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Neural correlates of arithmetic and language comprehension: A common substrate?

Juliana V. Baldo^{a,*}, Nina F. Dronkers^{a,b,c}

^a VA Northern California Health Care System, 150 Muir Road (126s) Martinez, CA 94553, United States

^b University of California, Department of Neurology, Davis, CA 95616, United States ^c University of California, Center for Research in Language, La Jolla, CA 92093, United States

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Abstract

There is debate as to the relationship between mathematical ability and language. Some research has suggested that common processes underlie arithmetic and grammar while other research has suggested that these are distinct processes. The current study aimed to address this issue in a large group of 68 left hemisphere stroke patients who were all tested on analogous arithmetic and language comprehension measures. The behavioral data revealed a significant correlation between performance on the comprehension and arithmetic measures, although a subset of patients showed a dissociation in performance on the two tasks. To determine the brain regions critical for performance on each measure, patients' lesions were analyzed using Voxel-based Lesion Symptom Mapping. Arithmetic was associated with a small number of foci, with the most significant region located in the left inferior parietal lobule (Brodmann areas 39 and 40). Comprehension was associated with a larger number of brain regions, most extensively in the left middle and superior temporal gyri. There was also overlap between the arithmetic and comprehension maps in a number of regions, such as the inferior frontal gyrus. Our findings suggest that arithmetic and language comprehension are mediated by partially overlapping brain networks. These findings are discussed in light of previous work on the neural basis of arithmetic ability and its relationship to language. Published by Elsevier Ltd.

Keywords: Aphasia; Arithmetic; Neuroimaging; Supramarginal gyrus; Inferior parietal cortex; Language comprehension

Does language underlie our ability to do arithmetic? This question has sparked debate among scientists from many fields. For example, recent research has suggested that people from cultures that do not use counting numbers are less able to perform calculations (Pica, Lemer, Izard, & Dehaene, 2004), suggesting a dependence of arithmetic on language. On the other hand, research in young children suggests that numerical understanding arises independently of language (Gelman & Butterworth, 2005), and a recent study showed that monkeys perform quantitative comparisons much like humans do (Cantlon & Brannon, 2005). Evidence concerning the relationship of language to arithmetic also comes from studies of brain-injured patients. Such studies were initially undertaken by Henschen (as described in Butterworth, 1999), who coined the term acalculia to describe deficits in mathematical ability. In support of the notion that arithmetic and language are inde-

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pendent processes, patients have been described who exhibit relatively preserved mathematical skills in the face of severe language impairment (Cappelletti, Butterworth, & Kopelman, 2001; Rossor, Warrington, & Cipolotti, 1995; Varley, Klessinger, Romanowski, & Siegal, 2005). Other patients exhibit the reverse dissociation, namely, a selective deficit in mathematical skills but relatively preserved language (Cipolotti, Butterworth, & Denes, 1991; Dehaene & Cohen, 1997; Lucchelli & De Renzi, 1993; Warrington, 1982). In contrast, some studies with braininjured patients have noted that arithmetic and linguistic deficits often co-occur (Dahmen, Hartje, Bussing, & Sturm, 1982; Delazer, Girelli, Semenza, & Denes, 1999). These latter studies have suggested that verbal skills play a role in arithmetic ability and/or that common processes subserve both abilities.

A recent study tested the notion that arithmetic and language rely on a common syntax (Varley et al., 2005). For example, knowing who pushed whom in the sentence, *The girl pushed the boy*, is analogous to solving 25 - 10 =. Both items require an understanding of two entities (girl, boy or 25, 10), the action being taken (push or subtract), as well as an appreciation of

^{*} Corresponding author. Tel.: +1 925 372 4649; fax: +1 925 372 2553. *E-mail address:* juliana@ebire.org (J.V. Baldo).

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order (i.e., 25 - 10 is not the same as 10 - 25, nor is a girl pushing a boy the same as a boy pushing a girl). In an attempt to test whether the *syntactic* rules for arithmetic and those for grammar are dissociable, Varley and colleagues tested three language-impaired patients on a series of math and language tasks. They found a dissociation in performance: The three patients were at chance on comprehension of reversible sentences such as those described above, but showed relatively good performance on calculation problems, including long, bracketed equations (e.g., $50 - [(4+7) \times 4]=$). Varley et al. concluded that syntax for language and syntax for arithmetic are distinct processes. Given such results, it was of interest to determine whether brain regions could be found to parallel these behavioral findings in a large patient set.

Previous studies of arithmetic and language have focused mostly on behavioral dissociations, and thus the anatomical basis of this dissociation has not been demonstrated in a single study. The patients in Varley et al.'s study had large left hemisphere lesions, encompassing frontal, temporal, and parietal cortex, and thus localization was not possible (Varley et al., 2005). Lesion and neuroimaging studies of calculation alone consistently point to the inferior parietal lobule and/or inferior parietal sulcus as a brain region critical to numerical ability (Chochon, Cohen, van de Moortele, & Dehaene, 1999; Dehaene & Cohen, 1997; Dehaene, Molko, Cohen, & Wilson, 2004; Delazer et al., 2003; Mayer et al., 2003; Pesenti et al., 2001; Rivera, Reiss, Eckert, & Menon, 2005; Zago et al., 2001). Rote arithmetical facts (e.g., multiplication tables) are sometimes localized in this same region but have also been associated with inferior frontal cortex (Chochon et al., 1999), subcortical regions (Dehaene, & Cohen, 1997), and the angular gyrus (Dehaene, Piazza, Pinel, & Cohen, 2003). Dehaene and colleagues have recently suggested that mathematical fact knowledge, such as overlearned multiplication tables, is mediated by language regions in the left hemisphere, while quantitative processing, which would include subtraction and division, is mediated by the intraparietal sulcal region bilaterally (Dehaene et al., 2004). Given these anatomical findings, one would predict that mathematical ability and language processes would overlap due to their common reliance on peri-Sylvian regions in the case of verbal fact retrieval (such as simple addition and multiplication tables) but not in the case of numerical manipulation (such as subtraction and division).

In the current study, we had the opportunity to look at the relationship between arithmetic and language comprehension in a group of 68 left hemisphere stroke patients on whom detailed neuroimaging and language data were available. Brain lesion data from patients' CT and MRI scans were analyzed using Voxel-based Lesion Symptom Mapping (VLSM), which provides a detailed, functional map of brain regions involved in a given task (Bates et al., 2003). It does so by performing a series of *t*-tests at every voxel, comparing the performance of patients with and without a lesion in each site. Voxels are then colorized according to the size of the resultant statistical values. Patients in the current study were tested on arithmetic (simple addition, subtraction, multiplication, and division) and language comprehension measures that would allow for replication of Varley et al.'s (2005) behavioral study. The measures were matched along a number of task demands: Both tasks were four-choice, forced choice recognition tasks, with two arguments (e.g., 5 and 3; *boy* and *girl*) and a single operator (e.g., +, -, ×, or \div ; a single verb), and neither task required oral output.

If arithmetic operations are indeed distinct from those used in language comprehension, then we should observe a dissociation in patients' performance on the two measures, and presumably a dissociation in the neural regions supporting that performance as well. In light of previous lesion and functional neuroimaging studies, we predicted that arithmetic would be associated with foci in left inferior parietal cortex and that language comprehension performance would be confined to regions within the temporal lobe. If, on the other hand, arithmetic and language comprehension rely on common operations for their execution, we should observe an overlap in brain regions supporting performance on these two measures. Based on previous work (e.g., Dehaene et al., 2004), we further hypothesized that simple addition and multiplication would overlap with temporal lobe language zones and that subtraction and division (requiring more quantitative processing) would be associated with regions in parietal cortex.

1. Methods

1.1. Participants

Participants were 68 patients (16 women and 52 men) who had suffered a single left hemisphere cerebrovascular accident (CVA). Patients were recruited and tested at the Center for Aphasia and Related Disorders, VA Northern California Health Care System. Inclusion criteria for the study included native English proficiency, pre-morbidly right-handed, a single left CVA, and no previous neurologic, psychiatric, or substance abuse history. Mean age of the patients was 61.3 years (range 31–80), mean time post-stroke was 57.4 months (range 4–273), and mean education was 14.2 years (range 5–20). Patients with low education were not excluded, but this variable was used as a covariate in statistical analyses.

The data analyzed in the current study were collected in accordance with the Helsinki Declaration and the Institutional Review Board at the VA. All patients signed informed consent forms prior to participation.

1.2. Materials and procedures

All patients had undergone extensive language and cognitive testing that included both standardized and experimental measures as part of an existing research protocol. In order to obtain a large patient sample sufficient to do detailed lesion analysis, we analyzed previously collected arithmetic and language data, and thus were somewhat constrained as far as stimulus materials. The arithmetic and language comprehension tasks were chosen because they bore the most resemblance to stimulus materials used by Varley et al. (2005) and because the two tasks were procedurally analogous. Thus, for the purposes of this study, arithmetic was defined as simple calculation with two operands, and language comprehension was defined as auditory comprehension of reversible sentences on a picture-matching task.

The language comprehension task required patients to point to one of four pictures that best matched a sentence spoken by the examiner (Curtiss-Yamada Comprehensive Language Evaluation, subtests 4.2 and 5.6; Curtiss & Yamada, 1988). The sentences were reversible and included both active (e.g. *The girl is pulling the boy*) and passive (e.g., *The boy is being pulled by the girl*) sentences. The four choices included a picture of the target (e.g., a picture of a girl pulling a boy) and three distractors, one of which was a reversed picture (e.g., a picture of a boy pulling a girl). The active and passive items were presented as blocked subtests and were administered with several other intervening subtests.

Arithmetic performance was measured by the calculation subtest from the Western Aphasia Battery (WAB; Kertesz, 1982). This task included 12 prob-

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lems of addition, subtraction, multiplication, and division (see Appendix A for stimuli). Patients saw a single problem printed on a card and had to point to the correct answer out of four choices. The three distractors included responses that represented a different mathematical operation (e.g., for the problem 6 - 2 =, the choices were 8, 4, 12, and 3).

Patients' overall speech and language status was evaluated with the WAB, which includes subtests that assess fluency, repetition, naming, and comprehension. Patients' classifications based on the WAB included Broca's aphasia (n = 17), Wernicke's aphasia (n = 7), conduction aphasia (n = 6), anomic aphasia (n = 14), global aphasia (n = 1), transcortical sensory aphasia (n = 1), unclassifiable (n = 3), and within normal limits (n = 19). This latter classification is given to patients who score above 93.7 on the WAB, although they may still have residual language symptoms (e.g., mild word-finding difficulty). Patients were excluded from the study if they did not understand task instructions.

Brain correlates of the arithmetic and language measures were investigated using VLSM methodology, which has been described previously (Bates et al., 2003). Patients' lesions were imaged by MRI or CT at least three weeks post-onset and typically within three months of behavioral testing. The lesions were then reconstructed onto standardized brain templates by a board-certified neurologist who was blind to the patients' behavioral presentation. Lesion reconstructions and behavioral data for all 68 patients were then analyzed using VLSM. VLSM performs a *t*-test at every voxel to compare behavioral performance in patients with and without a lesion in that voxel. The number of years post-stroke was used as a covariate in the VLSM analyses to ensure that this factor did not affect the findings. A colorized map was then generated based on the resultant *p*-values at each voxel. For the current study, a correction was performed such that the false discovery rate was set at p=.05 (Benjamini & Hochberg, 1995). Also, *t*-tests were confined to those voxels where there were at least 15 patients in each group (i.e., with and without a lesion).

2. Results

Data from the arithmetic and language comprehension measures were analyzed with percent correct on each measure as the dependent variable, where chance performance was 25% correct. Mean performance on arithmetic was 80.6% correct (range 0–100), and mean performance on language comprehension was 74.0% correct (range 20–100). The relationship between arithmetic and comprehension performance was analyzed with a Pearson correlation (two-tailed), which was significant, r = .48, p < .001, suggesting a relationship between these two measures (see Fig. 1). As can be seen, however, a number of patients







Fig. 2. Arithmetic and comprehension performance across aphasia subgroups. WNL = within normal limits on the Western Aphasia Battery; conduction = conduction aphasia. The sample sizes were as follows: anomic (n = 14), Broca's (n = 17), conduction (n = 6), Wernicke's (n = 7), and WNL (n = 19).

exhibited a dissociation in performance: some patients had high scores on arithmetic despite poor comprehension, while other patients had high scores on comprehension and relatively poor arithmetic performance.

To assess the impact of different language profiles on mathematical ability, we ran a mixed ANCOVA with aphasia subgroup as a between-subjects variable (anomic, Broca's, Wernicke's, conduction, WNL), measure (arithmetic versus comprehension) as a within-subjects variable, and age, education, lesion volume, and months post-onset as covariates. Patients with global aphasia (n = 1), transcortical sensory aphasia (n = 1), and those who were unclassifiable (n=3) were excluded due to their small ns. Also, gender was initially analyzed as a potential variable, but there were no significant effects or interactions, and thus the following analyses are collapsed across gender. There was a significant main effect of aphasia subgroup, F(4,(55) = 25.68, p < .001, as some subgroups performed more poorly (Broca's, and Wernicke's) relative to other subgroups (WNL and anomic). There was also a main effect of measure, F(1,(58) = 8.75, p < .01, although this appeared to be driven mostly by the reduced comprehension performance in Broca's and Wernicke's patients (see Fig. 2). Consistent with this effect, there was a significant interaction of aphasia subgroup and measure, F(4, 55) = 4.93, p < .01, as the discrepancy between arithmetic and comprehension scores varied for the different patient subgroups. Specifically, Broca's and Wernicke's patients performed better on arithmetic relative to comprehension, while the other subgroups performed comparably on both measures.

Due to the distinction made in the literature between numerical analysis versus rote arithmetic knowledge, we separately analyzed the four different operations: addition, subtraction, multiplication, and division. Subtraction and division tend to fall into the former category since they are not memorized, whereas simple addition and multiplication tend to be more automatic and overlearned. We analyzed the data with a 2×4 mixed ANCOVA with patient type as a between-subjects

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Table 1 Percent correct across arithmetic operations by aphasia subtype

	n	Addition	Subtraction	Multiplication	Division
WNL	19	100	100	100	93
Broca's	17	86	84	65	38
Anomic	14	95	95	86	64
Wernicke's	7	86	95	67	38
Conduction	6	83	89	72	33
Unclassifiable	3	89	100	100	78
TC sensory	1	100	100	0	0
Global	1	0	0	0	0
Total	68	91	92	79	59

variable (aphasic versus WNL), operation (addition, subtraction, multiplication, and division) as a within-subjects variable, and age, years of education, lesion volume, and months post-onset as covariates. There was a main effect of patient type, F(1, 61) = 4.47, p < .05, as patients with aphasia performed worse overall. There was no main effect of operation. There was a significant interaction of patient type × operation, F(3, 183) = 3.61, p < .05, as multiplication and division performance were disproportionately impaired in the aphasic patients (see Table 1 for a breakdown of scores by aphasia subtype). Next, we used VLSM to identify brain regions associated with performance on the arithmetic and comprehension measures in all 68 patients (see Fig. 3a–d). The overall arithmetic score was most significantly affected by lesions in the inferior parietal lobe (Brodmann areas (BA) 39 and 40), seen as the red area on slice 9 in Fig. 3a. In contrast, the comprehension measure was most affected by lesions in the middle and superior temporal gyri (BA 21, 22 and 37). However, there was also a considerable degree of overlap between the two measures, as both maps showed significant foci in inferior frontal cortex (BA 45/47), portions of the middle and superior temporal gyri (BA 21, 22 and 37), pre-and post-central gyri (BA 1–4), and inferior parietal cortex (BA 39 and 40).

In order to differentiate brain regions associated with arithmetic and language comprehension alone, we computed VLSM subtraction maps of arithmetic minus comprehension and comprehension minus arithmetic (see Fig. 3c and d). When comprehension was subtracted from arithmetic, the inferior parietal focus remained, along with small foci in inferior frontal cortex (BA 45/47) and the post-central gyrus. When arithmetic was subtracted from comprehension, foci in the middle and superior temporal gyri predominated, along with foci in the inferior frontal gyrus (BA 45/47) and post-central gyrus. Thus, there were distinct foci associated with arithmetic and compre-



Fig. 3. VLSM maps showing significant foci associated with arithmetic performance (a) and comprehension (b). Voxels with larger p-values are plotted as hotter colors on the maps. p-values are in $-\log 10$ scale. The bottom row shows VLSM subtraction maps for arithmetic minus comprehension (c), and comprehension minus arithmetic (d).

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Fig. 4. VLSM subtraction maps of subtraction minus comprehension (left) and division minus comprehension (right).

hension, as well as significant regions of overlap between the two maps.

Next, we generated separate VLSM subtraction maps for the four different math operations relative to language comprehension. Interestingly, the resultant addition and multiplication maps revealed no significant foci (except for a small area of white matter for multiplication on slice 5), suggesting that the brain regions mediating these arithmetic operations overlapped almost completely with those subserving the language comprehension measure. In contrast, the subtraction and division maps revealed a number of significant foci, including superior parietal cortex (BA 7), pre-central gyrus, and inferior frontal gyrus (BA 44) for subtraction, and inferior parietal cortex (BA 39 and 40) and inferior frontal cortex (BA 45/47) for division (see Fig. 4).

3. Discussion

The current study addressed the relationship between mathematical ability and language by comparing performance of a large group of left hemisphere patients on arithmetic and language comprehension measures. We found a significant correlation between the measures, suggesting a relationship between arithmetic and language. At the same time, however, there were a number of patients who showed a dissociation of performance, such that for some patients, their arithmetic performance was relatively good compared to their comprehension while other patients showed the reverse dissociation. Thus, the behavioral data evidenced three possible patterns of affected performance, namely, arithmetic impairment with preserved language comprehension, comprehension impairment with preserved arithmetic ability, and concomitant deficits of arithmetic and comprehension.

In order to understand the anatomical basis for the behavioral data, we analyzed brain regions associated with arithmetic versus language comprehension, using Voxel-based Lesion Symptom Mapping (VLSM). Arithmetic was associated with inferior parietal cortex (supramarginal and angular gyri). This area has been implicated in the literature as a region important for arithmetic ability (Chochon et al., 1999; Dehaene et al., 2004; Mayer et al., 2003). For example, patients with acalculia in the absence of aphasia have been reported to have lesions in this region

(Warrington, 1982). In contrast, the comprehension map showed a large number of significant foci that predominated in the middle and superior temporal gyri, which is consistent with previous studies of language comprehension (Dronkers, Wilkins, Van Valin, Redfern, & Jaeger, 2004).

There were also a number of brain regions in common between the arithmetic and comprehension maps, including portions of the middle and superior temporal gyri and the inferior frontal gyrus. These findings suggest that, to some degree, arithmetic and language processes rely on common substrates. Inferior frontal cortex in particular has been implicated in a number of studies of arithmetic (Chochon et al., 1999; Rickard et al., 2000; Tohgi et al., 1995), but it may also represent an amodal region subserving working memory and cognitive control functions. Depending on the way that arithmetic ability is tested in a particular study, this region may or may not be engaged. For example, if patients are allowed to write while they are working out math problems, the act of writing may act as a buttress for reduced working memory that would otherwise compromise arithmetic performance.

Previous studies of mathematical ability have observed a behavioral dissociation between knowledge for rote arithmetical facts (e.g., $5 \times 6 = 30$) versus the capacity for numerical manipulation (e.g., 23 - 16 = 7; Dehaene & Cohen, 1997; Venkatraman, Siong, Chee, & Ansari, 2006; but see van Harskamp, Rudge, & Cipolotti, 2002). This dissociation has also been discussed as that between semantic versus procedural memory, respectively (Diesfeldt, 1993). Dehaene and Cohen showed an anatomical dissociation between these abilities in two patients with acalculia. They found that rote arithmetic ability (e.g., multiplication tables) was associated with left subcortical structures while numerical manipulation (e.g., subtraction and division problems) was associated with bilateral inferior parietal pathways. In a newer version of their model, Dehaene and colleagues have focused on three separate aspects of numerical processing, each with its own putative anatomic substrate: (1) quantitative processing (e.g., magnitude comparison, subtraction) mediated by bilateral intraparietal sulci; (2) verbal fact knowledge (e.g., multiplication tables) mediated by left peri-sylvian regions; (3) spatial attention (e.g., capacity for number line understanding) mediated by superior parietal cortex (Dehaene et al., 2003,

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2004). We were not able to assess these three different components fully in the current study, since we analyzed standardized measures from archived data and there were limited data points. However, the VLSM comparison of the four different arithmetic subtests did provide some insight. First, simple addition and multiplication (relying more on verbal fact knowledge) overlapped almost completely with the language comprehension map. In contrast, subtraction and division (requiring more quantitative processing) were associated with a number of significant foci, which included superior and inferior parietal cortex, respectively. These findings are somewhat consistent with Dehaene et al.'s model. One inconsistency in the current data is the fact that, behaviorally, multiplication and division were the subtests most disproportionately impaired in aphasic patients relative to nonaphasic patients, which would lead one to think that these two subtests should be anatomically most associated with language areas. Further studies with a broader array of mathematical stimuli are clearly needed to address this discrepancy.

A limitation of the current study is that our analyses were confined to the left hemisphere. There is some evidence from functional neuroimaging studies that the right hemisphere is also engaged during arithmetic processing (Chochon et al., 1999; Pesenti et al., 2001; Zago et al., 2001). The more verbally-mediated the mathematical operation (e.g., multiplication tables), the more likely the left hemisphere is to play a role, while less automatic operations may engage more right hemisphere processes. However, given the majority of left hemisphere activations in neuroimaging studies of math as well as the lesion literature, there appears to be a much larger role for the left hemisphere in arithmetic ability overall.

Current results may shed light on some of the controversy in the literature regarding the relationship between arithmetic and linguistic abilities. That is, some previous work with braininjured patients has found a direct relationship between language and math (Dahmen et al., 1982; Delazer et al., 1999), while other work has suggested that these abilities rely on distinct cognitive substrates (Cappelletti et al., 2001; Varley et al., 2005). In the current study, there was a significant correlation between language comprehension and arithmetic performance across our large group of patients, which is consistent with the former position. However, inspection of individual data revealed that there were a number of patients who showed discrepant performance, which is consistent with the latter position. Which position is supported likely depends on the site and size of patients' lesions and the number of patients tested. Lesions that involve only the inferior parietal lobule with little infringement on temporal language areas may be more likely to lead to arithmetic deficits alone, whereas larger lesions that also involve nearby regions in left temporal cortex are likely to lead to concomitant comprehension deficits. Last, it may be possible to see arithmetic deficits in patients with lesions in the overlapping regions we observed, such as the inferior frontal gyrus (Tohgi et al., 1995).

In conclusion, we found behavioral and anatomical evidence consistent with the notion of partially overlapping networks subserving language comprehension and arithmetic. The extent of this overlap is likely dependent on which aspect(s) of mathematical ability is tested and the way it is evaluated. Along with previous findings, these data suggest that language is related to arithmetic ability but that it is not always critical for its execution.

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Appendix A

Arithmetic stimuli on the WAB calculation subtest.

Addition	Subtraction	Multiplication	Division	
5+4=	6-2=	4 × 2 =	8÷4=	
6+2=	9 – 7 =	$5 \times 3 =$	$64 \div 8 =$	
4 + 3 =	8 – 3 =	$6 \times 7 =$	$18 \div 3 =$	

References

- Bates, E., Wilson, S. M., Saygin, A. P., Dick, F., Sereno, M. I., Knight, R. T., et al. (2003). Voxel-based lesion-symptom mapping. *Nature Neuroscience*, 6(5), 448–450.
- Benjamini, Y., & Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society, Series B*, 57, 289–300.
- Butterworth, B. (1999). *What counts: How every brain is hardwired for math.* New York: The Free Press.
- Cantlon, J. F., & Brannon, E. M. (2005). Semantic congruity affects numerical judgments similarly in monkeys and humans. *Proceedings of the National Academy of Sciences USA*, 102(45), 16507–16511.
- Cappelletti, M., Butterworth, B., & Kopelman, M. (2001). Spared numerical abilities in a case of semantic dementia. *Neuropsychologia*, 39(11), 1224– 1239.
- Chochon, F., Cohen, L., van de Moortele, P. F., & Dehaene, S. (1999). Differential contributions of the left and right inferior parietal lobules to number processing. *Journal of Cognitive Neuroscience*, 11(6), 617–630.
- Cipolotti, L., Butterworth, B., & Denes, G. (1991). A specific deficit for numbers in a case of dense acalculia. *Brain*, 114(Pt 6), 2619–2637.
- Curtiss, S., & Yamada, J. (1988). *Curtiss-Yamada Comprehensive Language Evaluation* (unpublished test).
- Dahmen, W., Hartje, W., Bussing, A., & Sturm, W. (1982). Disorders of calculation in aphasic patients—spatial and verbal components. *Neuropsychologia*, 20(2), 145–153.
- Dehaene, S., & Cohen, L. (1997). Cerebral pathways for calculation: Double dissociation between rote verbal and quantitative knowledge of arithmetic. *Cortex*, 33(2), 219–250.
- Dehaene, S., Molko, N., Cohen, L., & Wilson, A. J. (2004). Arithmetic and the brain. *Current Opinion in Neurobiology*, 14(2), 218–224.
- Dehaene, S., Piazza, M., Pinel, P., & Cohen, L. (2003). Three parietal circuits for number processing. *Cognitive Neuropsychology*, 20, 487–506.
- Delazer, M., Domahs, F., Bartha, L., Brenneis, C., Lochy, A., Trieb, T., et al. (2003). Learning complex arithmetic—an fMRI study. *Cognitive Brain Research*, 18(1), 76–88.
- Delazer, M., Girelli, L., Semenza, C., & Denes, G. (1999). Numerical skills and aphasia. *Journal of the International Neuropsychological Society*, 5(3), 213–221.
- Diesfeldt, H. F. A. (1993). Progressive decline of semantic memory with preservation of number processing and calculation. *Behavioral Neurology*, 6, 239–242.

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- Dronkers, N. F., Wilkins, D. P., Van Valin, R. D., Jr., Redfern, B. B., & Jaeger, J. J. (2004). Lesion analysis of the brain areas involved in language comprehension. *Cognition*, 92(1–2), 145–177.
- Gelman, R., & Butterworth, B. (2005). Number and language: How are they related? *Trends in Cognitive Science*, 9(1), 6–10.

Kertesz, A. (1982). Western aphasia battery. New York: Grune & Stratton.

- Lucchelli, F., & De Renzi, E. (1993). Primary dyscalculia after a medial frontal lesion of the left hemisphere. *Journal of Neurology, Neurosurgery, and Psychiatry*, 56(3), 304–307.
- Mayer, E., Reicherts, M., Deloche, G., Willadino-Braga, L., Taussik, I., Dordain, M., et al. (2003). Number processing after stroke: Anatomoclinical correlations in oral and written codes. *Journal of the International Neuropsychological Society*, 9(6), 899–912.
- Pesenti, M., Zago, L., Crivello, F., Mellet, E., Samson, D., Duroux, B., et al. (2001). Mental calculation in a prodigy is sustained by right prefrontal and medial temporal areas. *Nature Neuroscience*, 4(1), 103–107.
- Pica, P., Lemer, C., Izard, V., & Dehaene, S. (2004). Exact and approximate arithmetic in an Amazonian indigene group. *Science*, 306(5695), 499– 503.
- Rickard, T. C., Romero, S. G., Basso, G., Wharton, C., Flitman, S., & Grafman, J. (2000). The calculating brain: An fMRI study. *Neuropsychologia*, 38(3), 325–335.

- Rivera, S. M., Reiss, A. L., Eckert, M. A., & Menon, V. (2005). Developmental changes in mental arithmetic: Evidence for increased functional specialization in the left inferior parietal cortex. *Cerebral Cortex*, 15, 1779–1790.
- Rossor, M. N., Warrington, E. K., & Cipolotti, L. (1995). The isolation of calculation skills. *Journal of Neurology*, 242(2), 78–81.
- Tohgi, H., Saitoh, K., Takahashi, S., Takahashi, H., Utsugisawa, K., Yonezawa, H., et al. (1995). Agraphia and acalculia after a left prefrontal (F1, F2) infarction. *Journal of Neurology, Neurosurgery, and Psychiatry*, 58(5), 629–632.
- van Harskamp, N. J., Rudge, P., & Cipolotti, L. (2002). Are multiplication facts implemented by the left supramarginal and angular gyri? *Neuropsychologia*, 40(11), 1786–1793.
- Varley, R. A., Klessinger, N. J., Romanowski, C. A., & Siegal, M. (2005). Agrammatic but numerate. *Proceedings of the National Academy of Sciences USA*, 102(9), 3519–3524.
- Venkatraman, V., Siong, S. C., Chee, M. W., & Ansari, D. (2006). Effect of language switching on arithmetic: A bilingual fMRI study. *Journal of Cognitive Neuroscience*, 18, 64–74.
- Warrington, E. K. (1982). The fractionation of arithmetical skills: A single case study. *Quarterly Journal of Experimental Psychology A*, 34(Pt 1), 31–51.
- Zago, L., Pesenti, M., Mellet, E., Crivello, F., Mazoyer, B., & Tzourio-Mazoyer, N. (2001). Neural correlates of simple and complex mental calculation. *Neuroimage*, 13(2), 314–327.