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The calculating hemispheres: Studies of a split-brain patient

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Abstract

The purpose of the study was to investigate simple calculation in the two cerebral hemispheres of a split-brain patient. In a series of four experiments, the left hemisphere was superior to the right in simple calculation, confirming the previously reported left hemisphere specialization for calculation. In two different recognition paradigms, right hemisphere performance was at chance for all arithmetic operations, with the exception of subtraction in a two-alternative forced choice paradigm (performance was at chance when the lure differed from the correct answer by a magnitude of 1 but above chance when the magnitude difference was 4). In a recall paradigm, the right hemisphere performed above chance for both addition and subtraction, but performed at chance levels for multiplication and division. The error patterns in that experiment suggested that for subtraction and addition, the right hemisphere does have some capacity for approximating the solution even when it is unable to generate the exact solution. Furthermore, right hemisphere accuracy in addition and subtraction was higher for problems with small operands than with large operands. An additional experiment assessed approximate and exact addition in the two hemispheres for problems with small and large operands. The left hemisphere was equally accurate in both tasks but the right hemisphere was more accurate in approximate addition than in exact addition. In exact addition, right hemisphere accuracy was higher for problems with small operands than large, but the opposite pattern was found for approximate addition.

Keywords: Number processing; Calculation; Mathematics; Callosotomy; Hemisphere; Laterality

The ability to calculate has typically been associated with left hemisphere function, and cortical areas involved in performing mathematical operations overlap considerably with cortical areas involved in linguistic processing. Brain-damaged individuals with aphasia generally exhibit calculation deficits (Dehaene & Cohen, 1997; Delazer, Girelli, Semenza, & Denes, 1999), and neuroimaging studies have found that overlapping left parietal regions are involved in verbal processing and the recall of arithmetic facts (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Zago et al., 2001). Even in individuals with atypical patterns of laterality, linguistic and arithmetic functions are generally co-localized in the same hemisphere (Delazer et al., 2005). However, calculation and linguistic processes are anatomically dissociable. A recent neuroimaging study found that different cortical regions within the intraparietal sulcus were involved in language and calculation (Simon, Mangin, Cohen, Le Bihan, & Dehaene, 2002). Similarly, individuals with semantic dementia may have preserved arithmetical abilities (Cappelletti, Butterworth, & Kopelman, 2001; Crutch & Warrington, 2002). Thus, although there is considerable overlap between the neural mechanisms underlying linguistic and calculation abilities, there are also functionally specific anatomical regions.

The tight coupling of left hemisphere cortical areas involved in linguistic and calculation processes suggests that the two cognitive processes involve similar types of neural computation. However, additional research suggests that the ability to perform numerical quantity comparisons is associated with bilaterally represented visuo-spatial processes, including a visual representation of number forms (Dehaene, Molko, Cohen, & Wilson, 2004). Indeed, recent research from our laboratory has shown that both hemispheres are able to make quantity comparisons regardless of stimulus coding (Arabic numerals, number words, arrays of dots) (Colvin, Funnell, & Gazzaniga, 2005). Such findings have led Dehaene and colleagues to propose that both language-dependent and language-independent

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components contribute to arithmetic processing (for review, see Dehaene, Spelke, Pinel, Stanescu, & Tsivkin, 1999). The language-dependent components are associated with left hemisphere function and include a verbal representation of number forms and an ability to generate phonological output. The language-independent components are bilaterally represented and include a visual representation of number forms.

Dehaene and colleagues' neural model of mathematical processing predicts differences between the left and right hemispheres' abilities to execute arithmetical operations and to perform exact (i.e. retrieval of arithmetic facts) and approximate arithmetic. Specifically, the model predicts that the right hemisphere will be able to independently perform subtraction and approximate calculation, as these processes rely on the quantity representation modules represented in both hemispheres. In contrast, the left hemisphere will be able to execute all of the arithmetic operations (addition, subtraction, multiplication and division) and perform both exact and approximate calculations since it has access to both language-dependent and language-independent modules. To date, there is limited support for these hypotheses. A combined ERP and fMRI study comparing cortical activity during exact and approximate arithmetic operations found that exact arithmetic elicited a more left-lateralized pattern of activity than approximate arithmetic (Stanescu-Cosson et al., 2000). Similarly, there are reports of aphasic patients with impaired exact addition but preserved approximation (Dehaene & Cohen, 1991). With regard to specific arithmetical operations, an fMRI study comparing cortical activity during subtraction and multiplication found bilateral parietal activity during subtraction and left-lateralized parietal activity during multiplication, although the direct comparison of the two tasks revealed no significant difference in cortical activity (Chochon et al., 1999).

The primary purpose of this study was to directly test the predictions of Dehaene and colleagues' model with regard to the left and right hemisphere's arithmetic abilities, by comparing the abilities of the two hemispheres of a split-brain patient to perform the four basic arithmetic operations (addition, subtraction, multiplication and division) as well as exact and approximate arithmetic. Split-brain patients provide an ideal opportunity for comparing the abilities of the two hemispheres, as each patient's corpus callosum has been surgically severed for the control of intractable epilepsy, leaving each cerebral hemisphere in relative functional isolation. The current study also represents an effort to extend and clarify previous research on arithmetic abilities with split-brain patients. An earlier study showed that the left hemisphere is able to add, subtract, multiply and divide, but that the right hemisphere is unable to perform any of these operations (Gazzaniga & Smylie, 1984). However, in that study, the arithmetic problems were presented verbally with the exception of one digit that was briefly presented to the right or left visual field. Because the left hemisphere is superior to the right in linguistic ability, a hemispheric difference in comprehension of the verbally presented information could account for the hemispheric difference observed in calculation performance. In addition, responses were made by pointing to an array of 22 numbers presented in the center of the visual field. This response method may have been confusing to the right hemisphere of the split-brain patients and also introduces the possibility that the contralateral hemisphere might influence the motor output of the responding hemisphere, thereby impacting response accuracy.

In this paper, the limitations of the previous study of calculation abilities in split-brain patients are addressed and the research is extended to test the more recent predictions of the Dehaene et al. (1999, 2004) neural model of mathematical processing. The abilities of the two hemispheres to perform basic visually presented arithmetic operations (addition, subtraction, multiplication and division) were tested using a variety of non-verbal response methods, including true/false verification, forced choice recognition and written responses. The abilities of the two hemispheres to perform exact and approximate addition were also tested. We predicted that the left hemisphere would be able to perform all of the arithmetic operations across response conditions, in addition to accurately performing exact and approximate addition. Critically, the right hemisphere would only be able to perform operations that could be solved using quantity representations, such as subtraction and approximate addition. Such findings would be consistent with previous research and the basic architecture of Dehaene and colleagues' neural model of mathematical processing.

Although divided visual field testing of neurologically normal adults could potentially contribute additional insights into the calculation abilities of the two hemispheres, we chose to limit our investigation to a case study of a split-brain patient because of the difficulties in revealing and interpreting hemispheric differences in neurologically normal adults (Efron, 1990). When the corpus callosum is intact, rapid interhemispheric transfer can allow the dominant hemisphere to compensate for lack of ability in the non-dominant hemisphere, thereby masking any hemispheric differences. In addition, the corpus callosum plays a significant role in interhemispheric inhibition (Hamzei et al., 2002; Pal et al., 2005) that can prevent the non-specialized hemisphere from demonstrating its full processing capabilities. When the corpus callosum is severed, as in split-brain patients, this source of interhemispheric inhibition is removed and each hemisphere's positive competencies can be revealed (Hellige, 1993).

1. Method

1.1. Participant

Patient J.W. is a right-handed male who was 47 years old at the time of testing. He successfully completed high school and has no reported learning disabilities. He had his first seizure at the age of 16, and at the age of 25, he underwent a two-stage resection of the corpus callosum for relief of intractable epilepsy. Complete sectioning of the corpus callosum has been confirmed by MRI (Gazzaniga, Holtzman, Deck, & Lee, 1985). This is critical, as studies have shown that even a small degree of callosal sparing can support interhemispheric information transfer (Funnell, Corballis, & Gazzaniga, 2000). Post-surgical MRI also revealed no evidence of other neurological damage. J.W. has been tested extensively and a complete case history is reported elsewhere (Gazzaniga, Nass, Reeves, & Roberts, 1984). Hemispheric differences observed in this patient have been consistent with findings from lesion patients and from studies with neurologically normal participants (e.g. language, Gazzaniga, Smylie, Baynes, Hirst, & McCleary, 1984; emotion, Stone, Nisenson, Eliassen, & Gazzaniga,