Review

Special Issue: Space, Time and Number

Foundational numerical capacities and the origins of dyscalculia

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One important cause of very low attainment in arithmetic (dyscalculia) seems to be a core deficit in an inherited foundational capacity for numbers. According to one set of hypotheses, arithmetic ability is built on an inherited system responsible for representing approximate numerosity. One account holds that this is supported by a system for representing exactly a small number (less than or equal to four4) of individual objects. In these approaches, the core deficit in dyscalculia lies in either of these systems. An alternative proposal holds that the deficit lies in an inherited system for sets of objects and operations on them (numerosity coding) on which arithmetic is built. I argue that a deficit in numerosity coding, not in the approximate number system or the small number system, is responsible for dyscalculia. Nevertheless, critical tests should involve both longitudinal studies and intervention, and these have yet to be carried out.

Why are people bad at learning arithmetic?

Low numeracy is a serious handicap for individuals and a major cost for nations (see [1] for data relevant to the UK). It makes individuals less employable, is a risk factor for depression in adulthood and significantly reduces lifetime earnings. In the UK, approximately 25% of adults have poor functional numeracy [2]. Low arithmetic attainment has been attributed in the past to a deficit in general cognitive abilities such as working memory (WM) [3] and executive function [4], and there is evidence that these factors affect arithmetic learning and scholastic attainment more generally [3]. Many social and cognitive factors affect arithmetic learning (Box 1). This means that the presenting symptoms can be very varied and the underlying causes are difficult to identify.

Arithmetic difficulties and disabilities frequently co-occur with other developmental disorders, especially reading and digit span deficits and attention deficit hyperactivity disorder [5]. Individuals seriously affected, such as those classified with developmental dyscalculia [6] or mathematics learning disability [7] (Table 1), which both identify the same construct, have a modal prevalence of approximately 6.5% [8].

Several strands of recent evidence argue that very low arithmetic attainment can be an isolated deficit. For instance, several studies have found low attainment in learners matched for IQ and WM [9]. Recent evidence suggests that factors specific to the domain of numbers and arithmetic make a major independent contribution to low arithmetic attainment. In a longitudinal study by Geary and colleagues, tests on understanding the numerosity of sets and on estimating the position of a number on a number line were two important predictors of low achievement in mathematics, affecting some 50% of the sample, and of mathematics learning disability, affecting approximately 7% of the sample [10]. Using multivariate genetic analysis in a sample of 1500 pairs of monozygotic and 1375 pairs of dizygotic 7-year-old twins, Kovas and colleagues found that approximately 30% of the genetic variance was specific to mathematics [11]. In a study of first-degree relatives of dyslexic probands, principal component analysis revealed that numerical abilities constituted a separate factor, with reading-related and naming-related tasks being the two other principal components [12].

Taken together, these studies raise the possibility that difficulties and disabilities in learning arithmetic could arise from selective impairment in a domain-specific

Glossary

Approximate numerosity tasks: tasks involving clouds of dots (or other objects) typically too numerous to enumerate exactly in the time available. One common task is to compare two clouds of dots. Addition and subtraction tasks for which the solution is compared with a third cloud of dots are also used. (The term approximate arithmetic is sometimes used when an exact answer is not available or not needed: e.g. is 73 + 98 closer to 180 or to 130?)

Cardinality principle: in the development of counting, understanding that the last word in the count represents the number of objects in the set counted.

Distance effect: number comparison, whether symbolic or non-symbolic, is slower and more error-prone as the number magnitudes become more similar (Figure 1).

Intraparietal sulcus (IPS): brain area for core number processing such as simple enumeration, estimation, subitizing and comparison. Functional specialization of the left and right IPS develops with time and experience.

Numerosity: number of objects in a set.

Problem size effect: arithmetic problems involving larger numbers are harder than those involving smaller numbers, even for highly practiced sums and multiplications. Explanations of the effect vary.

Weber's law, Weber fraction and numerical acuity: psychologist Ernst Weber stated 'equal relative increments of stimuli are proportional to equal increments of sensation.' That is, the difference threshold depends on the proportional and not the absolute difference between two quantities. The Weber fraction is the proportional difference that is reliably detected. Thus, the smaller the Weber fraction, the better is the discrimination between two quantities. Numerical acuity refers to the Weber fraction of two approximate numerosities.

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Box 1. Factors associated with poor arithmetic learning

The available evidence suggests that there are several factors underlying low numeracy. For example, low socioeconomic status, minority ethnic status and gender can all be associated with lower mathematics attainment [87]. Although it is difficult to assess the role of poor or inappropriate teaching, the fact that the introduction of detailed new national primary school strategy for numeracy in the UK has had only a minor and possibly nonsignificant effect on numeracy for the group studied is indicative [1]. Even relatively simple tasks that depend relatively little on the quality of educational experience, such as comparison of the magnitude of two single-digit numbers or enumerating a small array of objects, show wide variation [13,14].

This evidence suggests that individual cognitive characteristics play a major role in variation in individual attainment. For example, there is evidence to suggest that IQ and working memory (WM) contribute to arithmetic attainment [10]. In fact, the usual definitions of dyscalculia (or equivalent constructs) use discrepancy between arithmetic attainment and IQ as a criterion (Table 2) [7].

Many authors, most influentially, Piaget, have argued that understanding concepts of number and arithmetic is premised on general cognitive abilities, especially reasoning with class inclusion, transitive inference and quantitative seriation, and the way the child applies reasoning to interactions with the environment [31]. More recently, Gardner coupled arithmetic with logic to form one of seven types of intelligence (termed logical–mathematical) [88]. According to this approach, difficulties or disabilities in learning arithmetic would necessarily be associated with difficulties or disabilities in reasoning and cognitive domains that support it, including, presumably, WM. More strongly, if these domain-general capacities are sufficient to learn arithmetic, then the prediction would be that dyscalculic subjects all have a deficit in a domain-general ability. However, the data presented in the main text argue strongly against this conclusion.

capacity. Indeed, recent reviews have proposed that developmental dyscalculia follows from a core deficit in this domain-specific capacity [5,6,9,13,14].

Domain-specific foundational capacities for arithmetic

Here I briefly outline proposals for a domain-specific capacity for numbers before discussing whether this capacity is foundational for acquiring arithmetic ability.A foundational capacity for numbers is revealed in the ability of human infants to discriminate on the basis of the numerosity of a display [15] and to match numerosity across modalities [16], which suggests that the capacity is not tied to one modality and implies a relatively abstract understanding of numerosity Box 2.

There is also extensive evidence from converging sources of specialized neural networks for numerical processing and calculation. Neurological damage has identified the left parietal lobe as a critical area in calculation, in particular the left angular gyrus [17]. There is also evidence from case studies that the right parietal lobe is specifically involved in rapid enumeration [18]. Novel arithmetic problems, word problems and reasoning about arithmetic involve the prefrontal cortex [19]. Functional neuroimaging has confirmed a role for the left angular gyrus in calculation [20], especially for the retrieval of arithmetic facts [21], whereas simple number tasks, such as magnitude comparison, typically show bilateral intraparietal sulcus (IPS) implementation [20,22–24]. Simple enumeration is frequently found most prominently in the right IPS [25].

The existence of specialized neural networks for numerical processing is perhaps most clearly revealed in primate studies showing that number-related neural activity in monkeys carrying out numerical tasks occurs in brain networks homologous to those activated in humans carrying out similar tasks [26].

To be foundational, representations of numbers must be capable of being entered into arithmetic operations. Formally, arithmetic is interpretable in terms of manipulations on sets [27,28] and much of early learning is based on physical manipulation of sets of objects [29]. Therefore, representations must be capable of being entered into set-based operations. This will involve both number abstraction (the capacity to represent the numerosity of a set) from number reasoning (the capacity to use number representations in arithmetic operations) [30]. The typical development of arithmetic competencies for whole numbers is given in Table 2. Therefore, the relevant foundational capacities must be able to represent numerosities of sets abstractly (independently of the properties of the objects in the set) and must be able to carry out arithmetic operations on them, specifically the standard school operations of addition, subtraction, multiplication and division. Of course, arithmetic, even in primary school (K–6), involves fractions and decimals as well as whole numbers.

As preconditions, foundational capacities for number reasoning must be able to establish the numerical equivalence or non-equivalence of two sets through one-to-one correspondence, and to distinguish transformations that do and do not affect numerosity. These requirements, already identified by Piaget [31], constitute benchmarks against which to evaluate theoretical accounts of the foundational capacities supporting the development of arithmetic.

The approximate number system (ANS)

Although there is little doubt that we share with many nonhuman species a system for estimating and comparing approximate numerosities [26,32], the role this system plays in the development of arithmetic remains to be clarified. The ANS is one system of core knowledge of

Table 1. Definitions of dyscalculia and equivalent constructs

DSM-IV [84]	**Mathematics disability**: the child must substantially underachieve on a standardized test relative to the level expected given age, education, and intelligence and must experience disruption to academic achievement or daily living
International Classification of Diseases 10 [85]	**Specific disorder of arithmetical skills:** specific impairment in arithmetic skills that is not solely explicable on the basis of general mental retardation or of inadequate schooling
Department for Education and Skills UK [86]	**Dyscalculia:** condition that affects the ability to acquire arithmetic skills. Dyscalculic learners can have difficulty understanding simple number concepts, lack an intuitive grasp of numbers, and have problems learning number facts and procedures. Even if they produce a correct answer or use a correct method, they might do so mechanically and without confidence

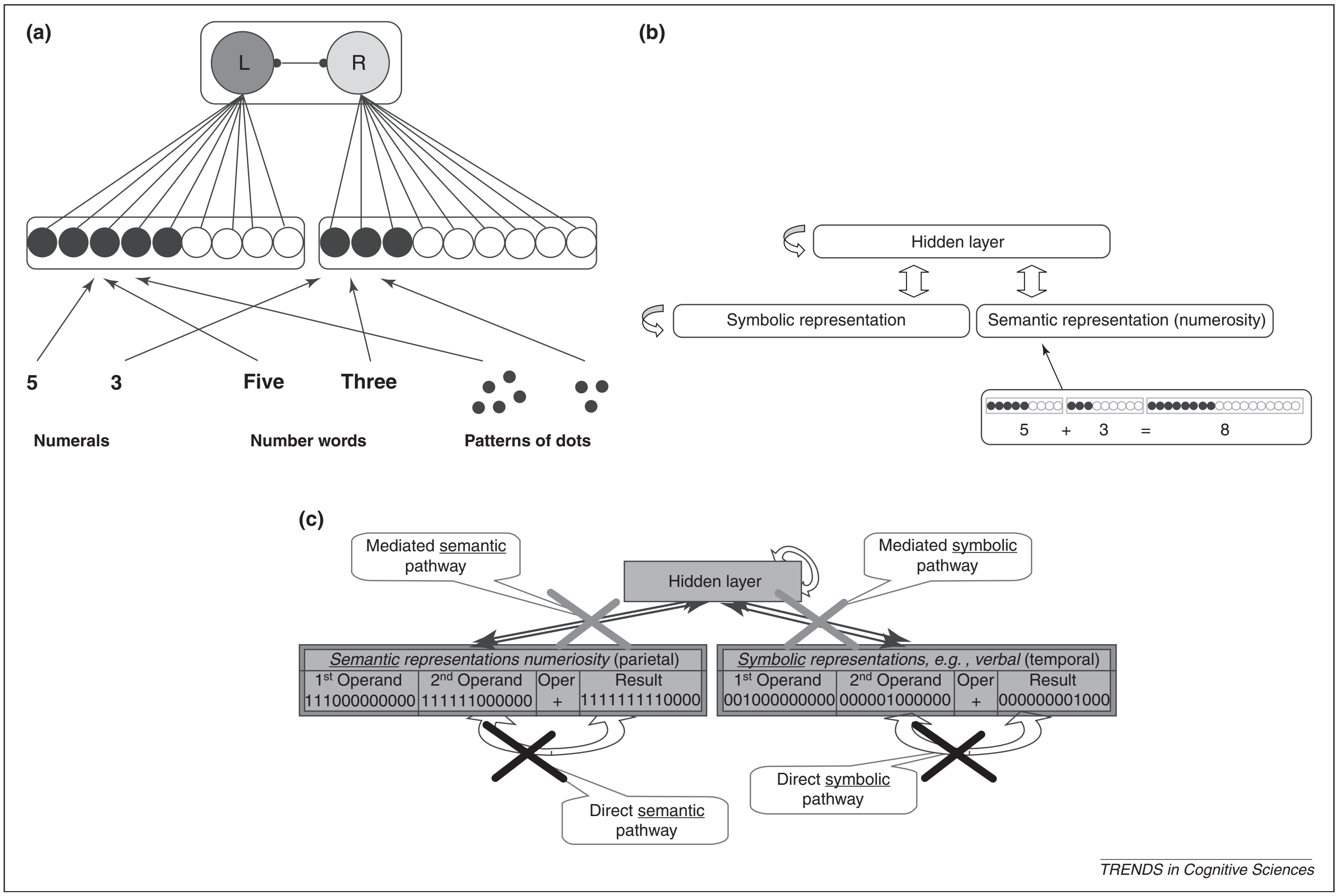

Figure 1. Numerosity coding. **(a)** Structure of numerosity coding in a neural network model [60,61]. Numeral, verbal and non-symbolic numbers are mapped onto an internal code that represents each numerosity as a set of discrete 'neurons'. For number comparison, each set contributes activation proportional to the number of neurons activated to a binary (in this example) decision procedure with reciprocal inhibition between nodes. Reaction times are modelled as the number of cycles for the decision process to settle into one state. This provides a good fit to human reaction time data [60]. Reproduced with permission from [61]. **(b)** The same internal coding can be used as part of a system for addition. Reproduced with permission from [61]. **(c)** To model verbal coding of addition facts, a symbolic route consists of arbitrary codes for the operands so that contribution of this coding can be evaluated. Reproduced with permission from [61]. The distinction between semantic and symbolic coding facilitates modelling of the effects of neural damage by reducing the connections between addends and sums. Network performance is worse the greater the damage, but the effect is greater when the connections within the semantic network are damaged. This reflects the findings in acquired dyscalculic patients that parietal lobe lesions affecting numerosity representation impair addition and subtraction, whereas damage to temporal lobe language areas affects mappings from symbolic input to output but not knowledge of arithmetic facts and procedures [62].

numbers [32] According to this approach, number-abstraction processes extract some kind of summary statistics from a scene (which, in principle, could be in a modality other than visual) that is separate from the processes implicated in analogue quantity estimation (how many objects vs how much stuff), but is nevertheless mapped onto analogue magnitude representations.

The strongest claim is that 'this nonverbal quantification system seems to constitute the phylogenetic and ontogenetic foundation of all further, more elaborate numerical skills' [26], which presumably includes arithmetic. In a number of studies, Spelke and colleagues correlated children's performance on tasks involving approximate arithmetic with tasks involving symbolic arithmetic. The method used to assess ANS functioning is typically non-symbolic number comparison, whereby the larger of two random arrays of objects, dots or squares systematically varied for area is selected. Either the accuracy of the response or its speed is used to determine individual numerical acuity. These scores are then correlated with performance on symbolic tasks [33]. Recent studies report a correlation between numerical acuity and mathematics attainment [34,35] (see also Piazza, this issue).

However, there are problems with ANS as a foundational capacity for arithmetic learning. First, the ANS system is primarily concerned with number abstraction and not at all with number reasoning. It is unclear how approximate numerosities, or their analogue representations, satisfy the two basic preconditions of arithmetic reasoning (see above). First, one-to-one correspondence cannot be carried out with approximate sets to establish their equality or inequality. Second, the effects of different types of transformations cannot be determined on approximate sets. Therefore, addition of one or subtraction of one might not be detectable. In any event, the idea that these transformations should affect numerosity cannot be captured by this type of representation. Conversely, transformations that do not affect numerosity might well affect estimations or judgments made by the ANS. It is known, for example, that the nature of objects to be enumerated [36] and their visual crowding reduce the accuracy of numerical estimation [37]. A third problem is that approximate numerosities

Box 2. Methodological problems

- Developmental hypotheses need longitudinal studies to determine whether the measures used are stable over time. That is, if a learner is in a slow group at age 5 years, will he or she still be in the slow group at 11 years or older? If they are not, that will be unhelpful for predicting outcomes in the long term.
- The stability of measures needs to be contrasted with their changes over time. Learners get faster and better as they get older. What are the typical and atypical trajectories of these changes?
- Are the slowest or lowest group at age 5 years simply delayed or are they qualitatively different on the basic measures? For example, will the parameters of their enumeration or number comparison performance always differ from their peers?
- Most studies use a single measure of underlying capacity, which might lead to artefacts. It is critical to use convergent measures, as determined by theory.
- Studies assume that graded differences in underlying capacity will lead to graded differences in arithmetic attainment. However, it might be that the underlying capacity only needs to be good enough. (According to the Matisse effect, having colour blindness will prevent you from being the next Matisse, but normal colour vision will not ensure that you are.)
- Studies of number reasoning are needed to complement studies of number abstraction.
- Prevalence studies should use a gold standard criterion based on stable predictive measures.

are held to be represented logarithmically [38], which makes the use of this representation problematic in addition and subtraction.

A main prediction from the ANS hypothesis is that dyscalculic subjects will have a deficit in approximate number tasks. ANS theory implies that approximate numerosities and symbolic numbers (e.g. 8 and eight) are mapped onto an analogue magnitude system that supports number comparison tasks. Thus, symbolic number comparison performance should index underlying numerical representations, and hence a foundational capacity relevant to arithmetic capability.

Recent studies have correlated the ability to discriminate approximate numerosities with low arithmetic attainment [33–35]. Conversely, some research has failed to find such an association. For example, approximate numerosity comparison did not discriminate typical from low-numeracy 7-year-old [39], 6–8-year-old [40] or 9-year-old children [41]. However, it is worth noting that symbolic number comparison using digits rather than arrays of objects is associated with arithmetic performance in children of 6–8 years [40].

In any event, correlations are not indicative of cause and it is unclear whether poor performance on ANS tasks is the cause or consequence of poor arithmetic ability. It is at least plausible that more work with numbers will lead to both better performance in number comparison tasks and better performance in arithmetic. It is worth noting that better counting skills are correlated with better approximate estimation [42]; again, more number work might lead to improvements in many areas of number skills.

Table 2. Typical development of whole number competencies in arithmetic [29]

Age	Typical development
0;0	Can discriminate on the basis of small numerosities
0;4	Can add and subtract one
0;11	Discriminates increasing from decreasing sequences of numerosities
2;0	Begins to learn sequence of counting words Can assign one-to-one correspondence in a sharing task
2;6	Recognizes that number words mean more than one ('grabber')
3;0	Counts out small numbers of objects Can recognize transformations that affect number
3;6	Can use the cardinality principle to establish numerosity of set
4;0	Can use fingers to aid adding
5;0	Can add small numbers without being able to count out sum
5;6	Understands commutativity of addition
6;0	Piagetian 'conservation of number'
6;6	Understands complementarity of addition and subtraction
7;0	Retrieves some arithmetic facts from memory

The small numerosity system

Arithmetic is about exact numbers, and to be foundational, representations of exact numbers need to be developed. How do approximate representations (of the type the ANS hypothesis proposes) develop into a sequence of numerosities, each with a unique successor?

One possibility is to exploit our ability to represent small numerosities without serial enumeration and with a high degree of precision; this is called subitizing (for a review see [43], but see [44]). It has therefore been proposed that the perceptual system underlying subitizing that keeps track of a small number (less than or equal to four) of individual objects [45] can have numerical content [46]. The argument is that there are distinct states of this system for individuating one, two, three or four objects [46]. This enables an individual to make inferences about addition or subtraction of one, two or three objects. Given that each state is distinct, a child will learn that distinct states of the system are associated with distinct number words: 'one' with one object, 'two' with two objects, 'three' with three objects, an so on [46].

Carey uses the concept of bootstrapping (a form of induction), so that a child infers from what she knows about the small numbers and applies this to large numbers [46] Thus, when she hears 'five' in a numerical context, and the approximate numerosity of about fiveness is active, she can figure out that the word must refer to an exact numerosity – such as one, two, three and four – and therefore conclude that the word 'five' refers not to approximately five but to exactly five (see [47,48] for assessments of this argument).

Carey and colleagues introduced a new notion called enhanced parallel individuation, whereby the contents of the small number system are treated as a set [49]. This process is called set-based quantification and enables application of the set-based properties of arithmetic. This seems to go beyond the two core systems of ANS and the small number system by introducing a third core system for both number abstraction and number reasoning that are not available in the former.

A main prediction arising from bootstrapping is that dyscalculic subjects will suffer from a deficit in the subitizing range. Although there is some evidence that the small number system is impaired in dyscalculic learners [50], enumeration of the entire range from one to nine is also typically impaired [9]. Even if a selective deficit in small numerosities is observed in dyscalculic subjects and others with delayed counting and arithmetic, this may be because subitizing enables early counters to check the result of their counting [51].

A second prediction from the small number hypothesis is that language impairments will affect number vocabulary, which in turn should affect the development of exact number concepts. However, studies of children with specific language impairment (SLI) suggest that they have no impairment in tasks on number comparison or numerical estimation [52]. Even more strikingly, they outperform learners matched for language in nonverbal number tasks [53], suggesting that grasp of the counting word sequence, for which their performance is generally poorer, is not the main driver of magnitude representation. However, they perform more poorly on many arithmetic tasks that depend on fact retrieval and more complex arithmetic procedures [54].

Numerosity coding

Piaget maintained that the concept of number, by which he meant cardinal number, is based on sets [31]. However, he thought that conservation of number under numerosity-irrelevant transformations was only possible at approximately the age of 4 years, when a particular stage in logical reasoning had been reached [31].

Since then, many studies have indicated that human infants can use the numerosity of visual arrays as a discriminative stimulus [15]. Moreover, infants can select collections of objects and treat them as a single unit [55,56]. These findings suggest that the idea of treating a collection of objects as a set might be present early in ontogeny. This would mean that a set can be a type of object that can itself take a property. This property need not be something common to the objects in the set, but could be a property of the set itself. One such property is its numerosity (a psychological way of talking about the logical concept of cardinality). Studies of infant behaviour suggest that these properties can be intermodal and therefore relatively abstract in the sense that the property of a set (e.g. eightness) is not the property of any member of the set [16,57].

The hypothesis that humans inherit a capacity to quantify over sets is not new. This was essentially the proposal of Gelman and Gallistel in 1978 [30], who hypothesized that pre-counting children, like many other species, possess numerons, an ordered sequence of numerosity concepts (e.g. the numeron for one, the numeron for two and so on). Learning to count is essentially a developmental process of learning to associate an ordered sequence of counting words with an ordered sequence of numerons. The concept of fiveness pre-exists acquisition of the knowledge that the word five refers to the numerosity fiveness.

More recently, Halberda and Feigenson suggested that the 'concept set is required and that this notion cannot come from object tracking, the approximate number system, or language... Conceiving of a set requires representing the hierarchical relationship between individual items and the larger structure into which they are bound' [58].

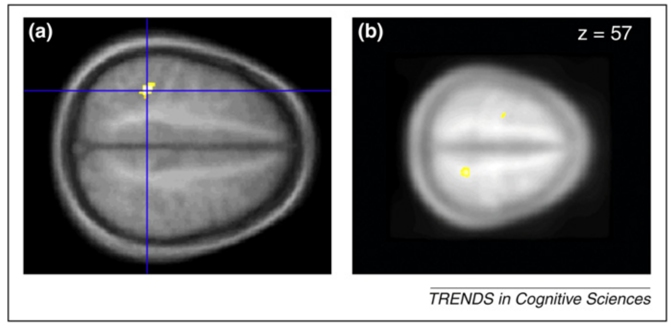

Figure 2. Structural abnormalities in young dyscalculic brains suggesting a critical role for the IPS. As noted in the text, both left and right IPS are implicated, possibly with a greater role for left IPS in older learners. **(a)** Small region of reduced grey matter density in left IPS in an adolescent dyscalculic. Reproduced with permission from [69]. **(b)** Right IPS with reduced grey matter density in a 9-year-old child. Reproduced with permission from [70].

There is also evidence showing that numerosity processing in the brain is distinct from the processing of continuous quantity, and that the numerosity of sets of objects distributed in time is processed by the same mechanisms as for sets distributed in space [59].

This conceptualization has been captured in a neural network model called the numerosity code [60,61]. The idea here is that mental representation of numerosities is a discrete set of neuron-like elements. Metaphorically, oneness is represented by one element, twoness by two elements, and so on (Figure 2). There is thus a step change from one numerosity to the next, unlike in the ANS. Although discrete, this type of representation can parametrically capture number comparison accuracy and reaction time (RT) data, as well as arithmetic accuracy and RT data, including the well-known problem size effect, in which RTs increase with the size of the sum (Glossary) [60,61]. Note that the model includes a standard decision procedure used widely in neural network modelling.

A main prediction arising from the numerosity coding hypothesis is that dyscalculic subjects will suffer from a deficit in enumerating sets. Although this might seem like a simple extension of small number coding, no upper limit or a role for attention is assumed. In fact, several studies of dyscalculia have shown this in group studies [9] and in individual cases [41].

The numerosity coding hypothesis further predicts that impaired numerosity representations will affect addition. The effects of impaired representations of numerosity on addition within the neural network model have been simulated [62]. Both semantic representations (numerosities) and symbolic representations are included in the model because it has been claimed that addition facts are represented as non-semantic verbal formulae [63]. In verbal representations, the form of the representation is arbitrary with respect to the magnitude of the addends or the results. The main result is that damage to even a relatively small proportion of the connections between the numerosity representations of addends and results affected accuracy, whereas damage to the symbolic connections had a much smaller effect, regardless of whether the answer was symbolic or semantic.

Numerosity coding also enables, although it does not entail, individuals to use fingers in arithmetic because it provides a set of elements that can be put in one-to-one correspondence with a set of fingers. The link between fingers and arithmetic is close in both development and the brain. Damage to the left angular gyrus has long been known to affect both in Gerstmann's syndrome [64] and recent research has shown that transcranial magnetic stimulation over the angular gyrus interferes with both [65]. It is not clear how either the ANS or the small number system could support the one-to-one relationship between the set of fingers (or other body parts) and the set involved in arithmetic.

A final prediction arising from the numerosity coding hypothesis is that poor finger representations in the brain (finger agnosia) will be associated with poor arithmetic skills. The link between fingers and numbers was described 90 years ago by Gerstmann, who observed frequent co-occurrence of finger agnosia, dyscalculia, left–right disorientation and apraxia following damage to the angular gyrus, A developmental form of this syndrome has been documented and poor finger gnosis in young learners predicts poor arithmetic [66]. Moreover, poor representations of numerosity might also hinder the development of finger use in early arithmetic, even where the learner has good finger representations, because the mapping between fingers and numerosities will be obscure. This hypothesis has still to be tested.

Role of language

The counting words, or what Carey calls the integer list, is held to play a special role in the emergence of exact arithmetic ability during child development [46]. Thus, a critical test of the role of language in the development of arithmetic ability is whether language impairments cause arithmetic disabilities. It is claimed that the role of language is to refine approximate representations through bootstrapping and regular association of a counting word with a particular approximate numerosity. If this is the case, then language impairments should affect very simple numerical tasks, such as numerosity comparison and set enumeration. Children with SLI invariably show slower and less accurate verbal counting, held to be the key element in the transition from approximate to exact representations of number. However, these learners perform as well as age-matched controls in number comparison and number reasoning, and better than younger language-matched controls [67].

Nevertheless, symbolization of numerosities is undoubtedly important in both individual and collective arithmetic skills because it can be used to think about numbers and to communicate facts about them [47]. Moreover, symbolization supports syntax, which in turn supports reasoning about large and small numbers that an individual has never before experienced and perhaps cannot know by direct experience. This might be particularly important in understanding fractions, decimals and division more generally. According to this notion, the development of arithmetic skills and knowledge could be affected by low language competence, even when mental representation of numbers is intact. This does seem to be the case [67,68].

As noted above, children can attain normal levels on non-symbolic comparison tasks yet show impaired symbolic digit comparison. Noël and colleagues have proposed that this might reflect a failure to link intact number concepts with their symbolic representations, which they suggest is at the root of dyscalculia [39]. However, as noted above, basic number concepts as measured by non-symbolic comparison tasks can also be defective, so linkage failure cannot provide a full explanation.

Neural basis of dyscalculia

Can studies of neural differences in structure or activation in dyscalculic subjects be used to decide among the foundational hypotheses? Structurally, reduced grey matter in dyscalculic individuals has been observed in areas involved in basic numerical processing, in the left IPS [69], in the right IPS [70] and in the IPS bilaterally (Figure 3) [71]. Moreover, there seem to be differences in connectivity between relevant regions as revealed by diffusion tensor imaging tractography [71].

Activation differences in non-symbolic number comparison in young learners have also been observed in the right IPS [72] and symbolic abnormalities in the left IPS [73]. The reason for these apparently conflicting findings is not yet clear. Two considerations might in time clarify the picture. First, the organization of numerical activity might change with age [74], shifting from right dominance to left dominance [75] as representations of numerosity link up with language [25]. Second, there might be residual specializations in the two parietal lobes, with the right specializing in subitizing and estimation [76,77] and the left in symbolic processing and calculation. If this is correct, longitudinal studies that combine neuroimaging with careful tests of basic numerical capacities might reveal different developmental trajectories depending on the locus of the neural abnormality. However, the representations of approximate numerosities, exact numerosities and their symbols occupy overlapping neural systems [23,78] so these cannot yet be used to decide among hypotheses.

Intervention

The efficacy of interventions designed to strengthen purported foundational capacities would constitute a critical test of the hypotheses discussed in preceding sections. For the ANS, Piazza and colleagues note that their 'findings lend support to remediation programs for developmental dyscalculia that include exercises aimed at retraining the core non-symbolic sense of number and to cement its links to the symbols used to denote it' [79]. The intervention they cite as appropriate is the Number Race game [80], a digital environment that is effective in promoting basic number skills [81]. However, this game uses relatively small exact numerosities rather than approximate numerosities. It would be interesting to see if training to improve the Weber fraction in approximate comparison improves arithmetic, as the ANS account would predict.

Other attempts to use digital media have also focussed on exact rather than approximate numerosities in numerical tasks involving some very simple arithmetic [82]. Similarly, the use of board games to promote numerical understanding has used small exact numerosities based on dice and counting with the aim of moving children away from approximate numerosities represented logarithmically to a

Box 3. Priorities for future research

- Establish developmental trajectories of key measures.
- Determine whether different aspects of number abstraction processes are critical at different stages in the development of arithmetic ability.
- Implement tests of number reasoning appropriate for different ages or stages.
- Use targeted interventions to help those with low arithmetic attainment and to test hypotheses about the domain-specific precursors to arithmetic ability.
- Establish the heritability of basic capacities using twin studies.

linear representation [83]. This preliminary evidence supports the idea that numerosity coding is foundational; however, systematic tests using approximate numerosities have yet to be attempted.

Concluding remarks

In summary, although the evidence is not yet conclusive, it seems that the ANS and small number systems are not sufficient to support the typical development of arithmetic skills. A system that represents sets, their numerosities and the effects of transformations on these sets seems to be required. Numerosity coding is such a system and there is extensive evidence that young humans possess this. However, we have only just begun to collect critical evidence from longitudinal and intervention studies of the developmental trajectory for typical and atypical learners. Definitive answers are therefore not yet available (Box 3).

Acknowledgements

I am grateful for helpful comments by and discussions with Randy Gallistel, Justin Halberda and Sashank Varma, and for comments on the manuscript by three anonymous referees.

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