Verbal and Nonverbal Representations of Numbers in the Human Brain

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Stanislas Dehaene

There is a domain of language in which we are all, in some sense, bilinguals: the domain of numbers. Like any other category of words, numbers can be spoken (/four/, /forty/) or spelled out (FOUR, FORTY). However, we are all familiar with a third symbolic notation, Arabic numerals (4, 40). Furthermore, numbers can also be conveyed in nonsymbolic ways such as sets of dots (::).

The human brain must contain mental representations and processes for recognizing, understanding, and producing these various notations of numbers and for translating between them. Hence the number domain provides a manageably restricted area within which to study the representation of symbolic information in the human brain and the interplay between verbal and nonverbal formats of representation. The lessons that numbers can teach us about the organization of symbol systems in the human brain may also turn out to be generalizable to other linguistic domains.

The Quantity Representation

Moyer and Landauer's (1967) seminal study of number comparison provided the first strong evidence for a quantity representation of numbers in human adults. Measuring the time that it takes to select the larger of two digits, they found a *distance effect:* number comparison becomes systematically slower as the distance between the two numbers decreases. It is easier to decide, say, that 9 is larger than 5 than to decide that 9 is larger than 8. The effect was later extended to two-digit numerals (Dehaene, Dupoux, and Mehler, 1990). The reaction time curve for deciding whether a two-digit number is larger or smaller than 65 is remarkably smooth and shows no significant discontinuities at decade boundaries. Reaction times are influenced by the ones digit, even though the tens digit is sufficient to respond: subjects respond "smaller" more slowly to 59 than to 51, although the 5 in the decades position readily indicates that both of these numbers are smaller than 65.

These results suggest that subjects do not compare numbers digit by digit. Rather, they appear to mentally convert the target Arabic numeral into a continuous quantity, which they then compare to the reference quantity using a psychophysical procedure similar to the one used for comparing line lengths, weights, or other physical quantities. Several models of number comparison suppose that the human brain incorporates an *analogical representation of numerical quantities* that may be likened to a number line. In this representation, numbers are represented not by discrete symbols such as digits or words, but by distributions of activation whose overlap indicates how similar the quantities are. Experiments with normal subjects confirm that the conversion from digits or number words to the corresponding quantities is fast and automatic and even occurs unbeknownst to the subject (review in Dehaene and Akhavein, 1995).

The Triple-code Model

The triple-code model was introduced by Dehaene (1992; Dehaene and Cohen, 1995) in an effort to provide testable hypotheses about the relationship between the various codes for numbers and their implementation in the human brain. The model postulates three main representations of numbers:

- A visual Arabic code, localized to the left and right inferior ventral occipito-temporal areas, and in which numbers are represented as identified strings of digits. This representation, which we call the visual Arabic number form by analogy with Shallice's

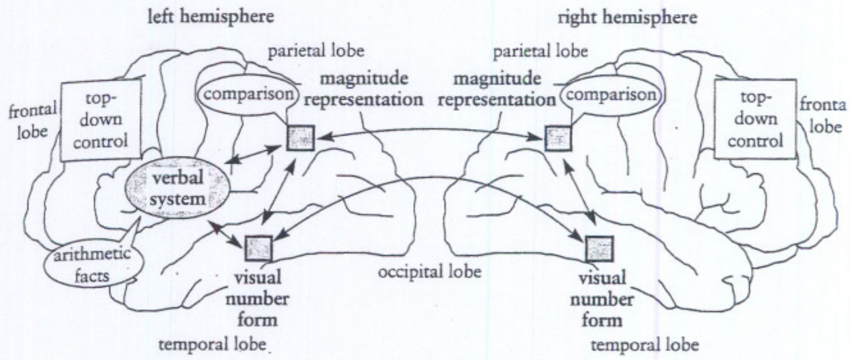

Figure 11.1. Schematic anatomical and functional architecture of Dehaene and Cohen's (1995) triple-code model. The three cardinal representations of number (two of them distributed bilaterally) are shown in light gray.

visual word form, is used during multidigit operations and parity judgments (for example, knowing that 12 is even because the ones digit is a 2).

- An analogical quantity or magnitude code, subserved by the left and right inferior parietal areas, and in which numbers are represented as points on an oriented number line. This representation underlies our semantic knowledge about numerical quantities, including proximity (for example, 9 close to 10) and larger-smaller relations (9 smaller than 10).
- A verbal code, subserved by left-hemispheric perisylvian language areas, in which numbers are represented as a parsed sequence of words. This representation is the primary code for accessing a rote verbal memory of arithmetic facts (for example, "nine times nine, eighty-one").

Figure 11.1 shows the patterns of interconnections that are postulated in the model. In the left hemisphere, all three cardinal representations (Arabic, verbal, and quantity) are interconnected by bidirectional translation routes, including a direct asemantic route for transcoding between the Arabic and verbal representations. In the right hemisphere, there are similar routes for translating back and forth between Arabic and quantity representations, but there is no verbal representation of numbers. Finally, it is assumed that the homologous Arabic and quantity representations in the two hemispheres are interconnected by direct transcallosal pathways. The system operates under the top-down control of frontal lobe and anterior cingulate, where the goals of the calculation and the information-processing pathways appropriate to implement them are specified.

Number Processing in Split-brains

A strength of the triple-code model is that it specifies cerebral localizations, however coarse, for the various representations of numbers. As a result, the model can predict the effect of specific anatomical lesions on number processing. A case in point is the "split-brain" syndrome. When the corpus callosum is severed, the model predicts that the left hemisphere should remain able to perform all sorts of calculations, because it contains the three cardinal representations of numbers (Arabic, verbal, and quantity). The right hemisphere, however, should be able to recognize Arabic numerals, to retrieve the quantity that they represent, but not to read aloud or to perform calculations dependent on the verbal code. This predicted pattern of results is exactly what is found, both in the classical literature on split-brains (Gazzaniga and Hillyard, 1971; Gazzaniga and Smylie, 1984; Seymour, Reuter-Lorenz, and Gazzaniga, 1994) and in a recent single-case study of number processing following an infarct of the posterior half of the corpus callosum (Cohen and Dehaene, 1996). When digits 5 and 6 are flashed in the left hemifield, the patients' right hemisphere can decide that 5 is smaller than 6, but it cannot read the digits aloud or calculate 5 + 6. Similar results suggesting a right hemispheric ability restricted to quantitative processing have been obtained in patients with extended left hemispheric lesions (Dehaene and Cohen, 1991; Grafman et al., 1989). Patient NAU, for instance, could not tell whether 2 + 2 was 3, 4, or 5—but he knew that it had to be smaller than 9.

Number Processing in Pure Alexia

Similar dissociations between impaired linguistic processing of numbers and preserved manipulation of numerical quantities are found in pure alexia (Cohen and Dehaene, 1995). Patients GOD and SMA suffered from highly similar infarcts of the left ventral occipito-temporal area, a region involved in high-level visual identification. Both were totally unable to read words. Arabic numerals were slightly better preserved: multidigit numerals were misread on 60–80 percent of trials and single digits on 8–18 percent of trials. Calculation on written operands was also impaired. For instance, when presented with 2 + 3, the patients might say *seven.* That these calculation errors were due to a misidentification of the digits was shown by (a) the patients' perfect ability to perform the same calculation with spoken operands, and (b) the patients' reading errors in calculation: for instance, 2 × 3 might be read *two times five* and then solved as *ten,* indicating that the patients correctly computed the sum of the operands that they had misread.

So far, this deficit might be understood as a selective impairment of the Arabic number identification module. Contradicting this hypothesis, however, but in agreement with the triple-code model's hypothesis of a right-hemispheric digit identification and quantity processing system, both patients GOD and SMA compared Arabic numerals with remarkable accuracy. For instance, when presented with 44 pairs of two-digit numerals, neither of them made any errors in pointing to the larger number, while they made respectively 89 percent and 91 percent errors in reading the very same pairs aloud. Some of the reading errors inverted the order of the numbers. For instance 78 76 was read as *seventy eight, seventy nine*—yet the patient correctly pointed to 78 as the larger number. These two pure alexia cases thus suggest that access to number semantics can be fully preserved, even when number identification for the purpose of reading is severely compromised. These observations have been replicated (Miozzo and Caramazza, 1998) and extended to show that even elementary calculations such as subtractions can remain preserved (for example, a pure alexic patient might read 3 – 1 incorrectly as *nine minus one,* but then go on to say the correct result, *two*) (Cohen and Dehaene, 2000).

In detail, how does the triple-code model account for these pure alexia cases? In those cases, the lesion affected the left ventral occipito-temporal area and therefore predictably impaired the left visual word and number identification system. Hence left-hemispheric verbal areas could not be directly informed about the identity of the visual word or digit, resulting in a severe impairment in reading aloud. Since the memory retrieval of rote arithmetic facts is assumed to depend on the verbal format, this reading deficit entailed a calculation deficit—the patients could not turn 3×3 into the verbal format *three times three*, which was necessary for them to retrieve the result *nine*. Yet the verbal circuit itself was intact and connected to auditory input/output circuits; it was only deprived of visual inputs. Hence the patients could still calculate when an arithmetic problem was read aloud to them. And finally, their right hemisphere was fully intact, including its visual identification and magnitude representation areas. According to the triple-code model, these preserved right-hemispheric circuits (and connections to the left-hemispheric quantity representation) were the basis for the patients' ability to compare the magnitudes of Arabic numerals that they failed to read aloud (Cohen and Dehaene, 1995).

A New Classification of Acalculias

The triple-code model also accounts for some of the types of acalculias and their anatomical correlates. According to the model, there are two basic routes through which a simple single-digit arithmetic problem such as $4 + 2$ can be solved. In the first, direct route, which works only for overlearned addition and multiplication problems, the operands 4 and 2 are transcoded into a verbal representation of the problem ("four plus two") which is then used to trigger completion of this word sequence using rote verbal memory ("four plus two, six"). This process is assumed to involve a left cortico-subcortical loop through the basal ganglia and thalamus. In the second, indirect semantic route, the operands are encoded into quantity representations held in the left and right inferior parietal areas. Semantically meaningful manipulations are then performed on these internal quantities, and the resulting quantity is then transmitted from the left inferior parietal cortex to the left-hemispheric perisylvian language network for naming. The model assumes that this indirect semantic route is used whenever rote verbal knowledge of the operation result is lacking, most typically for subtraction problems.

The two types of acalculic patients predicted by these two routes for calculation have now been identified (Dehaene and Cohen, 1997). There are several published cases of acalculia following a left subcortical infarct (Whitaker, Habiger, and Ivers, 1985; Corbett, McCusker, and Davidson, 1988; Hittmair-Delazer, Semenza, and Denes, 1994). In a recent case of a left lenticular infarct, Dehaene and Cohen (1997) showed that, as predicted by the model, only rote verbal arithmetic facts such as 3 × 3 were impaired (together with rote verbal knowledge of the alphabet, nursery rhymes, and prayers). Quantitative knowledge of numbers was fully preserved, as shown by the patient's intact number comparison, proximity judgment, and simple addition and subtraction abilities. Hittmair-Delazer, Semenza, and Denes (1994) likewise observed a preservation of conceptual, quantitative, and algebraic manipulations of numbers in their severely acalculic patient with a left subcortical lesion.

Conversely, the model predicts that lesions of the left inferior parietal area, typically resulting in Gerstmann's syndrome, affect calculation because they destroy quantitative knowledge while preserving rote verbal abilities. Indeed, Dehaene and Cohen (1997) observed a case of Gerstmann's syndrome who could still read aloud numbers and write them down to dictation, still knew rote addition and multiplication facts such as 2 + 2 and 3 × 3, and yet failed even in the simplest of quantitative tasks. He made 16 percent errors in larger-smaller comparison, 75 percent errors in simple subtractions (including gross errors such as 3 − 1 = 3 or 6 − 3 = 7), and 78 percent errors in number bisection (stating, for instance, that 3 falls in the middle of 4 and 8). The deficit was highly specific to the category of numbers, since the patient performed quite well in finding the middle of two letters, two days of week, two months, or two notes of the musical scale. We have now observed several such cases of severe number bisection deficits following lesion of the inferior parietal area. These cases support the triple-code model's hypothesis that this area is critical for representing and manipulating number as quantities.

Imaging the Parietal Representation of Quantities

Brain-imaging techniques now allow for the visualization of the cerebral circuits involved in number processing in normal subjects, without resorting to the study of pathological lesion cases. Imaging studies have confirmed that the inferior parietal lobe, in both hemispheres, is critically involved in the internal manipulation of numerical quantities. In an early study Roland and Friberg (1985), with a primitive PET (positron emission tomography) technique, reported bilateral frontal and inferior parietal activity during a repeated subtraction task, a result that has been confirmed in more recent fMRI (functional magnetic resonance imaging) studies (Burbaud et al., 1995; Rueckert et al., 1996). Most recently, we have found bilateral parietal activity during much simpler calculation tasks. In PET, intraparietal activation was found during multiplication of two single digits (Dehaene et al., 1996). In fMRI, similar activation is found when a single digit is flashed and subjects must compare it with 5, multiply it by 3, or subtract it from 11 (see Figure 11.2; see also Chochon et al., 1999). The accuracy of fMRI images obtained from single subjects allowed for a much tighter localization of the activated tissue, which is confined to the banks of the middle portion of the intraparietal sulcus, extending anteriorily into the depth of the postcentral sulcus. Activity is left-lateralized during multiplication, right-lateralized during comparison, and bilateral during subtraction, in agreement with previous studies using event-related potentials (Dehaene, 1996; Kiefer and Dehaene, 1997). Most interestingly, little or no parietal activation is found when subjects simply have to name a single Arabic digit. Hence, in agreement with the triple-code model, parietal activity is not found when subjects merely have to process numerical symbols (such as recognizing a digit or producing a number name), but only when they have to mentally represent and manipulate the corresponding quantity.

The triple-code model makes specific predictions concerning the nature of the parameters that should or should not affect parietal lobe activity during number processing. A first prediction is that the quantity representation should be more active during tasks that draw upon an approximate sense of numbers than during tasks that require exact arithmetic fact retrieval, which can be mediated at least in part by rote verbal memory processes. This prediction was recently confirmed with fMRI (Dehaene et al., 1999). Second, notational changes, such as presenting numbers in Arabic or in verbal form, should affect activity in visual and verbal areas, but not within the parietal system, which is supposed to encode numerical quantities in a notation-independent quantity code. The parietal system should, however, be affected by changes in the size of the numerical quantities involved, and in the dis-

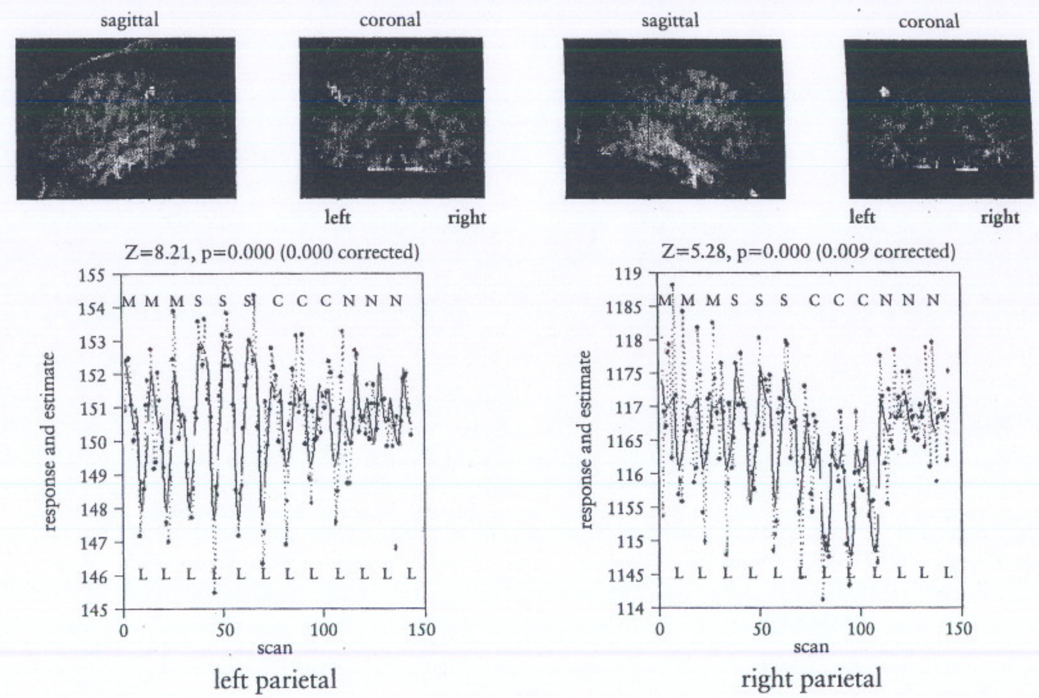

Figure 11.2. The banks of the intraparietal sulcus are active in both hemispheres during number-processing tasks (data from Chochon et al., 1999). Plots indicate activation as a function of time as the subject alternated blocks of comparison (C), multiplication (M), subtraction (S), and number-naming tasks (N) with blocks of letter-naming (L). Areas conjointly activated in the three calculation tasks (C, M, S) were determined with SPM96 software in an individual subject (voxelwise $p < 0.001$, corrected to $p < 0.05$). These areas are postulated to participate in the cerebral substrates of quantity knowledge.

tances between them. This prediction has been confirmed using event-related potentials. In a multiplication task, late event-related potentials recorded over left parietal electrodes were affected by the size of the operands (for example, 2×3 versus 7×9), but not by the auditory or visual modality in which they were presented (Kiefer and Dehaene, 1997). And likewise, in a number comparison task, electrical activity over left and especially right parietal electrodes was affected by the distance between the numbers to be compared (for example, 1 and 5 versus 4 and 5), but not by whether the numbers were presented visually as words or as digits (Dehaene, 1995). The latter variable only affected early visual ERPs: as predicted by the triple-code model, visual activity was bilateral for digits and left-lateralized for number words.

Conclusion

Neuropsychological and brain-imaging studies suggest that multiple brain areas are involved in representing numbers mentally. Each area contributes a different code for numbers, and different mental operations are preferentially executed using specific codes. The rich variety of arithmetical operations that can be executed by humans is presumably based on a constant interplay between symbolic and semantic representations for numbers. The human brain possesses both notation-specific cortices where specific number notations are recognized and/or produced, and notation-independent cortices, within the intraparietal sulcus, where numbers are represented in a nonsymbolic semantic quantity code. I speculate that other categories of knowledge, whether for persons, animals, actions, or colors, will be found to rest on a similar organization, with distributed cortical representations for the various input and output symbolic codes in which these concepts can be conveyed, as well as nonverbal category-specific cortical representations of their semantic dimension.

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