Towards an Anatomical and Functional Model of Number Processing

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A model is proposed for the mental processes and neuroanatomical circuits involved in number processing and mental arithmetic. The model elaborates on Dehaene's (1992) triple-code model and assumes that arabic and magnitude representations of numbers are available to both hemispheres, but that the verbal representation that underlies arithmetic fact retrieval is available only to the left hemisphere. Speculations as to the anatomical substrates and connections of these representations are proposed. We review a large number of single-case studies of acalculia and show that our model predicts in some detail the nature of the cognitive impairment in relation to the site of the lesion. The compatibility of our views with recent brain imaging studies of number processing in normal subjects is also examined.

INTRODUCTION

The architecture of the mental representation underlying simple number processing in adults is currently a highly controversial topic. There is little disagreement at the level of basic observations, since the main empirical findings in the domain of number processing have been remarkably replicable. However, the many models that have been proposed to account for these data disagree on at least two fundamental issues.

A first point of disagreement concerns the nature of the mental representations of numbers. Notation-specific representations and processes are clearly needed in order to account for the ability of normal human adults to comprehend and to produce spoken numerals and written numerals in either arabic or in alphabetical script. However, do we need to posit additional levels

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of representation beyond these, and if so how can we characterise them? Dehaene (1992) and McCloskey (1992) have both presented arguments suggesting that a representation of quantities is crucial in order to account for number-processing operations. Campbell and Clark (1992), on the other hand, have conjectured that many additional mental representations are involved in our daily use of numbers, including finger-counting, imaginal, and motoric codes.

A second point of disagreement concerns the architecture in which these representations are assembled for a given task. Is there a convergence towards a common format, for instance a quantity representation, regardless of the particular notation in which numbers are perceived or produced? McCloskey (1992) contends that an abstract quantity representation is central to any number processing task. Campbell and Clark (1992), on the other hand, propose that different tasks evoke quite different representations of numbers, and they have argued, in agreement with Noel and Seron (1993), that this mapping may even vary from subject to subject. Within a more constrained approach, Dehaene (1992) has made specific and testable proposals specifying which tasks rely on which number representation systems.

In the past, neuropsychological evidence has played a crucial role in testing these models or even in setting them forth (e.g. McCloskey, Caramazza, & Basili, 1985; McCloskey, Sokol, & Goodman, 1986; Campbell & Clark, 1988; Cohen & Dehaene, 1991; Dehaene & Cohen, 1991). However, most studies have until now been framed within the context of cognitive neuropsychology, which aims at understanding the behaviour of brain-lesioned patients at a purely functional level, without concern for brain localisation or lesion site. Accordingly, models of number processing have also been framed at a purely functional level. It seems to us, however, that this state of affairs is by no means necessary and that considerable insight into the functional architectures for number processing could be gained by considering the networks of brain areas that underlie them. A rich database of case reports, supplemented by some experiments using functional brain imaging techniques in normal subjects, is now available. It can and should be used to constrain the models.

The goal of the present paper is to provide an illustration of the form that a neuro-functional model of number processing could take. In attempting to review the data relevant to the neuroanatomy of number processing and calculation, we discovered that a simple set of principles could account for most of the available evidence. In the following, we shall first outline the proposed neuro-functional model of number processing. We shall then use this model as a framework for the interpretation of functional imaging studies and of single-case studies of patients with number processing impairments.

THE MODEL

The functional-anatomical model of number processing presented here is an extension of the triple-code model, a purely functional model of number processing introduced by Dehaene (1992). It essentially introduces functional precisions and hypothetical anatomical substrates to some components of the triple-code model. Hence it seems useful first to describe the functional postulates of this model before outlining its proposed cerebral implementation.

Functional Postulates of the Model

The triple-code model, schematised in Fig. 1, assumes that there are essentially three categories of mental representations[1] in which numbers can be manipulated in the human brain. First, there is a *visual arabic number form*, in which numbers are represented as strings of digits on an internal visuo-spatial scratchpad. At this level, the representation of number 52 as an ordered list of digit identities may be denoted as <5><2> (Caramazza & Hillis, 1990). Second, there is a *verbal word frame*, in which numbers are represented as syntactically organised sequences of words. At this level, the representation of number "fifty two" may be denoted as "Tens{5} Ones{2}" (McCloskey, Sokol, & Goodman, 1986; Cohen & Dehaene, 1991). In this notation, symbols such as "Ones" and "{2}" denote abstract addresses that together constitute a word lemma (Levelt, 1989) linked to the phonological and graphemic forms of the word (/tu/ vs. "two").

Under the assumptions of the triple-code model, neither the arabic number form nor the verbal word frame contain any semantic information. The meaning of

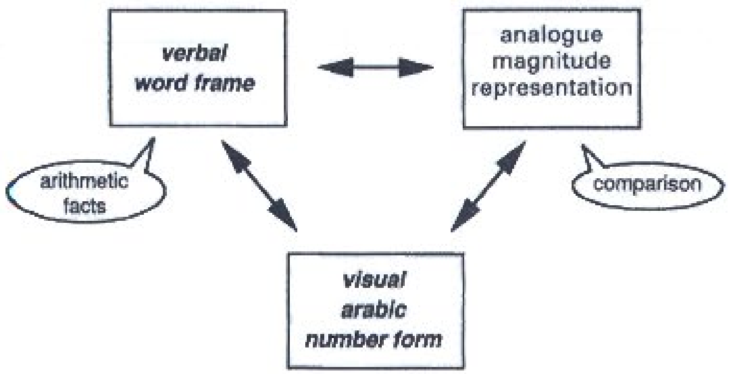

FIG. 1. A simplified diagram of the triple-code model of number processing (after Dehaene, 1992).

[1]Obviously, many numerical tasks, inasmuch as they involve general linguistic processes such as speech comprehension or production, incorporate additional levels of representation such as phonemic, articulatory, graphemic, and lexical codes. The claim, however, is that in order to understand what is genuinely numerical about number-processing tasks (e.g. the ability to compare or to calculate), only three cardinal representations suffice.

numbers is represented only in the third pole of the model, the *analogical magnitude representation*. At this level, the quantity or magnitude associated with a given number is retrieved and can be put in relation with other numerical quantities.[2] For instance, knowledge that 52 is smaller than 60, that it is about half-way between 0 and 100, and so on, is recovered at this level. The magnitude representation can be pictured as an oriented number line, with quantities being represented by local distributions of activation. Numerical relations are then implicitly represented both by the distance separating the peaks of activation, and by the overlap between two distributions of activation (Dehaene & Changeux, 1993). Based on evidence from normal subjects (for reviews see Dehaene, 1992, or Krueger, 1989), the number line is assumed to obey Weber's Law, such that the representation of larger and larger numerals becomes increasingly imprecise.

How are the arabic, verbal, and magnitude representations of numbers accessed from external stimuli? In the triple-code model, this depends on the format in which the numbers are presented. Visual identification processes allow arabic numerals to be mapped rapidly onto identified strings of digits in the visual arabic number form (and conversely, output routines allow strings of digits in the internal representation to be written down). Likewise, when a set of visual or auditory objects is presented, its numerosity can be extracted directly and represented on the "number line" by dedicated subitising and estimation processes (see Dehaene & Cohen, 1994, for a discussion of possible mechanisms). Finally, the verbal code is linked to input routines for parsing auditory or written sequences of number words, and to output routines for uttering them or for writing them down.

Thus, the first step in any task is the representation of input numbers into a notation-appropriate representation. Immediately afterwards, however, the triple-code model assumes that numbers can be transcoded into whatever internal code is required for the task at hand. For instance, the quantity associated with a given arabic or verbal numeral can be rapidly retrieved. Indeed, evidence from normal subjects indicates that activation of the quantity representation is a highly automatised process in human adults (e.g. Dehaene & Akhavein, in press). Conversely, subjects can retrieve the arabic or verbal label that represents a certain quantity. Most importantly, the model also assumes the existence of a direct route linking the arabic and verbal codes without passing through an intermediate quantity representation. In that respect, the triple-code model is similar to other so-called "multiple-route" models of reading in assuming that subjects can read or write arabic numerals without having to

[2]Number meaning is not limited to quantity knowledge. We may know, for instance, that 16 is a power of 2 and that 17 is a prime number. We also possess encyclopaedic knowledge of some numbers such as 1914 or 1789. This suggests that the semantic representation in our model should eventually be enriched with non-quantitative semantic features such as "power of 2," "prime," "famous date," and so on.

process information through a "semantic" representation of quantities (Cohen, Dehaene, & Verstichel, 1994; see McCloskey, 1992, for conflicting views).

Note that because the format in which numbers are encoded varies considerably in the three cardinal representations, the internal transcoding routes necessarily have very different properties. On the one hand, the direct arabic-verbal route works on non-interpreted sequences of symbols, either words or digits. It is ideally suited for transcoding unfamiliar numbers of any size and syntactic complexity between the arabic and the verbal notations using compositional rules. However, it manipulates arabic and word symbols "blindly," without knowledge of their meaning. On the other hand, the paths to and from the magnitude representation are supposed not to be syntactically sophisticated (Dehaene, 1992, p. 32). We assume that communications to and from the magnitude representation work by direct labelling. To each portion of the number line corresponds one or more labels such as "9," "nine," "about ten," and so on, that are appropriate to the quantity at hand (Dehaene & Mehler, 1992). Familiar numerals such as "nine," inasmuch as they represent a small enough quantity, may have a rich and precise internal semantic representation. Unfamiliar numerals such as "212," however, are necessarily rounded up to a more familiar quantity such as "200." Hence, the magnitude representation is not suitable for precise reading aloud or transcoding of arbitrary numerals, but it can be used for rounding up as well as for other approximation tasks.

Internal transcoding from one representation to the other is required, according to the triple-code model, because each elementary numerical operation is assumed to take its inputs from a specified code and also to provide its outputs in a specified code. Numerical comparison, for instance, is postulated to require two quantities for input. Thus, in order to determine which of two arabic digits is the largest, subjects must first translate them into an internal representation of the quantities that they represent. Similarly, and perhaps more controversially, in the triple-code model we suppose that arithmetic facts such as $2 \times 3 = 6$ cannot be retrieved unless the problem is coded into a verbal code "two times three. . . ," which then triggers the retrieval of the result "six" in the same verbal format.

Anatomical Implementation of the Triple-code Model

In the proposed neuro-functional model, the essential components of the triple-code model have been mapped onto their hypothetical anatomical locations on a schematic diagram of the two hemispheres (Fig. 2). Most importantly, some processes have been split in order to acknowledge that both hemispheres possess a copy of them (perhaps with variants). The critical postulates of the model are as follows:

1. **Both hemispheres possess effective visual identification procedures.** The left-hemispheric visual system can recognise all single digits, multi-digit numerals, and printed words. Its end product is a representation of the identities

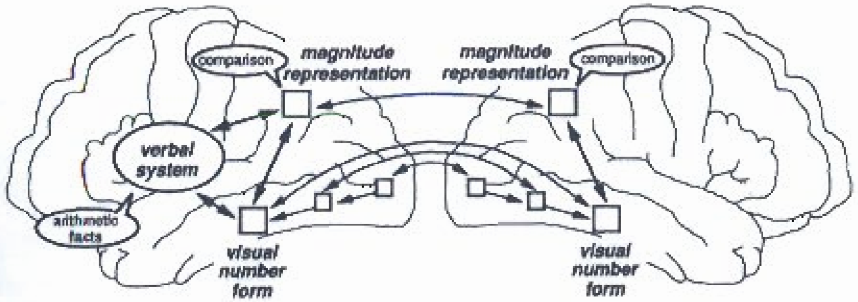

FIG. 2. Proposed anatomical distribution of the three cardinal number representations on an external view of the left and right hemispheres (see text for details).

and relative positions of symbols or groups of symbols in the stimulus, which has been called the visual word form (see e.g. Shallice, 1988) or, in the case of arabic numerals, the visual number form (Cohen & Dehaene, 1991). Anatomically, this system corresponds to a cascade of areas culminating in the left occipito-temporal region and belonging to the "ventral visual pathway" dedicated to visual recognition (Ungerleider & Mishkin, 1982). Homologous areas in the right hemisphere can also identify visual symbols such as arabic digits, some multi-digit numerals, and some words. However, for some as yet unknown reason, the size of their visual vocabulary for symbolic material, especially for words, seems highly limited (for discussion, see e.g. Farah, 1990).

2. Both hemispheres possess an analogical representation of numerical quantities or magnitudes, and a comparison procedure for deciding which of two quantities is larger or smaller. These processes are implemented in cortical areas grossly localised to the vicinity of the parieto-occipito-temporal junction of both hemispheres. The right hemisphere may be superior to the left in the processing of quantities (e.g. Kosslyn et al., 1989).

3. Only the left hemisphere possesses a representation of the sequence of words corresponding to verbal numerals, and procedures for identifying and producing spoken numerals. These procedures, which are not specific for numbers, are implemented within classical language areas of the left hemisphere, including inferior frontal and superior and middle temporal gyri as well as basal ganglia and thalamic nuclei.[3]

[3]We shall not attempt to provide a precise anatomical description of the circuits for spoken and written language processing, since this is currently the subject of much research and controversy. Correspondingly, pure impairments of spoken number comprehension or production will not be discussed, even though these have provided important information concerning the structure of the mental lexicon and grammar for verbal numerals (e.g. McCloskey et al., 1986). Let us simply note that the available evidence is consistent with a fine modular organisation of verbal input and output routines (McCloskey, 1992), the anatomical basis of which remains to be understood.

4. Mental arithmetic is intimately linked to language and to a verbal representation of numbers. The retrieval of arithmetic facts from memory relies on a subset of left-hemispheric language areas and cannot be performed by the right hemisphere alone. The procedures for multi-digit calculations are more complex and involve the coordination of visuo-spatial and verbal representations of the digits.

5. Within the left hemisphere, the visual, verbal, and magnitude representations are interconnected and can directly exchange information via dedicated transcoding pathways. In particular, the verbal system can be directly informed about digit identities by the left visual number form (asemantic route), without necessarily having to go through the magnitude representation (semantic route). Within the right hemisphere, connections and procedures exist only for linking the visual and magnitude representations.

6. In normal subjects, left and right visual representations are connected via the corpus callosum. Left and right magnitude representations are also connected in the same way. There are no other routes for exchanging numerical information across the two hemispheres. In particular there is no direct route linking the right-hemispheric visual number form to the verbal system.

The rest of this paper is dedicated to a justification of these assumptions and to a critical evaluation of their predictions against the relevant literature. We first examine single-case studies of brain-lesioned patients in the light of the model. We then review the (scarce) evidence from functional brain imaging of the normal human brain. For reasons of space, a discussion of the behavioural evidence from normal subjects could not be included here. It should be stressed, however, that the vast majority of data on the cognitive psychology of number processing is compatible with the present framework (for discussion, see e.g. Campbell, 1994; Dehaene, 1992; McCloskey, 1992; Logie, Gilhooly, & Wynn, 1994).

EVIDENCE FROM SINGLE-CASE STUDIES OF NUMBER PROCESSING

Neuropsychological studies provide a rich source of empirical constraints on models of number processing. In fact, these constraints are even stronger for neuro-functional models such as the one presented here, than for purely functional cognitive models. In the framework of cognitive neuropsychology, the goal is to explain the observed pattern of *behavioural* dissociations and deficits by assuming that one or more processes in the normal processing architecture have been impaired. However, the nature of the pathology and the site of the lesions are considered irrelevant, and indeed are sometimes not even reported. By contrast, our model claims both functional and anatomical validity. Not only should it describe, at a functional or behavioural level, the observed deficits, but it should do so by postulating impairments only to those processes that were supposedly subsumed by the lesioned brain areas. Ideally, a valid model should predict the nature of the behavioural deficits based solely on the site of the lesion. More realistically, given that lesions can be extended and that multiple functions can be implemented within close and often variable territories, the model should at least predict the range of possible deficits for each lesion type.

In accordance with this analysis, we have excluded from the present review cases with poorly localised lesions, degenerative diseases, or developmental disorders, as well as cases in which the cognitive deficit was not thoroughly analysed. We have focused on cases in which the lesion was unambiguously localised and in which sufficient cognitive tests were performed to provide a strong test of the model. For each neurological condition, we shall first outline the predictions that can be derived from the model, and then examine how they fit with the observed impairments and whether the data impose further theoretical refinements.

Split-brain Patients

In the case of a disconnection of the two hemispheres, the predictions of the model are straightforward. The left hemisphere contains a set of representations equivalent to the full triple-code model. Thus, it should perform adequately in all numerical tasks. The right hemisphere, on the other hand, contains only a visual arabic number form and a magnitude representation. Hence, it should be able to identify digits, to retrieve a representation of the quantities that they represent, and to compare these quantities. However, it should be unable to perform formal symbolic calculations and to read or produce numerals aloud.

The available evidence essentially conforms to this description. When a target digit is flashed to either hemifield, split-brain patients can point to the identical digit in a large set of other digits. Both hemispheres of split-brain patients can also decide if two digits are the same or different (Seymour, Reuter-Lorenz, & Gazzaniga, 1994). Such evidence implies that both hemispheres can identify digits. Both hemispheres can also decide which of two digits is the largest (Seymour et al., 1994), suggesting that both can represent numerical quantities (Fig. 3). By contrast, split-brain patients fail to point to the correct answer of simple arithmetic problems (addition, subtraction, multiplication, or division) when the operands are flashed in their left hemifield (Gazzaniga & Smylie, 1984; Fig. 3). This suggests that their right hemisphere cannot compute simple arithmetic operations.

Finally, most split-brains cannot name digits flashed in their left hemifield (e.g. Gazzaniga & Hillyard, 1971; Gazzaniga & Smylie, 1984). Some patients do succeed at reading aloud digits presented to the right hemisphere. Such evidence does not invalidate our model, however, because in at least one patient (LB), this ability could be traced back to a complex interhemispheric cross-cueing strategy (Gazzaniga & Hillyard, 1971). When targets were flashed in the

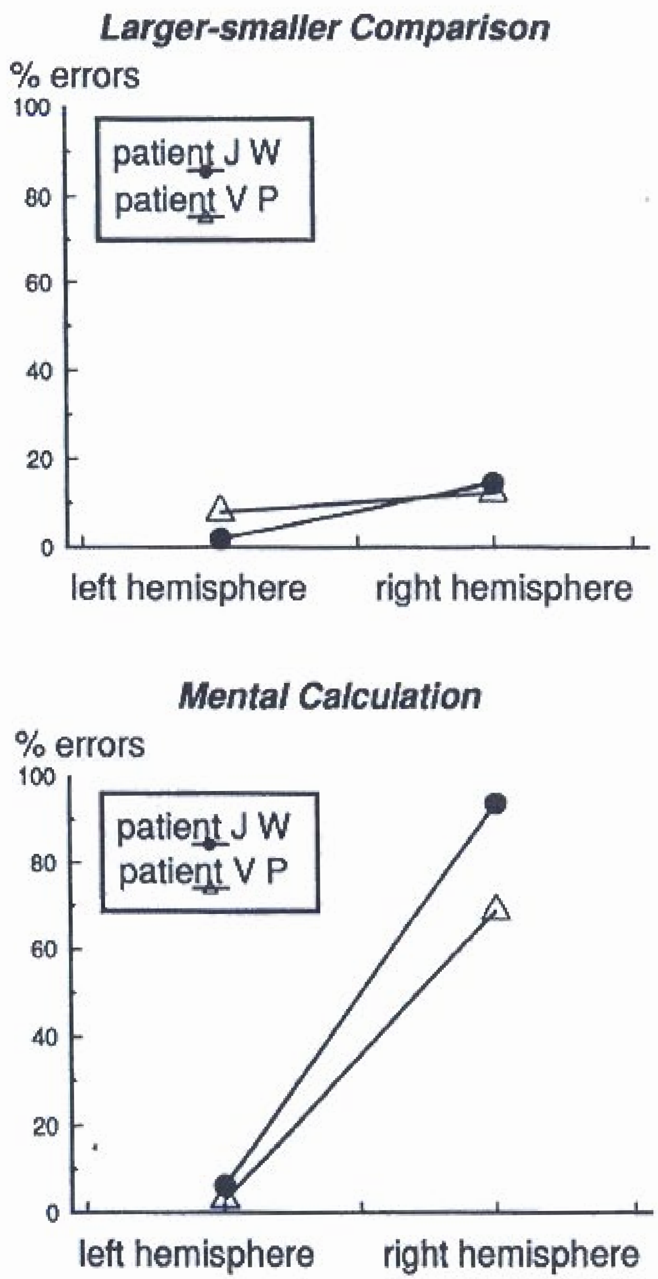

FIG. 3. Performance of two split-brain patients in number comparison and in mental arithmetic. Redrawn from data in Seymour et al. (1994) and in Gazzaniga and Smylie (1984).

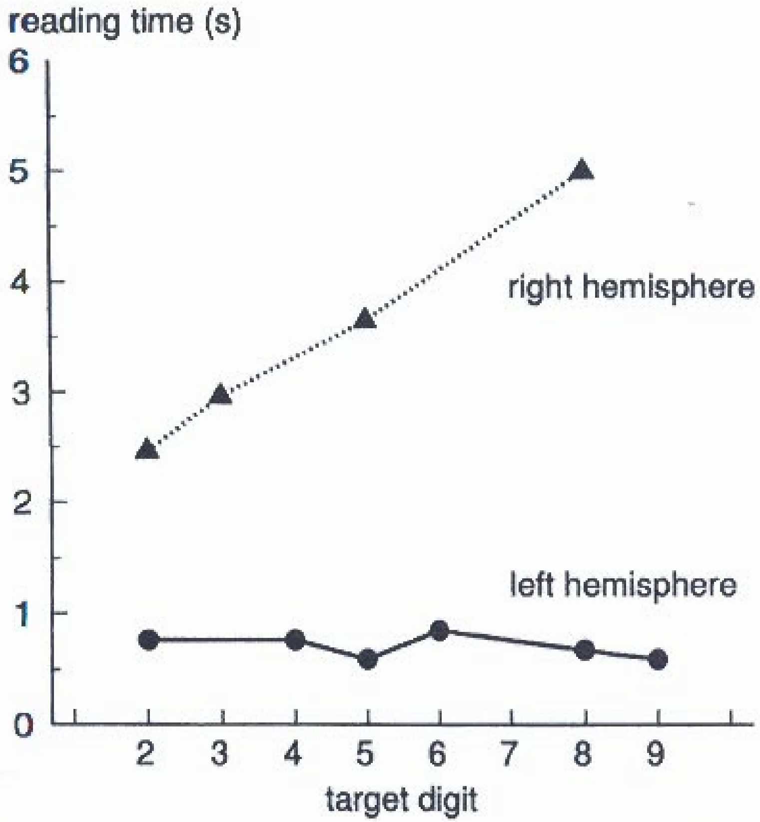

FIG. 4. Naming time for hemifield presentations of single arabic digits in a split-brain patient (redrawn from Gazzaniga & Hillyard, 1971).

right hemifield, LB's naming time was independent of the digit to be named. However, when targets were flashed in the left hemifield, naming time was much slower and increased linearly with numerical size (Fig. 4). Evidently, the patient was reciting the series of numbers, presumably using his left hemisphere. Each number was then cross-cued to the right hemisphere and compared to the target. Recitation stopped when a match was detected, at which point the patient could utter the result and therefore "name" the target. A similar naming-by-counting strategy has been reported in several patients with major left-hemispheric lesions (e.g. Dehaene & Cohen, 1991; Gott, 1973; Patterson, Vargha-Khadem, & Polkey, 1989; Seron & Deloche, 1987). The fact that patients have to resort to such an indirect strategy confirms that the right hemisphere alone does not possess any direct means of naming digits.

Some of these observations, in particular the ability of the right hemisphere to identify and compare digits, could in principle reflect an abnormal pattern of brain organisation prior to commisurotomy. Most commisurotomised subjects suffered from severe epilepsy throughout childhood, and this might have distorted the normal hemispheric lateralisation of number processing. This criticism, however, does not apply to a patient in whom the hemispheric disconnection resulted from an ischaemic lesion confined to the posterior half of the corpus callosum (Cohen & Dehaene, submitted). This patient, who was neurologically normal before the stroke, showed the classical symptoms of split-brain and had clear left-hemispheric dominance for language. The earlier observations on number processing were fully replicated with her. In particular she was good at comparing one- and two-digit arabic numerals that were flashed to her right hemisphere (respectively 94.1% and 79.5% correct), but she failed to read the same stimuli aloud (respectively 40.8% and 100% errors). Her performance with numerals flashed to her left hemisphere was excellent in all tasks.

Thus, split-brain studies fit globally with predictions of our model. Two points nevertheless deserve further study. First, split-brain patients offer a unique opportunity to compare the arabic and quantity representations that are computed in each hemisphere. As we shall see later, there are suggestions that the left visual number form may be more apt at representing long strings of digits than the right, and also that the right hemisphere may have superior magnitude representation abilities than the left. Such questions could be solved by appropriate chronometric experiments in split-brains. Second, some split-brain studies have suggested that coarse numerical information may be conveyed across the two hemispheres via non-callosal subcortical routes (e.g. Corballis & Sergent, 1992; Sergent, 1990). Although the bulk of the evidence so far does not support this point (Seymour et al., 1994), it deserves further scrutiny and may prompt a revision of the model.

Left Hemispherectomy

Following left hemispherectomy, our model predicts that only the right-hemispheric visual identification, magnitude representation, and number comparison routines should remain available. The verbal representation and the associated calculation routines should be destroyed. Essentially, such a patient should behave much as the isolated right hemisphere of a split-brain would.

Although number processing has not been thoroughly evaluated in hemispherectomy patients, Grafman et al. (1989) have described a case of "virtual left hemispherectomy" in a young man who suffered a severe gunshot wound during the Vietnam war. Most of the patient's left hemisphere was destroyed, except the occipital lobe and some parasagittal and mesial cortex. Yet the patient could still compare single-digit and even multi-digit numerals with excellent accuracy, confirming that digit identification and magnitude processing were intact. The patient was much less accurate with spoken or written words, confirming that the right hemisphere is quite poor at visual or auditory word recognition. Finally, the patient had severe difficulties in mental arithmetic and was largely unable to perform any multi-digit calculation, as predicted from the loss of left-lateralised verbal arithmetic routines.

The patient's number processing abilities, however, went slightly beyond those expected from our model. He could write down and name single digits and some multi-digit numerals. He could also solve very simple addition, subtraction, and some multiplication problems. In both cases, however, the patient could have relied on counting strategies or on estimation strategies using his intact right-hemispheric understanding of number magnitude. His response times, which might have provided important cues about the processes he used, were not reported. Finally, we note that the lesion occurred when the patient was in his late teens and that testing was performed more than 14 years later. Thus, the few number processing abilities that he exhibited above and beyond those predicted by our model may have been due to partial relearning.

Major Left-hemispheric Lesion

According to our model, consequences similar to hemispherectomy may result from extensive damage to the left hemisphere. Patient NAU (Dehaene & Cohen, 1991) fits in nicely with this prediction. NAU had a major lesion of the posterior left hemisphere, sparing some occipital, superior parietal, and anterior temporal cortex. He suffered from severe alexia and from speech comprehension and production deficits, as would be expected if the lesion affected temporal language areas as well as the left visual word form. Number reading was severely affected, although the patient could use the reading-by-counting strategy. As predicted by the model, he was very severely acalculic, to the extent that he would make errors with arithmetic problems as simple as 2+2. Explicitly computing the result of an addition, subtraction, or multiplication was virtually impossible. Finally, he was almost totally unable to judge if a digit was odd or even, which may be explained by supposing that parity judgments draw on the left-hemispheric visual number form (Dehaene, Bossini, & Giraux, 1993).

A variety of tests, however, showed that digit identification and understanding of number magnitudes, which supposedly could be performed by the right hemisphere, were indeed intact. The patient could compare single digits and two-digit arabic numerals with near perfection. He understood the quantity associated with two-digit numerals, as demonstrated by his ability to point to the corresponding location on a vertical line labelled 1 at the bottom and 100 at the top. He could also memorise a consecutive set of three digits and decide whether a probe digit belonged to the set or not, although he would make errors when the probe was close in magnitude to the memorised set (e.g. set 5 6 7, probe 4).

Patient NAU could also approximately answer questions probing his numerical knowledge. For instance, he said that one hour is 50 minutes, that a dozen eggs is 6 or 10 eggs, and when shown a 20 French francs note (with the arabic numeral hidden), he thought that its value was 30 FF. Although he made about 50% errors in such knowledge tasks, his responses were always close to correct. He was also perfect in judging the appropriateness of a given quantity to a real-world situation (e.g. nine children for a present-day mother →"it's too much"). Such evidence is compatible with the notion that the right hemisphere can compute a semantic representation of numerical magnitudes that is appropriate to the context in which a given number appears.

Patient NAU's results also gave evidence that the representation of number magnitudes is useful for more than just larger-smaller comparison. When presented with a grossly false addition such as 1 + 3 = 9, NAU readily rejected it even though other tests had showed that he did not know whether the addition result was 3, 4, or 5. Dehaene and Cohen (1991) suggested that he mentally represented the digits 1, 3, and 9 as magnitudes and then figured that the first two magnitudes, when combined, could not amount to anything as large as the third one. This implies the existence of a non-verbal system for doing approximate arithmetic by combining quantities. We speculate that a similar non-verbal system underlies simple arithmetic in animals (Davis & Pérusse, 1988; Dehaene & Changeux, 1993; Gallistel & Gelman, 1992) and in young infants (Wynn, 1992).

Our preferred interpretation is that NAU's preserved understanding of numerical quantities reflected processing in his intact right hemisphere. At present, however, the alternative hypothesis that his performance, in some or all tasks, reflected processing within partially intact left-hemispheric neural systems cannot be ruled out. It is even possible that the observed approximation behaviour reflected the impaired functioning of a lesioned semantic system rather than the existence of a preserved system for numerical approximation. Unless the entire left hemisphere is removed—and it could be argued that this was not even the case for Grafman et al.'s (1989) "virtual left hemispherectomy"—this alternative must remain open. However, in the face of independent evidence for quantitative number processing in the right hemisphere of split-brains and of normal subjects (see following), the hypothesis that patients with unilateral left-hemispheric lesion use their intact right hemisphere in tasks involving a representation of number quantities seems more parsimonious.

Although patient NAU was the first case of acalculia in which the preservation of number magnitude was systematically studied, "NAU-like" approximation behaviour seems to be an extremely frequent finding in acalculia. In acalculic patients with left-hemispheric lesions, whenever it was tested, the ability to select the larger of two digits was found to be intact (e.g. Cohen & Dehaene, 1991, submitted; Cohen et al., 1994; Dagenbach & McCloskey, 1992; Deloche et al., 1992; McCloskey et al., 1986 [patient HY]; Warrington, 1982). In some patients, additional evidence for the preservation of a magnitude representation was reported. Patient HY (McCloskey et al., 1986), who suffered from a speech production impairment, frequently produced erroneous number names that were close in numerical magnitude to the original arabic stimulus (Campbell & Clark, 1988). A similar effect of numerical nearness on speech production errors was found in patient RH (Macaruso, McCloskey, & Aliminosa, 1993). Warrington's (1982) patient, who often erred in simple calculations, always produced addition and subtractions errors of a reasonable magnitude. The patient, just like NAU, claimed that he often knew an approximate solution, but not the exact result. Our model predicts that the preservation of numerical magnitude knowledge should be observed in all patients with a left-hemispheric lesion, inasmuch as their right hemisphere is intact.[4]

Deep Dyslexia

The case of patient NAU, with his preserved approximate numerical knowledge, led us to re-examine in a broader perspective the nature of the semantic information conveyed by numbers. Arabic numerals can convey considerable information above and beyond their exact and approximate magnitude. For instance, French subjects may know that 1789 is a famous date, that 1664 is a brand of beer, etc. Would such encyclopaedic knowledge also be preserved following a large left-hemispheric lesion? Cohen et al. (1994) studied this question in a deep dyslexic patient with a lesion quite similar to that of patient NAU. Like patient NAU, and as predicted by our model, this patient excelled at comparing single or two-digit numerals. He could also verify simple written additions, although he did so very slowly, and we could not exclude that some form of counting strategy was operative. Thus, identification of arabic numerals and understanding of magnitudes was preserved.

However, this patient had severe difficulties in reading arabic numerals aloud. With elementary arabic numerals (those corresponding to a single ones, teens, or tens word), he often resorted, rather successfully, to a naming-by-counting strategy. With more complex and unfamiliar arabic numerals, however, he made a very large number of errors or even did not respond at all. Interestingly, however, when presented with complex but familiar numerals such as famous dates, brands of cars, zip codes, etc., the patient could often retrieve their meaning and occasionally name them. For instance, when presented with 504, the patient realised that it was a brand of car, that it was built by Peugeot, and eventually said "504." In some cases, he produced semantic errors, for instance correctly relating 1918 to the end of World War I, but then saying "1940." It

[4]The case described by Cipolotti, Butterworth, and Denes (1991) seems to go against this prediction because the patient, who suffered from a left fronto-parietal lesion, appeared unable to perform *any* numerical task, including larger-smaller comparison, when the target numbers exceeded 4. Such non-modularity of deficits is so unusual in neuropsychology and so incompatible with *all* current models, however, as to warrant deferring its discussion until other similar cases are reported.

should be noted that this patient suffered from deep dyslexia in word reading, and that he made similar semantic approaches and semantic errors when reading high-frequency and imageable words.[5]

The results reported by Cohen et al. (1994) indicate that the magnitude representation in the model should probably be enriched to include the variety of encyclopaedic knowledge available about numbers. Given the size of the lesion, it is plausible—though by no means certain—that the preserved knowledge was represented at least in part in the right hemisphere. Indeed, several authors have postulated a functional role for the right hemisphere in the residual reading abilities of deep dyslexics and pure alexics (e.g. Coltheart, 1980; Coslett & Monsul, 1994). In this context, our number-processing model may be considered as a particular case of the classical multiple-route models of word reading (Cohen et al., 1994). Examination of Fig. 2 shows that the model actually comprises three anatomical pathways by which an arabic numeral may be named: a direct route linking the left-hemispheric visual number form to the verbal system, a left-hemispheric "semantic" route going from the visual number form to the verbal system via the magnitude representation, and a right-hemispheric "semantic" route by which right visual identification areas can feed the right-hemispheric semantic representation, which then connects via callosal pathways to verbal production systems. In deep dyslexics, the direct arabic-to-verbal route would be impaired and the semantic routes would function only with familiar numerals whose meaning is stored in memory.

Pure Alexia

Further evidence for the dissociability of number reading pathways was provided recently by Cohen and Dehaene (submitted), who studied number-processing abilities in two patients suffering from pure alexia (see McNeil & Warrington, 1994, discussed later, for a similar case). The lesion sites were very similar in both cases and concerned the left infero-mesial occipito-temporal region. In the present framework, such lesions should predictably affect the formation of the visual word and number form, either by directly destroying the corresponding cerebral area or by deafferenting it (Fig. 5). Indeed, such an interpretation corresponds roughly to the classical account of pure alexia, as proposed for instance by Déjerine (1891, 1892).

What functional implications should such a lesion have for number processing? Clearly, the verbal system should fail to receive normal inputs from the visual word and number form. This should be reflected in a failure to read words and numerals as well as to perform simple arithmetic on written stimuli.

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[5]Patient NAU (Dehaene & Cohen, 1991) also made semantic errors in reading and would probably have been classified as a deep dyslexic, had word reading been documented in greater detail.

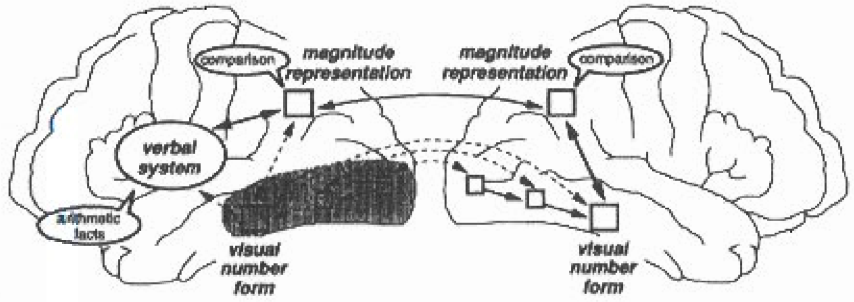

FIG. 5. Reconstruction of the lesioned circuits in two patients with pure alexia (Cohen & Dehaene, submitted). For simplicity, the lesioned visual number form area is shown in the lateral temporo-occipital region, whereas it is actually more inferior and medial. Note that the lesion disconnects the verbal system from direct visual inputs.

Arithmetic with auditorily presented numerals should be preserved, inasmuch as the verbal system itself is intact. Number comparison should also be preserved, since the intact right-hemispheric processes are sufficient to perform it.

The data from both patients fully supported these predictions. Word reading was dramatically impaired, although with unlimited exposure both patients managed to guess the identity of spelled-out number words with 80–90% accuracy by identifying their initial letter. Reading multi-digit arabic numerals was also severely impaired (67–80% errors). The vast majority of errors consisted in misidentifications of digits, which were often perseverated from one trial to the next (e.g. stimulus 39, response 69; stimulus 42, response 79; stimulus 32, response 79; etc). Nevertheless, the output was always a grammatically correct word string. This is consistent with our hypothesis that the verbal system was intact but did not receive appropriate information about digit identities from the impaired visual number form. Even the reading of single digits was not free of errors (8–18%), although the error rate was obviously much lower than with multi-digit numerals. We speculate that the transcallosal "semantic" route could transmit some information to the verbal system about single digits, which are highly familiar stimuli, but not about arbitrary multi-digit numerals.[6]

Just like split-brains and patients with major left-hemispheric damage, both the pure alexic patients could select the larger of two arabic numerals that they failed to read aloud. Most strikingly, they did not make any comparison errors with two-digit numerals, whereas their error rate when reading aloud the same

[6]Unfortunately, the reading of familiar multi-digit numerals such as dates was not tested in the two pure alexic patients. Our model would lead us to expect good identification of such material in pure alexics, at least in tasks not requiring a spoken output.

material was close to 90%. Our interpretation is that their intact right-hemispheric visual identification areas could contact the magnitude representation necessary to support number comparison, but that the digit identities could not be transmitted to the verbal system for naming. The left-hemispheric visual identification areas which normally serve to inform the verbal system were lesioned.

Both patients also made numerous errors in calculating with arabic numerals. For instance, when adding two arabic digits (which they could accurately compare), the patients made respectively 70% and 62.5% errors. This impairment was due to a misidentification of the operands and *not* to a faulty addition procedure, because addition performance was perfect when the same pairs of digits were presented auditorily. Furthermore, when the patients occasionally misread the digits aloud, they almost always produced an addition result consistent with their reading. For instance, when presented with the pair "2 3", one patient said "six and three makes nine". In our model, we interpret such performance as indicating that the intact arithmetic fact retrieval routines, which require verbally encoded inputs, were not properly informed about digit identities by the impaired visual number form.

It is worth emphasising the problems that these observations pose for models of number processing that do not take into account the known anatomical distribution of pathways in the two hemispheres. In such models, the fact that both patients could compare arabic numerals would entail that the comprehension of arabic numerals was preserved (McCloskey, 1992). The errors in reading and in calculating with arabic numerals should then be attributed to processes beyond stimulus comprehension, such as calculation or verbal production routines. However, the perfect performance on oral calculation with auditorily presented operands is totally inconsistent with this view. Rather, the data imply the existence of two distinct visual identification processes (here attributed to the left and right hemispheres) that contribute differentially to reading, comparison, and calculation tasks. An all-important practical consequence is that *intact comparison of arabic numerals does not imply preserved comprehension for all tasks*, contrary to what was tacitly assumed following the publication of McCloskey's model (e.g. Cohen & Dehaene, 1991; Deloche et al., 1992). As was anticipated, though not empirically proven, by Campbell and Clark (1988), "comprehension" cannot be assessed independently of the task performed by the patient. Multiple convergent tasks must be used if one wants to prove that both left and right visual number forms are intact.

One puzzle remains: Why couldn't pure alexic patients use their partially intact transcallosal reading pathway, which enabled them to achieve 82% to 92% accuracy in reading aloud single digits, to improve their addition performance? Further tests revealed a powerful effect of task demands on reading performance. When the patients were asked to read in the context of a comparison task ("read these two digits aloud and tell me which is the larger"), not only was the comparison performed accurately, but the *reading* itself improved (10% and 15% errors). By contrast, when the patients were asked to read in the context of a calculation task ("read these two digits aloud and add them"), reading performance deteriorated significantly (31% and 45% errors). This paradoxical result suggests that the selection of reading pathways can be affected by instructions and task demands (see Cipolotti, in press, for a similar argument). A comparison task biased the patients towards using the intact "semantic" transcallosal pathway, whereas a calculation task biased them to use the impaired direct route through the left-hemispheric visual number form. This interpretation is consistent with the known redistribution of brain activations in the human brain as a function of attention and of instructions, as observed for instance in PET (Postner & Raichle, 1994; see following).

Neglect Dyslexia

Cohen and Dehaene (1991) have reported on another case of number reading impairment that could be labelled "neglect dyslexia" but which, in retrospect, bears considerable similarity to the behaviour of pure alexics and can be interpreted within a similar framework. Their patient (YM) had undergone a left temporal lobectomy to remove a malignant tumour. After the operation, he presented with anomic aphasia, reading difficulties, and a mild speech comprehension impairment. Our study concentrated on his number reading deficit. In the context of our model, it may be assumed that the temporal lesion affected the visual word form area and possibly also the temporal language-processing networks. Thus, one should expect number reading difficulties similar to those found in pure alexia, with perhaps some mild speech comprehension, speech production, and calculation difficulties.

As a matter of fact, YM made many errors in reading arabic numerals. Several features of these errors were consistent with a visual identification deficit similar to that of pure alexics. First, the vast majority of reading errors were digit substitutions, and the output word string was always grammatically correct (e.g. stimulus 217, response 277). Second, many perseverations were again noted, which may be taken as an indication of confabulation about digit identities by the intact verbal systems. It is noteworthy that digit identities, not words, were perseverated. For instance we observed runs of errors in which digit 7 was repeatedly substituted for another digit, but was alternatively produced in French as "sept" and "soixante-dix". This suggested that the locus of the errors was in visual perception rather than in speech production.

Third, just like all of the earlier cases, the patient was perfect in choosing the larger of two arabic numerals, even those that he failed to read aloud. At that time, in keeping with McCloskey's model, we interpreted this dissociation (Cohen & Dehaene, 1991, p. 46) as indicating a "satisfactory comprehension of multi-digit Arabic numerals" and therefore implying that "the deficit [in reading aloud concerned] only a production component". We now think that it is best explained by a lesion of the left-hemispheric visual number form, and that the intact homologous right-hemispheric areas were sufficient for comparison but not for reading aloud or calculation. Thus, patient YM provides yet another example of the dissociation, predicted by our model, between impaired identification of arabic numerals for the purpose of reading and correct identification for the purpose of number comparison. Like the patients with pure alexia, YM was impaired in calculating with arabic numerals, a finding which, in our model, is consistent with an impaired arabic-to-verbal transcoding pathway. However, YM's case is less clearcut because errors were also observed in calculation with auditorily presented operands, suggesting that YM probably suffered from an additional calculation deficit.

A final feature clearly distinguished patient YM from patients with pure alexia, but nevertheless confirmed the visual origin of his reading errors. In reading multi-digit numerals, errors were not distributed randomly across all the digits. Rather, the vast majority of digit substitutions occurred on the left side of the string. That this was a genuinely *spatial* bias, rather than, say, a temporal deficit or an increasing difficulty with larger numbers, was confirmed by asking the patient to read aloud arabic numerals that had been printed vertically, one digit above the other. In this situation, the bias towards making more errors on the first digits vanished. This observation indicates that the deficit occurred at a level of processing in which the spatial positions of digits were still represented, namely the visual number form. In the word reading literature, a similar positional bias has often been reported under the label "neglect dyslexia" and has also been attributed to "neglect" in retrieving information from a spatially mapped representation of letter strings (e.g. Caramazza & Hillis, 1990).

Pure Anarithmetia

We now turn to what is often considered by neuropsychologists as the core feature of acalculia: Pure anarithmetia, or a specific inability to perform arithmetic calculations, ideally in the absence of aphasic or visuo-spatial disorders. This frequent category of impairment poses a special challenge to our model because, in apparent contradiction to our localisationist stance, it can be caused by lesions in a great variety of anatomical structures in the left hemisphere (inferior parietal, subcortical, or frontal). We are a long way from understanding the organisation of this network. In our opinion, however, much confusion has been generated by inappropriately grouping quite different impairments under the same heading of anarithmetia. Considerable clarification can be attained by introducing a distinction between levels of complexity in calculation tasks, and by considering the different processes that can contribute to calculation (e.g. Caramazza & McCloskey, 1987). Here we shall discuss four of them: rote verbal memory, semantic elaboration, working memory, and strategy choice and planning.

At the simplest level, studies of normal subjects have repeatedly suggested that most simple arithmetic facts such as $2 \times 3 = 6$ are stored and retrieved from memory (for review see e.g. Ashcraft, 1992). Addition and multiplication facts can be activated automatically even when they are irrelevant to the task (e.g. LeFevre, Bisanz, & Mrkonjic, 1988). Bilingual subjects, long after they have moved to a different country and shifted to a second language, often continue to activate arithmetic facts in the language in which they originally acquired them (Shannon, 1984). Such evidence is consistent with our hypothesis that rote arithmetic facts belong to the general class of rote verbal memories (Dehaene, 1992). Our model supposes that no semantic knowledge is required in order to retrieve the most simple of arithmetic facts. Rather, they can be recovered mechanically, without regard to the quantities involved.

At a second level of complexity, however, other arithmetic problems require a *semantic elaboration* before rote memory can be accessed (Fig. 6). Even for simple single-digit additions and multiplications, normal subjects do not possess a complete and error-free memory (e.g. Campbell & Graham, 1985). Hence, when faced with an unknown or irretrievable fact, subjects may resort to strategies other than memory retrieval (e.g. Siegler, 1988). For instance addition problems may be decomposed into simpler memorised facts (e.g. $9+7 = 9+1 + 7-1 = 10+6 = 16$). Such recoding strategies obviously require a good understanding of the quantities involved in the original problem (e.g. noticing that 9 is close to 10). Accordingly, we subsume them under the heading of "semantic elaboration." Semantic elaboration may be needed both before and after memory retrieval, in order to check the plausibility of a retrieved answer. In particular, accessing a representation of magnitudes may permit the filtering out of the grossly false results such as operation confusions (e.g. $5 + 6 = 30$; Winkelman & Schmidt, 1974). Thus, we postulate that success in arithmetic fact retrieval can be boosted considerably by accessing a semantic representation of the magnitude of the operands and of the tentative result.

At a third level of complexity, arithmetic problems often involve working memory. Working memory is obviously required when the operands are presented auditorily and must be remembered throughout the calculation. It is also needed for problems that require the temporary storage of intermediate results, for instance during carry or borrow operations. Research with normal subjects has demonstrated the involvement of a short-term verbal store, called the articulatory loop, in complex calculation (e.g. Hitch, 1978; Logie et al., 1994). A visuo-spatial store may also be used to maintain on-line the spatial layout and digits of an ongoing multidigit calculation.

Finally, at a fourth level of complexity, the most complex arithmetic problems require sequential planning and control processes. Multi-digit operations involve the resolution, in a strict order, of many single-digit problems. The selection and execution of each elementary operation must be controlled and possibly corrected. This also calls into play visuo-spatial resources, due to the spatial organisation of calculation algorithms. With considerable practice, parts of these

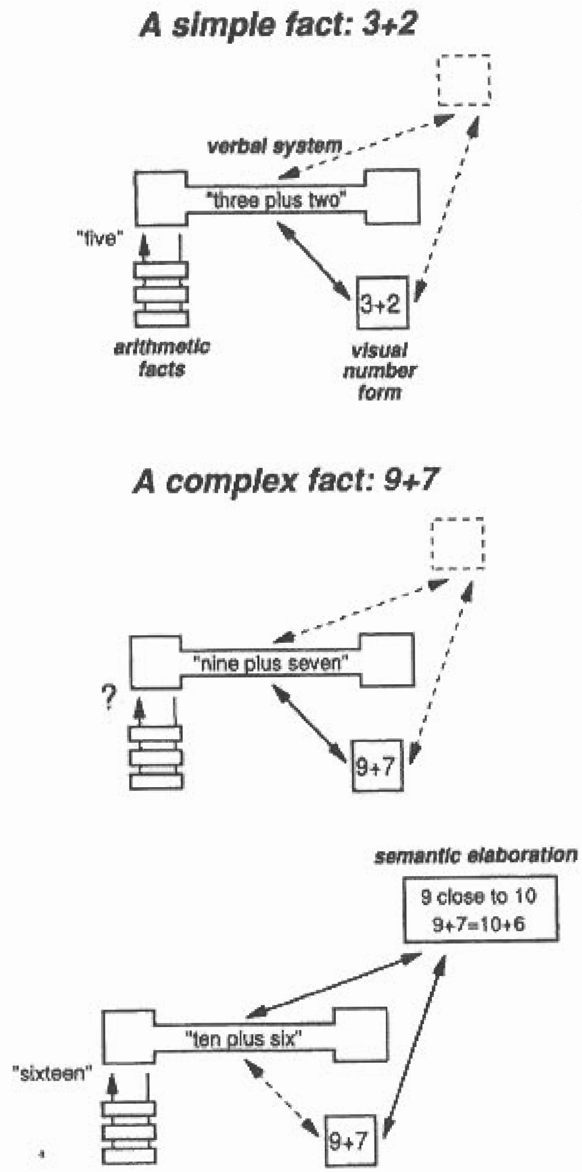

FIG. 6. Illustration of the possible role of semantic elaboration in arithmetic fact retrieval. Very simple problems such as 3 + 2 (**top**), once verbally encoded, may activate the corresponding verbal routine directly. More complex problems, such as 9 + 7 (**bottom**) may not be stored as such in rote memory. Semantic information, such as knowing that 9 is close to 10, may be used to recode the problem into a more familiar form.

algorithms may become routinised. For most of us, however, complex operations, especially subtraction and division, involve sequential trial and error processes (van Lehn, 1990). In yet other problems, such as word problems, the solution strategy is often not known or not transparent in the formulation, and a novel algorithm must be planned.

At present, we can only offer some very coarse speculations as to how these functionally defined levels of complexity map onto brain anatomy (Fig. 7). Considerable neuropsychological evidence outside of the numerical domain links planning and sequential control (level 4) to a "frontal network" involving prefrontal cortex, anterior cingulate, and subcortical nuclei (Shallice, 1982, 1988; Fuster, 1989). The articulatory loop of verbal working memory (level 3) has been localised by PET scan to a network of areas comprising the left supramarginal gyrus, the left inferior frontal region, the insula, and the left superior temporal gyrus (Paulesu, Frith, & Frackowiak, 1993), whereas visuo-spatial working memory may rely on a right-lateralised prefronto-parieto-occipital network (Jonides et al., 1993; McCarthy et al., 1994). As regards level 2 (semantic elaboration) and level 1 (rote arithmetic memory), their anatomical

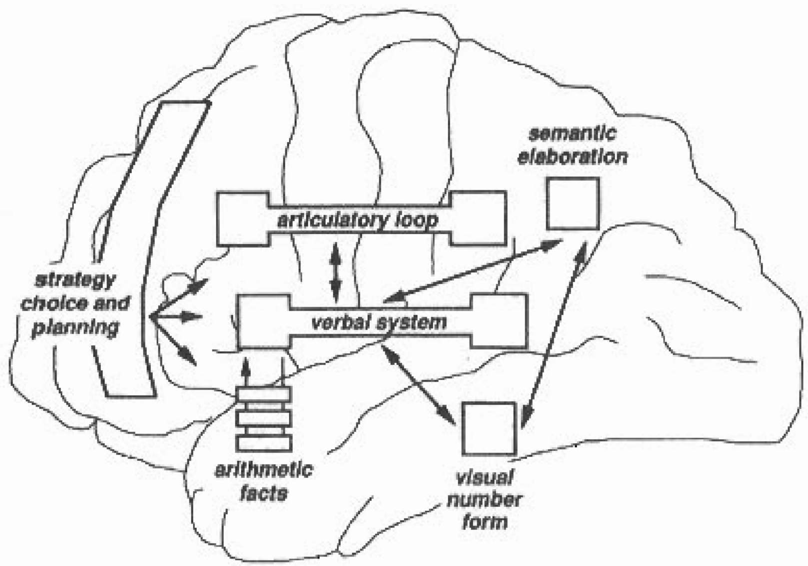

FIG. 7. Putative anatomical circuits involved in solving arithmetic problems of varying complexity. Perisylvian language areas provide a verbal encoding of problems. Retrieval of rote verbal arithmetic facts may be performed by a cortico-striatal loop through the left basal ganglia, and semantic elaboration and recoding of problems by left parieto-occipito-temporal areas. Operands and intermediate results may have to be stored in working memory via the articulatory loop or via the visual number form and other areas forming the "visuo-spatial scratchpad." Dorsolateral prefrontal circuits contribute to the planning, sequencing, and controlling of successive operations.

separation must remain tentative. We speculate, however, that the left inferior parietal region is usually involved in the computation of semantic relations between numbers, whereas a left cortico-striatal loop subserves rote arithmetic fact retrieval.

Whitaker, Habiger, and Ivers (1985), Corbett, McCusker, and Davidson (1988), and Hittmair-Delazer, Semenza, and Denes (1994) have each described a case of acalculia, including an inability to perform simple multiplications, following a left subcortical lesion in the basal ganglia. Both arithmetic facts and calculation procedures were impaired, although to a variable extent. Interestingly, Hittmair-Delazer et al.'s (1994) patient could still use conceptually elaborate strategies in order to sidestep his fact retrieval deficit (for instance computing 4×9 as either $9{\times}2 + 9{\times}2$ or as $90/2–9$). This indicates intact conceptual and operation sequencing resources. We therefore speculate that the circuitry of the basal ganglia is involved in the storage and retrieval of rote arithmetic memories and routine procedures, together with other routine "motor habits" (Mishkin & Appenzeller, 1987; Shallice, 1988). Alexander, Delong, and Strick (1986) have described cortico-striatal loops from cortex to the basal ganglia, the thalamus, and then back to cortex. One such loop, originating from cortical language areas of the left hemisphere and passing through the left basal ganglia, may contribute to the storage and retrieval of rote arithmetic facts. Note that this hypothesis predicts that a left thalamic lesion may also cause a fact retrieval impairment. Although we know of no case studies confirming this prediction, Ojemann (1974) has reported a disruptive effect of thalamic stimulation on mental arithmetic.

The most frequent lesion site for anarithmetia is the left inferior parietal region. In our model, part of this region is assumed to provide semantic relations between numbers, which can be used to inform and control rote fact retrieval by the cortico-striatal loop. Hence, lesions in this area might affect *access* to arithmetic memory (Warrington, 1982) or verification of its outputs, without necessarily destroying the rote facts themselves. Our model therefore predicts that such cases might remain able to recite, from rote memory, series of cells from the addition and multiplication tables. It also predicts that the calculation deficit should be all the more evident when patients' premorbid mastery of arithmetic facts was poor, so that they often had to rely on semantic backup strategies.

Analysis of left parieto-occipito-temporal cases, however, is often complex because multiple deficits may be involved. Patients with inferior parietal lesions often, but not necessarily, show a cluster of impairments known as Gerstmann's syndrome, which includes acalculia, agraphia, finger agnosia, and left-right disorientation (Benton, 1961, 1987, 1992; Cipolotti et al., 1991; Gerstmann, 1940). The observed number processing and calculation impairments may then be secondary to an agraphic or aphasic deficit (e.g. Benson & Denckla, 1969; Hécaen, Angelergues, & Houillier, 1961). Furthermore, verbal working memory may be affected if the lesion extends into the left supramarginal gyrus (Shallice & Vallar, 1990), perhaps explaining some multi-digit calculation impairments. Hence, reports of isolated calculation deficits (e.g. Takayama, Sugishita, Akiguchi, & Kimura, 1994) will have to be evaluated with great care.

We conclude with a brief consideration of left anterior cases of anarithmetia. Deficits in elementary calculation following a left frontal lesion seem to be relatively rare. Lucchelli and De Renzi (1993) have described a case of anarithmetia following a left medial frontal lesion, with a mild impairment of arithmetic fact retrieval and a severe deficit of calculation procedures. This may correspond to a mixed deficit, perhaps with partial impairment of the ability to plan and control the execution of arithmetic procedures. More often, the calculation difficulties of frontal patients show up mostly in non-routine arithmetic word problems (e.g. Fasotti, Eling, & Bremer, 1992; Fasotti, Eling, & van Houtem, 1994). According to Luria (1966), their impairment is due to an adherence to the surface form of the problems and an inability to conceive and execute non-obvious plans for a solution. This view is completely consistent with a deficit at level 4 in our hierarchical analysis.

Dissociations Between Operations

The distinction of levels of complexity within calculation processes obviously fits with the known double dissociation between simple arithmetic facts and calculation procedures (Caramazza & McCloskey, 1987). It may also be helpful in analysing dissociations between different arithmetic operations with single digits (e.g. Cipolotti & De Lacy Costello, in press; Dagenbach & McCloskey, 1992; Eshel, Gilad, & Sarova-Pinhas, 1994; McNeil & Warrington, 1994). The four basic operations of addition, multiplication, subtraction, and division, as taught at school, obviously put different emphasis on memory, semantic elaboration, and backup strategies. For multiplication, rote memory retrieval is the main strategy (e.g. Ashcraft, 1992; Campbell & Graham, 1985). Many simple additions are also memorised, but semantic elaboration and backup counting strategies are also available. Finally, subtraction and especially division are much less routinised and may be solved by counting or even by an "inversion" strategy of searching in memory for the converse addition or multiplication fact (e.g. 45/9 is solved by searching the 9 times table and retrieving $9 \times 5 = 45$).

It should thus be possible to explain dissociations between operations, not just with the ad hoc assumption that they are stored in different tables, but by appealing to the different functional and anatomical pathways on which they rely. For instance, assuming that a subject had always relied on fact retrieval for addition and multiplication, but had used more complex semantic strategies for subtraction, and that he persisted in doing so even after fact retrieval had become impaired, a selective impairment of addition and multiplication with preserved subtraction might ensue, as observed by Dagenbach and McCloskey

(1992), Lampl et al. (1994) and McNeil & Warrington (1994). Conversely, if rote arithmetic facts were preserved, but if semantic elaboration was impaired, a patient might be able to compute simple multiplications (e.g. 2 × 2 = 4) but not simple division (e.g. 4/2 = 2), as observed by Cipolotti and De Lacy Costello (in press), because he would lack the required ability to search his store of multiplication facts under semantic guidance. Obviously, such accounts are still sketchy and should be refined further using single-case studies and experiments with normal subjects.

Case HAR, described by McNeil and Warrington (1994), provides a good illustration of how the present model may account for seemingly bizarre dissociations in calculation. Patient HAR exhibited a selective deficit of addition and multiplication of written arabic digits, with preserved subtraction of written digits and with fully intact calculation on spoken operands. This dissociation pattern, however, unusual, fits perfectly with a lesion of the left visual number form of our model or with an impaired transmission from the visual number form to the verbal system, a functional lesion compatible with the large left parieto-occipital glioma observed in this patient. Hence, we interpret case HAR in a manner similar to the pure alexics discussed earlier (Cohen & Dehaene, submitted). Indeed, the similarities between HAR and the pure alexics are numerous. Both suffered from alexia without agraphia, both had a partially preserved reading of single digits, and both failed to read aloud multi-digit numerals. In both cases, the reading errors were digit substitutions with preserved number syntax, suggesting that the verbal system was largely intact and that the errors occurred in the transmission of digit identities to the verbal system. Like the pure alexics, HAR was perfect in magnitude comparisons of 1- and 2-digit numerals, indicating an intact arabic-to-magnitude pathway, possibly mediated by the right hemisphere. Finally, HAR performed almost perfectly in calculation with spoken operands (whether the response was spoken or written), indicating that, like the pure alexics, his calculation and number production abilities were intact.

How, then, can we account for the dissociation within written calculation? For both HAR and the pure alexics, additions and multiplications of written arabic digits were dramatically impaired. According to our model, arithmetic fact retrieval is triggered by a verbal encoding of the operands. Hence, we believe that, for addition and multiplication, the patients attempted to transcode the written arabic inputs into a verbal format. Because such transcoding was impaired, the arithmetic fact retrieval routine received wrong inputs and therefore the wrong result was retrieved. For instance, the problem 2 × 4 could be wrongly transcoded into "two times six" and therefore the erroneous result "twelve" was retrieved. Conversely, in patient HAR[7], the selective preservation of subtraction with written arabic operands, indicates that for subtraction

[7]Subtraction was not tested in the pure alexics reported by Cohen and Dehaene (submitted).

problems no such internal arabic-to-verbal transcoding was required. Lacking a memorised table of subtraction facts, the patient solved subtractions using semantic strategies rather than rote verbal memory. His very slow average reaction times for subtraction (21sec) are even compatible with counting. The resources required for the latter strategy—digit recognition, access to magnitude, verbal recitation—were well within the patient's grasp, as attested by his perfect arabic number comparison performance. Obviously, we should predict that HAR should also have been able to solve written additions by counting. The point, however, is that he did not normally do so because the normal strategy is to retrieve addition facts from verbal memory.

The Verbal Coding of Arithmetic Facts: Some Details

From a functional perspective, the dissociations observed in pure alexics and in patient HAR provide strong evidence in favour of an obligatory encoding of numbers in verbal format for the purpose of arithmetic fact retrieval. Indeed, if arithmetic facts could be accessed directly from the arabic or semantic representations, the patients should have been able to access arithmetic facts from written arabic operands because the recognition and attribution of meaning to written arabic digits, as assessed by the magnitude comparison task, were intact. The observation of a calculation impairment, specific to the visual modality, in patients whose deficit was in transcoding from visual inputs to spoken outputs, suggests that such transcoding is needed for accessing arithmetic memory from arabic operands.

Recently, however, Whalen, Lindemann, and McCloskey (in preparation) have gathered evidence that seems to run counter to this claim. They report several patients with impaired production of spoken numerals and who therefore erred in reading aloud arabic digits, but who could nevertheless *write down* the correct results of written calculations that they had misread. Patient KSR, for instance, was only 12% correct in reading aloud single-digit addition, subtraction, multiplication, or division problems. He was also severely impaired in rhyme judgements with arabic numerals (e.g. does 4 rhyme with the word "sour"?), indicating that he could not access a phonological representation from written arabic digits. Nevertheless, he was 99% correct in writing down the correct answer to written calculations, and his reaction times suggested that he retrieved most responses from memory. This dissociation therefore demonstrates that retrieving a correct phonological representation of the operands is *not* a first and compulsory step in arithmetic fact retrieval. Patients can have an incorrect phonological representation of an arithmetic problem, and yet retrieve the correct answer from memory.

We agree with Whalen and his colleagues that their observations essentially prove that arithmetic facts are not encoded in a phonological format. Does this, however, imply that the inputs and outputs of the arithmetic fact retrieval process are "abstract" semantic representations of numbers, as hypothesised in

McCloskey's (1992) model? Or could they still be verbal and yet be located at a level of processing more abstract than the phonological level? Many models of word production actually include such a level of verbal representation. It is called the filled syntactic frame in McCloskey et al.'s (1986) model of number word production, the filled word frame in Cohen and Dehaene's (1991) modified version of this model, and the "lemma" in Levelt's (1989) more general model of word production. At this level of processing, the verbal representation specifies "a plan for the production of words comprising the verbal numeral." (McCloskey, 1992, p. 137). The elements of this plan are addresses of the form "Tens:{6}" that specify both the lexical stack and the position within stack of each number word. Such addresses can then be used to retrieve the appropriate output representation or lexeme ("sixteen") from either the phonological or the graphemic output lexicon.

In order to reconcile our hypothesis of a verbal encoding of arithmetic facts with Whalen et al.'s new data, we therefore postulate that arithmetic facts are rote-memorised associations between filled word frame representations of the operands, rather than between their phonological representations. Figure 8 shows the hypothetical sequence of processing involved in reading aloud and in solving a simple multiplication problem. The visual stimulus, identified at the level of the visual number form, is used to compute a filled word frame representation of the arithmetic problem (see Cohen & Dehaene, 1991, for a precise model of this process). This verbal representation can then be used to trigger arithmetic fact retrieval, and the answer to the problem is retrieved in the same word frame format. The filled word frames of both the problem and the answer can then be used to access a phonological or graphemic output lexicon, depending on whether the problem and its answer must be read aloud or written down.

Within this more precise framework, pure alexics and patient HAR, on the one hand, would have a specific impairment in using visual number form information to fill out the word frame. Because such filling-out comes prior to fact retrieval, they would err in retrieving arithmetic facts from visually presented operands. Patients such as KSR, on the other hand, would have a specific impairment in using information in the filled word frame to access a phonological representation. Because phonological access comes after fact retrieval, such patients would have no difficulty in retrieving arithmetic facts from visually presented operands, nor in writing down the retrieved result.

Right-hemispheric Damage

Our entire discussion up to now has been focused on the consequences of *left-hemispheric* damage on numerical abilities. Indeed, a final seemingly trivial prediction of our model is that lesions of the right (non-dominant) hemisphere should have little or no effect on number processing. Since the dominant hemisphere supposedly contains a full copy of the three number representations

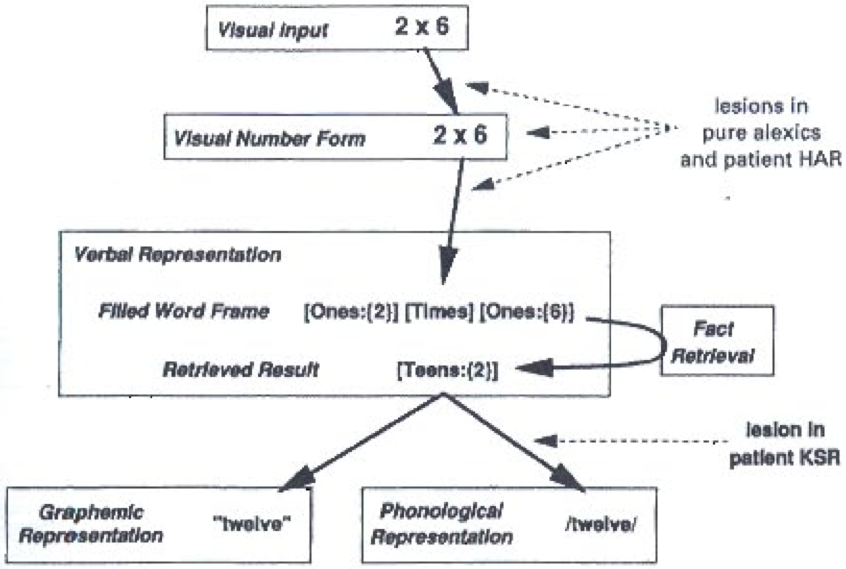

FIG. 8. Putative levels of representation involved in reading aloud and in retrieving the answers to simple written multiplications (based on Cohen & Dehaene, 1991). The proposed lesion sites for pure alexics and for patient KSR (Whalen et al., in preparation) are shown.

and of the associated calculation and comparison processes, it should be capable of performing any numerical task whether or not the non-dominant hemisphere is lesioned. This should at least be true in first approximation, since our model allows for some degree of differentiation between homologous left and right areas, such as a right-hemispheric advantage for representing continuous numerical quantities (e.g. Kosslyn et al., 1989).

Indeed, clinical studies of groups of patients have repeatedly confirmed that calculation impairments are much more likely to occur in left-hemisphere cases than in right-hemisphere cases (e.g. Dahmen, Hartje, Bussing, & Sturm, 1982; Grafman et al., 1982; Hécaen et al., 1961; Jackson & Warrington, 1986; Rosselli & Ardila, 1989). Jackson and Warrington (1986) even found that right-lesioned patients calculated just as well as age-matched controls. Some data suggest that larger–smaller comparison may be more affected by a right-hemispheric than by a left-hemispheric lesion (Dahmen et al., 1982; Rosseli & Ardila, 1989), consistent with a right-hemispheric superiority for quantitative representations. Nevertheless, aside from group studies, there are few reports of numerical impairments following a unilateral right-hemispheric lesion (e.g. Leleux, Kaiser, & Lebrun, 1979). Most often, these impairments fit with the definition of "spatial acalculia" (Hécaen et al., 1961), which is an impairment in the spatial layout of digits in writing or in calculation tasks with multi-digit numerals.

Although this condition indicates that right-hemispheric visuo-spatial areas contribute to complex calculations, it cannot be considered as a genuine acalculia because it very often derives from general spatial impairments such as neglect. Our model predicts that it is only in exceptional cases of right-hemispheric dominance for language that a unilateral right lesion may yield a specific numerical impairment. Thus, if the lesion extends into the right perisylvian region, crossed aphasia should invariably be observed.

Contrary to a common assumption, the rarity of numerical deficits in right-hemispheric cases does *not* imply that the right hemisphere is not involved with number processing in normal subjects. It is equally consistent with the presence of redundant numerical processes in the left and right hemispheres. In fact, our model predicts that the isolated right hemisphere possesses sophisticated processes for number identification and access to number meaning. Since the left hemisphere also possesses a copy of them, however, a right unilateral lesion alone has little or no effect on number processing.

EVIDENCE FROM FUNCTIONAL BRAIN IMAGING IN NORMAL SUBJECTS

We now turn to a different source of evidence on the cerebral organisation of number processing. In recent years it has become possible to study the activity of the normal human brain during the performance of cognitive tasks (Posner & Raichle, 1994). Numerical tasks have occasionally been studied using functional brain imaging techniques. The results provide direct evidence concerning the neuronal networks postulated in our model. Brain imaging data should be particularly useful for investigating the role of the right hemisphere in number processing. In patients with lesions of the left hemisphere, recovery processes can always be invoked to explain the involvement of right-hemispheric pathways. Functional brain imagery, however, can probe directly whether the right hemisphere contributes to numerical abilities in normal subjects.

Cerebral Blood Flow Studies

Roland and Friberg (1985), with the now outdated Xe^{133} technique, and Appolonio et al. (1994), using modern functional magnetic resonance imaging, have studied regional cerebral blood flow in normal volunteers during a complex calculation task. The task involved repeated subtractions starting with a given number (e.g. 50–3 = 47, 47–3 = 44, 44–3 = 41, etc). This was contrasted with resting in Roland and Friberg's study, and with forward counting in Appolonio et al.'s study.

The results showed extensive activations in the inferior parietal region and in prefrontal, premotor, and motor cortex. The activations were bilateral, although they tended to be larger in the left hemisphere. Globally, these results confirm that complex mental calculation involves an extended network of frontal and inferior parietal areas (Fig. 7). Unfortunately, from a cognitive perspective, the continuous subtraction task does not measure any well-defined neuropsychological component of number processing. It is heavily dependent on working memory and sequencing processes, and indeed it is often impaired in frontal patients who do not otherwise show acalculia (Luria, 1966). Thus, it is unclear which of the observed activations were specific to the numerical domain and which were related to global attentional, sequencing, and working memory factors.

Dehaene et al. (in preparation), using positron emission tomography, studied number processing in a more restricted setting. Pairs of arabic digits were flashed on a computer screen. The subjects were told either to multiply the two digits mentally, or to select the largest of the two digits. In both cases, subjects had to name the result covertly "in their head." These tasks therefore involved similar input-output processes, but a different internal operation (multiplication or comparison). The results were analysed by dividing each subject's MRI into anatomically defined regions of interest and then measuring variations in blood flow in each region and in each condition relative to a resting situation.

A number of regions were activated in both multiplication and comparison tasks: the left and right lateral occipital cortex, the supplementary motor area, and the left precentral gyrus (the right precentral gyrus was active during comparison but did not quite reach significance in multiplication). Such activations may correspond to processes common to the two tasks, for instance visual recognition, visual fixation, and attention orienting, and covert speech production. Whereas comparison, relative to rest, did not activate any additional areas, multiplication also activated the left inferior temporo-occipital region, the right internal occipital area, and the left and right inferior parietal areas (with a slight but non-significant tendency towards greater activation on the left).

Aside from the right internal occipital activation, which may be related to a left-to-right scanning of the problems, the areas that were found active during multiplication fit remarkably well with our review of the neuropsychological literature. The left inferior temporo-occipital activation fits with the fact that pure alexic patients with lesions restricted to this area can compare two visually presented digits, but fail to multiply them (Cohen & Dehaene, submitted; see earlier). We speculate that this activation reflects an attentional amplification of the left-hemispheric visual number form, which is supposedly critical for communicating digit identities to other left-hemispheric areas, notably those involved in arithmetic fact retrieval.

The left inferior parietal activation also fits with the many cases of anarithmetia from lesions of this area. As discussed earlier, our interpretation is that this region and the homologous right inferior parietal area are involved in semantic elaboration, which permits flexible access to rote verbal memories stored in a corticostriatal loop (Fig. 7). It is noteworthy that the left and right inferior parietal regions showed a smaller but nearly significant ($P = 0.076$)

increase in blood flow during number comparisons, supporting a putative role in semantic processing. Further research should determine if the activation of these regions decreases to a non-significant level, as predicted by our model, when retrieving only very simple rote arithmetic facts such as 2 × 2, which may not require semantic elaboration.

In our PET study, the activations during multiplication and comparison were also contrasted directly rather than relative to a resting situation. Higher blood flow was found during multiplication in the left basal ganglia (lenticular nucleus), in agreement with an involvement of cortico-striatal loops in arithmetic fact retrieval. Higher blood flow was also found during comparison in right inferior and anterior prefrontal regions, the right superior temporal gyrus, and the left and right middle temporal gyri. We do not know yet whether any of these areas play a specific role in number comparisons, or whether they were inactivated selectively during multiplication. However, the pattern of hemispheric asymmetries in all regions was compatible with a greater involvement of the left hemisphere in mental multiplication and with a more bilateral or even a right-lateralised pattern of activation during number comparison.

Electro-encephalography and Event-related Potentials

There is a long tradition of EEG studies of hemispheric lateralisation during calculation tasks (e.g. Papanicolaou, Schmidt, Moore, & Eisenberg, 1983; Shepherd & Gale, 1982; Inouye, Shinosaki, Iyama, & Mastumoto, 1993). The vast majority of such studies have showed a greater activation of the posterior left hemisphere during mental arithmetic, thus confirming classical neuropsychological findings. Inouye et al. (1993), for instance, reported EEG desynchronisation over the left temporo-centro-occipital area and increased coherence between the posterior left hemisphere and frontal areas during calculation relative to rest. However, the temporal unfolding of calculations and the specific cognitive mechanisms involved were not studied.

Recently, Dehaene (in press) has used high-density recordings of event-related potentials (ERPs) to study in finer detail the temporal unfolding of brain activations in number comparisons. ERPs were recorded from 64 scalp electrodes while subjects decided whether numbers were larger or smaller than 5. The experimental design was inspired by Sternberg's additive-factors method and incorporated three experimental factors: the notation used for the visual stimuli (arabic digits or spelled-out number words), the numerical distance of the target from the standard (close or far from 5), and the hand used for responding.

These three factors were found to have additive influences on reaction times. Furthermore, they had a significant effect on ERPs at well-ordered points in time (respectively about 120msec, 190msec, and 250–300msec after stimulus onset). This was in agreement with a sequential activation of stimulus identification, magnitude comparison, and motor programming processes, as predicted from our model.

Most critical to the current discussion is the localisation of the effects on the scalp. Number notation mainly affected the symmetry of an early posterior negative wave, the N1, peaking around 150–160msec. With number words, the N1 was much stronger over left infero-posterior electrodes than over the corresponding right electrodes, in agreement with a left lateralisation of the visual word form (e.g. Petersen, Fox, Snyder, & Raichle, 1990). With arabic digits, however, the N1 was symmetrical. In particular, a very strong N1 was recorded over the right hemisphere. This provides direct evidence that, in normals, both hemispheres are involved in visual digit recognition.

Slightly later in time, around 190msec post-stimulus, the ERPs to digits close and far from 5 diverged. It is well known that two numerically close digits are more difficult to compare than two digits that are further apart, a result which is taken as evidence for access to a semantic representation of number magnitude (e.g. Moyer & Landauer, 1967; Dehaene, Dupoux, & Mehler, 1990). Here, the distance effect was largest at electrodes situated near the parieto-occipito-temporal junction of both hemispheres, with a larger effect on the right. Most importantly, the topography and latency of this distance effect were quite similar whether the target numbers were presented in arabic or in alphabetical notation. Hence, the evidence was fully consistent with the subjects accessing a notation-independent magnitude representation grossly localised to left and right posterior parieto-occipito-temporal cortices. The observed rightward asymmetry was again consistent with a right-hemispheric superiority in processing quantitative information.

Kiefer and Dehaene (in prep.) have performed a similar ERP study of mental multiplication. Since speaking aloud would have caused movement artefacts, they used a verification task in which subjects were successively presented with the first operand, the second operand, and then a proposed multiplication result that they had to classify as correct or incorrect (e.g. 3, 6, 18). Simple and complex multiplications were contrasted by varying the size of the operands (e.g. 2×3 vs. 7×9). Although the results were considerably more complex than in the comparison task, a significant effect of multiplication difficulty was found about 400msec after the second operand on electrodes located near the *left* parieto-occipito-temporal junction. This effect is consistent with a greater activation of the left posterior cortices during complex multiplications, which presumably require semantic elaboration, than during simple ones. Taken together, the results of these two experiments provide support for several key aspects of the present neuro-functional model, notably the duplication of digit identification and magnitude comparison processes in the two hemispheres, and the left-hemisphere lateralisation of arithmetic fact retrieval.

CONCLUSION

We have outlined a model of the neuro-anatomical circuits underlying number processing in humans. This model was found to be in good agreement with brain-imaging experiments in normals and with neuropsychological case studies of acalculia. In particular, the cognitive number processing deficits of patients could be predicted with good accuracy based on the nature of their lesions. Various neurological conditions, including callosotomy, left hemispherectomy, major left-hemisphere damage, deep dyslexia, pure alexia, neglect dyslexia, and to a lesser extent left parietal-occipito-temporal and left fronto-subcortical damage, were shown to yield predictable impairments in the numerical domain. Even some notoriously difficult cases, such as McNeil and Warrington's (1994) modality- and operation-specific acalculia, fell to a relatively simple interpretation in our neuro-functional framework.

Contrary to an hypothesis tacitly endorsed by many cognitive scientists, the relations between cognitive functions and brain anatomy seem neither random nor dramatically variable across subjects, even in a high-level cultural domain such as number processing. However, our approach should not be construed as promoting a return to phrenology. Obviously, some of the labels on our anatomical schema are naive and will have to be replaced, in future versions of the model, by detailed accounts of the inner working of the corresponding brain areas (see e.g. Campbell & Oliphant [in press] for a model of arithmetic fact retrieval, or Dehaene and Changeux [1993] for a model of numerosity estimation, magnitude representation, and number comparison). We fully reject the phrenological notion of a "centre for calculation" or a single brain area where numerical knowledge would be concentrated. Rather, we believe that number processing results from the collective computation of widely distributed brain areas (Figs. 2 and 7), each of which performs only elementary transformations. Many such transformations need not be specific for numbers and may be called for by several different cognitive tasks. By comparing which tasks, whether numerical or not, rely on a given brain area and which do not, it should be possible to understand the elementary contribution of each area better. This should be pursued with brain imaging methods in preference to the lesion method, because in neuropsychology, the association of deficits is a notoriously poor indicator of their common origin (e.g. Benton, 1992; Shallice, 1988).

Within the numerical domain proper, we see two promising avenues for research. First, a recurrent finding in the literature is that most, if not all, acalculic patients are able to understand the quantities associated with simple arabic numerals and to compare them. In our model, this is attributed to a redundant bilateral representation of visual identification, quantity representation, and comparison processes. We therefore predict that the ability to understand and compare numerical quantities should break down in patients with bilateral posterior lesions or with diffuse brain damage. Such cases could provide currently missing information about the structure of semantic representations of numbers. A second direction for research concerns the brain circuits that are recruited during arithmetic calculation. Figure 7 provides testable predictions about the levels of complexity in arithmetic problems and the putative anatomical circuits that permit their solution. We have no doubt that further research will lead to substantial refutations and modifications of this diagram. The exact role of the left inferior parietal region in calculation, in particular, strikes us as an unsolved mystery.

Manuscript received December 1994
Revised manuscript received January 1995

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