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68 Cerebral Bases of Number Processing and Calculation

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ABSTRACT What is the cerebral basis of the human competence for mathematics? Cognitive neuroscientists have begun to address this issue in the small domain of elementary arithmetic. Chronometric experiments indicate that the human brain comprises an analogical representation of numbers, in which numerical quantities are internally manipulated as points on a mental "number line." Neuropsychological studies of number processing indicate that this representation is distributed in the two hemispheres and point to inferior parietal cortex as its dominant site. The intraparietal network may provide a category-specific semantic representation of numerical quantities. Recent neuroimaging experiments confirm that this area is specifically activated when normal subjects manipulate numbers, regardless of the particular notations used to convey them.

Mental arithmetic is a basic ability of the human brain. In daily life, we encounter numbers in a wide variety of situations: We punch phone numbers, check our change, balance our bank accounts, take a train, check our driving speed; and, sometimes, we even plan or analyze scientific experiments. Of the content words of language, number words are among the most frequent: In English, we utter the word "one" once in every 70 words, and the word "two" once in every 600 words (Dehaene and Mehler, 1992; frequencies are comparable in other languages). Arguably, numbers are one of humanity's most important cultural inventions, without which science or society as we know it would never have seen the light of day.

In recent years, experimental studies have begun to address an age-old puzzle–the origins of the human mind's competence for mathematics. Using the methods of cognitive neuroscience, we can now ask what internal representations are used to manipulate numbers mentally, when and how they develop, and what brain areas are involved. Space precludes an exhaustive description of cognitive neuroscience studies of numeracy (but see Campbell, 1992; Dehaene, 1997; Dehaene and Cohen, 1995); rather, this chapter focuses on two issues–category specificity and modularity–issues of general interest in cognitive neuroscience that have been addressed in the specific domain of numbers.

Category specificity refers to the hypothesis that different domains of knowledge–such as knowledge of animals, foods, actions, or objects–are subserved by dedicated mental processes, even by specific brain circuits. I have argued that the number domain provides a remarkable example of a biologically determined, category-specific domain of knowledge (Dehaene, Dehaene-Lambertz, and Cohen, 1998). Supporting evidence has accrued from multiple converging fields of research, including animal, infant, and adult human psychology, as well as lesion studies and brain imaging. This empirical evidence suggests that humans and animals possess a specific, biologically determined ability to attend to small numbers of objects or events in their environment. In humans, an internal representation of numerical quantities develops very rapidly in the first year of life; and, later in life, this representation underlies our ability to learn symbols for numbers and to perform simple calculations. It is specifically associated with neural circuitry in the inferior parietal lobule. Brain damage to these circuits can cause highly specific impairments in the representation and manipulation of numbers.

Arguably, then, biological evolution has internalized in our brains a dedicated cerebral system for number, comparable to the specialized cerebral devices that subserve color or stereo vision, auditory localization, or visuomotor transformations. Such a "number sense" is obviously useful to survival: It helps us make sense of a world composed, at the scale in which we live, largely of discrete objects forming sets whose combinations follow the rules of arithmetic.

The hypothesis of a dedicated brain system for quantity knowledge is superficially reminiscent of Gall and Spurzheim's phrenology. In phrenological diagrams, all knowledge of numbers and mathematics was attributed to a specific brain convolution. Of course, the present claim is quite different. According to the hypothesis developed here, the internal representation of numerical quantities, which is putatively linked to cortical tissue within the intraparietal sulcus, is not the only repository

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of arithmetic knowledge in our brains. Rather, it is assumed to be associated with a highly specific and limited mode of representation and manipulation of numbers, in the form of abstract quantities laid down on an analogical number line. Chronometric and neuropsychological studies indicate that the quantity representation is by no means the only internal code that humans use to manipulate numbers. Multiple representations, supported by a distributed cortical and subcortical network, underlie our ability to understand, produce, and mentally manipulate numbers in various formats, including arabic numerals (e.g., 32) and number words ("thirty-two"). Even extremely simple calculations, such as producing the result of 3 – 1, involve the coordination of multiple brain areas within a complex cognitive architecture.

This is the second key concept of cognitive neuroscience to which the study of numerical cognition has strongly contributed–the *modularity of the cognitive architecture* for verbal and nonverbal processing. Numbers constitute a small domain of language, with its own lexicon of thirty-some words, its restricted syntax, and its easily defined semantics. Fine-grained studies of number production, comprehension, and calculation tasks have provided strong evidence for a modular organization at each of these levels.

Number processing in normal subjects

Moyer and Landauer (1967) first characterized the semantic representation of numerical quantities in human adults. They presented subjects with pairs of arabic digits, such as 3:4, and asked them to indicate which number was larger (or smaller). Response times and error rates were strikingly affected by number size and number distance (figure 68.1). As the numbers to be compared represented closer and closer quantities (e.g., 2:8 vs. 4:5), the subjects' responses became increasingly slower and more error-prone. And when distance was kept constant, increasingly larger quantities again resulted in increasingly slower responses and larger error rates. Performance in comparing two numbers was determined by a Weber fraction, similar to that found when subjects have to compare physical parameters such as object size, line length, or tone height. Yet the number stimuli were presented in a symbolic notation, arabic numerals, whose surface form is largely arbitrary, conveying no information about number meaning. The distance effect suggested that subjects were converting the input numerals to an internal continuum, a mental "number line," and were performing a psychophysical comparison on this internal representation rather than on the surface form of the numbers.

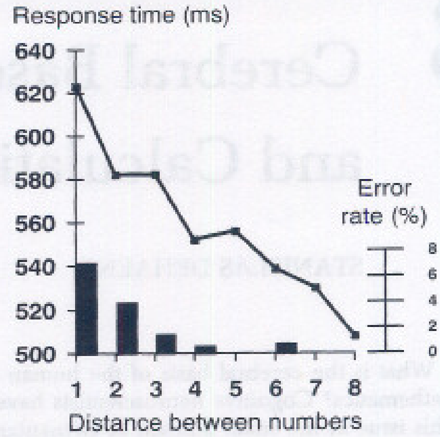


FIGURE 68.1 Distance effect: the amount of time it takes to decide which of two digits is larger is inversely related to the distance between them. Error rates show a similar trend. (Redrawn from Moyer and Landauer, 1967.)

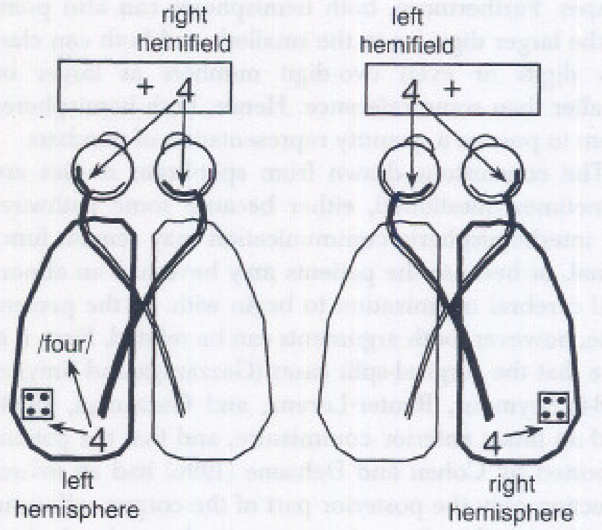
Subsequent work largely confirmed the hypothesis of an internal conversion to a notation-independent analogical representation of quantity. Buckley and Gillman (1974) measured the time to compare numbers that were conveyed either by arabic numerals or by the numerosity of dot patterns. Performance was remarkably similar, driven in both cases by numerical distance and size effects. In later work, parallel performance patterns were found when subjects compared arabic numerals and number words in various languages (Dehaene, 1996; Tzeng and Wang, 1983). Obviously, the mental representation on which subjects based their comparative judgments abstracted away from the symbolic surface form of the numerals and encoded their quantitative meaning only. A continuous distance effect was found even when subjects compared two-digit numerals. The two-digit number comparison results indicated that subjects did not rely on a digit-by-digit analysis of decades and units, but rather performed a holistic evaluation of numerical quantity (Dehaene, Dupoux, and Mehler, 1990; Hinrichs, Yurko, and Hu, 1981).

Beyond the number comparison task, chronometric experiments with various number processing and calculation tasks have revealed ubiquitous number size and distance effects, indicating that the quantity representation plays a pivotal role in numerical cognition. For instance, in a same–different judgment task (Dehaene and Akhavein, 1995; Duncan and McFarland, 1980), subjects were shown a pair of numbers, such as 2:5, and asked to say whether or not the two numbers were the same, responding as fast as they could. Conceivably, subjects can respond on the basis of visual similarity alone. Thus, in one version of the task, subjects were actually encouraged to rely on such a superficial visual analysis: They were asked to respond "different" to such pairs as "2:two," in which the numbers are numerically identical but physically different. Nonetheless, response times were always affected by a distance effect. When subjects responded "different," their responses were slower when the pair comprised two numbers that were numerically close (e.g., 2 and 3) than when it comprised two very different numbers (e.g., 2 and 8). Obviously, subjects could not prevent a mental conversion from digital symbols to the corresponding quantities.

Size and distance effects are also obvious when subjects calculate (Ashcraft and Battaglia, 1978). The time to perform an internal addition or multiplication operation varies considerably with the size of the numbers involved. Problems with small numbers, such as $2 + 3$ or 3×2, are solved much faster than problems with large numbers such as $6 + 8$ or 6×8. Of course, the greater practice we have with small arithmetic facts may contribute to this effect. The distance effect in calculation verification, however, cannot be explained by practice. When subjects are asked to verify whether an operation is true or false (e.g., $3 \times 6 = 72$?), responses are increasingly faster as the proposed result gets more distant from the true result of the operation. As with number comparison, number size and distance effects in calculation are similar whether numbers are presented as arabic digits or as number words, even though small but systematic differences seem to be found (for discussion, see Brysbaert, Fias, and Noel, 1998; Campbell, 1994; Noel, Fias, and Brysbaert, 1997; Vorberg and Blankenberger, 1993).

Hemispheric distribution of number processing abilities

While the existence of a mental representation of quantity has been known since the 1970s, cognitive neuropsychological studies have only recently begun to investigate the cerebral organization of number processing in the human brain. Perhaps the simplest question we can ask is, what is the hemispheric distribution of number processing abilities? Do both hemispheres have access to the quantity representation, and can both hemispheres calculate? This question has been examined in patients with callosal lesions. The corpus callosum is a large bundle of fibers that connects the two cerebral hemispheres. When it is lesioned or surgically sectioned, the cognitive abilities of each hemisphere can be assessed (Sperry, 1968). Numerical abilities were tested in a series of experiments initially performed with surgical split-brain cases (Gazzaniga and Hillyard, 1971; Gazzaniga and Smylie, 1984; Seymour, Reuter-Lorenz, and Gazzaniga, 1994). These results were recently replicated and extended in a study



left hemisphere		right hemisphere
99%	visual matching	99%
100%	pointing	100%
99%	comparison	96%
100%	reading	0%
94%	mental calculation	6%

FIGURE 68.2 Split-brain patients provide evidence about the hemispheric distribution of number-processing abilities (Cohen and Dehaene, 1996). When digits are presented in the right visual hemifield of a split-brain patient, hence contacting only the left hemisphere, the patient can perform any number processing task with them, including visual recognition, pointing to the digit in a random array, larger–smaller comparison, reading, and calculation. Thus, the left hemisphere contains visual, verbal, and quantity representations of numbers. But when digits are presented in the left hemifield, hence contacting only the right hemisphere, the patient may still recognize, point to, or compare them, but fails to read them or calculate with them. Although the right hemisphere has access to visual and quantity representations, it seems to lack a verbal representation of numbers as well as procedures for exact calculation. (Data from patient JW; Gazzaniga and Smylie, 1984; Seymour, Reuter-Lorenz, and Gazzaniga, 1994.)

of a patient who suffered a posterior callosal lesion in adulthood (Cohen and Dehaene, 1996). In both sets of experiments, digits were flashed in either the left or the right hemifield, thus contacting only the contralateral hemisphere, and the patients were asked to perform number processing tasks of varying complexity with them (figure 68.2).

An important conclusion of these experiments is that both hemispheres can process digits and quantities. When two digits are presented simultaneously *within* the same hemifield, split-brain patients experience no difficulty deciding whether they are the same or different (while their disconnection renders them completely unable to compare two digits *across* the two hemifields). Hence, both hemispheres can analyze digit shapes. Furthermore, both hemispheres can also point to the larger digit (or to the smaller), and both can classify digits or even two-digit numbers as larger or smaller than some reference. Hence, both hemispheres seem to possess a quantity representation of numbers.

The conclusions drawn from split-brain studies are sometimes questioned, either because some pathways for interhemispheric communication may remain functional, or because the patients may have had an abnormal cerebral organization to begin with. In the present case, however, both arguments can be refuted. First, it is true that the surgical-split cases (Gazzaniga and Smylie, 1984; Seymour, Reuter-Lorenz, and Gazzaniga, 1994) had an intact anterior commissure, and that the patient reported by Cohen and Dehaene (1996) had an infarct affecting only the posterior part of the corpus callosum. But the fact that the patients were at chance level when asked to compare arabic digits *across* the two hemifields offers clear evidence that the remaining pathways were not sufficient for the transmission of numerical information. Hence, their excellent performance when both stimuli were within the left hemifield cannot be attributed to transfer to the left hemisphere. The sharp dissociation between excellent within-hemifield performance and chance-level across-hemifield performance, indicating disrupted interhemispheric transmission, supports the hypothesis that both hemispheres can compare numbers. Second, while the patients studied by Gazzaniga and colleagues suffered from life-long neurological impairments, the patient studied by Cohen and Dehaene was neurologically normal prior to suffering a callosal lesion. Yet the number comparison results were identical in both cases. Hence, the ability of both hemispheres for number comparison does not seem to be an artifact of abnormal initial brain reorganization.

In only one callosal patient (to date) have the response times been recorded during the number comparison task and the distance effect analyzed (Cohen and Dehaene, 1996). A normal distance effect was observed in both hemispheres, with no significant difference in effect size between the two hemispheres. This suggests that the quantity representations of the left and right hemispheres may have similar characteristics. However, more evidence is needed before this point can be firmly accepted.

There are, however, at least two striking differences between the numerical abilities of the left and the right hemispheres. First, digits presented to the left hemisphere can be named normally by the patients, but digits presented to the right hemisphere cannot. This is in keeping with the well-known lateralization of speech production abilities to the left hemisphere. Second, split-brain patients can calculate only with digits presented to their left hemisphere. When digits are presented to their right hemisphere, the patients fail with operations as simple as adding 2, multiplying by 3, subtracting from 10, or dividing by 2. This is the case even when they merely have to point to the correct result among several possible results, or to indicate nonverbally whether a proposed result is correct or not. The only calculation ability that seems to be available to an isolated right hemisphere, at least occasionally, is approximation. A patient might not be able to decide whether 2 + 2 makes 4 or 5, but might still easily notice that 2 + 2 cannot make 9 (Cohen and Dehaene, 1996; Dehaene and Cohen, 1991).

Modular dissociations in brain-lesioned patients

Detailed single-case studies of patients with various cerebral lesions have indicated that the fractionation of calculation skills in neuropsychological cases is much greater than that seen in split-brain cases alone. The number processing skills of a normally educated adult include the ability to

read, write, produce, or comprehend numerals in both arabic (e.g., 12) and verbal ("twelve") formats, thus implying both lexical (single-word) and syntactic (multiple-word) processes;

convert numbers in these various formats to internal quantities, and vice-versa;

compute single-digit addition, subtraction, multiplication, and division operations;

coordinate several such elementary operations to solve a complex, multidigit arithmetic problem.

Most if not all of these abilities have been found to dissociate in brain-lesioned patients, often in a highly specific manner, indicating that there must be partially specific cerebral circuits associated with each of them.

As a detailed example, let us consider the case of patient HY (McCloskey, Sokol, and Goodman, 1986). When attempting to read an arabic numeral aloud, HY often erred, for instance, reading 5 as "seven" and 29 as "forty-nine." A careful analysis indicated that reading errors stemmed from a highly restricted impairment, affecting only one particular cognitive component of the processing chain that converts written arabic numerals into spoken words. First, HY could still decide which of two arabic numerals was the largest. She could also match an arabic digit to a written number word, verify written calculations, or select a number of poker chips corresponding to a given arabic numerals. Thus, identification of digits and access to quantity information were preserved. This narrowed down the reading deficit to an impairment at the level of producing spoken words. Indeed, McCloskey and his colleagues showed that, in a variety of tasks, HY was much more impaired when he had to produce the numerical answers aloud than when he had to write them down as arabic digits. For instance, when asked the number of eggs in a dozen, HY wrote 12 but said "sixteen."

A careful analysis of HY's number production errors revealed strong regularities. The vast majority of errors were substitutions of one number word for another, keeping the grammatical structure of the number intact. Not all substitutions were equally permissible. When the number fell between 1 and 9, so did HY's erroneous response. The categories of teens (10 to 19) and decades (20 to 90) was also respected. In the final analysis, the deficit could be explained by a highly selective impairment in selecting the appropriate number word in the output lexicon. When reading "15," for instance, the patient prepared to read aloud the fifth element of the teens category (eleven, twelve, thirteen, fourteen, *fifteen*), but he mistakenly selected, say, the eighth element *eighteen* instead. Only minor details of the word substitutions remained unexplained by this hypothesis (Campbell and Clark, 1988; Sokol, Goodman-Schulman, and McCloskey, 1989).

A wide variety of similar highly specific deficits of number processing have now been reported (Cipolotti and Butterworth, 1995; Cipolotti, Warrington, and Butterworth, 1995; Dehaene and Cohen, 1995; McCloskey, 1992). Most importantly, at virtually all levels of processing, dissociations have been observed between numbers and the rest of language, suggesting an amazing degree of modularity in the human brain. For instance, at the visual identification level, pure alexic patients who fail to read words often show a largely preserved ability to read and process digits (Cohen and Dehaene, 1995; Déjerine, 1891, 1892). Conversely, a case of impaired number reading with preserved word reading is on record (Cipolotti, Warrington, and Butterworth, 1995). In the writing domain, severe agraphia and alexia may be accompanied by a fully preserved ability to write and read arabic numbers (Anderson, Damasio, and Damasio, 1990). Finally, within the speech production system, patients who suffer from random phoneme substitutions, resulting in the production of an incomprehensible jargon, may produce jargon-free number words (Cohen, Verstichel, and Dehaene, 1998; Geschwind, 1965).

Selective impairments of the quantity representation

The aforementioned deficits concerned the processing of numerical symbols. But do some cases qualify as selective impairments of the semantic quantity representation of numbers? Laurent Cohen and I have proposed that patients with inferior parietal lesions and Gerstmann-type acalculia suffer from a category-specific impairment of the semantic representation and manipulation of numerical quantities (Dehaene and Cohen, 1995, 1997). From the beginning of this century, it has been known that parietal lesions, usually in the dominant hemisphere, can cause calculation deficits. Gerstmann (1940) reported the frequent co-occurrence of agraphia, acalculia, finger agnosia, and left–right confusion in parietal cases, a tetrad of deficits referred to as Gerstmann's syndrome (although the elements of the syndrome are now know to be dissociable; see Benton, 1992). The lesions that cause acalculia of the Gerstmann type are typically centered on the portion of the intraparietal sulcus that sits immediately behind the angular gyrus (Brodmann's area 39; see figure 68.3). In many cases, the deficit can be extremely incapacitating. Patients may fail to compute operations as simple as $2 + 2$, $3 - 1$, or 3×9. Several characteristics indicate that the deficit arises at a rather abstract level of processing. First, patients may remain fully able to comprehend and to produce numbers in all formats. Second, they show the same calculation difficulties whether the problem is presented to them visually or auditorily, and whether they have to respond verbally or in writing, or even merely have to decide whether a proposed operation is true or false. Thus, the calculation deficit is not due to an inability to identify the numbers or to produce the operation result.

Cohen and I, however, also believe that the patients' impairment is not best described as a specific deficit of calculation only ("anarithmetia" or "acalculia proper"). On the one hand, some calculation processes may remain preserved. Patient MAR, for instance (Dehaene and Cohen, 1997), remained able to retrieve simple multiplication results, such as $2 \times 3 = 6$ or $3 \times 9 = 27$, which he knew by rote. He was very specifically impaired with calculations that were not stored in rote memory and required an internal quantity manipulation, even if it was as simple as $3 - 1$ (he stated that this equaled 7). On the other hand, tasks that require a quantitative understanding of numbers, but are not typically associated with calculation per se, can be impaired in Gerstmann's syndrome patients. Patient MAR could not decide which number fell between 2 and 4 (number bisection task), even though he knew what letter fell between B and D, or what month fell between February and April. MAR also exhibited a discrete difficulty in number comparison, occasionally stating, for instance, that 5 was larger than 6.

The latter deficit suggests that MAR's understanding of the number line was impaired. Indeed, Cohen and I have suggested that inferior parietal cortex holds the

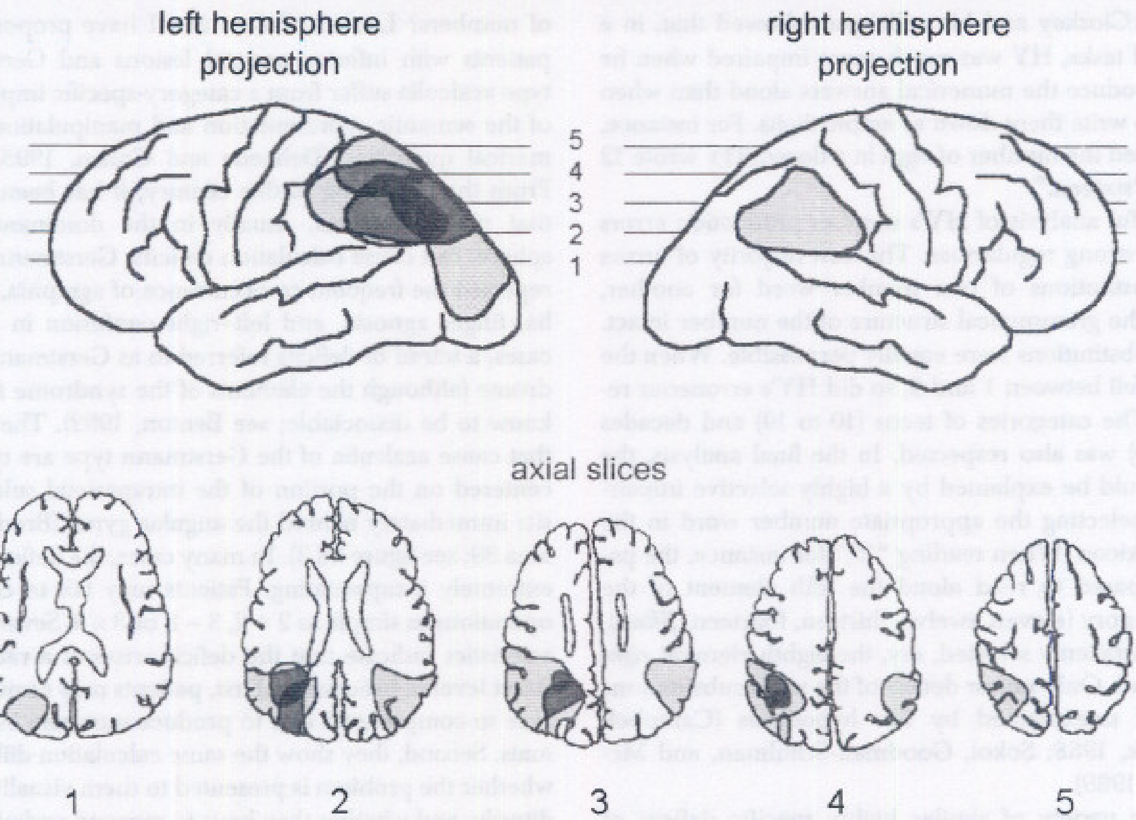


FIGURE 68.3 Overlapping lesions of five patients with Gerstmann's syndrome. All patients showed severe deficits in the comprehension and mental manipulation of numbers. The lesions overlap deep in the inferior lobule, in the vicinity of the intraparietal sulcus. (Redrawn from Dehaene and Cohen, 1997; Takayama et al., 1994.)

internal analogical representation of numerical quantities. Damage to this region causes calculation deficits only if the requested calculations call for internal manipulation of quantities, and not if the task merely involves the retrieval of rote arithmetic facts from verbal memory. Typically, then, subtraction and number bisection are severely impaired, while simple multiplication may be relatively preserved. The fact that interval bisection is affected only in the number domain, but not in the domain of the alphabet, months, or days of week, gives direct evidence that the deficit can be category-specific and not just task-specific.

A simple model of number processing circuits

Based on the variety of number-processing deficits that can be observed in patients, Laurent Cohen and I have proposed a tentative model of the cerebral circuits implicated in calculation and number processing: the *triple-code model* (see figure 68.4; Dehaene, 1992; Dehaene and Cohen, 1995). Initially developed as a purely cognitive model of the different types of representations involved in various number-processing tasks, this model also aims to explain chronometric data from normal subjects (Dehaene, 1992). A later version (Dehaene and Cohen, 1995) made specific proposals as to the putative cerebral substrates of these representations.

Functionally, the model rests on three fundamental hypotheses:

1. 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 number line; a verbal format, in which numbers are represented as strings of words (e.g., thirty-seven); and a visual Arabic number form representation, in which numbers are represented as a string of digits (e.g., 37).

2. Transcoding procedures allow information to be translated directly from one code to the other. For instance, the model supposes that one can mentally convert an arabic digit to the corresponding number word (from 3 to three) nonsemantically, without passing through the semantic representation of the quantity three. This hypothesis distinguishes the triple-code model from other modular models of number processing (e.g., McCloskey, Macaruso, and Whetstone, 1992)

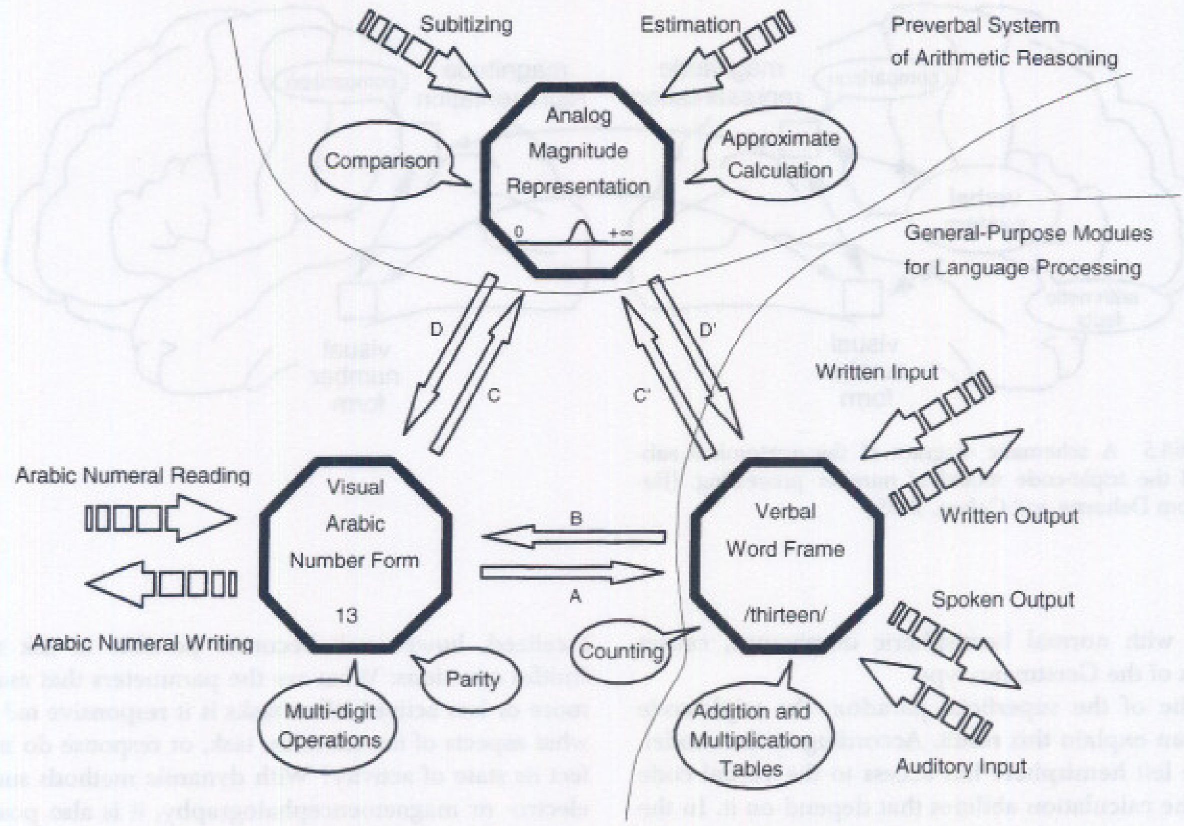


FIGURE 68.4 Functional architecture of the triple-code model of number processing. The three cardinal representations of numbers are represented by octagons. Direct input and output pathways to and from these representations are represented by thick arrows, while thin arrows represent the six possible transcoding pathways that link them. Specific processes putatively attached to a given level of representation are denoted by balloons. (Redrawn from Dehaene, 1992.)

and is more in line with multiple-route models of word processing. Recently, this aspect of the model has received strong support from the observation of patients who cannot convert directly from arabic to verbal numerals (e.g., cannot read arabic digits aloud), but can still convert back-and-forth between these representations and the corresponding quantities (Cipolotti and Butterworth, 1995; Cohen and Dehaene, 1995).

3. Each number-processing task is assumed to rest on a fixed set of input and output codes. For instance, number comparison is postulated to rely on numbers coded as quantities on the number line. Likewise, the model postulates that multiplication tables are memorized as verbal associations between numbers represented as a string of words; that subtraction, an operation that is not memorized by rote verbal learning, calls heavily on the quantity representation; and that multidigit operations are often performed mentally using the visual arabic code and a spatially laid-out representation of the aligned digits.

Neuropsychological observations have enabled us to flesh out the model and to associate tentative anatomical circuits to each function. Cohen and I speculate that the inferior occipitotemporal sectors of both hemispheres are involved in the visual identification processes that give rise to the arabic number form; that the left perisylvian areas are implicated in the verbal representations of numbers (as with any other string of words); and, most crucially, that the inferior parietal areas of both hemispheres are involved in the analogical quantity representation.

Note that the redundant representation of the visual and quantity codes in the left and right hemispheres can explain why, in callosal patients, number comparison remains feasible by both hemispheres (Cohen and Dehaene, 1996; Seymour, Reuter-Lorenz, and Gazzaniga, 1994). This bilaterality assumption does seem to raise a problem for interpreting acalculia cases, however. If there is a bilateral quantity representation, why does a *unilateral* inferior parietal lesion suffice to impair quantity manipulation in Gerstmann syndrome patients? Lesion data clearly indicate that, although the right hemisphere contains a representation of quantity (and although the right inferior parietal cortex is strongly activated during calculation), only a left-lateralized lesion, in

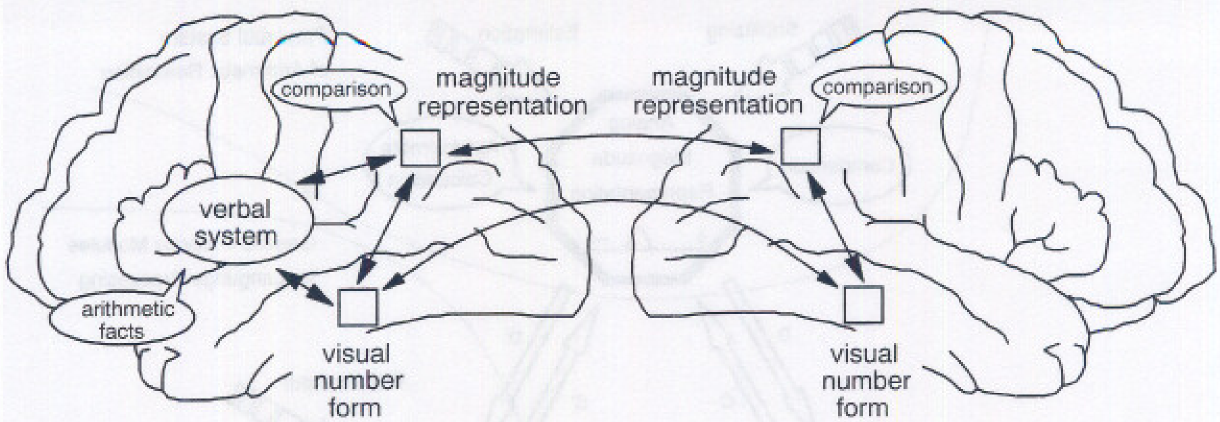


FIGURE 68.5 A schematic diagram of the anatomical substrates of the triple-code model of number processing. (Redrawn from Dehaene and Cohen, 1995.)

subjects with normal hemispheric dominance, causes acalculia of the Gerstmann type.

In spite of the superficial paradox, the triple-code model can explain this result. According to the model, only the left hemisphere has access to the verbal code and to the calculation abilities that depend on it. In the case of a unilateral left inferior parietal lesion, the model therefore predicts that the right-hemispheric parietal quantity representation, although intact, will be functionally disconnected from the left-hemispheric language system (see figure 68.5). Hence, such patients may remain largely able to compare number and perform other manipulations of pure quantities (this was the case with patient MAR, who was largely above chance in number comparison). Yet, according to the model, they are not able to use this quantity knowledge to guide arithmetic fact retrieval and number production, hence their striking deficit in simple arithmetic. The same argument also explains why the right hemisphere of callosal patients cannot read numbers aloud nor calculate with them. Only further research will tell whether this account of the special role of left parietal lesions in acalculia cases is valid. It should also help us grasp a better understanding of the respective roles of the left and right inferior parietal areas in number processing.

Brain imaging of calculation

Functional brain-imaging techniques now provide new tests of the organization of cognitive processes, including calculation processes. In itself, information about cerebral localization is not particularly interesting to cognitive scientists. Once a specific brain area has been localized, however, it becomes possible to ask some fruitful questions: What are the parameters that make it more or less active? What tasks is it responsive to? And what aspects of the stimulus, task, or response do *not* affect its state of activity? With dynamic methods such as electro- or magnetoencephalography, it is also possible to record how quickly and for how long a region activates. In all these respects, the triple-code model makes specific predictions. Most critically, it predicts that the left and right inferior parietal areas should be active during various quantitative number-processing tasks, and that their activation should depend purely on quantitative parameters such as number size and numerical distance, but not on input or output modality nor on the notation used for numbers.

Roland and Friberg (1985) were the first to monitor blood flow changes during calculation as opposed to rest. When subjects repeatedly subtracted 3 from a given number, activation increased bilaterally in inferior parietal and prefrontal cortex. These locations have been confirmed using fMRI (Burbaud et al., 1995; Rueckert et al., 1996). Because the serial subtraction task imposes a heavy load on working memory, it was not clear whether any of these activations were specifically related to number processing. However, experiments using simpler tasks have confirmed that the inferior parietal area seems to play a specific role involved in number processing. In a positron emission tomography study of multiplication and comparison of digit pairs, with little or no working memory component, my colleagues and I again found bilateral parietal activation confined to the intraparietal region (Dehaene et al., 1996). This confirmed results obtained with a coarser resolution EEG method (Inouye et al., 1993) as well as with single-unit recordings in neurological patients (Abdullaev and Melnichuk, 1996).

While these studies indicate that the left and right inferior parietal areas are active and presumably play an important role in calculation tasks, they do not establish the exact nature of their contribution. The triple-code model, however, makes the specific prediction that the inferior parietal cortex activation reflects the operation of an abstract quantity system independent of input and output modalities. Recently, my colleagues and I have begun to test this prediction.

In one study, we used high-density recordings of event-related potentials (ERPs) during a number comparison task to study the cerebral basis of the distance effect. An additive-factor design was used in which three factors were varied: number notation (arabic or verbal), numerical distance (close or far pairs), and response hand (right or left). The results revealed that inferior parietal activity was modulated by the numerical distance separating the numbers to be compared, but not by the notation used to present them (Dehaene et al., 1996). Notation did have a significant effect on the N1 wave, around 150 milliseconds after the visual presentation of the stimuli, indicating bilateral processing for arabic digits, but unilateral left-hemispheric processing for visual number words (in agreement with the triple-code model). By about 200 ms, however, ERPs were dominated by a parietal distance effect with a significant lateralization to the right, and without further influence of notation. Dipole models indicated that the scalp-recorded distance effect could be modeled by two bilateral dipoles located deep within the inferior parietal lobule, with the right-hemispheric dipole showing stronger activation than the left. The response hand effect, which emerged as early as 250 ms after the stimulus, provided an upper bound on the duration of the numerical comparison process.

A similar ERP study of number multiplication (Kiefer and Dehaene, 1997) showed that inferior parietal activity lasts longer during multiplication of two large digits than during multiplication of two small digits—again, regardless of the modality of presentation of the operands (auditory or visual). The main difference with the previous study of number comparison was that the ERP effects, though always bilateral, were stronger over the left inferior parietal area during multiplication, but stronger over the right parietal area during number comparison.

Recently, my colleagues and I replicated this modulation by task demands using fMRI (Chochon et al., 1999). We alternated 36-second blocks during which either single letters or single digits were flashed in the center of a screen. During the letter blocks, the subjects mentally named the letters. This served as a control for the various arithmetic tasks used during the digit blocks. On different runs, subjects were asked to name the digits, to compare them with 5, to multiply them by 3, or to subtract them from 11. In all subjects, fMRI identified a bilateral network that was very clearly pinpointed to the banks of the middle segment of the intraparietal sulcus (figure 68.6), in a location in excellent agreement with the result of lesion studies in Gerstmann's syndrome (figure 68.3). Importantly, however, the size and lateralization of this parietal activation was modulated by task demands. Relative to letter reading, digit comparison yielded greater activity in the right inferior parietal area, multiplication greater activity in the left parietal area, and subtraction a bilateral increase. In agreement with the hypothesis of a nonsemantic direct naming route, however, digit naming in itself did not significantly activate the parietal areas, although a small activation of the right intraparietal cortex was occasionally seen in some subjects.

Number: A biological determined category of knowledge?

In summary, number processing constitutes a remarkable example of the power of the cognitive neuroscience approach, in which a combination of methodologies borrowed from cognitive psychology, neuropsychology, and brain imaging is brought to bear on a single problem. Based on the converging evidence just reviewed, the following working hypotheses can be formulated:

1. The human brain contains an analogical representation of numerical quantities, which can be likened to a mental "number line." This representation is independent of, and common to, the multiple input and output notation systems we use to communicate numbers, such as words or arabic digits. It is subject to distance and magnitude effects.
2. Both the left and the right hemisphere have access to the mental representation of numerical quantity.
3. Lesions of the intraparietal cortex in the dominant hemisphere yield a specific impairment in the mental manipulation of quantities, particularly evident in subtraction and number bisection tasks.
4. The left and right intraparietal cortices are active when normal subjects perform simple calculation tasks. The strength, duration, and lateralization of their activation depends on the nature and difficulty of the operation involved, which in turn is related to the size and numerical distance of the numbers involved. It does not, however, depend on the modality or notation in which the numbers are presented.

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