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Abstract representations of numbers in the animal and human brain

Stanislas Dehaene, Ghislaine Dehaene-Lambertz and Laurent Cohen

There is evidence to suggest that animals, young infants and adult humans possess a biologically determined, domain-specific representation of number and of elementary arithmetic operations. Behavioral studies in infants and animals reveal number perception, discrimination and elementary calculation abilities in non-verbal organisms. Lesion and brain-imaging studies in humans indicate that a specific neural substrate, located in the left and right intraparietal area, is associated with knowledge of numbers and their relations ('number sense'). The number domain is a prime example where strong evidence points to an evolutionary endowment of abstract domain-specific knowledge in the brain because there are parallels between number processing in animals and humans. The numerical distance effect, which refers to the finding that the ability to discriminate between two numbers improves as the numerical distance between them increases, has been demonstrated in humans and animals, as has the number size effect, which refers to the finding that for equal numerical distance, discrimination of two numbers worsens as their numerical size increases.

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HOW SEMANTIC KNOWLEDGE is encoded in the human brain is a central issue in cognitive neuroscience. Recent neuropsychological and developmental findings have begun to provide a new perspective on this old problem. First, knowledge of different categories of words and objects such as persons, tools, animals and actions can be dissociated in brain-lesioned patients and is associated with distinct patterns of brain activation[1–3]. Thus, specific networks, similarly localized in different individuals[1], participate in the cerebral representation of distinct domains of knowledge in adults. Second, human infants have been found to possess elaborate world knowledge, for instance about objects, colors, faces and language[4]. This is compatible with the hypothesis that humans have been endowed by evolution with biologically determined predispositions to represent and acquire knowledge of specific domains.

In this paper, we review recent evidence suggesting that our knowledge of numbers and elementary arithmetic constitutes such a domain-specific cognitive ability. Supportive evidence includes its spontaneous emergence at a young age during development; its presence in animals, although in a simpler form; and its association to a specific cerebral substrate that can be identified reproducibly in different individuals, either by the lesion method or by functional brain imaging. Converging empirical findings from several areas of cognitive neuroscience arguably make elementary knowledge of arithmetic one of the best-validated candidates for a biologically determined, domain-specific ability. Without doubt, much of higher-level arithmetic is a cultural achievement specific to humans. Nevertheless, our claim is that the basics of 'number sense', the understanding of quantities and their inter-relations, are universal and shared by adult humans, animals and preverbal infants.

Criteria for an abstract representation of numbers

Attributing numerical representations to non-verbal organisms such as animals or infants remains highly

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controversial. Ever since the infamous 'clever Hans' episode, in which several psychologists incorrectly granted a horse the mastery of symbolic calculation, many scientists have considered number processing in animals as a last resort hypothesis[5], to be accepted only if all other non-numerical accounts fail to explain the observed behavior.

The legitimate concern that alternative non-numerical explanations should be tested and rejected can actually be turned into an experimental strategy for identifying genuinely numerical representations. Number can be defined as the only property of sets that remains invariant under substitutions of any items in the set. Thus, we can talk about three objects, three persons, three sounds, or three events: we can recognize that the cardinal of a set is three, regardless of its composition. Do infants or animals have an equally abstract representation of number? To find out, one can assess whether their behavior generalizes across significant variations in non-numerical physical parameters. Application of this strategy has resulted in a very rich body of experiments that demonstrate clearly the abstractness of infant and animal representations of number in the face of variation in object features (such as size, color or shape), spatial location, modality (auditory or visual) and mode of presentation (simultaneous or sequential).

The same strategy can also be used to define abstract semantic representations of number in adult humans. Adults can be said to rely on an abstract representation of number if their behavior depends only on the size of the numbers involved, not on the specific verbal or non-verbal means of denoting them. Indeed, strong evidence has been accrued for an abstract representation of numerical quantity in normal adults, a level of processing common to numbers presented or produced in the auditory or visual modalities, either as words, as Arabic digits or as sets of dots[6–8]. The same strategy has also been used in neuropsychological studies to identify brain-lesioned patients with 'central' deficits of number processing that generalize across various notations for numbers and across comprehension and production tasks[9–11]. Finally, brain-imaging experiments have identified brain systems involved in representing numerical quantities irrespective of notation and of the arithmetic task performed[12,13]. We will consider the application of this research agenda to infant, animals, normal adults, brain-lesioned patients and brain-imaging studies.

Number processing in infants

The received wisdom in developmental psychology, based on the Piagetian framework, was that infants are devoid of numerical competence. Indeed, Piaget's studies of young children's numerical representations suggested that abstract knowledge of arithmetic requires considerable learning and does not appear before 4–7 years of age[14]. The tests of number conservation and set inclusion on which this conclusion was based, however, have now been shown to be poor indicators of children's actual numerical competence. Less-demanding, non-verbal tests have indicated repeatedly that children between one and a half and four years of age have mastered number conservation[15–18]. Moreover, the last 20 years have seen a surge of experimental studies demonstrating numerical discrimination and elementary operation abilities even in preverbal infants[19–30].

Discrimination of visual numerosity was first demonstrated in 6–7-month-old infants using the classic method of habituation-recovery of looking time[19]. Infants watched as slides with a fixed number of dots (for example, two) were presented to them repeatedly until their looking time decreased, indicating habituation. At that point, the presentation of slides with a different number of dots (for example, three) was shown to yield significantly longer looking times, indicating dishabituation and therefore discrimination between two and three. In the princeps study, dot density, spacing and alignment were controlled for. In subsequent studies, the effect was replicated with newborns[20] and with various stimulus sets, including slides depicting sets of realistic objects of variable size, shape and spatial layout[21], and dynamic computer displays of random geometrical shapes in motion, with partial occlusion[22]. Because great care was taken to ensure that number was the only invariant parameter in the stimulus set, infants' behavior indicated genuine number discrimination.

The ability of infants' to discriminate numbers is 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[23]. Six-month-old infants also discriminate numbers of visual events, such as a puppet making two or three jumps[24]. Most importantly, there is some evidence for cross-modal numerosity matching in 6–8-month-old infants. When infants hear either two or three drumbeats, and are given a choice between looking at a slide with two visual objects or at another with three objects, they spend more time looking at the slide whose numerosity matches the number of sounds that they hear[25]. Although the replicability of this finding has been disputed[26], it has been backed up by re-analyses of older data as well as by more recent experiments[27]. As noted above, this finding is crucial because it suggests that in the first year of life, infants might already possess an abstract, amodal concept of number that bridges across the visual and auditory modalities. Further work will be needed, however, to determine whether infants' cross-modal numerosity matching is based on simple one-to-one pairings of objects and sounds, or whether it reflects a genuine amodal perception of number[27].

Another important issue concerns the extent to which infants' number representations can enter into internal arithmetic operations analogous to addition and subtraction. Wynn[28] used a violation-of-expectation paradigm to show that infants developed numerical expectations analogous to the arithmetic operations $1 + 1 = 2$ and $2 - 1 = 1$. To exemplify the $1 + 1 = 2$ operation, for example, five-month-old infants were shown a toy being hidden behind a screen, and then a second toy also being placed behind the same screen. To assess whether infants had developed the numerically appropriate expectation of two objects, their looking times were measured as the screen dropped and revealed either one, two or three objects (objects were added or removed surreptitiously, as needed). Infants looked longer at the unexpected outcomes of one or three objects than at the expected outcome of two objects. This suggests that they had computed internally an expectation of the outcome of two objects, although the two objects had not been presented together earlier.

One possible interpretation of Wynn's experiment is that infants maintain and update a detailed mental image of the objects behind the screen, including their identity, size and location. The detectable mismatch between this internal pictorial representation and the scene that appears when the screen drops would then be responsible for their surprise reaction and lengthened looking times. This non-numerical interpretation, however, has been refuted in two recent experiments. In one, objects were placed on a rotating tray so that their location behind the screen was unpredictable[29]. In the other, the identity of the objects was modified surreptitiously in some of the trials before the screen was dropped[30]. In both cases, infants still reacted to the numerically impossible events 1 + 1 = 1 and 2 – 1 = 2, while appearing to neglect changes in object location and identity. Thus, infants encode the scenes they see using an abstract, implicit or explicit representation of the number of objects in the scene, irrespective of their exact identity and location.

Number processing in animals

Evidence that animals also possess number discrimination, cross-modal numerosity perception and elementary arithmetic abilities comparable to those of human infants has been reviewed in detail elsewhere[5,31–34]. Only the most salient features of these data will be reported here. Like human infants, various animal species including rats, pigeons, raccoons, dolphins, parrots, monkeys and chimpanzees can discriminate the numerosity of various sets, including visual objects presented simultaneously or sequentially and auditory sequences of sounds. Several of these experiments included controls for non-numerical variables such as spacing, size, tempo and duration of the stimuli[35–37]. Although most experiments required extended training, numerically relevant behavior has also been observed in the wild[38] or in situations in which number appears to be extracted spontaneously by animals[36]. For example, in Meck and Church's experiments[36], rats were trained to press one lever in response to a short two-tone sequence and another in response to a long eight-tone sequence. Although duration discrimination was sufficient for that initial performance, subsequently, the rats generalized their behavior to novel, non-differentially rewarded sequences in which duration was fixed and only number varied. This suggests that the animals were representing number during the initial training phase.

Cross-modal extraction of numerosity has been observed in rats[35]. Rats trained initially on distinct auditory and visual discrimination tasks were shown later to generalize to novel sequences in which auditory and visual stimuli were mixed. Thus, a rat trained to press a lever on the left in response to two flashes or two sounds, and a lever on the right in response to four flashes or four sounds, spontaneously pressed the right lever when presented with a combination of two sounds and two lights. The rat's behavior was based on the abstract total number of four events, not on modality-specific representations.

Experiments of symbolic 'language' training also provide evidence for abstract numerical representations in animals. Monkeys[39] and chimpanzees[31,40] have been taught to recognize the Arabic digits 1–9 and to use them appropriately to refer to sets of objects. In controlled experiments, a parrot was even taught to recognize and produce a large vocabulary of English words including the first few number words. The animal could answer questions as complex as 'How many green keys?' when confronted with multiple objects of various colors. Symbolic labeling abilities such as these are exceptional, show considerable inter-individual and inter-species variability, require years of training and are never found in the wild. Thus, such experiments cannot be taken to indicate that exact symbolic or 'linguistic' number processing is within the normal behavioral repertoire of animals. However, they do indicate that abstract, presumably non-symbolic representations of number are available to animals and can, under exceptional circumstances, be mapped on to arbitrary behaviors that can then serve as numerical 'symbols'.

Like human infants, animals also exhibit some abilities for elementary mental arithmetic. They can apply to their internal representations of number simple operations of approximate addition, subtraction and comparison. For example, out of two sets, each composed of multiple piles of food morsels, chimpanzees spontaneously select the one with the greater total numerosity, indicating approximate addition of the number of morsels in each pile and comparison of these totals[41]. Abstract addition of simple fractions such as a quarter, a half and three quarters has also been recorded[42]. Chimpanzees trained with Arabic digits can even identify two Arabic digits such as 2 and 3 and point to their sum 5 amidst other Arabic digits[31]. Again, while some of these abilities require considerable training, a core of elementary arithmetic abilities seems to be available even to untrained animals. For example, Wynn's 1 + 1 = 2 and 2 – 1 = 1 experiments with infants[28] have been replicated using a very similar violation-of-expectation paradigm with untrained monkeys tested in the wild[38].

While the cerebral substrates of animals' numerical abilities are unknown, we speculate that occipito–parietal pathways for spatial visual processing play a crucial role in numerosity extraction, in agreement with the special role of bilateral inferior parietal cortices in number processing in human adults (cf. below). A neuronal network model of this process has been proposed[43]. In this model, numerosity is estimated by summing the activity over a neural map of space in which each object, regardless of its identity and size, is represented by a fixed population of neurons – a normalization which could be performed by the occipito–parietal 'where' pathway. The output of the simulation is a bank of units, each of which reacts to a given approximate number of objects of various sizes presented on the input layer. The model can be conditioned by reinforcement to acquire most numerical behaviors exhibited by animals[43].

Parallels between animal and human representations of number

How do animal abilities for number processing relate to arithmetic in adult humans? On the surface, the difference between animals and humans seems considerable, because animals are limited to elementary, approximate and non-symbolic calculations. Our

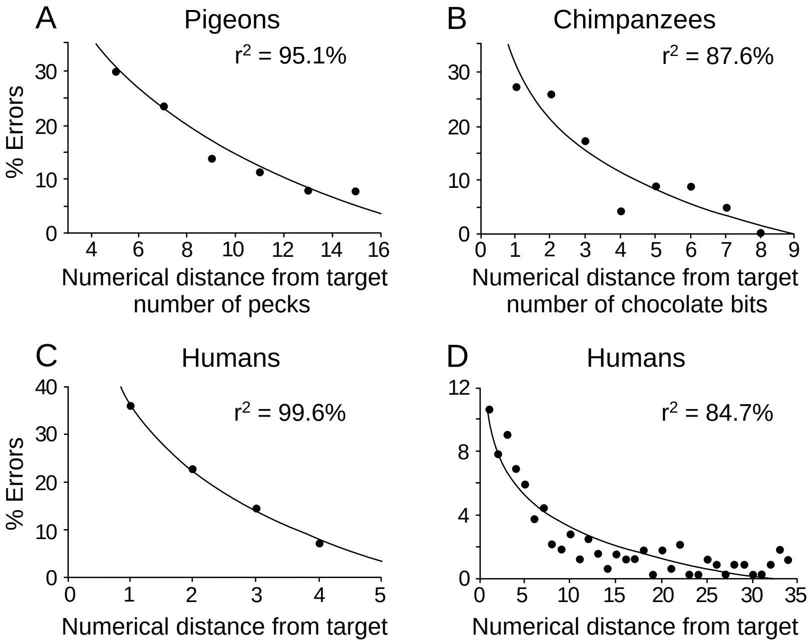

Fig. 1. ***Distance effect.*** *In all species, error rates in various number comparison tasks decrease monotonically as an approximately logarithmic function of the numerical distance between the numbers to be compared.* **(A)** *Pigeons compared their numbers of pecks to a fixed standard of 50 (Ref. 44).* **(B)** *Chimpanzees selected the larger of two small numbers of chocolate bits*[39]. **(C)** *Humans decided whether a pattern contained exactly 12 dots*[45]. **(D)** *Interestingly, humans also exhibit a distance effect when processing symbolic numerals, for instance when deciding if a two-digit Arabic numeral is larger than 65 (Ref. 46). Note the different scale, however, indicating that error rates are much lower when humans can rely on symbolic notation.*

claim, however, is that animal number processing reflects the operation of a dedicated, biologically determined neural system that humans also share and which is fundamental to the uniquely human ability to develop higher-level arithmetic. Support for the hypothesis of a shared evolutionary heritage for elementary arithmetic comes from the finding of deep and systematic parallels between human and animal number processing. Two such major parallels have been found to date: the numerical distance effect and the number size effect.

The numerical distance effect (Fig. 1) refers to the empirical finding that the ability to discriminate between two numbers improves as the numerical distance between them increases. Distance effects have been reported with 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[33]. Similar results have been obtained with adult humans, not only when comparing the numerosity of two sets of dots[45,47], but also when processing Arabic digits or number words[13,46–48]. Thus, it is faster and easier to compare four with eight than four with five, even after intensive training. The distance effect is found even with two-digit numerals[46]. Comparison times and error rates are a continuous, convex upward function of distance, similar to psychophysical comparison curves (Fig. 1).

The occurrence of a distance effect even when numbers are presented in a symbolic notation suggests that the human brain converts numbers internally from the symbolic format to a continuous, quantity-based analogical format. 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 the same or different[6], or in priming experiments in which the mere presentation of an Arabic digit or of a number word facilitates the subsequent processing of a numerically close target number[49,50].

The number size effect (Fig. 2) refers to the finding that, for equal numerical distance, discrimination of two numbers worsens as their numerical size increases. Thus, it is more difficult to tell which of the number eight or nine is the larger than to decide between two and three. This effect, which is a form of Weber's law, holds when various animal species are presented with different numbers of visual objects or sounds in various discrimination or comparison tasks[33]. It should be stressed here that animals are not limited to processing small numbers only. For example, pigeons can discriminate between 45 and 50 pecks[44]. However, the ability to discriminate decreases monotonically with number size.

The number size effect has not been studied systematically in human infants, although evidence suggests that they discriminate readily between two and three objects, occasionally between three and four (or four and five), but not between four and six[19]. In human adults, however, a growing imprecision for increasingly large numbers is found during identification or discrimination of two sets of dots[45,47]. The number size effect accounts for 'subitizing', our limited ability to perceive rapidly the exact number of objects when their number is below three or four, but not when it is above this number[54,55]. Most importantly, a similar number size effect is found when humans compare or calculate with numbers presented as Arabic digits or as number words[47,48,52]. Even in highly trained adults, adding, multiplying or comparing two large digits such as 8 and 9 is significantly slower and more error-prone than performing the same operations with digits 2 and 3, although the exact origin of this effect remains debated. Thus, cognitive psychological evidence indicates that, in various number processing tasks, humans quickly access a representation of numerical quantities similar to that of animals, which is organized by numerical proximity and gets increasingly fuzzier for increasingly larger numbers.

Deficits of semantic number processing in brain-lesioned patients

If the elementary understanding and manipulation of numerical quantities is part of our biological evolutionary heritage, does it also have a dedicated neural substrate? Two arguments suggest that number processing is associated with a specific cerebral network located in the inferior intra-parietal area of both hemispheres. First, neuropsychological studies of human patients with brain lesions indicate that the internal representation of quantities can be impaired selectively by lesions to that area[10,11,56,57]. Second, brain-imaging studies reveal that this region is activated specifically during various number processing tasks[12,13,58–60].

Lesions of the inferior parietal region of the language-dominant hemisphere often cause number processing deficits (Fig. 3). In some cases, comprehending, producing and calculating with numbers are all impaired[11]. However, in other cases, the deficit can be selective for calculation, with reading, writing, spoken recognition and production of Arabic digits and number words not being affected[10,56,57].

Recently, we suggested that the core deficit in parietal acalculia is a disorganization of an abstract semantic representation of numerical quantities rather than of calculation processes per se[10,61]. One of our patients, Mr M[10], experienced severe difficulties in calculation, especially with single-digit subtraction problems (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 presented visually and read out loud simultaneously, and because he failed in both overt production and covert multiple choice tests. Moreover, he also erred on tasks outside of calculation, such as deciding which of two numbers was the largest (16% errors) or what number fell 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 of the year, or letters of the alphabet (for example, what is between Tuesday and Thursday; February and April; B and D?), indicating that he suffered from a category-specific deficit for numbers.

Even in the number domain, patient M's rote verbal knowledge of arithmetic tables was preserved partially relative to his knowledge of quantities. Single-digit multiplication and addition problems, which are learned by rote in the French education system, were solved significantly better than subtraction problems. The patient could still recite 'three times nine is 27', although he claimed he no longer knew what that meant. This confirms our earlier suggestion that rote memory for arithmetic tables need not involve the parietal quantity system, but can be accessed non-semantically using a left perisylvian language circuit[10,61,62]. We have now made several observations of patients with dominant-hemisphere inferior parietal lesions and Gerstmann's syndrome. All of them showed specific impairments in subtraction and number bisection, suggesting disturbance to the central representation of quantities.

A 'developmental Gerstmann's syndrome', also called developmental dyscalculia, has been reported in children[63–66]. Some children show a highly selective deficit for number processing although they have normal intelligence, normal language acquisition and a standard level of education. For example, Paul[64] is a young boy who suffers no known neurological disease, has a normal command of language, and uses an extended vocabulary, but has experienced exceptionally severe difficulties in arithmetic since kindergarten. At the age of 11, he remained unable to multiply, subtract or divide numbers, and could only add some pairs of digits through finger counting. Paul can read non-words as well as infrequent and irregular words such as colonel. However, he makes word substitution errors only when reading numerals, for instance reading 1 as nine and 4 as two. Although there is little anatomo-pathological data on such developmental dyscalculia cases, it is tempting to view them as resulting from early damage to inferior parietal cortices that hold a representation of numbers.

Brain-imaging studies of number processing

Roland and Friberg[59] were the first to monitor blood flow changes during calculation as opposed to rest. When subjects repeatedly subtracted three from a

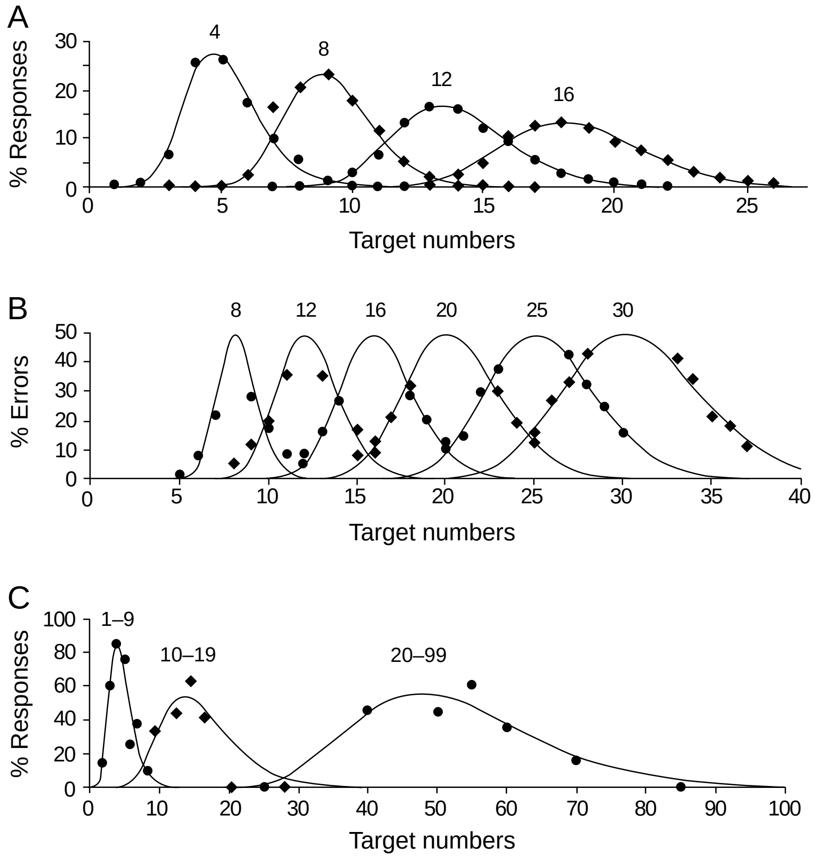

Fig. 2. ***Size effect.*** *In all species, performance in various number processing tasks becomes increasingly imprecise as the numbers involved get larger.* **(A)** *Rats compared their numbers of lever presses to a fixed standard of 4, 8, 12 or 16 (Ref. 51).* **(B)** *Humans compared the numerosity of a dot pattern to a fixed standard of 8, 12, 16, 20, 25 or 30 (Ref. 45). In both cases, the size effect is revealed by an increasing dispersion of the distribution of responses (Weber's law); scaling differences are related to minor differences in task demands and should be ignored. In general, when humans process symbolic numerals, the size effect is reflected only by lengthened response times and a small increase in error rates for increasingly larger numbers[47,48,52]. The data shown here* **(C)** *were obtained in the special case of Mr NAU, a patient with a larger left posterior lesion[53], who could still convert Arabic numerals to quantities but failed in exact calculation. In patient NAU, the normal distance effect was exacerbated, so that when asked to verify additions, he claimed that 2 + 2 = 5 was correct but recognized that 2 + 2 = 9 was false. The graph indicates that patient NAU's addition approximation performance was progressively less precise as the sums he was given went from single digits, to teens and then two-digit numbers.*

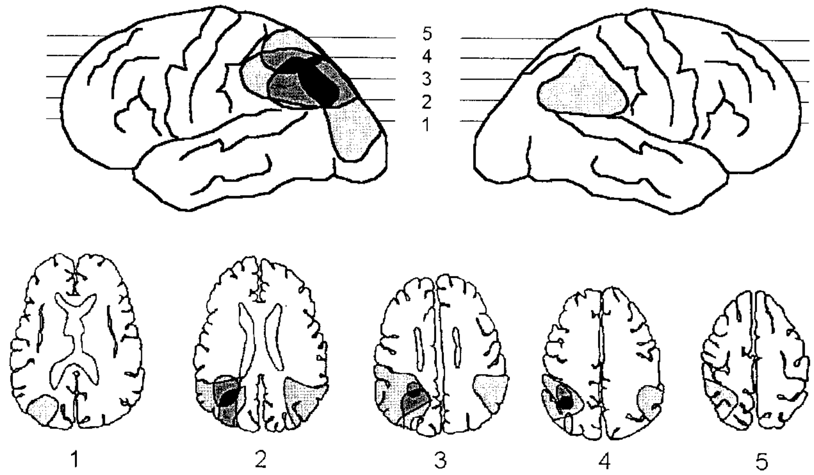

Fig. 3. ***Overlapping lesions of five patients with Gerstmann's syndrome*** (redrawn from Refs 10 and 57). *All patients could read Arabic numerals aloud and write them to dictation, and all suffered from a severe deficit of the processing of numerical quantities, evident in various calculation tasks. The lesions overlap deep in the inferior lobule, in the vicinity of the intraparietal sulcus, a location compatible with brain-imaging studies of calculation in normal subjects[58]. Note that the one patient with a right-hemispheric lesion (patient M; Ref. 10) was left-handed and suspected of right-hemispheric dominance for language.*

given number, activation increased bilaterally in the inferior parietal and prefrontal cortex. These localizations were later confirmed using functional magnetic resonance imaging (fMRI)[60,67]. A recent positron emission tomography study of multiplication and comparison of digit pairs has revealed bilateral parietal activation confined to the intraparietal region[58], in agreement with lesion data (Fig. 3).

More detailed studies have begun to examine the prediction that inferior parietal cortex activation reflects the operation of an abstract category-specific quantity system largely independent of input and output modalities and the specific arithmetic task involved. In a word categorization task, high-density recordings of event-related potentials (ERPs) revealed a late parietal activation specific to number words, which was not elicited by other categories of stimuli matched for length and frequency, such as proper names, verbs, animal names or consonant strings[68]. ERP recordings during a number comparison task revealed inferior parietal activity, which was modulated by the numerical distance separating the numbers to be compared, but not by the notation used to present them (Arabic numerals or written words)[58]. A similar study of number multiplication showed that inferior parietal activity lasted longer during multiplication of two large digits than during multiplication of two small digits, regardless of the modality of presentation of the operands (auditory or visual)[12]. Hence, both the distance effect and the number size effect can be traced back to the inferior parietal area.

Interestingly, the ERP effects, although always bilateral, were stronger over the left inferior parietal area during multiplication and over the right parietal area during number comparison. Recently, we replicated this modulation by task demands using fMRI (F. Chochon *et al.*, unpublished observations). Relative to letter reading, digit comparison yielded greater activity in the right inferior parietal area, multiplication yielded greater activity in the left parietal area, and subtraction yielded a bilateral increase. These lateralization effects are compatible with neuropsychological evidence that unilateral inferior parietal lesions are sufficient to disrupt exact arithmetic operations, but can leave intact the ability to compare two numbers. In spite of these variations, however, an extensive bilateral intraparietal network was common to all three tasks. We suggest that this network represents the cerebral basis of number sense.

Obviously, we are not promoting the phrenological idea that a single brain area underlies an entire domain of competence such as arithmetic. Presumably, only the core of number meaning – knowledge of numerical quantities and their relations – is encoded in the intraparietal cortex. A wide network of brain areas is known to be involved in other aspects of number processing such as digit identification, numeral comprehension and production, the spatial layout of multi-digit calculations, rote arithmetic memory and so on[61]. Even very simple calculations call for the coordination of many such areas. Indeed, neuropsychological dissociations confirm that arithmetic is a multifaceted domain. Algebraic knowledge [for example, $(a + b)^2 = a^2 + 2ab + b^2$] can be intact in patients with impaired number knowledge[69,70], suggesting that a distinct circuit is used. Likewise, in the triple-code model of number processing[61,71], arithmetic facts that have been learned repeatedly, such as the multiplication table, are thought to be stored in memory in a non-semantic way, in the form of rote sequences of words. A patient with lesioned left basal ganglia, but with an intact inferior parietal cortex, lost the ability to recite multiplication tables but could still compare numbers, solve simple addition and subtraction problems and bisect a numerical interval, thus completing the double dissociation with patient M (Ref. 10). Thus, the quantity representation in the intraparietal cortex is only one of the many cerebral codes for numbers – but it is the most crucial one, the representation of cardinal meaning out of which the whole of arithmetic can grow.

Some missing links and pointers to further research

The evidence reviewed above leads us to speculate that the inferior parietal cortex holds a biologically determined representation of numerical quantities; that this representation is available to animals and to infants before language acquisition; and that it underlies the acquisition of symbolic numerals and exact calculation algorithms in children and human adults. Owing to lack of space, the latter stage – how the preverbal approximate number representation connects to language and symbol systems – cannot be described here. The reader is referred to Ref. 34 for a more detailed discussion of how number words, early calculation algorithms, and so-called ‘prodigious’ calculation abilities are acquired in humans only.

Although empirical evidence supports a biologically determined cerebral basis for elementary number processing, there are still several unanswered questions and further research is necessary. In particular, directly parallel studies of animal, infant, and adult human behavior using identical experimental paradigms are still lacking. Most importantly, infant studies of arithmetic are confined to very small numbers (up to four or six). Our views predict that infants, like animals, should be able to discriminate large numbers provided the numerical distance between them is sufficiently large. This crucial prediction remains untested. In addition, although the role of the intraparietal cortex in number processing is supported by considerable evidence in adult humans, its involvement in infants and animals remains speculative. Non-invasive brain-imaging techniques applicable to infants[72] have not been applied to number processing. More surprisingly, in spite of the availability of excellent animal models of number processing, there is an absence of lesion and electrophysiological studies of number in animals. To the best of our knowledge, only a single study reported recordings of neurons responsive to a specific number of auditory or visual stimuli in the associative cortex of the anesthetized cat[73]. If this study could be replicated, it would provide a first-hand method for understanding the fine-grained networks underlying number processing.

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BOOK REVIEWS

Isolation, Characterization and Utilization of CNS Stem Cells

edited by F.H. Gage and Y. Christen, Springer, 1997. £52.50 (198 pages) ISBN 3 540 61696 9

This book is based on a meeting of the Fondation IPSEN held in Paris in 1995 and sets out to address issues relating to neural stem cells. The format is one of independent reports from different fields of research, seen very much from the contributing authors' viewpoint. This gives each chapter a specific 'flavour' and highlights the breadth of studies currently going on in this rapidly expanding field. Stem cells have been best studied in the haematopoietic system. Here there is a pluripotent 'mother of all stem cells' from which lymphoid and myeloid stem cells can be derived, which in turn give rise to progenitor cells with more limited capacity for division and differentiation. Weissman sets the scene in the opening chapter by describing succinctly the haematopoietic stem-cell biology and how this might relate to stem-cell biology in general. In the haematopoietic system, researchers bask in the luxury of over 100 cell-surface markers (established over a 35-year period of intensive research) which can track the development of pluripotent stem cells through progenitor stages and on to erythrocytes, monocytes and thymocytes.

The following chapters all deal with neural stem cells to some degree. Perhaps the most obvious topic for the second chapter would be to introduce the reader to neural stem-cell terminology and history, which is in fact covered much later in a concise report by McKay who outlines the origins of the CNS. Here we are introduced to the only marker of neuronal stem cells called nestin (an acronym for neuroepithelial stem cell protein) which, in contrast to the plethora of haematopoeitic extracellular markers, labels an intracellular intermediate-filament protein. As alluded to by the majority of authors in this book, a crucial issue facing neural stem-cell biology is the lack of definitions – which in part reflect the lack of markers for neural tissue at various stages of development. Even in the preface the terms stem cell, putative stem cell and progenitor cell are intermixed and in a later chapter by Snyder the term 'stem-like' cell is coined. Is there a consensus as to what a neural stem cell is? In a book devoted to this topic and including most of the senior workers in the field it is a shame that more effort has not been made to set global ground rules for these terms and perhaps include them in an appendix, although individual chapters do raise this issue separately. In broad terms any cell that can self-renew and give rise to neurones, astrocytes and oligodendrocytes is a good candidate for a neural stem cell. Just how long this cell has to self-renew *in vitro* to be a 'true' stem cell has not been addressed. Furthermore, in the haematopoetic system there are lineage-restricted lymphoid and myeloid stem cells, and so based on this terminology there could well be separate