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Cortical circuits for mathematical knowledge: evidence for a major subdivision within the brain's semantic networks

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Is mathematical language similar to natural language? Are language areas used by mathematicians when they do mathematics? And does the brain comprise a generic semantic system that stores mathematical knowledge alongside knowledge of history, geography or famous people? Here, we refute those views by reviewing three functional MRI studies of the representation and manipulation of high-level mathematical knowledge in professional mathematicians. The results reveal that brain activity during professional mathematical reflection spares perisylvian language-related brain regions as well as temporal lobe areas classically involved in general semantic knowledge. Instead, mathematical reflection recycles bilateral intraparietal and ventral temporal regions involved in elementary number sense. Even simple fact retrieval, such as remembering that 'the sine function is periodical' or that 'London buses are red', activates dissociated areas for math versus non-math knowledge. Together with other fMRI and recent intracranial studies, our results indicated a major separation between two brain networks for mathematical and non-mathematical semantics, which goes a long way to explain a variety of facts in neuroimaging, neuropsychology and developmental disorders.

This article is part of a discussion meeting issue 'The origins of numerical abilities'.

1. Introduction

Many scientists share the intuition that although mathematics is organized as a language, this language differs from, and even dispenses with, the structures of natural spoken language. In 1943, Hadamard asked his fellow mathematicians to introspect about their mental processes. Albert Einstein replied that 'words and language, whether written or spoken, do not seem to play any part in my thought processes. The psychical entities which seem to serve as elements in thought are certain signs and more or less clear images which can be 'voluntarily' reproduced and combined . . .. The above mentioned elements are, in my case of visual and muscular type' [1]. This famous quote is not isolated, and many mathematicians including Hadamard himself, have reported a similar introspection.

This view, however, has been highly debated and disagrees with an influential view in cognitive science that considers mathematics as an offshoot of the human capacity for language. According to Noam Chomsky, 'the origin of the mathematical capacity [lies in] an abstraction from linguistic operations' [2]. Indeed, although mathematics call upon a dedicated inventory of symbols and words, both natural language and mathematics share the need for a recursion operation that creates embedded tree structures [3]. Furthermore, some mathematical concepts seem to be language-dependent, for instance exact arithmetic facts may

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be stored in a language-specific form [4,5]. In particular, overlearned multiplication tables, which are learned by rote, put a greater emphasis on language areas than subtraction, which requires quantity manipulations [6,7].

In summary, the relationships between mathematical thinking and natural language processing remain uncertain. Here we review several recent fMRI and behavioural studies led in various populations that all converge in showing that mathematical thinking can be dissociated from sentence-level language processing and from general semantic thinking.

2. Imaging the brain of professional mathematicians

Recently, cognitive neuroscience has started to address the link between mathematics and language, mainly through studies of numerical abilities. However, many mathematicians argue that elementary arithmetic represents only a very small subset of the variety of domains that mathematics encompasses. In three fMRI experiments, we therefore studied the brain representation of advanced mathematical concepts in professional mathematicians [8].

(a) Experiment 1

In our first experiment [8], 15 professional mathematicians and 15 humanities specialists, all researchers or teachers, were presented with spoken mathematical and non-mathematical statements with high-level content and were asked to judge them as true, false or meaningless during a 4 s reflection period. Mathematical statements spanned four domains: algebra, analysis, topology and geometry, and non-mathematical statements enquired knowledge of nature and history (see [8] for a detailed description of stimuli, procedure and participants). At the end of the fMRI exam, participants were also presented with seven categories of images including words, numbers and mathematical formulae, and performed an additional localizer [9] including simple subtractions and sentence listening. After fMRI, they were presented again with all math and non-math statements and, for each of them, were asked to provide ratings about various aspects including their 'imageability' or their difficulty.

Within the group of mathematicians, we found that a specific set of brain regions was activated during mathematical reflection periods. These regions included bilateral intraparietal sulci (IPS), bilateral inferior temporal regions (IT), and bilateral sites in dorsolateral, superior and mesial prefrontal cortex (PFC). All of these regions showed greater activation to meaningful mathematical statements than to meaningful non-mathematical statements (figure 1). They also showed greater responses to meaningful compared to meaningless mathematical statements.

Two major characteristics of this particular set of brain areas have been identified. First, they dissociate from regions involved in the processing of general semantic knowledge. Indeed, examining regions activated by non-mathematical versus mathematical reflection, we found the inferior angular gyrus (AG), the anterior part of the middle temporal gyrus (aMTG), the ventral inferior frontal gyrus (IFG pars orbitalis) and an extended sector of mesial PFC (mesial parts of Brodmann's areas 9, 10 and 11). Similar results were found for the contrast of meaningful versus meaningless non-mathematical judgements. Crucially, there was virtually no intersection of the areas for meaningful > meaningless mathematical reflection and for meaningful > meaningless non-mathematical reflection.

Because the activations observed during mathematical reflection overlapped with a 'multiple demand system' [10] active during various difficult cognitive tasks involving executive control, it was important to control for task difficulty. We used participants' difficulty ratings to verify that easy math statements continued to activate the math-related network more than difficult non-math statements did. Our results therefore could not be due to a greater task difficulty for math relative to non-math statements.

This network for mathematical thinking also differed from the areas of the left temporal lobe and left IFG (Broca's area) classically involved in processing the syntax of spoken and written sentences [11,12]. A region-of-interest analysis performed in eight language-related regions during sentence presentation showed that, if anything, mathematics called less upon those language regions than did general semantic reasoning. Whole-brain imaging results confirmed that cerebral responses to mathematical reflection spared areas activated by sentence processing.

Second, brain regions activated by mathematical reflection activate for all math-related tasks, regardless of difficulty or any specific mathematical content. Indeed, all mathematical domains tested in this experiment (algebra, analysis, topology and geometry) activated these regions. Furthermore, even simple calculation (e.g. compute 7-3) or the mere presentation of mathematical formulae or numbers suffice to active them.

Does this result mean that our findings are artefactual and simply due to the presence of numbers in our mathematical stimuli? No. We carefully avoided any direct mention of numbers in our high-level mathematical statements, and the results remained essentially unchanged after excluding all statements containing indirect references to numbers or to fractions (e.g. $\mathbb{R}^2$, *unit* sphere, *semi*-major axis, etc). Thus, these overlapping activations could not be explained by a shared numerical component. Furthermore, the overlap was confirmed by sensitive single-subjects representational similarity analyses. In bilateral IPS and IT regions of interest, at the single-subject level, we found a high degree of similarity between the activation patterns evoked by mathematical reflection and those evoked by calculation or the recognition of numbers and mathematical expressions—compared to the activation patterns evoked by non-mathematical reflection, sentence listening, face or words recognition.

In summary, high-level mathematics, at a high level of detail, makes use of the very same regions involved in elementary arithmetic and number recognition. Indeed, the regions that were activated during the recognition of Arabic numerals in all subjects were expanded in professional mathematicians and became responsive to abstract expression such as integrals or differential equations. The findings are compatible with the idea that high-level mathematics 'recycles' brain areas involved in simpler concepts such as number or space [13].

(b) Control studies

In two further studies, we sought to replicate the observed dissociation between mathematical and general semantic processing, and to probe the nature of the boundary between language and mathematical processes [14].

In a first control experiment, similar to experiment 1, we probed the influence of semantic content on the math/

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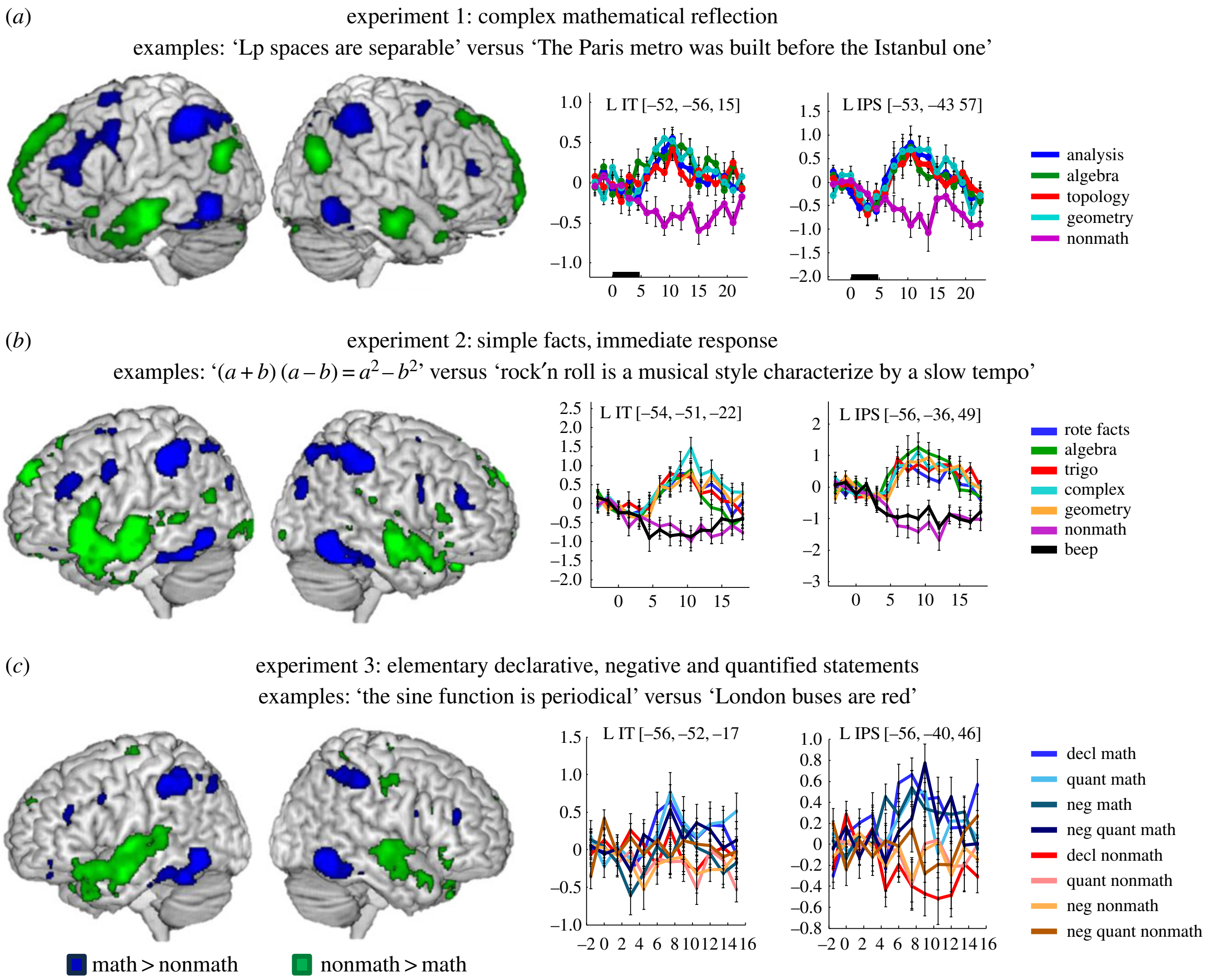

Figure 1. A reproducible dissociation between mathematical and general semantic knowledge. The figure shows brain activity in professional mathematicians evoked by (*a*) complex mathematical and general semantic statements [8], (*b*) simpler facts asking for an immediate response and (*c*) elementary declarative, negative and quantified statements. (Left) Brain maps showing areas of greater activation during reflection on mathematical statements versus non-mathematical statements (blue) or vice versa (green). (Right) Average fMRI signal in representative math-related areas. Top panel, Copyright © 2016 National Academy of Sciences.

language separation. Specifically, we assessed whether much simpler mathematical problems that even called upon rote memory also activated our math-related network. This time, spoken mathematical and non-mathematical statements were either true or false (meaningless statements were eliminated), and the mathematicians were asked to decide, as fast as possible (within 2.5 s) whether they were true or false. Mathematical statements consisted in well-known mathematical facts such as classical algebraic identities that are known by rote (e.g. $a^2 - b^2 = (a - b)(a + b)$), trigonometric formulae, properties of complex numbers and simple statements in non-metric Euclidean geometry. These were compared to declarative non-mathematical facts about arts. Low-level auditory controls consisting of series of beeps were also presented.

In a second control experiment, with the same subjects, we asked whether, within the statements of everyday language, the mere presence of some minimal logical operators could suffice to activate the math-related network. Specifically, we tested the influence of quantifiers and negation in mathematical and non-mathematical processing. Therefore, the true or false statements were either declarative sentences ('The sine function is periodical'; 'London buses are red.), or included the quantifier 'some' ('Some matrices are diagonalizable'; 'Some ocean currents are warm'), or a negation ('Hyperboloids are not connected'; 'Orange blossoms are not perfumed'), or both quantifier and negation ('Some order relations are not transitive'; 'Some plants are not climbing').

In both experiments, we replicated the extensive activations elicited by math more than non-math statements in bilateral IPS, bilateral IT regions and bilateral superior and middle frontal regions (BA 9 and 46) (figure 1). In the first control experiment, these regions again activated systematically for all types of math and deactivated for non-math judgements. In the second control experiment, they responded more to math than non-math statements, irrespective of the presence of quantifiers and negation. Interestingly, while frontal activation became weaker as the statements became easier, suggesting that frontal cortex was primarily called upon during intense and prolonged mathematical reflection, intraparietal and IT activations to mathematics remained strong even when subjects judged very simple and overlearned facts, suggesting that these regions are involved in the core knowledge of math.

The reverse contrast of non-math versus math reflection yielded activation in the bilateral anterior and posterior temporal lobe and bilateral inferior frontal areas in both experiments, largely replicating our previous findings [8] and previous meta-analyses of the brain areas for general semantic knowledge [15] (figure 1). Interestingly, as non-mathematical problems became easier, extensive anterior temporal

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activations remained, but activations at the temporo-parietal junction and in mesial frontal regions progressively disappeared, suggesting that the latter areas may be involved in sustained working memory and/or the mental inferences involved in plausible reasoning and intentional communication. A contrario, the bilateral anterior temporal lobe is confirmed as a core player in semantic knowledge—but at the exclusion of mathematical knowledge, which involves an entirely different network.

Taken together, these results indicate the presence of a common neural substrate for math processing in the intraparietal sulcus and ventral temporal cortex, independent of content and difficulty, with additional activations extending into dorsal PFC depending on the strategy and effort deployed to understand and solve the problem. Furthermore, this math-related network dissociates from other regions involved in sentence processing and semantic integration. This is true even in the case of very simple math and non-math statements that differ minimally in their surface form, and even in the presence of minimal logical operators such as quantifiers or negation.

3. Convergence with other studies

Several studies have shown a similar separation between mathematics and language. While space precludes a detailed appraisal, we now briefly review this convergence of data from a variety of fields.

(a) Brain-imaging studies of mathematical processing

In agreement with the present results, several brain-imaging studies indicate that separate neural substrates are involved in algebraic versus syntactic manipulations. For example, Maruyama *et al.* [16] showed that classical language areas were not recruited when students were asked to process the syntax of nested algebraic expressions such as '$(((3 + 4) - 2) + 5) - 1$'. Monti and collaborators [17–19] used fMRI to compare extremely well-matched tasks that required participants either to perform syntactic manipulations on sentences, or logical or algebraic manipulations on statements of equivalent complexity (e.g. '$x + y = z$; $y = z - x$; are these equivalent statements?). They found that left fronto-temporal perisylvian regions were more recruited by linguistic than by algebraic judgements, while the latter recruited areas such as the IPS, previously reported for numerical [20,21] or spatial [22,23] cognition.

A few observations have indicated that language-related areas such as the posterior temporal/angular gyrus region can be activated during the processing of number and arithmetic. A general rule-of-thumb, however, is that these activations occur whenever subjects process numerical materials in a rote manner, for instance when remembering exact addition facts such 'fifty-four plus thirteen is sixty-seven' [4] or when drilling multiplication facts [7]. Demonstrably, such rote learning involves a language-specific memory code [4,5]. The inferior frontal region ('Broca's area') is also activated when subjects name complex numerals such as 'three hundred twenty-four', in direct proportion to the complexity of the syntactic structures involved [24]. A contrario, the bulk of the evidence indicates that such language circuitry is not activated whenever a deeper, semantic representation of numbers is accessed and manipulated.

(b) fMRI of semantic networks

New data-driven analysis methods have been applied in order to clarify how different cortical sectors contribute to the semantic processing of words [25]. A large amount of fMRI data was recorded in individual subjects while they listened to narrative stories that referred to a great variety of contents, including an occasional mention of numerical information. The results revealed a systematic mapping of semantic information onto different sectors of the cortex. In particular, bilateral parietal, inferior frontal and inferior temporal regions were particularly selective to numerical information, along with words referring to units of measure, positions and distances (figure 2). On the contrary, social and relational words were particularly represented at various specialized sites along the superior and middle temporal region and the IFG. This separation into two distinct semantic networks appeared as a major principle of brain organization, because it corresponded to the first two principal components of variation in word-related brain activity [25] (figure 2).

(c) Intracranial recordings

Electrophysiological signals recorded from surface and depth electrodes in epilepsy patients confirm the joint contributions of the bilateral intraparietal sulcus and of the ventral infero-temporal cortex in number processing and calculation. Shum *et al.* [26] were the first to demonstrate the bilateral involvement of IT sites in number processing. These regions were initially called 'visual number form areas' because of their strong response to Arabic digits more than other visual stimuli, and of their proximity to the 'visual word form area' [27] and other category-specific regions of the ventral visual stream [28]. However, a similar activation has now been found in congenitally blind people trained to recognize roman numbers versus letters using a visual-to-music sensory-substitution device [29]. Furthermore, IT regions do not activate only during the visual recognition of numbers, but also during calculation [30,31] (figure 3) and during advanced mathematical reflection in professional mathematicians [8] (figure 1). Daitch *et al.* [30] report how different sectors of IT cortex respond specifically either to the presentation of numbers, to the presentation of operation symbols, or to calculation *per se*. These recent intracranial studies also show that (i) parietal and IT activity is modulated by problem difficulty [31]; (ii) number-active sites in ventral temporal regions exhibit a response pattern similar to and simultaneous with math-active parietal regions during elementary calculation [30]. Finally, in direct agreement with Huth *et al.*'s [25] fMRI findings, parietal electrodes sensitive to calculation are transiently and specifically activated whenever numbers and other quantities are mentioned in the midst of spontaneous speech production [32].

(d) Neuropsychological dissociations

Within the domain of neuropsychology, i.e. the study of cognitive deficits in brain-lesioned adults, double dissociations have been observed. It is, indeed, quite frequent for patients who suffer from acquired acalculia (impaired number processing and calculation, typically due to a left parietal lesion) to exhibit preserved language skills. With the exception of the multiplication table, whose impairment is frequently associated with deficits in other aspects of rote verbal memory, calculation

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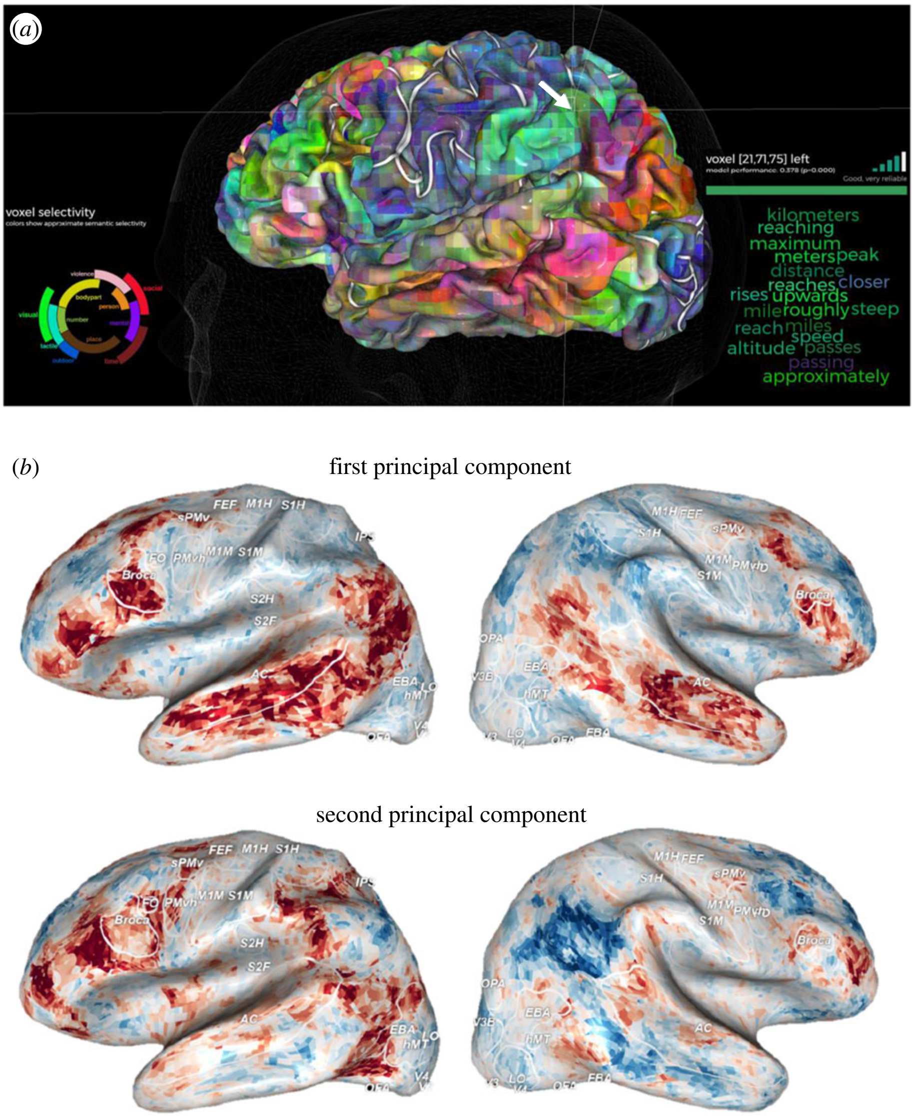

Figure 2. Brain activation elicited by word categories contained in naturalistic narrative stories [25]. (*a*) Snapshot from the explorer proposed by the Gallant lab (http://gallantlab.org/huth2016/), showing a parietal site sensitive to various quantity- and math-related concepts. (*b*) Brain maps of the first and second principal components of cerebral activation to narrative stories (image courtesy of Alexander Huth and Jack Gallant).

skills can be selectively impaired, or on the contrary, selectively spared relative to linguistic skills [33–35]. Most strikingly, patients with severe aphasia may exhibit preserved mathematical and algebraic skills [36,37]. In particular, these studies revealed the case of a patient with extensive lesions in the left temporal lobe, who failed in matching semantically reversible sentences such as 'the man killed the lion' to the corresponding pictures, but performed well on algebraic and calculation problems involving the four basic operations on either abstract, numerical or fractional terms, and even when those mathematical expressions required mental transformations or simplifications. Dissociations between impaired semantic knowledge and preserved knowledge of numbers and arithmetic are also observed in many cases of semantic dementia [38,39].

(e) Developmental deficits

Studies of developmental disorders such as dyscalculia versus dyslexia have also revealed a frequent dissociation between mathematical and linguistic processes. In one study [40], 8- and 9-year-old children with dyscalculia showed specific difficulties in task involving numbers and arithmetic, but not in non-numerical verbal tasks. Conversely, dyslexic children performed well in numerical calculation or comparison, but found all verbal tasks more challenging (including the naming of number words). At a later age, this dissociation may persist [41]: dyslexic students experience difficulties in associating letters with their sound but can normally associate Arabic numerals with their corresponding magnitude, whereas dyscalculic students show the reverse impairment.

The centrality of the dissociation between math and non-math knowledge is also reflected in the existence of developmental disorders of primarily genetic origin that cut through those two domains. For instance, children with Williams syndrome possess an extended vocabulary and sophisticated syntactic structures, yet their numerical and visuospatial cognition fails to develop normally, in agreement with the presence of cortical anomalies in the intraparietal sulcus [42,43]. Conversely, children with autism spectrum disorder, particularly Asperger syndrome, often exhibit preserved or even extraordinary developed numerical and visuospatial skills, in the face of severe deficits of language, communication, and social cognition, accompanied by cortical abnormalities along the superior temporal sulcus [44–46]. In the future, such observations may play a key role in the search for genes

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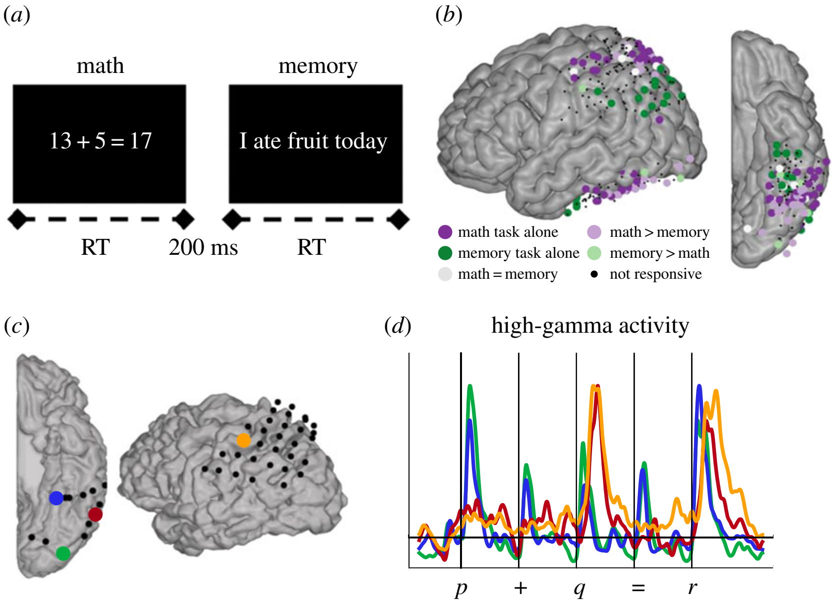

Figure 3. Intracranial evidence for a cortical network involved in mental arithmetic. (*a*,*b*) Parietal and ventrolateral temporal electrodes responding to math (purple) versus verbal memory (green) tasks. (*c*,*d*) High-frequency broadband time course in math-active sites within four anatomical regions in an exemplar subject ([30]; Copyright © 2016 National Academy of Sciences).

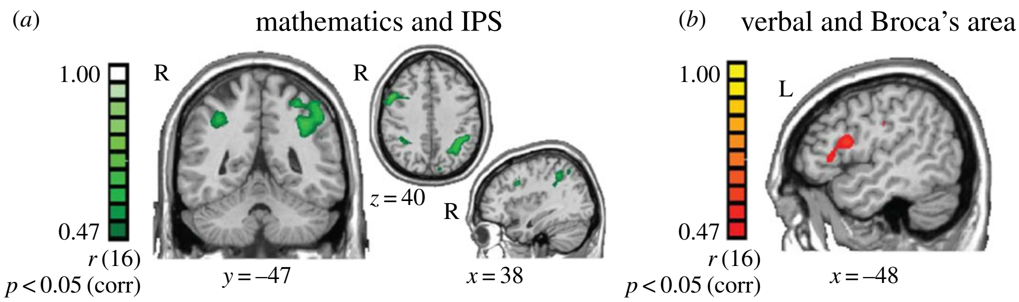

Figure 4. Dissociation between mathematical and verbal knowledge in 4- to 10-year-old children. Brain regions showing a significant correlation between children's neural maturity index (derived from fMRI signals) and their performance on mathematical test (*a*), and verbal test (*b*) ([51], reproduced with permission).

involved in the differential development of the corresponding brain circuits.

(f) Child development

Developmental studies have revealed that preverbal infants possess sophisticated proto-mathematical intuitions prior to language acquisition. For instance, newborns familiarized with a certain number of auditory syllables looked longer at an image containing the same number of objects than a different number [47]. They were thus able to transfer abstract numerical information from one modality to another. Furthermore, their performance was modulated by the ratio between congruent and incongruent numbers, in a way analogous to older children and adults. Neuroimaging studies of 6- and 7-month-old preverbal infants have also evidenced a numerical distance effect, following Weber's law, which appeared over right posterior sites in studies using electroencephalography [48] or near-infrared spectroscopy [49]. Later in childhood, brain imaging of 3-year-old children has shown neural tuning to numerosities in the intraparietal sulcus [50]. Crucially, an fMRI study of 4-year-old children watching 'Sesame Street' educational videos has revealed a dissociation comparable to the present one: whenever the videos talked about numbers, activation was found in intraparietal cortex, while letter-related materials elicited activation in Broca's area (figure 4). Furthermore, children's activity in parietal cortex predicted their performance in mathematical tests, while activity in Broca's area predicted performance in verbal tests [51].

(g) Cognitive anthropology

In the past decade, anthropological studies of Amazon tribes have brought another contribution to the idea that mathematics and language involve separate processes. Those studies show that human adults and children who are largely deprived of formal schooling and possess an impoverished lexicon for numerical and geometrical concepts may still possess sophisticated mathematical intuitions [52,53]. In particular, despite the fact that Munduruku speakers do not have number words above 5, they can estimate, represent, compare and even perform approximate arithmetical operations such as addition or subtraction with far larger numbers than they can name [52]. Similar conclusions can be made in the domain of geometry. Although Munduruku people do not have geometrical words in their language, they can spontaneously identify and use a wide range of geometrical concepts such as shapes (circle, square, right-angled triangle, etc.), Euclidean properties (parallelism, alignment, etc.), topological properties (closure, connectedness, etc.), metric properties (distance, proportion, etc.) and symmetries [53]. Our recent work suggests that the capacity to combine those mathematical primitives into

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nested structures is independent of other linguistic operations: memory for geometrical sequences involves a 'compression' of the information into a mental 'language of geometry', endowed with primitives and recursive combinatorial rules, but independent of natural language [54].

4. Discussion

Evidence from several domains of cognitive science converges to support the idea that the ability to understand the 'language of mathematics' dissociates from other aspects of linguistic or semantic processing. The studies reviewed here suggest that the behavioural dissociation between mathematical and linguistic skills is accompanied by a major neural dissociation between math-responsive brain regions and other areas involved in language processing and semantics. Such a clear-cut separation may explain why acquired or developmental mathematical impairments often leave other aspects of language processing and comprehension untouched, or vice versa. Indeed, this dissociation seems to operate at both syntactic and semantic levels. In the same way that algebraic or geometrical syntax does not seem to recruit linguistic syntax areas [16,55], mathematical semantic content elicits activation that spares classical regions involved in the semantic processing of words or sentences [15].

We note in passing that even if mathematical semantic storage is dissociated from other semantic storage, such a separation obviously does not imply that the math-related network is disconnected from the language network—on the contrary, our fMRI experiments imply that when subjects hear a mathematical statement, language areas are activated first, during the sentence processing period, and only then, if the content is mathematically relevant does processing continue within the math network [8]. An early proposal for the architecture of the number system, the triple-code model [56], postulated bidirectional exchanges between the intraparietal sulcus (representing quantity and other aspects of number meaning), the lateral IT regions (representing the visual number form of Arabic digits) and the left-hemispheric language system, including the left AG (involved in the representation and storage of numbers and arithmetic facts in verbal form). Our data do not contradict this model, given that listening to mathematical sentences activated language areas involved in syntax processing and multiword semantic integration such as the left perisylvian regions and the left AG. This activation was lower for mathematical than for non-mathematical sentences, but nevertheless significant, especially in the initial phase of sentence processing. More crucially, during the sentence listening period of our original experiment, a small transient activation was observed in the left AG in the contrast for meaningful compared to meaningless statements, both within math and non-math domains (see figure S12 in [8]). This finding agrees with previous suggestions that the AG might be involved in the semantic integration of individual words or concepts [57]. Surprisingly, however, rote algebraic facts did not activate the AG more than other mathematical statements in our second experiment, but continued to activate the classical math network. Prior findings indicated that the AG might be involved in the retrieval of verbal numerical facts such as multiplication facts [6,7], but the present results suggest that algebraic identities may not be stored in the same format.

Our results also challenge the triple-code model at the level of the lateral IT activation. While this region was thought to be associated with the visual form of numbers [26], we now see that it can also activate in the complete absence of visual stimuli, both during calculation and during high-level mathematics [8]. For semantics, it has been suggested that the left MTG/ITG/fusiform gyrus 'may be a principal site for storage of perceptual information about objects and their attributes' [58]. By extension, we suggest that lateral IT regions might also be a site for storage of information about the attributes of mathematical concepts [31].

Our fMRI findings, in turn, raise many questions regarding the operational definition and intrinsic characteristics of the fields of 'mathematics' and 'language', such that they activate two dissociated brain networks. First, what is the exact extension of the domain of mathematics? The math-responsive circuit that we observed in professional mathematicians also appears to be involved in a broad range of cognitive processes. It activates in a variety of effortful problem-solving tasks akin to IQ tests [10], as well as in domain-general logical, inferential or relational reasoning [19,59,60]. Even reflection on physics concepts such as 'energy' or 'wavelength' elicits partially similar activations [61]. Nevertheless, the hypothesis of a domain-general 'multiple demand' system [10] does not fit with the observation that this network fails to activate during equally flexible and long-lasting reflection on non-math-related concepts [8]. While arithmetic, logic, geometry, math, physics and IQ tests all share a family resemblance, identifying exactly what these different domains share, such that they solicit similar neural substrates, remains an open question for future research—indeed, one that may ultimately illuminate the classical philosophical debate on the nature of mathematical knowledge [62].

Second, where does language stop and mathematics begin? Though they involve distinct brain areas, language and mathematics are often intertwined. On the one hand, mathematical words are essential to the proper communication among mathematicians, and may also play a key role in conceptual change such as the acquisition of the ability to understand and compute with large numbers [4,5,52]. On the other hand, spontaneous discourse makes frequent recourse to mathematical concepts such as number, quantities, distances or measurement units—and when it does, math-responsive areas immediately activate [25,32]. Natural language also makes use of distinctions of geometrical, logical or numerical origin, such as spatial prepositions, quantifiers and the singular/dual/plural distinction. Delimiting, within natural language, the nature of the processes and concepts that do or do not activate the math-responsive network is a second open question that remains to be thoroughly investigated.

Data accessibility. This article has no additional data.

Competing interests. We declare we have no competing interests.

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