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Numerical processing in the two hemispheres: Studies of a split-brain patient

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Abstract

Neuroimaging and lesion studies have provided insights into the neural mechanisms underlying numerical processing, yet the roles of the right and left hemispheres have not been systematically investigated within a single study. To address this issue, we investigated subitizing and magnitude comparison abilities in a split-brain patient. The first experiment examined the two hemispheres' abilities to enumerate briefly presented sets of one to four stimuli. Both hemispheres were equally able to perform this task. The second and third experiments examined the hemispheres' abilities to make magnitude judgments about two simultaneously presented stimuli that were either identically coded (i.e., two Arabic numerals, two number words, or two arrays of dots) or differently coded (e.g., an Arabic numeral and a number word). Although the left hemisphere was more accurate than the right when the task involved number words, both hemispheres were able to make comparisons between numerical representations regardless of stimuli coding. In addition, both hemispheres exhibited a distance effect. The results are discussed in the context of Dehaene's triple-code model.

Keywords: Subitizing; Distance effect; Mathematics; Numerical processing; Callosotomy

1. Introduction

Mathematical ability can be deconstructed into many functionally and anatomically distinct cognitive components [for review, see (Dehaene, 2000)]. The most basic of these modules is the ability to represent numerical quantities. A mental representation of number magnitude is required for most mathematical processes, except those requiring the simple mnemonic retrieval of overlearned calculation facts (e.g., $2 + 2 = 4$) (Dehaene, 2000; Dehaene & Cohen, 1997). One question is whether both hemispheres of the brain are able to accurately represent quantitative knowledge. While calculation skill is typically associated with the left hemisphere (Gerstmann, 1940), there is substantial evidence suggesting that both hemispheres are able to perform rudimentary numerical comparisons [for review, see (Dehaene, 2000)]. Yet to date, no study has systematically and comprehensively investigated this question in complete callosotomy, or "split-brain" patients. These 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 the two cerebral hemispheres in functional isolation. In this study, we investigate whether the two hemispheres of a split brain patient are equally able to enumerate small sets and to make magnitude comparisons.

The ability to rapidly enumerate small sets of objects is known as subitizing (Kaufman & Lord, 1949). When the number of items in a briefly presented array does not

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exceed four, neurologically normal adults are able to rapidly and precisely quantify the number of items present (Mandler & Shebo, 1982). Historically, it has been debated whether subitizing is accomplished through a non-verbal counting mechanism (Gallistel & Gelman, 1992, 2000) or through a preattentive perceptual process (Dehaene & Cohen, 1994; Trick & Pylyshyn, 1993, 1994). While this debate is beyond the scope of this paper, from the standpoint of hemispheric asymmetries it is worth noting that both proposed mechanisms function independently of verbal ability. Preverbal human infants (Starkey & Cooper, 1980; Wynn & Bloom, 2002) and a variety of non-human species including chimpanzees and rats (Boysen & Berntson, 1989; Davis & Memmott, 1983; Matsuzawa, 1985; Pepperberg, 1987) are able to subitize. This suggests that the ability to subitize is present early in phylogenetic and ontogenetic development and is not dependent on higher-level cognitive processes, such as language. In addition, recent neuroimaging results indicate that subitizing elicits bilateral middle occipital and parietal activity (Piazza & Mechelli, 2002). Based on this evidence, we expect that the relatively non-verbal right hemisphere should not be at a disadvantage in enumerating small sets and that both hemispheres of a split-brain patient will be equally able to subitize.

In this paper, we also explore the ability of the two hemispheres to represent the ordinal properties of numbers. Again, developmental studies have demonstrated that pre-verbal human infants are able to discriminate between displays differing in numerosity. At a young age, infants are only able to make these discriminations when the numbers differ by a ratio of 2 (e.g., 8 vs. 16), but their sensitivity increases dramatically within the first year of life (Brannon, 2002; Lipton & Spelke, 2003; Xu, 2003; Xu & Spelke, 2000). Thus, one might expect that the right hemisphere's impoverished verbal skills would not impede magnitude judgments, at least for quantities differing by a substantial ratio. Neuroimaging studies of neurologically normal participants support this hypothesis, revealing bilateral parietal activity during magnitude judgments (Chochon & Cohen, 1999; Dehaene & Spelke, 1999; Pinel & LeClec'H, 1999; Pesenti & Thioux, 2000; Pinel & Dehaene, 2001).

Previous studies of partial and complete callosotomy patients support the hypothesis that the two hemispheres are equally able to make magnitude judgments when quantities are represented in an Arabic form (Cohen & Dehaene, 1996; Seymour & Reuter-Lorenz, 1994). However, additional research with a partial callosotomy patient and patients suffering from unilateral lesions has demonstrated that the right hemisphere's ability to make numerical comparisons is limited when numerical quantity is represented verbally (e.g., FOUR) (Cohen & Dehaene, 1996; Dellatolas & Deloche, 2001). Based on this and other research, Dehaene has proposed a triple-code model that includes three possible representations of numerical quantity: (1) visual Arabic number (e.g., 4), (2) verbal word frame (e.g., FOUR), and (3) analogical magnitude representation (e.g., a display of four dots). These numerical representations can be directly translated from one code to another (e.g., from 4 to four). According to the triple-code model, both hemispheres represent the visual and analogical representations, but only the left hemisphere can represent the verbal form. In the intact brain, callosal connections support the transfer of verbally represented numerical quantities to the right hemisphere. However, when the corpus callosum is damaged or severed, the triple-code model predicts that the right hemisphere will be limited to numerical manipulations that only require translations between the visual and analogical representations (e.g., quantity comparisons based on visually presented Arabic numerals). Without access to the verbal word form, the right hemisphere will be unable to perform tasks, including magnitude comparison, involving written number words or spoken numbers (Dehaene, 1992, 2000; Dehaene & Cohen, 1995).

Interestingly, Dehaene proposes that magnitude comparisons are accomplished by comparing analog magnitude representations along an internally represented number line (Dehaene & Dupoux, 1990). Magnitude comparisons thus require the automatic transcoding of verbal or visual representations to analog magnitude representations (Dehaene & Akhavein, 1995). Dehaene argues that each hemisphere can internally represent the number line. However, there is evidence that number line representation is influenced by linguistic ability. People whose languages are written from left to right show faster responses to small numbers with response keys on the left, and faster responses to large numbers with response keys on the right. This suggests that for native English speakers, mental representation of the number line increases in magnitude from left to right, with smaller numbers on the left. People whose native languages are written from right to left, however, show the opposite pattern, suggesting that their mental number line increases from right to left (Dehaene & Bossini, 1993). Thus, in humans, the ability to compare magnitudes is influenced by language function, raising the possibility that the non-verbal right hemisphere may represent the number line differently than the linguistic left hemisphere.

One way to investigate the internal representation of the number line in the two hemispheres is by examining the distance effect in each hemisphere. Moyer and Landaeur (1967) first demonstrated that humans are faster and more accurate in making magnitude judgments about quantities that numerically distant from each other (e.g., 2 vs. 9) than those that are comparatively close (e.g., 2 vs. 3) (Moyer & Landaeur, 1967). If the left and right hemisphere's internal representations of the number line differ, then one might expect that the numerical distance effect might also differ between the two hemispheres. To our knowledge, no previous study has examined the numerical distance effect in a complete callosotomy patient.

In this paper, we report a series of numerical processing studies conducted with a "split-brain" patient. These studies test the ability of the two hemispheres to rapidly enumerate small sets of items and to make magnitude judgments about differentially coded numerical quantities. Because subitizing does not rely upon verbal skills, we predict that both hemispheres will be able to rapidly enumerate small sets. Based on previous research, we also predict that both hemispheres will be able to make magnitude judgments involving Arabic numbers and analogical magnitude representations. In contrast, we expect the left hemisphere to be superior to the right for magnitude judgments about number words. Finally, we expect that the distance effect may differ between the two hemispheres.

2. Method

2.1. Participant

Patient J.W. is a right-handed male who was 47 years old at the time of testing. At the age of 25, he underwent a two-stage resection of the corpus callosum for relief of intractable epilepsy (see (Gazzaniga & Nass, 1984), for a case history). Post-surgical MRI confirmed that his corpus callosum was fully severed (Gazzaniga & Holtzman, 1985). This removes the possibility that callosal transfer is influencing the performance of one or both hemispheres as research has shown that even a few spared callosal fibers can support transfer of a fair degree of information from one hemisphere to the other (Funnell & Corballis, 2000). Structural brain imaging and neuropsychological testing reveal no evidence of other neurological damage. In addition, J.W. has been extensively tested in lateralized paradigms, and 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, 1984); emotion: (Stone & Nisenson, 1996); visuospatial: (Funnell & Corballis, 1999); face processing: (Gazzaniga & Smylie, 1983)]. For this reason, we are confident that patterns of hemispheric performance revealed in this patient can inform us as to normal neurological function.

2.2. General experimental design

The experiments were designed to assess each hemisphere's ability to process numerical information. To present information exclusively to either the left or right hemisphere, J.W. was seated 57 cm from the computer screen and asked to fixate on a central cross-hair. Stimuli were presented either to the left visual field (LVF) or to the right visual field (RVF) for 150 ms with the medial edges of the stimuli at least 2° (2 cm) to the right or left of fixation. This presentation time is too brief to permit the initiation of saccadic eye motions toward the lateralized stimuli, and the medial edges of the stimuli fall outside any zone of naso-temporal overlap. These arrangements therefore ensure that stimuli are perceived only by the hemisphere contralateral to the visual field of the presentation. That is, stimuli presented to the LVF are perceived only by the right hemisphere, and vice versa. J.W. made his responses via keypress using a standard keyboard placed comfortably in front of him. In each experiment, LVF and RVF trials were randomly intermixed. Each hemisphere received the same number of trials and the same combinations of numerical information, although the trial order to each hemisphere varied.

2.3. Data analysis

In Experiments 2 and 3, accuracy data were analyzed using a multidimensional χ^2 test, because these experiments involved single-subject data with multiple factors in which each hemisphere serves as a control for the other (Winer & Brown, 1991). The factorial design of the experiments allows higher-order interaction effects to be evaluated in a manner directly analogous to analysis of variance. The main effects are indexed by the interaction of response (top or bottom keypress), position of the correct stimulus (top or bottom), and the variable of interest (e.g., visual field). The interaction between two variables of interest is indexed by the interaction of response, position of the correct stimulus, and the variables of interest. The χ^2 analysis requires that there be two conditions and two response choices in order to set up a contingency table for analysis. In Experiment 1, there were four conditions and four response options so the χ^2 analysis was not possible. Accuracy data for this experiment were therefore analyzed using a paired t test.

Reaction time data for Experiments 2 and 3 were analyzed using a repeated measures analysis of variance. Only reaction times for correct responses were analyzed, and reaction times that were more than 3 standard deviations from the mean for each hand in each task were eliminated from the analysis. For experiments in which there were more than two levels of magnitude, univariate tests of significance were used with a Greenhouse–Geisser correction for the degrees of freedom in order to be conservative in determining whether main effects and interactions were significant.

2.4. Experiment 1: Subitizing

The purpose of this experiment was to assess the ability of the two hemispheres to rapidly identify the number of items in a small set. This ability, known as subitizing, is thought to rely on non-verbal mechanisms that allow for rapid enumeration of a set of one to four items (Dehaene & Cohen, 1994; Gallistel & Gelman, 1992, 2000; Trick & Pylyshyn, 1993, 1994). This ability has been demonstrated in preverbal human infants (Starkey & Cooper, 1980; Wynn, Bloom et al., 2002) and in a variety of non-human species including chimpanzees and rats (Boysen & Berntson, 1989; Davis & Memmott, 1983; Matsuzawa, 1985; Pepperberg, 1987). If the ability to subitize is indeed preverbal and present early in phylogenetic and ontogenetic development, then we would expect both hemispheres of humans to possess this capacity.

2.4.1. Method

The stimuli for this experiment were sets of red circles. Each stimulus set contained between 1 and 4 circles, and the sets of circles were presented to one or the other visual field for 150 ms. The arrangement of the circles was varied so that a set of 4 circles, for example, did not always look the same. This prevented decisions based on pattern recognition rather than numerosity. J.W. indicated how many items were in each stimulus set by pressing one of 4 response keys. Each response key was labeled with a number, beginning with 1 on the left-most key and proceeding to 4 on the right-most key. There were 64 trials in block with 32 in each visual field, 8 sets of each of the four quantities of circles (1–4). J.W. completed four blocks. In two blocks, he responded to all stimuli with his right hand, and in the other two blocks, he responded with his left hand.

2.4.2. Results and discussion

For the block in which J.W. responded with his left hand, stimuli presented to the left visual field were used for analysis and responses to stimuli presented to the right visual field were discarded. Similarly, for the block in which J.W. responded with his right hand, stimuli presented to the right visual field were used for analysis and responses to stimuli presented to the left visual field were discarded. This ensures that the hemisphere receiving the visual input also initiated the motor response. Using a paired t test, it was found that performance of the two hemispheres was equivalent (91.25% accuracy in both) and there was no significant difference between hemispheres ($t \approx 0, p \approx 1$). This suggests that both hemispheres are equally able to determine the number of items in small sets.

This finding is consistent with the idea that subitizing is a preverbal mechanism that is present early in ontogenetic and phylogenetic development. If it were dependent on higher level processes, a hemispheric difference might be expected since many higher level perceptual and cognitive processes are lateralized to one hemisphere or the other. Although the bulk of the relevant literature supports a bilateral mechanism, it has been suggested that the right hemisphere might have an advantage for subitizing. In a lateralized study of neurologically normal adults, Pasini and Tessari (2001) claim that their data support a left visual field/right hemisphere (LVF/RH) advantage for subitizing and a right visual field/left hemisphere (RVH/LH) advantage for determining numerosity of sets outside of the range of subitizing (Pasini & Tessari, 2001). In their analyses, however, they included responses from both hands in the data for each visual field (i.e., left visual field data included responses made by both the right and left hands). A more rigorous approach is to discard the responses from the contralateral hand (i.e., use only left hand responses for left visual field stimuli) since this ensures that the hemisphere receiving the visual input also initiates the motor response. When their data are considered in this more rigorous manner, there is no hemispheric difference in subitizing. Our data are consistent with this revised conclusion.

2.5. Experiment 2: Single code comparisons

The purpose of this experiment was to determine whether both hemispheres are able to make judgments of magnitude when comparing identically coded numerical information. Dehaene's triple-code model predicts that the right hemisphere will be unable to perform tasks involving written number words but will be able to make numerical judgments about Arabic numerals and analogical magnitude representations (Dehaene, 1992, 2000; Dehaene & Cohen, 1995). In contrast, the language-dominant left hemisphere should perform accurately with all three types of numerical representations. To characterize the numerical processing abilities of the two cerebral hemispheres, we measured accuracy and reaction times of each hemisphere when making magnitude judgments about Arabic numerals (digits), number words, and arrays of dots.

2.5.1. Method

The stimuli for this experiment were digits, ranging from 1 to 9, number words from one to nine, and arrays of one to four dots. In each trial, two numerical stimuli were presented one above the other within one visual field. J.W. was instructed to indicate via keypress which item in the pair was of a greater numerical magnitude. All trials within each set were of one type (i.e., there were separate sets of digits, number words and dots). J.W. completed 10 sets of each of the types of stimuli.

For the digits and the number words, the magnitude difference between the two stimuli ranged from 1 to 6. Each number appeared in four total combinations with another number. Each combination appeared four times in each visual field. The relative position of the two numbers (top or bottom) was the same for two of the four trials and the reverse for the remaining two trials. Therefore, for each magnitude difference (1–6), there were three possible number combinations that each appeared four times in each visual field (alternating the relative position of the numbers within each visual field), producing twelve trials for each magnitude difference in each visual field. Trials were randomly ordered. There were 144 trials in each set with 72 in each visual field (12 trials per magnitude difference in each field).

For the arrays of dots, the magnitude difference between the two stimuli was either 1 or 2. For each number of dots (1–4), there were six possible perceptual arrangements of dots. Each arrangement had high perceptual similarity both within number and across numbers so that all arrangements were the same size and had similar areas of positive space. Because the dot arrays ranged from one to four members, there were six possible combinations of arrays for both magnitude differences of one and two. Each combination appeared 16 times in each visual field. The relative position of the two arrays (top or bottom) was the same for eight of the trials and the reverse for the remaining eight trials. All possible combinations appeared before being repeated within field. There were 192 trials in each set with 96 per visual field (48 items per each magnitude difference in each field).

J.W. made his response to the presented stimuli using the hand ipsilateral to the field of presentation (i.e., responded with the left hand to stimuli presented in the LVF and vice versa). For each hand, there were two response keys, one located above the other. This arrangement corresponded to the arrangement of the numerical stimuli presented to each visual field. He was instructed to press the key corresponding to the item in the pair that represented the greater magnitude. That is, he was instructed to press the top key if the magnitude of the top item was larger, and the bottom key if the magnitude of the bottom item was larger. Both accuracy and reaction time were recorded for each stimulus type.

2.5.2. Results and discussion

Table 1 includes the results of statistical analysis of the accuracy data, and the data are depicted graphically in Fig. 1A. For each stimulus type, accuracy data were analyzed via multidimensional χ^2 analysis with visual field (right and left) and magnitude difference (6 levels for digits and number words, 2 levels for dots) as variables of interest. For the digits, there were no significant effects or interactions, and performance in both hemispheres was virtually at ceiling. The effect of magnitude was significant for both number words and arrays of dots, with accuracy better for larger magnitude differences than for smaller. The effect of visual field was significant only for number words, with performance in the RVF/LH better than that of the LVF/RH. This is likely due to the linguistic nature of the stimuli since the left hemisphere is superior to the right in processing written words. The interaction between visual field and magnitude difference was not significant, however, suggesting that both hemispheres are equally influenced by the relative size of the magnitude difference.

Table 1
Statistical analysis of response accuracy for Experiment 2

	χ^2 Value	p Value
Arabic digits		
Magnitude	1.67	.893
Field	0.01	.916
Magnitude × field	1.19	.946
Number words		
Magnitude	27.56	<.001*
Field	28	<.001*
Magnitude × field	1.76	.881
Arrays of dots		
Magnitude	5.85	.016*
Field	1.75	.186
Magnitude × field	0.25	.616

* The symbol signifies statistical significance.

Repeated measures analysis of reaction times included visual field and magnitude as factors. Table 2 includes the results of statistical analysis of the response time data, and the data are depicted graphically in Fig. 2A. In all conditions, J.W. responded faster with his right hand than with his left, resulting in a significant effect of visual field for all stimulus types. Both hemispheres exhibited a significant distance effect (effect of magnitude) for all three stimulus types. However, the size of the distance effect varied by hemisphere (interaction between visual field and magnitude) depending upon the stimulus coding. For Arabic numerals, both hemispheres demonstrated equivalent distance effects. For number words, the left hemisphere showed a larger distance effect than the right. This is likely due to the left hemisphere's superiority for linguistic processing since the stimuli in this experiment were words. Conversely, for the arrays of dots, the right hemisphere exhibited a larger distance effect than the left, probably reflecting the right hemisphere's superiority for perceptual processing.

In keeping with the predictions of Dehaene's triple-code model of numerical processing, the results of this experiment suggest that both hemispheres are capable of comprehending and processing numerical quantities when represented as Arabic digits or arrays of dots. There was no difference in accuracy between the two hemispheres for the digit task, indicating hemispheric equivalence in the ability to process these stimuli. The right hemisphere was more accurate than the left in responding to the arrays of dots, but both hemispheres performed at a high level of accuracy. However, while the left hemisphere was more accurate than the right in responding to number words, the performance of the right hemisphere was well above chance. Dehaene's

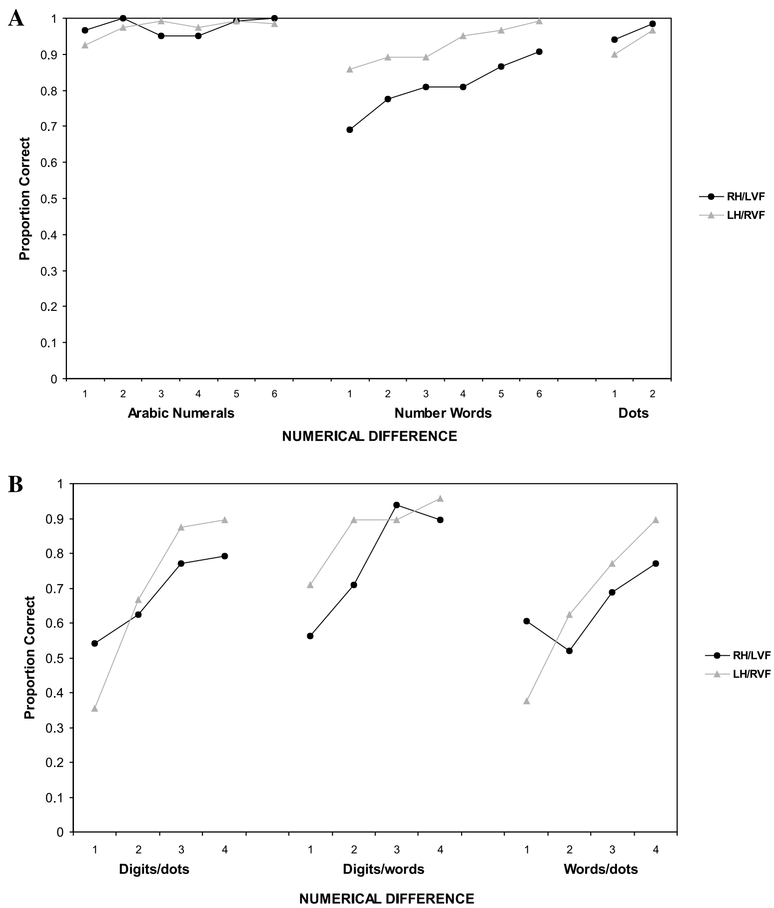

Fig. 1. (A) Experiment 2: Single code comparisons. Response accuracy for magnitude judgments of two stimuli coded in the same numerical format (Arabic digits, number words, and arrays of dots). In all the graphs, the *x*-axis represents the numerical difference between the two stimuli and the *y*-axis represents the proportion of correct responses. (B) Experiment 3: Transcode comparisons. Response accuracy for magnitude judgments of two stimuli coded in different numerical formats (digits/dots, digits/words, and words/dots).

Table 2
Statistical analysis of response accuracy for Experiment 2

	F Value	*p* Value
Arabic digits		
Magnitude	12.18	<.001*
Field	60.25	<.001*
Magnitude × field	1.38	.249
Number words		
Magnitude	14.72	<.001*
Field	153.15	<.001*
Magnitude × field	4.82	.018*
Arrays of dots		
Magnitude	5.21	.048*
Field	115.23	<.001*
Magnitude × field	7.38	.024*

* The symbol signifies statistical significance.

triple-code model predicts that the right hemisphere should be at chance for the number words task. Both hemispheres demonstrated a numerical distance effect for all three types of stimuli, but the magnitude of this effect differed between the hemispheres with hemispheric equivalence for Arabic numerals, left hemisphere advantage for number words, and right hemisphere advantage for arrays of dots. The data suggest that although one hemisphere may be superior to the other in processing a particular type of numerical representation, both can represent and compare all three types of numerical representations.

2.6. Experiment 3: Transcode comparisons

In Experiment 2, J.W. was asked to make magnitude judgements about similarly coded numerical stimuli. The purpose of Experiment 3 was to determine whether both hemispheres could make simple judgements of magnitude when comparing differently coded numerical stimuli. As in the previous experiment, J.W. was asked to indicate which of two presented numerical stimuli (Arabic numerals, words, or dot arrays) was larger. According to Dehaene's triple-code model, numerical representations can be directly transcoded from one format to another. For example, an Arabic number stimulus (e.g., 3) is directly converted to a verbal word frame

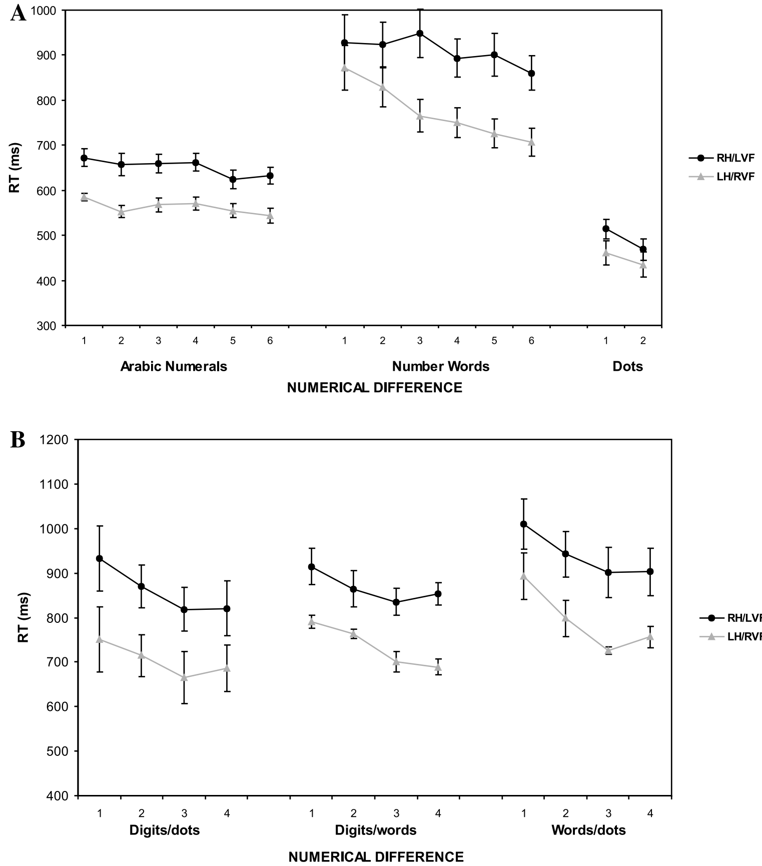

Fig. 2. (A) Experiment 2: Single code comparisons. Reaction times of correct responses for magnitude judgments of two stimuli coded in the same numerical format (Arabic digits, number words, and arrays of dots). (B) Experiment 3: Transcode comparisons. Reaction times of correct responses for magnitude judgments of two stimuli coded in different numerical formats (digits/dots, digits/words, and words/dots).

(e.g., three) without activating the analogical representation, and vice versa. The model predicts that the right hemisphere should be unable to identify, manipulate, and produce verbal word frame representations and therefore will also be unable to compare magnitudes of written number words to differently coded numerical representations. Both hemispheres, however, should be equally able to compare magnitudes of differently coded numerical stimuli as long as none of the stimuli are in the verbal word format. To test this prediction, we measured accuracy and reaction times of each hemisphere when making magnitude judgments about pairs of differently coded numerical representations.

2.6.1. Method

J.W. was asked to make magnitude judgments about two simultaneously presented stimuli. The method of presentation and response was the same as in Experiment 2. J.W. was tested on three types of magnitude comparison: digits and number words, digits and arrays of dots, and number words and arrays of dots. The range of quantity represented by each stimulus was between 1 and 6. The magnitude differences between two simultaneously presented stimuli ranged from 1 to 4. Each magnitude difference appeared equally in each visual field. The larger numerical quantity appeared equally as either code and in both within-field positions (top or bottom). Therefore, there were 32 possible combinations of visual field, position, magnitude difference, and code of correct response. Each combination appeared before being repeated within field. There were 128 trials in each set with 64 in each visual field (16 items per magnitude difference in each visual field). J.W. completed 6 sets of each type of magnitude comparison. In Experiment 2, the dots in the arrays varied in size and spatial arrangement so that the number of dots present could not be determined based on extraneous stimulus properties, such as the area subsumed by the dots. In this experiment, we presented the dots in specific patterns so that judgment of number of dots could be performed more rapidly and automatically.

2.6.2. Results and discussion

Table 3 includes the results of statistical analysis of the accuracy data, and the data are depicted graphically in Fig. 1B. For each type of numerical comparison (digits/dots, digits/words, words/dots), accuracy data were analyzed via multidimensional χ^2 analysis with visual

Table 3
Statistical analysis of response accuracy for Experiment 3

	χ^2 Value	*p* Value
Digits/dots		
Magnitude	19.56	<.001*
Field	0.05	.829
Magnitude × field	2.77	.429
Digits/words		
Magnitude	10.6	.014*
Field	1.51	.219
Magnitude × field	1.47	.688
Words/dots		
Magnitude	15.44	.011*
Field	0.08	.773
Magnitude × field	4.04	.257

* The symbol signifies statistical significance.

field (right and left) and magnitude difference (4 levels) as the variables of interest. Both hemispheres were equally able to make all three types of numerical comparison (no effect of visual field). In addition, both hemispheres exhibited significant distance effects (effect of magnitude) of equal size (no interaction between visual field and magnitude) for all three types of comparison.

Reaction time data were analyzed via repeated measures analysis of variance with visual field (left and right) and magnitude difference (one to four) as factors. Table 4 includes the results of statistical analysis of the response time data, and the data are depicted graphically in Fig. 2B. For all three types of numerical comparison, the effect of visual field was significant because J.W. responded faster with his right hand than with his left. For all three conditions, both hemispheres demonstrated significant distance effects (effect of magnitude) and the size of these effects were equivalent between hemispheres (no interaction between visual field and magnitude).

In Experiment 2, both hemispheres exhibited equal distance effects for Arabic numbers, but the left hemisphere showed a larger distance effect than the right for number words, while the right hemisphere showed a larger distance effect than the left for sets of dots. Based on this, it might have been expected that the left hemisphere would demonstrate a larger distance effect for the digit/word comparison and that the right hemisphere would demonstrate a larger distance effect for the digit/dot comparison. Neither of these predictions was borne out, however. Instead, the results of Experiment 3 suggest that both hemispheres are equally able to process and compare numerical information regardless of the format in which it is presented.

Table 4
Statistical analysis of response accuracy for Experiment 3

	F value	*p* Value
Digits/dots		
Magnitude	7.67	.002*
Field	122.01	<.001*
Magnitude × field	1.08	.389
Digits/words		
Magnitude	17.74	<.001*
Field	44.36	.001*
Magnitude × field	2.38	.159
Words/dots		
Magnitude	15.96	.001*
Field	122.01	<.001*
Magnitude × field	0.88	.405

* The symbol signifies statistical significance.

3. General discussion

The results of these three experiments suggest that both hemispheres are able to rapidly enumerate small sets of items and to process and compare numerical quantities regardless of the way in which they are coded (as digits, number words, or sets of dots). Further, the ability of the two hemispheres to compare quantities is similar whether the two quantities to be compared are coded in the same format or in different formats. There are, however, differences in the overall ability of each hemisphere to process specific numerical representations. Consistent with previous research [see (Gazzaniga, 2000) for review], the left hemisphere appears to be specialized for processing verbal material such as number words while the right is specialized for the visual processing necessary for determining the number of stimuli in a set of objects. For all types of numerical representation, however, the non-specialized hemisphere is able to make magnitude comparisons and shows the numerical distance effect.

The finding that both hemispheres are equally able to enumerate small sets of objects is consistent with previous research suggesting that the ability to subitize relies on non-verbal, lower-level processes which are likely to be bilaterally represented (Dehaene & Cohen, 1994; Gallistel & Gelman, 2000; Piazza, Mechelli et al., 2002). It has been suggested that while many higher level functions such as language and visuospatial processing are lateralized to one hemisphere or the other, basic perceptual and cognitive processes are likely to be equivalent in both hemispheres (Corballis, 2003; Corballis & Funnell, 2002). The ability to rapidly enumerate small sets of items can be considered to be a lower-level process since it is evident in non-human species (Boysen & Berntson, 1989; Davis & Memmott, 1983; Matsuzawa, 1985; Pepperberg, 1987) and in preverbal human infants (Starkey & Cooper, 1980; Wynn, Bloom et al., 2002). Our finding of hemispheric equivalence for subitizing supports this idea.

The results of Experiments 2 and 3 demonstrate that both hemispheres can make magnitude comparisons among different numerical representations. Surprisingly, the right hemisphere is capable of making comparisons involving number words, although the left hemisphere is superior for word/word comparisons. Nonetheless, these data provide evidence that the right hemisphere can process and understand verbal representations of number. This conclusion is not consistent with the triple-code model which predicts that both hemispheres can process Arabic numerals and analog representations of number, but only the left hemisphere can identify, manipulate and produce verbal word frame representations (Dehaene, 1992, 2000; Dehaene & Cohen, 1995). Our findings are, however, consistent with data from Cohen and Dehaene's (1995) patient who sustained a lesion of the posterior half of the corpus callosum. They tested the two hemispheres on same/different numerical judgments and magnitude comparisons. Number words were tested in both hemispheres using a matching and a comparison task. In both tasks, the right hemisphere was significantly impaired relative to the left, but performance was above chance. Interestingly, both hemispheres showed an equivalent distance effect in the magnitude comparison task with the number words (Cohen & Dehaene, 1995).

One possible explanation for Cohen and Dehaene's (1995) results is that the intact anterior portion of this patient's corpus callosum supported the transfer of the semantic number concepts to the non-verbal right hemisphere. Semantic transfer has been observed in other patients who have minimal rostral connections (Corballis & Corballis, 2001; Funnell, Corballis et al., 2000). Another explanation that is also consistent with our findings is that the right hemisphere is able to represent some numerical quantities in a verbal form. Evidence from patient populations and from neurologically normal subjects has demonstrated that the right hemisphere has linguistic capacities, including a lexicon (Gazzaniga, Smylie et al., 1984) as well as more complex semantic knowledge (Beeman, 1993; Beeman & Friedman, 1994). Although the right hemisphere's lexicon is not as extensive as that of the left, the right hemisphere is capable of associating meaning with words. While patient J.W. has more extensive linguistic abilities than many other callosotomy and unilateral lesion patients (Baynes, 1990), the posterior callosal lesion patient reported by Cohen and Dehaene (1995) does not (Cohen & Dehaene, 1995). Thus, it seems possible that the right hemisphere may have a limited ability to comprehend number words, at least those that are frequently encountered in everyday language and represent small quantities.

The results of Experiments 2 and 3 also illustrate that both hemispheres demonstrate a distance effect. While the results of Experiment 2 suggest that the magnitude of this effect may reflect a left hemisphere advantage for number words and a right hemisphere advantage for arrays of dots, the results of Experiment 3 suggest that this effect may be minimal or depend on task conditions. The overall findings do not support the hypothesis that the two hemispheres' internally represented analogical number lines significantly differ.

In summary, both hemispheres are able to rapidly enumerate small sets of items and make magnitude judgments regardless of the way in which numerical information is presented. Both hemispheres also demonstrate distance effects regardless of the stimulus coding. The functional specializations of each hemisphere do impact performance on specific tasks, but both hemispheres comprehend quantity and magnitude.

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References

Baynes, K. (1990). Reading in the right hemisphere: Highways or byways of the brain?. *Journal of Cognitive Neuroscience, 2*, 159–179.

Beeman, M. (1993). Semantic processing in the right hemisphere may contribute to drawing inferences from discourse. *Brain and Language, 44*, 80–120.

Beeman, M., Friedman, R. B., et al. (1994). Summation priming and coarse semantic coding in the right hemisphere. *Journal of Cognitive Neuroscience, 6*(1), 26–45.

Boysen, S. T., & Berntson, G. G. (1989). Numerical competence in a chimpanzee (pan-troglodytes). *Journal of Comparative Psychology, 103*(1), 23–31.

Brannon, E. M. (2002). The development of ordinal numerical knowledge in infancy. *Cognition, 83*, 223–240.

Chochon, F., Cohen, L., et al. (1999). Differential Contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience, 11*(6), 617–630.

Cohen, L., & Dehaene, S. (1995). Number processing in pure alexia: The effect of hemispheric asymmetries and task demands. *Neurocase, 1*(2), 121–137.

Cohen, L., & Dehaene, S. (1996). Cerebral networks for number processing: Evidence from a case of posterior callosal lesion. *Neurocase, 2*, 155–174.

Corballis, M. C., & Corballis, P. M. (2001). Interhemispheric visual matching in the split-brain. *Neuropsychologia, 39*(13), 1395–1400.

Corballis, P. M. (2003). Visuospatial processing and the right-hemisphere interpreter. *Brain and Cognition, 53*(2), 171–176.

Corballis, P. M., Funnell, M. G., et al. (2002). Hemispheric asymmetries for simple visual judgments in the split brain. *Neuropsychologia, 40*, 401–410.

Davis, H., & Memmott, J. (1983). Autocontingencies - rats count to 3 to predict safety from shock. *Animal Learning and Behavior, 11*(1), 95–100.

Dehaene, S. (1992). Varieties of numerical abilities. *Cognition, 14*, 1–42.

Dehaene, S. (2000). Cerebral bases of number processing and calculation. In M. Gazzaniga (Ed.), *The New Cognitive Neurosciences* (pp. 987–998). Cambridge, MA: MIT Press.

Dehaene, S., & Akhavein, R. (1995). Attention, automaticity, and levels of representation in number processing. *Journal of Experimental Psychology: Learning, Memory, and Cognition, 21*(2), 314–326.

Dehaene, S., Bossini, S., et al. (1993). The mental representation of parity and number magnitude. *Journal of Experimental Psychology: General, 122*(3), 371–396.

Dehaene, S., & Cohen, L. (1994). Dissociable mechanisms of subitizing and counting: Neuropsychological evidence from simultanagnosic patients. *Journal of Experimental Psychology: Human Perception and Performance, 20*(5), 958–975.

Dehaene, S., & Cohen, L. (1995). Towards an anatomical and functional model of number processing. *Mathematical Cognition, 1*, 83–120.

Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex, 33*, 219–250.

Dehaene, S., Dupoux, E., et al. (1990). Is numerical comparison digital? Analogical and symbolic effects in two-digit number comparison. *Journal of Experimental Psychology: Human Perception and Performance, 16*(3), 626–641.

Dehaene, S., Spelke, E., et al. (1999). Sources of mathematical thinking: Behavioral and brain-imaging evidence. *Science, 284*, 970–974.

Dellatolas, G., Deloche, G., et al. (2001). Assessment of calculation and number processing using the EC301 battery: Cross-cultural normative data and application to left- and right-brain damaged patients. *Journal of the International Neuropsychological Society, 7*(7), 840–859.

Funnell, M. G., Corballis, P. M., et al. (1999). A deficit in perceptual matching in the left hemisphere of a callosotomy patient. *Neuropsychologia, 37*, 1143–1154.

Funnell, M. G., Corballis, P. M., et al. (2000). Cortical and subcortical interhemispheric interactions following partial and complete callosotomy. *Archives of Neurology, 57*, 185–189.

Gallistel, C. R., & Gelman, R. (1992). Preverbal and verbal counting and computation. *Cognition, 44*, 43–74.

Gallistel, C. R., & Gelman, R. (2000). Non-verbal numerical cognition: From reals to integers. *Trends in Cognitive Sciences, 4*(2), 59–65.

Gazzaniga, M. S. (2000). Cerebral specialization and interhemispheric communication: Does the corpus callosum enable the human condition. *Brain, 123*, 1293–1326.

Gazzaniga, M. S., Holtzman, J. D., et al. (1985). MRI assessment of human callosal surgery with neuropsychological correlates. *Neurology, 35*, 1763–1766.

Gazzaniga, M. S., Nass, R., et al. (1984). Neurologic perspectives on right hemisphere language following surgical section of the corpus callosum. *Seminars in Neurology, 4*(2), 126–135.

Gazzaniga, M. S., & Smylie, C. S. (1983). Facial recognition and brain asymmetries: Clues to underlying mechanisms. *Annals of Neurology, 13*, 536–540.

Gazzaniga, M. S., Smylie, C. S., et al. (1984). Profiles of right hemisphere language and speech following brain bisection. *Brain and Language, 22*, 206–220.

Gerstmann, J. (1940). Syndrome of finger agnosia disorientation for right and left agraphia and acalculia. *Archives of Neurology and Psychiatry, 44*, 398–408.

Kaufman, E. L., Lord, M. W., et al. (1949). The discrimination of visual number. *American Journal of Psychology, 62*, 498–525.

Lipton, J., & Spelke, E. S. (2003). Origins of number sense: Large-number discrimination in human infants. *Psychological Science, 14*(5), 396–401.

Mandler, G., & Shebo, B. J. (1982). Subitizing: An analysis of its component processes. *Journal of Experimental Psychology: General, 111*, 1–21.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*(6014), 57–59.

Moyer, R. S., & Landaeur, T. K. (1967). Time required for judgments of numerical inequality. *Nature, 15*, 1519–1520.

Pasini, M., & Tessari, A. (2001). Hemispheric specialization in quantification processes. *Psychological Research, 65*, 57–63.

Pepperberg, I. M. (1987). Evidence for conceptual quantitative abilities in the African Grey parrot: Labeling of cardinal sets. *Ethology, 75*, 37–61.

Pesenti, M., Thioux, M., et al. (2000). Neuroanatomical substrates of arabic number processing, numerical comparison, and simple addition: A PET study. *Journal of Cognitive Neuroscience, 12*(3), 461–479.

Piazza, M., Mechelli, A., et al. (2002). Are subitizing and counting implemented as separate or functionally overlapping processes?. *NeuroImage, 15*, 435–446.

Pinel, P., Dehaene, S., et al. (2001). Modulation of parietal activation by semantic distance in a number comparison task. *NeuroImage, 14*(5), 1013–1026.

Pinel, P., LeClec'H, G., et al. (1999). Event-related fMRI analysis of the cerebral circuit for number comparison. *NeuroReport, 10*, 1473–1479.

Seymour, S. E., Reuter-Lorenz, P. A., et al. (1994). The disconnection syndrome: Basic findings reaffirmed. *Brain, 117*, 105–115.

Starkey, P., & Cooper, R. G. (1980). Perception of numbers by human infants. *Science, 210*(4473), 1033–1035.

Stone, V. E., Nisenson, L., et al. (1996). Left hemisphere representations of emotional facial expressions. *Neuropsychologia, 34*, 23–29.

Trick, L. M., & Pylyshyn, Z. W. (1993). What enumeration studies can show us about spatial attention: Evidence for limited capacity preattentive processing. *Journal of Experimental Psychology: Human Perception and Performance, 19*, 331–351.

Trick, L. M., & Pylyshyn, Z. W. (1994). Why are small and large numbers enumerated differently? A limited capacity preattentive stage in vision. *Psychological Review, 101*, 80–102.

Winer, B. J., Brown, D. R., et al. (1991). *Statistical principles in experimental design*. McGraw-Hill: New York.

Wynn, K., Bloom, P., et al. (2002). Enumeration of collective entities by 5-month-old infants. *Cognition, 83*, B55–B62.

Xu, F. (2003). Numerosity discrimination in infants: Evidence for two systems of representations. *Cognition, 89*, B15–B25.

Xu, F., & Spelke, E. S. (2000). Large number discrimination in 6-month-old infants. *Cognition, 74*, B1–B11.