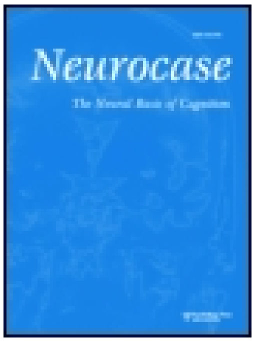

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Cerebral Networks for Number Processing: Evidence from a Case of Posterior Callosal Lesion

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Abstract

We report a study of number processing in a patient with a lesion selectively destroying the posterior half of her corpus callosum. This case provided an opportunity to study the cerebral distribution of numerical abilities across hemispheres, and their interhemispheric communication pathways. Tasks of interhemispheric same-different judgement with digits and sets of dots showed that exact digit identity could not be transferred between hemispheres, but that some approximate magnitude information could. With arabic numerals presented in the left visual field, reading aloud and arithmetic were severely impaired. In contrast, larger-smaller magnitude comparison was spared. With right-visual-field stimuli, the patient's performance was essentially normal in reading aloud, arithmetic and number comparison. These findings lend support to the hypothesis that both hemispheres are capable of identifying arabic digits, and of accessing and comparing the corresponding magnitudes. However, the verbal abilities which underlie overt naming and arithmetic computations are available only to the left hemisphere.

Introduction

Calculation is generally thought to rest primarily on the left hemisphere. In patients with a standard brain lateralization, acalculia is frequently observed following left-hemispheric lesions, while symmetrical right-hemispheric damage does not impede number processing (Hécaen *et al.*, 1961; Jackson and Warrington, 1986). The sole exception is the so-called spatial acalculia, an inability to position properly in space the digits of multidigit numerals, which is often observed following right posterior lesions. This disorder, however, is not a genuine number-processing deficit but a mere by-product of general visuo-spatial impairments.

The fact that right-hemispheric lesions do not affect number processing can be interpreted in one of two ways. Either right-hemispheric areas simply do not contribute to number processing, or alternatively, some processes may be redundantly represented in both hemispheres. In the latter case, a unilateral lesion selectively affecting those redundant processes may have no visible impact on behaviour. Indeed, there are converging indications that the right hemisphere is able to identify arabic digits and to access and manipulate the corresponding magnitudes (for a comprehensive review, see Dehaene and Cohen, 1995). Perhaps the clearest evidence for numerical abilities in the right hemisphere comes from a few studies with split-brain patients. If a pair of digits is flashed in the left visual field (LVF) of split-brain patients, and is therefore available to their right hemisphere only, such patients can decide accurately whether the two digits are identical (Sergent, 1990), and which of two different digits represents the larger magnitude (Seymour *et al.*, 1994). Such observations imply that the right hemisphere can recognize arabic digits, as well as represent and compare the corresponding quantities.

The split-brain evidence also suggests that not all numerical processes are available to both hemispheres. Split-brain patients are generally unable to read aloud digits presented in their LVF (Gazzaniga and Hillyard, 1971). Similarly, they cannot solve even simple arithmetic problems whose operands are presented in the LVF (Gazzaniga and Smylie, 1984). All the above tasks are easily performed when stimuli are flashed in the patients' right visual field (RVF), so as to be processed selectively by their left hemisphere. Thus, in keeping with the well known left-hemispheric specialization for language, the left

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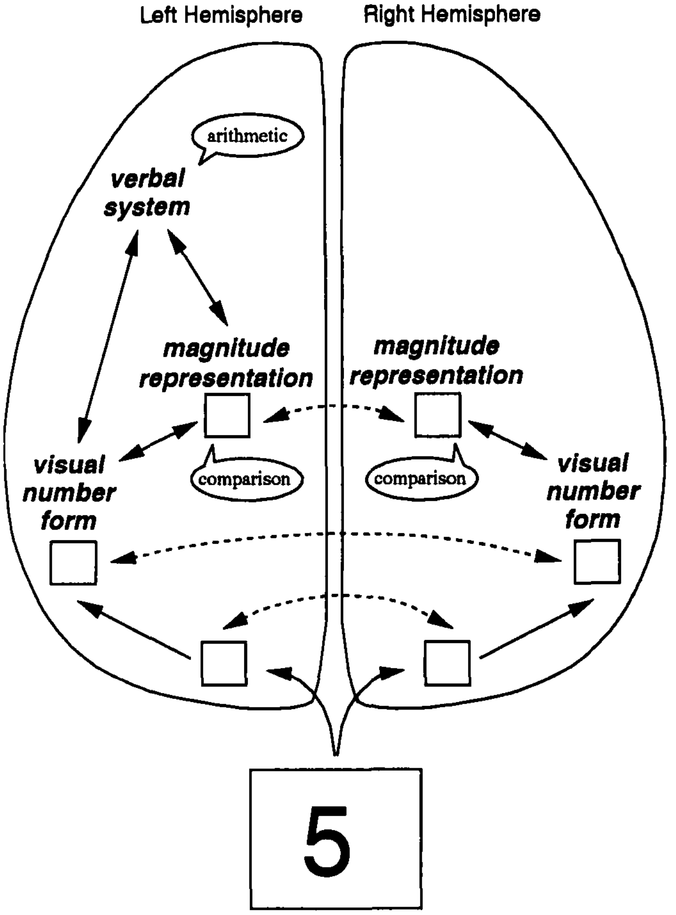

Fig. 1. Model of arabic number processing, featuring bilateral visual and magnitude representations, left-hemispheric verbal representation, and three interhemispheric pathways.

hemisphere, but not the right, appears to process numerals in a verbal form and to perform symbolic calculations.

Elaborating on such findings, we have recently proposed a model of the functional and anatomical architecture of the number processing system (Cohen and Dehaene, 1995; Dehaene and Cohen, 1995). This model makes explicit hypotheses relative to the distribution of numerical processes in the left and right hemispheres, as well as to the interhemispheric communication routes for numerical information (Fig. 1).

Following Dehaene's (1992) triple-code theory, we assume that numbers can be represented in the human brain in three distinct formats: as arabic numerals, as sequences of words, and as analogical representations of the corresponding magnitude. In the visual arabic code, numbers are encoded as strings of digits on an internal visuo-spatial scratchpad, which by analogy with the visual word form (Warrington and Shallice, 1980) is called the visual number form (Cohen and Dehaene, 1991). In the verbal code, they are encoded as sequences of number words. Finally, in the magnitude code, numbers are represented as analogical quantities in the same way as other continuous dimensions such as weight or size (Dehaene *et al.*, 1990; Dehaene and Changeux, 1993). The 'number line' (Restle, 1970) has been proposed as an adequate metaphor for the magnitude code. Numerical relations, such as knowing that 9 is larger than 5, are then implicitly represented by proximity relations on the number line.

The model assumes that these three cardinal representations are linked by direct transcoding routes that allow numbers to be rapidly re-encoded in different formats. Thus, a printed arabic numeral will always be initially identified and encoded in the visual arabic number form. Then, if the task requires assessing its magnitude, its identity will be transmitted and re-encoded on the quantity representation. If, in contrast, the task requires reading the numeral aloud, then its identity will be transmitted to the verbal system where an appropriate sequence of words will be generated. In the course of more complex tasks, such as multidigit multiplication, several such transcodings may take place back and forth between the three cardinal representations.

A crucial hypothesis of the model is that each of the three numerical representations is well suited for a different set of functions. The visual number form, holding a representation of the spatial layout of digits, is well suited for performing mental calculations with long arabic numerals. The verbal format, on the other hand, is postulated to be the obligatory entry code for accessing stored tables of rote arithmetic facts, encoded in the form of short sentences in verbal memory (e.g. 'two times three, six'). Finally, the analogical magnitude format is ideal for representing approximate numerical relations, such as knowing that 11 is about 10, or that 7 is slightly larger than 5.

Thanks to several single-case and brain imaging studies, reviewed in Dehaene and Cohen (1995), tentative proposals could be made about the network of brain areas underlying the triple-code model. The visual number form corresponds to a cascade of areas culminating in the mesial occipito-temporal region of both hemispheres. The analogical magnitude representation is computed by areas in the vicinity of the parieto-occipito-temporal junction of both hemispheres. Finally, the verbal word frame is computed by classical language areas in the perisylvian region of the left hemisphere. We also make the hypothesis that homologous left and right hemispheric regions are connected into single functional units by transcallosal fibres. Thus, information can be transferred across the corpus callosum in three different ways: at a low visual level, at the level of the visual number forms, or at the level of the magnitude representation. Within the left hemisphere, we also suppose the visual, verbal, and magnitude representations to be fully interconnected by dedicated neural pathways.

In this study, we report the case of a patient with an ischaemic lesion destroying the posterior half of her corpus callosum. Contrary to most split-brains, who suffered severe epilepsy throughout childhood, this patient was neurologically intact prior to her stroke. Thus her cerebral organization faithfully reflected the standard distribution of

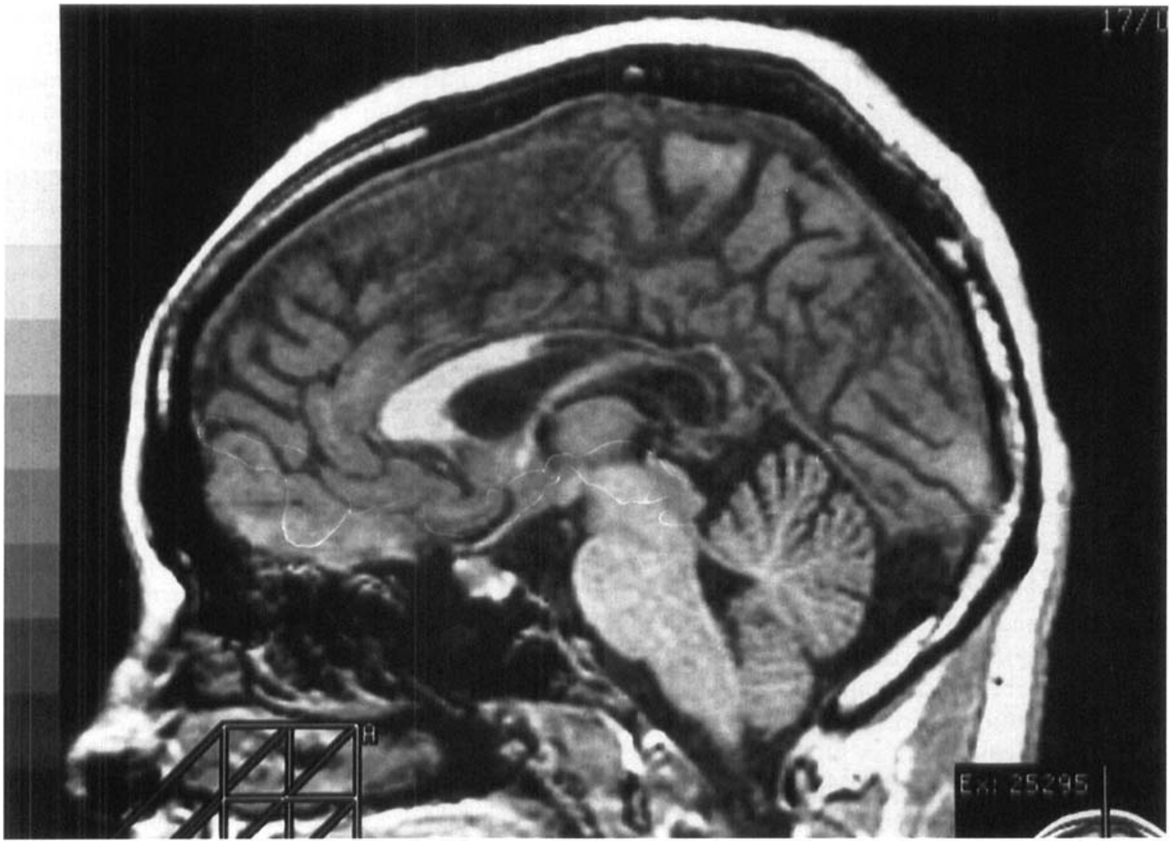

Fig. 2. Sagittal MRI section of the patient's brain, showing an infarct of the posterior half of the corpus callosum.

functions in the two hemispheres. The callosal lesion presumably left the number-processing systems of both hemispheres intact, although partially disconnected. This case therefore provides a unique opportunity to test several core predictions of our model about the cerebral distribution of number-processing modules and their interhemispheric communication pathways.

Medical history

The patient was a 30-year-old right-handed woman, with no significant medical history. She had been working for some time as a draughtswoman in a building company. One evening, she had a sudden feeling of sickness, followed by brief motor seizures affecting her right limbs. Over the few weeks following this episode, the patient probably suffered from a deficit of anterograde memory, and may have had some difficulties recognizing the faces of previously familiar individuals. These impairments receded completely, and the patient's only residual complaints concerned a general weariness, some visual discomfort on her right side, as well as a feeling of clumsiness when using her hands. In particular, she mentioned occasional difficulties in bimanual tasks such as getting dressed, or using forks and knives.

When the present study was carried out, there was no motor or sensory deficit. Goldmann perimetry disclosed a partial right superior quadrantanopia with macular sparing. Visual acuity was 10/10 bilaterally. There was some degree of visuo-motor ataxia when either hand reached for an object presented in the opposite visual hemifield. A left-sided extinction phenomenon could be elicited when the patient was asked to report the side of elementary visual or tactile stimulations.

Magnetic resonance imaging revealed an infarct affecting the left half of the posterior half of the corpus callosum (Fig. 2). Additionally, there was a small lesion in the left occipital cortex, just ventral to the anterior part of the calcarine sulcus, corresponding to the right quadrantanopia. Despite extensive investigations, the exact origin of this infarct could not be ascertained.

Assessment of callosal functions

A severe impairment of interhemispheric transfer could be demonstrated in several modalities. The visual, haptic and auditory modalities will be considered in turn, and followed by the description of a few additional motor tasks. Results are summarized in Table 1.

Visual transfer

In this and all following tests using visual stimuli, the patient was seated at a distance of about 55 cm in front of a

Table 1. Error rates (%) in tests of interhemispheric transfer in the visual, haptic and auditory modalities

Side of stimulation	Left	Right
Visual transfer		
Picture naming	32/43 (74.4)	6/42 (14.3)
Picture classificiation	2/85 (2.4)	0/85 (0.0)
Word naming	75/75 (100.)	23/75 (30.7)
Word classification	23/50 (46.0)	6/50 (12.0)
Letter naming	21/26 (80.8)	0/26 (0.0)
Pointing to letters	7/9 (77.8)	0/10 (0.0)
Naming complex numerals	40/40 (100.)	8/20 (40.0)
Haptic transfer		
Naming body parts	12/27 (44.4)	0/21 (0.0)
Object naming	8/20 (40.0)	0/20 (0.0)
Auditory transfer		
Unilateral stimulation	14/60 (23.3)	
Dichotic stimulation	59/60 (98.3)	3/60 (5.0)

computer screen. Various types of stimuli were flashed for 200 ms, randomly in one or the other visual hemifield. Eye fixation on a central crosshair was controlled visually by the experimenter. It remained remarkably stable and accurate throughout testing sessions. For all tests requiring a manual response, an equal number of sessions were run using the right and the left hands. No differences emerged between right- and left-hand responses, and data were therefore pooled.

There was a clear-cut left anomia. When the patient attempted to name line drawings of simple items flashed in her LVF, her performance was severely impaired (74.4% errors), although better than chance. She made only 14.3% errors when pictures were presented to her RVF [$\chi^2(1) = 31.1$, $P < 0.001$]. In order to establish whether her right hemisphere could identify the depicted objects more accurately than this poor naming performance would suggest, we asked the patient to decide simply whether each picture represented an animal or not (half the pictures actually depicted animals). She responded using a joystick which she tilted to the right or to the left depending on whether she thought she had seen an animal or not. The patient did not make a single error with RVF stimuli. More interestingly, she made only 2.4% errors with LVF stimuli. While approximate identification may be sufficient to classify pictures but not to name them, this performance discrepancy between naming and classification suggests that the patient could probably identify many of the pictures flashed to her right hemisphere, although she could not name them.

The patient also showed left alexia. She made 100% errors in reading aloud words presented in her LVF, and 30.7% errors when words were presented in her RVF [$\chi^2(1) = 79.6$, $P < 0.001$]. Furthermore, errors were qualitatively different between the two hemifields. In the RVF, almost all errors were orthographically close to the target (e.g. 'cratère'→'artère'). In the LVF, however, errors did not follow this pattern. About half of them were perseverations (i.e. repetitions of a previously produced answer), a phenomenon observed only once with RVF stimuli. Furthermore, although they were orthographically unrelated, stimuli and responses were significantly correlated in terms of length, as measured by the number of letters [$r(62) = 0.48$, $P = 0.0001$]. The same stimuli were used for an animal classification task (words in the two categories were matched for number of letters and syllables). The patient made only 12.0% errors in her RVF, whereas she performed at chance level in her LVF (46.0% errors). To summarize, reading errors in the RVF apparently resulted from the intrinsic visual difficulty of the task, with a likely contribution of the right-sided scotoma. In contrast, we found no evidence for word identification in the LVF.

A similar asymmetry prevailed when the patient was presented with single letters. She named flawlessly all letters presented in her RVF. She made as many as 80.8% errors with LVF stimuli, a performance which is, however, above chance level [$\chi^2(1) = 16.6$, $P < 0.0001$]. The contrast between hemifields persisted even when the patient was asked to respond by silently pointing with her left hand to the corresponding letter among a visually presented array [$\chi^2(1) = 9.2$, $P = 0.0024$]. This suggests that her right hemisphere was poor at identifying alphabetic characters, irrespective of the output modality.

The patient could not name correctly a single 2–4 digit long arabic numeral flashed in her LVF, while she made 40% errors in her RVF [$\chi^2(1) = 26.37$, Yates' correction applied, $P < 0.001$]. Errors obeyed the same pattern as in word reading. All errors in the RVF were visually similar to the target (e.g. 600→6000, 2818→2018). In the LVF, the patient resorted to a slow and ineffective guessing strategy. She produced frequent perseverations, and stimuli and responses were significantly correlated in terms of number of digits [$r(32) = 0.47$, $P = 0.0052$].

Haptic transfer

Unless otherwise stated, the following tests were performed with the patient's eyes closed. The patient could easily move a finger that had been touched by the examiner (0/17 errors). However, she made 59.1% (13/22) errors when asked to move the corresponding finger of the opposite hand [$\chi^2(1) = 15.1$, $P = 0.0010$]. When the examiner imposed a given posture to one of her hands, she was unable to reproduce it with the opposite hand. Furthermore, she could accurately describe postures imposed to her right but not to her left hand. Similarly, when asked to name the part of her body touched by the examiner, she performed flawlessly when the right half of her body was stimulated, while she made 44.4% errors on her left side. Left tactile anomia also appeared when the patient was asked to name familiar objects that she was allowed to manipulate with one hand only. There were no errors with her right hand, but 40.0% errors with her left

Table 2. Error rates (%) in tests of interhemispheric transfer of numerical information

Same–different judgement between hemifields		
Two digits	76/158 (48.1)	
Digit versus dot pattern	20/96 (20.8)	
Same–different judgement within hemifield		
Side of stimulation	Left	Right
Two digits (same font)	1/64 (1.6)	0/64 (0.0)
Two digits (different fonts)	19/128 (14.8)	7/128 (5.5)
Central digit versus dot pattern	4/48 (8.3)	1/48 (2.1)

hand. In another testing session, it appeared that when the patient had failed to name an object, she could nevertheless select it correctly among a set of visually presented items.

Dichotic listening

The patient was presented dichotically with digits, words and sentence fragments. She was almost totally unable to report stimuli presented to her left ear (98.3% errors, mostly absence of response), while she only made 5.0% errors with right-sided stimuli. When stimuli were presented to her left ear only, she made only 23.3% errors (mostly phonetically related to the target), indicating that her poor performance in the dichotic condition corresponded to an extinction phenomenon.

Limb praxis and writing

When tested for limb praxis, the patient showed some clumsiness and inaccuracy with her left hand, prevailing across all tasks (imitation of arbitrary hand postures, symbolic gestures, simulated and real object manipulation). The quality of gestures was generally improved on imitation. The patient could write normally with her right hand. With her left hand, however, she produced errors affecting both the shape of individual letters and occasionally the spelling of words.

To summarize, the patient showed a wide range of deficits of callosal transfer affecting the visual, haptic and auditory modalities (Degos *et al.*, 1987; Gazzaniga, 1995). Moreover, a variety of tasks requiring a verbal output or input demonstrated a clear-cut specialization of her left hemisphere for language. Thus, the patient seemed to provide an adequate source of data concerning the role of callosal transfer in various number-processing tasks.

Interhemispheric transfer of numerical information

In the model of numerical processing outlined in the introduction, numerical information can be conveyed across the corpus callosum in two different formats, in addition to low-level visual transfer. We postulate a posterior visual transcallosal route for the transfer of information in arabic notation, and a more anterior, semantic transcallosal route for the transfer of quantitative information (Sidtis *et al.*, 1981). In order to understand the functional consequences of the patient's lesion, it was therefore necessary first to assess the residual function of these two routes. We used several same–different judgement tasks, within or between hemifields, and concluded that the visual route was essentially unavailable, while the semantic route remained still partially functional. The results of this series of tasks are summarized in Table 2.

Same–different judgement between two arabic digits

As a simple test of callosal transfer, pairs of arabic digits were flashed to the patient, one digit in each hemifield. The two digits were different on 82/158 (51.9%) trials. All digits 1 through 9 were used, and the two digits in a pair differed by 1 to 4 units. The patients responded 'same' or 'different' by tilting a joystick. In this and all following experiments, we used the same tachistoscopic visual presentation technique as described before.

The patient made 76/158 errors (48.1%), a performance not different from chance. There was no significant latency difference between 'same' and 'different' trials [mean response time (RT) = 2982 ms and 2894 ms, respectively; $F(1, 154) < 1$]. Thus, there was a severe failure of communication between the visual representations built up by the two hemispheres.

It is important, however, to verify that each hemisphere was indeed able to process arabic digits, as predicted by our model. We tested this by running the same task with pairs of digits now presented within the same hemifield. The two digits were different on 50% of trials. All digits 1 through 8 were used, and the two digits in a pair differed by 1 to 4 units. The patient's responses were flawless with LVF (1.6% errors) as well as with RVF stimuli (0% errors). Latencies were longer with LVF than with RVF stimuli [mean RT = 983 ms and 635 ms, respectively; $F(1, 126) = 7.77$, $P = 0.0061$].

In a variant of this task using the same set of stimuli, the two digits in a pair were printed in different fonts, in order to encourage the patient to process the digits beyond a purely perceptual level. The patient made 14.8% errors with LVF stimuli and 5.5% errors with RVF stimuli [$\chi^2(1) = 6.16$, $P = 0.013$]. She was also slower with LVF than with RVF stimuli [mean RT = 1399 ms and 795 ms, respectively; $F(1, 254) = 43.1$, $P < 0.001$]. These data suggested that each hemisphere could process digits up to a font-independent structural level, although the right hemisphere was somewhat less accurate than the left when the task could not be performed on the basis of a purely visual match.

Overall, the dissociation between good within-hemifield and poor between-hemifield matching of two arabic digits replicated previous findings with split-brain patients (Seymour *et al.*, 1994; Corballis, 1995). It suggested that the visual transcallosal route was disrupted in our patient, as in previous surgical cases.

Same–different judgement between a digit and a dot pattern

It remains possible that the transcallosal route for transferring quantity information was partially spared, but was simply not used in the above digit-matching task. In order to induce the patient to transfer quantitative information between hemispheres – if this was at all possible – we designed a matching task in which the LVF and RVF stimuli could not be matched at a visual level. The patient was simultaneously presented with an arabic digit in one hemifield, and with a random pattern of dots in the other hemifield. Digits as well as sets of dots were in the range 1 to 6. Half the trials were matching. On non-matching trials, the digit and set of dots to be compared differed by 2 to 5 units. All dots appeared within a square in the lower quadrant of the visual field. The patient was asked to decide if the digit and the number of dots matched and to respond by tilting a joystick.

The patient made 11/48 errors (22.9%) when the dot pattern fell in her RVF (mean RT = 4142 ms), and 9/48 errors (18.8%) when it fell in her LVF [mean RT = 2740 ms; $F(1,92) = 11.5$, $P = 0.001$]. The overall performance of 20.8% was much higher than chance [$\chi^2(1) = 32.7$, $P < 0.001$]. Most importantly, it was significantly better than the patient's performance with pairs of arabic digits [$\chi^2(1) = 18.9$, $P < 0.001$], even when the analysis was restricted to comparable pairs of digits 1–6 [$\chi^2(1) = 7.9$, $P = 0.0048$]. This indicated that substantial interhemispheric transfer of quantitative information about numbers could still take place.

The patient's 20.8% error rate could arise from several sources. It might reflect a partial impairment in callosal transfer of quantity information. Alternatively, it could indicate a less than perfect perception of the numerosity of dot patterns (Mandler and Shebo, 1982). In order to disentangle these two influences, and to measure the ability of each hemisphere to extract numerosity, we devised a variant of the matching task that did not require interhemispheric transfer. On each trial, the patient was first presented for 2 s with an arabic digit at fixation point, presumably allowing both hemispheres to identify it. Then the digit disappeared and a random dot pattern was flashed for 200 ms in one hemifield, and the patient was again asked if its numerosity matched the digit.

In this intrahemispheric task, the error rate was 1/48 when the dot pattern appeared in the RVF (mean RT = 1409), and 4/48 when it appeared in the LVF (mean RT = 1226). There was no significant accuracy [$\chi^2(1) = 0.84$, NS] nor latency [$F(1,93) = 1.17$, NS] difference between hemifields. Importantly, the overall error rate of 5.2% was significantly lower than the 20.8% figure obtained in the interhemispheric version of the task [$\chi^2(1) = 10.3$, $P = 0.0013$]. This suggests that the limiting factor was not the ability of each hemisphere to extract numerosity information (see below). Rather, there seemed to be a moderate impairment in the ability to transfer quantitative information across the corpus callosum.

Discussion

Across a series of tasks, we asked the patient to decide whether two arabic digits, or one digit and a dot pattern, were matched or not. She responded accurately when the two stimuli were presented together within the LVF or RVF, that is when no callosal transfer was required. In contrast, as soon as the task required callosal transfer, the patient's performance deteriorated significantly. Transfer was impossible when the task was performed at a visual level. Some partial interhemispheric communication was observed when quantitative processing was encouraged.

Three conclusions arise from these observations (Fig. 3). First, in keeping with the model outlined in the intro-

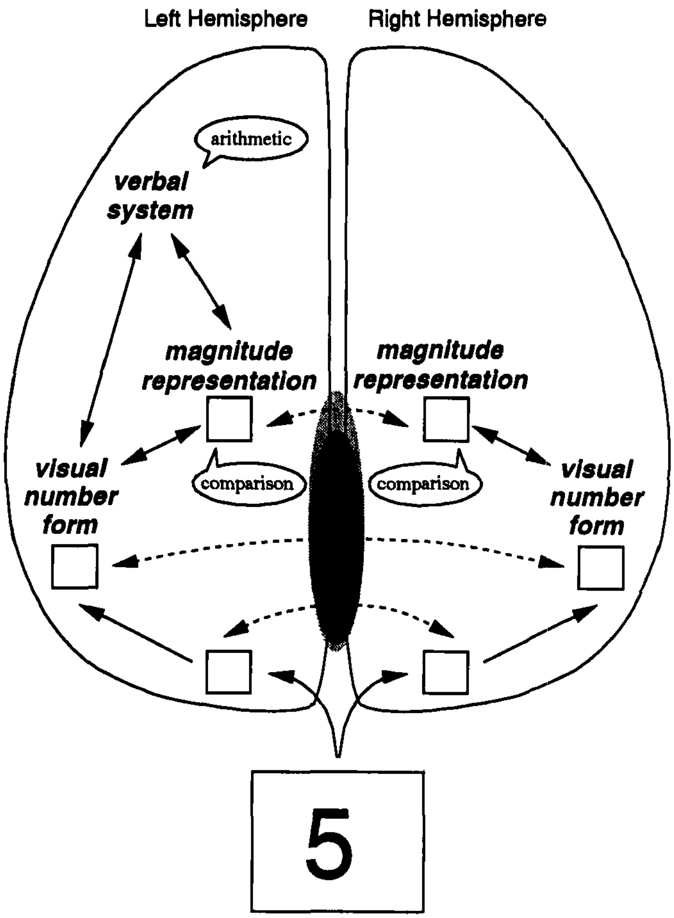

Fig. 3. Schematic representation of the patient's lesion. Only the more anterior interhemispheric pathway is relatively preserved, allowing for the transfer of magnitude information.

duction, both hemispheres were able to identify digits. Second, the disruption of the visual callosal pathway precluded any interhemispheric transfer of numerical information in the format of arabic digits. Third, the transfer of some quantitative information was still possible through a relatively preserved, presumably more anterior, segment of the corpus callosum.

Now that the functional correlate of the callosal lesion has been approximately delineated, we may derive specific predictions on the patient's performance in a variety of numerical tasks. Since the left hemisphere is thought to comprise a complete number-processing system, no callosal transfer should ever be necessary with arabic numerals presented in the RVF. Hence, with RVF stimuli, the patient's performance should be essentially normal whatever the task. In contrast, with LVF stimuli, the patient's performance should crucially depend on task demands. On the one hand, tasks that are within the reach of an isolated right hemisphere, such as magnitude comparison, should be performed satisfactorily. On the other hand, tasks that exceed the abilities of the right hemisphere, such as reading aloud or solving arithmetic problems, require callosal transfer of numerical information. The performance in such tasks should be impaired if visual transfer is required, but should benefit from the preserved transfer of magnitude information.

Number comparison

The prediction that magnitude comparison should be performed satisfactorily with digits presented in either hemifield was directly tested by asking for a larger–smaller judgement of single digits presented within one hemifield.

All digits 1 to 9, excluding digit 5, were presented in each hemifield, in random order. The patient decided whether each target was smaller or larger than 5 and responded by tilting a joystick to the right for targets larger than 5, and to the left for targets smaller than 5. As shown in Table 3, she made 5.9% errors in her LVF and 1.3% errors in her RVF. Although performance was significantly worse in the LVF [$\chi^2(1) = 10.15$, $P = 0.0014$], it was clearly excellent on both sides.

In normal subjects, a distance effect in number comparison has been repeatedly demonstrated (e.g. Moyer and Landauer, 1967): comparison times decrease monotonically with larger numerical distances. This is one of the main findings that suggest that comparison operates on the magnitudes associated with numbers, with numerically close numbers sharing partially overlapping magnitude representations (Dehaene *et al.*, 1990). The patient's reaction times for correct responses, excluding four responses slower than 10 s, were submitted to an analysis of variance with two factors: hemifield and absolute numerical distance between target and standard 5. Latencies were somewhat longer for LVF than for RVF stimuli [1166 ms versus 1014 ms, $F(1, 607) = 4.37$, $P = 0.037$]. There was a significant effect of distance [$F(3, 607) = 5.14$, $P = 0.0016$]. Latencies decreased with numerical distance [$r(613) = -0.14$, $P < 0.001$]. This distance effect held for both RVF and LVF [$r(314) = -0.14$, $P = 0.013$; $r(297) = -0.14$, $P = 0.012$ respectively], and there was no interaction of distance and hemifield in the analysis of variance [$F(3, 607) = 1.41$, $P = 0.24$]. Thus, digits in either hemifield yielded a normal and essentially identical distance effect.

Table 3. Error rates (%) in magnitude comparison tasks

Side of stimulation	Left	Right
Comparison of digits with 5	19/320 (5.9)	4/320 (1.3)
Comparison of digits with 5 and naming	8/80 (10.0)	3/80 (3.8)
Comparison of digit pairs	13/96 (13.5)	0/96 (0.0)
Comparison of two-digit numbers with 55	36/176 (20.5)	1/176 (0.6)

We similarly tested the comparison of two-digit numerals to a standard of 55. Numerals 11 to 99, excluding 55, were presented in the RVF or LVF, in random order. The patient decided whether each target was smaller or larger than 55 and responded by tilting a joystick to the right for targets larger than 55, and to the left for targets smaller than 55. As shown in Table 3, she made 20.5% errors in her LVF and 0.6% errors in her RVF [$\chi^2(1) = 37.00$, $P < 0.001$]. Thus, two-digit numerals presented in the LVF were processed less accurately than single digits, but still way above chance level [$\chi^2(1) = 61.5$, $P < 0.001$].

Reaction times for correct responses, excluding one response slower than 10 s, were submitted to an analysis of variance with two factors: hemifield, and absolute numerical distance between the tens digit of the target and 5. Latencies were longer for LVF than for RVF stimuli [1614 ms versus 1228 ms, $F(1, 305) = 13.05$, $P < 0.001$]. There was a significant effect of distance [$F(4, 305) = 8.16$, $P < 0.001$]. Error rates were higher [$r(3) = -0.98$, $P = 0.0035$] and latencies longer the smaller the numerical distance [$r(313) = -0.26$, $P < 0.001$]. This distance effect on reaction times held for both RVF and LVF [$r(173) = -0.42$, $P < 0.001$; $r(138) = -0.18$, $P = 0.031$ respectively], and there was no interaction of distance and hemifield in the analysis of variance [$F(4, 305) < 1$].

Finally, we used a third, more complex task probing the ability of each hemisphere to compare pairs of digits. Pairs of horizontally aligned digits were flashed in one hemifield, and the patient was asked to tilt a joystick in the direction of the larger digit. All digits 1 through 8 were used, and the two digits in a pair differed by 1 to 4 units. As shown in Table 3, she did not make a single error when the digit pairs appeared in her RVF, and 13.5% errors with pairs presented in her LVF [$\chi^2(1) = 13.9$, $P = 0.0002$]. RVF pairs were compared at a fairly normal speed (868 ms), and with a normal distance effect on RTs

[$r(94) = -0.24$, $P = 0.021$]. In contrast, LVF pairs were compared much more slowly [2842 ms; $F(1, 190) = 142$, $P < 0.0001$], and the distance effect did not reach significance.

In summary, all three experiments showed that the patient could compare digits, and to some extend two-digit numerals, presented in either hemifield. Given the previous evidence for total lack of visual transfer, these results imply that each hemisphere was capable of accessing a representation of the magnitude associated with an arabic digit. With LVF stimuli, comparison of two-digit numerals was not as good as comparison of single digits. However, we did not collect sufficient data to ascertain whether the right hemisphere was computing the full magnitude corresponding to the whole number, possibly less accurately than the left hemisphere, or just relied on the magnitude of the tens digit (see Dehaene *et al.*, 1990).

One minor issue remains open. Because callosal transfer of magnitude information was not completely disrupted, the present case does not allow us to establish whether number comparison was performed on two independent comparison processes located within each hemisphere, or by a single process. We note, however, that patients with complete surgical callosal sections are still able to compare pairs of digits flashed in either hemifield (Seymour *et al.*, 1994; Corballis, 1995). Such complete cases, where callosal magnitude transfer is impossible, provide better evidence for a duplication of number comparison abilities in the two hemispheres.

In the present case, the existence of two distinct comparison systems may be the cause of the differences in reaction times between the LVF and RVF. In single-digit comparison, both LVF and RVF stimuli produced short latencies and a normal distance effect. However, in comparison of digits pairs, LVF stimuli were processed much more slowly. This asymmetry might reflect a basic inability of the right hemisphere to process two numbers in parallel, a hypothesis that should receive attention in further research. It does not, however, invalidate our conclusion that both hemispheres were able to represent numbers as magnitudes.

Reading aloud arabic digits

According to our model, while number comparison can be performed by both hemispheres, reading digits aloud is critically dependent on left-hemisphere structures. The normal pathway for reading involves the encoding of a word or number stimulus as a parsed string of characters in the left visual word or number form, followed by the transmission of such information to the left-hemispheric verbal system. When the left visual form is lesioned, deprived of inputs, or disconnected from the verbal system, reading is severely impaired, as exemplified by the syndrome of pure alexia (e.g. Dejerine, 1892; Geschwind, 1965; Warrington and Shallice, 1980; Coslett *et al.*, 1993; Cohen and Dehaene, 1995). This deficit can be partially compensated, however, by entering the verbal system from an alternative semantic pathway, which in the case of numbers conveys mainly magnitude information. This semantic reading provides the theoretical basis for classical accounts of the deep dyslexia syndrome (Coltheart, 1980; Cohen *et al.*, 1994).

Table 4. Error rates (%) in naming arabic numerals and the numerosity of dot patterns

Side of stimulation	Left		Right	
Naming single digits	84/200	(42.0)	0/200	(0.0)
Comparing and naming single digits	39/80	(48.7)	0/80	(0.0)
Naming two-digit numerals	97/108	(89.8)	5/108	(4.6)
Naming the numerosity of sets of dots	45/144	(31.2)	34/138	(24.6)

In this framework, given her callosal lesion, our patient should have difficulty in reading aloud digits presented in her LVF. These digits should not be able to gain direct access to the left-hemispheric visual number form which is the gateway to the normal reading route. We expected her, however, to compensate partially for this deficit by using her partially preserved interhemispheric transfer of magnitude information from the right to the left hemisphere.

We therefore asked the patient to read aloud the same list of digits as in the above single-digit comparison task. She did not make a single error with RVF stimuli, whereas she made as many as 42.0% errors with LVF stimuli (see Table 4). This percentage cannot be directly compared with her 5.9% error rate in the number comparison task, because chance levels were different. However, in almost half of her naming errors (16.5% of trials), the incorrect response was larger than 5 whereas the target was smaller than 5, or vice versa. In this respect, performance was significantly worse in the reading task than in the comparison task [$\chi^2(1) = 15.26$, $P < 0.001$].

In an additional set of 80 trials in which naming latencies were measured, mean RTs were considerably longer in the LVF than in the RVF [2044 ms versus 598 ms; $F(1, 75) = 35.14$, $P < 0.0001$]. Relative to published data (e.g. Mandler and Shebo, 1982), naming speed appeared normal for RVF stimuli, but abnormally slow for LVF stimuli. Naming latencies were not correlated with the numerical magnitude of the stimuli, as may occur when patients resort to a counting strategy (Gazzaniga and Hillyard, 1971).

The patient only produced names of digits 1–9 as responses. Chance performance could therefore be evaluated at 11.1%, and her score of 58.0% correct with LVF stimuli was clearly well above this level. According to our model, this could only result from partial interhemispheric transfer of visual or magnitude information about the target.

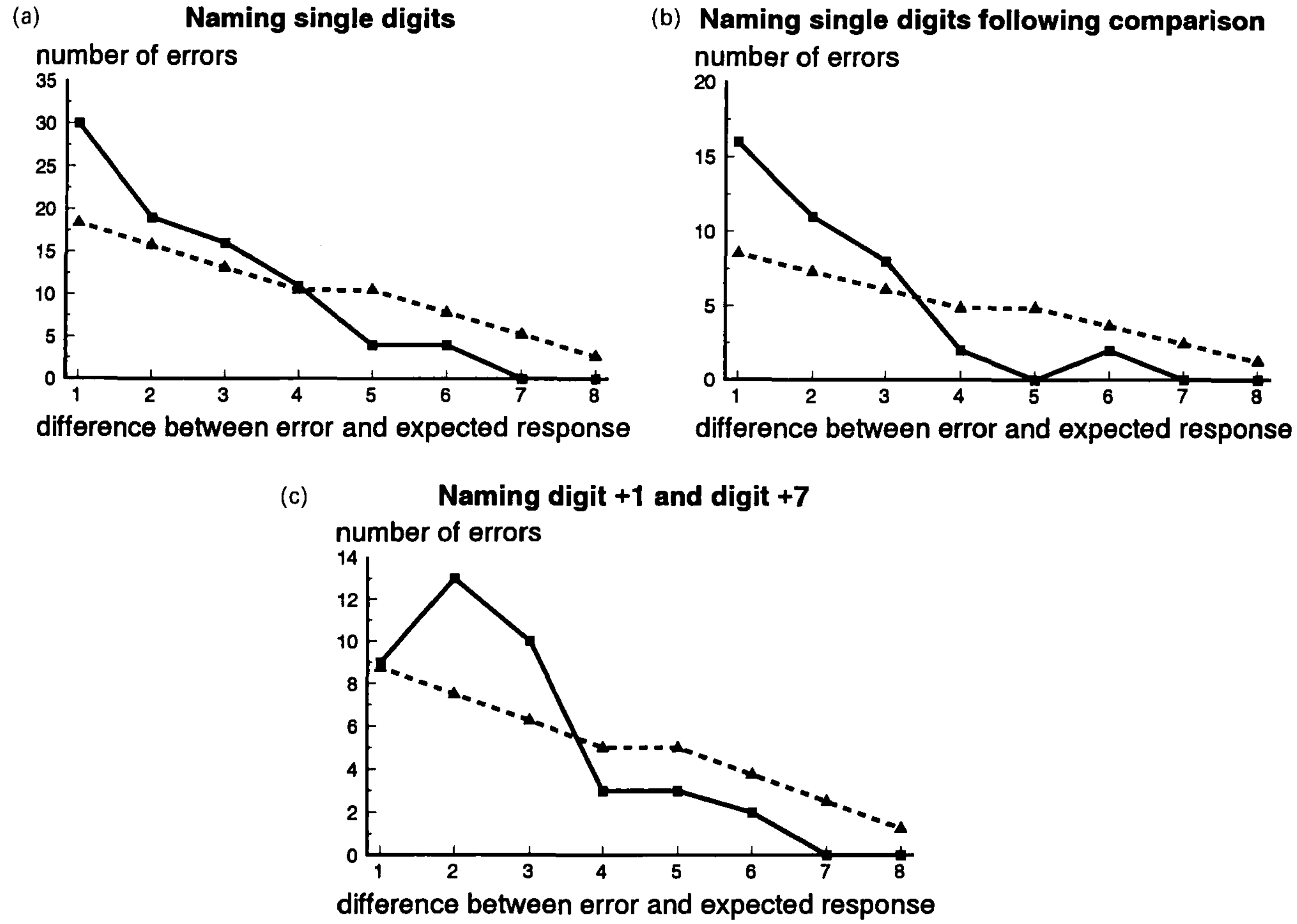

Fig. 4. Distribution of errors with LVF digits as a function of their numerical distance from the expected response. (a) Naming task; (b) naming following comparison; (c) naming the digit plus 1 or plus 7. The observed distributions (solid lines) are compared with the distributions expected if responses were selected randomly (broken lines). The patient produced errors numerically close to the expected response more often than chance, reflecting the transfer of magnitude information from the right to the left hemisphere.

Visual transfer was assessed by counting the number of errors for each possible stimulus–response pair, and by submitting these data to a regression analysis with a published measure of visual similarity between arabic digits (Campbell and Clark, 1988). There was no significant influence of visual similarity on the frequency of errors [$r(62) = 0.15$, $P = 0.25$].

Transfer of magnitude information was assessed by counting the number of errors for each value of the absolute difference between error and expected response. Many erroneous responses were numerically quite close to the target (e.g. stimulus 2, response 3). This effect was tested by comparing the observed distribution of differences between errors and expected responses with the distribution that would be expected under the null hypothesis that responses were selected at random (Fig. 4a). The difference was significant [$\chi^2(5) = 21.4$, $P < 0.001$], reflecting the clustering of errors at small distances from the target.

In summary, these results conformed exactly to the expectations based on our model. First, naming of RVF stimuli was fast and accurate. Second, naming of LVF stimuli was slow and error-prone. Third, there was no evidence for visual transfer, but the responses were influenced by the magnitude of the target digit. This accords with our previous conclusion that digits flashed in the LVF are processed up to the level of a magnitude representation which may, in the case of a partial posterior callosal lesion, still be transferred in part to the left hemisphere.

How did the patient eventually select a response, given that magnitude transfer obviously did not suffice to select a unique number word for response? We found that the patient's responses were affected by consistent biases and perseverations. As shown in Fig. 5, she did not select all possible answers with equal frequency. For instance, she responded 'seven' 44 times, and 'two' only eight times, although digits 7 and 2 were both presented 25 times. She also sometimes produced the same response repeatedly within a short time interval. Such behaviour, which was also seen when the patient attempted to read words and multidigit numerals in her LVF, has been interpreted as reflecting confabulation by the verbal system when it is partially deprived in inputs (Geschwind, 1965).

In a final test with the same stimuli, the contrast between good extraction of magnitude and poor naming was

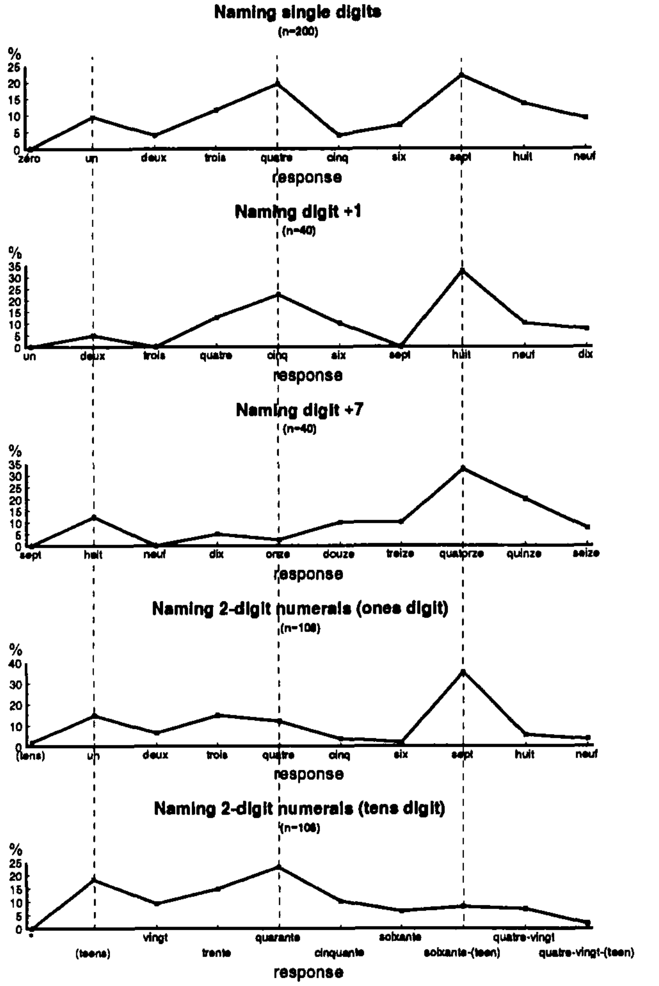

Fig. 5. Biases affecting response selection in naming and arithmetic tasks with LVF arabic numerals. A similar pattern of preferences prevailed across a variety of tasks implying a verbal encoding of stimuli. Note for instance a recurrent preference for 'seven'.

demonstrated within each trial. The patient was asked, on each trial, first to decide whether the target was larger or smaller than 5, and then to read it aloud. As shown in Tables 3 and 4, number comparison was good in both hemifields (RVF: 3.8% errors; LVF; 10.0% errors), whereas reading was selectively impaired for LVF stimuli [RVF: 0% errors; LVF: 48.7% errors; $\chi^2(1) = 51.57$, $P < 0.001$]. Analysis of the distribution of differences between errors and expected responses showed that the patient tended to produce errors at small distances from the expected response [$\chi^2(4) = 19.21$, $P < 0.001$; Fig. 4b], again suggesting partial interhemispheric transfer of magnitude information. Interestingly, the patient tended to use her larger–smaller responses to select her verbal responses. In 27/39 (69.2%) errors, the patient's response was on the same side of number 5 as the target digit (e.g. 7→/larger/ 'eight'). The 8/39 (20.5%) trials where the response was on the opposite side of number 5 corresponded exactly to those trials where the patient made a comparison error. Hence, magnitude information was used to constrain naming.

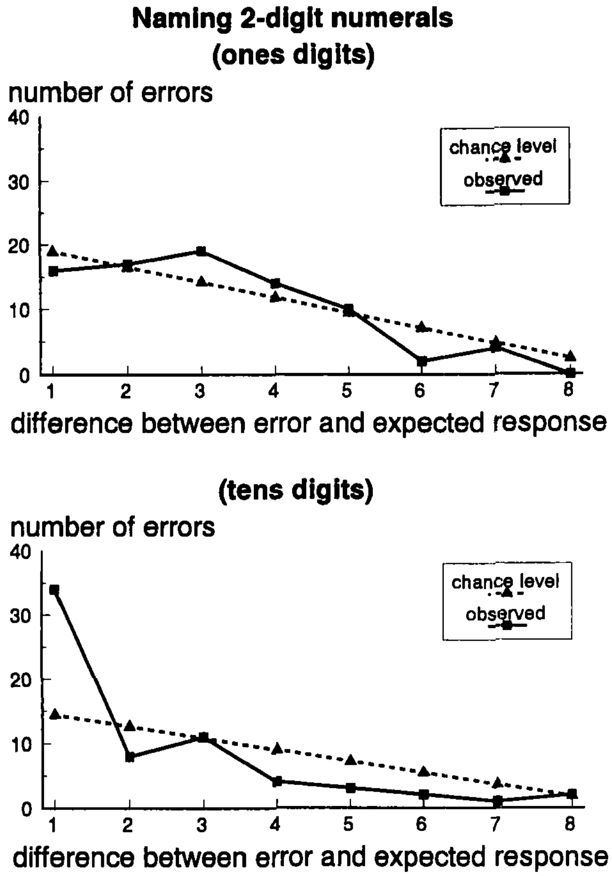

Fig. 6. When naming two-digit numerals flashed in her LVF, the patient produced tens digits, but not ones digits, numerically close to the expected response.

Reading aloud two-digit numerals

We similarly tested reading aloud of two-digit arabic numerals that were flashed in the patient's LVF or RVF. All numerals 11 through 99 (except 55) were presented at least once. She made only 4.6% errors with RVF stimuli, whereas she made 89.8% errors with LVF stimuli (see Table 4). The following analyses concentrated only on LVF trials.

All errors consisted of legal two-digit numbers. The patient misread the tens digit in 65/108 trials (60.2%), and the ones digit in 85/108 trials (78.7%). Note that both of these error rates were higher than the 42.0% error rate in reading aloud single digits [$\chi^2(1) = 9.3$, $P = 0.0023$ and $\chi^2(1) = 38.1$, $P < 0.001$ respectively]. Such a disproportionate difficulty in reading multidigit numerals relative to single digits is a frequent finding in patients with pure alexia (for discussion of possible mechanisms, see Cohen and Dehaene, 1995).

Since reading of both the tens and the ones digits was above chance [$\chi^2(1) = 103.6$, $P < 0.001$ and $\chi^2(1) = 14.6$, $P < 0.001$ respectively], we looked for indications of visual or magnitude transfer. Visual transfer was assessed by counting the number of errors for each possible stimulus–response pair, and by submitting these data to a regression analysis with a measure of visual similarity (no values available for digit 0; Campbell and Clark, 1988). This was done separately for the tens and for the ones digits. No significant influence of visual similarity was found [$r(70) = -0.16$, $P = 0.19$; $r(70) = -0.10$, $P = 0.41$, respectively].

In order to assess transfer of magnitude information, an analysis of the distribution of differences between errors and expected responses was done separately for the tens and for the ones digits (Fig. 6). With tens digits, there was a significant clustering of errors at a distance of 1 from the target [$\chi^2(4) = 36.7$, $P < 0.001$]. In contrast, with ones digits, no significant distance effect was observed [$\chi^2(4) = 4.9$, $P = 0.30$].

We examined whether, as in naming single digits, the patient's responses were influenced by biases and perseverations. As shown in Fig. 5, the choice of the ones digit in the patient's response followed a preference pattern highly similar to the one observed in single-digit naming [$r(8) = 0.76$, $P = 0.011$]. For instance, the patient's favourite ones digit was again 'seven'. The pattern for the tens digit was less clear. The correlation of the preference profiles for tens and for single digits was not significant ($r(8) = 0.50$, $P = 0.15$], mostly due to the absence of a peak for 'seventy'. This is perhaps related to the absence of an equivalent for the word 'seventy' in French, where seventies are expressed by combining the word 'soixante' (sixty) and a teen word [e.g. 73 = 'soixante-treize' (sixty thirteen)]. When the special French tens 70, 80 and 90 were excluded, the preference profile for tens digits was now correlated with that observed for single digits [$r(5) = 0.90$, $P = 0.0053$].

In summary, the naming of two-digit numerals obeyed the same principles as the reading of single digits. Reading was accurate with RVF stimuli, but severely impaired with LVF stimuli. The latter impairment appeared to be due to an inability to transfer visual information about the target. However, there was some transfer of global magnitude information, which was conveyed by the tens digit. The ones digit of the patient's erroneous responses was totally uncorrelated with the ones digit of the target, and was affected by the same verbal biases as in single-digit reading.

Naming the numerosity of sets of dots

We further pursued the dissociation between visual and magnitude interhemispheric transfer by contrasting digit reading with naming the numerosity of random sets of dots. Both tasks share the same left-hemispheric verbal output, and both therefore require callosal transfer when the stimulus appears in the LVF. However, according to our model, the two tasks normally involve different transcallosal routes (Fig. 7). The normal pathway for reading aloud digits, on the one hand, involves a visual-to-verbal route which, for LVF stimuli, was interrupted by the callosal lesion in our patient. The normal pathway for numerosity naming, on the other hand, involves the representation of the stimulus in a magnitude format and the transmission of this information to the verbal system. Given the above evidence that the interhemispheric transfer of magnitude information was partially preserved, one may expect a relatively better performance in numerosity naming than in digit reading.

Random patterns of 1–6 dots were flashed in the patient's LVF or RVF. She was simply asked to say how many dots she had perceived. Vocal reaction times were measured in a subset of 192 out of 299 trials.

As shown in Table 4, the patient made 24.6% errors with RVF stimuli (mean RT = 1270 ms), and 31.2% errors with LVF stimuli (mean RT = 1318 ms). There was thus no difference in accuracy [$\chi^2(1) = 1.53$, $P = 0.22$] nor in naming latency [$F(1, 173) < 1$] between the two hemifields. This was quite different from digit reading and suggested that, in the case of dots, there was little cost for callosal transfer. Indeed, as in normals, errors in both hemifields appeared mostly due to the difficulty of discriminating large numerosities. Error rate increased with the number of dots [$r(10) = 0.80$, $P = 0.0018$]. The patient made 2.1% errors with sets of 1–2 dots, 24.2% errors with sets of 3–4

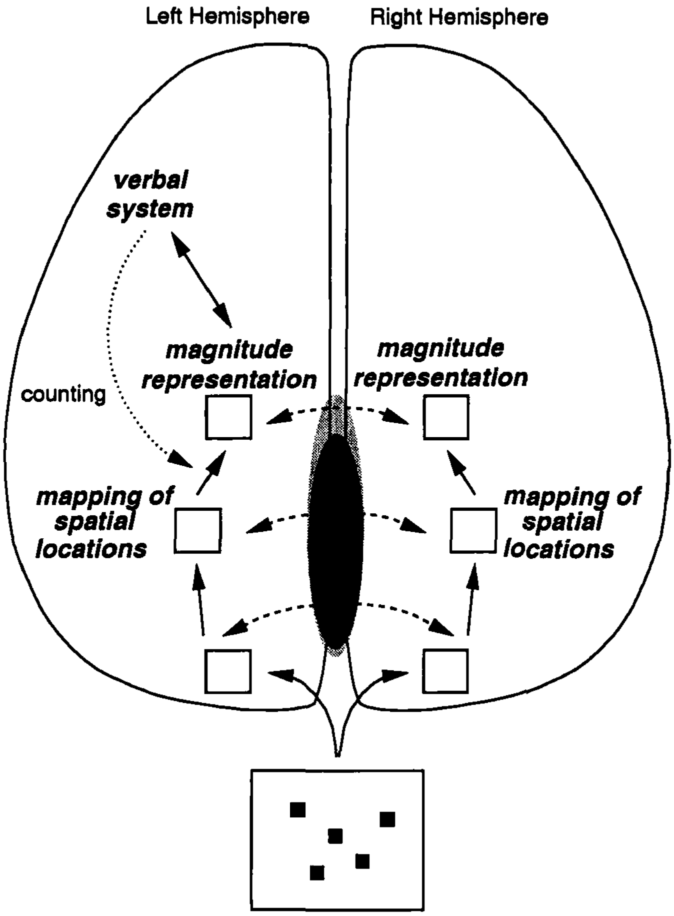

Fig. 7. Model of the numerical processing of sets of dots. Interhemispheric transfer of magnitude information, which was spared in the present case, is presumably the default pathway for naming the numerosity of LVF sets.

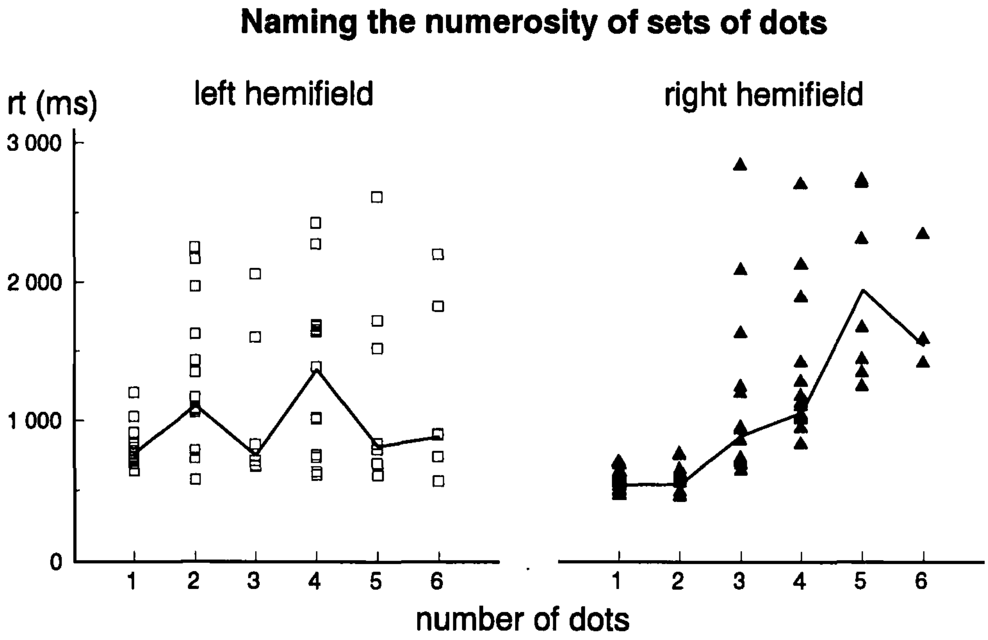

Fig. 8. Vocal reaction times in naming the numerosity of sets of dots. Solid lines represent the median values. With RVF stimuli, but not with LVF stimuli, latencies increased with numerosity, suggesting that counting may be available to the left hemisphere only.

dots, and as many as 60.0% errors with sets of 5–6 dots. As in normal subjects, most erroneous responses differed from the target by only one unit (94.1% of RVF and 86.7% of LVF errors).

We predicted that with LVF stimuli, the patient should make fewer errors in numerosity naming than in digit naming. A global analysis verified this prediction [45/144 versus 84/200 errors, $\chi^2(1) = 4.13$, $P = 0.042$]. However, this analysis could be criticized on the ground that stimuli ranged from 1 to 9 (excluding 5) in the digit-reading task, and from 1 to 6 in the present numerosity naming task. In an effort to circumvent this shortcoming, we restricted the analysis to matched sets of stimuli (1, 2, 3, 4 and 6) (note, however, that the range of possible responses was still 1–9 for digits and 1–6 for dots). In fact, the advantage of numerosity naming over digit reading was even more striking [45/144 versus 61/125 errors, $\chi^2(1) = 8.6$, $P = 0.0033$]. The contrast between the two tasks was clearest for numbers 1 and 2, where the patient was perfect with dot patterns (0/48 errors), while still severely impaired with arabic digits [25/50 errors, $\chi^2(1) = 32.2$].

In summary, numerosity naming differed from digit naming in two respects. First, numerosity-naming performance did not differ between the two hemifields, whereas digit naming showed a very significant LVF impairment. Second, for targets in the LVF, numerosity naming was significantly better than digit naming. Both results indicate that the two tasks rest on different routes for callosal transfer, a posterior visual route for digit naming and a more anterior magnitude route for numerosity naming.

As an aside, we note that the present data are relevant to the issue of the cerebral mechanisms for enumerating sets of visual objects. Research with normal subjects (e.g. Mandler and Shebo, 1982) and with brain-lesioned patients (Dehaene and Cohen, 1994) has documented several enumeration strategies. From one to three items, the so-called 'subitizing range', normal numerosity naming times are fast and increase very moderately with numerosity. Above that limit, RTs increase linearly with numerosity, reflecting serial counting. Finally, when large sets are briefly presented, subjects can estimate numerosity, as evidenced by an asymptote in RTs and a sharp increase in errors. The present case of visual disconnection provided some indications as to which of these processes are available to each hemisphere. An analysis of variance was performed on the patient's correct RTs, with numerosity and hemifield as factors. There was no main effect of hemifield ($F < 1$), but there was a significant interaction of hemifield with numerosity [$F(5, 123) = 6.04$, $P < 0.0001$]. Post hoc analyses indicated a significant effect of numerosity with RVF [$F(5,65) = 14.4$, $P < 0.0001$], but not with LVF stimuli [$F(5,58) = 1.9$, $P = 0.10$]. As shown in Fig. 8, RTs increased linearly with numerosity in the RVF [$r(69) = 0.66$, $P < 0.0001$; slope 344 ms], but not in the LVF.

Thus, although their overall performance was comparable, the two hemispheres probably resorted to different procedures. Serial counting, as evidenced by linearly increasing RTs, seemed to be used only by the left hemisphere. Indeed, counting probably requires the use of verbal labels that, according our model, are not available to the right hemisphere (Fig. 7). The latter probably used some kind of estimation strategy, as attested by constant RTs over 1 s and slightly elevated error rates. Unfortunately, our data were too scarce to assess the presence of a 'subitizing range' in either hemifield. Further research is

Table 5. Error rates (%) in calculation tasks

Side of stimulation	Left	Right
Mental addition (plus 1)	20/40 (50.0)	0/40 (0.0)
Mental addition (plus 7)	20/40 (50.0)	0/40 (0.0)
Addition verification	45/80 (56.2)	4/80 (5.0)
Pointing to an addition result	23/48 (47.9)	0/48 (0.0)

needed to clarify the contribution of the two hemispheres to object enumeration.

Calculation

A prediction of our model is that mental arithmetic is dependent on the left-hemispheric verbal system. Hence, calculation tasks should yield results very similar to the above naming tasks. The patient should not be impaired in calculation with operands presented in her RVF. In contrast, calculation with LVF stimuli should be severely impaired. This deficit should be entirely traceable to the difficulty in transferring digit identities from the right hemisphere to the left verbal system. The results of the following series of calculation tasks are summarized in Table 5.

Mental addition

In order to depart minimally from the digit-naming task, we presented the patient with the same digit stimuli and asked her mentally to add 1 to the target digit and to name the result of this operation. In another session, we asked her to name the target plus 7.

The patient did not make a single error out of 80 trials when digits were presented in her RVF. When digits were flashed in her LVF, she made 50.0% errors (20/40 when adding 1, and 20/40 when adding 7). This error rate was not different from the error rate observed in digit naming [$\chi^2(1) = 1.48$, $P = 0.22$].

Our model also predicts that the *nature* of errors should be similar for naming and for calculation. In both cases, upon seeing a digit such as '6', right-hemisphere processes would correctly extract digit identity and magnitude information, but fail to transfer this identity to the left verbal system, resulting in an erroneous verbal representation of the stimulus (e.g. 'seven'). This representation would then be processed normally, either for direct production (naming) or for arithmetic calculation. We therefore predicted that the patient's responses in the addition task, once reduced by 1 or 7, should be similar to her responses in the simple naming task.

Several observations suggest that this was the case. First, once reduced by 1 or 7, the patient's responses all fell within the 1–9 range of the stimuli. Second, a distance effect emerged, just as in the naming task. Analysis of the distribution of differences between errors and expected responses showed that erroneous responses (reduced by 1 or 7) clustered at small numerical distances from the stimulus more often than would be expected by chance ($\chi^2(5) = 11.98$, $P = 0.035$; Figure 4c). Thus, there was again a partial transfer of magnitude information. Third, the profile of verbal preferences was strikingly similar across the simple naming, the 'plus 1', and the 'plus 7' tasks [reading and 'plus 1': $r(8) = 0.895$, $P = 0.0005$; reading and 'plus 7': $r(8) = 0.62$, $P = 0.055$; 'plus 1' and 'plus 7': $r(8) = 0.63$, $P = 0.053$]. For instance, as shown in Fig. 5, the patient's favourite response was 'seven' in the simple naming task, 'eight' (i.e. $7 + 1$) in the 'plus 1' task, and 'fourteen' (i.e. $7 + 7$) in the 'plus 7' task. This observation implies that verbal biases affected a stage of processing earlier than the computation of the addition result. It provides a strong confirmation of the processing sequence proposed in our model, by showing that simple calculation involves a preliminary encoding of the operands into a verbal format. Such verbal encoding, which is common to calculation and naming tasks, was affected by identical biases and distance effects.

Addition verification

It could be argued that the poor performance in calculation with LVF stimuli was related to the requirement of responding verbally. We also used an addition verification task which does not require producing an addition result aloud, and may therefore reveal putative calculation abilities of the right hemisphere. The model predicts that the verification of additions presented in the RVF should be performed as in a normal subject. However, the verification of additions presented in the LVF should still be severely impaired.

Simple addition problems were flashed randomly in the patient's RVF or LVF. The operands were horizontally aligned and the proposed sum was displayed below. The operands were single digits whose sum was also a single digit. On half of the trials, the proposed sum was the true result of the addition, while on the other half the proposed sum was false.

We first report the results for stimuli presented in the RVF. The error rate was 5.0%, and the mean reaction time was 1616 ms. A close analysis showed that calculation in the left hemisphere obeyed exactly the same principles as found in normal subjects (Ashcraft, 1992). Normal subjects are faster and more accurate when the operands are small than when they are large. Beyond this so-called problem size effect, tie problems – problems with two identical operands – are also especially easy. Both of these effects were found for stimuli presented in the patient's RVF. Mean correct latencies were significantly slower for larger problems, whether problem size was measured by the product of the operands [$r(74) = 0.371$, $P = 0.0010$] or by their sum [$r(74) = 0.355$, $P = 0.0017$]. Mean correct latencies were also significantly faster for tie than for non-tie problems [$F(1, 74) = 7.65$, $P = 0.0071$]. The very small number of errors prevented such an analysis to be performed on error rates.

The same analyses were performed for trials with stimuli presented in the LVF. The error rate was 56.2%, which is at chance level, and the mean reaction time was 4530 ms. This performance was significantly poorer than in the RVF [RTs: $F(1, 158) = 149$, $P < 0.0001$; error rates: $\chi^2(1) = 49.5$, $P < 0.0001$]. The exceedingly long RTs suggested that problems were processed differently in the two hemifields. Indeed, contrary to what prevailed with stimuli presented in the RVF, there was no influence of problem size or tie versus non-tie status, neither on accuracy nor on response latencies. Hence, there was no evidence for any addition verification abilities in the right hemisphere.

Pointing to an addition result

As a final non-verbal test of arithmetical abilities, the patient was presented in her RVF or LVF with a pair of digits whose sum was also a single digit. She was asked to point towards the sum of the two digits among a random array of digits 1–9 in free-field vision. She made no errors with RVF stimuli, but 47.9% errors with LVF stimuli [$\chi^2(1) = 30.2$, $P < 0.0001$]. The latter performance was severely defective. It was still above chance, however, which may appear surprising in view of the patient's random performance in addition verification. We believe, however, that the pointing task left considerable time for various strategies, including partial interhemispheric transfer and cross-cueing. For instance, the right hemisphere could direct eye or finger movements towards the operand digits on the response array, thus informing the left hemisphere of their identity. Various analyses unveiled no systematic relation between the erroneous and expected responses, except that the patient performed significantly better with ties (77.8% correct) than with non-ties [36.7% correct: $\chi^2(1) = 7.62$, $P = 0.0058$]. This might perhaps reflect the greater facility of transferring just one, rather than two, digit identities to the left hemisphere.

Summary of addition performance

In summary, addition problems presented in the RVF were solved as in normal subjects, in keeping with the hypothesis that the left hemisphere possesses a complete calculation system. In contrast, addition problems presented in the LVF were solved very slowly, with frequent errors, and without the qualitative features of normal calculation such as the problem size effect. Such evidence is consistent with the hypothesis that by and large the right hemisphere lacks effective calculation routines.

Processing of spelled-out numerals

As a final point, we now turn to the processing of spelled-out number words. While arabic digits can clearly be

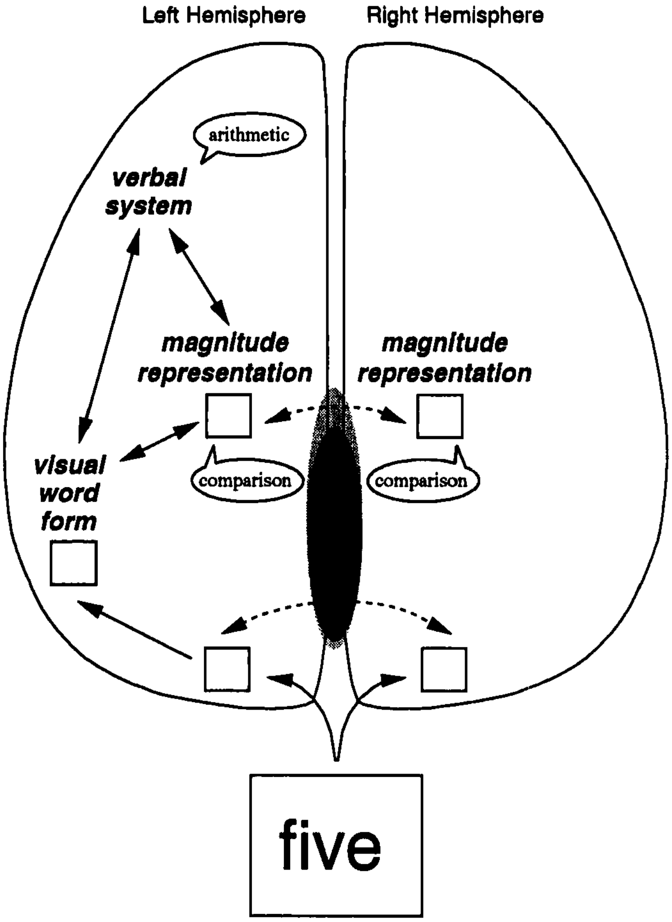

Fig. 9. Model of processing of spelled-out numerals. The right hemisphere is unable to recognize numbers expressed in this notation.

identified by both hemispheres, the situation is less clear-cut for number words. The right hemisphere does not seem totally devoid of word identification abilities, and may possess a small visual lexicon dealing mostly with frequent and concrete words (Gazzaniga, 1995). However, it is unclear whether number words figure in this right-hemispheric lexicon. In the only study to have addressed this issue, Cohen and Dehaene (1995) found that two patients with pure alexia resulting from left occipito-temporal infarcts could still recognize arabic digits, but not spelled-out number words unless they resorted to letter-by-letter reading. This suggested that their right hemisphere was unable to recognize number words (Fig. 9). We re-examined this hypothesis with the present patient using number matching, comparison, and naming tasks (see Table 6).

Same–different judgement within hemifield

The patient was asked to perform a same–different judgement on pairs of vertically aligned numerals, flashed in her RVF or LVF. All numerals 1 – 'un' through 8 – 'huit' were used. Half the trials were matching. On non-matching trials, the two numerals differed by 1 to 4 units.

Table 6. Error rates (%) in tasks using spelled-out numerals

Side of stimulation	Left		Right	
Same–different judgement with a digit	51/128	(39.4)	10/128	(7.8)
Comparison with 5	29/96	(30.2)	1/96	(1.0)
Naming	33/48	(68.7)	0/48	(0.0)

On half the trials the upper numeral was spelled-out and the lower one arabic, and conversely on the other half of the trials.

The patient made 7.8% errors with RVF stimuli, and as many as 39.4% errors with LVF stimuli. LVF performance was better than chance [$\chi^2(1) = 5.28$, $P = 0.022$]. The patient was also much slower with LVF than with RVF stimuli [4006 ms and 1355 ms respectively; $F(1, 249) = 143.8$, $P < 0.0001$]. With RVF stimuli, the patient was as accurate as when performing a same–different judgement with two arabic digits printed in different fonts [$\chi^2(1) = 0.57$, NS]. In contrast, with LVF stimuli, performance was much worse in the present task [$\chi^2(1) = 20.1$, $P < 0.0001$].

These results are compatible with the hypothesis that the right hemisphere is much poorer at identifying spelled-out than arabic numerals. However, it is difficult at this point to determine precisely why the patient performed somewhat better than chance with LVF stimuli.

Comparison of spelled-out numerals to a standard

All numerals 'un' (1) through 'neuf' (9), excluding 'cinq' (5), were flashed 12 times in the patient's LVF and RVF. She was simply asked to decide whether each target was larger or smaller than 5, and to respond using a joystick.

The patient made 1.0% errors with RVF stimuli, and 30.2% errors with LVF stimuli. Performance in the LVF was above chance level [$\chi^2(1) = 15.04$, $P < 0.001$]. Latencies were significantly longer with LVF than with RVF stimuli [1710 ms versus 915 ms, $F(1, 154) = 51.23$, $P < 0.001$]. There was a significant effect of distance on reaction times [$F(3, 154) = 3.90$, $P = 0.010$], and no interaction of distance and hemifield [$F(3, 154) = 1.20$, $P = 0.31$]. Latencies were longer the smaller the numerical distance, globally [$r(160) = -0.22$, $P = 0.0046$], and both in the RVF [$r(93) = -0.29$, $P = 0.0042$] and in the LVF [$r(65) = -0.29$, $P = 0.016$].

With RVF stimuli, the patient was as accurate as when performing the same task with arabic digits [$\chi^2(1) = 0.03$, NS]. With LVF stimuli, however, performance was much worse with spelled-out numerals [$\chi^2(1) = 42.6$, $P < 0.0001$].

Thus, the patient's right hemisphere seemed unable to access satisfactorily the magnitudes associated with spelled-out numerals. As in the same–different matching task described above, it is again difficult to determine whether the patient's better than chance performance with LVF stimuli reflected right hemisphere processing or interhemispheric transfer.

Naming spelled-out numerals

All numerals 'un' (1) through 'neuf' (9), excluding 'cinq' (5), were flashed six times in each of the patient's hemifields, in random order. Her naming performance was flawless with RVF stimuli, while she made 68.7% errors with LVF stimuli. The latter errors all fell in the range 'un' (1) to 'neuf' (9), except for seven occurrences of the word 'dix' (10). Although severely defective, performance with LVF stimuli was significantly better than chance [$\chi^2(1) = 24.1$, $P < 0.001$].

As in the two previous tasks, performance was as good as with arabic digits in the RVF (0% errors in both cases), while in the LVF it was significantly worse than with arabic digits [$\chi^2(1) = 11.1$, $P < 0.0001$].

Response choice was not influenced by the same factors as in the arabic digit-naming task. Errors did not tend to be numerically close to the target [$\chi^2(4) = 3.92$, $P = 0.42$]. Moreover, the profile of response preferences was not correlated with that observed with arabic digits ($r(8) = 0.003$, NS). Rather, just as when reading ordinary words, the patient tended to produce erroneous responses with a number of letters correlated with that of the target [$r(31) = 0.58$, $P = 0.0005$]. Furthermore, we noticed that the patient produced a response containing the letter 'x' ['deux' (2), 'six' (6), and 'dix' (10)] more often when the target itself contained the letter 'x' than when it did not [$\chi^2(1) = 11.43$, $P < 0.001$].

Discussion

In summary, a similar pattern of results emerged from the three tasks that we used to explore the processing of spelled-out numerals. In all three tasks, responses to RVF stimuli were as accurate with spelled-out number words as with arabic digits. In contrast, with LVF stimuli, the patient's performance was significantly worse with spelled-out than with arabic numerals. This indicates that identification of spelled-out numerals by the right hemisphere was, at best, very limited.

If the right hemisphere had accessed the magnitudes corresponding to spelled-out numerals, a numerical distance effect should have obtained in the reading task, just as with arabic numerals. The fact that this was not the case suggests that identification of spelled-out numerals by the right hemisphere was actually negligible. The patient's better than chance reading performance apparently resulted from a strategy based on the transfer of some crude information to the left hemisphere, where a tentative and generally faulty identification of the stimulus took place. Given previous tests, it seems unlikely that the information transferred was visual in nature. Rather, information about the number of letters could have been transferred as an abstract magnitude, like the numerosity of a set of dots. The fact that the patient also took into account the presence or absence of a final 'x' can be related to the patient's above-chance performance in LVF letter reading. Although we cannot strictly exclude the possibility of visual transfer, we consider it more likely that more abstract information such as position in the alphabet was used.

Such limited interhemispheric transfer, operative in the reading task, is sufficient to account for the better than chance performance in the comparison to standard 5. In 35.4% of reading trials, the response fell on the wrong side of number 5, a percentage not different from the 30.2% errors in the comparison task [$\chi^2(1) = 0.40$, NS]. Thus, we obtained no evidence for any identification of spelled-out numerals in the patient's right hemisphere.

General discussion

Summary and general interpretation

In view of the patient's multimodal disconnection syndrome, we first tried to determine which kind of numerical information, if any, could be transferred across hemispheres despite the posterior callosal lesion. The patient did not perform better than chance when trying to decide whether two digits, presented one in each hemifield, were identical. This indicated that the exact identity of digits could not be communicated from one hemisphere to the other. However, when the patient was asked to compare a digit and the numerosity of a set of dots displayed in opposite hemifields, and was thus forced to process stimuli up to a magnitude representation, her performance improved significantly. This was taken as evidence that some magnitude information could still be transferred across hemispheres.

The patient was then submitted to various numerical tasks with stimuli flashed in one hemifield only. With digits presented in her RVF, the patient was flawless in magnitude comparison, reading aloud, and arithmetic tasks. This fits with our hypothesis that the left hemisphere contains a complete, self-sufficient, number-processing system. With LVF digits, however, the patient's performance was excellent in magnitude comparison, but impaired in reading aloud and arithmetic tasks. According to our model, comparison can be performed by an isolated right hemisphere without requiring callosal transfer, while reading aloud and exact arithmetic demand a participation of the left-hemispheric verbal system and hence require a right-to-left interhemispheric transfer. Such transfer was largely defective in our patient. Only some magnitude knowledge was transferred, as manifested by the patient's production of naming errors numerically, but not visually, close to the target digits.

Although this study was chiefly devoted to the processing of single digits, we extended our investigations to other representations of number.

With *two-digit numerals* flashed in the LVF, magnitude comparison with 55 was relatively preserved. Reading aloud, while severely impaired, again showed a marked effect of numerical proximity. These findings suggest that the right hemisphere was able to extract some magnitude information about two-digit numerals and to transfer it to the left hemisphere. However, in view of the less than perfect performance with two-digit numerals, it seems possible that only the leftmost digit of the stimulus was actually processed.

With *spelled-out numerals* flashed in the LVF, the patient's performance was uniformly low across all tasks. This suggests that numbers in such notation could simply not be understood by the right hemisphere.

When presented with a *set of dots*, the patient could name its numerosity and match it to an arabic digit displayed in the same or in the opposite hemifield with reasonable proficiency, whatever the side of presentation. Hence, both hemispheres appeared able to quantify sets of up to 6 dots, and the resulting quantity could be transferred across hemispheres. Finally, analysis of naming times suggested that when enumerating sets of dots, the left hemisphere relied on serial counting while the right hemisphere was using some parallel estimation strategy.

Anterior callosal transfer of semantic information

Despite our patient's lesion, quantity information could still be transferred across hemispheres, presumably through the anterior segment of the corpus callosum. Such transfer was evidenced in naming one- or two-digit numerals, in the plus-1 and plus-7 addition task, and in the same–different judgement between a digit and a set of dots displayed in opposite hemifields. We suggest that quantity transfer is but a particular case of the general ability of the anterior callosum to transfer abstract knowledge across hemispheres (Sidtis *et al.*, 1981). Indeed, apart from the specific meaning of familiar numbers such as famous dates or brands of cars, the essential semantic value of numbers is the quantity that they represent. This semantic transfer allows patients with selective posterior callosal lesions to express verbally some semantic knowledge of stimuli presented to their right hemisphere, provided that the right hemisphere is able to identify those stimuli and access their meaning.

For instance, patients with posterior callosal lesions name LVF digits more accurately than letters (Damasio *et al.*, 1980; Levine and Calvanio, 1980). This observation was confirmed in the present case. The advantage of digits over letters may be due to the fact that, contrary to digits, letters have little semantic content to be transferred across hemispheres (for a discussion of other possible explanations, see Cohen and Dehaene, 1995). Similarly, Japanese patients with posterior callosal lesions are significantly better at naming LVF words written in kanji ideograms than in kana phonograms (Sugishita *et al.*, 1978; Abe *et al.*, 1986). Presumably, the right hemisphere can access and transfer the meaning of kanji words, but cannot decode a phonological script such as kana. It may be noted that arabic numerals are akin to an ideographic writing system, since each digit corresponds to an entire word rather than to a phonological segment. It is therefore not surprising that the relative preservation of digit naming is paralleled by a relative preservation of kanji naming (Cohen *et al.*, 1994).

Perhaps the most dramatic evidence for the involvement of the anterior corpus callosum in semantic transfer comes from a study by Sidtis (1981) of a patient (JW) who underwent a two-stage callosotomy. Preoperatively, JW could read aloud words displayed in his LVF normally. After complete callosotomy, he denied perceiving such stimuli. Of interest was his behaviour at an intermediate stage when only the posterior half of his corpus callosum had been sectioned. At this point, he was anatomically and functionally similar to the patient we have described in the present study. When the word 'knight' was flashed to his right hemisphere, JW responded 'I have a picture in mind, but can't say it ... Two fighters in a ring ... Ancient ... Wearing uniforms and helmets ... on horses ... trying to knock each other off ... Knights?'. These words were a verbal formulation of semantic data communicated from the right to the left hemisphere through the anterior callosum. We propose that our patient's tendency to produce errors numerically close to the target when attempting to name LVF digits is an equivalent, in the numerical domain, of JW's elaborate and semantically guided verbal behaviour.

Given the evidence for semantic transfer of number information, we may ask why our patient responded at chance level when judging whether two digits presented in opposite hemifields were identical or different. Corballis (1995) described a patient (DK) with a posterior callosal lesion who, contrary to the present case, performed well above chance in a comparable task. Evidently, DK resorted to more effective cognitive strategies than our patient. As Corballis (1995) reports, 'he appeared to be having difficulty early in the first block until he suddenly remarked that he could perform the task by naming the digits' (p. 1478). Our patient failed in interhemispheric digit comparison because she tried to compare the visual identities of the RVF and LVF digits, notwithstanding the fact that visual transfer was impossible for her. Unlike DK, she never had the insight of abandoning her default visual strategy. DK's greater cognitive flexibility may be related to his being tested 9 years after surgery, while our patient was tested within 2 years of her stroke.

A similar explanation may account for the contrast between our patient's poor naming of arabic digits in the LVF and her much better naming of the numerosity of sets of dots in the LVF. We speculate that each cognitive task relies on a preferred set of brain areas and connections and that the patient continued to use the same task sets as before her stroke. Whenever the task relied on an impaired processing component such as visual transfer, performance was therefore disrupted, even if resorting to other available routes might have resulted in fewer errors. For instance, in spite of her visual transfer impairment, the patient still named LVF digits by relying mostly on the normal direct visual-to-verbal transcoding route, although relying more heavily on the indirect semantic route through the quantity representation might have led to a better performance. Other examples of task-dependent selection of number-processing routes have been presented in the context of pure alexia (Cohen and Dehaene, 1995). This suggests that it might be possible to improve patients' performance using rehabilitation tasks designed to induce them to rely more on their intact processing routes.

Converging evidence for numbers processing in the right hemisphere

This study helps delineate the numerical abilities of the right hemisphere, and their limits. Our results are in good agreement with previous studies of number processing in patients with complete callosotomy, as reviewed in the introduction. As in the present case, these patients' left hemisphere was excellent in all numerical tasks, while their right hemisphere could compare digits (Seymour *et al.*, 1994; Corballis, 1995), but not name them aloud or solve arithmetic problems (Gazzaniga and Hillyard, 1971; Gazzaniga and Smylie, 1984). In most surgical callosotomy cases, there is a doubt that the abnormal neurological status of the patient prior to surgery was in part responsible for the hemisphere distribution of cognitive functions. Our results, however, were obtained with a patient who was neurologically intact prior to her stroke. The remarkable convergence of results with previous studies suggests that processing of number magnitudes belongs to the cognitive abilities of the normal right hemisphere.

There is some remaining uncertainty about the exact extent of calculation abilities in the right hemisphere. Acalculic patients with major left-hemispheric lesions have been shown to verify (Dehaene and Cohen, 1991) or even to solve (Grafman *et al.*, 1989) some elementary addition problems. On this basis, Dehaene and Cohen (1991) suggested that the right hemisphere can make use of its magnitude-processing abilities in order to approximate the result of simple additions. In the experiment reported above, no evidence was ever found that the right hemisphere was able to solve even very simple addition problems. However, in one pilot block of 32 addition verification problems including either true problems (e.g. $1 + 1 = 2$) or grossly false problems (e.g. $1 + 1 = 9$), the patient made only one error out of 16 LVF trials. It is highly unlikely that such a performance occurred only by chance ($P < 0.0003$). It seems that this pilot block of trials saw the transient disclosure of a right hemispheric ability to approximate addition problems, something that could never be replicated on subsequent tests. Perhaps responses were systematically selected on the basis of left-hemispheric rather than right-hemispheric arithmetic computations on later tests. Given this ambiguity, the possibility that the right hemisphere possesses some elementary abilities for arithmetic should be left open for further research.

We noted that, although our patient's right hemisphere was quite accurate in number comparison, it performed slightly but significantly worse than her left hemisphere. This fact was also observed in the patients studied by Seymour *et al.* (1994) and Corballis (1995). In a same–different judgement task between two arabic digits printed in different fonts, our patient was also somewhat better with RVF than with LVF stimuli. Hence, these results converge to suggest a small left-hemisphere advantage for identifying digits, which may explain the slight asymmetry in the comparison task.

Another source of converging evidence is the studies of number-processing abilities of patients with pure alexia. In pure alexia, the left-hemisphere visual word and number form are destroyed or deafferented. Although such patients cannot read words aloud, they occasionally show residual word-processing abilities in tasks such as lexical decision or semantic classification (Coslett *et al.*, 1993, for review). One theory proposes that residual processing takes place, at least in its initial stages, within the right hemisphere. According to our model, pure alexic patients should be able to transfer the semantic information extracted by the right hemisphere to the left hemisphere, using the very same pathway that is operating when patients with posterior callosal lesions attempt to name LVF stimuli. Indeed, testing of pure alexics in conditions similar to those used in this study have yielded a pattern of behaviour very similar to the one reported here with LVF stimuli (Cohen and Dehaene, 1995). In a nutshell, number comparison was again preserved, while naming and arithmetic were severely impaired. The same pattern also prevails in patients with large left-hemispheric lesions (Grafman *et al.*, 1989; Dehaene and Cohen, 1991; Cohen *et al.*, 1994), although a right-hemispheric involvement can only be tentatively proposed in such cases.

Finally, the present data are in good agreement with brain activation studies in normal subjects, which suggest that both hemispheres contribute to number processing. Roland and Friberg (1985), using Xe^{133}, and Appolonio *et al.* (1994), using functional magnetic resonance imaging, have obtained bilateral inferior parietal and frontal activations during complex calculations. Using positron emission tomography, Dehaene *et al.* (1996) have also observed a bilateral inferior parietal activation. Moreover, the overall pattern of asymmetry suggested a greater involvement of the left hemisphere in mental multiplication, and a more bilateral activation during number comparison.

Using high-density recordings of event-related potentials (ERPs) during number comparison, Dehaene (1996) showed that arabic digits elicit symmetrical posterior N1 components, suggesting that both hemispheres contribute to digit identification. In contrast, spelled-out numerals evoked an essentially left-sided N1, in keeping with the neuropsychological observation that only the left hemisphere can recognize such stimuli. Later in time, Dehaene (1996) found a significant parieto-temporo-occipital difference between the ERPs recorded during easy versus difficult comparisons. This was interpreted as reflecting a bilateral inferior parietal involvement in a quantitative representation of numbers. In contrast, recording of ERPs during mental multiplication revealed a left-lateralized effect of problem difficulty, in agreement with a left-hemispheric specialization for arithmetic (M. Kiefer and S. Dehaene, submitted for publication).

Conclusion

Neuropsychological evidence from split-brains indicates that digit identification and magnitude-processing abilities are duplicated in both hemispheres, although perhaps not in identical forms. In addition, functional brain-imaging studies in normals have demonstrated bilateral activations during numerical tasks. Altogether, these observations lend direct support to the idea that the cerebral network for number processing comprises several distributed brain areas, some of which belong to the right hemisphere. According to our working hypothesis, it is only when numbers have to be processed in verbal form, such as during calculation or overt naming, that a superiority in favour of the left hemisphere is found.

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Cerebral networks for number processing: evidence from a case of posterior callosal lesion

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Abstract
The authors report a study of number processing in a patient with a lesion selectively destroying the posterior half of her corpus callosum. This case provided an opportunity to study the cerebral distribution of numerical abilities across hemispheres, and their interhemispheric communication pathways. Tasks of interhemispheric same–different judgement with digits and sets of dots showed that exact digit identity could not be transferred between hemispheres, but that some approximate magnitude information could. With arabic numerals presented in the left visual field, reading aloud and arithmetic were severely impaired. In contrast, larger–smaller magnitude comparison was spared. With right-visual-field stimuli, the patient's performance was essentially normal in reading aloud, arithmetic and number comparison. These findings lend support to the hypothesis that both hemispheres are capable of identifying arabic digits, and of accessing and comparing the corresponding magnitudes. However, the verbal abilities which underlie overt naming and arithmetic computations are available only to the left hemisphere.

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Primary diagnosis of interest
Impaired number processing abilities following callosal lesion in a patient who was neurologically intact prior to her stroke

Author's designation of case
None

Key theoretical issue
- Both hemispheres are capable of identifying arabic digits, of accessing and comparing the corresponding magnitudes. However, the verbal abilities which underlie overt naming and arithmetic computations are available only to the left hemisphere.

Key words: corpus callosum; language; acalculia; reading; numbers

Scan, EEG and related measures
MRI

Standardized assessment
Neurological examination

Other assessment
Tests of callosal transfer in the visual, haptic and auditory modalities

Lesion location
- Posterior half of the corpus callosum

Lesion type
Stroke

Language
English