Mind and Language

Précis of " The number sense "

Stanislas Dehaene

INSERM U.334
Service Hospitalier Frédéric Joliot
CEA/DSV
4 Place du Général Leclerc
91401 cedex Orsay
France

Phone +33 1 69 86 78 73
Fax +33 1 69 86 78 16
dehaene@shfj.cea.fr

Abstract

" Number sense " is a short-hand for our ability to quickly understand, approximate, and manipulate numerical quantities. My hypothesis is that number sense rests on cerebral circuits that have evolved specifically for the purpose of representing basic arithmetic knowledge. Four lines of evidence suggesting that number sense constitutes a domain-specific, biologically-determined ability are reviewed: the presence of evolutionary precursors of arithmetic in animals; the early emergence of arithmetic competence in infants independently of other abilities, including language; the existence of a homology between the animal, infant, and human adult abilities for number processing ; and the existence of a dedicated cerebral substrate. In adults of all cultures, lesions to the inferior parietal region can specifically impair number sense while leaving the knowledge of other cognitive domains intact. Furthermore, this region is demonstrably activated during number processing. I postulate that higher-level cultural developments in arithmetic emerge through the establishment of linkages between this core analogical representation (the " number line ") and other verbal and visual representations of number notations. The neural and cognitive organization of those representations can explain why some mathematical concepts are intuitive, while others are so difficult to grasp. Thus, the ultimate foundations of mathematics rests on core representations that have been internalized in our brains through evolution.

Introduction

Number is a fundamental parameter by which we make sense of the world surrounding us. Not only can we quickly and accurately perceive the numerosity of small collections of things; but all languages have number words ; all of us have learned, more or less spontaneously, to calculate on our fingers ; and most of us have strong arithmetic intuitions which allow us to quickly decide that 9 is larger than 5, that 3 falls in the middle of 2 and 4, or that 12+15 cannot equal 96, without much introspection as to how we perform those feats. I collectively refer to those fundamental elementary abilities or intuitions about numbers as “ the number sense ” (Dehaene, 1997, hereafter TNS).

My hypothesis is that number sense qualifies as a biologically determined category of knowledge. I propose that the foundations of arithmetic lie in our ability to mentally represent and manipulate numerosities on a mental “ number line ”, an analogical representation of number ; and that this representation has a long evolutionary history and a specific cerebral substrate. “ Number appears as one of the fundamental dimensions according to which our nervous system parses the external world. Just as we cannot avoid seeing objects in color (an attribute entirely made up by circuits in our occipital cortex, including area V4) and at definite locations in space (a representation reconstructed by occipito-parietal neuronal projection pathways), in the same way numerical quantities are imposed on us effortlessly through the specialized circuits of our inferior parietal lobe. The structure of our brain defines the categories according to which we apprehend the world through mathematics. ” (TNS, p. 245).

In this *précis*, I shall first briefly summarize the multiple sources of evidence that support this claim. These include the presence of evolutionary precursors of arithmetic in animals; the early emergence of arithmetic competence in infants independently of other abilities, including language; the existence of a homology between the animal, infant, and human adult abilities for number processing ; and the existence of a dedicated cerebral substrate, as inferred from studies of brain-lesioned patients with acquired deficits of number sense, as well as from brain imaging studies of calculation in normal subjects. I shall then briefly discuss how the biologically determined number representation interacts with cultural factors such as language acquisition and schooling to yield the specifically human ability for higher-level arithmetic.

Evolutionary precursors of arithmetic

If the human ability for arithmetic has a specific cerebral substrate which is partially under genetic control, then one should find precursors of this ability in animals. At the scale at which most animals live in, the world is made of collections of movable physical objects. The evolutionary advantages of being able to extract the numerosity of such collections are obvious, were it only to track found sources, predators, or potential mates. It was therefore proposed that evolutionary pressures must have lead to the internalization of numerical representations in the brain of various animal species (Gallistel, 1990).

The search for animal arithmetic became an obvious goal of scientific inquiry soon after Darwin's publication of *The Origin of species.* This quest initally met with failure and growing skepticism (in TNS, I tell the famous story of Clever Hans, a horse who was initially thought to be able to count and read, but was later discredited). In the modern literature, however, considerable evidence indicates that animals possess numerosity discrimination, cross-modal numerosity perception, and elementary arithmetic abilities (for review see Boysen & Capaldi, 1993; Davis & Pérusse, 1988; Gallistel, 1989; Gallistel, 1990; Gallistel & Gelman, 1992). Various animal species including rats, pigeons, raccoons, dolphins, parrots, monkeys and chimpanzees have been shown to discriminate the numerosity of sets, including simultaneously or sequentially presented visual objects as well as auditory sequences of sounds. Cross-modal extraction of numerosity was observed, for instance in rats (Church & Meck, 1984). Most such experiments included controls for non-numerical variables such as spacing, size, tempo, and duration of the stimuli (Church & Meck, 1984; Mechner & Guevrekian, 1962; Meck & Church, 1983).

Some animals have also been shown to use their internal representations of number to compute simple operations such as approximate addition, subtraction and comparison. At least some of those experiments required little or no training, suggesting that the numerical representation is present in naive animals. For instance, the ability to compute 1+1 and 2-1 was demonstrated using a violation-of-expectation paradigm in monkeys tested in the wild (Hauser, MacNeilage, & Ware, 1996). In some experiments that did require training, there is excellent evidence that animals can generalize beyond the training range. A case in point is the remarkable recent experiment by Brannon and Terrace (1998). Monkeys were initially trained to press cards on a tactile screen in correct numerical order : first the card bearing one object, then the card bearing two, and so on up to four. Following this training, the monkeys were transferred to a novel block with numerosities five to nine. Although no differential reinforcement was provided, the monkeys readily generalized their smaller-to-larger ordering behavior to this new range of numbers. Such evidence suggests that a genuine understanding of numerosities and their relations can be found in monkeys.

What does require years of training, however, and is never found in the wild is the ability to learn symbols for numbers. Although a variety of species, including monkeys (Washburn & Rumbaugh, 1991), chimpanzees (Boysen & Berntson, 1996; Boysen & Capaldi, 1993; Matsuzawa, 1985), and even dolphins (Mitchell, Yao, Sherman, & O'Regan, 1985) and a parrot (Pepperberg, 1987) have learned the use of abstract numerical symbols, including Arabic digits, to refer to numerical quantities, this always required huge amounts of training. Hence, it cannot be taken to indicate that exact symbolic or 'linguistic' number processing is within animals' normal behavioral repertoire. It does indicate, however, that abstract, presumably non-symbolic representations of number are available to animals and can, under exceptional circumstances, be mapped onto arbitrary behaviors that can then serve as numerical 'symbols'.

Numerical abilities in preverbal infants

It is remarkable that the elementary numerical abilities that can be demonstrated in animals are almost strictly identical to those that have been found in preverbal infants in the first year of life. Discrimination of visual numerosity was first demonstrated in 6-7 month-old infants using the classical method of habituation-recovery of looking time (Starkey & Cooper, 1980). Infants watched as slides with a fixed number of dots, say 2, were repeatedly presented to them until their looking time decreased, indicating habituation. At that point, presentation of slides with a novel number of dots, say 3, was shown to yield significantly longer looking times, indicating dishabituation and therefore discrimination of 2 versus 3.

In order to demonstrate that numerosity is the crucial parameter that drives behavior, it is crucial to exclude all other potentially confounding variables in the stimulus design. In the infant literature, this is still a matter of controversy, because many experiments were not fully controlled, and in some of them at least, replications suggest that the original behavior was imputable to confounds. Still, in the original study, dot density, spacing, and alignment were controlled for. In subsequent studies, numerosity discrimination was replicated with newborns (Antell & Keating, 1983) and with various stimulus sets, including slides depicting sets of realistic objects of variable size, shape and spatial layout (Strauss & Curtis, 1981), and dynamic computer displays of random geometrical shapes in motion, with partial occlusion (van Loosbroek & Smitsman, 1990).

Infants' numerosity discrimination abilities are not limited to visual sets of objects. Newborns have been shown to discriminate two- and three-syllable words with controlled phonemic content, duration and speech rate (Bijeljac-Babic, Bertoncini, & Mehler, 1991). Six month-olds also discriminate the numerosity of visual events, such as a puppet making two or three jumps (Wynn, 1996). There is also evidence for cross-modal numerosity matching in 6-8 month-old infants (Starkey, Spelke, & Gelman, 1983; Starkey, Spelke, & Gelman, 1990), although its replicability has been disputed (Mix, Levine, & Huttenlocher, 1997; Moore, Benenson, Reznick, Peterson, & Kagan, 1987).

Like many animal species, human infants have also be shown to perform elementary computations with small numerosities. Wynn (1992) used a violation-of-expectation paradigm to show that infants developed numerical expectations analogous to the arithmetic operations 1+1=2 and 2-1=1. When shown a physical transformation such as two objects being successively placed behind a screen, 4-½ month olds expected the numerically appropriate number of objects (here two) and were surprised if another number was observed. Later replications demonstrated that this behavior could not be explained either by biases in the location of the objects (Koechlin, Dehaene, & Mehler, 1997), or in their identity (Simon, Hespos, & Rochat, 1995). Infants still reacted to the numerically impossible events 1+1=1 and 2-1=2 when changes in object location and identity were introduced. Thus, infants seem to encode the scenes they see using an abstract representation of the number of objects on the scene, irrespective of their exact identity and location.

There has been some discussion as to whether these experiments reflect a genuine representation of numerosity in infants. Instead, many of these results could be thought to indicate merely that infants have a capacity to keep track of up to 3 or 4 objects through a representation of " object files " -- a representation in which numerosity would only be implicitly encoded, not explicity represented (Koechlin et al., 1997; Simon, 1997; Simon et al., 1995; Uller, Huntley-Fenner, Carey, & Klatt, 1999). Space precludes a full discussion of this issue here. Suffice it to say, however, that several experiments, notably those demonstrating discrimination of auditory signals, temporal events, or large numbers such 8 versus 16 visual objects (Xu & Spelke, in preparation), are not directly conducive to such an explanation. Thus, the object file interpretation, even if it turned out to be correct for many experiments with small numerosities, would still have to be supplemented with an additional genuinely numerical mechanism.

Homology or analogy ?

To demonstrate that human abilities for arithmetic have a biological basis with a long evolutionary history, it is not sufficient to demonstrate that animals and preverbal infants possess rudimentary number processing abilities. One must also show that there are profound homologies between human and animal abilities that suggest a phylogenetic continuity. In fact, two striking shared characteristics of number processing in humans and animals have been identified : the distance effect and the size effect. The distance effect is a systematic, monotonous decrease in numerosity discrimination performance as the numerical distance between the numbers decreases. The size effect indicates that for equal numerical distance, performance also decreases with increasing number size. Both effects indicate that the discrimination of numerosity, like that of many other physical parameters, obeys Fechner's Law.

Distance and size effects have been reported in various animal species whenever the animal must identify the larger of two numerical quantities or tell whether two numerical quantities are the same or not (review in Gallistel & Gelman, 1992). It should be stressed here that animals are not limited to processing small numbers only. Pigeons, for instance, can reliably discriminate 45 pecks from 50 (Rilling & McDiarmid, 1965). The number size effect merely indicates that, as the numbers get larger, a greater numerical distance between them is necessary to achieve the same discrimination level. Number size and distance effects have not been systematically studied in human infants yet, but the available evidence already suggests that they readily discriminate 2 versus 3 objects, occasionally 3 versus 4 or 4 versus 5, but not 4 versus 6 (Starkey & Cooper, 1980). A recent study indicates that infants can discriminate 8 versus 16 visual objects even when all size, density and occupation cues are controlled (Xu & Spelke, in preparation).

The distance and size effects indicate that animals and infants seem to possess only a fuzzy representation of numbers, in which imprecision grows proportionally to the number being represented. As a consequence, only very small numbers (up to about 3) can be represented accurately, while other numerical quantities are increasingly imprecise. Superficially, this analogical mode of representation may seem to differ radically from the kind of representation that adult humans use in arithmetic. Animals are severely limited to elementary, approximate, and non-symbolic calculations, while we can make symbolic calculations with arbitrary accuracy. Why, then, do I claim that the distance and size effect indicate continuity, rather than discontinuity, between the human and animal representations of number ? This is because, quite counter-intuitively, those effects do hold with humans, not only when representing the numerosity of sets of objects (Buckley & Gillman, 1974; van Oeffelen & Vos, 1982), but even when processing Arabic digits or number words (Buckley & Gillman, 1974; Dehaene, 1996; Dehaene, Dupoux, & Mehler, 1990; Moyer & Landauer, 1967). For instance, when comparing Arabic digits, it is faster and easier to decide that 8 is larger than 4 than to decide that 8 is larger than 7, even after intensive training. The distance effect is found even with two-digit numerals (Dehaene et al., 1990). Comparison times and error rates are a continuous, convex upward function of distance, similar to psychophysical comparison curves. The number size effect relates to 'subitizing', our ability to rapidly name the numerosity of a set of simultaneously presented objects when it is below 3 or 4, but not beyond (Dehaene & Cohen, 1994; Mandler & Shebo, 1982). It is also found when humans calculate. Even in highly trained adults, adding, multiplying, or comparing two large digits such as 8 and 9 is significantly slower and error-prone than performing the same operations with digits 2 and 3. Furthermore, we exploit numerical distance to approximate additions and to reject grossly false results, such as 4+6=39 (Ashcraft & Stazyk, 1981; Dehaene, Spelke, Stanescu, Pinel, & Tsivkin, 1999).

That human behavior obeys distance and size effects even when the numbers are presented in a symbolic notation suggests two conclusions. First, the adult human brain contains an analogical representation of numerical quantity very similar to the one observed in animals and in young infants, organized by numerical proximity and with increasing fuzziness for larger and larger numbers. Second, when presented with number words and Arabic numerals , the human brain converts these numbers internally from their symbolic format to the analogical quantity representation. This internal access to quantity seems to be a compulsory step in number processing, because a distance effect is found even when subjects merely have to say whether two digits are same or different (Dehaene & Akhavein, 1995), or in priming experiments in which the mere presentation of a digit or of a numeral facilitates the subsequent processing of a numerically close target number (Brysbaert, 1995; Dehaene et al., 1998b; den Heyer & Briand, 1986; Koechlin, Naccache, Block, & Dehaene, 1999).

A cerebral basis for number sense

One final piece of evidence is required to demonstrate that the understanding and manipulation of numerical quantities is part of our biological evolutionary heritage. One should show that it has a dedicated neural substrate. A specific cerebral circuit should be reproducibly associated with the representation and acquisition of knowledge about numerical quantities and their relations. Although the demonstration is still far from complete, two arguments support the hypothesis that the intraparietal cortex of both hemispheres participates in such a circuit. First, neuropsychological studies of human patients with brain lesions indicate that the internal representation of quantities can be selectively impaired by lesions to that area. Second, brain-imaging studies reveal that this region is specifically activated during various number processing tasks.

It has been known for at least 80 years that lesions of the inferior parietal region of the dominant hemisphere can cause number processing deficits (Gerstmann, 1940; Hécaen, Angelergues, & Houillier, 1961; Henschen, 1920). In some cases, comprehending, producing and calculating with numbers are globally impaired (Cipolotti, Butterworth, & Denes, 1991). In others, however, the deficit may be selective for calculation and spare reading, writing, spoken recognition and production of Arabic digits and numerals (Dehaene & Cohen, 1997; Hécaen et al., 1961; Takayama, Sugishita, Akiguchi, & Kimura, 1994; Warrington, 1982). My colleague Dr. Laurent Cohen and I have recently suggested that the core deficit in left parietal acalculia is a disorganization of an abstract semantic representation of numerical quantities rather than of calculation processes per se (Dehaene & Cohen, 1995; Dehaene & Cohen, 1997).

One of our patients, Mr. Mar (Dehaene & Cohen, 1997), experienced severe difficulties in calculation, especially with single-digit subtraction (75% errors). He failed on problems as simple as 3-1, with the comment that he no longer knew what the operation meant. His failure was not tied to a specific modality of input or output, because the problems were simultaneously presented visually and read out loud, and because he failed in both overt production and covert multiple choice tests. Moreover, he also erred on tasks outside of calculation per se, such as deciding which of two numbers is the larger (16% errors) or what number falls in the middle of two others (bisection task: 77% errors). He easily performed analogous comparison and bisection tasks in non-numerical domains such as days of the week, months, or the alphabet (What is between Tuesday and Thursday? February and April? B and D?), suggesting that his deficit was rather specific for the category of numbers. There are now several observations of patients with dominant-hemisphere inferior parietal lesions and Gerstmann's syndrome (e.g. Delazer & Benke, 1997, Cohen and Dehaene, unpublished observations). All of them showed severe impairments in number processing, most clearly in subtraction, compatible with a disturbance of the central representation of numerical quantities.

Brain imaging evidence provides independent support for the idea that the region of the intraparietal sulcus may be a crucial cerebral site for the representation and manipulation of numerical quantity. Since the inception of brain imaging techniques, this region has been known to be activated bilaterally whenever subjects calculate (Roland & Friberg, 1985). The localization of this activity has been refined to the banks of the left and right intraparietal sulcus using the modern techniques of positron emission tomography (Dehaene et al., 1996) and functional magnetic resonance imaging (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene et al., 1999; Pinel et al., 1999; Rueckert et al., 1996) (figure 1). There is even a report of single neurons in this area firing specifically during simple calculations (Abdullaev & Melnichuk, 1996).

Most importantly, several findings support the idea that this region is not just related to calculation in general, but more specifically to the quantity representation or " number line ". First, intraparietal activation is higher during an approximation task that requires quantity estimation than during an exact calculation task of similar complexity, but which can be performed at least in part by rote retrieval (Dehaene et al., 1999). Second, the inferior parietal region has been shown to be unaffected by the notation used for the numbers, suggesting involvement at an abstract notation-independent level of processing (Dehaene, 1996; Pinel et al., 1999). Third, the duration and intensity of activation in this region is sensitive to distance and number size effect, as predicted from its putative role in encoding the mental analogical " number line " (Dehaene, 1996; Kiefer & Dehaene, 1997; Pinel et al., 1999).

Two additional facts are relevant to my hypothesis that inferior parietal cortices contribute to a biologically determined numerical representation. First, the association of arithmetic with the intraparietal sulcus is remarkably reproducible. If arithmetic was just a cultural activity without a strong foundation in brain architecture, one would expect considerable variation as a function of learning, education, and culture. Yet reports from research groups in various countries suggest that, in most if not all cultures throughout the world, the sites of the lesions causing Gerstmann-type acalculia, as well as the sites of brain activation during calculation, systematically fall in the inferior parietal region.

Second, although neuroscientists currently place considerable emphasis on the concept of brain plasticity, the evidence suggests that the contribution of inferior parietal cortices to number processing is highly specific and cannot be easily transferred to other brain regions. If an early brain lesion disrupts parietal circuitry, lifelong difficulties in arithmetic may follow. Indeed, a " developmental Gerstmann syndrome ", also called developmental dyscalculia, has been reported in children (Benson & Geschwind, 1970; Spellacy & Peter, 1978; Temple, 1989; Temple, 1991). Some of these children show a highly selective, category-specific deficit for number processing in the face of normal intelligence, normal language acquisition, and standard or even special education. Although there is a dearth of accurate brain imaging data on developmental dyscalculia, in at least one case the deficit has been clearly related to early damage to inferior parietal cortex (Levy, Reis, & Grafman, 1999). Such evidence bolsters my postulate that this area holds a biologically determined quantity representation, and that early lesions to that region cause an inability to understand the core meaning of numbers.

Against phrenology : the triple-code model of number processing

The above discussion should not be construed as a modern defense of phrenology, with a single brain area – inferior parietal cortex – encoding all knowledge of arithmetic. The view that I defend in TNS is exactly opposite. Multiple brain areas contribute to the cerebral processing of numbers ; the inferior parietal quantity representation is only one node in a distributed circuit. The triple-code model of number processing, which was developed by Laurent Cohen and I (Dehaene, 1992; Dehaene & Cohen, 1995), makes explicit hypotheses about where these areas lie, what they encode, and how their activity is coordinated in different tasks (see figure 2).

Functionally, our model rests on three fundamental hypotheses. First, numerical information can be manipulated mentally in three formats: an analogical representation of quantities, in which numbers are represented as distributions of activation on the mental number line; a verbal format, in which numbers are represented as strings of words (e.g. thirty-seven); and a visual Arabic representation, in which numbers are represented as a string of digits (e.g. 37). Second, transcoding procedures enable information to be translated directly from one code to the other. Third, each calculation procedure rests on a fixed set of input and output codes. For instance, the operation of number comparison takes as input numbers coded as quantities on the number line. Likewise, the model postulates that multiplication tables are memorized as verbal associations between numbers represented as string of words, and that multi-digit operations are performed mentally using the visual Arabic code.

Neuropsychological and brain-imaging observations have permitted us to associate tentative anatomical circuits to each node of the triple-code model. We speculate that the ventral occipito-temporal sectors of both hemispheres are involved in the visual Arabic number form; that the left perisylvian areas are implicated in the verbal representations of numbers (like any other string of words); and, most crucially, that the intraparietal areas of both hemispheres are involved in the analogical quantity representation.

Although this model remains very simple, it can explain a variety of behavioral and neuropsychological observations, including quite counter-intuitive ones. For instance, the model predicts that the rote memorization of arithmetic facts depends on a linguistic code for numbers and on left-hemispheric language areas ; conversely, the ability to approximate orders of magnitude, to compute novel operations such as subtraction through quantity manipulation, and more generally to achieve an understanding of conceptual relations between numbers, relies on the quantity code provided by inferior parietal areas. Recent experiments have largely confirmed this prediction. Brain lesions to the predicted areas can dissociate rote calculation from conceptual understanding of quantities (Delazer & Benke, 1997), exact calculation from approximation (Dehaene & Cohen, 1991), and even multiplication from subtraction (Dehaene & Cohen, 1997). Furthermore, brain imaging patterns during exact and approximate calculation confirms that distinct circuits are involved (Dehaene et al., 1999). When subjects approximate an addition, the bilateral intraparietal quantity circuits shows greater activation that when subjects retrieve the exact result, in which case greater activation is seen in left-lateralized language-related circuits. Experiments in bilinguals also indicate that rote calculation is learned in a language-specific fashion and does not easily generalize to a new language, while the ability to approximate is language-independent and transfers without cost (Dehaene et al., 1999).

Another prediction of the triple-code model is that the right hemisphere of a split-brain patient (with a severed corpus callosum) should be able to compare Arabic numerals that it cannot read (see figure 2). This is indeed the case (Cohen & Dehaene, 1996; Seymour, Reuter-Lorenz, & Gazzaniga, 1994). Even more counter-intuitively, the models predicts that following a left inferior temporal lesion, a patient should lose the ability to read words and

Arabic numerals (a deficit known as pure alexia), and also the ability to multiply, but not necessarily the ability to compare or to subtract numbers. Again, we have recently demonstrated that this is the case (Cohen & Dehaene, 1995; Cohen & Dehaene, submitted; see also McNeil & Warrington, 1994). Some patients can subtract numbers that they cannot read ! That we can explain, and even predict, the occurrence of such strange cases attests that one can go a long way with a simple model that assumes a distribution of processing in multiple parallel representations and pathways.

The construction of higher-level number concepts

How does the coordination of these multiple brain areas emerge during child development ? The hypothesis developed in TNS is that all children are born with a quantity representation which provides the core meaning of numerical quantity. Exposure to a given language, culture, and mathematical education leads to the acquisition of additional domains of competence such as a lexicon of number words, a set of digits for written notation, procedures for multi-digit calculation, and so on. Not only must these abilities be internalized and routinized ; but above all, they need to be coordinated with existing conceptual representations of arithmetic. The constant dialogue, within the child's own brain, between linguistic, symbolic, and analogical codes for numbers eventually leads, in numerate adults, to an integrated set of circuits that function with an appearance of non-modularity. Before such a flexible integration is achieved, however, the hypothesis of a modularity and lack of coordination of number representations can explain many of the systematic errors or difficulties that children encounter in the acquisition of arithmetic.

The reader is referred to TNS for a description of some of the difficulties that children go through as they successively acquire single number words, number syntax, the counting sequence, finger-counting algorithms, memorized arithmetic facts, multidigit calculation algorithms, and higher-level number concepts such as zero, negative numbers, or fractions. Here I shall only discuss one example, the memorization of the multiplication table. Why is it so difficult to learn the small number of single-digit multiplication facts ? Leaving out multiplications by 0 and by 1, which can be solved by a general rule, and taking into account the commutativity of multiplication, there are only 36 facts such 3x9=27 that need to be learned. Yet behavioral evidence indicates that even adults still make over 10% errors and respond in more that one second to this highly overtrained task.

What I think is happening is that our intuition of quantity is of very little use when trying to learn multiplication. Approximate addition can implemented by juxtaposition of magnitudes on the internal number line, but no such algorithm seems to be readily available for multiplication. The organization of our mental number line may therefore make it difficult, if not impossible, for us to acquire a systematic intuition of quantities that enter in a multiplicative relation. (This hypothesis is supported by the fact that patients can have severe deficits of multiplication while leaving number sense relatively intact ; in particular, patient NAU (Dehaene & Cohen, 1991), who could still understand approximate quantities despite aphasia and acalculia, was totally unable to approximate multiplication problems). In order to memorize multiplication facts, we therefore have to resort to other strategies based on non-quantitative number representations. The strategy that cultures throughout the world have converged on is to acquire multiplication facts by rote verbal learning. That is, each multiplication fact is recited and remembered as a rote phrase, a specific sequence of words in the language of teaching. This is still a difficult task, however, because the 36 facts to be learned all involve the same number words in slightly different orders, with misleading rhymes and partial overlap. Error analyses indeed indicate that interference in memory is the most frequent cause of multiplication error. When we err, say, on 7x8, we do not produce 55 or 57, which would be close matches, but we typically say 63, which is the correct multiplication result of the wrong operation, 7x9 (Ashcraft, 1992; Campbell & Oliphant, 1992).

It can be argued that our memory never evolved to acquire a lot of tightly inter-related and overlapping facts, as is typical of the multiplication table. Our long-term semantic memory is associative and content-adressable : when cued with a specific episode, we readily retrieve memories of related contents based on the semantic similarity. In particular, we generalize approximate additions based on numerical proximity. Hence, we can readily reject 34+47=268 as false, even though we have never been exposed to this particular fact, because our representation of quantity immediately allows us to recognize that the proposed quantity, 268, is too distant from the operands of the addition (Ashcraft & Battaglia, 1978; Dehaene et al., 1999). In the case of exact multiplication, however, the organization of memory by proximity is detrimental to performance. It would be desirable to keep each multiplication fact separate from the others ; yet our memory is designed so that, when we think of 6x7, we co-activate 6x8 and 5x7. In summary, our cerebral organization can explain both why exact multiplication facts are so confusing and difficult to learn, and why approximation and understanding of quantities are highly intuitive operations.

Individual differences in mathematical achievement

Can empirical studies of the number sense also shed some light on individual differences in mathematics ? In TNS, a whole chapter is dedicated to the peculiar case of talented mathematicians and calculating prodigies. The study of such cases is crucial because at first sight it seems to run against my main argument. If the basic architecture of our brain imposes such strong limits on our understanding of arithmetic, why do a few children seem to thrive in mathematics? How did outstanding mathematicians such as Gauss, Einstein, or Ramanujan attain such an extraordinary familiarity with mathematical objects? And how do some retarded or autistic children with an IQ of 50 manage to become experts in mental calculation? Do we have to suppose that some people started in life with a distinct brain architecture, a biological predisposition for calculation and mathematics?

In all fairness, it should be said that, at present, very little is known about this issue. However, having reviewed the available evidence, I do not believe that that much of our individual differences in mathematics are the result of differences in an initial "talent". At present, at any rate, there is very little evidence that great mathematicians and calculating prodigies have been endowed with a distinct neurobiological structure for numbers. On the contrary, there is strong empirical evidence that like all of us, experts in arithmetic have to struggle with long calculations and abstruse mathematical concepts. A beautiful illustration is provided by a recent single case study which probed the major domains of numerical competence, from single- and multi-digit calculation (including acquisition of new algorithms) to working memory and long-term memory, in a calculating prodigy (Pesenti, Seron, Samson, & Duroux, 1999). In all these domains, the subject exhibited the response time and error characteristics of any normal subject, such as size and distance effects. Training seemed to have reduced the size of these effects, but their basic characteristics remained unaltered. For instance, the subject’s short-term memory span for digits was 11, but it did not exceed the normal value of 7 for letters, a domain for which the subject had no particular training. This suggests that his excellent memory for numbers was most likely due to extensive training rather than to an innate distinct biological organization.

My hypothesis, then, is that talented people succeed largely because they devote a considerable time, attention and effort to their topic of predilection. Through training, they develop well-tuned algorithms and clever short-cuts that any of us could learn if we tried, and that are carefully devised to take advantage of our brain’s assets and get around its limits. What is special about them is their disproportionate and relentless passion for numbers and mathematics – a passion which is occasionally of pathological origin, as clearly seen in retarded autistic children with calculation skills. Training experiments indicate that, with a similar amount of training, normal subjects can also enhance their memory and calculation speed (Chase & Ericsson, 1981; Staszewski, 1988).

Chapter 6 in TNS contains many examples of the algorithms and short-cuts that underlie “ prodigious ” calculation. Rather than reiterating them here, let me propose here a novel reinterpretation of the famous dialogue between Ramanujan and Hardy. The prodigious Indian mathematician Ramanujan was slowly dying of tuberculosis when his colleague Hardy came to visit him at the sanatorium. Not knowing what to say, Hardy made the following reflection: "The taxi that I hired to come here bore the number 1729. It seemed a rather dull number". "Oh no, Hardy", Ramanujan immediately replied, "it is a captivating one. It is the smallest number that can be expressed in two different ways as a sum of two cubes" !

1729 is indeed equal to $10^3 + 9^3$ and to $12^3 + 1^3$. But how did Ramanujan compute this complicated mathematical fact in a matter of seconds, from his hospital bed ? Such anecdotes tend to support the belief that geniuses are of a different breed. Yet there is a more plausible explanation. Having worked for decades with numbers, Ramanujan evidently had memorized scores of facts, including the cubes of small integers. He therefore knew that 729, 1000, and 1728 are cubes ($10^3 = 1000$ is obvious ; likewise $12^3 = 1728$ is familiar because, since there are 12 inches in a foot,1728 is the number of cubic inches in a cubic foot ; $9^3 = 729$ is less obvious, but clearly easy to compute). Hence, Ramanujan could readily see that 1729 is one unit off a cube, and that its last three digits are also a cube. From this, it should be absolutely obvious to someone with Ramanujan's training that 1729 is the sum of two cubes in two different ways, namely 1728+1 and 1000+729. Proving that it is the smallest such number is more difficult, but can be verified by trial and error. Eventually, the magic of this anecdote dissolves when one learns that Ramanujan had written this fact in his adolescence notebooks (Kanigel, 1991). Hence, contrary to the legend, Ramanujan did not discover it on the spur of the moment : he already knew it ! I expect that in-depth studies of normal mental algorithms will lead to the debunking of many similar cases, which can and should brought back within the range of the normal human competence.

Concluding thoughts on the nature of the mathematical enterprise

In conclusion, I would like to briefly discuss how cognitive neuroscience studies of number processing can be relevant to wider issues in the philosophy of mathematics. The nature of mathematical objects has been the subject of considerable controversy amongst philosophers and the mathematicians themselves. Traditional approaches to the nature of mathematics have disregarded the psychological or neurological constraints on the brain of the practicing mathematician. My strong belief, though still clearly speculative at this point, is that our improved understanding of the neuropsychological bases of number sense can provide a new “ naturalistic ” approach to the problem of the foundations of mathematics.

Many mathematicians still adhere to the philosophical tradition of platonism. They believe that mathematical objects have an independent reality outside of the human mind : they are abstract, transcend our human descriptions, and predate the evolution of the human brain. Mathematicians do not invent them, but merely discover them through progressive explorations of the mathematical realm. Several features of this point of view are open to criticism, however. Most crucially, Platonism encounters considerable difficulty explaining exactly what this abstract realm of mathematical objects consists of, and, worse yet, how a physical device such as the human brain could ever interact with this non-physical space of pure ideas and know some mathematical truths.

Another approach called formalism considers mathematics as a symbolic game with little or no meaning. By modifying symbol strings according to the adequate rules, mathematicians can derive new theorems from a given set of axioms, but it would be misleading to search for transcendental truth in this play with symbols. This point of view may perhaps account for the development of some recent areas of pure mathematics. It cannot however explain why mathematical objects are so often exquisitely adapted to our understanding of the physical world. “How is it possible that mathematics, a product of human thought that is independent of experience, fits so excellently the objects of physical reality?” Einstein asked in 1921. The physicist Eugene Wigner likewise marveled about the “unreasonable effectiveness of mathematics in the natural sciences.” Examples of this effectiveness abound. My personal favourite is Kepler’s approximation of the trajectories of planets. Kepler discovered empirically – and Newton soon proved from first principles -- that ellipses provide an excellent model of the trajectories of the planets around the sun. Yet the properties of ellipses were first described, for an entirely different purpose, by the Greek mathematician Appolonius about 20 centuries before Kepler’s time! Why did these mathematical objects, which originally described the sections of a cone by a plane, succeed so well in mimicking astronomical reality ?

My point of view is that the mystery of the efficiency of mathematics partly dissipates if one adheres to a naturalistic philosophy of mathematics, firmly grounded in cognitive neuroscience. According to this view, our ability to make sense of the world through mathematics is due to the internalization of representations in the human mind and brain in the course of evolution. These representations are “ unreasonably effective ” in understanding our environment because they have been selected precisely for their representational adequacy. Indeed, two consecutive levels of evolution and selection explain the amazing adequacy of our present mathematics : first, the biological evolution of elementary representational abilities, and second, the cultural evolution of higher-level mathematics (see also Changeux & Connes, 1995).

In the course of biological evolution, selection has shaped our brain representations to ensure that they are adapted to the external world. I have argued that arithmetic is such an adaptation. At our scale, the world is mostly made up of separable objects that combine into sets according to the laws of arithmetic. Representing these combinatorial operations is useful to many organisms. Pressures of selection therefore lead to the emergence of an internal system for elementary arithmetic in the brain of many animal species, including humans. Representational systems have also evolved for the mental manipulation of space, time, motor actions, and many other domains yet. I believe that the ultimate foundations of mathematics are to be found in these largely innate core representational systems.

Specific to the human species, however, is a second level of evolution at the cultural level. As humans, we are born with multiple intuitions concerning numbers, sets, continuous quantities, iteration, logic, or the geometry of space. Through language and the development of new symbols systems, we have the ability to build extensions of these foundational systems and to draw various links between them. In the course of centuries, mathematicians have generated a great variety of such cultural constructions. Those were then selected according to various criteria including their non-contradiction, simplicity, elegance, but also their productivity in capturing physical phenomena. This Darwinian view of the history of mathematics, with an initial, largely unconstrained generation of pure mathematics followed by the selective propagation of its most adequate products, may partially account for the efficiency of our present-day mathematics. " Year after year, mathematical constructions that are self-contradictory, inelegant, or useless are ruthlessly tracked down and eliminated. Only the strongest stand the proof of time. (...) If today's mathematics is efficient, it is perhaps because yesterday's inefficient mathematics has been ruthlessly eliminated and replaced. " (TNS, pp. 246 & 251).

Obviously, we are still very far from understanding how the biological organization of the human brain allows us to make sense of the world through mathematics. At present, only the most elementary of all mathematical concepts, the small integers, have been submitted to a cognitive neuroscience analysis. Yet a similar analysis could be attempted for other domains of mathematics. Topology and geometry, for instance, might be plausibly related to the representations of space computed by our parietal and peri-hippocampal cerebral regions. As our understanding of the neuropsychological foundations of mathematics deepens, not only may we reach a better comprehension of the nature of the mathematical enterprise ; but I also hope that, once the assets and limits of our cognitive apparatus are better known, our ability to teach this notoriously difficult domain will improve.

Acknowledgements. I gratefully acknowledge collaborations with F. Chochon, L. Cohen, E. Koechlin, D. Le Bihan, L. Naccache, P. Pinel , E. Spelke and R. Stanescu. This work is supported by a James S. McDonnell Centennial Fellowship.

References

Abdullaev, Y. G., & Melnichuk, K. V. (1996). Counting and arithmetic functions of neurons in the human parietal cortex. NeuroImage, 3, S216.

Antell, S. E., & Keating, D. P. (1983). Perception of numerical invariance in neonates. Child Development, 54, 695-701.

Ashcraft, M. H. (1992). Cognitive arithmetic: A review of data and theory. Cognition, 44, 75-106.

Ashcraft, M. H., & Battaglia, J. (1978). Cognitive arithmetics: evidence for retrieval and decision processes in mental addition. Journal of Experimental Psychology : Human Learning and Memory, 4, 527-538.

Ashcraft, M. H., & Stazyk, E. H. (1981). Mental addition : A test of three verification models. Memory And Cognition, 9, 185-196.

Benson, D. F., & Geschwind, N. (1970). Developmental Gerstmann syndrome. Neurology, 20, 293-298.

Bijeljac-Babic, R., Bertoncini, J., & Mehler, J. (1991). How do four-day-old infants categorize multisyllabic utterances. Developmental Psychology, 29, 711-721.

Boysen, S. T., & Berntson, G. G. (1996). Quantity-based interference and symbolic representations in chimpanzees (*Pan trogolodytes*). Journal of Experimental Psychology: Animal Behavior Processes, 22, 76-86.

Boysen, S. T., & Capaldi, E. J. (1993). The development of numerical competence: Animal and human models. Hillsdale N.J.: Erlbaum.

Brannon, E. M., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. Science, 282(5389), 746-749.

Brysbaert, M. (1995). Arabic number reading: On the nature of the numerical scale and the origin of phonological recoding. Journal of Experimental Psychology: General, 124, 434-452.

Buckley, P. B., & Gillman, C. B. (1974). Comparison of digits and dot patterns. Journal of Experimental Psychology, 103, 1131-1136.

Campbell, J. I. D., & Oliphant, M. (1992). Representation and retrieval of arithmetic facts: A network-interference model and simulation. In J. I. D. Campbell (Ed.), The nature and origin of mathematical skills (pp. 331-364). Amsterdam: Elsevier.

Changeux, J. P., & Connes, A. (1995). Conversations on Mind, Matter and Mathematics. Princeton N.J.: Princeton University Press.

Chase, W. G., & Ericsson, K. A. (1981). Skilled memory. In A. J. R. (Ed.), Cognitive skills and their acquisition (pp. 141-189). Hillsdale N.J.: Erlbaum.

Chochon, F., Cohen, L., van de Moortele, P. F., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. Journal of Cognitive Neuroscience, in press.

Church, R. M., & Meck, W. H. (1984). The numerical attribute of stimuli. In H. L. Roitblat, T. G. Bever, & H. S. Terrace (Eds.), Animal Cognition . Hillsdale N.J.: Erlbaum.

Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. Brain, 114, 2619-2637.

Cohen, L., & Dehaene, S. (1995). Number processing in pure alexia: the effect of hemispheric asymmetries and task demands. NeuroCase, 1, 121-137.

Cohen, L., & Dehaene, S. (1996). Cerebral networks for number processing: Evidence from a case of posterior callosal lesion. NeuroCase, 2, 155-174.

Cohen, L., & Dehaene, S. (submitted). Calculating without reading: unsuspected residual abilities in pure alexia. Cognitive Neuropsychology.

Davis, H., & Pérusse, R. (1988). Numerical competence in animals: Definitional issues current evidence and a new research agenda. Behavioral and Brain Sciences, 11, 561-615.

Dehaene, S. (1992). Varieties of numerical abilities. Cognition, 44, 1-42.

Dehaene, S. (1996). The organization of brain activations in number comparison: Event-related potentials and the additive-factors methods. Journal of Cognitive Neuroscience, 8, 47-68.

Dehaene, S. (1997). The number sense. New York: Oxford University Press.

Dehaene, S., & Akhavein, R. (1995). Attention, automaticity and levels of representation in number processing. Journal of Experimental Psychology: Learning, Memory, and Cognition, 21, 314-326.

Dehaene, S., & Cohen, L. (1991). Two mental calculation systems: A case study of severe acalculia with preserved approximation. Neuropsychologia, 29, 1045-1074.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting - Neuropsychological evidence from simultanagnosic patients. Journal of Experimental Psychology: Human Perception and Performance, 20, 958-975.

Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. Mathematical Cognition, 1, 83-120.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. Cortex, 33, 219-250.

Dehaene, S., Dehaene-Lambertz, G., & Cohen, L. (1998a). Abstract representations of numbers in the animal and human brain. Trends in Neuroscience, 21, 355-361.

Dehaene, S., Dupoux, E., & Mehler, J. (1990). Is numerical comparison digital: Analogical and Symbolic effects in two-digit number comparison. Journal of Experimental Psychology: Human Perception and Performance, 16, 626-641.

Dehaene, S., Naccache, L., Le Clec'H, G., Koechlin, E., Mueller, M., Dehaene-Lambertz, G., van de Moortele, P. F., & Le Bihan, D. (1998b). Imaging unconscious semantic priming. Nature, 395, 597-600.

Dehaene, S., Spelke, E., Stanescu, R., Pinel, P., & Tsivkin, S. (1999). Sources of mathematical thinking: Behavioral and brain-imaging evidence. Science, 284, 970-974.

Dehaene, S., Tzourio, N., Frak, V., Raynaud, L., Cohen, L., Mehler, J., & Mazoyer, B. (1996). Cerebral activations during number multiplication and comparison: a PET study. Neuropsychologia, 34, 1097-1106.

Delazer, M., & Benke, T. (1997). Arithmetic facts without meaning. Cortex, 33(4), 697-710.

den Heyer, K., & Briand, K. (1986). Priming single digit numbers: Automatic spreading activation dissipates as a function of semantic distance. American Journal of Psychology, 99, 315-340.

Gallistel, C. R. (1989). Animal cognition: The representation of space, time, and number. Annual Review of Psychology, 40, 155-189.

Gallistel, C. R. (1990). The organization of learning. Cambridge (Mass.): MIT Press.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. Cognition, 44, 43-74.

Gerstmann, J. (1940). Syndrome of finger agnosia disorientation for right and left agraphia and acalculia. Archives of Neurology and Psychiatry, 44, 398-408.

Hauser, M. D., MacNeilage, P., & Ware, M. (1996). Numerical representations in primates. Proceedings of the National Academy of Sciences USA, 93, 1514-1517.

Hécaen, H., Angelergues, R., & Houillier, S. (1961). Les variétés cliniques des acalculies au cours des lésions rétro-rolandiques: Approche statistique du problème. Revue Neurologique, 105, 85-103.

Henschen, S. E. (1920). Klinische und anatomische Beitraege zur Pathologie des Gehirns. Stockholm: Nordiska Bokhandeln.

Kanigel, R. (1991). The man who knew infinity: a life of the genius Ramanujan. New York: Charles Scribner's Sons.

Kiefer, M., & Dehaene, S. (1997). The time course of parietal activation in single-digit multiplication: Evidence from event-related potentials. Mathematical Cognition, 3, 1-30.

Koechlin, E., Dehaene, S., & Mehler, J. (1997). Numerical transformations in five month old human infants. Mathematical cognition, 3, 89-104.

Koechlin, E., Naccache, L., Block, E., & Dehaene, S. (1999). Primed numbers: Exploring the modularity of numerical representations with masked and unmasked semantic priming. Journal of Experimental Psychology: Human Perception and Performance, in press.

Levy, L. M., Reis, I. L., & Grafman, J. (1999). Metabolic abnormalities detected by H-MRS in dyscalculia and dysgraphia. Neurology, in press.

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. Journal of Experimental Psychology: General, 111, 1-21.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. Nature, 315, 57-59.

McNeil, J. E., & Warrington, E. K. (1994). A dissociation between addition and subtraction within written calculation. Neuropsychologia, 32, 717-728.

Mechner, F., & Guevrekian, L. (1962). Effects of deprivation upon counting and timing in rats. Journal of the Experimental Analysis of Behavior, 5, 463-466.

Meck, W. H., & Church, R. M. (1983). A mode control model of counting and timing processes. Journal of Experimental Psychology: Animal Behavior Processes, 9, 320-334.

Mitchell, R. W., Yao, P., Sherman, P. T., & O'Regan, M. (1985). Discriminative responding of a dolphin (*Tursiops truncatus*) to differentially rewarded stimuli. Journal of Comparative Psychology, 99, 218-225.

Mix, K. S., Levine, S. C., & Huttenlocher, J. (1997). Numerical abstraction in infants: Another look. Developmental Psychology, 33, 423-428.

Moore, D., Benenson, J., Reznick, J. S., Peterson, M., & Kagan, J. (1987). Effect of auditory numerical information on infant's looking behavior: contradictory evidence. Developmental Psychology, 23, 665-670.

Moyer, R. S., & Landauer, T. K. (1967). Time required for judgements of numerical inequality. Nature, 215, 1519-1520.

Pepperberg, I. M. (1987). Evidence for conceptual quantitative abilities in the african grey parrot: Labeling of cardinal sets. Ethology, 75, 37-61.

Pesenti, M., Seron, X., Samson, D., & Duroux, B. (1999). Basic and exceptional calculation abilities in a calculating prodigy: A case study. Mathematical Cognition, in press.

Pinel, P., Le Clec'H, G., van de Moortele, P. F., Naccache, L., Le Bihan, D., & Dehaene, S. (1999). Event-related fMRI analysis of the cerebral circuit for number comparison. NeuroReport, in press.

Rilling, M., & McDiarmid, C. (1965). Signal detection in fixed ratio schedules. Science, 148, 526-527.

Roland, P. E., & Friberg, L. (1985). Localization of cortical areas activated by thinking. Journal of Neurophysiology, 53, 1219-1243.

Rueckert, L., Lange, N., Partiot, A., Appollonio, I., Litvar, I., Le Bihan, D., & Grafman, J. (1996). Visualizing cortical activation during mental calculation with functional MRI. NeuroImage, 3, 97-103.

Seymour, S. E., Reuter-Lorenz, P. A., & Gazzaniga, M. S. (1994). The disconnection syndrome: basic findings reaffirmed. Brain, 117, 105-115.

Simon, T. J. (1997). Reconceptualizing the origins of number knowledge: A "non-numerical" account. Cognitive Development, 12, 349-372.

Simon, T. J., Hespos, S. J., & Rochat, P. (1995). Do infants understand simple arithmetic? A replication of Wynn (1992). Cognitive Development, 10, 253-269.

Spellacy, F., & Peter, B. (1978). Dyscalculia and elements of the developmental Gerstmann syndrome in school children. Cortex, 14, 197-206.

Starkey, P., & Cooper, R. G. (1980). Perception of numbers by human infants. Science, 210, 1033-1035.

Starkey, P., Spelke, E. S., & Gelman, R. (1983). Detection of intermodal numerical correspondences by human infants. Science, 222, 179-181.

Starkey, P., Spelke, E. S., & Gelman, R. (1990). Numerical abstraction by human infants. Cognition, 36, 97-127.

Staszewski, J. J. (1988). Skilled memory and expert mental calculation. In C. M., G. R., & F. M. J. (Eds.), The nature of expertise . Hillsdale N.J.: Erlbaum.

Strauss, M. S., & Curtis, L. E. (1981). Infant perception of numerosity. Child Development, 52, 1146-1152.

Takayama, Y., Sugishita, M., Akiguchi, I., & Kimura, J. (1994). Isolated acalculia due to left parietal lesion. Archives of Neurology, 51, 286-291.

Temple, C. M. (1989). Digit dyslexia: A category-specific disorder in development dyscalculia. Cognitive Neuropsychology, 6, 93-116.

Temple, C. M. (1991). Procedural dyscalculia and number fact dyscalculia: Double dissociation in developmental dyscalculia. Cognitive Neuropsychology, 8, 155-176.

Uller, C., Huntley-Fenner, G., Carey, S., & Klatt, L. (1999). What representations might underlie infant numerical knowledge. Cognitive Development, in press.

van Loosbroek, E., & Smitsman, A. W. (1990). Visual perception of numerosity in infancy. Developmental Psychology, 26, 916-922.

van Oeffelen, M. P., & Vos, P. G. (1982). A probabilistic model for the discrimination of visual number. Perception & Psychophysics, 32, 163-170.

Warrington, E. K. (1982). The fractionation of arithmetical skills: A single case study. Quarterly Journal of Experimental Psychology, 34A, 31-51.

Washburn, D. A., & Rumbaugh, D. M. (1991). Ordinal judgments of numerical symbols by macaques (*Macaca mulatta*). Psychological Science, 2, 190-193.

Wynn, K. (1992). Addition and subtraction by human infants. Nature, 358, 749-750.

Wynn, K. (1996). Infants' individuation and enumeration of actions. Psychological Science, 7, 164-169.

Figure legends

Figure 1 : Anatomical substrates of the number sense in the parietal lobe. All images are horizontal slices through the brain (i.e. parallel to the eye-ear plane), with the front of the brain on top and the left side shown to the left. Sites of activation, indicated by white spots, are mostly concentrated in the intraparietal sulcus, a fissure that runs deep within the left and right parietal lobes (here shown at the bottom of each image). Bilateral activation of the intraparietal sulcus is observed when subjects solve simple arithmetic problems such as subtracting a single digit from 11 (left column, from Chochon et al., 1999) or when they approximate additions (middle column, from Dehaene et al., 1999). In both cases, activation is found relative to a letter manipulation task which does not involve number processing, but is matched to the main task in input and output requirements. The active site in the left parietal lobe coincides roughly with the site of lesions causing acalculia of the Gerstmann type (right, from Dehaene, Dehaene-Lambertz, & Cohen, 1998a).

Figure 2 : Schematic functional and anatomical architecture of the triple-code model (Dehaene & Cohen, 1995). The localization of the main areas thought to be involved in the three numerical codes is depicted on a lateral view of the left and right hemispheres (i.e., as seen from the outside). This schematic diagram is meant as an aid to memory rather than a detailed anatomical depiction. The verbal system, depicted here as a single ellipse, actually is known to involve multiple areas close to the sylvian fissure, including inferior frontal, insular, and superior and middle temporal cortices. The parietal quantity system and the occipito-temporal visual form system, shown here in projection, actually involve deeper cortical areas, respectively in the intraparietal sulcus and in the fusiform gyrus. Finally, the arrows indicate a functional transmission of information across numerical codes and are not meant as a realistic depiction of existing neural fiber pathways, whose organization is not fully understood in humans.

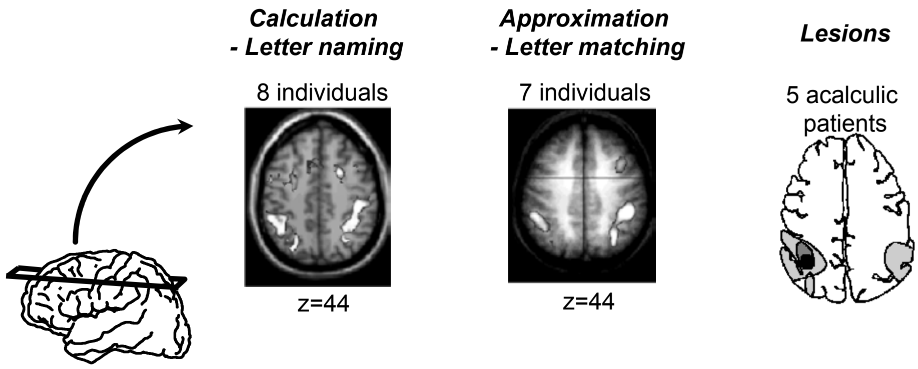
Calculation
- Letter naming
8 individuals
z=44
Approximation
- Letter matching
7 individuals
z=44
Lesions
5 acalculic
patients

figure 1

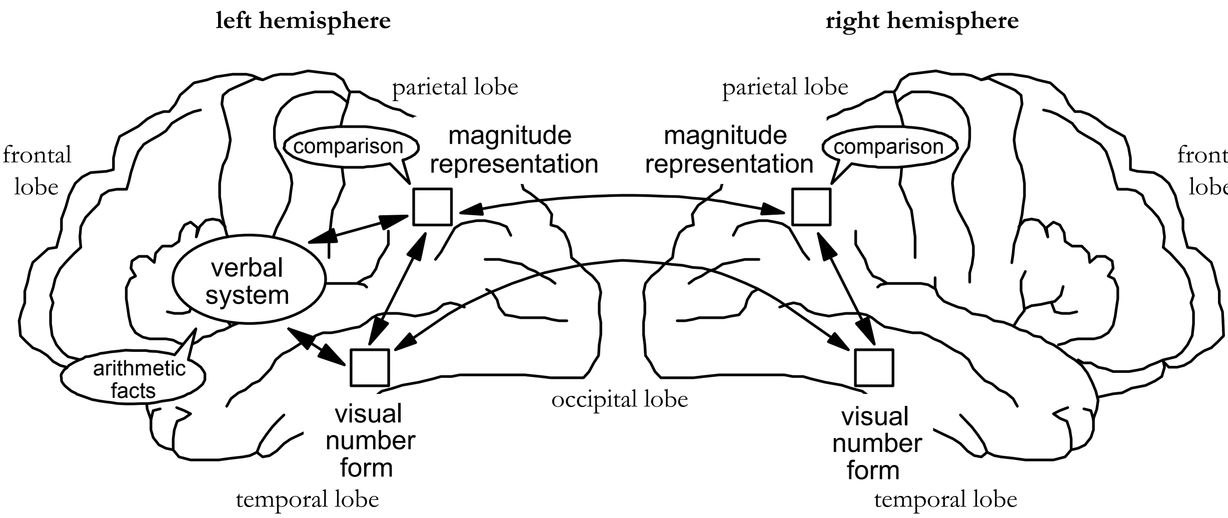
left hemisphere
right hemisphere
parietal lobe
parietal lobe
frontal lobe
frontal lobe
comparison
magnitude representation
magnitude representation
comparison
verbal system
arithmetic facts
visual number form
occipital lobe
visual number form
temporal lobe
temporal lobe

figure 2