Review

Special Issue: Space, Time and Number

Neurocognitive start-up tools for symbolic number representations

Manuela Piazza[1,2]

[1] INSERM, U562, Cognitive Neuroimaging Unit, CEA/SAC/DSV/DRM/Neurospin Center. Bât 145, Point Courier 156. F-91191 Gif-sur-Yvette Cedex, France
[2] Center for Mind/Brain Sciences and Dipartimento di Scienze della Cognizione e della Formazione University of Trento, Palazzo Fedrigotti - corso Bettini 31, I-38068 Rovereto (TN), Italy

Attaching meaning to arbitrary symbols (i.e. words) is a complex and lengthy process. In the case of numbers, it was previously suggested that this process is grounded on two early pre-verbal systems for numerical quantification: the approximate number system (ANS or 'analogue magnitude'), and the object tracking system (OTS or 'parallel individuation'), which children are equipped with before symbolic learning. Each system is based on dedicated neural circuits, characterized by specific computational limits, and each undergoes a separate developmental trajectory. Here, I review the available cognitive and neuroscientific data and argue that the available evidence is more consistent with a crucial role for the ANS, rather than for the OTS, in the acquisition of abstract numerical concepts that are uniquely human.

Neurocognitive start-up tools

Current theories of cognitive development posit that knowledge acquisition is based on a limited set of 'core knowledge' systems, defined as domain-specific representational priors that guide and constrain the cultural acquisition of novel representations [1,2]. This notion fits well with a recent proposal that cultural learning occurs by a partial reconversion ('cortical recycling') of a few cerebral circuits initially selected to support evolutionary relevant functions, but sufficiently plastic for changing their coding scheme and acquiring new functions [3]. The combination of these two ideas defines the notion of a 'neurocognitive start-up tool'. In the specific case of numbers, I review the features of two pre-verbal systems for numerical quantification, the approximate number system (ANS) and the object tracking system (OTS), and critically assess their role in the cultural learning of symbolic numbers. Although the evidence is as yet inconclusive, I argue that the currently available cognitive and neural data are more consistent with a foundational role of the ANS, rather than the OTS, in the acquisition of more elaborate numerical concepts.

The approximate number system

Approximate number, much like colour or shape, is a basic feature of the environment to which animals appear wired to attend to: spontaneous extraction of an approximate

Corresponding author: Piazza, M. (manuela.piazza@gmail.com).

Glossary

Cardinality: a property of sets indicating the number of elements in the set.
Dyscalculia: a specific learning disability that affects the acquisition of knowledge about numbers and arithmetic.
MVPA algorithm: classification algorithm based on the distributed pattern of activation over multiple voxels within a given brain region.
Phonological awareness: an individual's awareness of the phonological structure of words. It includes the ability to distinguish different units of speech, such as individual phonemes in syllables, syllables in words and rhymes between words. Phonological skills are crucial for the development of reading, as they are an important and reliable predictor of later reading ability [88,89].
Scalar variability: a property of the response distribution in estimation tasks (including numerosity estimation), whereby the mean responses and standard deviation of the responses are proportional to each other as the quantity to be estimated varies, such that the coefficient of variation (standard deviation/mean) is constant across a range of quantities. Scalar variability is an instance of Weber's law [90].
Subitizing: the rapid, accurate and confident judgment of the number of items in small collections 'at a glance', without counting. Subitizing is thought to emerge from the ability to allocate attention over multiple individual items in parallel (i.e. the OTS system) [34,91].
Successor function: a rule establishing the existence of a minimal quantity, ONE, which corresponds to the minimal distance between two successive numbers.
Weber fraction: the smallest variation to a quantity that can be readily perceived. When performing numerosity discrimination threshold experiments, the first analysis is often aimed at establishing whether Weber's law holds for that set of discriminations. If it does, the next step is to determine what the Weber fraction is. The Weber fraction can be straightforwardly derived from the accuracy performance as the difference between the two closest discriminable numerosities normalized by their size, and can also be expressed as a percentage. Better fits of numerosity response functions can be obtained by modeling the task with more refined psychophysical functions, including some free parameters accounting for response biases that, in particular conditions, might influence performance [23,92,93]. The measure derived by this method has been labeled 'internal Weber fraction' to differentiate it from the 'behavioral Weber fraction'. Irrespective of the method used to estimate the Weber fraction, different studies find broadly convergent results that an average adult can reliably discriminate sets with a numerical ratio of 7:8 (a Weber fraction of ~ 0.15) [22,23,64,91,92].
Weber's law: a psychophysical law describing the relationship between the physical and the perceived magnitude of a stimulus. It states that the threshold of discrimination (also referred to as 'smallest noticeable difference') between two stimuli increases linearly with stimulus intensity. Weber's law (as first demonstrated by Gustav Fechner [14]) can be accounted for by postulating a logarithmic relation between the physical stimulus and its internal representation.
$Dp = K*\Delta S/S$: where Dp is the smallest noticeable difference; ΔS is the physical difference and S is the stimulus intensity.

1364-6613/$ – see front matter doi:10.1016/j.tics.2010.09.008

number of objects in sets is reported in several species, both in the wild and in more controlled laboratory settings (reviewed in [4]). For example, macaque monkeys spontaneously match the approximate number of individuals they see to the number of individuals' voices that they hear [5]; they also sum up visual and auditory stimuli to estimate their total number, without previous training [6]. The evolutionary relevance of such ability is clear: appreciation of number (e.g. of ingroup versus outgroup members) can be crucial for social behavior [7,8], foraging [9] and reproductive strategies [10]. Although not precise, number representations in non-human animals can be mentally combined to perform complex operations, such as comparison, addition and subtraction across sets [11,12]. In humans, a similar spontaneous detection of the approximate number of objects in sets, even across different sensory modalities, is reported surprisingly early, from the first hours of life [13]: newborn babies habituated for some minutes to auditory sequences of a given number (e.g. six syllables), look longer at numerically matching visual sets (e.g. six dots) subsequently presented to them than to non-numerically matching sets (e.g. 18 dots). However, they fail with sets differing numerically by smaller ratios; for example, 6 versus 12 elements. This suggests a shared evolutionarily ancient innate system for approximate number: the ANS.

The most important defining feature of the ANS is that it represents number in an approximate and compressed fashion, in such a way that two sets can be discriminated only if they differ by a given numerical ratio, according to Weber's law (see Glossary). Weber's law (as first demonstrated by Fechner [14]) can be accounted for by postulating a logarithmic relation between the physical stimulus and its internal representation. Most current models of the internal representation of number assume that such logarithmic relation comes from the compressed nature of the internal representation of numerosity itself. For some models, this takes the form of equally spaced mental magnitudes with increasing noise [15] whereas for other models, it takes the form of logarithmically spaced mental magnitudes with fixed noise [16,17]. Taking a different perspective, other researchers have suggested that the origin of the weberian nature of numerosity compression is to be found in the computational processes engaged

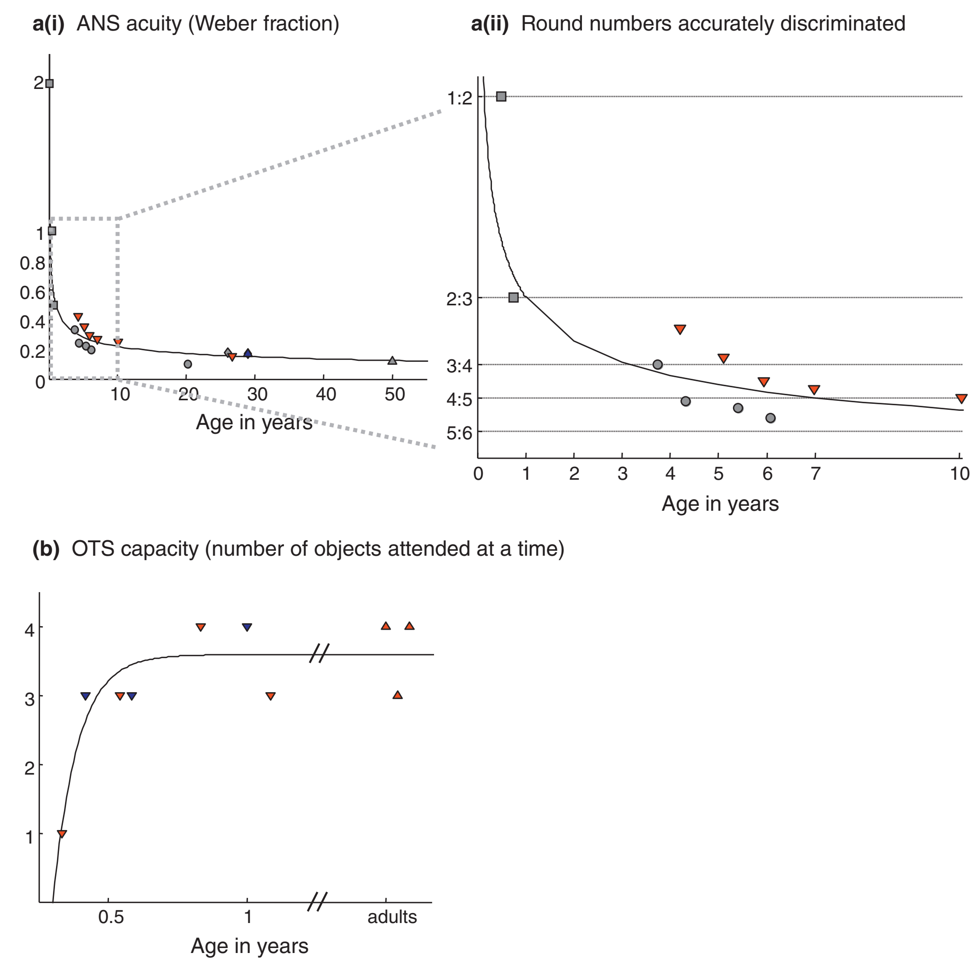

Figure 1. ANS and OTS development. The ANS acuity increases during the life-span with an sharp improvement during the first years of life, followed by a progressively smaller but long-lasting effect reaching plateau during adulthood, while the OTS reaches its adult-like capacity already around the first year of life. **(ai)** Estimated Weber fractions (measuring ANS acuity) are reported from different studies as a function of subjects' age. In (ii), Weber fractions are expressed as the two closest round numbers accurately discriminated in the age range between zero and ten years old. Solid black line indicates power function fit. Data from: grey squares, infants [13,25]; red triangles [19,22]; grey triangles [92]; grey circles [21]; blue triangles [92]. **(b)** Estimates of OTS capacities are reported from different studies as a function of subjects' age. Solid black line shows exponential function fit. Data from: inverted red triangles [36]; blue triangles [38]; red triangles [34,35,39].

during the judgment of relative numerical magnitude [18]. Although theoretically possible, this hypothesis is not supported by neuroimaging data, which show a weberian neural response to number even in conditions in which subjects do not perform any explicit computations on the stimuli but simply observe sets of different numbers [19].

Irrespective of the specific model of the internal representation of number assumed, the Weber fraction can be safely taken as an index of ANS acuity. Interestingly, the ANS acuity varies across individuals, and this variability is present from early in life [20–22]. Moreover, it is not stable across the life span but increases consistently during development [22,23], most dramatically during the first years of life: whereas newborns can discriminate sets differing by a minimal numerical ratio of 1:3 at birth [13], at six months their acuity increases to 1:2, and to 2:3 at approximately 9 to 12 months of age [20,24,25]. Between the third and fourth year, children can discriminate reliably between sets with a 3:4 ratio, and can become sensitive to an adult-like 7:8 ratio at approximately 20 years of age [22,23] (Figure 1).

Neuroimaging techniques have been used to investigate extensively the neuronal underpinnings of the ANS in humans. Converging results using passive fixation [19], as well as tasks such as numerosity comparison [26], or approximate calculation [27] of dot patterns or sequentially presented stimuli [28], consistently point to regions in the mid intraparietal sulcus as the source of approximate number representations in both adults and infants (Figure 2; recently reviewed in [29,30]).

The object tracking system

The OTS is a mechanism by which objects are represented as distinct individuals that can be tracked through time and space. This core system for representing objects centers on the spatio-temporal principles of cohesion (objects move as bounded wholes), continuity (objects move on connected, unobstructed paths), and contact (objects do not interact at a distance). These principles enable human infants, as well as other animals, to perceive object boundaries, and to predict when objects will move and where they will come to rest [1].

One of the defining properties of this system is that it is limited in capacity to three or four individual objects at a time. This property has been confirmed using several different tasks, such as visual short-term memory (VSTM) tasks, whereby simple features (such as colour or orientation) of a small, limited number of objects can be accurately retained in memory ('visuo-spatial short-term memory

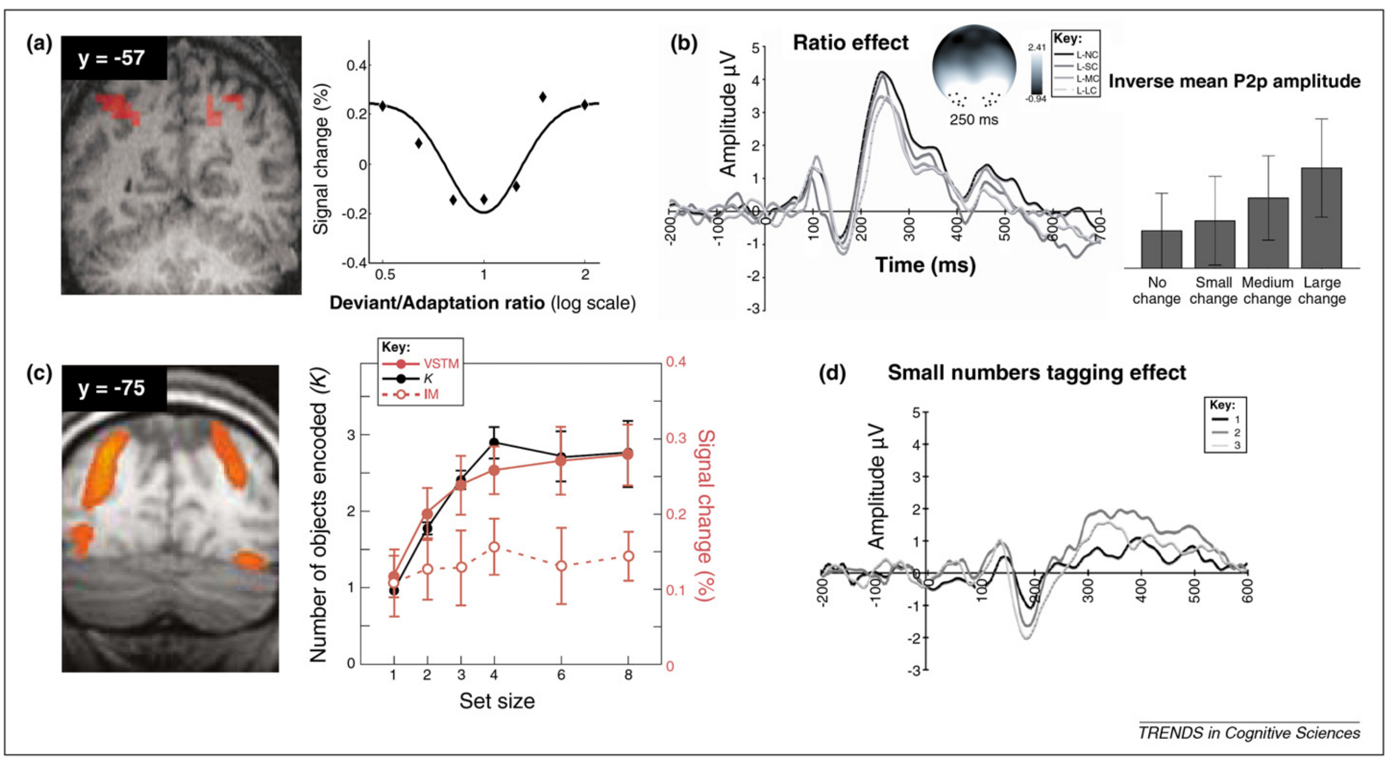

Figure 2. The neural basis of the ANS and the OTS. **(a)** Mid-Parietal regions showing weberian responses to non-symbolic numerical quantity in an fMRI number adaptation experiment investigating the neural underpinning of the ANS in human adults. Adaptation stimuli were sets with a fixed number of dots, whereas deviant stimuli, presented rarely, were sets of variable number along a continuum spanning from half to double the adaptation values. Parietal activation for deviant numerical stimuli was a direct function of the ratio between the deviant and the adaptation number, according to Weber's law [19] **(b)** ERP recordings of activity evoked by numerically deviant stimuli embedded in sequences of repeated numerically fixed stimuli (EEG adaptation) characterize the time course of brain activation associated with the ANS, showing that parietal electrodes are modulated by the size of the numerical change between the deviant and the adaptation number (L-NC: large number, no change; L-SC: large number, small change; L-MC: large number, medium change; L-LC: large number, large change) at ~250 ms after stimulus onset (at the level of the N1 to P2p transition zone) [48]. **(c)** Posterior parietal regions which activity shows OTS signature (linearly increasing response for sets with one to three or four items and leveling off thereafter) in an fMRI visual short term memory (VSTM) experiment [39]. Subjects were shown sets of one to eight colored dots and, after a short retention period were subsequently asked to detect a change in color of one of the items. Paralleling behavioral responses, measured as the estimated number (K) of encoded colored dots at each set size, posterior parietal activation shows a set-size limit at approximately three or four items. The same regions did not show the same response when subjects were performing an iconic memory (IM) task consisting of detecting the presence of a given color in the same displays used for the VSTM. **(d)** Electrophysiological signatures of the OTS. ERP recordings of activity evoked by numerically deviant stimuli embedded in sequences of repeated numerically fixed stimuli (EEG adaptation) show that for small sets of one to three items, the amplitude of an early (150 ms post-stimulus) negative peak (N1), over parietal electrodes is not modulated by the size of the numerical change, as it is the case for large numerositieis, but it is modulated by the absolute number of items (set size effect) [48].

Box 1. The ANS and the OTS: two different systems?

There has been an ongoing debate about whether subitizing and the OTS reflect a mechanism dedicated to small sets, or whether they instead reflect the ANS, which, owing to its Weberian nature, encodes small numbers with a higher precision than it does for larger numbers [49,94]. More recently, however, behavioral evidence for a non-estimation-like process responsible for subitizing has been reported: first, in dual task conditions, attentional manipulations affect subitizing but not estimation [91]; second, in the small one to four subitizing range, the variability of the estimates (or coefficient of variation) is lower than that in the large 10–40 range, even when the ratios between numbers is identical across ranges; finally, the interindividual variability in subitizing span and in large numerosity estimation precision does not correlate across subjects [34]. Interestingly, the absence of correlation between the ANS and the OTS has been recently replicated in infants as young as nine months [20].

Further behavioral support for the distinction between the ANS and the OTS comes from studies of young infants conducted mainly by Feigenson and colleagues (reviewed in [51]). First, for small sets falling within the limits of the OTS (less than four), but not for large sets, when certain such features (such as surface area or contour length) are pitted against number, infants sometimes attend more automatically to those and thus fail to respond to number. Second, if, of two sets to be compared or matched, one falls within the OTS capacity (e.g. less than four objects) and the other one beyond (more than four objects), the infants also fail to attend to number, or need extremely large numerical ratios to succeed [95]. This suggests that the OTS is automatically recruited whenever the number of items falls within its limits and, under some occasions, might even mask the ANS, thus interfering with otherwise perfectly feasible numerical operations.

SPAN') [31], or multiple object tracking (MOT) tasks, whereby a few moving items can be tracked in parallel throughout the display ('multiple objects tracking capacity') [32]. The existence of the OTS is also evident in enumeration tasks: subjects can determine the number of objects in small collections of three or four items with high accuracy and high speed, even in conditions of very briefly presented or masked stimuli (a phenomenon called 'subitizing') [33,34]. For sets with more than three or four items, enumeration is only possible either via exact counting, which implies a serial scanning of the display, or via approximate estimation, which falls under the computational constraints of the ANS, thus reflecting Weber law's through scalar variability (Box 1).

Similarly to the ANS, the OTS also varies across individuals [21,34,35], and is also subject to maturation: using preferential looking paradigms, researchers have shown that the capacity limit of the OTS develops quickly over the first year of life, such that the OTS capacity at six months is limited to a single object, whereas its capacity reaches an adult-like limit of three or four items at approximately 12 months [36–38] (Figure 1). The neural underpinnings of the OTS are less clearly defined, but appear to be distinct from the neural substrates of the ANS. Several neuroimaging studies using object tracking tasks report capacity-limited neural activation, paralleling behavioral measures, in the posterior parietal and occipital regions bilaterally [35,39–42]. By contrast, other researchers associate subitizing to regions of the right temporo-parietal junction [43,44]. Neuropsychological studies indicate a crucial role for the posterior parietal cortex in the OTS, as the inability to track multiple items in parallel (a disorder called 'simultanagnosia' [45]) typically emerges following lesions to the bilateral posterior parietal cortex [46]. Interestingly, patients with simultanagnosia also appear to have a restricted subitizing range (at approximately two items) [47].

Electroencephalography (EEG) recordings also support a separation between the neural signatures of the ANS and OTS. For example, using an adaptation paradigm, Hyde and colleagues showed that the amplitude of an early (150 ms post-stimulus) negative peak (N1), centered over the parietal cortex, was modulated by the absolute number of elements in the display for small numbers; by contrast, the amplitude of a later (250 ms post-stimulus) positive peak (P2p), also centered over parietal cortex, showed an ANS signature in that it was modulated by the ratio of change in the large number range, regardless of the absolute number of objects presented [48]. Source reconstruction of the EEG event-related potentials (ERPs) was not performed in this study, and this did not enable any conclusions to be drawn on the anatomical dissociation between the ANS and the OTS.

In sum, although somewhat inconsistently across studies, the OTS appears to be associated with regions of the posterior parietal and occipital cortices that do not appear to overlap with regions involved in the ANS. The electrophysiological signatures of the two systems also appear to be distinct.

The role of the ANS and the OTS in the acquisition of symbolic number representations

Most existing proposals of the acquisition of symbolic number (here the term 'symbolic numbers' stands for positive integers) claim that the symbols for numbers acquire meaning by being mapped onto the pre-existing core quantity representations: some proposals highlight the role of the ANS [15,17,49], others the role of the OTS [2,50], whereas others consider the combination of the two systems as crucial [1,51] [see [52] for a concise review of the different positions, [53] for a proposal that neither the ANS nor the OTS has any role in learning symbolic numbers, and Butterworth (this issue) for the proposal of an innate representation of large exact number].

Here, I focus on the question of whether the ANS and OTS are foundational (i.e. act as start-up tools) in symbolic number acquisition. In critically reviewing the existing cognitive and neuroscientific literature, I assess two criteria that are definitional for neurocognitive start-up systems [3]: (i) their integrity should be a necessary (albeit not sufficient) condition for efficient learning in a given domain. Thus, early impairments in a foundational system should systematically lead to specific learning difficulties (in this case, dyscalculia); and (ii) their computational constraints should predict speed and ease of cultural knowledge acquisition in children, and they could also be observed even in adults after successful learning.

Evidence for a foundational role of the ANS in symbolic number processing

Traces of the ANS signature in symbolic number processing

Behavioral evidence Traces of the ANS signature in symbolic number processing appear to arise almost as soon as

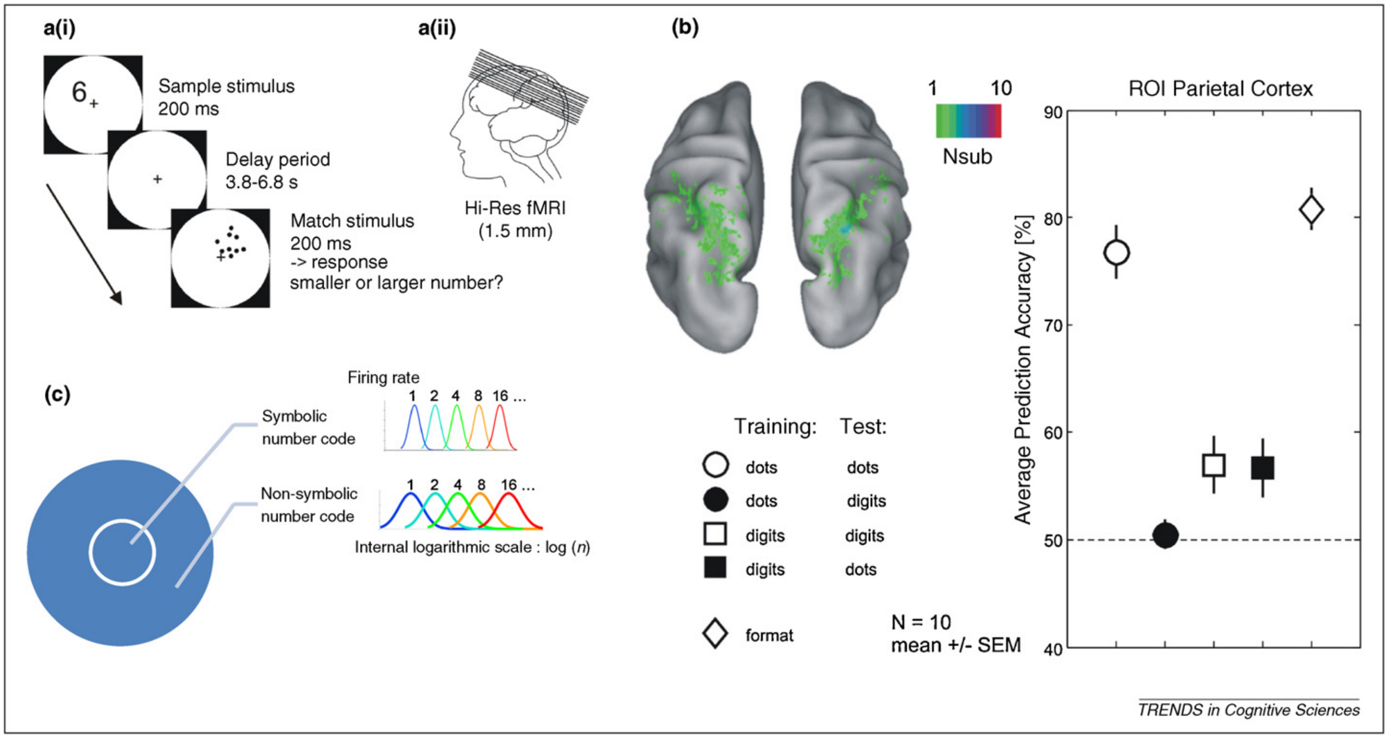

Figure 3. Neural evidence for a convergence between symbolic and non-symbolic number representations. **(ai)** Example of stimuli in a high-resolution fMRI experiment in which subjects performed a delayed comparison task with Arabic digits and dot patterns; (ii) the scanned brain region [26]. **(b)** Regions active during the comparison task and the across-subject overlap of voxels (color coding indicates the number of subjects activating the corresponding voxel). Pairwise discrimination of mean-corrected activation patterns for different numerosities was significant for training and testing with data from dot pattern stimuli, but not for training with data from dot pattern stimuli and testing with data from digits. Training and testing with data from digits were significantly above chance but less accurate than for dot patterns, as was generalization from digits to dot patterns. Discrimination of the stimulus format (symbolic versus non-symbolic) for the same number was also significant and accurate. **(c)** Possible scenario accounting for the asymmetric pattern of generalization reported in (b) [26]. A subset of parietal neurons initially encoding approximate number undergo a process of tuning sharpening during the acquisition of symbolic number such that numerical quantity accessed by symbolic numbers is coded in a more precise, quasi-categorical fashion, consistent with the simulation by Verguts and Fias [17].

children acquire symbolic numbers. In a series of studies, Gilmore and colleagues showed that four- to five-year-old children, although they had not yet been taught the principles of exact calculation, solved simple arithmetical operations on large symbolic two-digit numbers relying on an approximate, ratio-dependent representation of quantity, and that they did so spontaneously [54]. Moreover, and crucially, performance with non-symbolic numerical tasks (measuring ANS acuity) predicted children's mastery of number words and symbols as well as performance in school-level mathematics tasks done some months later, and is independent of achievement in reading or general intelligence ({Gilmore [55]}, but see [56] for failure to observe such correlation in six- to eight-year-old children).

As children undergo formal mathematical training, they solve symbolic numerical tasks with high precision. However, traces of the ANS remain discernible even in adulthood. For example, Moyer and Landauer [57] established early on that, when adults are asked to determine which of two symbolic numbers (Arabic digits or number words) is larger, they are faster and make fewer errors when their ratio is high. Symbolic ratio effects also emerge in priming contexts, in that the speed of processing of a target number (digit or number word) is influenced directly by the numerical distance to a prime number [58,59]. Such symbolic priming effects are already present in first graders (six to seven years old), and their size remains stable across development [60]. This suggests a rapid crystallization of the internal representation of symbolic numbers according to an internal scale that inherits some key properties of the scale that governs the pre-existing representation of approximate quantity (i.e. that of being approximate and compressed).

Neuroimaging evidence Complementary evidence that symbolic numbers map onto a core quantity code comes from neuroimaging studies showing a format invariant parietal response to numerical quantity. First, the same parietal brain regions and similar ERP responses are modulated by the distance and magnitude effects for both Arabic digits and non-symbolic numerical quantities [61–63]. Second, and more importantly, quantity-related responses of the mid-intraparietal cortex transfer across symbolic and non-symbolic formats. Thus, in an adaptation paradigm, the parietal response to quantity is proportional to the numerical ratio between novel and repeated quantities even when they are represented in different formats [64]. Interestingly, this effect is not fully bidirectional (especially in the left hemisphere): whereas adaptation to dots extends to Arabic digits, the opposite does not occur.

A similar asymmetric effect was reported by an fMRI 'decoding' study in which a multi-voxel pattern classifier trained on parietal cortex activation was used to predict which Arabic was presented to subjects at any given trial. The numerosity of dot patterns was also correctly classified, but not vice versa [26] (Figure 3). These data are consistent with the idea that the parietal quantity code accessed by symbolic numbers is more precise than the one

Box 2. Refining the approximate number code: neural mechanisms

One crucial step towards the construction of a representation of exact numbers is achieved when children understand the counting principles. This then enables them to perform exact quantification on sets of any cardinality, thus overcoming the low resolution of ANS acuity. The mechanisms underlying this achievement are still largely unknown. A possibility is that one key aspect would involve a quick re-tuning of the coding schemes of a subset of parietal ANS neurons, such that through interaction with a precise symbolic system, where any number n is distinguished categorically from its neighbors $n-1$ and $n+1$, the tuning curves of a subset of numerosity detector neurons would become sharper, and the number representations would segregate into categorically quasi-distinct domains for the entire number range.

This proposal, also modeled by means of a neuronal network simulation [17], is consistent with a recent neuroimaging study reporting that, whereas MVPA algorithms trained to discriminate symbolic numbers on the basis of the activity of a distributed set of parietal cortex voxels, could accurately predict the corresponding non-symbolic numerical quantities, the contrary was not possible [26]. This suggests that, in the parietal cortex, intermingled populations encoding numerical quantities show different coding schemes: broader for non-symbolic numbers, and sharper, but with preserved analog response properties, for numerical symbols.

The emergence of such new coding schemes might be mediated by feedback 'tuning sharpening' projections from categorical coding neurons in the frontal cortex [87,96,97], as suggested by higher frontal cortex activation reported in children compared with adults during both symbolic and non-symbolic comparison tasks [98–100]. The changes of parietal quantity coding schemes and the changes in their coupling with inferior frontal cortex activity should be visible using fine neuroimaging techniques during development.

Box 3. The Bootstrapping account of Carey and colleagues

Carey and colleagues suggest that children acquire the meaning of the first number words (one to four) by constructing and storing in long-term memory a mental model of a set of individuals for each number, along with a procedure that determines that the number words can be applied to any set that can be put in one-to-one correspondence with this model [2]. For example, a mental model for the number word 'two' has the form of {j k}, and a new set of two elements (e.g. of two apples) is associated with its corresponding number ('two') by one-to-one correspondences between individual objects of the external set (each apple) and individual objects of the internal model ({j k}). Although it is currently unstated in the theory whether the one-to-one correspondence is itself a parallel or a serial process, the emerging representation is not intrinsically numerical, but rather, it is a 'model of individuals' [52].

Once the child has constructed these models, the number words associated with them are then aligned with the ordered number words in the numerical sequence, which the child initially lean by route. This happens via a mechanism called 'bootstrapping'. In the case of numbers, the place-holder structure is held to be the counting list (initially acquired as a meaningless sequence of sounds), whereas the pre-constructed concepts are the small number representations, issuing from the OTS, stored in long-term memory together with the one-to-one correspondence rule. When children notice the correspondence between the first number words that refer to long-term memory representations of sets, and the first number-words in the numerical sequence, they try to align those two independent representations. The alignment between order on the number list and order in a series of sets related by additional individual, allows the children to make the induction: for any word in the count list that refers to set with cardinality n, the next word in the list refers to set with cardinality $n+1$. Children are thus able to attribute meaning to any new number word.

for non-symbolic quantity [17], even if the former maintains some degree of fuzziness and compression (Box 2).

The relation between the developmental trajectory of the ANS and the initial stages of symbolic number acquisition

One puzzling feature of lexical acquisition in the number domain is that it is a slow process. After they understand that the number words refer to numerical quantities (at approximately two years of age), and before they discover the counting principles (at approximately four years of age), children learn to map numbers one to four to the corresponding cardinalities one after the other, and it might take them up to six months to move onto the next number [65,66]. Some researchers suggested that the cause underlying this difficulty is the need to reconcile two mutually incompatible systems: the ANS, providing approximate representations of number, and the OTS, limited in capacity to three to four items, supporting operations on individual objects and providing an indirect notion of exact number [2,51,52]. Others hold that lexical acquisition is built upon the OTS without any contribution from the ANS, and attribute the seriality of this process to the fact that children have to learn the successor function. This comes from learning the count list by rote first, which is itself a serial process [2,52] (Box 3).

An alternative view, which I propose here, is that two features of the ANS alone might account for the lexical acquisition process before understanding the counting principles: first, the ANS is not restricted to large numbers, but extends to all numerosities [67–70]; and second, by virtue of its weberian code and its increase in precision during the lifespan, it comes to represent small numbers with high precision by the first years of life. A representation of (exact) number N, which is a necessary condition for lexical acquisition of numbers, emerges only if children can consistently discriminate the set of N from the numerically adjacent sets (N-1 and N+1). Thus, children should be able to understand accurately the numeral 'three' only when they can reliably distinguish a set of three from a set of two and a set of four (i.e. when they become sensitive to a 3:4 ratio). This occurs, according to the fit to the existing available data, after the third year of life (Figure 1). Indeed, children become 'three-knowers' at about this age [52,66]. The present proposal further predicts that it should be difficult to teach new number words to children if their ANS does not enable a precise discrimination of the corresponding quantities, a prediction that was recently confirmed [71]. A final testable prediction also follows: ANS acuity should tightly correlate with the interindividual variability of lexical acquisition of number during the first years of life.

The ANS and developmental dyscalculia

A strong prediction from the hypothesis that the ANS is a start-up system in symbolic number processing is that ANS impairment should engender difficulties in symbolic number acquisition. Thus, children with dyscalculia [72] should show impairments in the ANS. This prediction received recent support [22,73,74] (see, however, [75,76] for failure to detect ANS impairments in individuals with dyscalculia, and [62] for no relationship between non-sym-

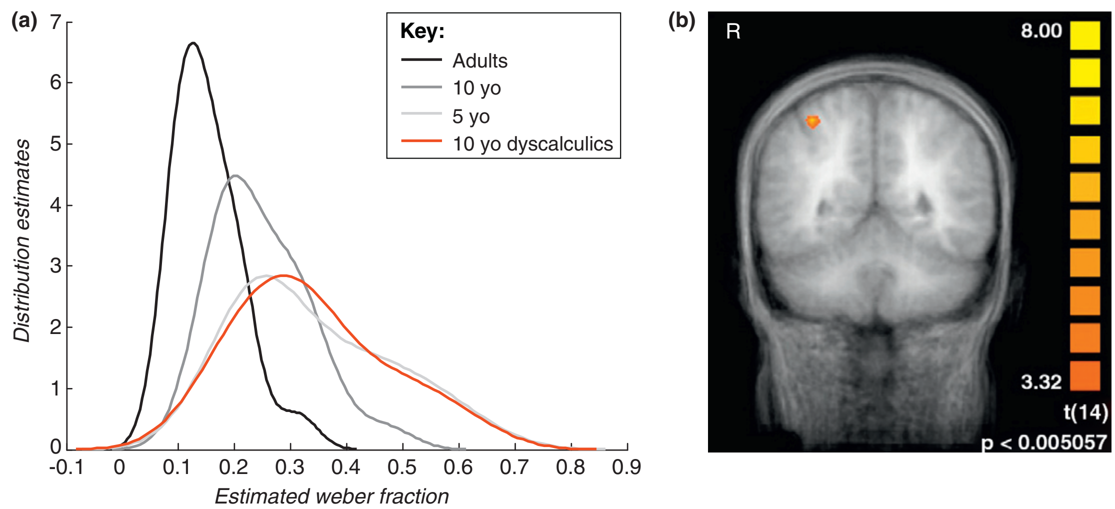

Figure 4. ANS impairments in dyscalculia. **(a)** Estimated Weber fraction distribution in four populations (using the same dots comparison task): normally developing adults (black line; $n = 20$); five-year-old children (pale-grey line; $n = 26$); ten-year-old children (dark-grey line; $n = 26$); and ten-year-old, age- and IQ-matched children with developmental dyscalculia (red line; $n = 23$) [22]. The ANS acuity in children with dyscalculia is lower than that of age- and IQ-matched controls, and identical to that of kindergarten children who are five years younger. **(b)** Right parietal regions showing decreased ratio effect in non-symbolic number comparison in children with dyscalculia compared with age- and IQ-matched controls [78].

bolic number discrimination and individual differences in children's mathematical achievement). In one study, a cohort of children aged approximately ten years old with dyscalculia was tested, diagnosed with a standardized battery probing knowledge of symbolic numbers and calculation. The performance of this group was compared to a group of age- and IQ-matched normally developing children as well as a group of five-year-old children [22]. The ANS acuity (derived from performance in a dot comparison test) of the children with dyscalculia was severely impaired compared with that of their age-matched controls and showed a five-year delay (Figure 4). Moreover, the size of the ANS impairment predicted symbolic number comparison impairments, consistent with another recent study reporting both non-symbolic and symbolic number comparison deficits in children with dyscalculia [77]. Consistently, dyscalculia is associated with decreased mid-parietal activation during both quantity comparison tasks [78] and symbolic calculation [79], as well as anatomical alterations in mid-parietal cortex (reduced gray matter, abnormal gyrification and sulcal depth) compared with control, non-dyscalculic subjects [79,80].

However, owing to the correlational nature of these results, it is at present impossible to establish firmly the direction of the causal links between dyscalculia, ANS impairments, and altered parietal function and structure. ANS impairments, together with the related parietal dysfunctions might be both the cause and the consequence of lack of learning to manipulate symbolic numbers, inasmuch as in the dyslexia literature lack of phonological awareness as well as altered activation in posterior perisilvian areas are seen both as a putative cause of the reading impairment, but also as a consequence of lack of learning to read [81].

In sum, although several strands of behavioral and neuroimaging evidence point toward an important and long-lasting role of the ANS in symbolic numerical thinking, the ultimate proof of its foundational role in the acquisition of symbolic numbers will only be provided by longitudinal investigations. At present, the only existing longitudinal study reporting a specific correlation between ANS acuity and mathematical achievement relates the ANS acuity of 14-year-old children to their mathematical proficiency earlier on (extending back to kindergarten) [21]. However, in light of the previously discussed issues of circular causality, it would be important to know whether ANS acuity as measured early in life, and crucially before the acquisition of symbolic numbers, can reliably predict subsequent success in arithmetical tasks (Box 4).

Evidence for a foundational role of the OTS in symbolic number processing

Some theories of the acquisition of symbolic numbers propose that the OTS is foundational because it provides the notion of exact number and enables the endorsement of the successor [11] relations between adjacent numbers [2,50–52] (Box 3). Indeed, it is often claimed that the ANS cannot provide semantic foundation to the

Box 4. Questions for future research

- Does ANS acuity increase smoothly during development or are there any developmental discontinuities? If so, what are they related to?
- What is the direction of the causal relation between the ANS and mathematical achievement? Is ANS acuity as measured early in life a reliable and specific predictor of later mathematical achievement?
- Does the refinement of the ANS during the lifespan reflect maturation or is it driven by training with symbolic numbers?
- Do early impairments in the OTS engender developmental dyscalculia?
- What are the neural underpinnings of the OTS in adults and children?
- Currently, there is only evidence that the neural code for approximate representations becomes less noisy, but there is no evidence that it becomes exact. How does the brain support representations of exact numbers?

representations of symbolic natural numbers because it lacks these two properties [50].

Traces of OTS signatures in symbolic number processing

The most important computational constraint of the OTS is that it is limited to small sets. Evidence for an important role of the OTS in symbolic number processing has been that the first number words are acquired initially for the small cardinalities one to four and only after the discovery of the counting principles, to larger sets [65,66]. When the counting principles are acquired, however, traces of the OTS in symbolic number processing appear to disappear: to date, there have been no reports of abrupt differences in behavioral or neural signatures of processing small one to four versus larger symbolic numbers in tasks such as comparison, naming, or arithmetic. Instead, distance and magnitude effects, reflecting a continuous approximate and compressed scaling of numbers, typically characterize symbolic number processing. Furthermore, there is no neuroimaging evidence in either children or adults showing activation specific to symbolic numbers that reflects a discontinuity around the numbers three or four in regions previously tentatively associated with the OTS, such as posterior parietal, occipital, or right temporo-parietal cortex. Instead, a progressive recruitment of mid and inferior parietal cortex, partially overlapping with the cerebral circuits of the ANS, especially of the left hemisphere, together with a progressive reduced activation in frontal regions appears to support the progressive mastering of symbolic numbers during development (reviewed in [82]). Data from neuropsychological studies are no more encouraging: acquired dyscalculia is neither systematically, nor even frequently, associated with disorders of multiple object tracking. As discussed above, multiple object tracking deficits (simultanagnosia) typically occur after bilateral lesions in the posterior occipito parietal cortex [45,46], and are not typically associated with calculation or number representation disorders.

The relation between the developmental trajectory of the OTS and the initial stages of symbolic number acquisition

The capacity limit of the OTS develops quickly over the first year of life: on average, infants have an adult-like multiple object tracking capacity limit of three or four items already at 12 months of age [36–38]. This means that, by the first year of life, children already have three or four ‘attentional pointers’ that could be used to track up to four objects in parallel and thus to discriminate sets of one to three or four items. Thus, if lexical acquisition in young children were to build upon the OTS, as suggested [2], then children should be able to attach the words ‘one’, ‘two’, ‘three’, and maybe ‘four’, to the corresponding sets at once and with little effort. Instead, as reviewed, lexical acquisition for the first numbers is slow and strictly serial [65,66]. Accounts that the seriality of number acquisition is caused by the seriality of the acquisition of verbal counting [2,52] are unconvincing because the numerical sequence is acquired earlier than numerical meaning, such that children understanding only the meaning of number ‘one’ already know how to recite the number sequence of numbers up to eight or nine [52]. Moreover, in younger children and infants, there is evidence that the OTS can be detrimental in numerical tasks. As reviewed above, objects are represented in the OTS as distinct individuals, with a given set of physical features, such as identity, colour, surface area, contour length, and so on. It was shown that, for small sets falling within the limits of the OTS (less than four) when certain such features (e.g. surface area or contour length) are pitted against number, infants sometimes automatically attend to those and thus fail to respond to number (reviewed in [51]). It is difficult to understand how a system that often interferes with numerical tasks might be relevant for learning more complex numerical representations.

OTS and developmental dyscalculia

In contrast to evidence for impairments in the ANS in dyscalculia, there appears to be no evidence to date for impaired OTS. Such evidence could take the form of impairments in subitizing, the adult measure of OTS capacity, in visuo-spatial short-term memory capacity, also correlated with subitizing across subjects in adults (Piazza *et al.* unpublished data), or in the MOT task, where subjects are asked to track the position of multiple objects moving along independent trajectories on the display. However, impairments in subitizing have not been convincingly reported in dyscalculia. By contrast, dyscalculia appears to be associated with slowed serial counting for sets of more than four items [83,84]. As for visuo-spatial short-term memory, the studies that report impairments in dyscalculia are plentiful, but they typically use tasks (such as the Corsi test; e.g. [85,86]) that do not assess pure visuo-spatial span, but rather more complex abilities, such as sequential order processing and complex visuo-motor coordination. This enables no strict conclusions to be drawn on whether children with dyscalculia have a reduced OTS. In sum, current data do not strongly support a foundational role of OTS in symbolic number acquisition.

Concluding remarks

Humans are born with strong intuitions on approximate numerical quantities and their relations. There is evidence to suggest that culture-based acquisition of symbols representing exact numerical quantities is grounded on these pre-existing intuitions, whereas there is little evidence for a foundational role of the parallel individuation system. Current neuroimaging data suggest that representations of exact numbers emerge through important modifications of the pre-existing parietal coding schemes for approximate numerical quantity. Under current investigation is the role of language and of visuo-spatial operations, such as serial pointing and serial individuation, instantiating the one-to-one correspondence principle in counting. This might be mediated initially by frontal cortex regions acting as a ‘tuning sharpener’ [87] of the core parietal approximate number code.

However, despite the current evidence suggesting the ANS rather than the OTS is foundational in the construction of symbolic numerical thinking, there is a need for behavioral and neuroimaging data that would clarify the nature of the cognitive and neural changes occurring during the crucial period when children acquire the fist symbolic numbers and learn the counting principles. Longitudinal studies mapping the exact status of knowledge before, during and after the crucial period of between two and five years of age, when natural number concepts are acquired, would be important to understand the relative role of the early quantification systems, how they account for the speed and accuracy of cultural learning, and if and how they are modified in turn by cultural learning. This will be the starting point for new and exciting discoveries of how humans, even though constrained by the limitations imposed by the functional architecture of their primate brains, manage to construct and combine a rich set of abstract representations.

References

1 Spelke, E. and Kinzler, K. (2007) Core knowledge. *Dev. Sci.* 10, 89–96
2 Carey, S. (2009) *The Origin of Concepts*, Oxford University Press
3 Dehaene, S. and Cohen, L. (2007) Cultural recycling of cortical maps. *Neuron* 56, 384–398
4 Brannon, E. and Roitman, J. (2003) Nonverbal representations of time and number in animals and human infants. In *Functional and Neural Mechanisms of Interval Timing* (Meck, W.H., ed.), pp. 143–182, CRC
5 Jordan, K. *et al.* (2005) Monkeys match the number of voices they hear to the number of faces they see. *Curr. Biol.* 15, 1034–1038
6 Jordan, K. *et al.* (2008) Monkeys match and tally quantities across senses. *Cognition* 108, 617–625
7 McComb, K. *et al.* (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. *Anim. Behav.* 47, 379–387
8 Wilson, M. *et al.* (2002) Chimpanzees and the mathematics of battle. *Proc. R. Soc. Lond. B. Biol. Sci.* 269, 1107–1112
9 Krebs, J. and Davies, N. (1993) *An Introduction to Behavioural Ecology*, Wiley-Blackwell
10 Lyon, B. (2003) Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature* 422, 495–499
11 Cantlon, J. and Brannon, E. (2007) Basic math in monkeys and college students. *PLoS Biol.* 5, e328
12 Flombaum, J. *et al.* (2005) Rhesus monkeys (*Macaca mulatta)* spontaneously compute addition operations over large numbers. *Cognition* 97, 315–325
13 Izard, V. *et al.* (2009) Newborn infants perceive abstract numbers. *Proc. Natl. Acad. Sci. U. S. A.* 106, 10382–10385
14 Fechner, G.T. (1860) *Elemente der Psychophysik*, Breitkopf & Hartel
15 Gallistel, C.R. and Gelman, R. (1992) Preverbal and verbal counting and computation. *Cognition* 44, 43–74
16 Dehaene, S. (2003) The neural basis of the Weber-Fechner law: a logarithmic mental number line. *Trends Cog. Sci.* 7, 145–147
17 Verguts, T. and Fias, W. (2004) Representation of number in animals and humans: a neural model. *J. Cogn. Neurosci.* 16, 1493–1504
18 Zorzi, M. and Butterworth, B., (1999) A computational model of number comparison. In *Proceedings of the Twenty-First Annual Conference of the Cognitive Science Society* (Hahn M, S.S., ed.), pp. 772–777, Erlbaum.
19 Piazza, M. *et al.* (2004) Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 44, 547–555
20 Libertus, M.E. and Brannon, E.M. (2010) Stable individual differences in number discrimination in infancy. *Dev. Sci.* DOI: 10.1111/j.1467-7687.2009.00948.x
21 Halberda, J. *et al.* (2008) Individual differences in non-verbal number acuity correlate with maths achievement. *Nature* 455, 665–668
22 Piazza, M. *et al.* (2010) Developmental trajectory of number acuity reveals a severe impairment in developmental dyscalculia. *Cognition* 116, 33–41
23 Halberda, J. and Feigenson, L. (2008) Developmental change in the acuity of the 'Number Sense': The Approximate Number System in 3-, 4-, 5-, and 6-year-olds and adults. *Dev. Psychol.* 44, 1457–1465
24 Lipton, J. and Spelke, E. (2003) Origins of number sense: large number discrimination in human infants. *Psychol. Sci.* 14, 396–401
25 Xu, F. and Spelke, E.S. (2000) Large number discrimination in 6-month-old infants. *Cognition* 74, B1–B11
26 Eger, E. *et al.* (2009) Deciphering cortical number coding from human brain activity patterns. *Curr. Biol.* 19, 1608–1615
27 Knops, A. *et al.* (2009) Recruitment of an area involved in eye movements during mental arithmetic. *Science* 324, 1583–1585
28 Dormal, V. *et al.* (2010) Mode-dependent and mode-independent representations of numerosity in the right intraparietal sulcus. *Neuroimage* 52, 1677–1686
29 Piazza, M. and Izard, V. (2009) How humans count: numerosity and the parietal cortex. *Neuroscientist* 15, 261–273
30 Dehaene, S. (2009) Origins of mathematical intuitions. *Ann. N.Y. Acad. Sci.* 1156, 232–259
31 Alvarez, G. and Cavanagh, P. (2004) The capacity of visual short-term memory is set both by visual information load and by number of objects. *Psychol. Sci.* 15, 106–111
32 Scholl, B. (2001) Objects and attention: the state of the art. *Cognition* 80, 1–46
33 Pylyshyn, Z. (2001) Visual indexes, preconceptual objects, and situated vision. *Cognition* 80, 127–158
34 Revkin, S.K. *et al.* (2008) Does subitizing reflect numerical estimation? *Psychol. Sci.* 19, 607–614
35 Vogel, E. and Machizawa, M. (2004) Neural activity predicts individual differences in visual working memory capacity. *Nature* 428, 748–751
36 Ross-Sheehy, S. *et al.* (2003) The development of visual short-term memory capacity in infants. *Child Dev.* 74, 1807–1822
37 Oakes, L. *et al.* (2006) Rapid development of feature binding in visual short-term memory. *Psychol. Sci.* 17, 781–787
38 Rose, S. *et al.* (2001) Visual short-term memory in the first year of life: capacity and recency effects. *Dev. Psychol.* 37, 539–549
39 Todd, J. and Marois, R. (2004) Capacity limit of visual short-term memory in human posterior parietal cortex. *Nature* 428, 751–754
40 Xu, Y. and Chun, M.M. (2006) Dissociable neural mechanisms supporting visual short-term memory for objects. *Nature* 440, 91–95
41 Piazza, M. *et al.* (2003) Single-trial classification of parallel pre-attentive and serial attentive processes using functional magnetic resonance imaging. *Proc. R. Soc. Lond. B. Biol. Sci.* 270, 1237–1245
42 Sathian, K. *et al.* (1999) Neural evidence linking visual object enumeration and attention. *J. Cogn. Neurosci.* 11, 36–51
43 Vetter, P. *et al.* (2010) A candidate for the attentional bottleneck: set-size specific modulation of the right TPJ during attentive enumeration. *J. Cogn. Neurosci.* X, 1–9
44 Ansari, D. *et al.* (2007) Linking visual attention and number processing in the brain: the role of the temporo-parietal junction in small and large symbolic and nonsymbolic number comparison. *J. Cogn. Neurosci.* 19, 1845–1853
45 Coslett, H.B. and Saffran, E. (1991) Simultanagnosia: to see but not two see. *Brain* 114, 1523–1545
46 Rizzo, M. and Vecera, S. (2002) Psychoanatomical substrates of Balint's syndrome. *Br. Med. J.* 72, 162–178
47 Dehaene, S. and Cohen, L. (1994) Dissociable mechanisms of subitizing and counting: neuropsychological evidence from simultanagnosic patients. *J. Exp. Psychol. Hum. Percept. Perform.* 20, 958–975
48 Hyde, D. and Spelke, E. (2009) All numbers are not equal: an electrophysiological investigation of small and large number representations. *J. Cogn. Neurosci.* 21, 1039–1053
49 Dehaene, S. and Changeux, J.P. (1993) Development of elementary numerical abilities: a neuronal model. *J. Cogn. Neurosci.* 5, 390–407
50 Carey, S. (2001) Cognitive foundations of arithmetic: evolution and ontogenisis. *Mind Lang.* 16, 37–55
51 Feigenson, L. *et al.* (2004) Core systems of number. *Trends Cog. Sci.* 8, 307–314
52 Le Corre, M. and Carey, S. (2007) One, two, three, four, nothing more: an investigation of the conceptual sources of the verbal counting principles. *Cognition* 105, 395–438
53 Rips, L. *et al.* (2008) From numerical concepts to concepts of number. *Behav. Brain Sci.* 31, 623–642
54 Gilmore, C.K. *et al.* (2007) Symbolic arithmetic knowledge without instruction. *Nature* 447, 589–591

55 Gilmore, C.K. *et al.* (2010) Non-symbolic arithmetic abilities and mathematics achievement in the first year of formal schooling. *Cognition* 115, 394–406
56 Holloway, I.D. and Ansari, D. (2009) Mapping numerical magnitudes onto symbols: the numerical distance effect and individual differences in children's mathematics achievement. *J. Exp. Child Psychol.* 103, 17–29
57 Moyer, R.S. and Landauer, T.K. (1967) Time required for judgements of numerical inequality. *Nature* 215, 1519–1520
58 Van Opstal, F. *et al.* (2008) Dissecting the symbolic distance effect: Comparison and priming effects in numerical and nonnumerical orders. *Psychon. Bull. Rev.* 15, 419–425
59 Reynvoet, B. *et al.* (2002) Semantic priming in number naming. *Q. J. Exp. Psychol. A* 55, 1127–1139
60 Reynvoet, B. *et al.* (2009) Children's representation of symbolic magnitude: the development of the priming distance effect. *J. Exp. Child Psychol.* 103, 480–489
61 Libertus, M. *et al.* (2007) Electrophysiological evidence for notation independence in numerical processing. *Behav. Brain Funct.* 3, 1
62 Temple, E. and Posner, M.I. (1998) Brain mechanisms of quantity are similar in 5-year-olds and adults. *Proc. Natl. Acad. Sci. U. S. A.* 95, 7836–7841
63 Notebaert, K. *et al.* The magnitude representation of small and large symbolic numbers in the left and right hemisphere: an event-related fMRI study. *J. Cogn. Neurosci.* (in press)
64 Piazza, M. *et al.* (2007) A magnitude code common to numerosities and number symbols in human intraparietal cortex. *Neuron* 53, 293–305
65 Wynn, K. (1990) Children's understanding of counting. *Cognition* 36, 155–193
66 Wynn, K. (1992) Children's acquisition of the number words and the counting system. *Cogn. Psychol.* 24, 220–251
67 vanMarle, K. and Wynn, K. (2009) Infants' auditory enumeration: evidence for analog magnitudes in the small number range. *Cognition* 111, 302–316
68 Cantlon, J.F. and Brannon, E.M. (2006) Shared system for ordering small and large numbers in monkeys and humans. *Psychol. Sci.* 17, 401–406
69 Izard, V. *et al.* (2008) Distinct cerebral pathways for object identity and number in human infants. *PLoS Biol.* 6, e11
70 Cantlon, J. *et al.* (2010) Spontaneous analog number representations in 3-year-old children. *Dev. Sci.* 13, 289–297
71 Huang, Y. *et al.* (2010) When is four far more than three? *Psychol. Sci.* 21, 600–606
72 Butterworth, B. (2005) Developmental dyscalculia. In *Handbook of Mathematical Cognition* (Campbell, J.I.D., ed.), pp. 455–467, Psychology Press
73 Mazzocco, M. *et al.* Impaired acuity of the approximate number system underlies mathematical learning disability. *Child Dev.* (in press)
74 Mussolin, C. *et al.* (2010) Symbolic and nonsymbolic number comparison in children with and without dyscalculia. *Cognition* 115, 10–25
75 Rousselle, L. and Noel, M.P. (2007) Basic numerical skills in children with mathematics learning disabilities: a comparison of symbolic vs non-symbolic number magnitude processing. *Cognition* 102, 361–395
76 Iuculano, T. *et al.* (2008) Core information processing deficits in developmental dyscalculia and low numeracy. *Dev. Sci.* 11, 669–680
77 Mussolin, C. *et al.* (2010) Symbolic and nonsymbolic number comparison in children with and without dyscalculia. *Cognition* 115, 10–25
78 Price, G.R. *et al.* (2007) Impaired parietal magnitude processing in developmental dyscalculia. *Curr. Biol.* 17, R1042–R1043
79 Molko, N. *et al.* (2003) Functional and structural alterations of the intraparietal sulcus in a developmental dyscalculia of genetic origin. *Neuron* 40, 847–858
80 Isaacs, E.B. *et al.* (2001) Calculation difficulties in children of very low birthweight: a neural correlate. *Brain* 124, 1701–1707
81 Castles, A. and Coltheart, M. (2004) Is there a causal link from phonological awareness to success in learning to read? *Cognition* 91, 77–111
82 Ansari, D. (2008) Effects of development and enculturation on number representation in the brain. *Nat. Rev. Neurosci.* 9, 278–291
83 Landerl, K. *et al.* (2004) Developmental dyscalculia and basic numerical capacities: a study of 8-9-year-old students. *Cognition* 93, 99–125
84 Maloney, E. *et al.* (2009) Mathematics anxiety affects counting but not subitizing during visual enumeration. *Cognition* 114, 293–297
85 Bull, R. *et al.* (1999) Exploring the roles of the visual-spatial sketch pad and central executive in children's arithmetical skills: views from cognition and developmental neuropsychology. *Dev. Neuropsychol.* 15, 421–442
86 McLean, J. and Hitch, G. (1999) Working memory impairments in children with specific arithmetic learning difficulties. *J. Exp. Child Psychol.* 74, 240–260
87 Freedman, D. *et al.* (2001) Categorical representation of visual stimuli in the primate prefrontal cortex. *Science* 291, 312–316
88 Ziegler, J. and Goswami, U. (2005) Reading acquisition, developmental dyslexia, and skilled reading across languages: a psycholinguistic grain size theory. *Psychol. Bull.* 131, 3–29
89 Bradley, L. and Bryant, P.E. (1983) Categorizing sounds and learning to read – a causal connection. *Nature* 301, 419–421
90 Izard, V. and Dehaene, S. (2008) Calibrating the mental number line. *Cognition* 106, 1221–1247
91 Burr, D. *et al.* (2010) Subitizing but not estimation of numerosity requires attentional resources. *J. Vision* 10, 1–10
92 Pica, P. *et al.* (2004) Exact and approximate arithmetic in an Amazonian indigene group. *Science* 306, 499–503
93 Dehaene, S. (2007) Symbols and quantities in parietal cortex: elements of a mathematical theory of number representation and manipulation. In *Attention and Performance Vol XXII* (Patrick Haggard, Yves Rossetti, and Mitsuo Kawato, eds), pp. 527-574, Harvard University Press
94 Gallistel, C.R. and Gelman, R. (1991) The preverbal counting process. In *Thoughts Memories and Emotions: Essays in Honor of George Mandler* (W., K., *et al.*, eds), pp. 65-81, Lawrence Erlbaum Associates
95 Cordes, S. and Brannon, E.M. Two systems or one? Infants discriminate small from large numerosities. *Dev. Psychol.* (in press)
96 Meyers, E. *et al.* (2008) Dynamic population coding of category information in inferior temporal and prefrontal cortex. *J. Neurophysiol.* 100, 1407–1419
97 Diester, I. and Nieder, A. (2007) Semantic associations between signs and numerical categories in the prefrontal cortex. *PLoS Biol.* 5, e294
98 Cantlon, J. *et al.* (2009) The neural development of an abstract concept of number. *J. Cogn. Neurosci.* 21, 2217–2229
99 Ansari, D. and Dhital, B. (2006) Age-related changes in the activation of the intraparietal sulcus during nonsymbolic magnitude processing: an event-related functional magnetic resonance imaging study. *J. Cogn. Neurosci.* 18, 1820–1828
100 Ansari, D. *et al.* (2005) Neural correlates of symbolic number processing in children and adults. *Neuroreport* 16, 1769–1773