrimination depends on abstract representations of numerosity. Furthermore, these abstract representations support number-relevant computations. Infants recognize ordinal relationships between numerosities [8], and form expectations about the outcomes of simple arithmetic problems such as 5 + 5 (Figure 1b) [9].

These hallmarks of approximate number representations are instantiated in models representing numerosity as a fluctuating mental magnitude, akin to a 'number line', shared across modalities [10–14]. There are

Box 1. Infants' computation of discrete versus continuous quantities

Early experiments on infants' quantitative abilities did not fully disentangle discrete and continuous variables, leaving the source of infants' responses ambiguous. More recent studies with stringent controls illustrate that infants can represent both types of information.

In tasks involving large numbers of elements, infants compute discrete number. With total surface area, contour length, display size, item size and item density all neutralized, infants dishabituate to changes between 8 versus 16 dots [2] and sounds [6]. That these activate infants' approximate representations of numerical magnitude is suggested by the signature of ratio-dependent performance. Furthermore, large-number arrays appear spontaneously to trigger numerical representations only; infants have difficulty extracting information about the continuous properties of large number arrays when number is controlled for [66].

Whereas the first core system outputs specifically numerical representations, the second system allows for the representation of continuous variables *and* of discrete number. Evidence comes from tasks producing the set-size signature of the system for representing small numbers of individuals. In some of these tasks, infants respond based on the total continuous properties of the array. Given a choice between two quantities of food, infants opt to maximize the total quantity of food rather than the number of pieces of food [20]. And when continuous variables are pitted against number in habituation and violation-of-expectation tasks, infants respond to continuous variables, such as total contour length or area [23,24]. However, the system for representing numerically distinct individuals also supports discrete numerical computations. Infants search for hidden objects based on the number of objects hidden, not on the total amount of continuous 'object-stuff' hidden [22]. And in a habituation task with strict controls for continuous variables, infants respond to discrete number if the array contains objects with highly dissimilar features (Feigenson, unpublished).

Why do infants sometimes compute continuous extent and sometimes compute number over representations of small numbers of individuals? Although no definitive answer has been found, infants' performance can be interpreted in light of the stimuli presented and the behavior required. Computing total continuous extent over arrays of food objects makes sense if the goal is to maximize the amount one gets to eat. Computing number when searching for objects makes sense when the goal is to obtain an individual object, rather than a detached quantity of 'stuff.' Still, because no single rule decides when infants will compute continuous versus discrete properties of a small-number array, this area is ripe for future investigation.

currently two competing mathematical formulations of the number line (Figure 2), although their behavioral predictions are highly similar. The linear model with scalar variability represents the number line as a series of equally spaced distributions with increasing spread. The logarithmic model with fixed variability represents successive numerosities on a logarithmic scale subject to a fixed amount of noise. In both models, larger numerosities are represented by distributions that overlap increasingly with nearby numerosities. This variability increases the likelihood of confusing a target with its neighbors, yielding infants' ratio-dependent performance.

Core system 1 in older children and adults

Older children and adults share this system for representing large, approximate numerosities [3,10,15–17]. When shown arrays of dots or sequences of sounds under conditions that prevent counting, adults discriminate numerosities when continuous variables are controlled, their discrimination is subject to a ratio limit, and the ratio limit is identical for arrays from different modalities. Like those of infants, adults' numerical representations therefore show two hallmarks: they are ratio-dependent and are robust across multiple modalities of input.

What is the relationship between this approximate number system and the system of symbolic number that supports exact enumeration and arithmetic? Early work showed that adults are faster to determine which of two Arabic digits is larger when the numerosities are small and/or more distant from each other [18]. These two factors collapse into the same ratio dependence that is observed with visual or temporal arrays, now seen with numerosities presented in symbolic form. Ratio dependence in symbolic numerical comparison has also been revealed in children as young as 5 years [17], suggesting that children quickly learn to map symbolic numbers onto their pre-existing representations of numerical magnitude. Recent evidence suggests that this mapping is initially logarithmic but becomes linear during the elementary school years, consistent with the thesis that the mental number-line is logarithmically compressed, and that children and adults learn to compensate for this compression [19].

Core system 1: Summary

To sum up, the findings indicate that infants, children and adults share a common system for quantification. This system yields a noisy representation of approximate number that captures the inter-relations between different numerosities, and is robust across modalities and across variations in continuous properties. This system

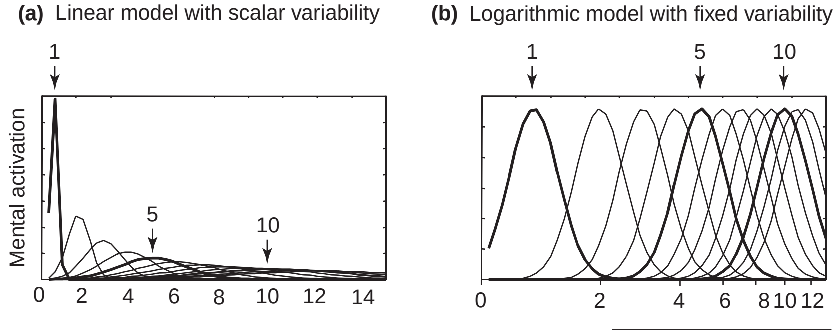

Figure 2. Two models of the mental number line (Core system 1), a linear model **(a)** and a logarithmic one **(b)**, depicting mental activation as a function of numerosity.

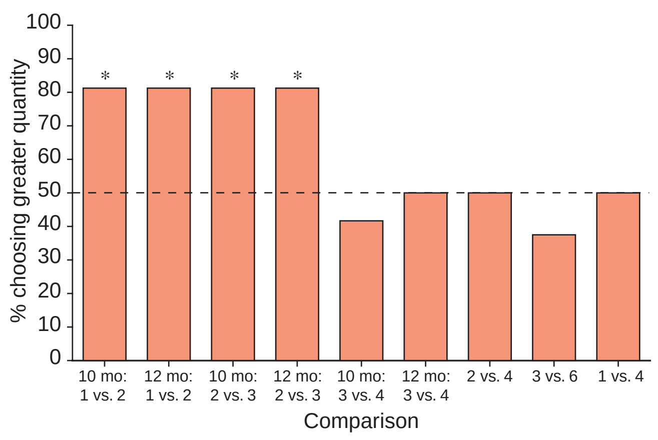

Figure 3. Infants' choices in the experiment by Feigenson *et al.* [20]. Bars represent the percentage of infants in each comparison group (at two different ages, 10 and 12 months, for the smaller quantities) choosing the greater quantity of crackers. Infants' choices demonstrate the set-size signature of the system for representing small numbers of numerically distinct individuals (Core system 2), in that infants performed randomly (dotted line at 50%) when either array contained more than 3 objects, even with highly discriminable ratios between the quantities. Asterisks denote significance levels of $P < 0.05$. Adapted with permission from [20].

shows a signature ratio limit that is probably explained by logarithmic compression of its underlying representation of numerical magnitude. Finally, the first core system becomes integrated with the symbolic number system used by children and adults for enumeration and computation.

Core system 2: Precise representations of distinct individuals

Core system 2 in infants

The approximate system is not our only source of numerical information. Infants and adults have a second system for precisely keeping track of small numbers of individual objects and for representing information about their continuous quantitative properties.

In one experiment, 10- and 12-month-old infants chose between two quantities of hidden crackers (Figure 1c) [20]. Infants watched an experimenter sequentially hide, for example, one cracker in a bucket on the left, and $1 + 1 = 2$ crackers in a bucket on the right. With choices of 1 vs. 2 and 2 vs. 3 equal-sized crackers, infants spontaneously chose the larger quantity. However, with choices of 3 vs. 4, 2 vs. 4, 3 vs. 6, and even 1 vs. 4 crackers, infants chose randomly despite the highly discriminable ratio between the quantities (Figure 3) [20].

This performance pattern differs dramatically from that observed with large numerosities in the studies reviewed above, because infants' success depended not on numerical ratio but on the absolute number of items presented, with an upper-bound of 3. This striking limit on infants' small number quantification appears in at least two other paradigms. First, infants successfully discriminate 2 vs. 3 but not 4 vs. 6 items in a habituation task [21], despite the identical ratio difference. Second, the 3-item limit was found in a task in which infants saw objects hidden sequentially in a box and then searched to retrieve them (Figure 1d) [22]. Fourteen-month-olds matched their searching to the number of objects hidden, but only for numerosities 1, 2 and 3. Infants' search patterns show that they successfully represented the hiding of 'exactly 1', 'exactly 2', and 'exactly 3' objects. However, when 4 objects were hidden, infants retrieved one of them and then stopped searching. Importantly, in this experiment the continuous extent of the objects was controlled for. Thus, in this task, infants base their searching on the exact number of objects hidden and not on continuous variables (Box 1).

Besides computing numerosity, infants also compute the total continuous extent of small object arrays. In the cracker task described above, infants presented with one large cracker versus two crackers totaling half the area of the large one reliably preferred the bucket with one [20]. As infants succeeded in this task only when 3 or fewer crackers were hidden in either location, this suggests that they represented the crackers as distinct individuals, up to a limit of 3, and then summed across these to represent the amount of total cracker material in each bucket. This sensitivity to continuous variables has been observed in many paradigms, including habituation and violation-of-expectation, demonstrating the importance of this computation when representing small numbers of objects (Box 1) [5,23,24].

Like the first core system, the system for representing small numbers of distinct individuals yields a consistent signature across abstract representations. Just as with object arrays, infants precisely represent the individuals in visual-event and auditory sequences (e.g. puppet jumps and sounds) [25]. Here again, infants fail to represent arrays greater than 3, fail to represent number when continuous variables are controlled, and often respond instead to summary representations of amount of motion or amount of sound. Nevertheless, there are limits on the types of individuals that can be represented by this system. Streams of continuous substances or objects that come into and go out of existence are not successfully tracked either by adults [26,27] or by infants [28,29]. These shared constraints provide further evidence for the deployment of the second core system across development (see also [30–32]).

Core system 2 in adults

One long-standing and still unanswered question concerns the role of exact small-number representations in adults' symbolic number processing. When adults enumerate elements in dot arrays, performance is fast and nearly perfect for the numerosities 1–4, after which error rate or response time rise sharply and climb with increasing numerosity [33,34]. This discontinuity has led to the suggestion that small numbers are processed differently from large numbers via subitizing, a process allowing for their immediate and accurate recognition. Subitizing has been proposed to depend on the system for representing and tracking small numbers of individuals discussed above [34], but this claim remains controversial [12,15]. An alternative explanation for the fast and accurate enumeration of numerosities 1–4 is that, like larger numerosities, they are represented by the first core system, but that the variability in the read-outs of these small numbers is sufficiently small that they can be recognized with little error. At present, therefore, it is not known whether the second core system is recruited in symbolic number tasks.

Dissociations between systems 1 and 2

In summary, infants' processing of large versus small numbers exhibits two dissociations. First, large approximate number discrimination varies relative to the ratio between numerosities, whereas small-number discrimination varies relative to the absolute number of individuals, with a limit of about 3. Second, large-number discrimination is robust over variations in continuous variables, whereas small-number discrimination is often affected by such continuous properties. These dissociations suggest that large and small numerosities are the province of different systems with different functions: large arrays primarily activate a system for representing sets and comparing their approximate cardinal values. Small arrays primarily activate a system for representing and tracking numerically distinct individuals, which allows for computations of either their continuous quantitative properties or of the number of individuals in the array.

The core systems' shared heritage

Core representations of number are common across many species. When given tasks comparable with those presented to human infants and adults, animals show the same signature limits, suggesting that core knowledge of number depends on mechanisms with a long phylogenetic history.

Core system 1 in non-human animals

Many animal species represent numerical magnitudes. Rats trained to press a lever N times produce presses normally distributed around the target number. Further, the standard deviation of these response distributions is a linear function of the target number, showing that the rats rely on imprecise representations that grow noisier as numerosity increases [35]. And like those of human infants and adults, rats' numerical magnitude representations are abstract [13]. Rats trained to respond to numbers of noise bursts later experienced sequences that mixed noise bursts with a stimulus from a new modality, cutaneous shocks. Rather than enumerating only the trained auditory stimuli, rats spontaneously enumerated both the noises and shocks.

Primates also use approximate magnitudes to represent number, as illustrated by experiments testing ordinal knowledge in rhesus monkeys. Monkeys were trained to touch arrays of 1–4 elements in ascending numerical order [36]. Next, they saw pairs of novel stimuli containing two numerosities between 5 and 9. Monkeys spontaneously touched these new arrays in ascending numerical order, and the speed and accuracy of their responses was a function of numerical ratio, mirroring the effect obtained with human adults (Figure 4). Similar ratio-dependence has been found in untrained cotton-top tamarins presented with auditory sequences [37].

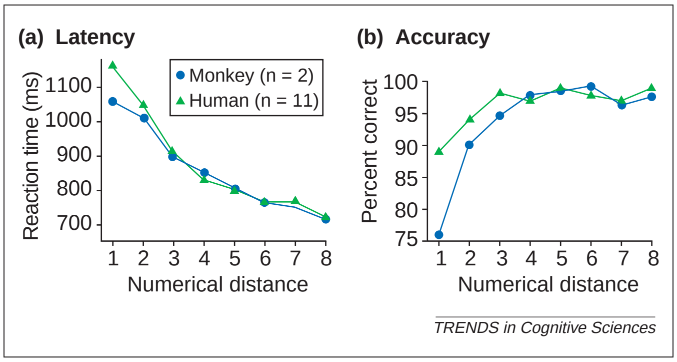

Figure 4. Latency and accuracy to the first response in a pairwise numerical comparison task. Both species were required to order two numerosities on a touch-sensitive screen. Accuracy increased (**b**) and latency decreased (**a**) with increasing numerical disparity for both monkeys (blue circles) and humans (green triangles). Reprinted with permission from [68].

Core system 2 in non-human animals

Animals also represent small numbers of distinct individuals. In the task on which Feigenson *et al.* [20] based their cracker experiments with infants, rhesus monkeys saw apple slices sequentially hidden in two locations and then chose between them [38]. With choices of 1 vs. 2, 2 vs. 3, and 3 vs. 4, monkeys preferred the larger quantity. But with 3 vs. 8 and 4 vs. 8, they were at chance. Therefore, although demonstrating a slightly higher capacity than human infants, monkeys presented with these relatively small numerosities (arrays containing up to 8 items) were limited to tracking 4 or fewer per location, regardless of the ratio between the quantities. The same 4-item limit was also found when monkeys watched simple addition problems, in which they succeeded at discriminating the correct outcomes of $1+1$ ($=2$ or 3), and $2+1$ ($=3$ or 4), but failed with $2+1+1$ ($=3$ or 4 or 5) [39].

The abrupt limit on the number of entities monkeys represented in the above tasks implicates the small-number system as the source of their performance. Monkeys' restriction to the numerosities 1–4 in situations involving small arrays, coupled with their capacity to create noisy representations of large sets, suggests that monkeys, like humans, have two distinct systems for representing number. The two core number systems therefore offer a strong case of representational continuity across development and across species.

Cerebral bases of the core systems

Recently, neuroimaging and neurophysiological techniques have begun to provide access to the neuronal underpinnings of the core number systems. The system for representing approximate numerical magnitudes has become well characterized and is associated by a convergent series of results with the bilateral horizontal segment of the intraparietal sulcus (HIPS; for a review see [40]). This brain region is implicated by both event-related potentials [41,42] and fMRI [43,44] as the source of the numerical distance and size effects that are observed behaviorally. In adults, the HIPS is activated equally well by numerical symbols in the auditory and visual modalities [45], and by sets of visual items [46]. This area thus lies at the convergence of multimodal symbolic and non-symbolic input pathways for approximate number.

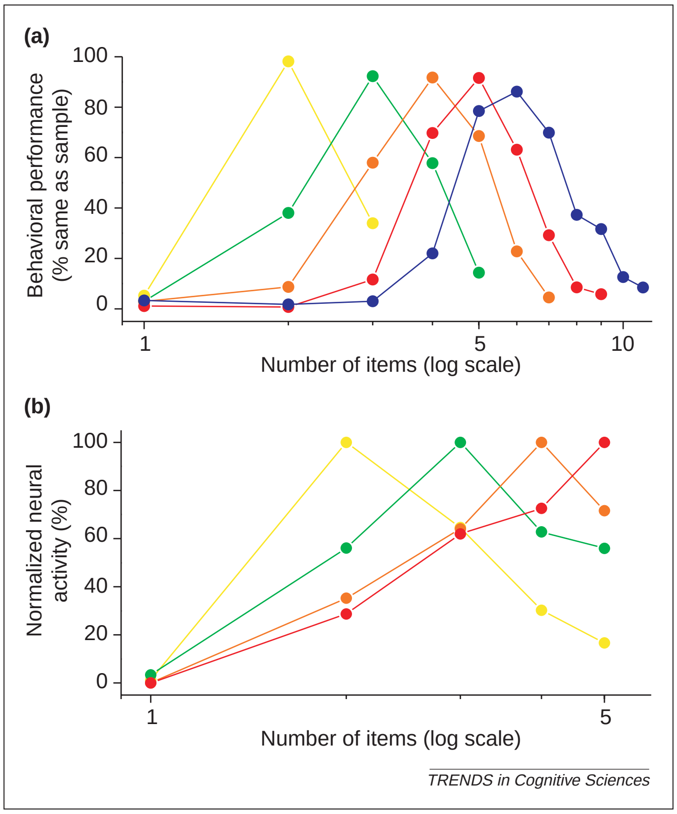

Figure 5. Behavioral and neural numerical filter functions. **(a)** The behavioral performance for two monkeys indicated whether they judged the first test stimulus (in a delayed match-to-numerosity task) as containing the same number of items as the sample display. The function peaks indicate the sample numerosity at which each curve was derived. Behavioral filter functions are plotted on a logarithmic scale. **(b)** Single-neuron representation of different numerosities in the prefrontal cortex of the same behaving monkeys. Population neural filter functions were derived by averaging the normalized single-unit activity for all neurons that preferred a given numerosity and transforming them to a logarithmic scale. Reprinted with permission from [52].

Lesion data concur with these findings. Many adult patients with acalculia suffer from lesions in the IPS vicinity. In particular, a subcategory of patients with deficits in elementary operations such as subtraction, bisection, or comparison seem to suffer more specifically from a deficit of the numerical magnitude system [47,48]. Even simple non-symbolic tasks involving the enumeration of large-number dot arrays can be impaired in such patients [49]. Furthermore, early pathologies of this system might cause developmental dyscalculia, a severe deficit in learning arithmetic in otherwise normally developing children. Loss of gray matter in the IPS has been identified in two medical conditions associated with dyscalculia: prematurity [50] and Turner's syndrome [51].

In a crucial step towards elucidating the internal organization of this system for representing approximate numerosities, the first electrophysiological recordings of number-related neurons in awake monkeys indicate the existence of neurons tuned to approximate numerosity (Figure 5) [52–54]. In a numerosity-matching task, for instance, about a third of prefrontal neurons and up to 15% of neurons in the depth of the IPS fired selectively after a certain numerosity of dots was presented visually [52,53]. Furthermore, the neurons had identically short firing latencies for all of the numerosities tested, indicating parallel extraction of numerosity across the entire display, and the faster latencies for IPS neurons than for prefrontal neurons suggests that numerosity is first computed in parallel in parietal cortex, then is transmitted and held online by prefrontal delay activity [54].

Crucially, numerical tuning is approximate and is broader for larger numerosities. The ratio signature of Weber's law is observed, with the breadth of the tuning curves increasing linearly with the neurons' preferred numerosity. Mathematically, the tuning curves can be described as Gaussians with a fixed width on a logarithmic scale of number. This property, together with the lack of any discontinuity between numbers below 3 and above 4, associates this neural code unambiguously with the first core number system. It provides evidence, moreover, that this system can represent the magnitude of the smallest numerosities as well as larger ones, at least in monkeys that receive extensive training.

By contrast, the neural bases of the second core system are not yet clear. In neuropsychological patients, representations of small numbers are sometimes disproportionately spared relative to large numerosities [55,56]. And conversely, some children with developmental dyscalculia show impairments to subitizing that are so severe that the children had to count to assess the numerosity of arrays of even 2 or 3 objects [57,58]. However, imaging of the neural substrates of subitizing has proven inconclusive [46], perhaps because this activity is a basic, automatic function of early extrastriate areas [59]. Indeed, the representation of distinct objects is so fundamental to perception and cognition that it might elude current neuroimaging methods, which work best when one can devise control tasks in which the target system is not activated.

Conclusion

Why is number so easy and yet so hard? Although studies of human infants have not definitively answered this question (see Box 2), they offer several suggestions. First, number is *easy* because it is supported by core systems of representation with long ontogenetic histories. One system serves to represent approximate numerical magnitudes independently of non-numerical quantities. Because this system is active early in infancy, humans are attuned to the cardinal values of arrays from the beginning of life. The other system serves to represent numerically distinct individuals of various types, and allows multiple computations over these representations. These computations include forming summary representations of the

Box 2. Questions for future research

- What is the relationship between representations of large, approximate numerosities and representations of small numbers of numerically distinct individuals? Can information be transferred from one core system to the other?
- What factors determine which representational system is deployed in a given situation?
- How does each of the two core number systems contribute to the creation of more sophisticated numerical knowledge?
- Do impairments to either core system lead to different types of deficits in the development of mature number knowledge?

individuals' continuous properties, and representing the number of individuals in an array. Because this second system is also active in infancy, concepts of 'enumerable individual' and 'adding one' are accessible throughout our lifetimes. Numerical reasoning might be easy, and numerical intuitions transparent, when they rest on one of these systems.

Second, number is *hard* when it goes beyond the limits of these systems. When one attempts to represent an exact, large cardinal value, one must engage in a process of verbal counting and symbolic representation that children take many years to learn [60,61], that adults in different cultures perform in different ways [62], and that people in some remote cultures lack altogether (Gordon, unpublished). When humans push number representations further to embrace fractions, square roots, negative numbers and complex numbers, they move even further from the intuitive sense of number provided by the core systems.

What drives humans beyond the limits of the core systems? If the human mind were endowed only with a single system of core knowledge, then humans might never venture beyond its bounds. We are endowed, however, with two core systems of numerical knowledge and with other systems for reasoning about physical, living and intentional beings (e.g. [63–65]). As we apply these different systems to the same objects, events and scenes, we appear to be driven to reconcile the representations that they yield. Three-year-old children might show this drive when they struggle with their representations of approximate magnitudes and of numerically distinct individuals so as to learn the meanings of words like 'seven', a concept whose meaning is guaranteed by neither core system. Newton and Leibniz may have shown a similar impulse when they independently invented the calculus, stretching their systems of numerical and mechanical knowledge so as to reconcile them. Nothing guarantees, however, that the intuitions provided by distinct core systems can be reconciled into a single system of consistent, transparent and accessible truths. Despite the great advances in human physical and mathematical concepts over cultural and intellectual history, this consilience continues to elude us.

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