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Marie Amalric

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Université Pierre et Marie Curie

École Doctorale Cerveau Cognition Comportement

NeuroSpin / Unicog

ÉTUDE DES MÉCANISMES CÉRÉBRAUX D'APPRENTISSAGE ET DE TRAITEMENT DES CONCEPTS MATHÉMATIQUES DE HAUT NIVEAU

Par Marie AMALRIC

Thèse de doctorat de neurosciences cognitives

Dirigée par Stanislas DEHAENE

Présentée et soutenue publiquement le 8 septembre 2017

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Université Pierre et Marie Curie

École Doctorale Cerveau Cognition Comportement

NeuroSpin / Unicog

STUDY OF THE BRAIN MECHANISMS INVOLVED IN THE LEARNING AND PROCESSING OF HIGH-LEVEL MATHEMATICAL CONCEPTS

Marie AMALRIC

Dissertation submitted for the degree of Doctor of Philosophy

in Cognitive Neurosciences

Supervised by Pr. Stanislas DEHAENE

Publicly defended on the 8th of September 2017

Jury:

Pr. Elizabeth SPELKE	Harvard University	Rapporteur
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Abstract

How does the human brain conceptualize abstract ideas? In particular, what is the origin of mathematical activity, especially when it is associated with high-level of abstraction? Cognitive sciences have now started to investigate this question that has been of great interest to philosophers, mathematicians and educators for a long time. While studies have so far focused on arithmetic processing, my PhD work aims at further investigating the dissociation between mathematical and language processing in the case of advanced mathematical knowledge, which gives better account for the diversity of mathematical activities (analysis, algebra, topology, geometry ...) than simple arithmetic. My PhD work is based on two main axes: (1) identifying the cognitive mechanisms and neural correlates of high-level mathematical reflection; (2) studying the learning processes of abstract mathematical rules.

In a first part, I present three fMRI studies that involved professional mathematicians (including the exceptional case of three blind mathematicians), in which subjects had to evaluate the truth-value of advanced spoken mathematical and nonmathematical statements. Even formulated as sentences, all mathematical statements, regardless of their difficulty, domain, or participants' visual experience, activated a reproducible set of bilateral intraparietal and ventrolateral temporal regions that completely dissociated from areas related to language and general-knowledge semantics, but rather coincided with sites activated by simple arithmetic. Conversely, all nonmathematical statements focusing on history, arts or everyday general knowledge, even including logical operations such as quantifiers or negation, activated bilateral middle and superior temporal sulci and left inferior frontal gyrus.

In a second part, I investigate the human acquisition of mathematical rules in a non-linguistic context. I present a behavioral study – involving 5-years-old children, adults and teenagers from the Amazon who lack formal education and have impoverished numerical and geometrical lexicon as well as French adults – suggesting that the human understanding of regular geometrical spatial sequences, regardless of participants' age or school education, relies on the compression of these sequences to minimal description length in a recursive language of thought independent of natural spoken language.

The results reported in the present work tend to show that mathematical activity recycles brain areas involved in basic knowledge of number and space, and dissociates from language processing at both syntactic and semantic level. They also pave the way to further investigation of mathematical learning processes and raise new questions regarding the operational definition of the fields of “mathematics” and “language” at the brain level.

Résumé

Comment le cerveau humain parvient-il à conceptualiser des idées abstraites ? Quelle est en particulier l'origine de l'activité mathématique lorsqu'elle associée à un haut niveau d'abstraction ? Cette question qui intéresse depuis longtemps philosophes, mathématiciens et enseignants, commence aujourd'hui à être abordée par les neurosciences cognitives, et ce, en grande partie par le biais d'études portant sur l'arithmétique élémentaire. Toutefois, les mathématiques recouvrent de nombreuses disciplines telles que l'algèbre, l'analyse ou la géométrie et ne sauraient être réduites à la compréhension des nombres. Aussi dans mon travail de thèse, j'ai privilégié l'étude de la manipulation d'idées mathématiques plus avancées et des processus cérébraux impliqués dans leur apprentissage. Ma thèse s'organise autour de ces deux axes principaux.

La première partie vise à identifier les corrélats neuronaux de la réflexion mathématique de haut niveau. Je présente les résultats de trois expériences en IRMf, menées chez des mathématiciens professionnels (dont trois mathématiciens non-voyants) qui devaient évaluer la valeur de vérité d'affirmations mathématiques et non-mathématiques énoncées oralement. Même formulées comme des phrases, toutes les affirmations mathématiques, quels que soient leur difficulté, domaine ou l'expérience visuelle des participants, impliquent systématiquement des régions bilatérales intrapariétales et inféro-temporales. Ces régions sont totalement dissociées des aires reliées au langage et au traitement sémantique, mais coïncident avec des zones activées par l'arithmétique élémentaire. A l'inverse, même lorsqu'elles comprennent des opérateurs logiques (quantificateurs, négation), les affirmations non-mathématiques (portant sur l'histoire, les arts, la géologie, la faune etc...), activent les sillons temporaux supérieurs bilatéraux et le gyrus frontal inférieur gauche.

La seconde partie étudie les mécanismes d'apprentissage de règles mathématiques abstraites. Je présente une étude comportementale menée chez des enfants de 5 ans, chez des adultes et adolescents vivant en Amazonie, dont le langage est pauvre en mots numériques et géométriques et qui disposant d'un accès limité à l'éducation, ainsi que chez des adultes français. Les résultats suggèrent que le cerveau humain est muni d'un « langage de la pensée » récursif, indépendant du langage parlé naturel, qui lui permet de compresser et ainsi de comprendre et mémoriser des séquences spatiales présentant des régularités géométriques.

En conclusion, l'activité mathématique semble « recycler » des aires cérébrales impliquées dans la connaissance élémentaire des nombres et de l'espace et se dissocier de la manipulation du langage, tant au niveau sémantique que syntaxique. Ces résultats ouvrent finalement la voie à une étude plus approfondie des mécanismes d'apprentissage des mathématiques à l'école ou encore de ce que signifie réellement "faire des mathématiques" pour le cerveau humain.

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Publications of the author

Articles included in the thesis

Some chapters included in this thesis have been accepted in or submitted to international peer reviewed journals and were slightly adapted to increase consistency and facilitate readability.

CHAPTER 1. **Amalric, M.** & Dehaene, S. *Origins of the brain networks for advanced mathematics in expert mathematicians*. PNAS, 04/2016; 113(18). DOI:10.1073/pnas.1603205113

CHAPTER 2. **Amalric, M.** & Dehaene, S. *Dissociated cortical networks for mathematical and non-mathematical knowledge*. In prep.

CHAPTER 3. **Amalric, M.**, Denghien, I., Dehaene, S. *On the role of visual experience in mathematical development: Evidence from blind mathematicians*. Developmental Cognitive Neuroscience, in press.

CHAPTER 4. **Amalric M.**, Wang, L., Pica, P., Figueira, S., Sigman, M., Dehaene, S. *The language of geometry: Fast comprehension of geometrical primitives and rules in human adults and preschoolers*. Plos Computational Biology, 2017. DOI:10.1371/journal.pcbi.1005273

Other articles

Amalric M., & Dehaene S. *Cortical Circuits for Mathematical Knowledge: Evidence for a Major Subdivision within the Brain's Semantic Networks*. Philosophical Transactions of the Royal Society B, in press.

Wang L., **Amalric M.**, Fang W., Jiang X., Pallier C., Figueira S., Sigman M., Dehaene S. *Representation of spatial sequences using nested rules in human prefrontal cortex*. In prep.

Romano, S., Salles, A., **Amalric, M.**, Dehaene, S., Sigman, M., Figueira, S., *Bayesian selection of grammar productions for the language of thought*. Behavior Research Methods, submitted.

Introduction

Literature review

Where have mathematical ideas originated from and how did they emerge? These questions of already great interest of intellectuals in Antiquity nowadays continue to spark attention of educators, philosophers and scientists.

1. Mathematical foundations in the brain

1.1. Number and space as universal mental constructions

Looking at mathematical history, it appears that numbers and space have been at the center of mathematics in many human civilizations around the world. The oldest trace of Mathematics might even go back to Upper Paleolithic. The 20,000 years-old Ishango bone, with its three columns carved all along, made archaeologists think that it might be a tally stick, used to construct a specific numerical system. Later, in the Fertile Crescent, contemporaneously with cuneiform script, appeared the first – sexagesimal – positional numerical system. 2000 years before Christ, Babylonian already knew the four operations (addition, subtraction, multiplication and division) and even invented algorithms to extract square roots or to solve second order equations. At the same time, Egyptians invented a – decimal – additional system, knew the four operations, extracted square roots, solved simple equations, used fractions, and addressed many geometrical problems related to areas and volumes. Chinese, from the XIth century B.C., invented a binary system in which they were able to represent even negative, decimal and large numbers, and developed sophisticated algorithms and abacus to solve geometrical, trigonometrical and algebraic problems. In pre-Columbian civilizations, mathematics was essentially numerical and mostly concerned architecture and astronomy. Mayas invented a base 20 numerical system and were the first to use a number zero. Later, Incas formalized a decimal system for statistical purpose and kept track of it thanks to knotted ropes. All these examples tend to show that, behind the diversity of formalisms, numerical and spatial knowledge encompasses universal core concepts.

1.1.1. The case of numbers and arithmetic

Numbers have first been studied by cognitive sciences. Over the past decades, the existence of a “number sense”, shared by many animal species including human babies and adults, has been suggested. Indeed, number appears to be one of the fundamental parameters through which human perceive the external world. Some recent studies have shown that the human brain automatically extracts sets numerosity, i.e. the numerical perceptual parameter contained in object sets. A visual

illusion on sets of dots, created by Burr and Ross, suggested that there exists a brain system that extracts and can adapt to numerical information (Burr and Ross, 2008). Number actually seems to be more easily perceived than other visual dimensions such as surface, size or spacing (Park et al., 2016). In this last study, authors have shown that 3 orthogonal dimensions – numerosity, size and spacing – could represent the entire parameter space describing the perception of dot arrays. Authors then probed how variations in these three properties quantitatively changed participants' event-related-potentials (ERPs), and suggested that very precocious ERP activity was more sensitive to numerosity than to other visual dimension.

The brain system perceiving numerosity seems to be present in all human adults and babies. Indeed, 5-years-old infants proved to be able to manipulate abstract amodal representations of numbers to compare quantities or perform simple nonsymbolic additions (Barth et al., 2005). Moreover, Jordan and Brannon (2006) have shown that 7-month-old babies are able to match the number of faces they saw with the number of voices they heard. A similar result was also found in 6-month-old babies (Feigenson, 2011). In a seminal study, 5-month-old also proved to be able to perform basic arithmetical operations with small numbers (Wynn, 1992a). Even 2-days-old human babies are already able to represent numerical information (Izard et al., 2009). In this last experiment, babies were first exposed to auditory series containing a fixed number of syllables (“tu-tu-tu-tu”; “ra-ra-ra-ra”). They were then presented with visual stimuli containing a certain number of objects. Babies looked longer when visual and auditory numbers were matched than when they sufficiently differed (e.g. 4 vs 12). All these findings tend to show that infants are able to detect numerosity, in an abstract manner independent of modality.

Moreover, ethology has revealed that many animal species, from insects, amphibians, birds and fishes, to mammals, including horses, felines and non-human primates, also possess numerical abilities. For example, studies of lions and hyenas in the wild have shown that they can adapt their behavior according to their estimations of the relative number of their intruders. This results in greater vigilance when they have lower numerical advantage, or more risky attitude and even attack when they evaluate pertaining to the largest group (Benson-Amram et al., 2011). Agrillo et al. (2010) have also shown that newborn fishes can discriminate small quantities up to 3, and can identify larger quantities after 40 days of life when they are reared in groups. Rugani et al. (2009) have used imprinting to familiarize newborn chicks to certain numbers, meaning that chicks were reared from birth with a certain number (here 5) of identical objects that were spontaneously considered as “social companions”. After a few days of life, chicks were placed in front of two opaque screens behind which experimenter made imprinted objects disappear either one by one or all at a glance, so that one screen hid 3 objects and the other hid 2 objects. In both conditions, chicks preferentially

headed to the screen hiding the biggest amount of imprinted objects, thus suggesting that they were able to discriminate sets of 3 versus 2 objects, without any training, even when sets were not directly visible but memorized. Finally, a lot of research has now been conducted with monkeys. For example, Cantlon et al. (2016) have shown that rhesus monkeys can approximately perform additions and subtractions. Moreover, Matsuzawa and colleagues have shown that chimpanzees can be trained to recognize and associate Arabic numerals from 0 to 19 to corresponding sets of objects (Biro and Matsuzawa, 2001). They can also understand ordinal aspects of numbers and perform very well in tasks requiring sorting numerals in ascending order (Inoue and Matsuzawa, 2007).

Interestingly, numerical perception in all animal species shares the same characteristic: a distance effect measured on a logarithmic scale (Feigenson et al., 2004). In other words, the larger and closer numbers are, the more difficult is the task (figure 0.1). Moyer and Landauer (1967) were the first to verify that Weber’s law applies to number discrimination in adults, whose reaction time was systematically influenced by both the distance and the absolute magnitude of the values represented by two Arabic numerals they were asked to compare. These effects have then been observed in different numerical notations (Buckley and Gillman, 1974; Dehaene et al., 1990; Hinrichs et al., 1981).

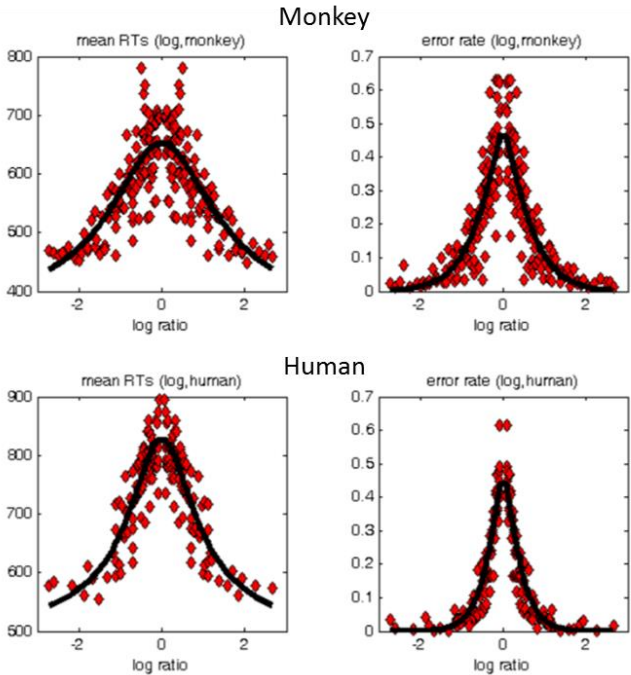


Figure 0.1. Extreme similarity between humans’ and monkeys’ behavior during numerosity comparison task. Adapted from (Dehaene, 2007) reanalyzing data from (Cantlon and Brannon, 2006). Both error rates and reaction times show distance effects in both humans and monkeys. Indeed, error rate and reaction time increase whenever the log ratio between compared numerosities gets closer to 0 (i.e. compared numerosities are close).

These effects have also been observed in monkeys. In particular, untrained monkeys have proved to be able to discriminate numerosities with accuracy depending on their ratio (Hauser et al., 2003). Interestingly, Cantlon and Brannon (2006) have directly compared humans’ and rhesus macaques’ performance and have shown that macaques were able to choose the smaller of two sets of dots,

regardless of covariate parameters such as density, surface or perimeter, with a distance effect similar to humans performing the same comparison task. Indeed, both groups exhibited decrease in accuracy and increase in response time as the ratio between sets approached 1 (figure 0.1). Furthermore, classical effects of human arithmetic have been found in rhesus macaques trained to perform non-symbolic additions and subtractions (Cantlon et al., 2016) and untrained monkeys who spontaneously compute additions of large numbers (Flombaum et al., 2005). Adapting Wynn's seminal paradigm (Wynn, 1992a) originally introduced to study additions and subtractions in human infants, Flombaum et al. (2005) have shown that rhesus macaques looked longer at impossible compared to possible results of additions of two sets of lemons, only when values were large and differed by a ratio of 1:2 but not when they differed by a ratio of 2:3. According to (Cantlon et al., 2016), monkeys exhibited a ratio effect for addition and subtraction; they exhibited a residual size effect (i.e. systematic decline of accuracy as the magnitude of operands increase) after the ratio effect was regressed out; and they also performed better when the two operands in additions were identical, revealing a classical tie effect. Altogether, these results tend to show that the human brain system for numerosity is inherited from evolutionarily ancient system.

This system has therefore been considered as one of the fundamental "core systems" that all humans possess. According to Spelke's "core knowledge theory", there are five such innate domain-specific and encapsulated systems for objects, actions, social partners, numbers and space (or geometry).

1.1.2. The case of space and geometry

The idea that some geometric intuitions are available in human minds from birth can already been found in Antique Greece. In *the Meno*, Plato leads a young uneducated slave to discover by himself how to double the surface of square, suggesting that some geometric properties are spontaneously accessible. In the past decades, cognitive studies conducted in animals, babies and uneducated adults have revealed that all humans are endowed with evolutionarily ancient basic geometrical intuitions about spatial relations, shapes and their properties.

Three main paradigms have been used in these studies: reorientation tasks, map tasks and intruder tasks. In reorientation tasks, the subject explores a room that has a specific geometric shape, in which a target is hidden (it can be a toy for kids, food for animals). The subject is then disoriented and reintroduced into the room where he is asked to grab the target. In map tasks, subjects are presented with a minimal abstract map constituted of geometrical shapes showing the location of an object they will have to search for or place in a room whose configuration is depicted by the map. Finally, in intruder tasks, subjects are showed a slide with 6 different visual objects that

all share a specific geometric property but one. This different one, the intruder, has to be picked by the subject.

These different types of tasks have revealed the existence of two separate core knowledge systems for geometry: one navigational system that extracts information about distances and directions, and one system responsible for the detection of shapes and their properties such as length, angles, symmetries or topology.

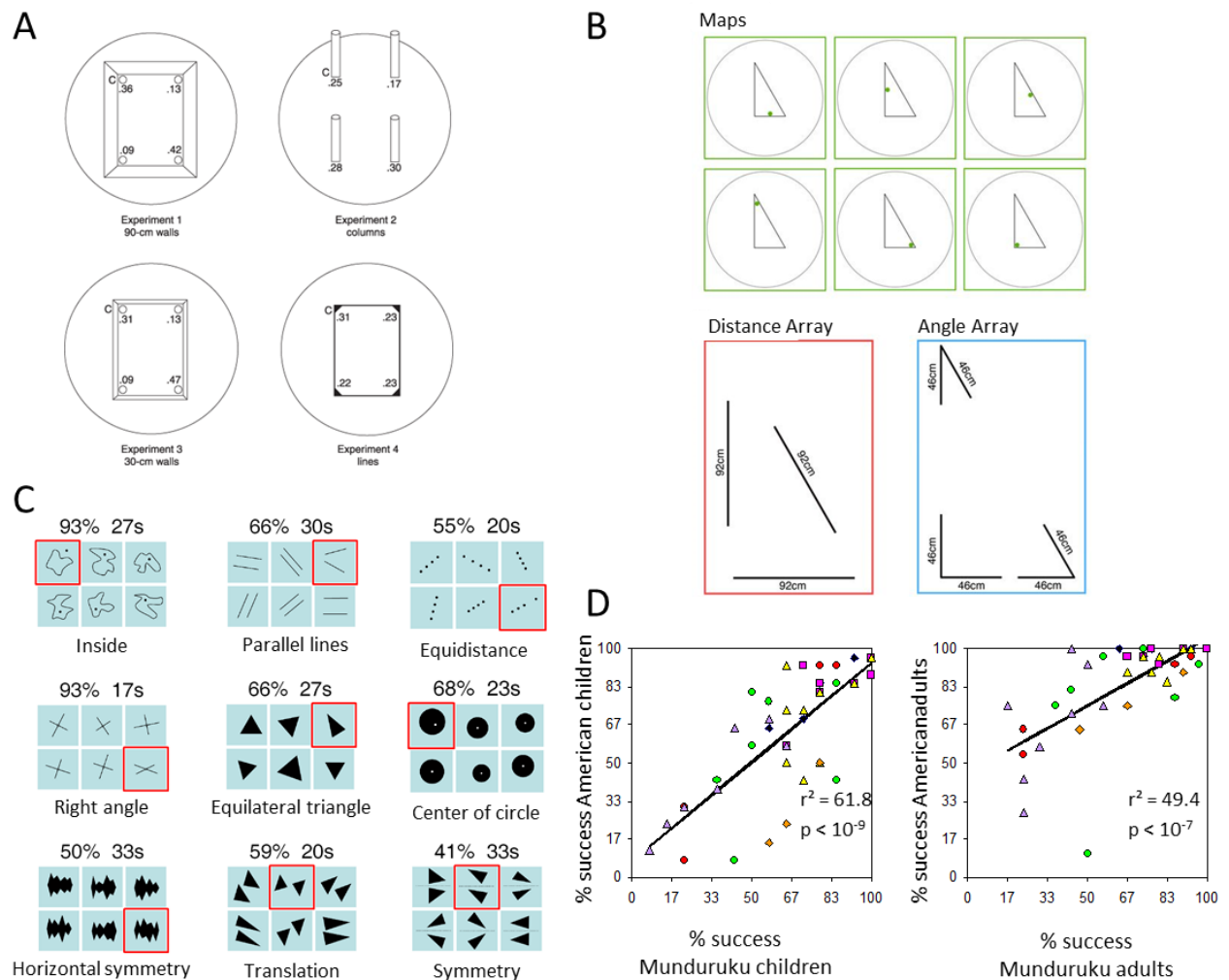


Figure 0.2. Typical paradigms used in studies investigating geometrical skills. (A) adapted from (Lee and Spelke, 2008): exemplar of reorientation task comparing different environment layouts over a rectangular shape. (B) adapted from (Dillon et al., 2013): exemplar of map task. In this experiment, children used six different maps to navigate within triangular arrays. (C), (D) adapted from (Dehaene et al., 2006): intruder task. (C) Examples of slides in which 5 images share a geometric property that is absent from the last image. (D) Strong correlation between performances of Mundurucu and American children and adults in this intruder task.

In reorientation tasks, subjects proved to make primary use of geometrical cues such as distance and orientation to navigate the environment, before using visual landmarks such as colors or distinctive signs. Interestingly, these geometric information failed to be extracted from 2D layouts, and information about length and angles led subjects to systematic and typical errors (Lee and

Spelke, 2008; Spelke and Lee, 2012, figure 0.2). For example, 30-month-old children will look for a sticker in every four corners of a square room delimited by walls of different lengths, but they will look for the sticker only in two diagonal pertinent corners in a fragmented rectangle made of walls of the same length but at different distances (Lee et al., 2012). Similar findings underlying spontaneous sensitivity to geometrical cues have been exhibited in several animal species including monkeys (Deipolyi et al., 2001), rats (Cheng, 1986), chicks (Chiandetti and Vallortigara, 2007), fishes (Sovrano et al., 2002) and even ants (Wystrach and Beugnon, 2009). Adaptation of such navigation tasks to computer testing has revealed that even 5-month-old children devoid of experience with independent locomotion, were sensitive to geometrical cues present in an enclosed triangular layout (Lourenco and Huttenlocher, 2008).

Intruder tasks have nevertheless suggested that humans possess spontaneous intuitions of 2D shapes and their properties. In particular, a seminal study have revealed that, although Amazonian Mundurucu people are largely deprived of formal schooling and possess an impoverished lexicon for numerical and geometrical concepts, they can spontaneously identify 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 (Dehaene et al., 2006). Notably, arguing for a certain universality of the patterns of difficulty of the tested geometrical concepts, strong correlations were found between Mundurucus children and adults' performance, and American children and adults' performance (Dehaene et al., 2006, figure 0.2). This original intruder task was then adapted to test specifically for the human ability to extract information about angles, length and direction (or sense) from 2D displays (Izard et al., 2011a). In trials where the intruder varied only in size, angle or sense, as well as in trials where another dimension interfered so that various deviants could be picked, all age groups (from 3 to 30) proved to detect better angle and size intruders than sense deviants. In particular young 3/4-years-old children used only angle and size, thus confirming the existence of two separate geometrical systems, one that recollects direction and orientation from 3D navigational environment, and another that extracts length and angle from 2D shapes (Spelke et al., 2010). Note that these results find support in previous habituation tasks showing the sensitivity to angle and length of young and even a few-hours-old infants (Newcombe et al., 1999; Slater et al., 1991)

Finally, map tasks have revealed that children and uneducated adults are able to read and use geometrical information contained in abstract maps, even though it is the first time they are presented with such tool, to locate a target object (Dehaene et al., 2006; Izard et al., 2014). Interestingly, 4-years-old children provided with a geometrical map show flexible use of the two core knowledge systems to navigate in a triangular room delimited either by three distant walls or three

distinct corners (figure 0.2). Although there is no evidence for any transfer from one system to another, they were able to extract in both situations pertinent information respectively about distance and angle (Dillon et al., 2013).

1.1.3. Other intuitive mathematical components: probabilities and inferences

Recent studies have suggested that babies are able, very early in their development, to internalize and update probabilities of external events, to evaluate the plausibility of simultaneous hypotheses and to use probabilities to generate predictions and compare them to incoming external data. In particular, babies exhibit sensitivity to statistical regularities and are able to make bidirectional probabilistic inferences.

First, an important study conducted by Saffran et al. (1996) has revealed that 8-month-old infants are able to learn temporal statistical regularities. Infants were presented with a succession of syllables constituted of four different 3-syllabic “words” randomly chained, such that within a given “word” the transition probability between syllables was equal to 1, but transition probabilities between the last syllable of a “word” and the first syllable of another “word” was equal to 1/3. Authors showed that infants’ looking time was greater for new or rare isolated words than for words of the initial sequence. Their result therefore suggested that young infants spontaneously and quickly built an internal representation of statistical information available in the sequence and used it to detect novel words that did not follow initial probabilities. Moreover, Marcus et al. (1999) have suggested that this capacity for statistical learning does not only apply to specific items but can also underlie the acquisition of more abstract “algebraic patterns”, i.e. the abstract rule, underlying a set of specific sequences. By 7 months of age, infants can already understand that the set {aab, ccd, eeg} includes sequences systematically composed with a repetition of any two items followed by a third one. Such capacity for regularity learning does not seem to be grounded in a specific sensory modality but is rather abstract. Indeed, a few hours-old newborns were already able to identify regularities in a visual sequence of geometrical shapes forming pairs presented in random order (Bulf et al., 2011).

Second, using situations in which subjects were confronted to random sampling of collections of objects with different properties, some studies have now suggested that young children possess a certain sense of probabilistic inference (Denison et al., 2013; Denison and Xu, 2010; Kushnir et al., 2010; Teglas et al., 2011; Téglás et al., 2007; Xu and Denison, 2009; Xu and Garcia, 2008). In 2007, Téglás and Bonatti have shown that 12-month-old babies can anticipate the probability of a forthcoming event. In their experiment, babies are presented with objects of different colors colliding in a box, e.g. 3 blue objects and a yellow one. The box then becomes opaque and one object gets out of the box. When the least probable object gets out of the box, e.g. the only

yellow one; babies look longer, therefore indicating their surprise (figure 0.3). Authors showed that neither physical characteristics of the final screen nor frequency played a role in infants' behavior, which was instead driven by a feeling of improbability (Téglás et al., 2007).

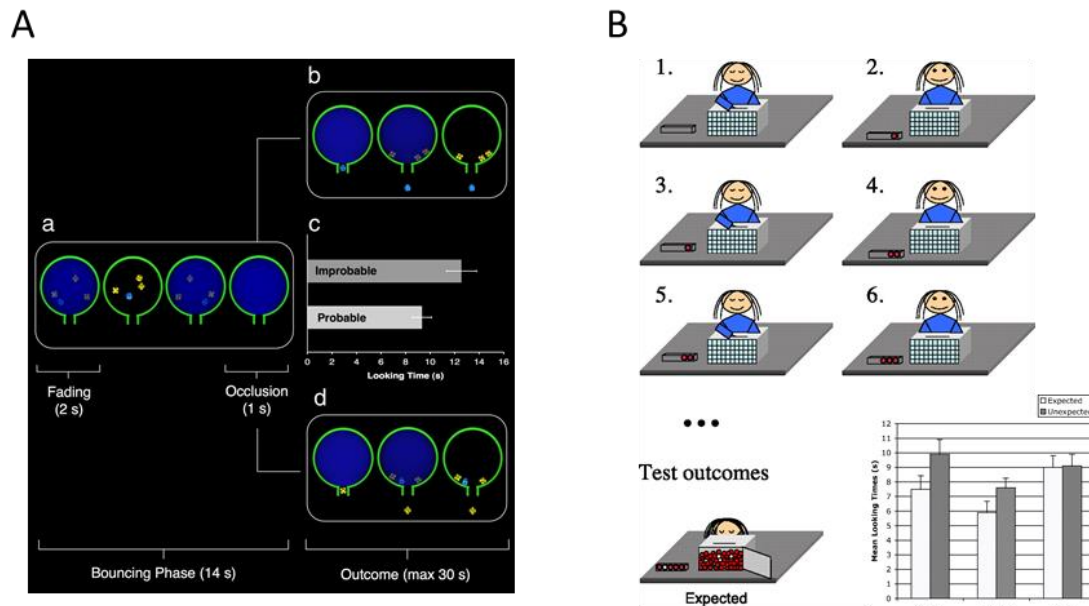


Figure 0.3. Examples of paradigms revealing infants' sensitivity to probability. (A) Adapted from (Téglás et al., 2007): mean looking time of infants (c) when presented with probable (b) or improbable (d) outcome of a lottery (a). (B) Adapted from (Xu and Garcia, 2008): infants look longer when the population of red and white balls mismatched the sample.

In 2008, similar results have been found in 8-month-old babies. In their experiment, Xu and Garcia had first familiarized babies with boxes containing a majority of either red or white balls. At the beginning of each trial, the content of boxes was hidden. The experimenter then designated one box, closed his eyes, and picked 5 balls from the box, 4 in one color and 1 in the other color. After revealing the content of the box, babies looked longer when it did not match the sample (figure 0.3). Conversely, babies could also use information about the whole population to predict what samples were most probable. Indeed, when the content of the box was visible from start, babies looked longer when the picked sample was improbable (Xu and Garcia, 2008).

These findings have suggested that young babies are able to perform bidirectional probabilistic inferences. In 2014, Fontanari and collaborators have also shown that Mayan subjects, devoid of any mathematical training, were able to indicate better than chance from which set a red object was more likely to be picked, even in situation where set size was incongruent with the proportion of red objects relative to black objects. In a second experiment, authors also showed that when subjects were asked to indicate whether two objects picked out of one specific set would have the same color or not, the subjective probability of their answer was tuned to the objective probability computed by enumerating the relative number of colored objects in the set (Fontanari et al., 2014).

Human capacity to perform probabilistic inference appears to be grounded in two other mathematical abilities. First, it could be linked to a specific intuition for proportions, i.e. ratios between set numerosities (Denison and Xu, 2014). Recently, Hubbard, Matthews and colleagues have shown that humans have perceptual access to non-symbolic ratio magnitudes and can estimate and compare ratios, in symbolic and non-symbolic contexts, with typical distance effect (Lewis et al., 2016; Matthews and Chesney, 2015).

The ability of young infants to perform probabilistic inference also leans on intuitions of logical reasoning. Cognitive sciences have started to address this issue in infants. Gopnik and colleagues have notably shown that 2.5-years-old children are able to perform quick and sophisticated inferences. In their experiments, children were presented with a “blicket” detector and various objects that were to be labeled or not as “blicket”. In the first condition, one object alone activated the “blicket” detector, another object alone did not, and both objects together activated the detector. In the second condition, one object systematically activated the detector and another object activated the detector only 66% of the time. In the first condition, toddlers correctly labeled only the first object as “blicket” and both objects in the second condition (Gopnik et al., 2001).

Some work led on great apes has revealed that humans share such intuitions of logical inference with other animal species. In particular, Call placed two cups in front of orangutans, chimpanzees, gorillas or bonobos, presented them with food, hid the food in one of the two cups and closed them, before revealing the content of either both or only one cup. Results notably suggested that, when presented with the empty cup, great apes were able to reason by exclusion to look for food in the other cup (Call, 2004). Certain forms of deduction, such as transitive inference (“ $A < B < C < D$ ”), have also been observed in rats (Davis, 1992), birds (Bond et al., 2003), and fishes (Grosenick et al., 2007).

1.2. Neuroimaging of mathematical processing

1.2.1. Neural correlates of numerical processing

Early neuropsychological and fMRI works have led to the hypothesis that parts of the intraparietal sulcus (IPS) play a central role in the representation of numbers (figure 0.4).

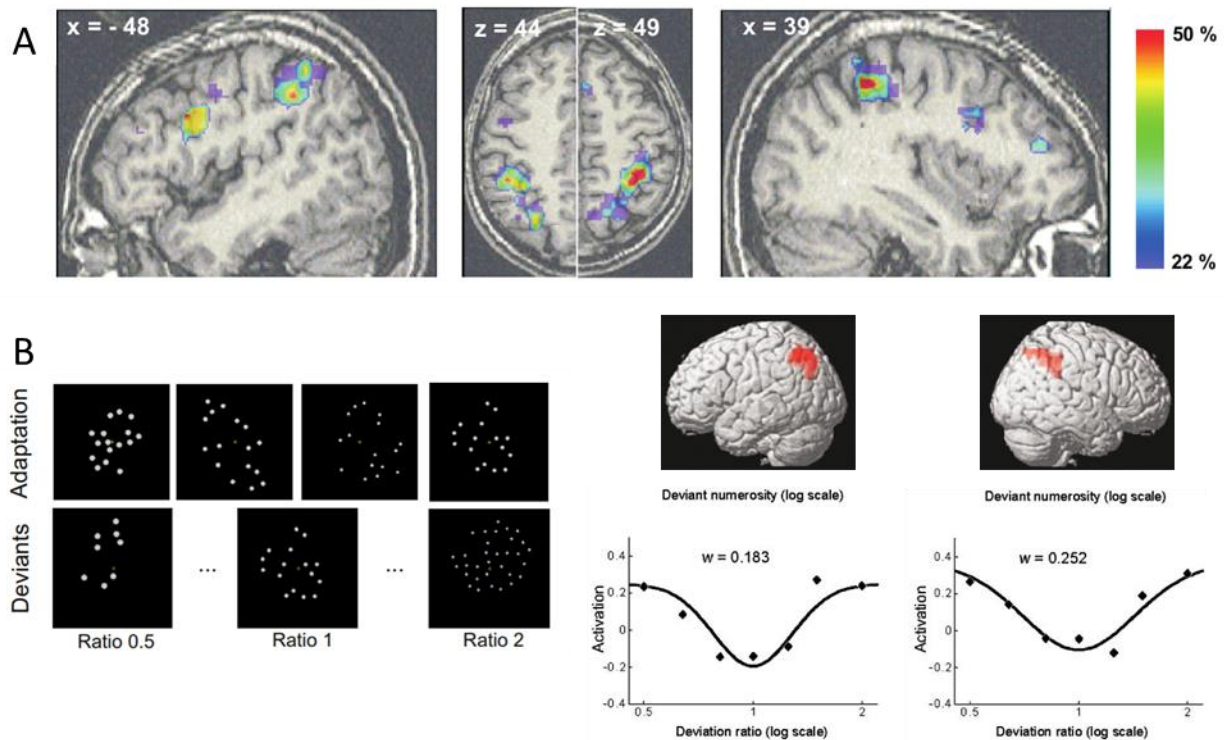


Figure 0.4. The role of IPS in the representation of numerical information. (A) adapted from (Dehaene et al., 2003): result of a meta-analysis revealing that bilateral IPS is involved in all numerical tasks (estimation, comparison, calculation, ...) either symbolic or non-symbolic. The amount of IPS activity is directly correlated with operations difficulty. (B) adapted from (Piazza et al., 2004): typical distance effect in fMRI signal change exhibited by bilateral IPS during the release from adaptation to constant number of dots.

Since then, converging evidence from three different fMRI approaches have suggested that bilateral IPS are indeed involved in a wide range of symbolic and non-symbolic numerical tasks. First, fMRI contrasts have been used to study the preferential activation of IPS for numbers versus other control conditions. In particular, IPS have proved to be more activated during the passive viewing or listening of numbers than by active detection of letters or colors (Eger et al., 2003). Quantitatively comparing two stimuli irrespective of their format (angle size, line length or digit numbers) also jointly activated a site in left IPS (Fias et al., 2003). Comparing estimation (respectively exact counting) to non-numerical but equally attentional demanding matching task in both auditory and visual modalities also revealed the involvement of right (respectively left) IPS (Piazza et al., 2006).

Second, fMRI adaptation techniques benefit from neural habituation to repeated exposure to a same or related stimulus, here typically a constant number of items with various low-level features, followed by signal rebound when a novel unrelated stimulus is presented, here a different number of items. Such change in numerosity has found to elicit activity rebound in IPS, in a way that follows Weber's law. Indeed, after repeated presentations of 16 items, the IPS responds to different new numbers of items (8, 13, 16, 20, 32) according to their distance (i.e. log ratio) with the reference. In other words, the more distant numbers are, the more IPS is activated (Piazza et al., 2004, figure

0.4). Neuroimaging studies in 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 (Libertus et al., 2008) or near-infrared spectroscopy (Hyde et al., 2010). Furthermore, 3 to 6-years-old children exhibited a strong relation between neural numerosity tuning curves and behavioral numerosity tuning curves, as well as a strong correlation between neural and behavioral Weber fractions in bilateral IPS (Kersey and Cantlon, 2016). Such adaptation to numerosity also extends to various aspects of quantity processing including ratios (Jacob and Nieder, 2009), symbolic numerical processing (Arabic digits and number words), and transfer across formats (Piazza et al., 2007).

Third, multivoxel pattern recognition techniques that directly compare activation patterns across multiple voxels between conditions, combined with either comparison, matching or simple viewing tasks, have again suggested that IPS codes for numerical information. For example, Eger et al. (2009) have presented subjects with different numerosities they had to keep in mind. Authors have first applied support vector machine classification to discriminate these numerosities then a multivariate searchlight analysis has revealed differences in activation patterns mostly in IPS.

At a finer-grained level, Nieder and collaborators have started to unravel the neuronal basis of numerical skills thanks to macaque neurophysiology (Nieder, 2005; Nieder and Miller, 2004). In particular, Nieder and Miller (2004) have recorded responses of single neurons in PFC and IPS in rhesus monkeys trained to perform a match-to-numerosity task. Monkeys had to memorize the numerosity of a first dot array and respond when a second array contained the same number of dots. In IPS, 20% of neurons were found to be tuned to numerical information with log-Gaussian tuning curves compatible with the idea that numerosity comparison is based on ratio perception. Such results tend to confirm that posterior parietal cortex is involved in number coding.

At human brain level, electrocorticography in patients implanted with subdural electrodes has revealed systematic activations of neural populations within the intraparietal sulcus whenever participants performed simple arithmetic calculation, and even when they were presented with numerical content embedded in natural spontaneous conversation (Dastjerdi et al., 2013).

Using 7-teslas fMRI, Harvey et al. (2013) have scanned subjects during passive viewing of sequences of dot arrays with increasing or decreasing numerosity. They then estimated the selectivity of individual voxels by extracting numerosity tuning from signal time courses. This original method allowed authors to describe a certain "numerotopy" for small numbers in right superior parietal lobule (SPL). In other words, authors have exhibited that, locally, SPL voxels showing selectivity to specific numbers are spatially organized in the same order as the numbers they are

selective to (figure 0.5). This layout was very similar across multiple stimulus sets (with constant dot size, area, circumference, regardless of density, and with items of any shape), it was shown only for small numbers, and no equivalent layout was found for symbolic numbers.

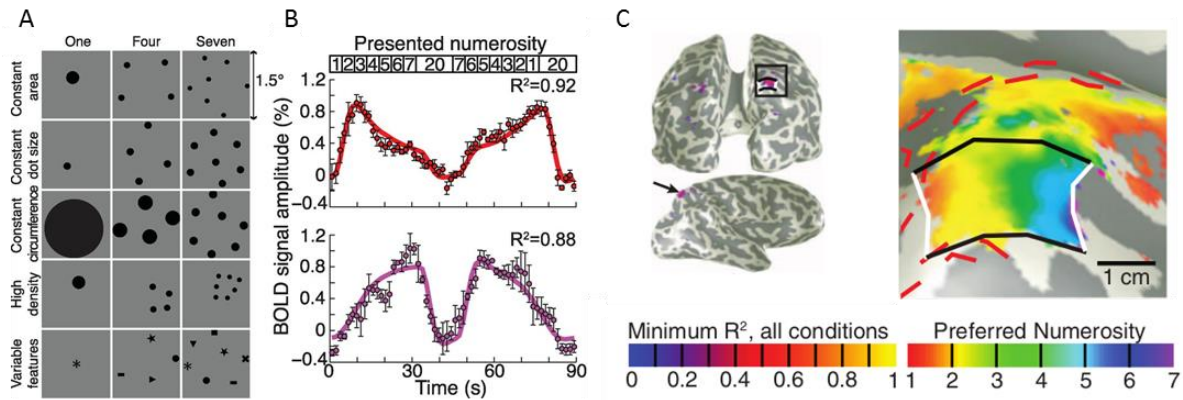


Figure 0.5. Small numbers numerotopy in right parietal cortex. Adapted from (Harvey et al., 2013). (A) Stimulus conditions. (B) Exemplar time courses of fMRI signal from two voxels distant of 2 cm in the posterior parietal cortex that prefer either a single dot (top) or seven dots (bottom). (C) Continuous layout responsive to ordered numerosities from medial to lateral sites of SPL in an exemplar subject.

Human IPS therefore appears to encode abstract numerical information, across formats and modalities. The triple code model, proposed by Dehaene (1992), hypothesized that these abstract representations of numbers in IPS are interfaced with symbolic representations that call upon temporal sites that would encode the verbal representation of numbers, and to lateral inferotemporal regions that would recover visual symbols associated to numbers. Only recently, Park et al. (2012) have identified such a region responding more to Arabic numbers than letters in the right hemisphere (figure 0.6). Electrophysiological recordings in epileptic patients have also revealed that some electrodes localized in inferotemporal gyrus responded more to Arabic digits than to letters or false fonts (Shum et al., 2013, figure 0.6) and more to calculation than to sentence reading (Hermes et al., 2015).

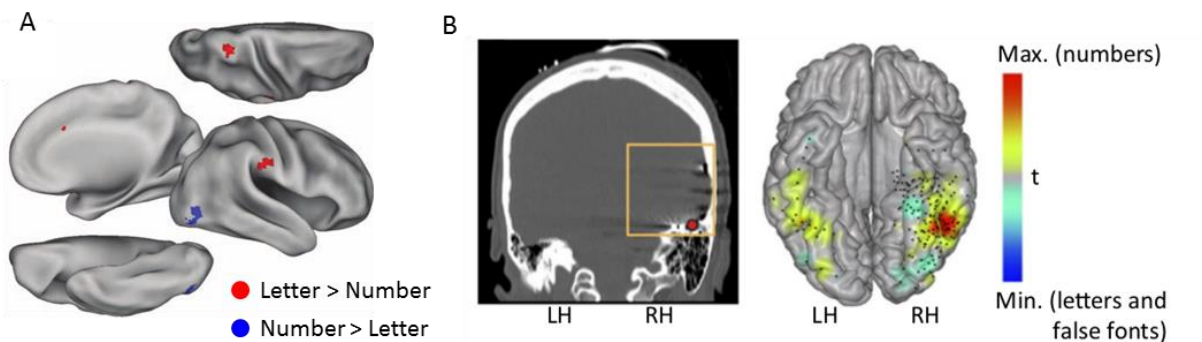


Figure 0.6. Evidence for visual recognition of number form in human adults. (A) adapted from (Park et al., 2012): inferior-temporal region responding more to visual numbers than letters. (B) adapted from (Shum et al., 2013) and (Hannagan et al., 2015): (right) selectivity for numbers versus false fonts in the right inferior temporal gyrus. (left) Location of one electrode.

These regions have been called “Visual Number Form Areas” because they are supposed to recollect the visual form of numeric symbols.

1.2.2. Neural correlates of geometrical and spatial processing

Up to date, the neural correlates of geometrical processing per se have not been directly investigated. However, entire fields of cognitive neurosciences are investigating spatial navigation and shape perception, two processes that underlie the two core knowledge systems of geometry described by Elizabeth Spelke. Although it is not the purpose of the present thesis to review all results in these fields, I will provide a brief overview of main findings.

Activation in two sets of brain areas have been correlated with spatial location and navigation. First, entorhinal and parahippocampal cortices are recruited for navigation. In particular, it is now well documented that rats medial entorhinal cortex contains a neuronal map of their spatial environment that takes the form of hexagonal « grid cells » firing at specific locations (Hafting et al., 2005). Similar conclusions have been reached also in monkeys (Killian et al., 2012). In humans, electrodes implanted in entorhinal cortex of epileptic patients have revealed a grid-like pattern of activity during spatial navigation in virtual environment (Jacobs et al., 2013). This kind of tasks, combined with fMRI, has also proved, among other brain regions, to activate parahippocampal cortex, especially when navigation used landmarks recognition (Maguire et al., 1999). Moreover, parahippocampal cortex has proposed to be the privileged focus for integrating visuo-spatial information, constructing scenes and recognizing places. Among other findings, the parahippocampal place areas (PPAs) have been found to respond to depiction of scenes, landscape images, pictures of places or houses (Epstein et al., 1999). More directly linked with geometry, an original study has also revealed that increased gray matter density in parahippocampal cortex strongly correlated with the intensity of classical geometrical illusions such as Muller-Lyer or Ebbinghaus (Axelrod et al., 2017).

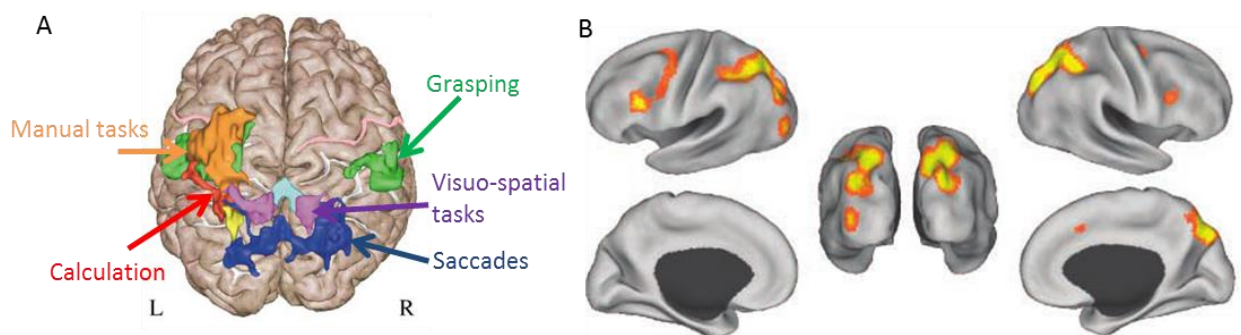


Figure 0.7. Spatial processes in the parietal cortex. (A) adapted from (Simon et al., 2002): spatial relation between calculation, visuo-spatial processes and eye movements in the parietal cortex. (B) Adapted from (Zacks, 2008): meta-analysis showing regions responding in mental rotation tasks.

Second, besides numbers, parietal cortices also proved to be recruited by a wide range of spatial processes (Husain and Nachev, 2007) including mental projection in space (Gauthier and Wassenhove, 2016), spatial direction of attention and eye movements (Culham and Kanwisher, 2001; Simon et al., 2002). Moreover, among other regions, left intraparietal sulcus has notably found to be associated with the visual perception of some geometrical characteristics of shapes such as the presence of crossing, and right intraparietal sulcus with the number of segments drawn to copy a given geometrical shape (Tzagarakis et al., 2009). Finally, a meta-analysis conducted by (Zacks, 2008) on all studies using the task of mental rotation introduced by (Shepard and Metzler, 1971), has demonstrated that such geometrical transformations recruit a large parietal region centered in intraparietal sulcus and extended through the superior parietal lobule.

1.2.3. Neural correlates of deductive reasoning

Cognitive neurosciences have investigated the neural underpinnings of abstract deductive reasoning for a few decades now. Since the advent of non-invasive neuroimaging techniques, fMRI studies have consistently used arguments constituted of two premises and one conclusion, successively displayed on a screen in order to distinguish between premises integration (display of the second premise) and deduction (task performed on the conclusion). Different types of reasoning have been examined, including syllogistic deduction (“all P are B; all B are D; all P are D”) (Goel, 2004; Goel et al., 2000; Reverberi et al., 2010; Rodriguez-Moreno and Hirsch, 2009), conditional reasoning (Modus Ponens: “if A then B; A; then B”) (Monti et al., 2007; Noveck et al., 2004; Prado et al., 2010a; Reverberi et al., 2010, 2007) or relational reasoning (“A is on top of B; B is on top of C; A is on top of C”) (Goel and Dolan, 2001; Prado et al., 2010a). To isolate abstract reasoning, experimental designs are usually complex, contrasting either simultaneously or separately such arguments with baseline arguments made of unrelated premises and conclusion (Goel, 2004; Goel et al., 2000; Noveck et al., 2004; Prado et al., 2010a; Reverberi et al., 2010), abstract and concrete content (Goel et al., 2000; Goel and Dolan, 2001; Monti et al., 2007), logically valid and invalid arguments (Goel et al., 2000; Noveck et al., 2004; Rodriguez-Moreno and Hirsch, 2009), or different reasoning types (Goel, 2004; Goel and Dolan, 2001; Prado et al., 2010a; Reverberi et al., 2010, 2007).

Probably because of all these differences in experimental designs, and although deduction seems to be a fundamental human ability shared with many other animal species, no consensus has yet been reached on which brain areas underlie deductive reasoning. (Goel, 2007) has written that all studies “implicate some combination of occipital, parietal, temporal and frontal lobes, basal ganglia, and cerebellar regions in logical reasoning, and several implicate all of these regions”. However, (Monti and Osherson, 2012) have overcome these differences and have proposed the existence of two sets of brain areas involved in deductive reasoning regardless of content. First, left rostralateral

and medial prefrontal cortices have been proposed to constitute “core” regions underlying logical operations necessary to derive conclusion from premises. Second, a set of fronto-parietal regions have been hypothesized to provide additional support to mere deduction reasoning, allowing representing and maintaining the content-independent structure of arguments.

2. The emergence of advanced mathematics

The fact that every human possess from birth a proto-mathematical intuitions grounded in dedicated brain circuits is now well admitted. Mathematics in humans also goes well beyond these approximate intuitions, in a way that seems unique among animal species.

1.1. Core knowledge of number and space as building bricks of advanced mathematics

1.1.1. Evidence from behavioral studies

Recent work has suggested that formal mathematics builds upon the core set of non-verbal proto-mathematical abilities that all humans are endowed with from birth. Indeed, many studies have exhibited a relation between math achievement at schools and number sense acuity (Feigenson et al., 2013; Gilmore et al., 2010; Libertus, 2015; Starr et al., 2013, figure 0.8). At group level, dyscalculic children generally possess less accurate lower Weber fraction than typically developing children (Piazza et al., 2010). The acuity of the approximate number system also appears to be a good predictor of individual differences in formal mathematical performance in typically developing children (Starr, 2015), in teenagers tested across ten years since they were in kindergarten (Halberda et al., 2008), and even within a group of mathematically gifted adolescents (Wang et al., 2017). Furthermore, training the approximate number system appears to enhance performance in exact symbolic arithmetic in children (Hyde et al., 2014) and adults (Park and Brannon, 2014).

In geometry, Dillon et al. (2013) have suggested that non-symbolic knowledge of geometry predicts the ability to use symbolic geometrical cues in 4-years-old children. In more details, authors have shown that children performances in a reorientation task within a rectangular array and in a classical intruder task asking to identify properties of visual shapes, strongly correlated with children performances in symbolic map tasks asking to use respectively distance and angle cues to navigate within a triangular array. However, no correlation was found between performances on symbolic distance and angle map tasks. These results thus show that children made separate use of the two core geometric systems for navigation and shapes whenever symbolic tasks required it.

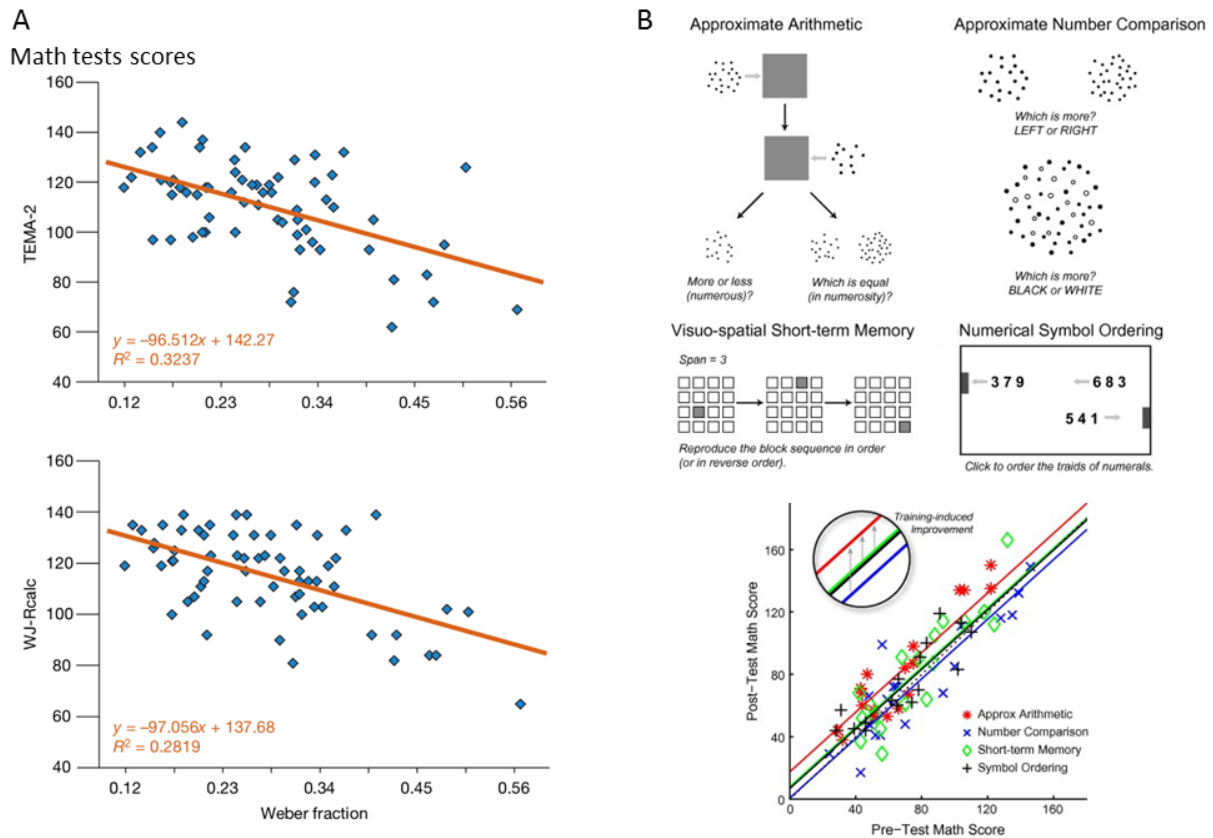


Figure 0.8. Relation between approximate number sense acuity and symbolic math performance. (A) adapted from (Halberda et al., 2008): individual Weber fractions correlate with symbolic math abilities in children tested during 10 years from kindergarten. (B) adapted from (Park and Brannon, 2014): training approximate number system enhances arithmetic performance in adults more than training numerical comparison, numerical matching, or visuo-spatial short-term memory.

Interestingly, proto-mathematical intuitions of number and space seem to persist and even transfer to symbolic abstract concepts acquired during life. As suggested by Kersey and Cantlon (2016), adults' nonsymbolic numerosity processing is similar to young children', and remains quite stable during development. Moreover, typical numerical distance effect remains when human adults are asked to compare symbolic numbers to a reference: it is for example harder to say that 70 is greater than 65 than to say that 99 is greater than 65 (Dehaene et al., 1990). Finally, abstract geometrical representations of parallels on a sphere in educated adults show universal biases (Izard et al., 2011b).

These findings are compatible with mathematical history that shows how mathematical concepts developed following a pyramidal construction. In Ancient Greece, mathematicians studied primarily abstract objects of arithmetic and geometry. Pythagoreans were interested in properties of rational number and integers, regular polygons, etc... In Euclid Elements that summarized all mathematical knowledge of this era, all objects were ideal and well defined and axioms implied properties. Importantly, at this time, a first formal link between number and length was made. From this point when all foundations of mathematics were laid, mathematicians started to build on top of

them. Arabic mathematicians drew the foundational principles of algebra from Greek, Indian and Chinese mathematics, trying to fill the gap between arithmetic and geometry. During 10th to 12th centuries, their works were then transmitted to European intellectuals who developed over many centuries, new concepts and fields like complex numbers, infinitesimal calculus or analysis...

1.1.2. Neuronal recycling hypothesis

These behavioral findings are also compatible with the theory of neuronal recycling of evolutionarily ancient systems. This theory stipulates that recent human cognitive abilities such as reading or arithmetic, which are unlikely to have implied any adaptation of our brain architecture at such short time scale, actually reuse parts of the brain whose primary function was pertinent to the recently evolved function (Dehaene, 2005). For example, when humans learn to read, they learn to recognize new types of symbols, namely letters and words. Doing so, within the ventral visual pathway that appears to be composed of a mosaic of specific visual detectors (Kanwisher and Dilks, 2012), a region called “visual word form area” specifies to this new function. Indeed, evidence show that this area of the left lateral occipito-temporal sulcus evolves, at human time scale, by learning to read (Dehaene et al., 2010).

The neuronal recycling hypothesis can particularly account for the fact that bilateral IPS and neighboring regions are systematically activated by any type of numerical computation: comparisons, additions, subtractions and multiplications encoded either symbolically or non-symbolically. Indeed, recent studies in monkeys have suggested that the human competence for symbolic calculation recycles evolutionarily old regions that support numerosity processing and internal representation of space during eye movements, namely IPS, VIP and LIP (Dehaene and Cohen, 2007). Recent work focusing on the connectivity between frontal and parietal regions also tends to support the neuronal recycling hypothesis. Indeed, connectivity mediated by the superior longitudinal fasciculus increases in the course of normal numerical and mathematical education and in mathematically gifted students relative to others (Emerson and Cantlon, 2012; Matejko and Ansari, 2015; Prescott et al., 2010). The neuronal recycling hypothesis could also explain the specialization for numerical symbols in the ventrolateral temporal cortex, either because of pre-existing connectivity with bilateral intraparietal sites, or because the ventral occipito-temporal pathway is pre-wired to extract abstract amodal representations of invariant shape features (Hannagan et al., 2015).

2.1. Possible vector of mathematical development: language

While it seems reasonable that basic intuitions of number and space serve as foundations of more advanced mathematical concepts, the way humans conceive, formalize and learn these concepts still remains unknown.

2.1.1. Language might be necessary to the representation of exact numerical concepts

For Noam Chomsky, “the origin of the mathematical capacity [lies in] an abstraction from linguistic operations” (Chomsky, 2006). Actually, it has been often proposed that the faculty of language reflects a broader human-specific ability to represent and acquire recursive structure or a combination of abstract symbols. For Hauser et al. (2002), the same neural mechanisms operating over linguistic structures, namely recursion, would be used for both language and mathematics. In 2001, Spelke and Tsivkin stated that natural language is the “most striking combinatorial system” of the human mind and claimed that formal mathematics might be one of its “richest and most dramatic outcomes”. Arithmetical facts, for example, can be abstracted from language by “preserving the mechanisms of discrete infinity and eliminating the other special features of language” (Chomsky, 2006). In particular in algebra, a widespread idea is that syntactical routines allowing to understand sentences such as “The girl kissed the boy who offered her roses”, are directly used to interpret algebraic expressions such as $2 \times (3 \times (6 + 2) - 5)$.

Some behavioral studies have suggested that learning number words seems to be an essential process of arithmetical development. In children, two simultaneous observations have been made that can support this idea. First, the ratio between two distinguishable large quantities drastically increases during the first years of life (Piazza et al., 2013). Second, children slowly and progressively learn to match number words with the corresponding quantities, starting with “one” around 2.5 years of life, “two” at 3 years old, etc... and finally understand general counting principles around 4 years-old (Wynn, 1992b). It is tempting to say that the acquisition of number words meaning allow children to conceive discrete categories of numbers instead of an indistinct continuum. But it is hard to disentangle whether refinement of infants’ numerical system is an effect of general brain maturation or progressive language acquisition. Studies conducted with adults who speak a language with impoverished numerical lexicon, such as some Amazonian populations might help answer this question. Such studies have revealed that the lack of number words impairs exact representation and calculation with numbers larger than 5 (Pica et al., 2004). While Mundurucu people show performances similar to French adults when asked to estimate, compare or approximatively calculate with large numbers, their performance drastically drops when they are asked to perform exact subtractions. Furthermore, when asked to place numbers represented either non-symbolically or symbolically on a line between 1 and 10, Mundurucu Indians propose a relation between number and space that is different from the one exhibited by American control adults, but very similar to the one exhibited by young children (Siegler and Opfer, 2003). This relation is systematic, revealing a classical SNARC (Spatial Numerical Association of Response Code) effect, with small numbers on the left and large numbers on the right, but is not linear (Dehaene et al., 2008). It is probable that understanding that there is a same spacing between 1 and 2 than between 8 and 9

builds upon the understanding of exact quantities, and thus upon the acquisition of number words. Taken together, these results suggest that language may contribute to shape the spatial representation of numbers as linear and to underlie exact calculation.

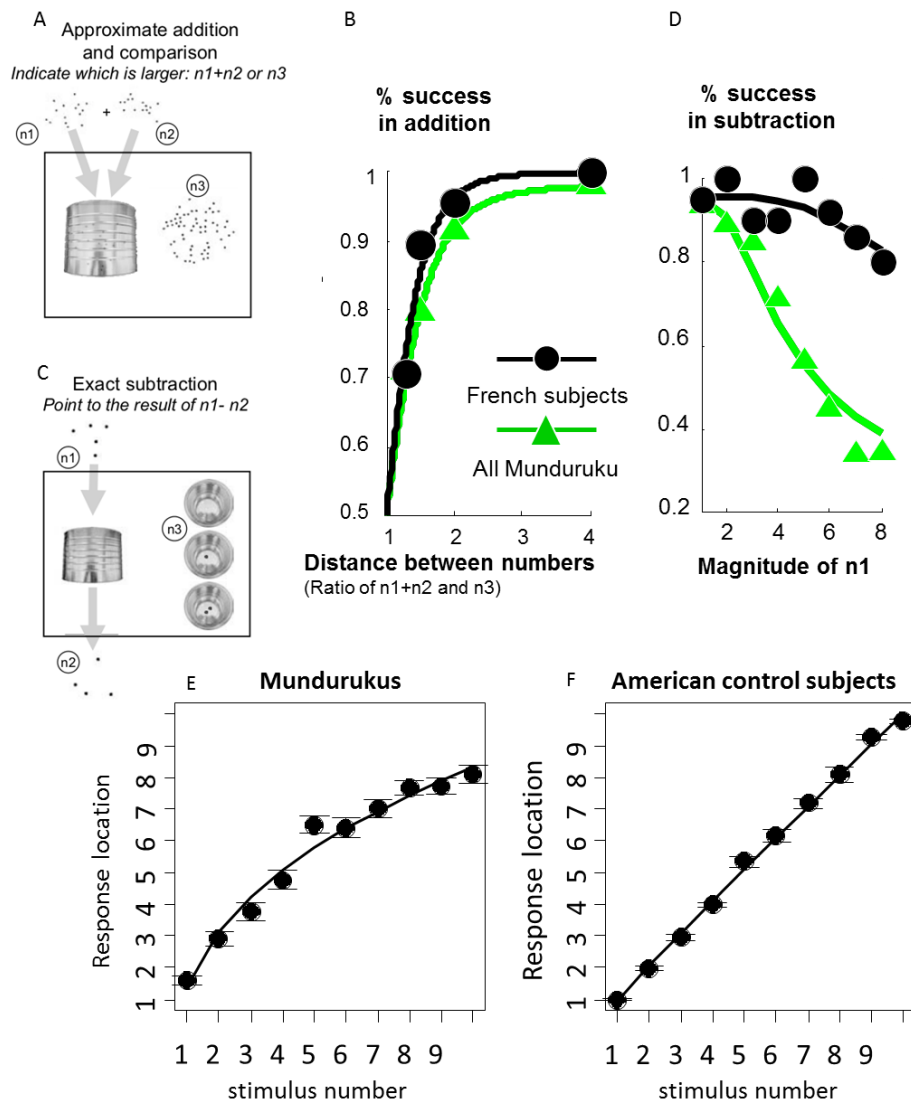


Figure 0.9. Arithmetic skills in Mundurucu people. (A), (B), (C), (D) adapted from (Pica et al., 2004): Mundurucus perform similarly to French subjects (B) in approximate addition (A), but failed (D) with approximate subtraction (C). (E), (F) adapted from (Dehaene et al., 2008): Average location of numbers on a horizontal segment differs between Mundurucu (E) and American participants (F).

Studies investigating the role of language in bilingual contexts have also revealed that there is an advantage for doing exact arithmetic in the language in which it was taught (Bernardo, 2001; Spelke and Tsivkin, 2001). In the latter, Russian-English bilinguals were either taught new numerical procedures such as approximating cube roots or learning addition tables of large numbers, trained to perform exact and approximate additions and multiplications, or taught historical and geographical facts possibly containing exact large and small numbers, objects, spatial relations, temporal information or proper names. Half of items were taught in Russian and the other half in English, and

participants' knowledge of taught items and new items was then tested in both languages. Interestingly, while no effect of language was observed when retrieving information about approximate numbers and non-numerical facts, knowledge about exact numbers was more accurately and efficiently retrieved in the language of training.

At the brain level, a few observations have indicated that language-related areas such as the posterior temporal/angular gyrus region can be activated during the processing of numerical materials in a rote manner, for instance when remembering exact addition facts such as “fifty four plus thirteen is sixty-seven” (Dehaene et al., 1999) or when drilling multiplication facts (Delazer et al., 2005; Ischebeck et al., 2006). Demonstrably, such rote learning involves a language-specific memory code (Dehaene et al., 1999). 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 (Hung et al., 2015). Finally, neuroimaging studies of mental arithmetic in bilinguals have exhibited different activation patterns in each language. Venkatraman et al. (2006) have trained Chinese-English bilinguals to perform mental arithmetic in both languages and have revealed that left IFG was more activated when solutions were retrieved in the untrained than in the trained language. Van Rinsveld et al. (2017) very recently showed that Luxembourgian bilinguals who all received school instruction first in German and then in French, recruited more their left temporal regions to perform simple additions in German, and more some frontal regions and their occipital cortex to perform complex additions in French. These results thus suggested that different solving procedures were involved in the language in which participants had learnt the basis of arithmetic (German) and in the language in which they had learnt more complex mathematical notions (French).

2.1.2. Cognitive and functional dissociation between school math and language

(Adapted from Amalric and Dehaene, accepted, *Cortical circuits for mathematical knowledge: Evidence for a major subdivision within the brain semantic networks*, Philosophical Transactions of Royal Society B)

First, 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 skills can be selectively impaired, or on the contrary, selectively spared relative to linguistic skills (Dehaene and Cohen, 1995; Dehaene, S. and Cohen, L., 1997; Lemer et al., 2003). Most strikingly, patients with severe aphasia may exhibit preserved mathematical and algebraic skills (Klessinger et al., 2007; Varley et al., 2005). 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 (Cappelletti et al., 2012, 2001).

Studies of developmental disorders such as dyscalculia versus dyslexia have also revealed a frequent dissociation between mathematical and linguistic processes. In one study (Landerl et al., 2004), 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 (Rubinsten and Henik, 2006): 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. Furthermore, a 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 (Jackowski et al., 2009; Meyer-Lindenberg et al., 2004). 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 (Iuculano et al., 2014; Lombardo et al., 2011; Zilbovicius et al., 2006). In the future, such observations may play a key role in the search for genes involved in the differential development of the corresponding brain circuits.

In the past decade, anthropological studies of Amazon tribes have brought another contribution to the idea that mathematics and language involve separate processes. While Mundurucu people seemed unable to perform exact calculation in the absence of dedicated lexicon, they still proved to possess sophisticated mathematical intuitions (Dehaene et al., 2006; Pica et al., 2004). In particular, despite the fact that Mundurucu 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 (Pica et al., 2004). Similar

conclusions can be made in the domain of geometry. Although Mundurucu 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 (Dehaene et al., 2006).

Finally, some brain-imaging studies have indicated that separate neural substrates are involved in algebraic versus syntactic manipulations. For example, Maruyama et al. (2012) 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 (2012, 2009; 2012) 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 judgments, while the latter recruited areas such as the intraparietal sulci, previously reported for numerical (Dehaene et al., 2003; Nieder and Dehaene, 2009) or spatial (Culham and Kanwisher, 2001; Hubbard et al., 2005) cognition. Interestingly, one developmental study has also revealed that 4-year-old children watching “Sesame Street” educational videos focusing on numbers and letters have exhibited 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. Furthermore, children’s activity in parietal cortex predicted their performance in mathematical tests, while activity in Broca’s area predicted performance in verbal tests (Cantlon and Li, 2013).

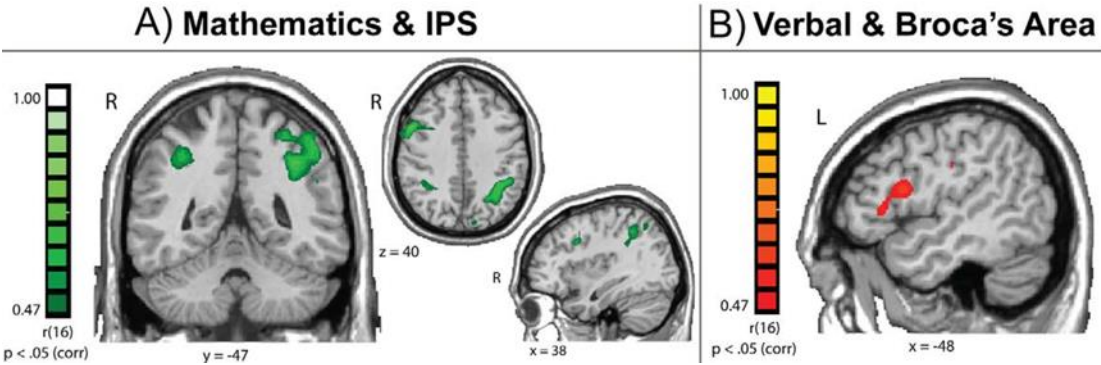


Figure 0.10. Dissociation between mathematical and verbal knowledge in 4- to 10-year-old children. Brain regions showing a significant correlation between children’s neural maturity index (derived from fMRI signals) and their performance on mathematical test (left), and verbal test (right) ((Cantlon and Li, 2013), reprinted with permission).

2.2. Possible vector of mathematical development: visual experience

Another possible explanation of how formal mathematics emerges from proto-mathematical systems for numbers and space is that mathematical representations are rooted in visuospatial thinking and develop through visual experience.

2.2.1. The role of visual experience in shaping mathematical concepts

In 1945, Albert Einstein wrote to fellow mathematician Jacques Hadamard that "[t]he psychological entities which seem to serve as elements of my 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". As for Albert Einstein, mathematical objects appear to be advantageously encoded in a visual way for many mathematicians and physicists. One can therefore think that visual experience of the world heavily contributes to shape the human representation of mathematical concepts. It seems particularly true for geometry which is popularly seen as "visual".

First, it has long been argued that the detection of symmetries might be essential to the perception of shapes. Gestalt theory has proposed that the presence of symmetries tend to serve as grouping cues to perceive a figure (Palmer, 1990). Later research has shown that our visual system spontaneously extracts symmetrical properties and in particular the vertical mirror symmetry, in a reliable and quick manner (Machilsen et al., 2009), and even in the case of skewed figures (Sawada and Pizlo, 2008). Human participants also spontaneously generate patterns that contain symmetries (Westphal-Fitch et al., 2012, figure 0.11). Finally, symmetry detection has proved to influence drastically shape perception. For example, a square with sides at 45° to horizontal and vertical axes will be perceived as a diamond. In that case, Giaquinto (2005) argued that our visual system spontaneously extracts a symmetrical axis drawn through opposite vertices and interpret it as the vertical axis.

Second, Howe and Purves (2005) have also suggested that human conceptualization of angles and orientation could originate from natural-scene perception (figure 0.11). They have counted occurrences of different values of angles formed by intersecting straight lines a massive database of natural scenes made of landscape pictures and scenes containing human constructions. Probabilities of each given angle occurrence have proved to predict certain specificities of angle perception such as the overestimation of acute angles, underestimation of obtuse angles or misinterpretations of line orientation in famous visual illusions.

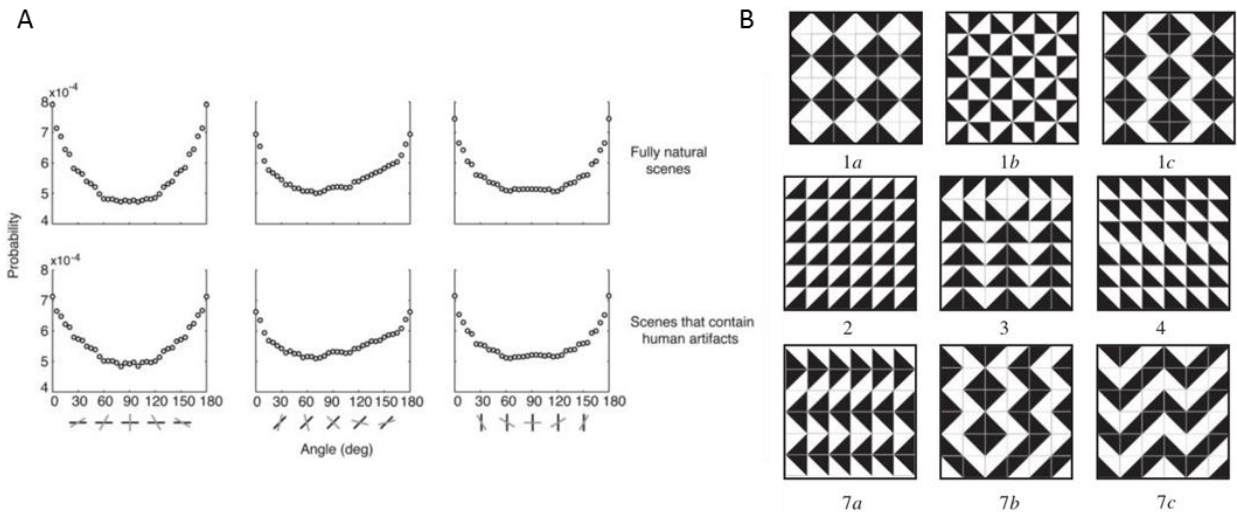


Figure 0.11. Visual perception influences geometrical conceptualization. (A) adapted from (Howe and Purves, 2005): Probability of occurrence of angles in natural scenes. (B) adapted from (Westphal-Fitch et al., 2012): spontaneous production of symmetrical figures.

Visual experience can also prove relevant to build numerical representations. For example, numerical concepts per se can build upon the visual decomposition and integration of our environment as showed by Stoianov and Zorzi (2012) who managed to build a deep learning network developing classical representations of numerosity only from its exposure to visual arrays containing different numbers of objects. Numerical calculation seems also to be extremely sensitive to visual perception. Indeed, arithmetic tasks have been showed to involve eye movements that may “reflect a fast understanding of arithmetic constituent structure” (Schneider et al., 2012). Solving simple algebraic equations also seem to rely on eye movements and even mental movement of constituents from one side to the other of the equal sign in order to isolate the unknown variable. In fact, it becomes harder to solve an equation written on a background moving in a direction that is incongruent with constituent movement (Goldstone et al., 2010) or to perform arithmetic calculation when spacing does not match operators precedence (Landy et al., 2008).

Finally, visual representations enclosed in diagrams have hypothesized to be a major support of geometrical and topological reasoning. For example, Euclid made a systematic use of diagrams in the geometrical proofs of his “Elements” (Manders, 2008) in a way that makes the underlying ideas spontaneously accessible to every reader (Hamami and Mumma, 2013). De Toffoli and Giardino (2014) even proposed that, in knot theory, knots diagrams with their allowed movements and space they define, might not only help identifying equivalent knots but could also promote the invention of new topological objects.

2.2.2. Some evidence that numerical and spatial processing do not rely on vision

There is now much evidence that pre-verbal infants and animals perceive numerosity in both visual and auditory modalities and are even able to extract numerical information from one modality and transfer it to the other modality. For example, we remind here that Izard et al. (2009) have shown that a few days-old babies are able to match visual arrays containing a given number of objects with the same number of sounds. Jordan et al. (2008) have also shown that rhesus monkeys can represent number abstractly, matching numerosities across sensory modalities. Furthermore, Vallortigara et al. (2009) have revealed that rearing experience with right angles and metrically distinct surfaces is not required for chicks to deal efficiently with geometric information during navigation tasks.

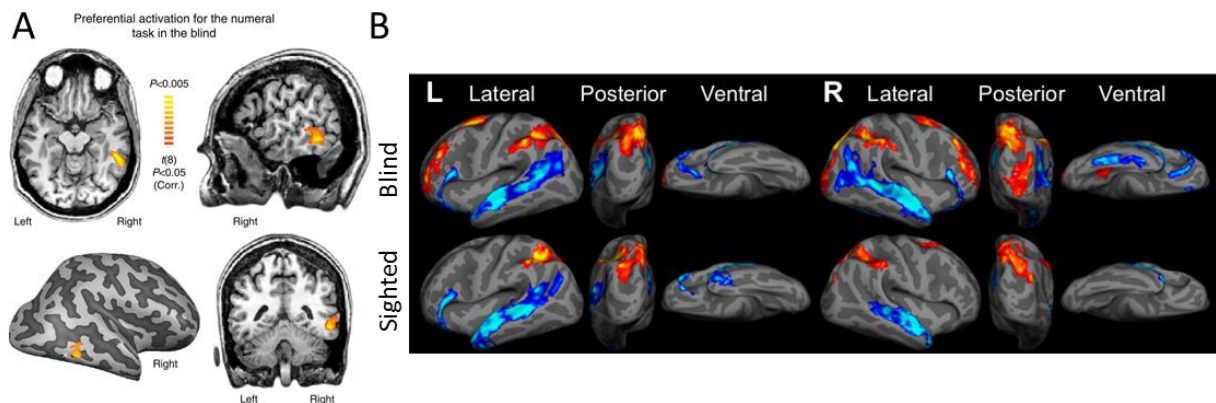


Figure 0.12. Arithmetic in the blind. (A) adapted from (Abboud et al., 2015): preferential activation for roman numerals over letters encoded by EyeMusic in congenitally blind subjects. (B) adapted from (Kanjlia et al., 2016): similar activation in frontal and parietal areas of blind and sighted participants performing mental arithmetic.

Crucially, direct evidence that numerical and spatial conceptualization does not necessarily requires vision comes from studies conducted with blind people. For example, Landau et al. (1981) have shown that a 2.5-year-old blind child, who was first walked through a room to discover the location of four objects forming a diamond shape, was then able to take on her own new paths between objects. As blindfolded adults and 3-year-old children demonstrated the same ability, authors concluded that spatial navigation does not rely on visual cues, but rather on abstract metric knowledge of space. Moreover, Castronovo and Seron (2007a) have shown that blind and sighted adults exhibit the same classical distance and SNARC effects when they perform simple comparison tasks, thus suggesting that visual modality is not necessary to integrate numerical and spatial dimensions. Such integration of numbers and space might even not at all reflect a visuospatial mechanism but rather an abstract mechanism useful to extend working memory capacities (Dijck et al., 2014; Fias et al., 2011; van Dijck and Fias, 2011). Finally, figure 0.12. shows fMRI studies that have revealed that congenitally blind adults, just like sighted subjects, also recruit IPS to perform simple

calculation (Kanjlia et al., 2016) and visual number form areas to recognize number symbols (Abboud et al., 2015).

Introduction to the experimental contribution and overview of the thesis

Recent neuroimaging developments have offered new ways to investigate the long-debated issue of the origins of mathematics in the human brain. Together with behavioral studies, we have seen that neuroimaging techniques such as fMRI, EEG, NIRS and EcoG have already allowed elucidating many questions regarding numerical abilities. However, simple numerical knowledge seems hardly representative of the variety of domains that modern mathematics embraces.

The originality of the chapters 1, 2 and 3 of this thesis is therefore to explore, for the first time, how the human brain represents advanced concepts from diverse domains constitutive of mathematics such as analysis, algebra, geometry or topology. This specific framework offers new perspectives on the long-debated questions of the relations between mathematics and language or between mathematics and vision. In particular, chapters 1, 2 and 3 of the present work address a series of questions such as: Is mathematical language similar to natural language? Are language areas used by mathematicians when they do mathematics? On the contrary, does advanced mathematical reflection recycle core regions for number and space processing? Does the brain comprise a generic semantic system that stores mathematical knowledge alongside knowledge of history, geography, or famous people? Do mechanisms underlying mathematical reflection vary among domains? Is visual experience necessary to advanced mathematical reflection? In these three chapters, I report the results of fMRI experiments conducted with professional mathematicians, three of them being blind, who performed fast semantic judgments on spoken advanced mathematical and nonmathematical statements. The first chapter interrogates the relations of advanced mathematical concept processing to general semantics and language processing, and to simple calculation and visual recognition of numbers and equations. The second chapter questions the observed dissociation between mathematics and general semantics, trying to draw the limit between mathematical and linguistic processing. Finally, the third chapter assesses the impact of visual experience on mathematical development in the brain, comparing three exceptional cases of professional blind mathematicians with a group of sighted mathematicians.

Chapter 4, in turn, lays the foundation for investigating a novel question. In this chapter, we bring two observations together. First, studies of sequence learning have suggested that humans are endowed with an abstract ability to extract complex structures from sequential inputs. Young infants have indeed proved to be able to learn temporal regularities using statistical information available in

auditory or visual sequences and can even grasp the “algebraic pattern”, i.e. the abstract rule, underlying a set of specific sequences. Interestingly, it has been suggested that this ability relies on the progressive scaffolding of internal tree-like representations. Second, the importance of identifying structures and their properties is particularly salient in mathematics. In particular, algebra is considered since the XXth century as the mathematical domain studying algebraic structures such as groups, fields, vector spaces or algebras, i.e. all types of structures composed of a set endowed with composition laws and satisfying certain axioms. In fact, the salience of structures is not only relevant to mathematicians or students in mathematics at university, but also to humans who spontaneously perceive the analogy existing between sequences of increasing numbers and increasing length (de Hevia and Spelke, 2010), or understand the properties of parallel lines in the plane (Izard et al., 2011b), or even who discover that integers are linearly organized (Dehaene et al., 2008), or that positions of objects on a surface can be represented by a Euclidian plane.

Combining these two observations, we therefore start to ask whether the human ability to identify the abstract and deep structure underlying a set of stimuli could underlie the acquisition of mathematical principles.

Chapter 1. Origins of the brain networks for advanced mathematics in expert mathematicians

1. Introduction to the article

In this chapter, we introduce a novel paradigm to assess the brain representation of advanced mathematical concepts. For the first time, we have proposed to professional mathematicians to think about advanced mathematical problems while undergoing fMRI scanning. We chose to present mathematical problems from analysis, algebra, topology and geometry in linguistic format, through auditory sentences that were true, false, or meaningless. We compared mathematicians' reflection on mathematical statements with their reflection on control statements from nonmathematical domains such as history or geography. We also compared mathematicians to nonmathematician control subjects with similar academic standing but devoid of mathematical training beyond high school when they process advanced mathematical concepts as long as basic numerical processing.

2. Abstract

The origins of human abilities for mathematics are debated: some theories suggest that they are founded upon evolutionarily ancient brain circuits for number and space, others that they are grounded in language competence. To evaluate what brain systems underlie higher mathematics, we scanned professional mathematicians and mathematically naïve subjects of equal academic standing as they evaluated the truth of advanced mathematical and non-mathematical statements. In professional mathematicians only, mathematical statements, whether in algebra, analysis, topology or geometry, activated a reproducible set of bilateral frontal, intraparietal and ventrolateral temporal regions. Crucially, these activations spared areas related to language and to general-knowledge semantics. Rather, mathematical judgments were related to an amplification of brain activity at sites that are activated by numbers and formulas in non-mathematicians, with a corresponding reduction in nearby face responses. The evidence suggests that high-level mathematical expertise and basic number sense share common roots in a non-linguistic brain circuit.

3. Introduction

The human brain is unique in the animal kingdom in its ability to gain access to abstract mathematical truths. How this singular cognitive ability evolved in the primate lineage is currently

unknown. According to one hypothesis, mathematics, like other cultural abilities that appeared suddenly with modern humans in the upper Paleolithic, is an offshoot of the human language faculty – for Noam Chomsky, for instance, “the origin of the mathematical capacity [lies in] an abstraction from linguistic operations” (Chomsky, 2006). Many mathematicians and physicists, however, disagree and insist that mathematical reflection is primarily non-linguistic – Albert Einstein, for instance, stated: « Words and language, whether written or spoken, do not seem to play any part in my thought processes. » (Hadamard, 1945).

An alternative to the language hypothesis has emerged from recent cognitive neuroscience research, according to which mathematics arose from an abstraction over evolutionarily ancient and non-linguistic intuitions of space, time, and number (Dehaene, 2011; Dillon et al., 2013). Indeed, even infants and uneducated adults with a drastically impoverished language for mathematics may possess abstract proto-mathematical intuitions of number, space and time (Dehaene et al., 2006; Pica et al., 2004). Such “core knowledge” is predictive of later mathematical skills (Gilmore et al., 2010; Halberda et al., 2008; Starr et al., 2013) and may therefore serve as a foundation for the construction of abstract mathematical concepts (Spelke, 2003). Advanced mathematics would arise from core representations of number and space through the drawing of a series of systematic links, analogies and inductive generalizations (Dehaene et al., 2008; Lakoff and Núñez, 2000; Piaget, 1952; Piaget and Inhelder, 1948).

The linguistic and core-knowledge hypotheses are not necessarily mutually exclusive. Linguistic symbols may play a role, possibly transiently, in the scaffolding process by which core systems are orchestrated and integrated (Carey, 2009; Spelke, 2003). Furthermore, mathematics encompasses multiple domains, and it seems possible that only some of them may depend on language. For instance, geometry and topology arguably call primarily upon visuospatial skills, while algebra, with its nested structures akin to natural language syntax, might putatively build upon language skills.

Contemporary cognitive neuroscience has only begun to investigate the origins of mathematical concepts, primarily through studies of basic arithmetic. Two sets of brain areas have been associated with number processing. Bilateral intraparietal and prefrontal areas are systematically activated during number perception and calculation (Dehaene et al., 1999), a circuit already present in infants and even in untrained monkeys (Nieder and Dehaene, 2009). Additionally, a bilateral inferior temporal region is activated by the sight of number symbols such as Arabic numerals, but not by visually similar letters (Shum et al., 2013). Those regions lie outside of classical language areas, and several fMRI studies have confirmed a double dissociation between the areas involved in number sense and language (Cantlon and Li, 2013; Monti et al., 2012). Only a small part of our

arithmetic knowledge, namely the rote memory for arithmetic facts encoded in linguistic form (Dehaene et al., 1999; Spelke and Tsivkin, 2001). The bulk of number comprehension and even algebraic manipulations can remain preserved in patients with global aphasia or semantic dementia (Cappelletti et al., 2012; Lemer et al., 2003; Varley et al., 2005). Contrary to intuition, brain-imaging studies of the processing of nested arithmetic expressions show little or no overlap with language areas (Friedrich and Friederici, 2009; Maruyama et al., 2012; Nakai and Sakai, 2014). Thus, conceptual understanding of arithmetic, at least in adults, seems independent of language.

Many mathematicians, however, argue that number concepts are too simple to be representative of advanced mathematics. To address this criticism, here we study the cerebral representation of high-level mathematical concepts in professional mathematicians. We collected functional magnetic resonance images (fMRI) in 15 professional mathematicians and 15 non-mathematicians controls of equal academic standing, while participants performed fast semantic judgments on mathematical and non-mathematical statements (figure 1.1A). On each trial, a short spoken sentence was followed by a 4-second reflection period during which the participants decided whether the statement was true, false or meaningless. Meaningful and meaningless statements were matched on duration and lexical content, but meaningless statements could be quickly dismissed, while meaningful statements required in-depth thinking, thus presumably activating brain areas involved in conceptual knowledge. Statements were generated with the help of professional mathematicians and probed four domains of higher mathematics: analysis, algebra, topology, and geometry. A fifth category of non-math sentences, matched in length and complexity, probed general knowledge of nature and history. Two additional fMRI runs evaluated sentence processing and calculation (Pinel et al., 2007) and the visual recognition of faces, bodies, tools, houses, numbers, letters, and written mathematical expressions.

4. Methods

4.1. Participants

We scanned a total of 30 French adult participants. 15 were professional mathematicians (11 male, 4 female, age range 24-39, mean = 28.1) and 15 were humanities specialists (10 male, 5 female, age range 24-50, mean = 30.1). Their ages did not significantly differ ($t = 0.8397$, $p = 0.41$).

Professional mathematicians were full-time researchers and/or professors in mathematics. All had a PhD in Mathematics and/or had passed the French national examination called “aggregation” which is the last qualification exam for professorship. The 15 control subjects had the same education level, but had specialized in humanities and had never received any mathematical courses since high school. Their disciplines were: literature ($n = 3$), history ($n = 3$), philosophy ($n = 1$),

linguistics (n = 2), antiquity (n = 1), graphic arts and theatre (n = 3), communication (n = 1) and heritage conservation (n = 1). All subjects gave written informed consent and were paid for their participation. The experiment was approved by the regional ethical committee for biomedical research.

4.2. Visual runs

Seven categories of images were presented: faces, houses, tools, bodies, words, numbers, and mathematical formulas, plus a control condition consisting of circular checkerboards whose retinotopic extent exceeded that of all other stimuli.

All stimuli were black on a white background. Faces, tools, houses and bodies were highly contrasted gray-level photographs matched for overall number of gray level. Faces were front or slightly lateral views of non-famous people. Houses consisted in outside views of houses or buildings. Tools were common hand-held household object such as a hair-dryer. Bodies were front pictures of headless standing bodies. Numbers, words and formulas were strings of 5 or 6 characters. All numbers were decimal forms of famous constants (e.g. $3.14159 = \pi$). Formulas were extracted from classical mathematical equations or expressions (e.g. binomial coefficients or the Zeta function). Words were written either with upper or lower case letters and were of high lexical frequency (mean = 28.3 per million; <http://lexique.org>).

Although numbers, words and formulas were inevitably arranged horizontally relative to other images, the mean width of horizontal images was not significantly different from the mean length of vertical images or the mean side of the square ones, so that they were all inscribed in a circle of 310 pixels diameter, equivalent to a visual angle of 5° .

The stimuli were presented in short mini-blocks of eight stimuli belonging to the same category. Within each block, the subject's task was to click a button whenever he/she detected an image repetition (one-back task). Each of the seven categories of images comprised twelve items, among which eight items were randomly picked on a given mini-block. Each image was flashed for 300 ms and followed by a 300 ms fixation point, for a total duration of 4.8 s. The category blocks were separated by a brief resting period with a fixation point only, whose duration was randomly picked among 2.4 s, 3.6 s or 4.8 s.

4.3. Auditory runs

Subjects were presented with 72 mathematical statements (18 in each of the fields of analysis, algebra, topology and geometry) and 18 non-mathematical statements. Within each category, 6 statements were true, 6 were false, and 6 were meaningless. All meaningless statements (in math or non-math) were grammatically correct but consisted in meaningless associations of words extracted from unrelated meaningful statements. All meaningful statements bore upon non-trivial facts which were judged unlikely to be stored in rote long-term memory and therefore required logical reflection. Reference to numbers or to other mathematical concepts (e.g. geometrical shapes) was purposely excluded. A complete list of statements, translated from the original French, is presented in appendix.



Figure 1.1. Main paradigm and behavioral results. (A) On each trial, subjects listened to a spoken statement and, four seconds later, classified it as true, false or meaningless. (B) Performance in this task (% correct). (C, D) Mean d' -prime values for discrimination of meaningful versus meaningless statements (C) and, within meaningful statements, of true versus false statement (D). *, $p < 0.05$ (student t -tests). Error bars represent one standard error of the mean (SEM).

All statements were recorded by a female native French speaker who was familiar with mathematical concepts. Statements from the different categories were matched in syntactic construction, length (mean number of words: math = 12.4, non-math = 12.6, $t = 0.24$, $p = 0.81$) and duration (mean duration in s: math = 4.70, non-math = 4.22, $t = 1.93$, $p = 0.056$).

The experiment was divided into 6 runs of 15 statements each, which included one exemplar of each sub-category of statements (5 categories [analysis, algebra, geometry, topology, or general knowledge] \times 3 levels [true, false, or meaningless]). On screen, the only display was a fixation cross on a black background. Each trial started with a beep and a color change of the fixation cross (which turned to red), announcing the onset of the statement. Following auditory presentation, a fixed-

duration reflection period (4 seconds) allowed subjects to decide whether the statement was true, false or meaningless. The end of the reflection period was signaled with a beep and the fixation cross turning to green. Only then, for 2 seconds, could subjects give their evaluation of the sentence (true, false, or meaningless) by pressing one of three corresponding buttons (held in the right hand). Each trial ended with a 7-second resting period (figure 1.1A).

4.4. Localizer scan

This 5-minute fMRI scan is described in detail elsewhere (Pinel et al., 2007). For present purposes, only two contrasts were used: language processing (sentence reading + sentence listening relative to rest) and mental calculation (mental processing of simple subtraction problems such as 7-2, presented visually or auditory, and contrasted to the processing of non-numerical visual or auditory sentences of equivalent duration and complexity).

4.5. Post-MRI questionnaire

Immediately after fMRI, all the statements that had been presented during fMRI were reexamined in the same order. For each of them, participants were asked to rate their comprehension of the problem itself within the noisy environment of the fMRI machine; their confidence in their answer; whether the response was a well-known fact or not (variable hereafter termed “immediacy”); the difficulty of the statement; its “imageability”; and the kind of reasoning that they had used on an axis going from pure intuition to the use of a formal proof.

4.6. fMRI data acquisition and analysis

We used a 3-Tesla whole body system (Siemens Trio) with a 32 channel head-coil and high-resolution multiband imaging sequences developed by the Center for Magnetic Resonance Research (CMRR) (Xu et al., 2013) (multiband factor = 4, Grappa factor = 2, 80 interleaved axial slices, 1.5 mm thickness and 1.5 mm isotropic in-plane resolution, matrix = 128x128, TR = 1500 ms, TE = 32 ms).

Using SPM8 software, functional images were first realigned, normalized to the standard MNI brain space, and spatially smoothed with an isotropic Gaussian filter of 2 mm FWHM.

A two-level analysis was then implemented in SPM8. For each participant, fMRI images were high-pass filtered at 128s. Then, time series from visual runs were modelled by regressors obtained by convolution of the 8 categories of pictures plus the button presses with the canonical SPM hemodynamic response function (HRF) and its time derivative. Data from the auditory runs was modelled by two regressors for each sentence, one capturing the activation to the sentence itself (kernel = sentence duration) and the other capturing the activation during the reflection period (4-s rectangular kernel). We then defined subject-specific contrasts over specific sentences, either comparing the activation evoked by any two subsets of sentences (during sentence presentation or

during the post-sentence reflection period), or evaluating the impact of a continuous variable such as subjective difficulty on a subset of sentences. Regressors of non-interest included the six movement parameters for each run. Within each auditory run, two additional regressors of non-interest were added to model activation to the auditory beeps and to the button presses.

For the second-level group analysis, individual contrast images for each of the experimental conditions relative to rest were smoothed with an isotropic Gaussian filter of 5 mm FWHM, and separately for visual and auditory runs, entered into a second-level whole-brain ANOVA with stimulus category as within-subject factor. All brain-activation results are reported with a clusterwise threshold of $p < 0.05$ corrected for multiple comparisons across the whole brain, using an uncorrected voxelwise threshold of $p < 0.001$.

5. Results

5.1. Behavioral results

5.1.1. Behavioral results in auditory runs

With mathematical statements, mathematicians performed way above chance level ($63.6 \pm 2.8\%$ [mean \pm standard error]; chance = 33.3%; Student's t test, $t = 11.3$, $p < 0.001$, figure 1.1B), while control subjects unsurprisingly fell close to chance level ($37.4 \pm 1.6\%$, $t = 2.6$, $p = 0.02$; difference between groups: $t = 8.5$, $p < 0.001$). With non-mathematical statements, both groups performed equally well (mathematicians: $65.4 \pm 3.1\%$, $t = 10.6$, $p < 0.001$; controls: $63.7 \pm 3.8\%$, $t = 8.3$, $p < 0.001$; no difference between groups: $t = 0.4$, $p = 0.7$). Importantly, mathematicians performed identically with math and non-math statements ($t = 0.5$, $p = 0.6$), thus suggesting that math and non-math problems were well-matched in objective difficulty level.

Above-chance performance could arise from a discrimination of meaningful and meaningless statements, from a discrimination of true versus false statements, or both. To separate these effects, we applied signal detection theory (SDT). First, we quantified subjects' ability to discriminate whether the statements were meaningful (pooling across true and false statements) or meaningless. We considered hits as "meaningful" responses to statements that were indeed meaningful, and false alarms as "meaningful" responses to meaningless statements. For both mathematics and non-mathematics, mathematicians' judgments of meaningfulness were highly above chance ($d'_{math} = 2.68 \pm 0.18$, $t = 15.9$, $p < 0.001$; $d'_{non-math} = 3.56 \pm 0.28$, $t = 13.0$, $p < 0.001$). On the contrary, controls' judgments of meaningfulness dropped nearly to 0 for mathematics ($d'_{math} = 0.67 \pm 0.17$, $t = 3.9$, $p = 0.002$), but were highly above chance for general knowledge ($d'_{non-math} = 3.16 \pm 0.47$, $t = 6.99$, $p < 0.001$). There was no significant difference comparing mathematicians and controls' capacity to discriminate meaningful non-mathematical sentences ($t = 0.76$, $p = 0.45$). However, mathematicians

were significantly better than controls at discriminating meaningful mathematical statements ($t = 8.44, p < 0.001$) (figure 1.1C).

We also applied SDT to evaluate the subjects' capacity to discriminate true and false statements. This analysis was restricted to meaningful statements that were judged meaningful. We considered hits as true statements correctly classified as true, and false alarms as false statements incorrectly classified as true. Mathematicians showed weak but significantly positive d -primes for mathematics ($d'_{math} = 0.78 \pm 0.16, t = 5.0, p < 0.001$), and for non-mathematics ($d'_{non-math} = 0.68 \pm 0.31, t = 2.30, p = 0.04$). Controls did not show a significantly positive d -prime for mathematics but they did for non-mathematics ($d'_{math} = 0.38 \pm 0.23, t = 1.72, p = 0.11$; $d'_{non-math} = 0.52 \pm 0.15, t = 3.48, p = 0.004$). The difference between mathematicians and controls failed to reach significance, either for mathematics ($t = 1.46, p = 0.15$) or for general knowledge ($t = 0.49, p = 0.63$) (figure 1.1D).

In summary, mathematicians performed equally well with both types of sentences. Within the allotted time period of 4 seconds, they managed to discriminate meaningful mathematical statements from meaningless ones, as well as to distinguish true statements from false ones. Controls only managed to understand and classify the non-mathematical sentences. Most importantly, the results indicate that mathematical statements and non-mathematical sentences were well matched in term of objective difficulty, as evaluated by percent success, and that mathematicians and control subjects were well matched in terms of their performance with non-mathematical statements.

5.1.2. Behavioral results in visual runs

SDT was also used to evaluate subjects' ability to perform the visual one-back task. Pooling across the groups, d 's for each category were significantly greater than 0 (minimum d' averaged across subjects = 2.4, all $p < 10^{-12}$), meaning that participants correctly detected repetitions within each visual category. An ANOVA on d 's, with category as a within-subject factor and group as a between-subjects factor, indicated that neither mathematical expertise nor the category of pictures influenced the performance, and that both groups performed equally well in detecting repetitions regardless of the visual category (group: $F = 0.18, p = 0.67$; category: $F = 0.29, p = 0.94$; interaction group x category: $F = 0.69, p = 0.66$). An ANOVA on reaction time showed equivalent results (group: $F = 1.63, p = 0.20$; category: $F = 0.67, p = 0.67$; interaction group x category: $F = 0.54, p = 0.78$). Obviously, the one-back task was simple enough that, in spite of their mathematical expertise, mathematicians performed no better than controls in detecting repetitions, even with numbers ($t = 0.83, p = 0.41$) or formulas ($t = 0.83, p = 0.41$).

5.1.3. Subjective variables reported during the post-MRI questionnaire

For mathematical statements, mathematicians gave higher ratings than controls for all subjective variables (all p s < 0.001) (figure S0). For non-mathematical sentences, ratings of understanding, immediacy and imageability were equivalent for both groups, and controls responded with higher ratings than mathematicians for confidence, ease of responding, and reflection (p s < 0.05). Those findings suggest that each group was more at ease with its respective domain of expertise (figure S0).

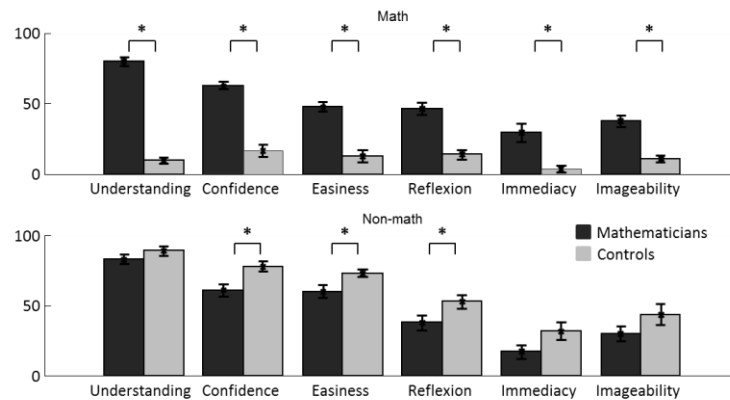


Figure S0. Participants' subjective ratings. Subjective ratings of understanding, confidence, ease of responding, intuition, immediacy and imageability for math (top) and nonmath (bottom) statements in both mathematicians (black) and control subjects (gray).

To evaluate the reliability of subjective ratings, which were collected after the fMRI, we correlated them with objective performance to the same statements. Within the group of professional mathematicians, we observed that objective performance during fMRI was positively correlated with subsequent ratings of confidence (logistic regression, $r = 0.36$; $p < 0.001$) and comprehension ($r = 0.21$; $p < 0.001$) of the same statements, and negatively correlated with subjective difficulty ($r = -0.28$; $p < 0.001$) and intuition ($r = -0.11$; $p < 0.001$). Those relations indicate that subjective variables were reliable and that, unsurprisingly perhaps, mathematicians showed increasingly better performance on sentences that they understood better, rated as easier, were more confident about, and for which they deployed explicit reasoning rather than mere intuitive judgments.

5.2. fMRI activations associated with mathematical reflection

Within the group of professional mathematicians, we first searched for greater activations to math than to non-math judgments during the reflection period. This contrast identified an extensive set of areas involving the bilateral intraparietal sulci (IPS), bilateral inferior temporal (IT) regions, bilateral dorsolateral, superior and mesial prefrontal cortex (PFC), and cerebellum (figures 1.2 and S1; table S1).

Examination of the time course of activity indicated that, at all sites of the shared math network, the fMRI signal rose sharply after a mathematical statement and remained sustained for ~15 seconds (figures 1.2C and S1).

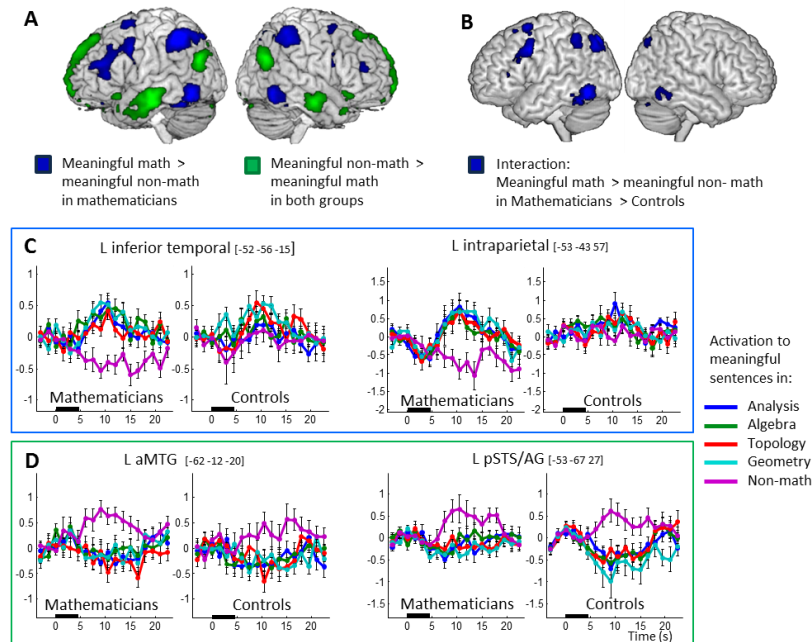


Figure 1.2. Distinct brain areas for mathematical expertise and for general semantic knowledge. (A) Whole-brain view of areas activated during reflection on mathematical statements (blue) versus general knowledge (green). In this figure and all subsequent figures, brain maps are thresholded at voxel $P < 0.001$, cluster $P < 0.05$ corrected for multiple comparisons across the brain volume. (B) Mathematical expertise effect: Interaction indicating a greater difference between meaningful math and nonmath statements in mathematicians than in controls. (C and D) Average fMRI signals in representative areas responsive to math (C) and to nonmath (D) (see SI Appendix, Fig. S1 for additional areas). Black rectangles indicate sentence presentation.

Contrariwise, for non-mathematical statements, a slow deactivation was seen (figure 1.2C). Thus, this network was strongly activated by all domains of mathematics, but remained inactive during reflection on matched non-mathematical problems. Furthermore, an interaction with group (math>non-math X mathematicians>controls) showed that this activation pattern was unique to subjects with mathematical expertise (figure 1.2B, table S1).

In control subjects, the math > non-math contrast identified a set of cortical areas involving right pre-central and left postcentral sulci, bilateral mesial parietal, middle occipital gyri, lingual gyri, insula overlapping with BA13, different frontal sites in BA10, parts of orbitofrontal prefrontal cortex and middle frontal gyrus, and subcortical regions, especially bilateral putamen (Figure S2A, Table S1). Those activations partly resemble the activations evoked by meaningless general-knowledge statements. Indeed, the meaningless > meaningful non-math contrast revealed activations in the right supramarginal gyrus, bilateral mesial parietal, right lingual gyrus, left anterior superior temporal gyrus (aSTG), near temporal pole, right pre-central and left post-central sulci. Activation maps for

these two contrasts overlapped in the right pre-central and left post-central sulci, bilateral mesial parietal and right lingual gyrus (figure S2B). In aSTG, we observed a strong deactivation for meaningless non-math and no activation for math (figure S2C).

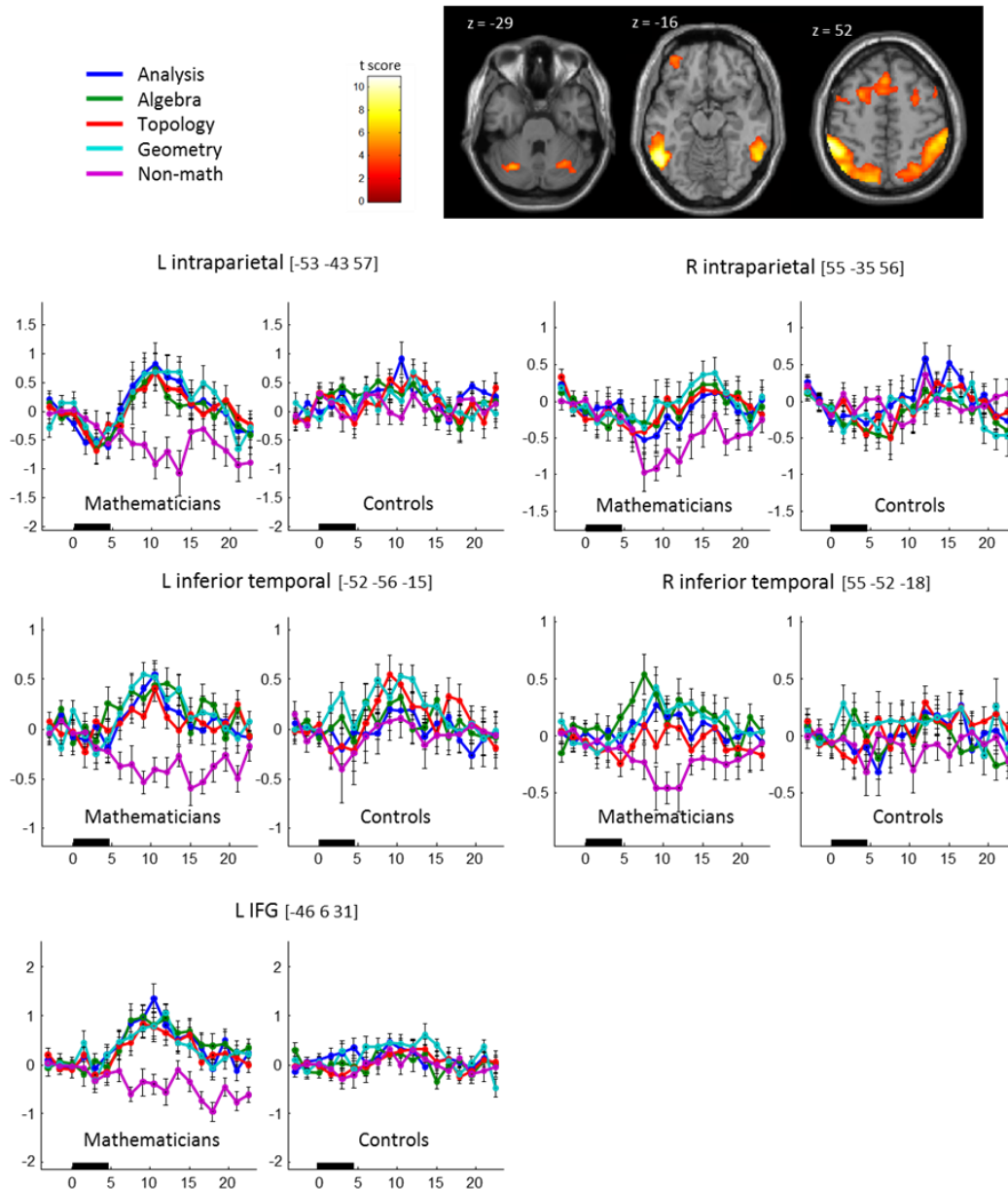


Figure S1. Activation profiles in areas activated by mathematical reflection in professional mathematicians. (Top) Axial slices showing voxels where activation was higher during reflection on math statements relative to non-math statements (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level). (Bottom) Plots show the fMRI signal (mean \pm one standard error) at the main peak of the main significant clusters. Time scale starts 3 seconds before the presentation of the sentence and lasts until the end of a trial. Black rectangles indicate the approximate time of sentence presentation.

These results suggest that control subjects, when listening to mathematical statements (1) do not activate the same bilateral intraparietal and inferior temporal regions as professional

mathematicians; and (2) process both meaningful and meaningless mathematical statements in a manner similar to meaningless non-mathematical statements.

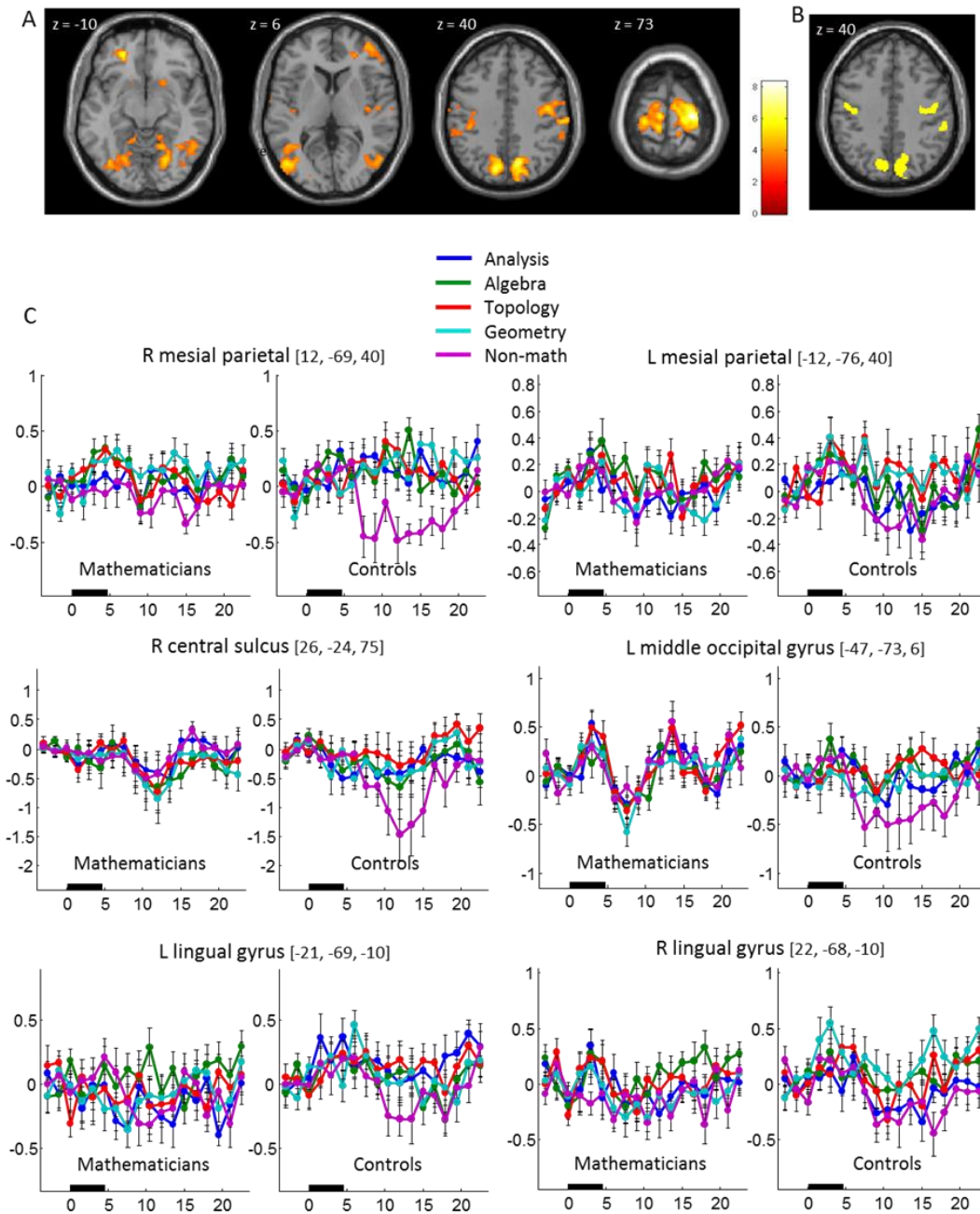


Figure S2. Brain areas showing a difference math > non-math in control subjects. (A) Axial slices showing voxels where activation was higher during reflection on math statements relatively to non-math sentences (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level) in control subjects. (B) Slice showing commonalities between the math > non-math contrast and the meaningless > meaningful non-math contrast in control subjects. (C) Plots showing the temporal profile of activation at the main peak of each significantly activated region.

5.3. Variation in brain activation across mathematical problems

Figure 1.3 shows that the majority of the mathematical expertise network was activated jointly by all four mathematical domains, as evidence by an intersection analysis (contrasts of algebra, analysis, geometry and topology, each relative to non-math, in mathematicians during the

reflection period; each at $p < 0.001$; cluster size > 200 voxels). An F-test was used to identify the putative differences between those four contrasts at the whole-brain level. This test revealed significant differences in bilateral parietal posterior regions (peaks at 23, -72, 52; $F = 8.39$, uncorrected $p < 0.001$; and at -11, -75, 58; $F = 8.73$, uncorrected $p < 0.001$) and left inferior temporal regions (-50, -63, -5; $F = 12.01$, uncorrected $p < 0.001$) (figure 1.3A). Examination of the activation profiles, as well as further t-tests, revealed that this pattern was primarily due to a greater activation to geometry problems than to the other three domains combined (at -50, -63, -5, $t = 6.39$, $p < 0.001$; at 23, -72, 52, $t = 4.39$, $p < 0.001$; at -11, -75, 58, $t = 4.28$, $p < 0.001$). This contrast also revealed regions showing more activation to geometry than to the other domains of math in bilateral IT, bilateral superior parietal, right intraoccipital sulcus, left supramarginal gyrus, and left inferior parietal cortex. In addition, statements in analysis also induced greater activation than other domains in a mesial frontal orbital region, and statements in topology in the left middle frontal gyrus (table S2, peaks at $p < 0.001$; cluster size > 200 voxels, corresponding to clusterwise $p < 0.05$ corrected).

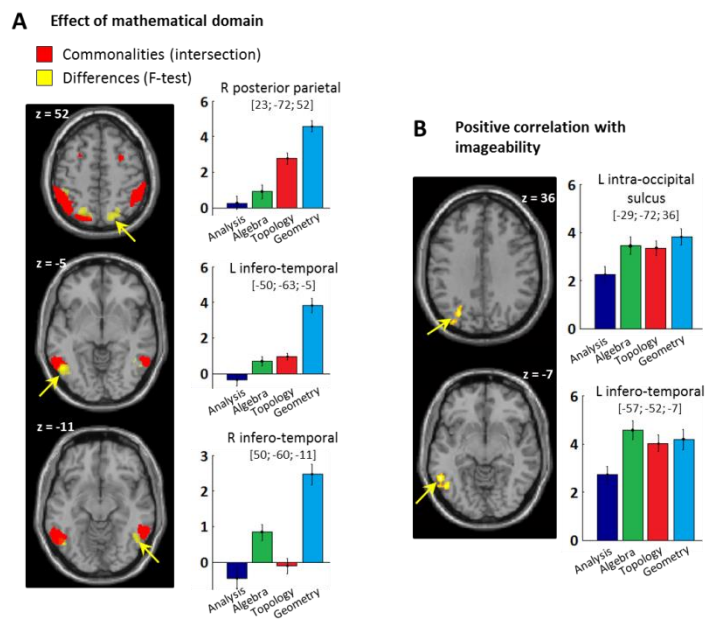


Figure 1.3. Variation in brain activation across mathematical problems. (A) Cortical sites where responses were common (red) or different (yellow) between analysis, algebra, topology, and geometry. The commonalities of the four mathematical domains were assessed by the intersection of activation maps for the contrasts analysis $>$ nonmath, algebra $>$ nonmath, topology $>$ nonmath, and geometry $>$ nonmath (each $P < 0.001$). Differences in cortical responses across mathematical domains were evaluated by an F-test at the whole-brain level (voxel $P < 0.001$, cluster $P < 0.05$ corrected). Bar plots show the activation for each mathematical domain at the principal peaks of three main regions identified in the latter F-contrast (R posterior parietal, L and R infero-temporal). (B) Cortical sites that showed a positive correlation between activation during math reflection and subjective imageability ratings within the meaningful statements in mathematicians.

We also evaluated whether the mathematicians' subjective ratings in the post-MRI questionnaire correlated with brain activity evoked by different mathematical statements. We tested this potential correlation, in mathematicians only, for meaningful math statements, with each of the 6 subjective variables that were rated (comprehension, confidence, difficulty, intuition, immediacy and imageability). Only a single contrast revealed a significant positive correlation between imageability and brain activation, at two sites in the left inferior temporal cortex (peak at -57, -52, -7, $T=7.38$, $p < 0.001$) and in the left intra-occipital sulcus (peak at -29, -72, 36, $t = 6.06$, $p < 0.001$) (figure 1.3B).

5.4. fMRI activations associated with meaningful mathematical reflection

As a second criterion for brain areas involved in mathematical expertise, we compared the activations during reflection on meaningful versus meaningless mathematical statements. This contrast, which is orthogonal to the previous one and controls for lexical content, fully replicated the results obtained with the contrast of meaningful math > nonmath.

In mathematicians, activation was stronger in bilateral IPS, IT and PFC for meaningful than for meaningless math statements (figure 1.4A; table S1), with the latter inducing only a transient activation in most areas (figure 1.4C, no activation at all in right IPS; figure S3). The same contrast yielded no significant difference in controls, resulting in a significant group X meaningfulness interaction in the same brain regions (figure 1.4B; table S1).

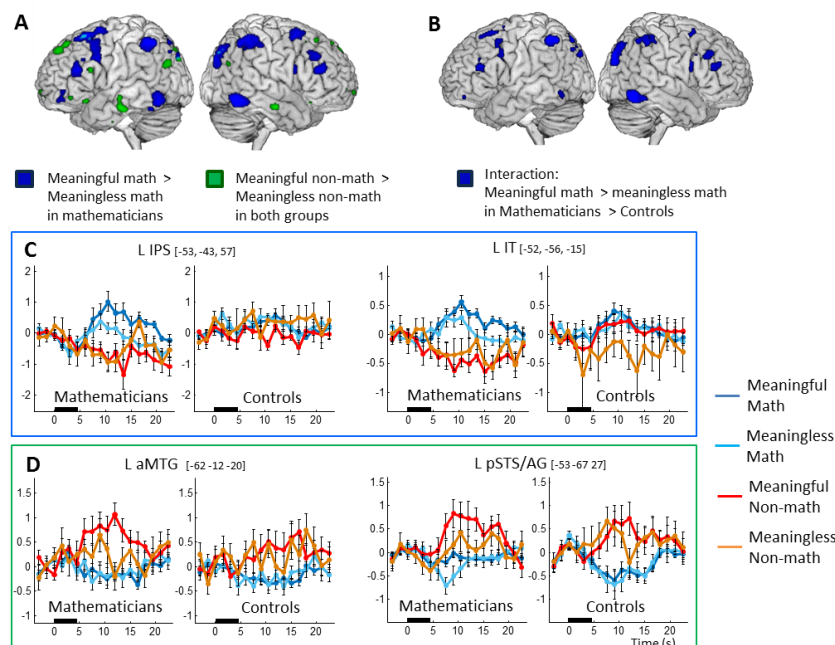


Figure 1.4. Math and nonmath semantic effects. (A) Whole-brain view of semantic effects (meaningful > meaningless) for math statements in professional mathematicians (blue) and for nonmath statements in both groups (green). (B) Mathematical expertise effect: Interaction indicating a large difference between meaningful and meaningless math statements in mathematicians than in controls. (C and D) Average fMRI signals in representative areas responsive to math (C) and to nonmath (D) (see SI Appendix, figure. S3 and S6 for additional areas).

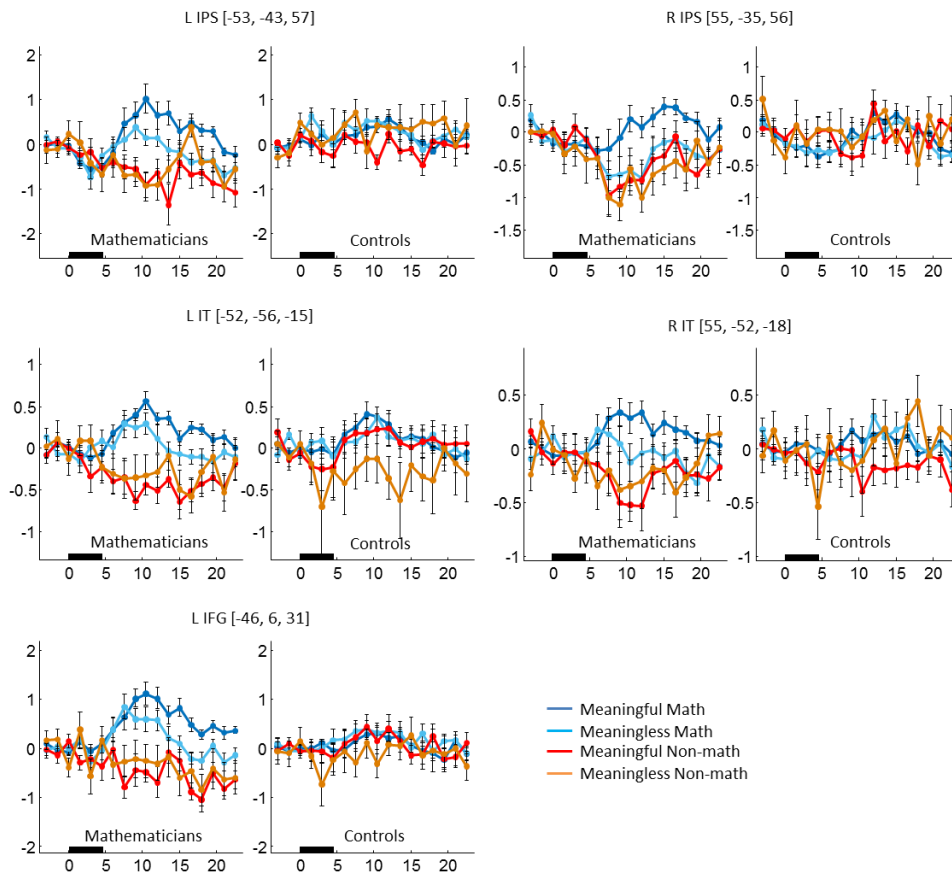


Figure S3. Activation profiles for meaningful and meaningless statements in brain areas responsive to mathematical statements. For both groups, plots at the peaks of the 5 main regions identified in the contrast of math > non-math in mathematicians (same coordinates as figure S1).

5.5. Controls for task difficulty

The activations observed during mathematical reflection overlap with a set of areas which have been termed the “multiple demand system” (Duncan, 2010). Those regions are active during a variety of cognitive tasks that involve executive control and task difficulty (Fedorenko et al., 2013). It is therefore important to evaluate whether our results can be imputed to a greater task difficulty for math relative to non-math statements. As noted in the behavioral section, objective task difficulty, as assessed by percent correct, was not different for math and non-math statements within the mathematicians, and for non-math statements across the two groups of mathematicians and control subjects. However, subjective difficulty, as reported by mathematicians after the fMRI, was judged as slightly higher for the math problems than for the non-math problems (on a subjective scale converted to a 0-100 score: subjective difficulty = 52.4 ± 3.4 for math, and 40.0 ± 4.5 for non-math; $t = 2.4$, $p = 0.03$). Nevertheless, several arguments suggest that this small difference fails to account for our brain-activation results.

First, once the meaningless statements were excluded, difficulty did not differ significantly between meaningful math and non-math statements (subjective difficulty = 53.9 ± 2.8 for meaningful

math, versus 49.4 +/- 4.7 for meaningful non-math; $t = 0.8$, $p = 0.5$). In other words, the small difference in subjective difficulty (math > non-math) was due only to the greater perceived simplicity of the meaningless general-knowledge statements, whose absurdity was more immediately obvious than that of meaningless math statements. Yet when we excluded the meaningless statements from the fMRI analysis, the difference in brain activation between math and non-math statements remained and was in fact *larger* for meaningful than for meaningless statements (figures 1.2 and 1.4).

Second, to directly evaluate the impact of difficulty on the observed brain networks, within each subject, we sorted the meaningful math and non-math statements into two levels of subjective difficulty (easy or difficult, i.e. below or above that subject's mean of the corresponding category). As expected, the easiest math statements were rated as much easier than the difficult non-math statements (figure 1.5A).

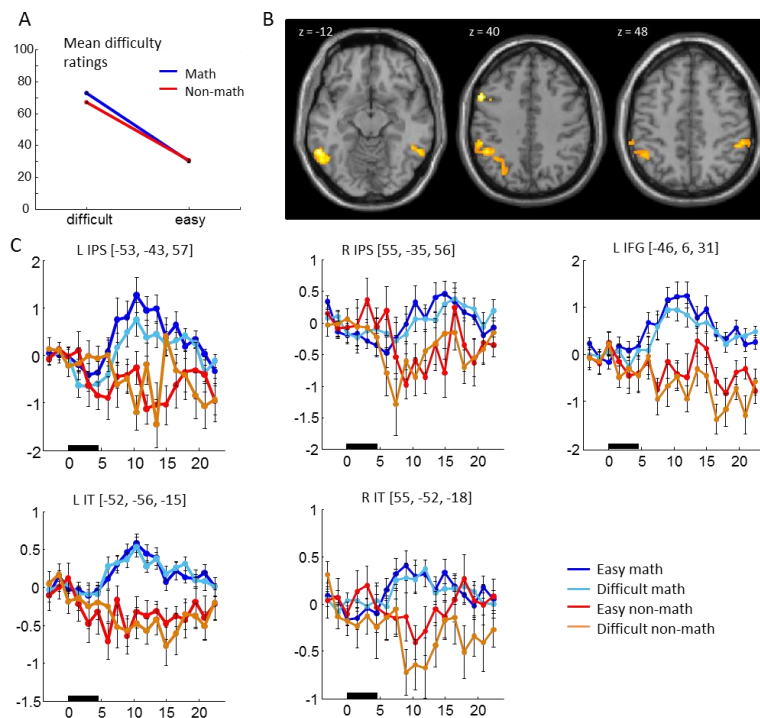


Figure 1.5. Control for task difficulty. For each subject, math and nonmath statements were sorted into two levels of difficulty (easy versus difficult) depending on whether their subjective rating was below or above the subject's mean. (A) Mean difficulty ratings for easy and difficult math and nonmath statements. The results indicate that activation is organized according to domain (math versus nonmath) rather than difficulty. (B) Axial slices showing the principal regions activated in the contrast "easy math > difficult nonmath" in mathematicians across all meaningful problems (voxel $P < 0.001$, cluster $P < 0.05$ corrected). This contrast revealed virtually the same sites as the ones that were activated for the standard math > nonmath contrast. (C) Plots report the temporal profile of activation at the principal peaks identified in the contrast of math > nonmath in mathematicians (same coordinates as figure S1).

In spite of this difference, the contrast of meaningful easy math > meaningful difficult non-math again revealed the same sites as those which were activated for the standard math > non-math contrast (figure 1.5B). Thus, those sites were activated even during simple mathematical reflection,

and their greater activation for math than for non-math occurred irrespective of task difficulty. Indeed, the time course of fMRI signals in the 5 main regions identified by the math > non-math contrast (figure 1.5C) showed no effect of difficulty. This was confirmed by the contrast of difficult > easy math and difficult > easy non-math which revealed no significant sites. Similar results were obtained when problems were sorted by objective performance (figure S4).

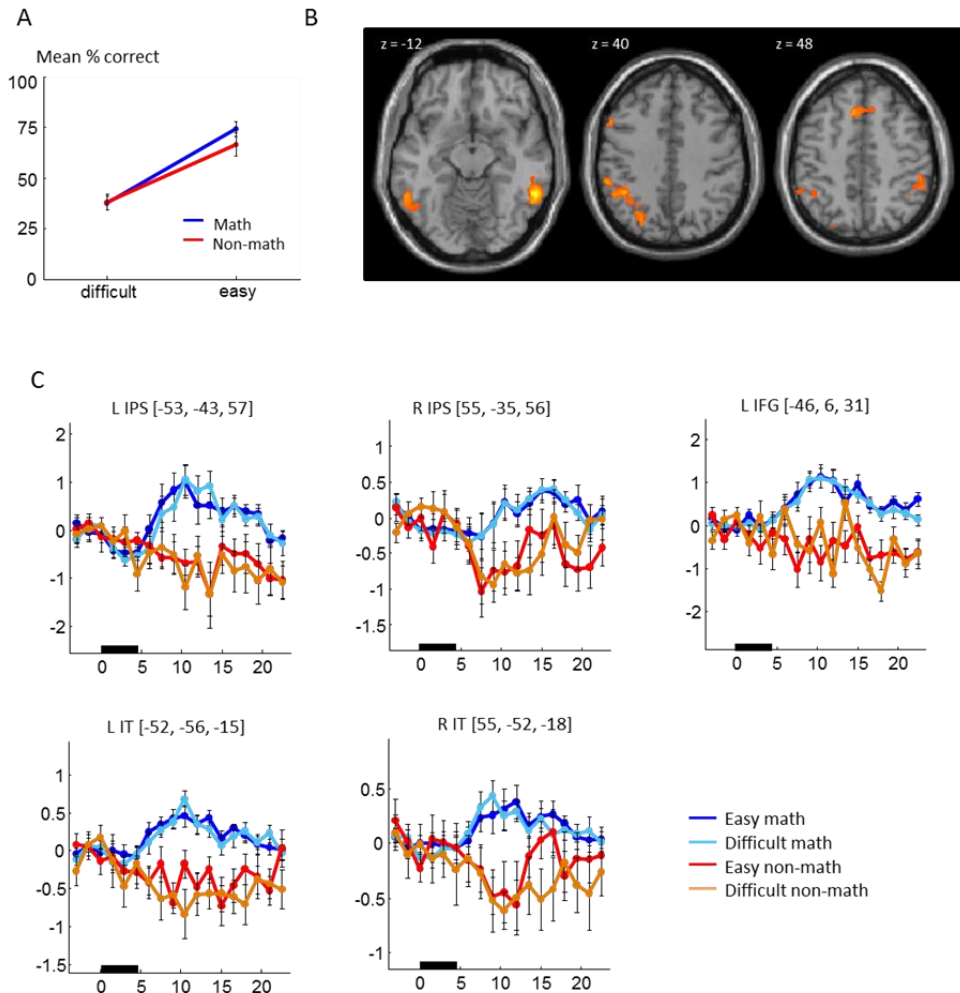


Figure S4. Control for task difficulty. For each subject, math and non-math statements were sorted into two levels of difficulty (easy versus difficult) depending on whether mean performance on a given statement was below or above the global percent correct. (A) Mean correct rates for easy and difficult math and non-math statements. The results again indicate that activation is organized according to domain (math versus non-math) rather than difficulty. (B) Axial slices showing the principal regions activated in the contrast “easy math > difficult non-math” in mathematicians across all meaningful problems (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level). This contrast revealed virtually the same sites as those which were activated for the standard math > non-math contrast. (C) Plots report the temporal profile of activation at the principal peaks of the 5 main regions identified in the contrast of math > non-math in mathematicians (same coordinates as figure S1).

5.6. Dissociation with the areas activated during non-mathematical reflection

We next examined which regions were activated by non-math statements. Pooling across the two groups, areas activated bilaterally by non-math > math reflection included the inferior angular gyrus (AG, near the temporo/parietal junction), the anterior part of the middle temporal gyrus

(aMTG), the ventral inferior frontal gyrus (IFG pars orbitalis, overlapping Brodmann's area 47), an extended sector of mesial prefrontal cortex (PFC; mesial parts of BA 9, 10 and 11) and cerebellum Crus I (figures 1.2A and S5; table S3), consistent with previous studies of semantic networks (Monti et al., 2012; Vandenberghe et al., 1996).

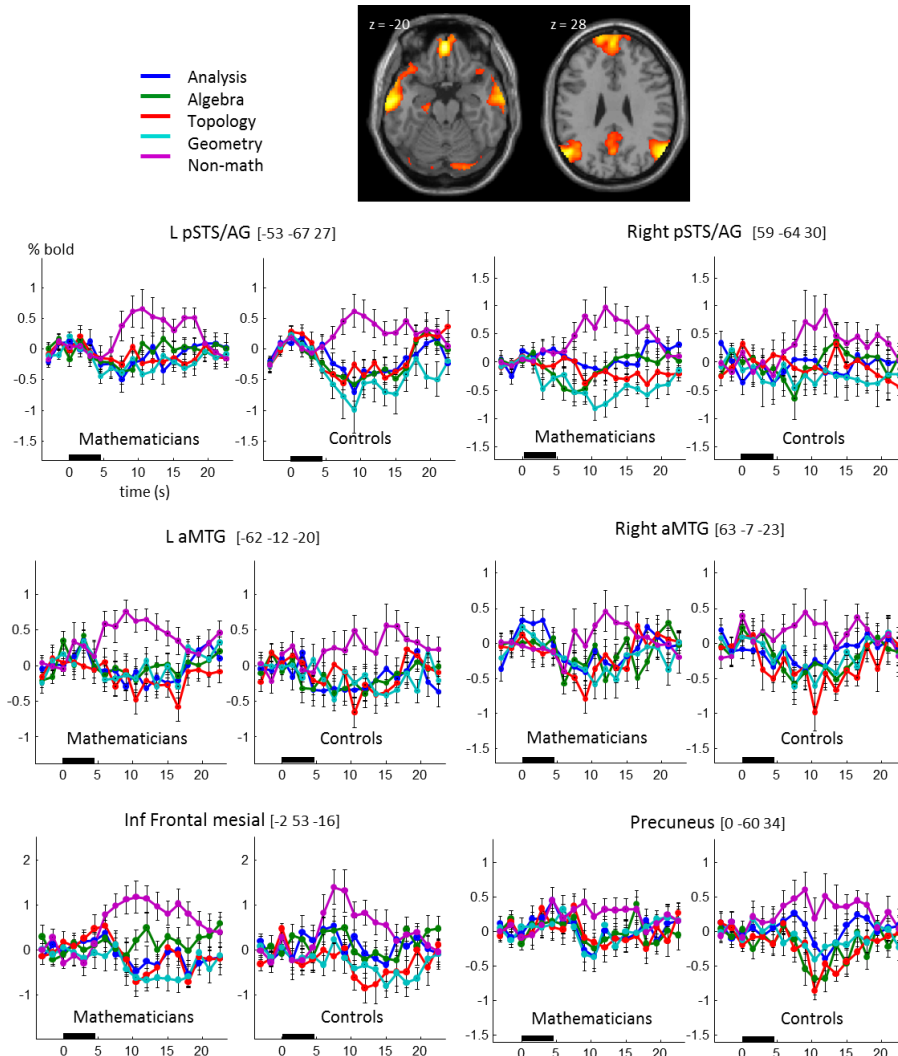


Figure S5. Activation profiles within areas of the general-knowledge network. Axial slices show voxels where activation was higher during reflection on non-math sentences relatively to math statements (voxel $p < 0.001$, cluster $p < 0.05$ corrected for multiple comparisons at the whole-brain level) in control subjects. Plots report the time course of activation at the principal peak of the activated areas.

The majority of these regions showed no difference between groups (table S3). Their time course indicated a significant activation just after non-math statements, and a systematic deactivation to all four types of math statements (figure 1.2D). The contrast meaningful > meaningless non-math statements, which provides an orthogonal means of identifying general-knowledge semantics, pointed to virtually the same sites (figure 1.4A; table S3) and did not differ across groups (figure S6; table S3).

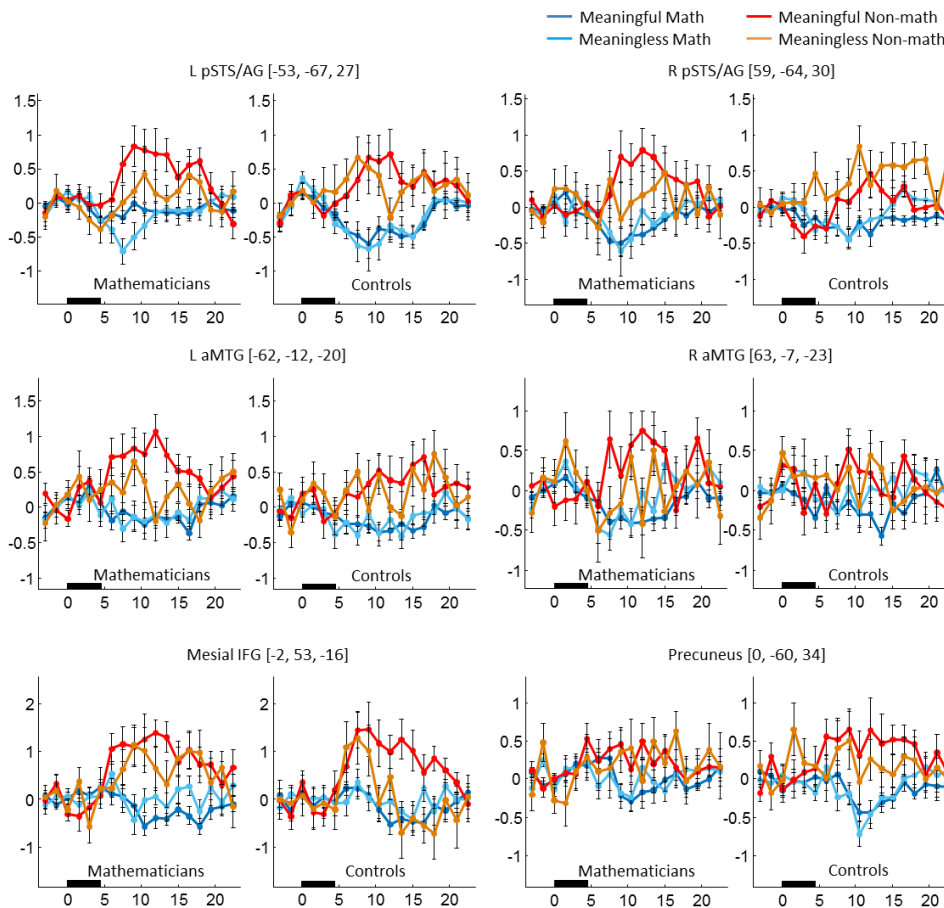


Figure S6. Activation profiles for meaningful and meaningless statements in brain areas mainly responsive to non-mathematical statements during the reflection period. Plots at the peaks of the 6 main regions identified in the contrast of non-math > math in both groups during the reflection period.

Thus, two converging criteria identified a reproducible set of bilateral cortical areas associated with mathematical expertise and that differ from the classical language semantics network. The dissociation, within mathematicians, between the networks for math and non-math was tested formally through the appropriate interactions, i.e. (meaningful - meaningless math) – (meaningful – meaningless non-math) and the opposite contrast (table S4). Stronger activations for meaningful math were again seen in bilateral IT, bilateral IPS, right posterior superior frontal, and left lateral IFG/MFG, while stronger activations for meaningful non-math were in right pSTS/AG, bilateral anterior MTG and ventro-mesial PFC. Crucially, there was essentially no intersection at $p < 0.001$ of the areas for meaningful > meaningless math and for meaningful > meaningless non-math (figure 1.4A, tables S1, S3). The only small area of intersection, suggesting a role in generic reflection and decision-making, was observed outside the classical language network, in bilateral superior frontal (BA 8) and left inferior MFG. Even at a lower threshold ($p < 0.01$ uncorrected), the intersection extended to part of posterior parietal and dorsal PFC but spared perisylvian language cortex.

5.7. Activation profile in language areas

To further probe the contribution of language areas to math, we used a sensitive region-of-interest (ROI) analysis. We selected left-hemispheric regions previously reported (Pallier et al., 2011) as showing a language-related activation proportional to constituent size during sentence processing (temporal pole [TP]; anterior superior temporal sulcus [aSTS]; posterior superior temporal sulcus [pSTS]; temporo-parietal junction [TPj]; inferior frontal gyrus pars orbitalis [IFGorb] and pars triangularis [IFGtri]), plus the left Brodmann area 44 (Amunts et al., 2003). We then used an independent functional localizer (Pinel et al., 2007) to identify subject-specific peaks of activation to sentences (spoken or written) relative to rest, and finally tested the contribution of those language voxels to the main reasoning task.

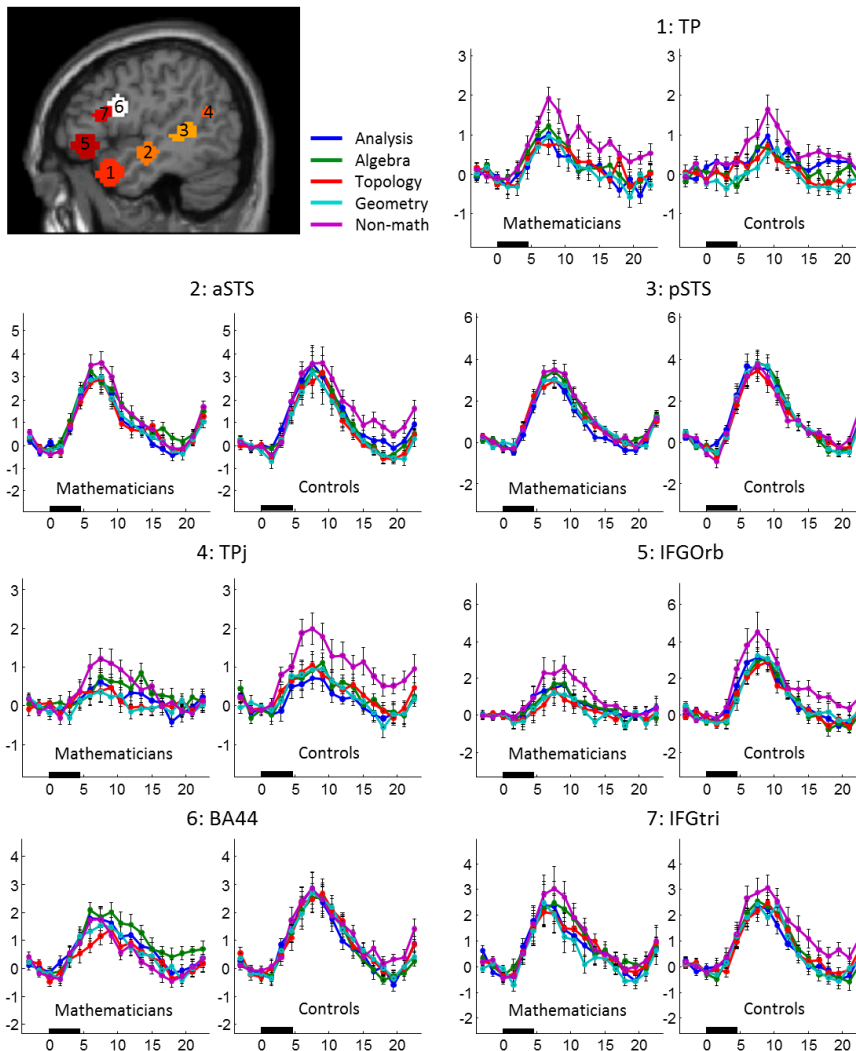


Figure S7. Activation evoked by mathematical and non-mathematical statements in classical language-related regions. The brain slice shows the localization of the seven cortical regions of interest: TP, aSTS, pSTS, TPj, IFGorb, BA44 and IFGtri. Within each region, plots show the temporal profile of activation for the four domains of math and non-math, averaged across subjects, at the subject-specific peak of activity during an independent localizer for sentence processing. None of these regions appear to be specifically activated during mathematical reflection. On the contrary, several of them show greater activation by non-math than by math statements (see table S5 for statistics).

Figure S7 shows the temporal profile of activation, averaged across participants, at the peak subject-specific voxel, and table S5 presents the corresponding statistics. At this single-voxel level, none of these language regions showed evidence of a contribution to mathematical reflection. In fact, during the reflection period, in mathematicians, TP, pSTS, and IFGorb responded significantly

more to non-math than math. In controls, only aSTS and IFGtri responded more to non-math than to math. We also looked for differences between groups, but the only trends were in the direction of significantly greater activation in controls than in mathematicians (in aSTS and BA44 for non-math statements; and in TP for math statements; uncorrected $p < 0.05$). There was no interaction between group and category in any region. Furthermore, no significant activation was found in those regions for meaningful versus meaningless math statements, neither in mathematicians, nor in controls. However, for meaningful versus meaningless non-math, a significant activation was found in aSTS, and to a lesser extent in pSTS in mathematicians (table S5).

This sensitive ROI approach thus confirmed that language networks do not contribute to mathematical reflection. It could be, however, that these regions have a transient role during the processing of the mathematical statements themselves. We therefore replicated the above analyses with contrasts measuring activation during sentence presentation (table S5, lower part). None of the ROIs were engaged in math listening more than non-math listening, nor in meaningful > meaningless math listening, neither in mathematicians, nor in controls. The only effects were in the converse direction: there was more activation for non-math than for math in aSTS, pSTS, TPJ, IFGOrb, IFGtri and BA44 for mathematicians, and in TPJ and IFGOrb for control subjects. Only IFGOrb showed a group effect, activating less in mathematicians than in controls both during math listening and during non-math listening, without any significant interaction (table S5).

Overall, these results provide no indication that language areas contribute to mathematics, and in fact suggest that, if anything, they activated less for mathematics and/or less in mathematicians.

Whole-brain imaging confirmed a near-complete spatial separation of areas activated by mathematical judgments and by sentence processing (figure S8). A very small area of overlap could be seen in the left dorsal Brodmann area 44 (figure S8B), an area also singled-out in previous reports (Wang et al., 2015) and which should certainly be further investigated in future research. Note, however, that this small overlap was only present in smoothed group images and failed to reach significance in higher-resolution single-subject results (table S5).

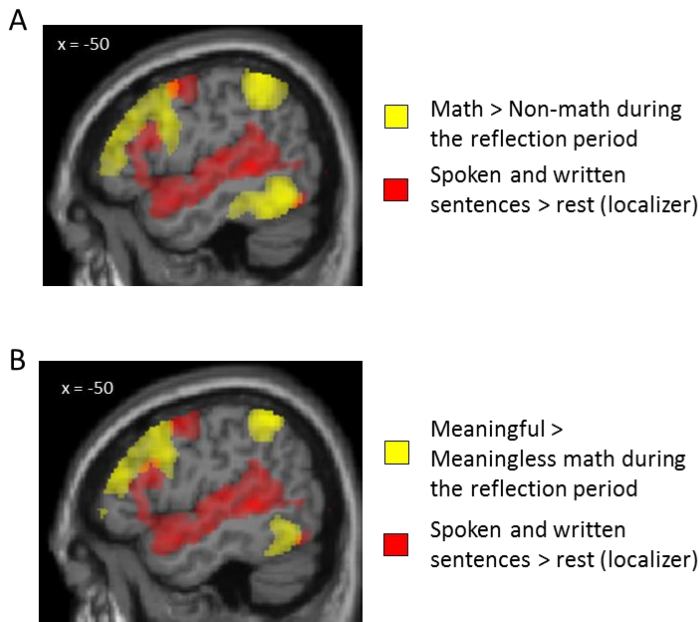


Figure S8. Spatial relationship between the math and language networks. The sagittal slices show, in red, the contrast of spoken and written sentences relatively to rest during an independent functional localizer scan and in yellow, (A) the contrast of math > non-math statements (during the reflection period) and (B) the contrast of meaningful > meaningless math statements (during the reflection period). A very small area of overlap appears in orange in superior frontal cortex mostly in A. The images show how the contours of the math network, in the frontal lobe, spare language-related areas in the left inferior frontal gyrus.

5.8. Relationships between mathematics, calculation, and number detection

We next examined the alternative hypothesis of a systematic relationship between advanced mathematics and core number networks. To this aim, we compared the activations evoked by math versus non-math reflection in mathematicians, with those evoked either by calculation relative to sentence processing (Pinel et al., 2007) or by numbers relative to other visual categories in both mathematicians and controls (after verifying that these groups did not differ significantly on the latter contrasts). Both calculation and simple number processing activated bilateral IPS and IT, thus replicating early observations of number-sense and number-form areas (figure 1.6). Remarkably, those activations overlapped entirely with those activated by higher-level mathematics in mathematicians only (figure 1.6).

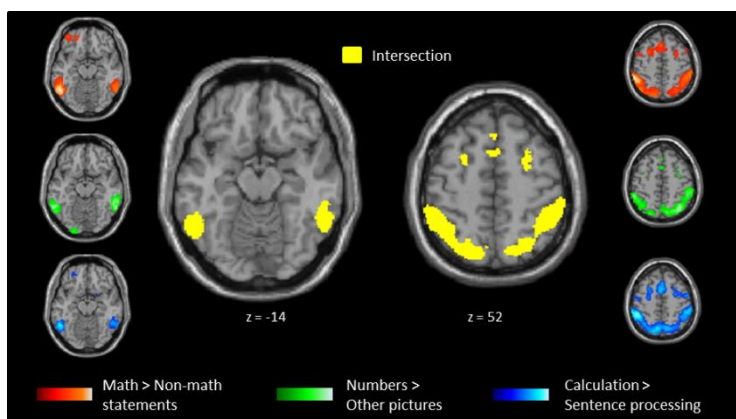


Figure 1.6. Overlap of the mathematical expertise network with areas involved in number recognition and arithmetic. Red, contrast of math versus non-math statements in mathematicians; green, contrast of Arabic numerals versus all other visual stimuli in both mathematicians and controls; blue, contrast of single-digit calculation versus sentence processing in the localizer run, again in both groups; yellow, intersection of those three activation maps (each at $P < 0.001$).

Our mathematical statements carefully avoided any direct mention of numbers or arithmetic facts (see appendix), but some still contained an occasional indirect reference to numbers or to fractions (e.g. \mathbb{R}^2 , *unit sphere*, *semi-major axis*, etc). We therefore reanalyzed the results after systematic exclusion of such statements. The activation evoked by mathematical reflection remained virtually unchanged (figure S9, table S6). Thus, the overlapping activations to number and to

advanced math cannot be explained by a shared component of numerical knowledge, but indicate that high-level mathematics recruits the same brain circuit as basic arithmetic.

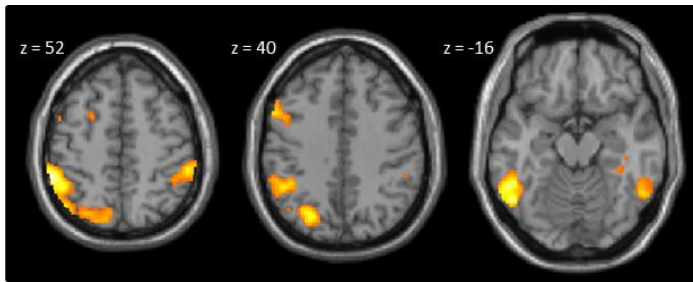


Figure S9. Activation for math > non-math in mathematicians, after removal of sentences containing occasional reference to numbers. Axial slices showing the principal regions activated in the math > non-math contrast in mathematicians, after having removed all statements that contained a reference to numbers. This analysis revealed virtually the same sites as those activated for the overall math > non-math contrast.

Because group-level overlap of activation can arise artificially from inter-subject averaging, we next turned to more sensitive within-subject analyses. First, thanks to independent localizer scans performed in a different cohort of 83 subjects (Pinel et al., 2007), we defined 13 math-related regions in left and right Intraparietal sulci (IPS), infero-temporal cortex (IT), inferior, middle and superior frontal lobes (IFG, MFG, and SFG), mesial supplementary motor area (SMA) and bilateral foci in Cerebellum. In particular within left and right IPS and IT, we verified that the subject-specific voxels activated during simple arithmetic also showed a significant activation during mathematical reflection and during number and formula recognition, and did so more than in the corresponding control conditions (respectively non-math reflection and non-symbolic pictures; table S7).

Second, we used representational similarity analysis to probe whether a similar pattern of activation was evoked, within each subject, by all math-related activities, i.e. mathematical reflection, calculation, and numbers or formula recognition. At subject level, within each of the 13 regions of interest, we computed correlation coefficients between the activations evoked by our main experimental conditions: math and non-math statements, simple calculation and sentence processing, and formulas, numbers, words and non-symbolic pictures. We then compared the correlation of math statements with other math-related condition to the correlation of math statements with the corresponding non-math control condition (figure 1.7). The results revealed that, in all 13 regions, the activation evoked by mathematical reflection was more correlated to the activation evoked by simple calculation than to spoken or written sentence processing (all p s < 0.011 uncorrected, table S7). In particular, in bilateral IPS and IT, we first found that the activation topography during the reflection period was more strongly correlated across the four domains of mathematical statements (analysis, algebra, topology and geometry) than between any of those domains and the general-knowledge non-math statements. Second, the activation during mathematical reflection was better correlated with that evoked by simple arithmetical problem solving than with the activation evoked by non-numerical spoken or written sentences in left and right IPS and IT. Third, it was also better correlated with the activation during number recognition (in

all four regions) and formula recognition (in left IPS and bilateral IT) than with the activation evoked by non-symbolic pictures or by written words (in bilateral IT only). Similar effects were also observed in other regions: e.g. left IPS, MFG and Cerebellum for formulas or all regions except right Cerebellum for numbers in the comparison with pictures (see table S7). Finally, in bilateral IPS and IT,

the activation during simple calculation was better correlated with that evoked by numbers or formulas, than with that evoked by non-symbolic pictures or written words (all p s < 0.027 uncorrected, bottom panel of figure 1.7, table S7). Similar correlations with numbers were observed in the other regions except right cerebellum; and left frontal regions also exhibited a stronger correlation with formulas than with pictures (see table S7).

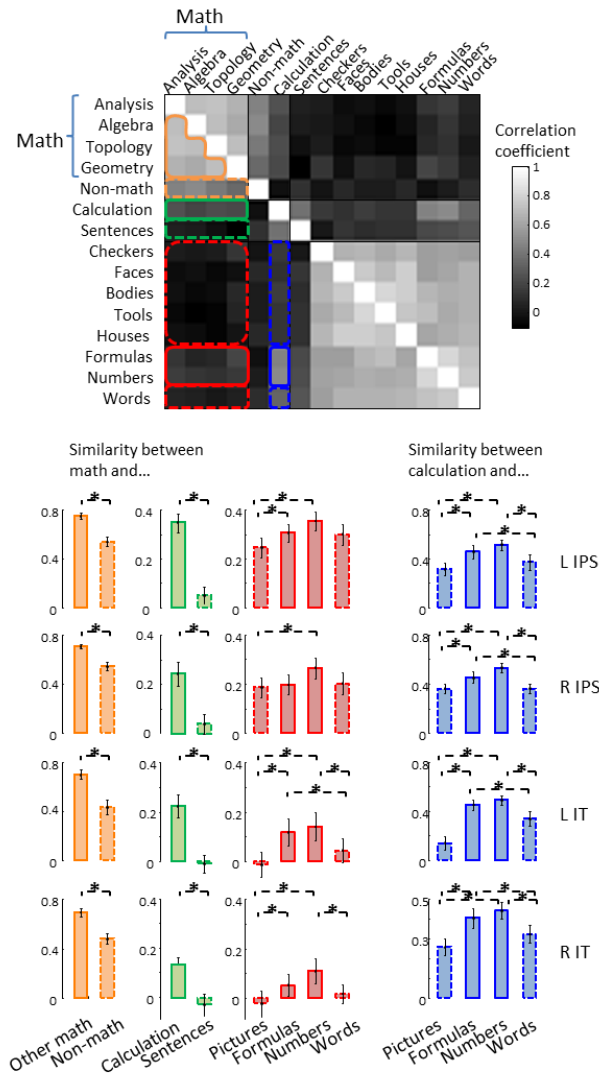


Figure 1.7. Representational similarity analysis. (Top) Sample similarity matrix in left infero-temporal cortex showing the mean, across subjects, of the correlation between the spatial activation patterns evoked by the 15 experimental conditions of the whole experiment: four domains of math plus nonmath presented in auditory runs, calculation and spoken and written sentences from the localizer, and all pictures and symbols tested in visual runs. (Bottom). Mean correlation coefficients are shown in representative regions of interest of the math network. Colors indicate the provenance of the data in the similarity matrix. ROIs (left and right intraparietal sulci and infero-temporal cortices) were defined using a calculation localizer in a different group of subjects. * $P < 0.05$ (Student t tests). Error bars represent one SEM.

Overall, these high-resolution single-subject analyses confirm that advanced mathematics, basic arithmetic and even the mere viewing of numbers and formulas recruit similar and overlapping cortical sites in mathematically trained individuals.

5.9. Activations during the sentence-listening period

We also analyzed activations during sentence listening, prior to the reflection period. Our conclusions remained largely unchanged. Indeed, in mathematicians, the contrast math > non-math indicated that a subset of the areas involved in math reflection already activated during the auditory presentation of the statements: bilateral IT (-57, -58, -10, $t = 10.53$; 59, -55, -17, $t = 8.42$); bilateral IPS (left: -59, -37, 46, $t = 7.42$ and -29, -73, 37, $t = 8.08$; right: 39, -61, 54, $t = 4.17$ and 29, -75, 42, $t =$

4.88); and bilateral PFC foci (left: -45, 37, 16, $t = 7.09$ and -48 8 25, $t = 6.92$; right: 51, 7, 24, $t = 6.40$) (figure S10). Though activation was mostly bilateral, time courses of activation in bilateral intraparietal sulcus suggested that the math network activated early in the left hemisphere and then spread to the right hemisphere (figure S1). Moreover, the bilateral and mesial superior frontal foci that we found activated during reflection were not present during sentence presentation. Conversely, we found an additional activation during sentence presentation in the right head of the caudate nucleus (12, 25, 1, $t = 6.79$).

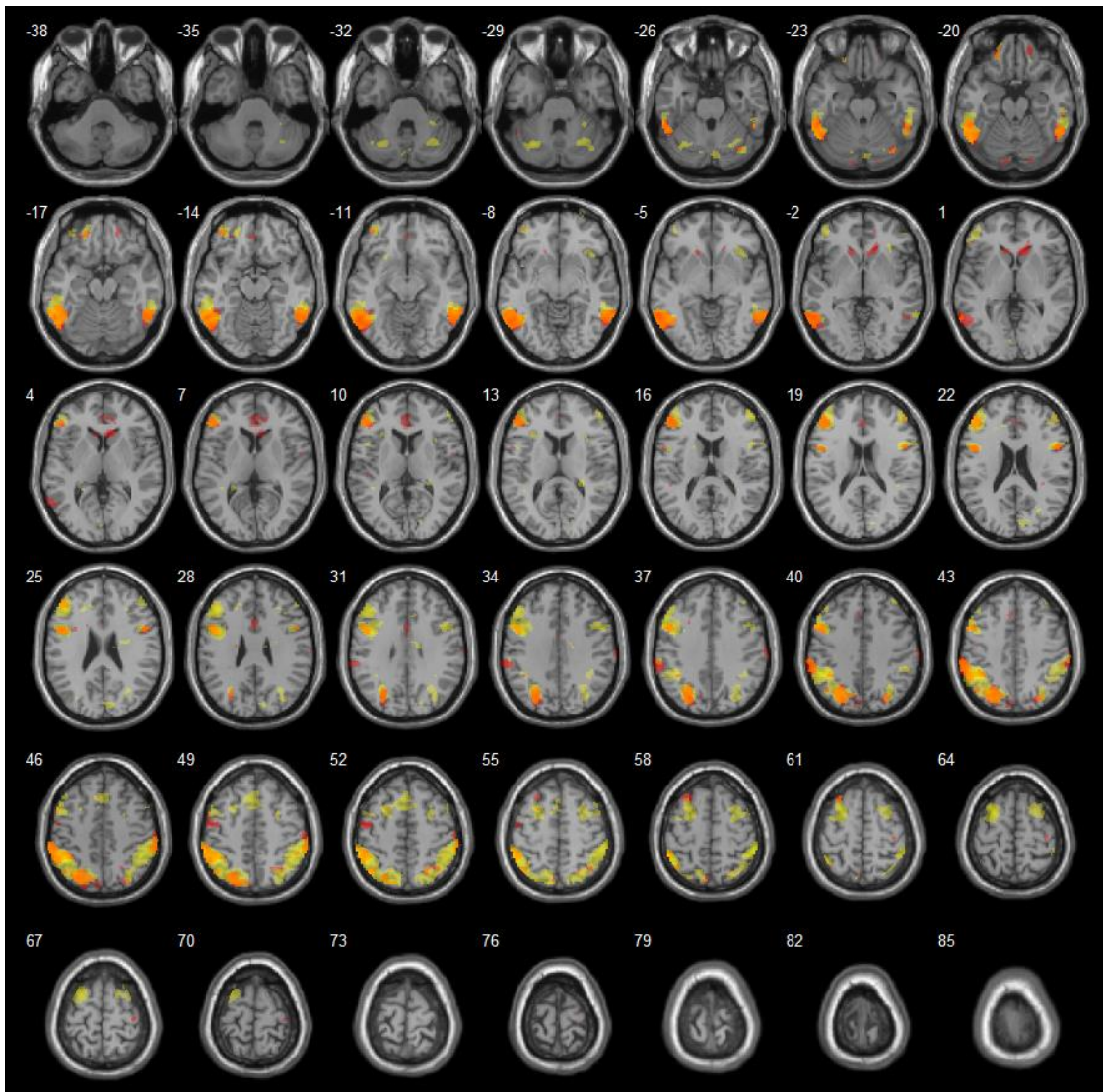


Figure S10. Superposition of the math > non-math contrasts in mathematicians during statement presentation and during the subsequent reflection period. Axial slices show the math > non-math contrasts in mathematicians, separately for activations evoked during sentence presentation in red, and during the reflection period in yellow. The intersection (in orange) reveals that most areas involved in mathematical reflection, particularly in the left hemisphere, were already activated when mathematicians listened to the statements.

For control subjects, the contrast of math > non-math during sentence presentation revealed again a completely different set of areas than the previously identified math network. Some of these

areas were found during reflection and thus seemed to activate early, such as the bilateral middle occipital gyri and bilateral insula. Other regions seemed to activate only during sentence presentation. Notably, we found activation in different sub-cortical nuclei including bilateral thalamus (left: -18, -16, 4, $t = 5.06$; right: 18, -22, 6, $t = 5.18$), amygdala (left: -29, -6, -26, $t = 5.48$; right: 27, -1, -28, $t = 4.99$) and left hippocampus (-39, -30, -10, $t = 5.67$).

Concerning the non-math statements, the contrast of non-math > math in mathematicians revealed a network that we previously described for non-math > math during the reflection period. We found bilateral temporal activation: anterior MTG (left: -59, -7, -14, $t = 10.8$; right: 56, -6, -17, $t = 9.68$), posterior MTG (left: -59, -39, 1, $t = 5.52$; right: 60, -34, -2, $t = 5.55$), angular gyrus and temporo-parietal junction (left: -47, -61, 22, $t = 10.1$; right: 48, -63, 25, $t = 6.59$). We also found frontal activation: IFGOrb (left: -47, 25, -13, $t = 9.28$; right: 39, 35, -13, $t = 8.11$), IFGtri (left: -54, 20, 24, $t = 7.79$; right: 54, 23, 21, $t = 6.06$), and mesial frontal sites (superior frontal: -6, 56, 39, $t = 8.07$; orbitofrontal: -5, 55, -13, $t = 5.76$). In control subjects, we found additional sites around the calcarine sulcus (-3, -69, 22, $t = 6.78$), bilateral lingual gyri (left: -15, -57, 3, $t = 7.30$; right: 12, -49, 3, $t = 6.03$) and bilateral head of the caudate nucleus (left: -9, 17, -1, $t = 5.19$; right: 9, 13, -1, $t = 5.41$).

Two additional effects emerged only during sentence presentation. First, a group X problem type interaction revealed a striking group difference in the bilateral head of the caudate nucleus (figure S11). This region was active in mathematicians only when they were exposed to math statements, and in control subjects only when they were exposed to non-math statements. This effect was confirmed by an examination of the SPM interaction of group and the math > non-math contrast, which was highly significant in the head of the caudate nucleus bilaterally (left: -11, 20, -1, $t = 5.95$; right 15, 25, -1, $t = 7.39$), and by plots of temporal profiles of fMRI signals for math and non-math stimuli over the whole regions of interest (figure S11).

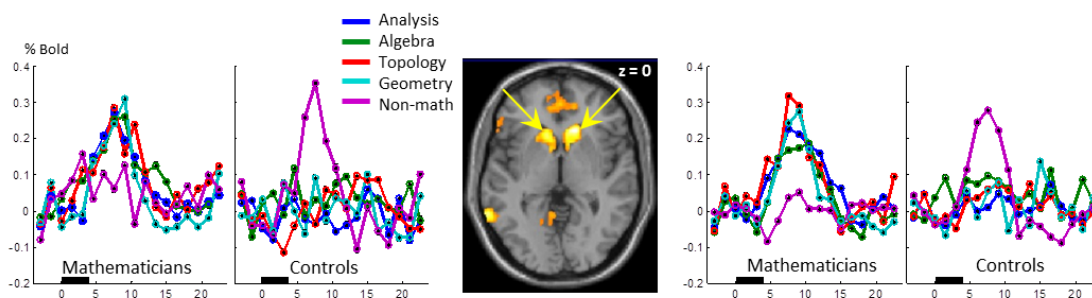


Figure S11. Interaction between group and problem type during statement presentation in the head of the caudate nucleus. The axial slice shows a bilateral activation during statement presentation in the head of the caudate nucleus in the interaction (math>non-math) X (mathematicians – controls) (voxel $p < 0.001$, cluster corrected $p < 0.05$). Plots show the corresponding temporal profile of fMRI signals for the four different domains of math and non-math, separately in mathematicians and control subjects. Signals were averaged across the entire caudate cluster.

The engagement of this subcortical region, which is known to participate in motivation and executive attention, thus shifted radically towards the subject’s preferred domain.

Second, another group difference concerned the left angular gyrus. It was deactivated by meaningless compared to meaningful general-knowledge statements in both groups, as previously reported (Pallier et al., 2011; Seghier, 2013). Indeed, studying the contrast of meaningful > meaningless non-math during sentence presentation, the most important cluster was found in the left angular gyrus. It extended to middle occipital gyrus and middle temporal gyrus (in mathematicians: -48, -60, 16, $t = 5.28$; in controls: -38, -75, 28, $t = 4.75$; in both groups together: -39, -76, 31, $t = 6.12$). In mathematicians, it was the only cluster revealed by this contrast. We found additional clusters in control subjects, including three sites exhibiting a significantly greater difference between meaningful and meaningless non-math in controls than in mathematicians: the bilateral middle temporal sulcus (left: -44, -23, -5, $t = 5.85$; right: 53, -19, 3, $t = 4.85$), and right Heschl’s gyrus (36, -31, 9, $t = 4.95$). However, in mathematicians only, bilateral angular gyri (left: -48, -60, 16, $t = 5.52$; right: 44, -79, 22, $t = 4.35$) also showed a greater activation for meaningful than for meaningless math (figure S12), along with the head of the left caudate nucleus (-14, 19, -2, $t = 5.28$), some mesial frontal foci (superior frontal: -3, 68, 15, $t = 4.95$; orbitofrontal: 9, 44, -11, $t = 4.28$) and middle temporal region (-69, -18, -14, $t = 4.74$).

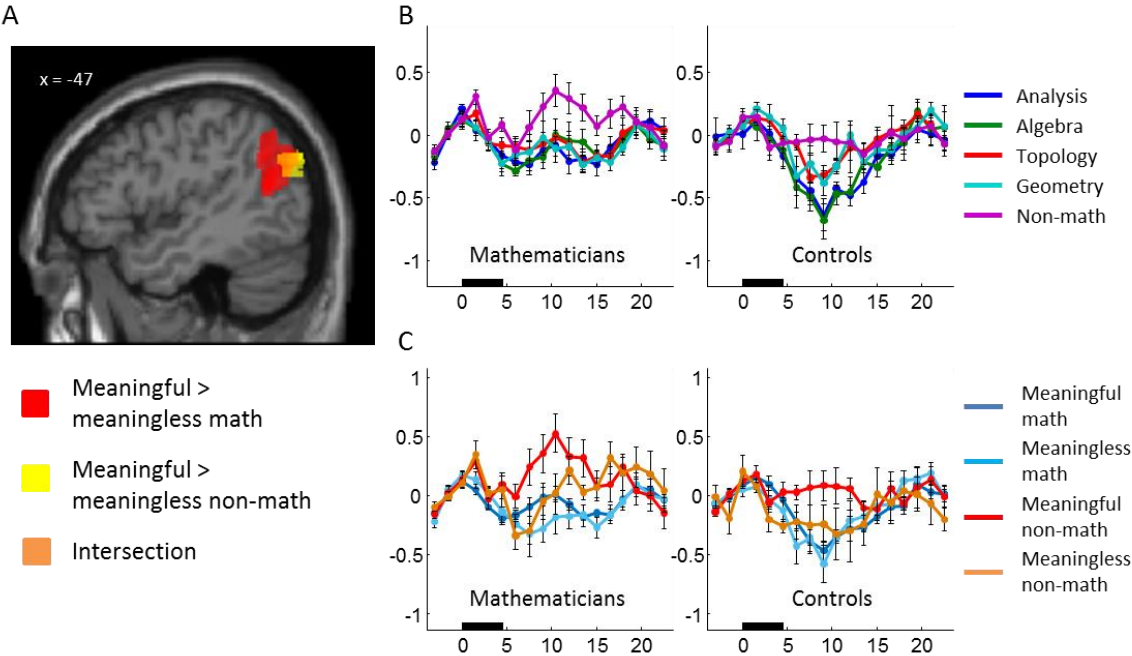


Figure S12. Transient effect of meaningful versus meaningless statements during sentence presentation in the angular gyrus. (A) Sagittal slice centered on the left angular gyrus showing activations to meaningful > meaningless math (in red) and to meaningful > meaningless non-math (in yellow) during sentence presentation (voxel $p < 0.001$, cluster corrected $p < 0.05$). The intersection of both contrasts maps appears in orange. (B) Time course of the mean activation within the voxels belonging to the intersection presented in panel A, for the four domains of math and non-math statements in both groups. (C) Time course of the mean activation to meaningful and meaningless math and non-math statements. A transient difference between meaningful and meaningless math is seen only in mathematicians.

Those sites were essentially different from the ones observed during the reflection period, and interestingly, the left angular gyrus appeared in the intersection of meaningful > meaningless contrasts for math and for non-math (figure S12A). In order to clarify the role of this region, we plotted the temporal profiles of the average fMRI signals within that intersection (figure S12B & C).

Such plots revealed that the observed differences occurred in the general context of a deactivation for all mathematical statements relative to baseline, particularly marked in the control subjects. Indeed, we found more deactivation for math in controls than in mathematicians within this region. Moreover, we observed a deactivation for both math and non-math meaningless statements in mathematicians and for all math and meaningless non-math statements in control subjects. In mathematicians, the only group able to distinguish meaningless from meaningful math statements, there was a small transient effect of greater activation to meaningful than to meaningless math. These results therefore suggest that this region is involved in semantic processing of sentences and distinguishes meaningful from meaningless sentences regardless of their mathematical or non-mathematical content. This interpretation fits with previous observations on this area (Humphries et al., 2006; Pallier et al., 2011; Seghier, 2013), which demonstrate an increasing activation in this area in direct proportion to the amount of semantic information available in the stimulus and a systematic deactivation to meaningless materials (e.g. pseudowords or delexicalized “Jabberwocky” sentences), presumably reflecting the contribution of this region to semantic reflection in the resting state. Moreover, mathematical expertise seems to enable the left angular gyrus to extend its function to mathematical statements. Importantly, this is only a transient contribution, restricted to the sentence comprehension period, as this area was deactivated during mathematical reflection.

5.10. Differences between mathematicians and controls in ventral visual cortex

Since high-level mathematics recruits ventral areas of the inferior temporal gyrus involved in the recognition of numbers and expressions, a final question is whether the activation of those regions varies as a function of mathematical expertise. During a one-back task involving the visual presentations of numbers, formulas and other visual stimuli, both mathematicians and controls showed a typical mosaic of ventral occipito-temporal preferences for one category of visual stimuli over all others (figure 1.8A, table S8). Those regions included the right-hemispheric fusiform face area (FFA), bilateral parahippocampal place areas (PPA), bilateral extrastriate body areas (EBA), bilateral lateral occipital cortices for tools (LOC), and left-hemispheric visual word form area (VWFA). Importantly, with high-resolution fMRI, we also found a strong number-related activation in bilateral regions of the inferior temporal gyrus, at sites corresponding to the left and right visual number form areas (VNFA) (Hermes et al., 2015; Shum et al., 2013). We also observed bilateral responses to formulas > other stimuli in both groups at bilateral sites partially overlapping the VNFA. A whole-

brain search for interactions with group (mathematicians versus controls) revealed that some of these visual contrasts differed with mathematical expertise. First, the left inferior temporal activation to written mathematical formulas was significantly enhanced in mathematicians relative to controls (-53 -64 -17, $t = 4.27$; figure 1.8B). Single-subject ROI analyses verified that this effect was not simply due to greater variance in anatomical localization in controls compared to mathematicians, but to a genuine increase in the volume of bilateral IT cortex activated by mathematical formulas (table S8). We presume that this region was already present in control subjects because they had received higher education and could therefore recognize basic arithmetic expressions which have been previously related to IT and IPS regions (Maruyama et al., 2012). Just like reading expertise massively enhances the left ventral visual response to written letter strings (Dehaene et al., 2010), mathematical expertise leads to a bilateral enhancement of the visual representation of mathematical symbols.

For numbers, no significant difference between groups was observed using a whole-brain SPM analysis. However, once identified by the overall contrast “number>others”, the VNFA peak in the left hemisphere exhibited a small but significant group difference, with more activation in mathematicians than in controls for number > non-symbolic pictures (i.e. excluding formulas and words; $t = 2.31$, $p = 0.028$; no such effect was found at the peak of the right VNFA). Both left and right VNFA also responded more to formulas than to other stimuli in mathematicians relative to controls (left: $t = 3.82$, $p < 0.001$; right: $t = 2.72$, $p = 0.01$; figure 1.8E). Thus, mathematical expertise is associated with a small expansion of number representations in the left VNFA and a bilateral recruitment of the VNFA by mathematical formulas.

Finally, because literacy has been shown to induce a hemispheric shift in face responses (Dehaene et al., 2010), we also examined face processing in our mathematicians. While there was no significant difference between the two groups at the principal peak of the right FFA, a whole-brain search indicated that responses to faces were significantly reduced in mathematicians relative to controls in right-hemispheric IT (44 -45 -17, $t = 4.72$, figure 1.8D). There was also an enhanced response to tools in mathematicians relative to controls in left LOC, just posterior to the activation by formulas (-45 -73 -5, $t = 5.12$, figure 1.8C). These intriguing differences must be considered with caution, as their behavioral impact and causal link to mathematical training remains presently unknown.

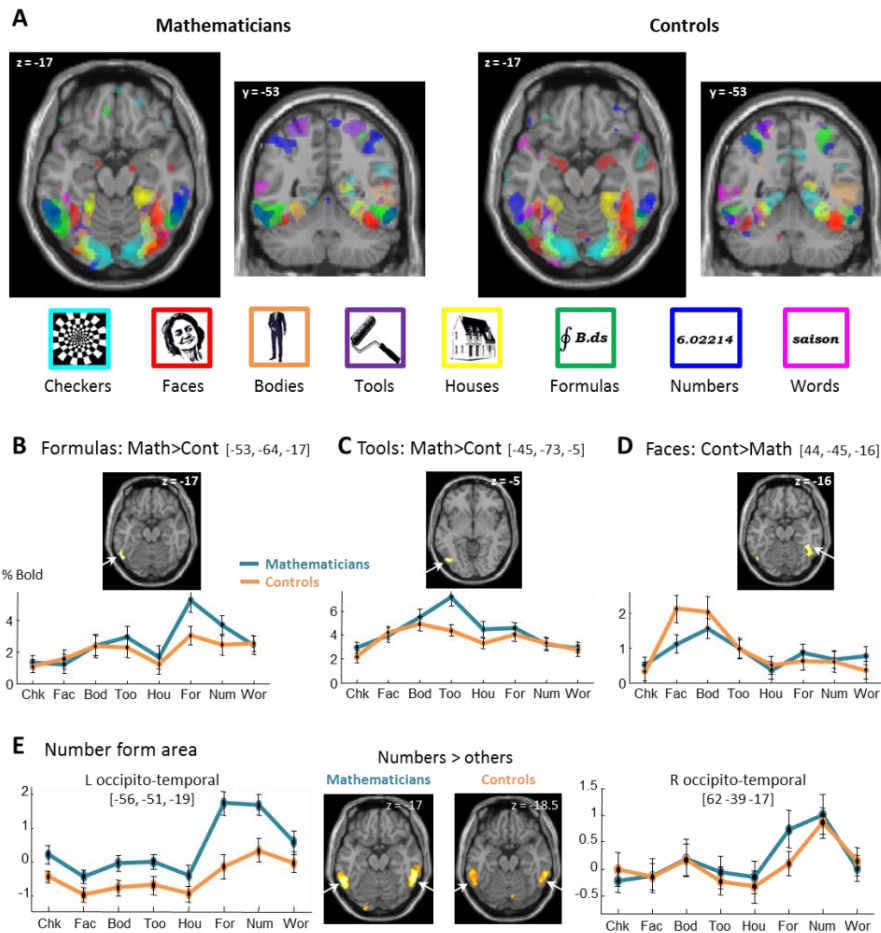


Figure 1.8. Effects of mathematical expertise on the ventral visual pathway. (A) Mosaic of preferences for different visual categories in ventral visual cortex. Slices show the activation for the contrast of a given category (represented by a specific color) minus all others. (B and C) A whole-brain search for larger responses in mathematicians than in controls revealed an effect for formulas in left ventral occipito-temporal cortex (B) and for tools in left lateral occipital cortex (C). Plots show the activation to each category relative to rest at the selected peak for mathematicians and controls. (D) A whole-brain search for smaller responses in mathematicians than in controls revealed an effect for faces in the right fusiform face area (FFA). (E) Slices showing the bilateral visual number form areas (VNFAs) in mathematicians and in controls, assessed by the contrast of numbers minus all other categories. At the peak of the left VNFA, a larger activation was found in mathematicians relative to controls for both numbers and formulas.

6. Discussion

Using high-resolution whole-brain fMRI, we observed the activation of a restricted and consistent network of brain areas whenever mathematicians engaged in high-level mathematical reflection. This network comprised bilateral intraparietal, inferior temporal, and dorsal prefrontal sites. It was activated by all domains of mathematics tested (analysis, algebra, topology and geometry) and even, transiently, by meaningless mathematical statements. It remained silent, however, to non-mathematical statements of matched complexity. Instead, such problems activated distinct bilateral anterior temporal and angular regions.

Our main goal was to explore the relationships between high-level mathematics, language, and core number networks. In mathematicians, we found essentially no overlap of the math-

responsive network with the areas activated by sentence comprehension and general semantic knowledge. We observed, however, a strong overlap and within-subject similarity of the math-responsive network with parietal and inferior temporal areas activated during arithmetic calculation and number recognition (table S7). In particular, bilateral ventral inferior temporal areas corresponding to the visual number form area (Hermes et al., 2015; Shum et al., 2013) were activated by high-level mathematics as well as by the mere sight of numbers and mathematical formulas. The latter activations were enhanced in mathematicians. Correspondingly, a reduced activation to faces was seen in the right fusiform gyrus. Those results are analogous to previous findings on literacy, showing that the acquisition of expertise in reading shifts the responses of left ventral visual cortex towards letters and away from faces. (Dehaene et al., 2010; Dundas et al., 2013; Pegado et al., 2014)

Our findings shed light on the roots of mathematical abilities. Some authors argued that mathematics rests on a recent and specifically human ability for language and syntax (Chomsky, 2006), while others hypothesized that it is a cultural construction grounded upon evolutionary ancient representations of space, time and number (Dehaene, 2011; Dillon et al., 2013; Lakoff and Núñez, 2000). In our task, language areas were only activated transiently during the presentation of auditory statements, whether mathematical or non-mathematical. Rather, the activations that we observed during mathematical reflection occurred in areas previously associated with number coding in humans and other animals. Bilateral intraparietal and dorsal prefrontal regions are active during a variety of number-processing and calculation tasks (Dehaene et al., 1999) and contain neurons tuned to numerical quantities (Nieder and Dehaene, 2009). Bilateral inferior temporal regions have been termed “visual number form areas” (VNFA) because they activate to written Arabic numerals much more than to letter strings or other pictures (Hermes et al., 2015; Shum et al., 2013). The VNFAs were previously difficult to detect with fMRI because they lie close to a zone of fMRI signal loss (Shum et al., 2013). However, using a fast high-resolution fMRI sequence that mitigates these difficulties, we found that the VNFAs are easily detectable and are activated bilaterally not only by Arabic numerals, but also by algebraic formulas, arithmetic problems and, in mathematicians only, during high-level mathematical reasoning.

While we only investigated, within our subjects, the relationship between the cortical territories for high-level mathematics, formulas and number processing, previous work strongly suggests that the representation of geometrical relationships and visuo-spatial analogies also calls upon a similar bilateral dorsal prefrontal and intraparietal network (Krawczyk et al., 2011; Watson and Chatterjee, 2012). Indeed, representations of cardinal number, ordinal knowledge, and spatial extent overlap in parietal cortex (Harvey et al., 2015; Prado et al., 2010b). Given those prior findings,

our results should not be taken to imply that number is the sole or even the main foundation of higher mathematical abilities; more likely, a complex integration of numerical, ordinal, logical and spatial concepts is involved (Lakoff and Núñez, 2000).

Although one might have thought that the relationship between language and math would depend strongly on the domain of mathematics under consideration, we found no support for this hypothesis. Except for a small additional activation in posterior inferotemporal and posterior parietal cortex for geometry statements, all problems in algebra, analysis, topology and geometry induced correlated and overlapping activations that systematically spared language areas. Using elementary algebraic and arithmetic stimuli, previous fMRI and neuropsychological research in non-mathematicians also revealed a dissociation between mathematical and syntactic knowledge (Klessinger et al., 2007; Maruyama et al., 2012; Monti et al., 2012; Varley et al., 2005). Together, those results are inconsistent with the hypothesis that language syntax plays a specific role in the algebraic abilities of expert adults. Importantly, however, they do not exclude a transient role for these areas in the acquisition of mathematical concepts in children (Spelke, 2003). Imaging studies of the learning process would be needed to resolve this point.

Our results should not be taken to imply that the IPS, IT and PFC areas that activated during mathematical reflection are specific to mathematics. In fact, they coincide with regions previously associated with a « multiple-demand » system (Duncan, 2010) active in many effortful problem-solving tasks (Fedorenko et al., 2013) and dissociable from language-related areas (Fedorenko et al., 2012). Some have suggested that these regions form a “general problem solving” or “general purpose network” active in all effortful cognitive tasks (Hugdahl et al., 2015). Several arguments, however, question the idea that this network is fully domain-general. First, we found no activation of this network during equally difficult reasoning with non-mathematical semantic knowledge. In fact, the easiest mathematical problems caused more activation than the most difficult non-mathematical problems (figure 1.5), and even meaningless mathematical problems caused more activation than meaningful general-knowledge problems (figure 1.4). Second, other studies have found a dissociation between tightly matched conditions of linguistic versus logical or arithmetical problem solving (Monti et al., 2012, 2009). Overall the existing literature suggests that the network we identified engages in a variety of flexible, abstract, and novel reasoning processes that lie at the core of mathematical thinking, while contributing little to other forms of reasoning or problem-solving based on stored linguistic or semantic knowledge.

Our conclusions rest primarily on within-subject comparisons within the group of professional mathematicians (e.g. between math and non-math reasoning, meaningful and meaningless math, etc.). As an additional control, we also presented the same stimuli to a gender-

and age-matched group of non-mathematically trained but equally talented researchers and professors in humanities and related disciplines. Although mathematicians and controls may still differ on dimensions such as IQ, musical talent, hobbies, etc., such putative differences are irrelevant to our main conclusion of a dissociation between general-knowledge and mathematical reasoning *within* the mathematicians. They also seem unlikely to account for the enhanced ventral visual responses to numbers and math formulas, which most plausibly reflect the much higher frequency with which mathematicians process such symbols.

Previous explorations of the brain mechanisms underlying professional-level mathematics are scarce. One fMRI study scanned 15 professional mathematicians, focusing entirely on their subjective sense of beauty for math expressions (Zeki et al., 2014). The results revealed a medial orbito-frontal correlate for this subjective feeling, but could not determine which brain areas are responsible for the mathematical computations that precede it. The network we observed appears as a plausible candidate that should be tested in further work.

The regions we observe also fit with those showing increased gray matter in mathematicians relative to control subjects of equal academic standing (Aydin et al., 2007). During elementary problem-solving tasks, fronto-parietal activations at locations similar to ours were enhanced in mathematically gifted subjects (Descio et al., 2011). Inter-individual variations in this network predict corresponding variations in fluid intelligence (Duncan, 2010; Gray et al., 2003), which is a major correlate of mathematical skills independently of other language skills. The connectivity between those regions, mediated by the superior longitudinal fasciculus, also increases in the course of normal numerical and mathematical education and in mathematically gifted students relative to others (Emerson and Cantlon, 2012; Matejko and Ansari, 2015; Prescott et al., 2010).

The fact that these brain areas are jointly involved in higher mathematics and basic arithmetic may explain the bidirectional developmental relationships that have been reported between pre-linguistic number skills and later mathematical skills, whereby intuitive number sense predicts subsequent mathematical scores at school (Gilmore et al., 2010; Halberda et al., 2008; Hyde et al., 2014; Starr et al., 2013) and, conversely, mathematical education enhances the precision of the non-verbal approximate number system (Piazza et al., 2013). Educational research also provides ample correlational and interventional evidence suggesting that early visuo-spatial and numerical skills can predict later performance in mathematics. The present results provide a putative brain mechanism through which such links may arise.

7. Supplementary tables

Table S1. Main activation peaks for the math > non-math and the meaningful > meaningless math contrasts.

	Mathematicians								Controls								Mathematicians > Controls							
	Math > Non-math				Meaningful > Meaningless math				Math > Non-math				Meaningful > Meaningless math				Math > Non-math				Meaningful > Meaningless math			
	x	Y	z	t	x	y	z	T	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t
L IPS	-53	-43	57	10.9	-50	-51	52	9.07	-	-	-	-	-	-	-	-	-27	-75	52	7.88	-51	-46	54	6.68
R IPS	50	-36	56	7.30	51	-40	51	7.90	-	-	-	-	-	-	-	-	33	-73	49	5.43	53	-40	51	5.45
L IT	-53	-57	-16	10.4	-56	-58	-16	7.88	-	-	-	-	-	-	-	-	-53	-60	-17	8.26	-62	-57	-10	4.64
R IT	52	-52	-19	7.50	60	-54	-13	9.46	-	-	-	-	-	-	-	-	56	-39	22	5.27	60	-54	-11	7.22
L MFG/ BA46	-44	31	27	7.81	-48	37	22	7.57	-	-	-	-	-	-	-	-	-45	-26	28	7.14	-47	13	36	4.88
L MFG/ BA9	-47	7	31	8.21	-50	10	33	7.33	-	-	-	-	-	-	-	-	-54	14	39	8.57	-53	37	22	5.11
L SFS	-24	8	64	7.11	-26	5	63	7.39	-	-	-	-	-	-	-	-	-27	11	66	7.45	-27	14	60	5.10
R SFS	32	5	56	4.97	30	8	57	9.88	-	-	-	-	-	-	-	-	-	-	-	-	30	8	57	5.79
R MFG/ BA46	50	47	16	6.74	48	38	22	7.60	-	-	-	-	-	-	-	-	-	-	-	-	48	37	22	5.14
R MFG/ BA9 - BA10	50	10	21	6.03	51	11	22	6.61	42	47	25	4.91	-	-	-	-	-	-	-	-	51	11	25	5.45
SMA	-2	23	51	6.12	0	26	49	7.24	-	-	-	-	-	-	-	-	-2	23	51	6.87	-	-	-	-
BA10	-20	47	-16	5.78	-42	55	-13	6.25	-22	44	-10	6.26	-	-	-	-	-	-	-	-	-	-	-	-
L Cereb. 6th lobule	-29	-66	-29	6.00	-3	-81	25	5.22	-	-	-	-	-	-	-	-	-5	-82	-26	6.28	3	-79	-25	4.61
R Cereb. 6th lobule	39	-73	-26	5.24	14	-82	-25	6.03	-	-	-	-	-	-	-	-	8	-81	-23	7.04	8	-78	-28	4.10
L mesial parietal	-	-	-	-	-	-	-	-	-12	76	40	6.50	-	-	-	-	-	-	-	-	-	-	-	-
R mesial parietal	-	-	-	-	-	-	-	-	12	-69	40	6.94	-	-	-	-	-	-	-	-	-	-	-	-
R pre- central sulcus	-	-	-	-	-	-	-	-	26	-24	75	8.34	-	-	-	-	-	-	-	-	-	-	-	-
L post- central sulcus	-	-	-	-	-	-	-	-	-63	0	28	5.85	-	-	-	-	-	-	-	-	-	-	-	-
L MOG	-	-	-	-	-	-	-	-	-47	-73	6	5.50	-	-	-	-	-	-	-	-	-	-	-	-
R MOG	-	-	-	-	-	-	-	-	53	-67	-4	5.56	-	-	-	-	-	-	-	-	-	-	-	-
L Lingual gyrus	-	-	-	-	-	-	-	-	-21	-69	-10	4.50	-	-	-	-	-	-	-	-	-	-	-	-
R Lingual gyrus	-	-	-	-	-	-	-	-	22	-68	-10	5.12	-	-	-	-	-	-	-	-	-	-	-	-
L insula/	-	-	-	-	-	-	-	-	-38	-19	12	5.47	-	-	-	-	-	-	-	-	-	-	-	-

Table S3. Main activation peaks for the non-math > math and the meaningful > meaningless non-math contrasts

	Mathematicians								Controls								Mathematicians > Controls							
	Non-math > Math				Meaningful > Meaningless non-math				Non-math > Math				Meaningful > Meaningless non-math				Non-math > Math				Meaningful > Meaningless non-math			
	x	y	z	t	x	y	z	T	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t
L inferior AG/TP	-56	-70	25	8.30	-	-	-	-	-51	-66	27	8.53	-42	-69	28	4.58	-	-	-	-	-	-	-	-
R inferior AG/TP	60	-64	22	9.83	57	-67	27	4.79	50	-70	33	5.90	41	-66	34	4.01	56	-69	21	5.45	-	-	-	-
L aMTG/STS	-59	-4	-19	9.16	56	-15	-23	4.69	-63	-7	-10	6.66	-63	-10	-8	5.19	-	-	-	-	-	-	-	-
R aMTG/STS	60	-9	-25	8.95	-	-	-	-	63	4	-13	5.16	-	-	-	-	60	-7	-25	4.91	-	-	-	-
Precuneus	2	-60	42	6.90	-	-	-	-	-2	-60	34	6.35	-	-	-	-	-	-	-	-	-	-	-	-
L IFGOrb / BA47	-	-	-	-	-51	43	-11	4.95	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
R FGOOrb / BA47	-	-	-	-	-	-	-	-	53	25	33	5.39	-	-	-	-	-	-	-	-	-	-	-	-
L SFG	-	-	-	-	-14	43	52	4.96	-18	58	34	7.88	-21	43	48	4.61	-	-	-	-	-	-	-	-
R SFG	-	-	-	-	26	31	57	4.19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Mesial BA 9, 10	0	55	34	7.70	-	-	-	-	2	53	16	5.26	-	-	-	-	-	-	-	-	-	-	-	-
Mesial frontal Orb/ BA 11	3	59	-7	9.52	-8	41	-16	5.20	-2	53	-16	8.46	-6	44	-17	5.37	-	-	-	-	-	-	-	-
L Cereb. Crus I	-18	-88	-29	6.78	-	-	-	-	-6	-84	-25	7.88	-	-	-	-	-	-	-	-	-	-	-	-
R Cereb. Crus I	27	-79	-34	6.11	-	-	-	-	23	-85	-26	9.08	-	-	-	-	-	-	-	-	-	-	-	-
L MOG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-47	-72	6	4.86	-	-	-	-
R MOG	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	56	-69	21	5.45	-	-	-	-
L para-central /BA4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-15	-31	70	5.04	-	-	-	-
R pre-central	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	26	-24	75	7.21	-	-	-	-
SMA	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-18	52	5.04	-	-	-	-
Heschl / Rolandic Oper	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-39	-18	12	4.99	-	-	-	-
Anterior cingulate	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	37	-7	4.39	-	-	-	-

Table S4. Interaction of meaningfulness by math vs. non-math in mathematicians

Mathematicians	Meaningful > Meaningless math - Meaningful > Meaningless non-math				Meaningful > Meaningless non-math - Meaningful > Meaningless math			
	X	y	z	t	x	y	z	t
L Intraparietal sulcus	-62	-34	42	7.78	-	-	-	-
R Intraparietal sulcus	65	-37	46	6.94	-	-	-	-
L inferior temporal	-60	-58	-8	5.00	-	-	-	-
R inferior temporal	59	-57	-10	5.22	-	-	-	-
L lateral IFG/MFG	-44	50	22	5.14	-	-	-	-
R SF sulcus	26	4	55	4.71	-	-	-	-
R pSTS/AG	-	-	-	-	59	-66	27	5.46
L aMTG	-	-	-	-	-57	-15	-11	4.34
R aMTG	-	-	-	-	57	-10	-19	4.64
Mesial frontal Orb	-	-	-	-	2	67	-13	5.4
Mesial superior frontal	-	-	-	-	-14	43	51	4.07

Table S5. Results of regions-of-interest (ROI) analysis in left-hemispheric language regions during reflection.

The table shows the results of contrasts applied to activation from either the reflection period (top) or the sentence presentation period (bottom) of the main task (math/non-math truth value judgment) in voxels isolated in a subject-specific manner, with each ROI, for their responsiveness to spoken or written sentences. A negative sign in the t test indicates an effect in the direction opposite to that indicated in the column title. Significant trends are highlighted in yellow ($p < 0.05$, uncorrected) and in green ($p < 0.05$ with Bonferroni correction for multiple comparisons across the 7 ROIs).

During reflection period																
	Non-math > Math				Meaningful > Meaningless non-math				Meaningful > Meaningless math				Controls > Mathematicians			
	Mathematicians		Controls		Mathematicians		Controls		Mathematicians		Controls		During math		During non-math	
	p	t	p	t	p	T	p	t	p	t	p	t	p	t	p	t
TP	0.039	2.29	0.119	1.67	0.272	1.15	0.248	1.21	0.080	-1.90	0.859	0.18	0.039	2.17	0.227	1.24
aSTS	0.082	1.89	0.003	3.53	0.009	3.09	0.669	0.44	0.289	1.10	0.931	0.09	0.114	1.64	0.031	2.27
pSTS	0.001	4.11	0.862	0.18	0.051	2.15	0.068	1.98	0.426	0.82	0.167	1.46	0.378	0.90	0.957	0.05
TPJ	0.080	1.91	0.083	1.95	0.169	1.46	0.458	0.78	0.993	-0.01	0.799	-0.26	0.468	0.74	0.380	0.90
IFGorb	0.024	2.65	0.380	0.91	0.544	0.63	0.442	-0.80	0.313	-1.06	0.578	-0.57	0.386	-0.88	0.254	-1.17
IFGtri	0.289	1.11	0.029	2.46	0.468	0.75	0.568	0.59	0.451	0.78	0.311	1.06	0.955	0.06	0.512	0.67
BA44	0.077	-1.97	0.492	0.71	0.219	1.31	0.807	-0.25	0.111	1.75	0.967	-0.04	0.442	0.78	0.014	2.64

During sentence presentation																
	Non-math > Math				Meaningful > Meaningless non-math				Meaningful > Meaningless math				Controls > Mathematicians			
	Mathematicians		Controls		Mathematicians		Controls		Mathematicians		Controls		During math		During non-math	
	P	t	p	t	p	T	p	t	p	t	p	t	p	t	p	t
TP	0.169	1.46	0.141	1.57	0.888	0.14	0.304	-1.07	0.192	-1.38	0.309	1.06	0.090	-1.76	0.286	-1.09
aSTS	0.002	3.98	0.257	1.18	0.087	-1.85	0.671	0.43	0.029	-2.46	0.540	-0.63	0.647	0.46	0.956	0.06
pSTS	0.033	2.38	0.123	1.64	0.123	-1.65	0.096	-1.78	0.354	-0.96	0.693	-0.40	0.486	0.71	0.507	0.67
TPJ	0.013	2.91	0.002	4.21	0.460	0.76	0.267	-1.18	0.071	1.98	0.179	1.46	0.132	1.57	0.173	1.41
IFGorb	0.001	4.79	0.042	2.27	0.439	-0.81	0.092	-1.83	0.325	-1.04	0.898	-0.13	0.045	2.12	0.033	2.27
IFGtri	0.026	2.57	0.568	0.59	0.109	-1.75	0.220	-1.29	0.634	-0.49	0.545	-0.62	0.947	-0.07	0.794	-0.26
BA44	0.046	2.28	0.960	-0.05	0.052	-2.20	0.357	0.95	0.034	-2.45	0.143	1.55	0.185	1.36	0.399	0.86

Table S6. Main peaks for math > non-math and meaningful > meaningless math, after removal of occasional references to numbers, in mathematicians

Mathematicians	Math > Non-math				Meaningful > Meaningless math			
	X	y	z	t	x	y	z	t
L Intraparietal sulcus	-53	-43	57	8	-50	-51	52	7
R Intraparietal sulcus	50	-42	58	5.4	51	-40	52	5.8
L inferior temporal	-56	-49	-19	6.9	-57	-57	-16	7.1
R inferior temporal	53	-51	-19	5.2	60	-58	-13	7.1
L MFG/BA46	-48	39	23	5.6	-49	34	21	5.8
L MFG/BA9	-47	7	31	5.6	-47	18	50	6.3
L SF sulcus	-24	4	64	4.8	-24	4	61	5
R MFG/BA46	-	-	-	-	51	38	21	5.7
R MFG/BA9 - BA10	-	-	-	-	53	11	21	4.4
R SF sulcus	-	-	-	-	30	8	58	7.2
SMA/Frontal Sup mesial	-	-	-	-	-2	28	51	4.8
BA10	-	-	-	-	-41	50	-14	5.3

Table S7. Subject-specific analyses of the relationships between advanced mathematics, simple arithmetic, and number and formula recognition in mathematicians

The top part of the table shows the activations evoked by mathematical reflection, numbers, and mathematical formulas, in subject-specific voxels isolated by their activation during simple arithmetic, within specified regions of interest (ROIs). The bottom part shows, in the same ROIs, comparisons of activation patterns similarity in several math-related stimuli and tasks, versus math and non-math-related stimuli and tasks. Significant trends are highlighted in yellow ($p < 0.05$, uncorrected) and in green ($p < 0.05$ with Bonferroni correction for multiple comparisons across the 13 ROIs). All approaches indicates that advanced mathematics evokes very similar patterns of activity as simple arithmetic, number recognition, and the recognition of mathematical formulas, particularly in bilateral IPS and IT cortex.

			L Intraparietal sulcus	R Intraparietal sulcus	L inferior temporal	R inferior temporal	L MFG/BA46	L MFG/BA9	L SF sulcus	R MFG/BA46	R MFG/BA9 - BA10	R SF sulcus	SMA/Frontal Sup mesial	L Cerebellum 6th lobule	R Cerebellum 6th lobule	
Activation	mathematicians at best localizer peaks for calculation	Math > Non-math reflection	p 0.001	3E-04	0.002	0.009	0.003	1E-04	3E-04	0.006	0.001	0.016	0.063	0.784	0.655	
			t 4.10	4.72	3.92	3.04	3.51	5.17	4.75	3.27	3.98	2.73	2.02	0.28	0.46	
		Numbers > others	p 0.001	4E-05	0.007	7E-05	0.013	4E-04	0.001	3E-04	0.047	0.004	0.011	0.006	0.115	
			t 4.40	5.91	3.14	5.57	2.85	4.64	4.35	4.79	2.18	3.43	2.92	3.28	1.68	
		Formulas > others	p 0.018	0.029	0.011	4E-04	0.146	0.026	0.203	0.249	0.469	0.821	0.075	0.919	0.914	
			t 2.67	2.43	2.97	4.76	1.55	2.49	1.34	-1.21	-0.75	-0.23	1.95	-0.10	0.11	
	Statistics on similarity patterns	math* math	> p	1.4E-11	3.9E-11	7.0E-10	3.1E-09	3.0E-10	2.6E-08	1.8E-09	9.2E-13	3.3E-10	1.8E-10	5.3E-10	4.5E-13	8.2E-10
			t	19.59	18.19	14.64	13.07	15.59	11.07	13.63	23.96	15.51	16.25	14.95	25.24	14.47
math* calculation		> p	2E-05	1E-04	3.4E-04	0.001	7E-05	7E-06	0.001	0.002	0.001	0.001	4E-04	1E-04	0.011	
		t	6.46	5.19	4.71	4.04	5.57	6.92	4.15	3.88	4.05	4.04	4.57	5.23	2.92	
math * formulas		> p	0.014	0.301	0.003	0.001	0.003	0.011	0.074	0.651	0.058	0.085	0.077	0.025	0.842	
		t	2.82	1.07	3.53	4.18	3.66	2.91	1.93	0.46	-2.06	1.85	1.91	2.50	-0.20	
math * non-symbolic pictures		> p	5E-04	0.002	0.001	2E-04	0.002	0.002	4E-04	0.002	0.013	0.029	0.003	0.034	0.072	
		t	4.51	3.88	4.06	5.02	3.75	3.81	4.65	3.72	2.84	2.44	3.65	2.34	1.95	
math * formulas		> p	0.807	0.910	0.033	0.179	0.083	0.147	0.292	0.541	0.095	0.273	0.645	0.109	0.228	
		t	0.25	-0.11	2.36	1.41	1.87	1.53	1.09	0.63	-1.79	1.14	0.47	1.71	-1.26	
math * numbers		> p	0.062	0.094	0.011	0.021	0.058	0.015	0.006	0.017	0.085	0.129	0.036	0.110	0.669	
		t	2.03	1.80	2.91	2.61	2.06	2.77	3.24	2.71	1.85	1.62	2.32	1.71	0.44	
calculation * formulas		> p	0.001	0.001	2E-06	9E-05	0.006	2E-05	0.006	0.374	0.020	0.930	0.059	0.116	0.427	
		t	4.34	4.29	7.88	5.41	3.23	6.20	3.21	0.92	2.62	-0.09	2.06	1.67	0.82	
calculation * numbers		> p	6E-06	5E-07	3E-07	4E-06	0.002	6E-05	3E-05	0.001	0.001	0.010	0.001	0.014	0.067	
		t	6.98	8.70	9.14	7.27	3.86	5.66	6.02	4.23	4.15	3.00	4.37	2.82	1.99	

	formulas * (numbers – non-symbolic pictures)	p	5E-06	4E-05	7E-05	1E-04	0.002	6E-05	0.010	0.001	0.003	5E-05	8E-07	0.072	0.513
		t	7.14	5.93	5.57	5.25	3.73	5.67	2.98	4.10	3.52	5.76	8.36	1.95	0.67
	calculation * formulas > calculation * words	p	0.029	0.027	0.006	0.041	0.079	0.222	0.236	0.425	0.454	0.074	0.828	0.063	0.298
		t	2.43	2.48	3.22	2.25	1.90	1.28	1.24	0.82	0.77	1.93	-0.22	2.02	1.08
	calculation * numbers > calculation * words	p	0.003	0.001	0.003	0.002	0.031	0.102	0.015	0.018	0.041	0.002	0.026	0.003	0.091
		t	3.66	4.07	3.55	3.91	2.39	1.75	2.77	2.67	2.25	3.77	2.49	3.62	1.82

Table S8. Volume of activation to different visual stimuli in mathematicians and control subjects

	Principal peaks in both groups				Mathematicians		Controls		Mathematicians > Controls	
	x	y	Z	t	volume (mm ³)	Standard error	volume (mm ³)	Standard error	p	t
L EBA	-50	-76	7	19.1	2846	46	2785	63	0.843	0.20
R EBA	54	-67	3	16.8	2961	45	3055	68	0.768	-0.30
L FFA	-38	-49	-20	10.3	261	14	295	15	0.685	-0.41
R FFA	42	-48	-22	13.4	509	16	521	26	0.918	-0.10
L formulas	-51	-61	-11	11.6	2276	90	1334	63	0.035	2.21
R formulas	55	-55	-17	9.36	803	30	394	22	0.008	2.85
L LOC	-48	-73	-5	9.98	3719	120	2401	141	0.076	1.84
R LOC	50	-70	-7	6.33	1125	62	955	50	0.587	0.55
L PPA	-29	-49	-7	12.4	2739	121	1347	86	0.022	2.42
R PPA	29	-49	-8	13.1	2594	130	2393	132	0.781	0.28
L VNFA	-56	-51	-19	7.94	812	46	591	28	0.303	1.05
R VNFA	62	-39	-17	8.44	643	35	341	19	0.060	1.96
VWFA	-42	-45	-17	4.76	82	6	99	7	0.645	-0.47

Annex: statements used in fMRI experiments

1. Analysis

1.1. True

Statement 1. The Fourier series expansion of a continuous and piecewise C^1 function f converges pointwise to f .

Statement 2. Any real-valued function locally polynomial is polynomial.

Statement 3. The function $\frac{1}{\Gamma(z)}$ admits an analytic continuation to the whole complex plane.

Statement 4. Any compact topological group admits a unique probability measure invariant under left-translations.

Statement 5. The set of test functions is dense in every space L^p , for $p \geq 1$.

Statement 6. A smooth function whose derivatives are all non-negative is analytic.

1.2. False

Statement 7. The spaces \mathcal{L}^p are separable.

Statement 8. The Fourier transform is an isometry from $L^1(\mathbb{R}^n)$ onto itself.

Statement 9. The topological dual of $L^1(\mathbb{R})$ is $L^1(\mathbb{R})$.

Statement 10. An inequality between two functions remains valid for their primitives.

Statement 11. There exists a continuous map from the unit ball into itself without any fixed point.

Statement 12. The distributional derivative of the Heaviside step function is the Heaviside step function.

1.3. Meaningless

Statement 13. Any Dirac's Heaviside function admits a Taylor expansion in L^p .

Statement 14. The space $L^1(\mathbb{R}^n)$ admits a locally polynomial, separable and analytic measure.

Statement 15. In finite measure, the series expansion of the roots of a holomorphic map is reflexive.

Statement 16. The topological dual of a Fourier series admits an analytic continuation.

Statement 17. The trace of the unit ball diverges for some $p \in \{1, \infty\}$.

Statement 18. Any compact polynomial space is isometric to a unique space L^p .

2. Algebra

2.1. True

Statement 19. A square matrix with coefficients in a principal ideal domain is invertible if and only if its determinant is invertible.

Statement 20. For even n , any sub-algebra of $M_n(\mathbb{C})$ of dimension ≤ 4 admits a non-trivial centralizer.

Statement 21. The square matrices with coefficients in a field that are equivalent to a nilpotent matrix are the non-invertible matrices.

Statement 22. Up to conjugacy, there only exist 5 crystallographic groups of the plane.

Statement 23. There exists a 13-dimensional algebra of 4×4 -complex matrices.

Statement 24. \mathbb{Q} can be canonically embedded into any field of characteristic zero.

2.2. False

Statement 25. There exists a group of order 169 whose center is reduced to one element.

Statement 26. Any matrix with coefficients in a principal ideal is equivalent to a companion matrix.

Statement 27. A group of which all proper subgroups are abelian is abelian.

Statement 28. In the algebra $M_n(\mathbb{C})$, if two sub-algebras commute, the sum of their dimensions is not greater than n^2 .

Statement 29. Any square matrix is equivalent to a permutation matrix.

Statement 30. There exists an infinite order group that admits a finite number of sub-groups.

2.3. Meaningless

Statement 31. Any square invertible ring admits a hexadecimal expansion.

Statement 32. Any matrix with cardinality greater than 3 is factorial.

Statement 33. The field of fractions of an immatricial algebra is embedded in the space of projections.

Statement 34. Any algebra of dimension not greater than 4 is a linear combination of three projections.

Statement 35. There only exist 5 nilpotent canonically additive groups.

Statement 36. The field $\mathbb{R}[i]$ admits a free noetherian centralizer over \mathbb{Q} .

3. Topology

3.1. True

Statement 37. A finite left-invariant measure over a compact group is bi-invariant.

Statement 38. The boundary of the Cantor set equals itself.

Statement 39. There exist non-discrete spaces whose connected components are reduced to one point.

Statement 40. The union of a family of pairwise non-disjoint connected subsets of \mathbb{C} is connected.

Statement 41. Any locally finite bounded set of \mathbb{R} is finite.

Statement 42. The quotient of a topological group by its identity component is totally disconnected.

3.2. False

Statement 43. Any continuous bijection between two Hausdorff spaces is a homeomorphism.

Statement 44. There exists a continuous function from the unit sphere onto itself without any fixed point.

Statement 45. Any convex compact set of a Euclidean space is the intersection of a family of closed balls.

Statement 46. In any topological space, every subspace homeomorphic to an open set is also an open set.

Statement 47. Every complete graph can be embedded into the unit sphere of \mathbb{R}^3 .

Statement 48. Any infinite set of real numbers admits at least one accumulation point.

3.3. Meaningless

Statement 49. Every non-decreasing morphism of the Cantor set is conjugated to a homeomorphism of the unit ball.

Statement 50. Every finite measure on a Hopf algebra is locally modelled on the Haar measure.

Statement 51. The boundary of a homeomorphism has empty interior.

Statement 52. A subset of \mathbb{C} is always left-invariant and right-continuous.

Statement 53. The graph of the completion of a compact group is dense in a partially connected open set.

Statement 54. Every non-countable measure is the intersection of a family of compact groups.

4. Geometry

4.1. True

Statement 55. Any vector field on an even-dimensional sphere vanishes.

Statement 56. The eccentricity of a rectangular hyperbola equals $\sqrt{2}$.

Statement 57. In an ellipse, the ratio of the distance from the center to the directrix equals half the major axis over the eccentricity.

Statement 58. The set of points that are equidistant from two given disjoint lines of \mathbb{R}^3 is a hyperbolic paraboloid.

Statement 59. A vector bundle whose base is contractible (for instance, a ball) is trivializable.

Statement 60. The Euclidean orthogonal group has exactly two connected components.

4.2. False

Statement 61. The stereographic projection of the sphere minus one point in the Euclidean space is bounded.

Statement 62. A holomorphic function on a Riemann surface is constant.

Statement 63. Any compact surface is diffeomorphic to an algebraic surface.

Statement 64. At any point P of a directrix of a hyperbola, two tangent lines intersect.

Statement 65. The orthogonal projection of the focus of a parabola on one of its tangents is on the directrix.

Statement 66. Any C^1 vector field on a torus admits a singularity.

4.3. Meaningless

Statement 67. Any Riemannian metric is conjugated to the Haar measure.

Statement 68. The stereographic projection admits $\sqrt{2}$ as Euler characteristic.

Statement 69. The set of points equidistant from two Riemann surfaces is compatible with a paraboloid.

Statement 70. Any holomorphic compact fiber bundle is a particular sphere.

Statement 71. Any variety locally contractible is included in a two-sheeted hyperboloid.

Statement 72. Any locally ellipsoidal submersion is the exponential of a Riemann surface.

5. Non-math

5.1. True

Statement 73. In all Ancient Mediterranean cultures, bulls were considered deities.

Statement 74. In Ancient Greece, a citizen who could not pay his debts was made a slave.

Statement 75. The VAT is a French invention and is a direct consumption tax.

Statement 76. The flag of the Esperanto community is predominantly green.

Statement 77. Apart from the Vatican, Gibraltar is the world's smallest country.

Statement 78. The concept of robots and avatars was already present in Greek mythology.

5.2. False

Statement 79. The Paris metro was built before the Istanbul one.

Statement 80. All borders in Europe, except for Yugoslavia, were set at the end of World War II.

Statement 81. The poet Aragon never joined the Communist party.

Statement 82. The end of the Council of Trent coincides with the fall of the Western Roman Empire.

Statement 83. All members of the Club des Cordeliers were guillotined during the "Terror".

Statement 84. In every society, the market is considered an essential and founding institution.

5.3. Meaningless

Statement 85. The potato flag was guillotined at the end of the Council of Trent.

Statement 86. The institutionalized market drinks Western Roman avatars.

Statement 87. Every indebted green beans have a scientific background.

Statement 88. The Greek mythology is the smallest alcohol derived from the VAT.

Statement 89. Most of the robotic bulls never met Yugoslavia.

Statement 90. A poet is a predominantly green tax over the metro.

Chapter 2. Dissociated cortical networks for mathematical and non-mathematical knowledge

1. Introduction to the article

In the previous chapter, we have identified, for the first time, a set of brain areas involved in high-level mathematical processing. This math-related network includes bilateral fronto-parietal regions and bilateral inferior temporal regions, and drastically dissociates from classical language areas and from areas that classically store and process general semantics.

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.

2. Abstract

The relation between language and mathematics in human cognition is an essential issue of cognitive sciences. While it has been argued that mathematics emerges as an offshoot of human linguistic abilities, recent evidence tends to show that language and mathematics have evolved independently and even build upon dissociated neural substrates. Here, we question this dissociation with two fMRI experiments in which professional mathematicians had to judge the truth value of mathematical and nonmathematical spoken statements. First, we verified that mathematical processing systematically call upon bilateral intraparietal sulci and inferior temporal regions, regardless of math domain, problem difficulty, or the solving strategy (i.e. rote memory, calculation or visualization). Second, the classical language areas proved to be involved in parsing both nonmathematical and mathematical statements with an intensity that directly reflected syntactical complexity. Finally, we confirmed that the math-responsive regions were not engaged to solve nonmathematical problems, even when they contained minimal mathematical operators such as quantifiers or negation. Instead, main effects of quantifiers and negation were respectively observed in right angular gyrus and left IFG.

3. Introduction

Language and advanced mathematical reasoning are both typically human abilities. How they relate is a leading debate in Cognitive Sciences. On the one hand, mathematics can be seen as an outcome of language, as suggested by (Hauser et al., 2002) or (Spelke and Tsivkin, 2001). In the first, authors explain that recursive computation, which lies at the core of linguistic abilities, also underlies mathematical competence. In the second, authors stated that mathematics might be one of the

“richest and most dramatic outcomes” of language which is the human “most striking combinatorial system”. Moreover, some studies have suggested that language would play an essential role in creating large exact number concepts (Carey, 1998).

On the other hand, many studies have now suggested that mathematics and language are independent. First, patients who exhibit deficits in mathematical skills can have preserved language (Dehaene and Cohen, 1997). Conversely, other patients with severe aphasia but preserved mathematical skills have been described (Klessinger et al., 2007; Varley et al., 2005). In the latter for instance, the authors tested language impaired patients who were unable to understand reversible sentences but performed relatively well on calculation problems. Moreover, recent studies conducted in pre-verbal infants, in adults without access to education and with a poor numerical lexicon and in a variety of non-human animal species, have exhibited a shared capacity to estimate numerosity and to perform simple arithmetical operations over these quantities. These results thus suggest that numerical comprehension arises independently of language (Cantlon and Brannon, 2005; Gelman and Butterworth, 2005; Izard et al., 2009; Pica et al., 2004). Similarly, all humans and various animal species are endowed with basic geometrical intuitions (Dehaene et al., 2006; Lee and Spelke, 2008; Spelke and Lee, 2012).

Recent brain imaging studies tend to confirm the behavioral dissociation observed between mathematics and language. When participants were asked to evaluate whether pairs of linguistic or algebraic propositions were either equivalent or grammatically well-formed, algebraic equivalence recruited bilateral intraparietal sulci, whereas linguistic equivalence recruited left fronto-temporal perisylvian regions (Monti et al., 2012). More recently, a similar separation between brain networks processing linguistic versus mathematical problems has been found. Indeed, Amalric and Dehaene (2016) have shown that a group of professional mathematicians, who were asked to judge the semantic truth value of advanced mathematical and nonmathematical spoken statements, exhibited activations in bilateral intraparietal sulci and infero-temporal regions when they were thinking about math whereas bilateral superior temporal sulci and angular gyri were activated by nonmath reflection.

How can we explain the dissociation observed between math and nonmath statements? To assess this question, we need to further interrogate the intrinsic characteristics of math and nonmath problems. Given that our math-responsive network largely coincides with a “multiple-demand system”, active in various effortful domain-general problem-solving tasks (Duncan, 2010; Fedorenko et al., 2013), could it be that solving math problems intrinsically require more attentional and cognitive resources than solving nonmath problems? Or do different semantic contents (math versus nonmath) systematically call upon separate neural substrates as suggested by some studies

showing that recognition of letters versus numbers lead to a dissociation in visual cortices (Abboud et al., 2015; Park et al., 2012; Shum et al., 2013)? Where is the boundary between language and math processes? Are there math problems, putatively relying on verbal knowledge, that activate more language areas than the math-responsive network? On the contrary, do some minimal operators systematically activate the math-responsive network even in nonmathematical context? To address these issues, we proposed two fMRI experiments, similar to the one proposed by Amalric and Dehaene (2016), to a group of professional mathematicians who had to judge, as quickly as they could, whether simple spoken mathematical and nonmathematical statements were true or false.

4. Experiment 1: Simple mathematical facts

4.1. Introduction

In this experiment, we used simple mathematical facts to probe the influence of both the semantic content and the strategy used to solve mathematical problems on the math/language separation.

Previous fMRI studies have suggested that some arithmetical problems rely more on verbal knowledge than calculation. Ischebeck et al. (2006) revealed that arithmetical fact retrieval (trained multiplication) recruited the left angular gyrus whereas arithmetic calculation (subtraction) elicited activation in the intraparietal sulci. In particular, the strategy used to solve the problem seems to have a direct impact on cerebral activation. Indeed, in the latter study, subtraction also elicited more activation in occipital cortex and precuneus than multiplication, therefore suggesting that subtraction relies more on visual strategies than multiplication. Moreover, Delazer et al. (2005) exhibited more activation in the intraparietal sulci when a complex novel arithmetical operation was learnt using calculation strategies, while learning by drill induced more activation in the angular gyri.

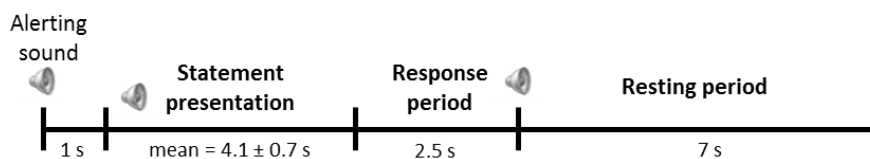
In the present experiment, we therefore ask whether mathematical facts that were learnt by heart rely more on verbal memory and call upon classical semantic regions. On the contrary, are there some mathematical problems that do not recruit language areas at all? Do mathematical problems that involve mental imagery recruit visual cortex? To address these issues, mathematical statements in this experiment included, inter alia, simple facts that participants knew by heart (e.g. classical algebraic identities) or simple problems that required visualizing the solution (e.g. on the trigonometric circle).

4.2. Methods

A group of 14 professional mathematicians, i.e. full-time researchers and/or professors in mathematics participated in this study.

Participants were exposed to spoken mathematical and nonmathematical statements and were given 2.5 seconds to classify each of them as true or false (figure 2.1). They were asked to press a button in their right hand for true and in their left hand for false. Each trial began with a “beep” announcing the presentation of the statement and ended with a 7-second resting period.

Various mathematical statements were proposed: (1) well-known facts such as classical algebraic identities (e.g. “ $(a+b)^2$ equals a^2+b^2+2ab ”) or trigonometric formulae (“ $\cos(a+b)$ equals $\cos(a)\cos(b)-\sin(a)\sin(b)$ ”), (2) algebraic equations (“ $(z-1)^2$ equals $z^2 - 2z + 1$ ”), (3) simple facts requiring to visualize the solution on the trigonometric circle (“ $\sin(x+\pi)$ equals $-\sin(x)$ ”), (4) the complex plane (“the angle between i and $1+i$ equals $\pi/4$ ”), or (5) concerning geometrical shapes (“Any equilateral triangle can be divided into two right triangles”). These were compared to nonmathematical facts about music, painting, literature or movies (“Pantomime relies on attitude and gesture, without speaking”). Ascending or descending series of beeps were also presented to probe activation in primary auditory regions. Participants were asked to classify ascending series as true and descending series as false. (see appendix for a complete list of statements).



Statements of experiment 1:

- | | |
|---------------------------|--|
| 1) Algebraic facts: | $(a+b)(a-b) = a^2 - b^2$ |
| 2) Algebraic calculation: | $(x-1)(x+1) = x^2 - 1$ |
| 3) Trigonometry: | $\sin(x+3\pi/2) = -\cos x$ |
| 4) Complex numbers: | $Re(e^{i\pi/4}) = Im(e^{i\pi/4})$ |
| 5) Euclidean geometry: | The section of a sphere by a plane is always a point |
| 6) General knowledge: | Rock'n'roll is a musical style characterized by a slow tempo |

Statements of experiment 2:

	Math	vs	Non-math
1) declaratives:	The sine function is periodical		Londonian buses are red
2) quantified declaratives:	Some matrices are diagonalizable		Some ocean currents are warm
3) negatives:	Hyperboloids are not connected		Tigers are not carnivores
4) quantified negatives:	Some infinite sets are not countable		Some green plants are not climbing

Figure 2.1. Experimental paradigm. (top) Procedure of experiments 1 and 2: subjects listened to a statement announced with a beep, and were asked for a speeded response during a 2.5s period ending with a beep. (bottom) Exemplar statements from each category tested in both experiments.

4.3. Results

4.3.1. Behavior

Overall performance for the math statements reached $80.1 \pm 4.6\%$ correct and $86.3 \pm 2.4\%$ for the nonmath statements. $90.9 \pm 2.8\%$ of correct responses were given for the classical algebraic

identities (called rote facts in figure 2.2). $85.2 \pm 2.3\%$ of the algebraic equations and $83.3 \pm 4.4\%$ of the problems on complex number properties were correctly classified. Performance on the geometrical statements reached $81.1 \pm 2.4\%$. The trigonometric formulae were the most difficult statements, with an average performance of $59.9 \pm 3.1\%$ correct. Overall, an ANOVA with problem type as between factor and subject as within factor revealed a significant effect of problem type ($F(4,52) = 14.3$, $p < 0.001$, figure 2.2). This effect was mainly due to the trigonometric problems, given that an ANOVA performed on math problems excluding trigonometry did not reveal any significant effect of problem type ($F(3,39) = 1.66$, $p = 0.19$). Again excluding the trigonometric problems, no difference was found between the math and nonmath problems ($t(13) = 0.41$, $p = 0.69$; $F(4,52) = 1.42$, $p = 0.24$).

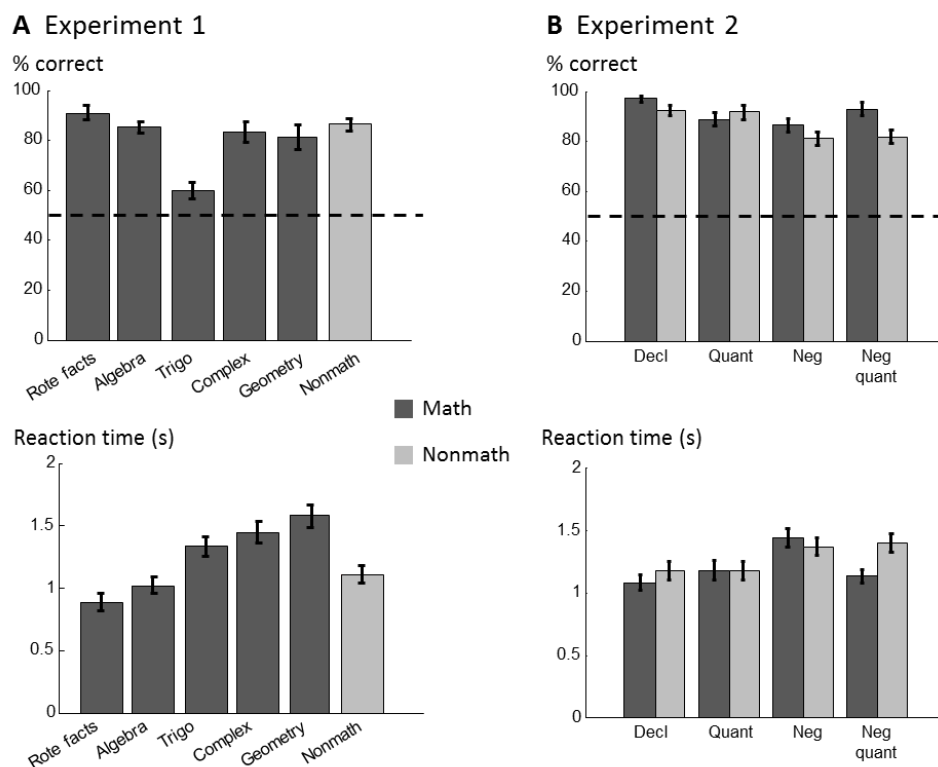


Figure 2.2. Behavioral results. (A) Percentage of correct responses and mean response times per category in experiment 1 (error bars = one standard error of the mean). Dashed lines represent the chance level. Dark gray bars stand for mathematical statements and light gray bars for nonmathematical statements. (B) Same format for experiment 2.

Analysis of response time confirmed that the rote facts were the easiest problems with only $0.88 \pm 0.07s$. The algebraic equations took $1.02 \pm 0.07s$ for mathematicians to answer; the trigonometric problems took $1.33 \pm 0.07s$; the problems on complex numbers took $1.44 \pm 0.08s$; and the geometrical problems took $1.57 \pm 0.09s$. In average, participants answered to the mathematical statements in $1.25 \pm 0.1s$, and significantly faster to the nonmathematical statements in $1.11 \pm 0.06s$ ($t(13) = 36$, $p < 0.001$). Within mathematical problems, an ANOVA revealed a significant effect of problem type on response time ($F(4,52) = 30.9$, $p < 0.001$).

4.3.2. Dissociation between brain activations to math and nonmath reflection

At group level, pooling across all types of math, we first searched for activations elicited more by math than nonmath statements and found extensive activations in bilateral intraparietal sulci, bilateral inferior temporal regions, and bilateral superior, and middle frontal regions (Brodmann areas 9 and 46) (figure 2.3). These regions activated systematically for all types of math as revealed by the contrasts of each math domain versus nonmath (figure S1). Notably, principal peaks of each contrast within each math-responsive region were remarkably close (figure S1). These findings are summarized in figure 2.3 by a conjunction analysis of each math domain versus nonmath (figure 2.3). Furthermore, plots of temporal course of average activation in characteristic math-responsive regions (previously and independently defined from (Amalric and Dehaene, 2016)), showed that signal rose quickly for all types of math at the beginning of the trials and remained strong until the end of the trials. On the contrary, no activation or even a deactivation was seen for the nonmath statements and series of beeps.

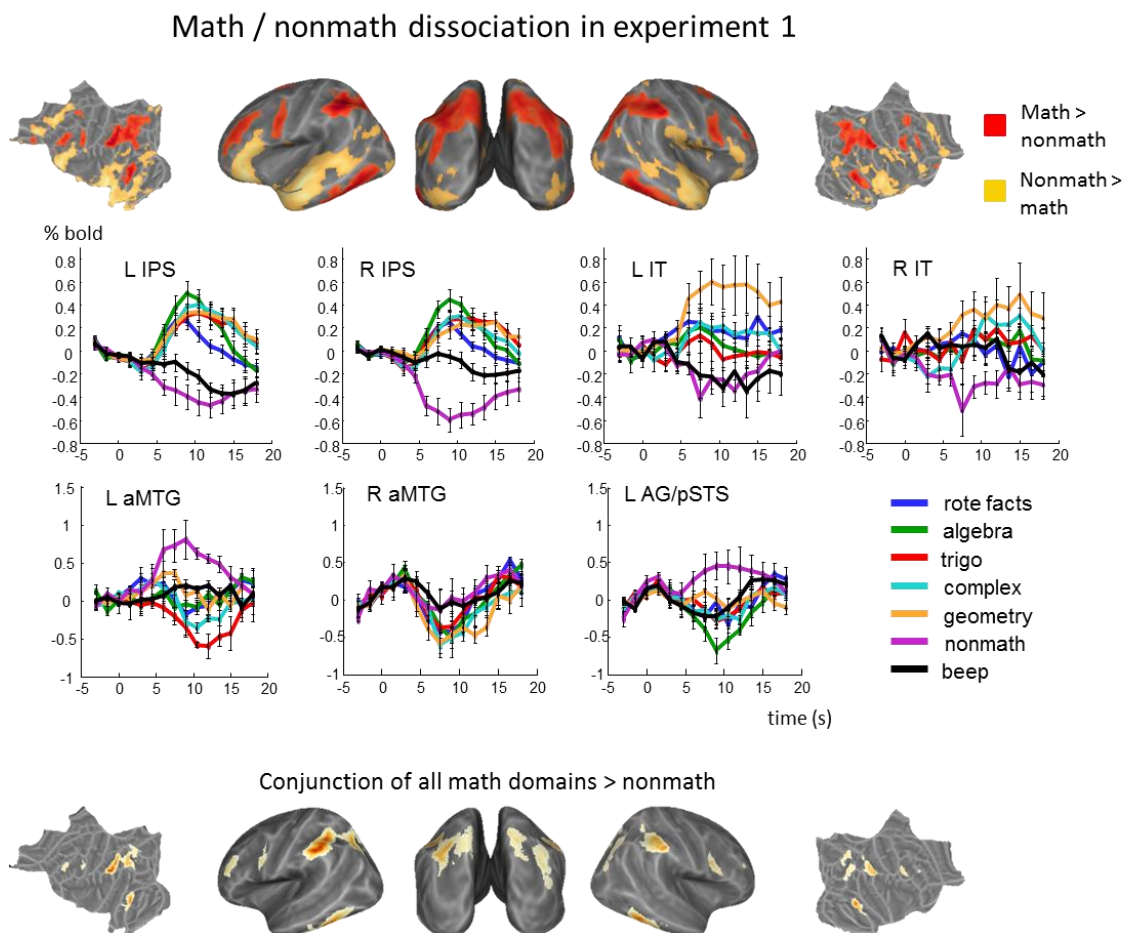


Figure 2.3. Dissociation between math and nonmath semantic networks in experiment 1. (top) Flattened and inflated brain maps showing the contrasts of math > nonmath processing (red) and nonmath > math processing (yellow) (uncorrected $p < 0.001$ voxelwise, corrected $p < 0.05$ clusterwise). (middle) Temporal course of bold signal for each category of statements in representative brain areas of the networks responsive to math and general-semantics. (bottom) Flattened and inflated brain maps showing the conjunction of the five contrasts of each math category versus nonmath (uncorrected $p < 0.001$ voxelwise, corrected $p < 0.05$ clusterwise for each separate contrast).

The reverse contrast of nonmath versus math reflection yielded activation all along bilateral superior temporal sulci, in bilateral inferior frontal gyri and mesial orbital gyrus (figure 2.3). From our previous study (Amalric and Dehaene, 2016), we retrieved the functional regions of interest representative of activation to general semantics (contrast of meaningful versus meaningless nonmath). In these regions, the average fMRI signal remained sustained above zero only for the nonmath statements. For the math statements, if anything, the activity was only transient during statement listening.

4.3.3. Effect of difficulty

Analysis of the participants' accuracy and response time has revealed that some math statements were more difficult than others. We thus searched for an effect of difficulty in the brain response. We first used the individual reaction times for each statement and computed the corresponding individual contrasts before performing a t-test at group level. This whole-brain approach did not reveal any significant cluster. We then performed a more sensitive analysis to test directly whether problem difficulty has an impact on the activity of math-related parietal regions that presumably overlap with Duncan's multiple system (Duncan, 2010). For each statement, we extracted the mean beta value from our bilateral intraparietal region of interests, and evaluated whether it correlated with the participants' mean correct rate and response time. No such correlation was found ($R(\text{beta}, \% \text{ correct}) = 0.074$, n.s.; $R(\text{beta}, \text{RT}) = -0.35$; n.s.), therefore reaffirming that the math-responsive network activates independently of problem difficulty.

4.3.4. Differences between math types

To test for differences in brain activation between math types in our experiment, we first performed an F-test on all math types. At whole brain level, we found differences in the left anterior temporal lobe (temporal pole and anterior superior temporal sulcus), the left inferior frontal gyrus (pars orbitalis, triangularis and opercularis), the right temporal pole, bilateral angular gyri, and a large mesial swath of occipital cortex from the calcarine sulcus to the cuneus (figure 2.4). We then compared each math stimuli type against all others. We observed that activation in language regions (left IFG, TP, aSTS and pSTS) were due to geometry more than other math types. This contrast of geometry > other math also revealed activation in left inferior-temporal regions including the fusiform gyrus (figure 2.4). Conversely, other math types together elicited more activation than geometry in a right parietal region (figure 2.4). No significant cluster was found for rote facts or algebra compared to other math statements. Trigonometry versus other math types yielded an extensive activation in the mesial precuneus, and complex numbers activated more regions alongside the calcarine sulcus and bilateral angular gyri than the rest of math statements.

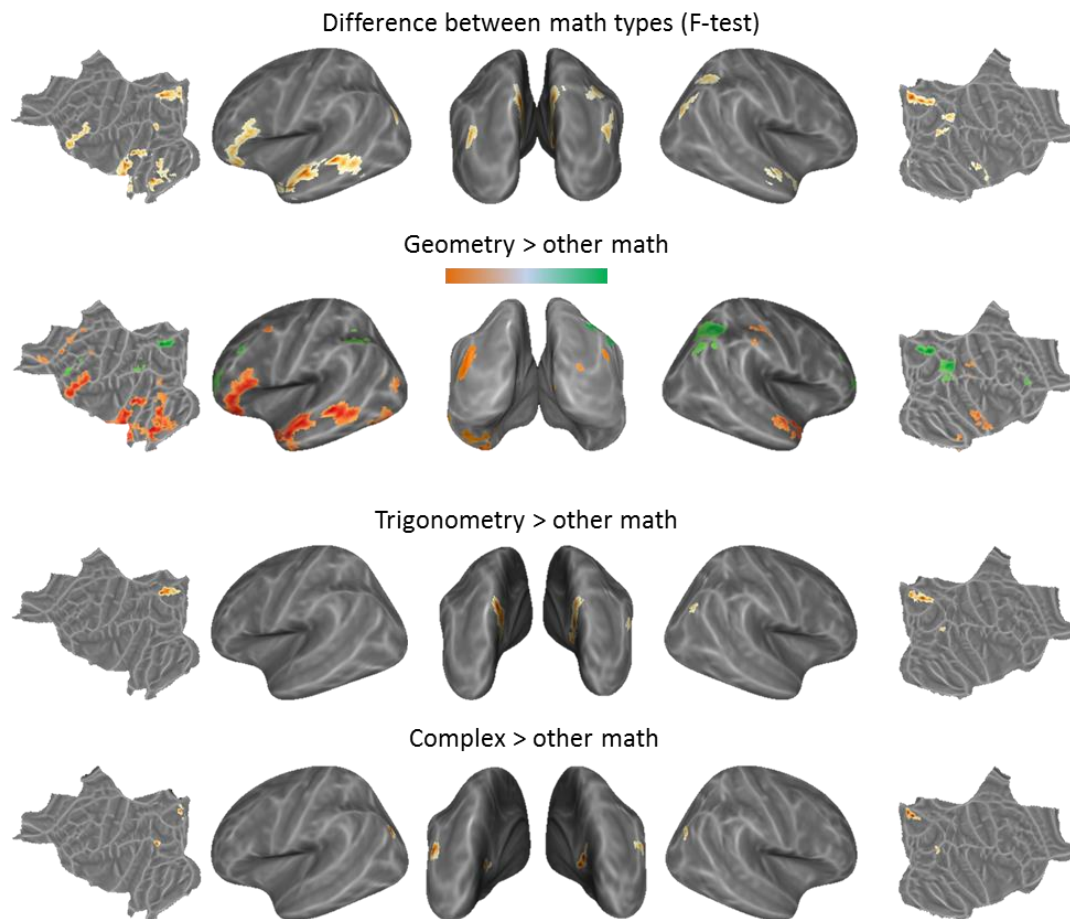


Figure 2.4. Activity differences between math types. From top to bottom: flattened and inflated brain maps of (1) the result of global F-test on math statements; (2) temporal activation elicited more by geometry than other math statements; (3) occipital responses to trigonometry more than other math categories; (4) additional activation in angular gyri for complex numbers compared to other math statements. (uncorrected $p < 0.001$ voxelwise, corrected $p < 0.05$ clusterwise).

To further investigate the effect of the strategy used to solve mathematical problems, we pooled together all statements related to trigonometry and complex numbers and compared them to rote facts and algebra. We observed activation in bilateral angular gyri and many occipital sites, alongside the calcarine sulcus, to more dorsal regions (figure 2.5). Figure 2.5 also displays activation changes for all categories of statements in each significant cluster of activation. Interestingly, plots of beta estimates alongside the calcarine sulcus revealed activation for complex numbers, geometry and nonmath statements. This cluster extended towards more dorsal sites which significantly activated for trigonometry alone. Finally, there was a global deactivation for all kind of statements in the right angular gyrus, and the left angular gyrus activated for the complex numbers and geometrical problems (figure 2.5).

A unique significant cluster of activation was found for the reverse contrast of rote facts and algebra versus trigonometry and complex numbers, located in the right posterior temporal sulcus (around $[65, -37, -4]$). Analysis of the betas estimates for each category of statements has revealed

that this cluster did not activate only for algebra and rote facts, but also for geometrical and nonmath statements and deactivated for trigonometry and complex numbers.

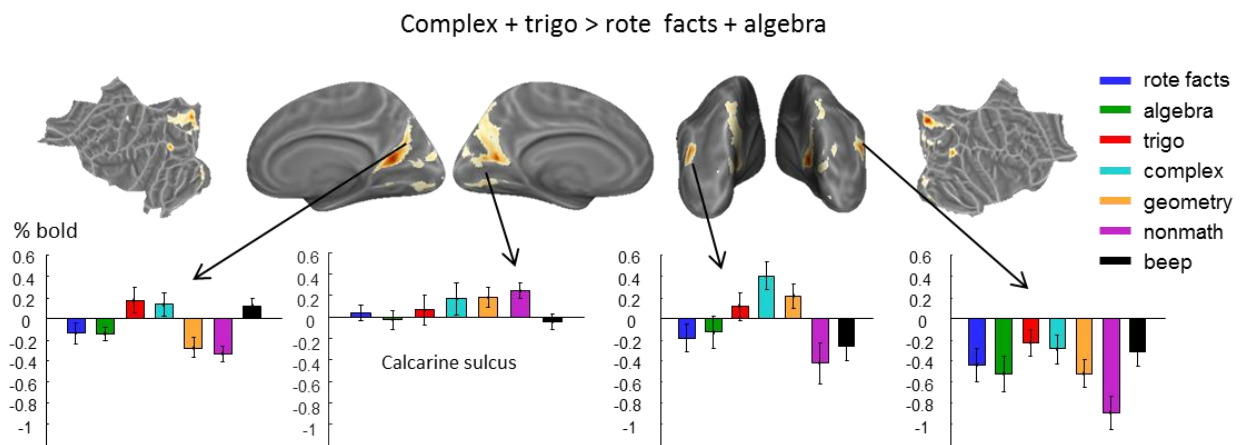


Figure 2.5. Activation profile in occipital regions. (top) Flattened and inflated brain maps of the contrast complex + trigonometry > rote facts + algebra. (bottom) Mean beta estimates extracted from the principal activated clusters.

4.3.5. Activation profile in language areas

The activation to geometry located in classical language regions might simply be explained by syntactic differences between geometrical and other math statements. Indeed, the geometrical statements contained more verbs and more clauses than other math statements (see appendix for a complete list of statements). To further investigate the relation of math statements to language, we performed a sensitive analysis in 7 regions of interest associated with syntactical processing in previous studies: temporal pole (TP), anterior and posterior superior temporal sulcus (aSTS and pSTS), temporo-parietal junction (TPJ), inferior frontal gyrus pars orbitalis and triangularis (IFGorb and IFGtri) and Brodmann area 44 (BA 44) (Fedorenko et al., 2011; Pallier et al., 2011). We used an independent syntax localizer (see the methods section for more details) to identify subject-specific peaks of activation to spoken sentences relative to rest and tested the contribution of those language voxels to math reflection. Figure 2.6 shows the average beta for each category of statements in each region of interest. Three different patterns of activation can be identified. First, TP, TPJ and IFGorb exhibited very little or no activation for rote facts, algebra, trigonometry and complex numbers, significantly more activation for geometry (except in TPJ, all p s < 0.02 with Bonferroni correction for multiple comparisons over the 7 regions of interest), and even significantly more activation to nonmath than all types of math (except in TP for nonmath > geometry, all p s < 0.02 with Bonferroni correction). Second, in aSTS, pSTS and IFGtri, all categories exhibited a significant activation (all p s < 1.10^{-6} with Bonferroni correction). Geometry elicited systematically more activation than other math types (except for complex numbers in aSTS, all p s < 0.04 with Bonferroni correction) but was not significantly different from nonmath. Finally, BA 44 exhibited a radically different pattern of activation: geometrical statements induced significantly greater

activation than any other category except complex numbers (all p s < 0.015 with Bonferroni correction), and no difference was found between other math types and nonmath ($F(4,44) = 1.6$, n.s.).

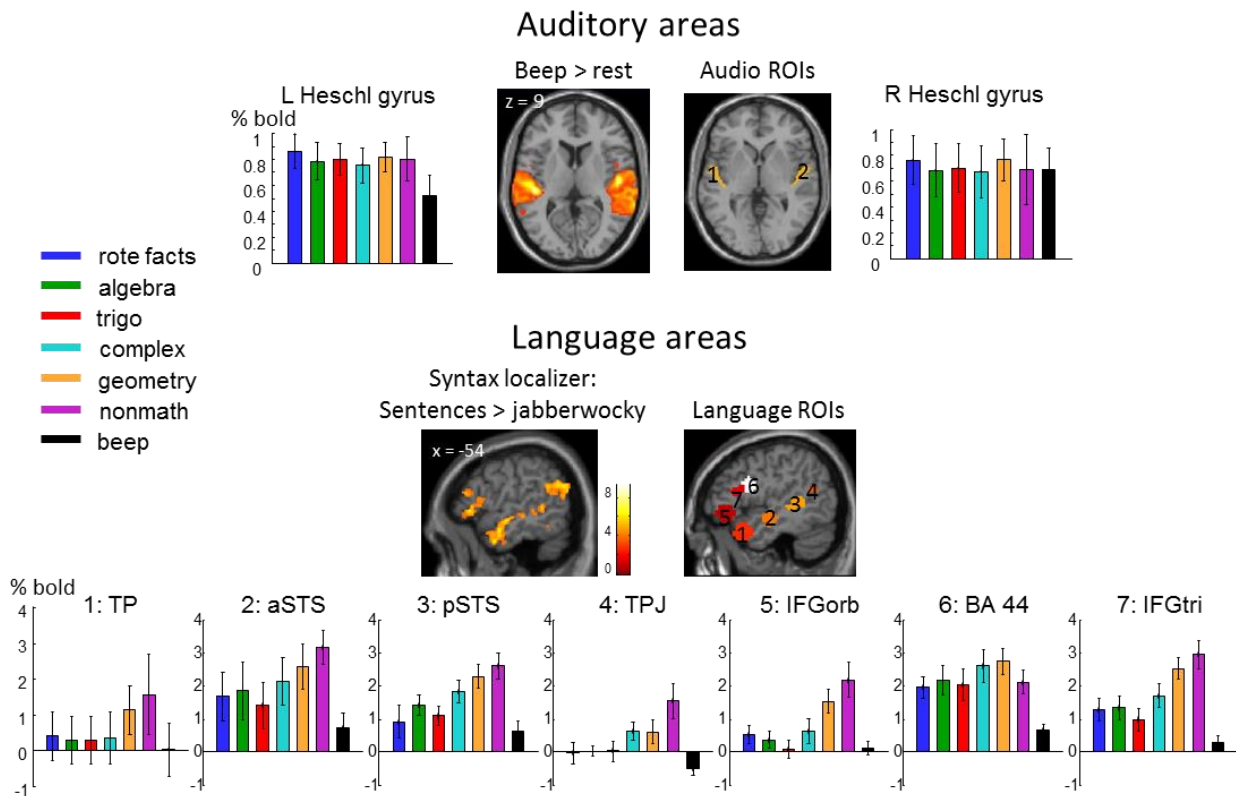


Figure 2.6. Activation profile in auditory and language areas. (top) Axial slices showing activation in Heschl gyri for series of beeps versus rest (left) and anatomical regions of interest (right) from which beta estimates of each category were extracted (bar plots). (bottom) Sagittal slice showing 7 language regions of interest (right) and the contrast of sentences versus jabberwocky (i.e. grammatical sentences with pseudo-words) in our syntax localizer (left) that served to select best activated voxels in individual subjects. Bar plots represent beta estimates extracted from these regions.

Interestingly, this analysis has revealed that certain types of mathematical statements, such as rote facts, algebra or trigonometry, make virtually no or little use of the language regions. First, we verified that the activation differences between categories of stimuli were not due to low level auditory differences. We thus probed activation to each category in bilateral Heschl gyri (figure 2.6). In both hemispheres, no difference was found between sentence categories (left: $F(5,55) = 1.23$, $p = 0.31$, right: $F(5,45^1) = 1.51$, $p = 0.21$) thus indicating that auditory responses to all statements were similar.

Then, to examine whether some intrinsic characteristics of the statements could explain our findings, we dissected activation elicited by each individual statement over the 6 language areas that showed similar relative amount of activation between categories (i.e. TP, aSTS, pSTS, TPJ, IFGorb and

¹ Note that degrees of freedom may vary because certain participants did not systematically exhibit, within each region of interest, one significantly activated voxel in the contrast of sentences > jabberwocky of our syntax localizer.

IFGtri). Figure S2 shows the mean betas over these 6 regions for each statement, sorted in ascending order. We notably observed that statements were grouped per category, suggesting a strong reproducibility of brain response to statements within each category. Series of beeps activated the least language regions, followed closely by a mix of trigonometry, rote facts and algebra, afterwards came the group of statements related to complex numbers, then geometrical statements, to finish with the group of nonmath statements. When enumerating grammatical morphemes (i.e. grammatical markers such as verb endings or plural markers) in each statement, we found a strong correlation with mean beta values ($R = 0.71$, $p = 5.10^{-12}$). This result may suggest that the differential activation in language areas is due to differences in syntactical complexity among categories of statements.

4.3.6. Activation profile in math-responsive areas

Comparatively, a similar analysis conducted in the math-responsive regions (left and right IPS, left and right IT, again a priori defined from (Amalric and Dehaene, 2016)) revealed a completely different ordering (see figure S3). Indeed, we confirmed that nonmath statements and series of beeps systematically deactivated these regions, while math statements systematically activated these regions regardless of their content. Each region exhibited a significant activation for all categories of math (except for geometry in right IPS, all $ps < 0.015$ with Bonferroni correction for multiple comparisons over 4 regions of interest). Conversely, nonmath statements systematically deactivated all of these math-responsive regions (all $ps < 0.05$ corrected). Moreover, in the left and right IT, activation to all math categories was similar (left: $F(4,48) = 1.44$, n.s.; right: $F(4,48) = 0.74$, n.s.). In the left and right IPS, rote facts, algebra, trigonometry and complex numbers elicited similar activation (left: $F(3,36) = 1.85$, n.s.; right: $F(3,36) = 1.51$, n.s.), and elicited more activation than geometry (left: $ps < 0.015$ corrected for algebra and complex numbers $>$ geometry; right: all $ps < 0.004$ corrected). These results may suggest that while IT activates regardless of statements format, IPS is sensitive to their surface form. Indeed, the amount of activation in right IPS was negatively correlated with the number of grammatical morphemes in the math statements ($r = -0.48$, $p = 0.0001$).

4.4. Conclusion

This first experiment indicates that activation in the math-responsive network found in our previous study (Amalric and Dehaene, 2016) is highly reproducible even when simple and well-known mathematical facts are processed. In particular, our results suggest that there is a common neural substrate for math processing independent of content and difficulty. An additional activation can be found in occipital regions for statements that required a certain visual processing.

Furthermore, rote algebraic facts, algebraic or trigonometric calculation or the problems on complex numbers activate the language areas to a lesser extent than our geometrical and nonmath sentences, and even do not activate at all TP, TPJ and IFGOrb. One can partly explain this result arguing that sentences from these categories had a lower syntactical complexity than the geometrical or nonmathematical sentences. In the following experiment, to avoid any syntactical effect, we have proposed mathematicians to listen to mathematical and nonmathematical statements that had the exact same syntactic structures.

5. Experiment 2: effect of minimal combinatorial operations such as quantifiers and negation.

5.1. Introduction

The math-responsive network has proved to coincide with activations elicited by a wide range of problem-solving tasks (Duncan, 2010), and in particular in several recent studies using reasoning tasks, even in nonmathematical context (Goel, 2004; Goel and Dolan, 2001; Monti et al., 2007). For example, Goel (2004) suggested that deductions like “No humans can get osteoporosis; Some humans are men; Some men cannot get osteoporosis”, compared to the integration of two related and a third unrelated statements, induced activations in bilateral superior parietal cortex. These results may thus suggest that, under some conditions, logical reasoning about nonmath problems can elicit the math-responsive network.

An important characteristic of logical reasoning is the presence of logical operators such as negation, conjunction or quantifiers. Some recent neuroimaging studies have exhibited parietal activations in response to quantifiers (Hubbard et al., 2008; McMillan et al., 2005; Troiani et al., 2009; Wei et al., 2014). For example, bilateral intraparietal sulci activations correlate with numerical quantifiers (“at least three”, “more than two”, etc...) according to Troiani et al. (2009). While this result might simply be due to the presence of numbers in numerical quantifiers, McMillan et al. (2005) have further shown that all types of quantifiers (“some”, “every”, “more than”, etc...) share activation in the inferior parietal cortex.

In this second experiment, we aimed investigating whether some logical operators, that are used in both mathematical and general contexts, such as quantifiers and negation, suffice to activate the math-responsive network. To address this issue, it was crucial that our statements differed only in terms of content (math/nonmath) and of the presence of quantifiers or negation. We thus took extra caution in matching syntax between math and nonmath statements.

5.2. Method

The same participants as in experiment 1 were again exposed to a set of spoken true or false mathematical and non-mathematical statements (figure 2.1), following the same procedure. These statements were either mere declarative sentences (“The sine function is periodical”; “Londonian buses are red”), included one quantifier (“Some matrices are diagonalizable”; “Some ocean currents are warm”), one negation (“Hyperboloids are not connected”; “Orange blossom is not perfumed”), or both a quantifier and negation (“Some order relations are not transitive”; “Some green plants are not climbing”). Note that we were extremely careful that math and nonmath statements were fully syntactically matched within each category. Indeed, they contained, in pairs, the exact same number of words, of the exact same grammatical categories.

5.3. Results

5.3.1. Behavior

The group of mathematicians performed almost perfectly in this experiment, with an overall performance of $88.9 \pm 2.9\%$ correct (math: $91.1 \pm 2.6\%$ correct; nonmath: $86.6 \pm 3.0\%$ correct; figure 2.2). In details, the mathematicians classified correctly each category (math declarative: $96.9 \pm 1.2\%$ correct; nonmath declarative: $92.2 \pm 2.1\%$ correct; quantified math: $88.5 \pm 2.8\%$ correct; quantified nonmath : $91.5 \pm 2.9\%$ correct; math negative : $86.4 \pm 2.5\%$ correct; nonmath negative: $81.0 \pm 2.8\%$ correct; quantified math negative: $92.8 \pm 2.7\%$ correct; quantified nonmath negative: $81.5 \pm 2.8\%$ correct).

Overall, an ANOVA with problem type as between factor and subject as within factor revealed a significant effect of conditions ($F(7,91) = 6.69$, $p < 0.001$) and a T-test revealed that the math statements were significantly better classified than the nonmath statements ($t(55) = 3.0$, $p = 0.004$). In more details, no significant difference was found between the math and nonmath statements neither in the declarative condition ($t(13) = 1.87$, $p = 0.08$), in the quantified condition ($t(13) = 1.23$, $p = 0.24$), nor in the negative condition ($t(13) = 1.85$, $p = 0.09$). But math and nonmath significantly differed in the quantified negative condition ($t(13) = 3.42$, $p = 0.005$). Both within math and nonmath statements, condition had a significant effect (math: $F(3,39) = 5.05$, $p < 0.005$; nonmath: $F(3,39) = 7.72$, $p < 0.001$).

A small but significant difference in response time was found between the math and nonmath statements (math: 1.21 ± 0.08 s; nonmath: 1.28 ± 0.08 s; $t(13) = 2.32$, $p = 0.024$, figure 2.2). Within each condition, however, no difference was found between math and nonmath response times, except for quantified negation ($t(13) = 5.18$, $p < 0.001$).

5.3.2. Math versus nonmath dissociation

We first searched for regions exhibiting more activation to math than nonmath statements, and found the now classical math-responsive network: bilateral IPS, IT, superior and middle frontal regions (figure 2.7). Similar results were found within each condition (declarative, negative, quantified declarative and quantified negative) for the contrast of math versus nonmath (figure S4). Furthermore, the conjunction of math > nonmath contrasts in all four categories again revealed activation in bilateral inferior-temporal regions and the left intraparietal sulcus (figure 2.7).

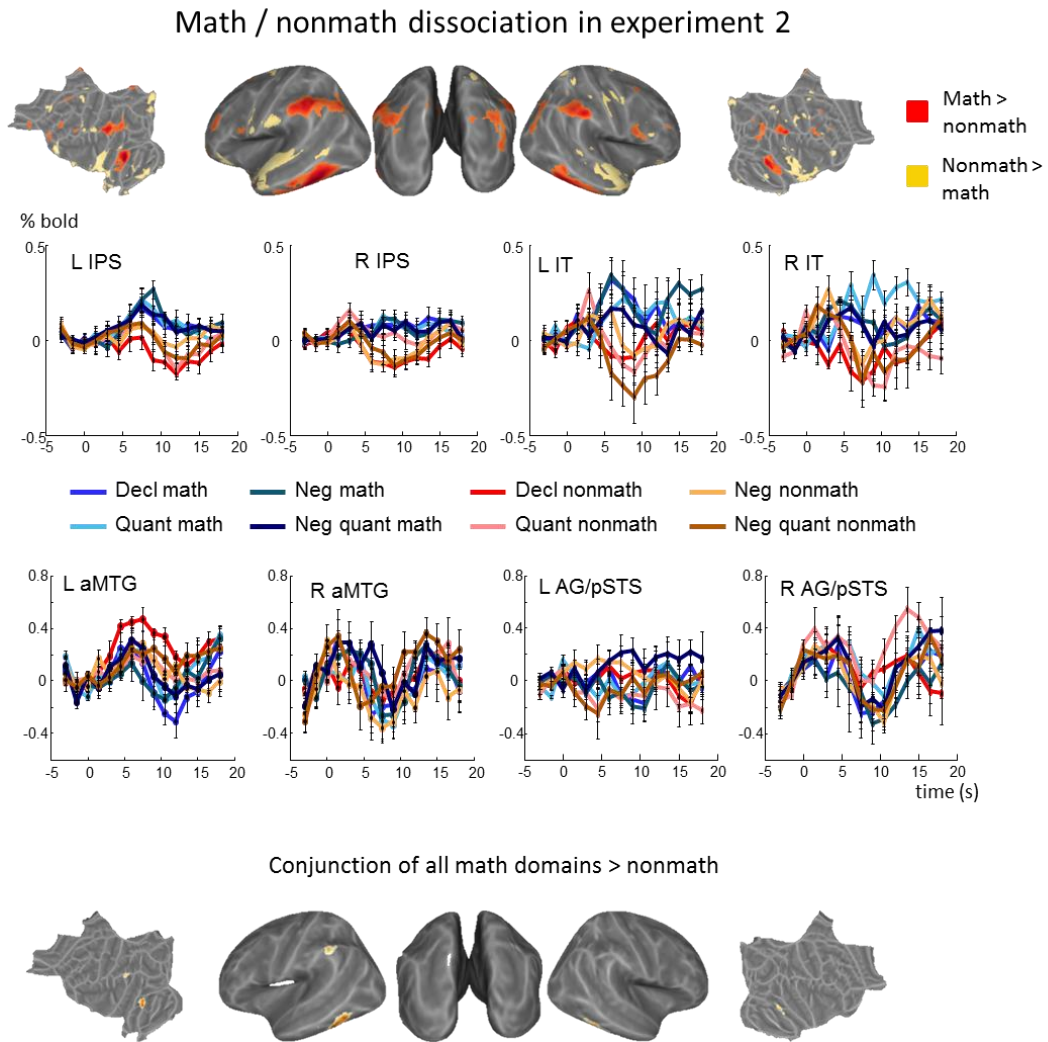


Figure 2.7. Dissociation between math and nonmath semantic networks in experiment 2. (top) Flattened and inflated brain maps showing the contrasts of math > nonmath processing (red) and nonmath > math processing (yellow) (uncorrected $p < 0.001$ voxelwise, corrected $p < 0.05$ clusterwise). (middle) Temporal course of bold signal for each category of statements in representative brain areas of the networks responsive to math and general-semantic. (bottom) Flattened and inflated brain maps showing the conjunction of the four contrasts of math > nonmath within each condition (uncorrected $p < 0.001$ voxelwise, corrected $p < 0.05$ clusterwise for each separate contrast).

In the math-related regions, plots of temporal course of activation revealed a systematic activation for mathematical conditions and, contrariwise, a systematic deactivation for nonmathematical conditions (figure 2.7). The analysis and sorting of the mean betas associated with

each statement over the 4 main math-related regions (i.e. bilateral IPS and IT) confirmed this result (see figure S6). Indeed, virtually all non-math statements had negative betas while almost all math statements, with a few exceptions, came at the top of the ranking.

Conversely, the brain regions exhibiting greater activation for nonmath than math statements were bilateral superior temporal sulci and the left IFGOrb. Similar clusters of activation were found in bilateral superior temporal poles for nonmath > math reflection when restricting to declarative or quantified statements. For negative statements, only a small difference between nonmath and math statements in the left temporal pole was observed, and no such difference was seen for quantified negative statements. Note that the main contrast of nonmath versus math statements elicited less extended activation in the semantic-related regions than the equivalent contrast in experiment 1 (figure S5). In particular, no activation in bilateral angular gyri was found this time. Examination of temporal activation in regions of interest extracted from nonmath > math reflection in our previous study (Amalric and Dehaene, 2016) revealed noisy and indistinct signal (figure 2.7), suggesting that the nonmath statements activated slightly different regions in the present experiment. Only in the left anterior superior temporal sulcus, activation for the nonmath statements remained sustained until the end of the trials and was especially high for the declaratives, while the math statements induced an only transient activation, followed by a systematic deactivation (figure 2.7).

5.3.3. Activation profile in auditory and language areas

We first checked whether auditory responses differed between categories in the Heschl gyri, and found similar responses to all statements in the right hemisphere ($F(7,70) = 0.44$, n.s), and slight but significant difference in the left hemisphere ($F(7,84) = 2.70$, $p = 0.03$ with Bonferroni correction over 2 regions, figure 2.8). We then performed an ROI analysis in the 7 same syntactical regions that were used in experiment 1 (i.e. TP, aSTS, pSTS, TPJ, IFGorb, BA44 and IFGtri). Figure 2.8 shows the average betas of each statements types within each region. All categories elicited significant activation in all 7 regions but TPJ (all p s < 0.04 corrected over 7 regions of interest), and ANOVAs performed in each region revealed no significant differences between categories.

This result was finally confirmed by dissecting activation elicited by each individual statement over all 7 language areas. After sorting corresponding betas in ascending order, no clear segregation appeared, either between categories or between math and nonmath statements. Contrariwise, the math and nonmath statements were almost completely stirred (figure S6).

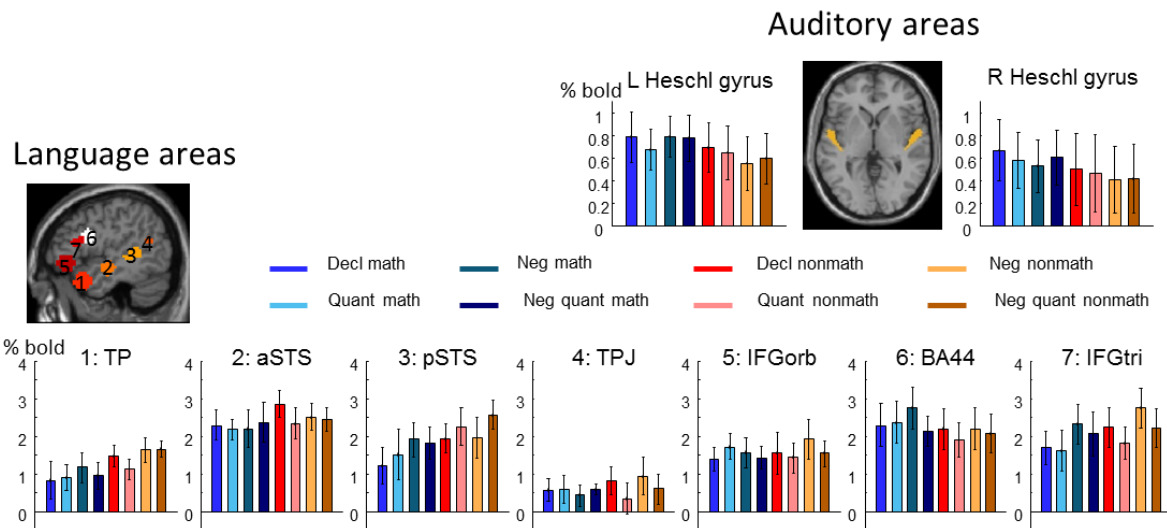


Figure 2.8. Activation profile in auditory and language areas. (top) Axial slices showing auditory anatomical regions of interest, i.e. Heschl gyri, from which beta estimates of each category were extracted (bar plots). (bottom) Sagittal slice showing the 7 language regions of interest used to extract beta estimates represented in bar plots.

5.3.4. Effect of quantifiers

We studied the main effect of quantification by comparing all statements that contained a quantifier (i.e. quantified plus negative quantified math and nonmath statements) to all other statements. This contrast revealed a cluster of activation in the right angular gyrus (figure 2.9). Interestingly, this activation totally spared math-related regions as suggested by the superposition of brain maps showing the math > nonmath contrast and the main effect of quantifiers (figure 2.9). Similar activation was found when restricting to math statements, and no significant effect of quantifiers was found within nonmath statements. Plots of average betas in this cluster revealed that the quantified statements induced less deactivation than simple declaratives or negatives (figure 2.9).

5.3.5. Effect of negation

We first searched for regions of which activity was modulated by the presence of negation, regardless of the math/nonmath distinction. The comparison of all negative statements (math and nonmath, quantified or not) versus all other statements revealed activation lying at the intersection of the left IFG pars triangularis, Opercularis and Orbitalis (figure 2.9). Then, restricting to the math statements, activation was found only in IFG Triangularis (around [-45 22 -1], $t = 4.04$), while restricting to the nonmath statements, we found activation only in the IFG Orbitalis (around [-44 52 3], $t = 4.33$).

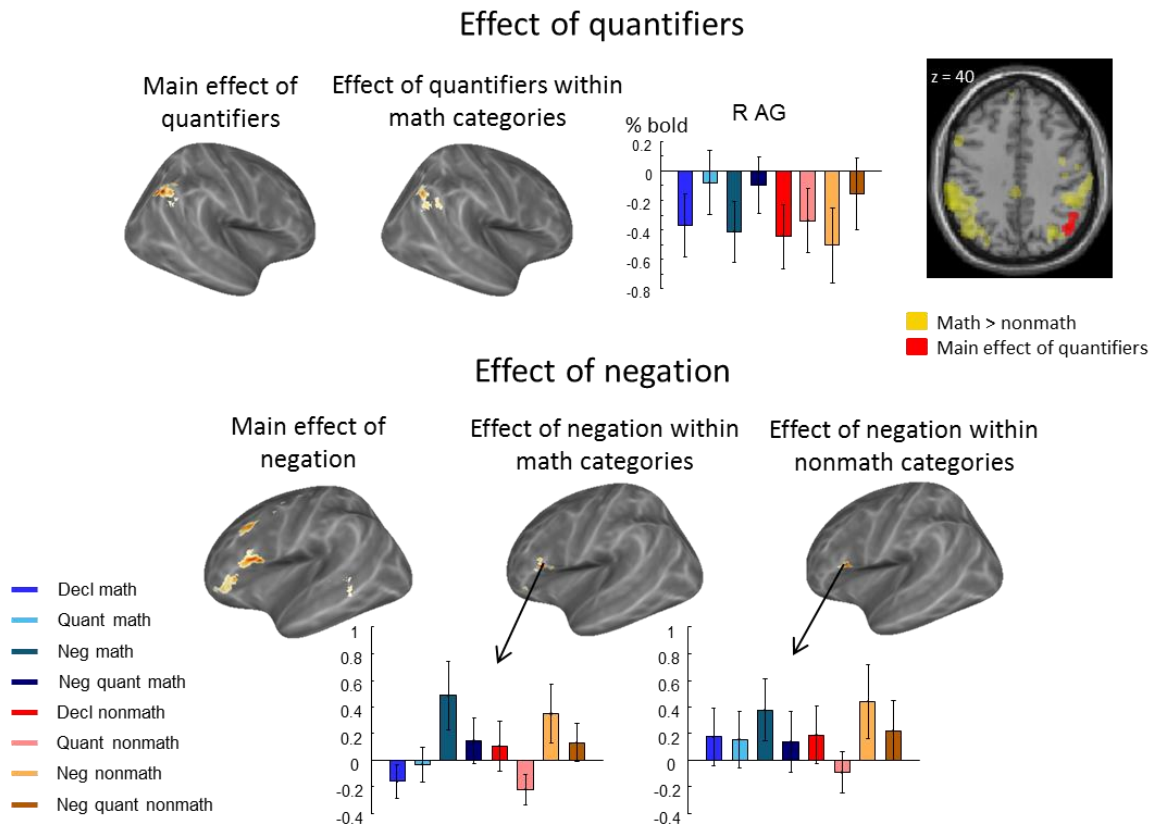


Figure 2.9. Main effects of quantifiers and negation. (top) Inflated brain maps showing the main effect of quantifiers among math and nonmath statements, and the effect of quantifiers within math categories only. Bar plot displays the mean beta values obtained in this specific cluster of activation. (top right) Axial slice showing the relative spatial extent of the activation induced by the main effect of quantifiers and the activation elicited more by math than nonmath statements. (bottom) Inflated brain maps showing the main effect of negation among math and nonmath statements, and the effect of negation within math and nonmath categories separately. These separate contrasts have exhibited activation left IFG from which bar plots represent the extracted mean beta values.

5.4. Conclusion

In this experiment, while all statements were perfectly matched in syntax and elicited similar activation in the classical language areas, only the math statements were processed in bilateral intraparietal and inferior temporal regions. This result therefore reinforces the idea that there is a math-responsive network in the brain constituted of bilateral IPS and IT regions that systematically process math-related semantic content.

Furthermore, the presence of minimal mathematical operators such as quantifiers and negation was not enough to elicit activation in the math-responsive regions in a nonmathematical context. Negation correlated with activation in the left IFG, suggesting a syntactical complexity effect. Quantifiers correlated with less deactivation in the right angular gyrus, a very same region than the one previously found by (McMillan et al., 2005), that did not overlap with parietal activation engaged in mathematical reflection.

6. Discussion

We start by summarizing the main findings of the present fMRI studies. First, we replicate the dissociation that was previously observed between brain circuits involved in math and nonmath reflection (Amalric and Dehaene, 2016), in the case of simple math statements. This dissociation was even more drastic in the case of rote algebraic facts or algebraic calculation which elicited virtually no activation in the language areas. On the contrary, the nonmath problems did not engaged the math-responsive regions, even when they contained minimal mathematical operators such as quantifiers or negation. Instead, main effects of quantifiers and negation were respectively observed in the right angular gyrus and the left IFG. Finally, trigonometry and complex numbers, that required some visualization, induced additional activation in the occipital cortex.

Our findings consolidate the idea that the intraparietal sulci and bilateral lateral inferior temporal regions constitute a core math-related network, activated regardless of mathematical domain or problem difficulty. Indeed, whether mathematical problems were easy or difficult, retrieved from memory, resulting from calculation or visualized, these four brain regions were systematically activated. Interestingly, comparing the brain circuits activated for mathematical reflection in our previous study with the activation observed in the present studies, we notice a decreased activation in frontal regions as mathematical statements get simpler, while activation in the bilateral intraparietal and inferior temporal regions remains.

Moreover, math-related regions appeared to be exclusively used for mathematical purpose in our experiments, and were never used to process nonmathematical statements, even when such statements contained minimal logical operators. Negation, that automatically increases the number of words in a sentence compared to simple or quantified declaratives, induced more activation in the left IFG (Broca's area). This result might therefore suggest a mere effect of syntactical complexity. Quantifiers, in turn, appeared to deactivate less than other statements a right parietal region that did not overlap with the math-related network.

A subject-specific analysis in the math-responsive regions also seems to indicate the existence of two subsets of core mathematical regions. Indeed, IPS and IT did not respond similarly to all types of math problems. Indeed, while bilateral IT did not show evidence of sensitivity to differences in math statements formulation, bilateral IPS, in particular in the right hemisphere, responded less to the geometrical statements with greater linguistic complexity.

In the present studies, we have also confirmed that mathematical reflection on advanced concepts does not call upon the classical semantic areas – the anterior part of superior and middle temporal sulcus, and the temporo-parietal junction/angular gyrus (Binder et al., 2009). While

bilateral anterior temporal lobe was consistently involved in general semantic processing in our previous (Amalric and Dehaene, 2016) and present experiments, sensitive analysis in language regions of interest extracted from a previous study by (Pallier et al., 2011), revealed that algebra, trigonometry and complex numbers made virtually no use of left TP, TPJ and IFGOrb in the first experiment of the present study. Note that (Pallier et al., 2011) showed that left TP, aSTS and TPJ exhibited no effect of constituent size in jabberwocky sentences (i.e. meaningless sentences with pseudo-words but preserved syntax), again suggesting that these regions are sensitive to semantics. Our results thus tend to reinforce previous findings suggesting that mathematical semantics dissociate from general semantics in the brain (Amalric and Dehaene, 2016).

We note in passing that while Ischebeck et al. (2006) found that the retrieval of verbal arithmetic facts versus untrained calculation involved the angular gyri, we did not verify such a result here for rote algebraic facts that activated the now classical math network. This result could suggest that algebraic identities may not be stored in a verbal format.

We also verify here that mathematics and language are not completely disconnected in the brain. Indeed, in experiment 1, listening to math statements activated some language areas (aSTS, pSTS, IFGTri) to an extent that reflected their syntactical complexity. Moreover, in experiment 2, ROI analysis in the language areas showed no difference between math and nonmath statements, thus reflecting the extreme similarity of the math and nonmath statements in terms of syntactical construction.

We note here that additional activation in the occipital cortex was found for the problems concerning complex numbers, trigonometry or geometry. To be solved in 2.5s, these mathematical problems would require visualizing the solution, thus suggesting that occipital cortex activations may reflect a certain visual imagery. This interpretation strengthens our previous findings that problems imageability, rated by participants after fMRI exam, correlated with brain activity in a parieto-occipital region (Amalric and Dehaene, 2016).

The main effect of quantifiers may seem surprising. Indeed, while we found a cluster of activation in a region very similar to what was reported by McMillan and colleagues, we acknowledge for two major differences compared to their findings (McMillan et al., 2005). First, inspection of the beta estimates in this region revealed no activation for statements that contained a quantifier but a strong deactivation for declarative and negative statements. Second, McMillan and colleagues described brain activation to quantifiers as located in inferior parietal lobule, a result they interpreted as the existence of a common numerical basis for numbers and quantifiers. However, what they called inferior parietal lobule actually seems closer to the angular gyrus than to the

intraparietal sulcus. Furthermore, our results suggested that the region showing a main effect of quantifiers was not included in the math-responsive network. Altogether, these observations query the idea that quantifiers would call upon numerical processes.

Finally, comparing our three experiments, we observe that activation in bilateral angular gyri for the nonmathematical statements has disappeared in the second experiment. In experiment 2, the nonmath statements were easier than in experiment 1, which were also easier than in our previous experiment. Given that the angular gyrus has been suggested to play a general role in the integration of semantic information and was particularly found to respond to semantic combination of nouns or nouns and adjectives (Boylan et al., 2017), decreasing activity in the angular gyrus might be an effect of decreasing difficulty of the nonmath statements. Another explanation could be link to the statements content itself. According to Binder et al. (2005), bilateral angular gyri were more activated when participants were presented with concrete words than abstract words. However, this finding cannot account for our results given that the nonmath statements in experiment 2 elicited less activation in the angular gyri than experiment 1 while they contained more concrete words (such as “plant”, “ocean”, “fruit”, “tiger”, ...) than experiment 1 (“pantomime”, “rock’n’roll”, “Ancient Greece”, “still-life painting”, ...). A radically different explanation could be that nonmathematical statements of experiment 2 were less contextualized than other experiments (examples from (Amalric and Dehaene, 2016): “in Ancient Greece”, “all borders in Europe”,...). Such contextualization might involve other cognitive processes such as self-reflection and self-projections in time and space that were both suggested to involve the angular gyrus. Indeed, according to Saxe and Wexler (2005), the right temporo-parietal junction has a special role in “Theory of Mind” reasoning. Moreover, activation in the angular gyrus proved to be modulated by the distance in spatial and temporal mental projections (Gauthier and Wassenhove, 2016). Unfortunately, the present data are simply insufficient to validate one or the other hypothesis.

Regarding our original question, however, our findings unequivocally support previous observations that brain regions responsive to mathematical versus linguistic semantic content are dissociated.

7. Methods

7.1. Ethics statement

All experiments were approved by the regional ethical committee for biomedical research, and subjects gave informed consent after they read consent information.

7.2. Stimuli

All statements were recorded using Audacity by a female native French speaker who was familiar with mathematical concepts. Within each experiment, the statements from the different categories were as far as possible matched in number of syllables and duration. A complete list of stimuli can be found in appendix.

The spoken statements of experiment 1 lasted 4.12 ± 0.68 s in average, and the statements of experiment 2 lasted 4.47 ± 0.62 s in average.

7.3. Procedure

In both experiments, screen only displayed a fixation cross on a black background, which participants had to fixate continuously. Each trial started with a beep and a color change of the fixation cross (which turned to red), announcing the onset of the statement. Participants were then asked to answer as quickly as they could. A maximum of 2.5 seconds was left for the reflection and the response. The response period ended with a beep, and was signaled by the fixation cross turning to green. Subjects gave their evaluation of the sentence (true, false) by pressing a button held in the right hand for true, and held in the left hand for false. Each trial ended with a 7-second resting period (figure 2.1).

Experiment 1 was divided into 3 runs of 32 statements each, including exactly two exemplars of each sub-category (math/nonmath x true/false x 4 conditions).

Experiment 2 was divided into 7 runs of 12 statements each, including at least one exemplar of each sub-category.

7.4. Syntax localizer

At the end of the fMRI exam, participants performed a syntax localizer. In a unique run of 14 minutes, participants listened to correct sentences, jabberwocky sentences (i.e. sentences composed of pseudo-words with preserved grammatical markers), and jabberwocky in random order (in which the grammatical structure is degraded). At the beginning of each trial, they heard a word or pseudo-word, followed by a sentence or pseudo-sentence in which they had to detect the target word or pseudo-word. Trials ended with a 7-second resting period. Targets always pertained to the last third of sentences in order to maintain participants' concentration until the end of the trial. To keep participants focused throughout the whole session, sentences did not systematically include the target which was absent of 10% of the sentences and pseudo-sentences. Sentences and pseudo-sentences had purposely complex syntax. They all contained 14 words and relative clauses.

7.5. fMRI data acquisition and analysis

We used two 3-Tesla whole body systems (Prisma) with high-resolution multiband imaging sequences developed by the Center for Magnetic Resonance Research (CMRR) (Xu et al., 2013) (multiband factor = 4, Grappa factor = 2, 80 interleaved axial slices, 1.5 mm thickness and 1.5 mm isotropic in-plane resolution, matrix = 128x128, TR = 1500 ms, TE = 32 ms), with 64 channel head-coil.

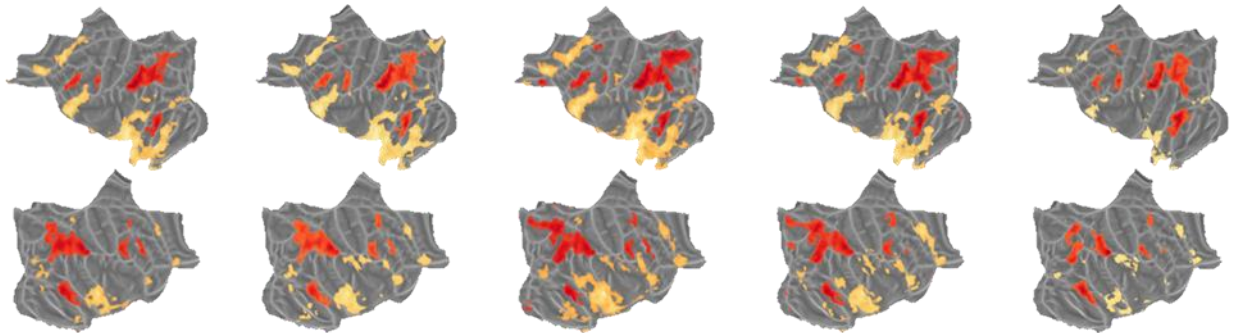
Using SPM8 software, functional images were first corrected for slice timing, realigned, normalized to the standard MNI brain space, and spatially smoothed with an isotropic Gaussian filter of 2 mm FWHM. A two-level analysis was then implemented in SPM8. For each participant, fMRI images were high-pass filtered at 128s. Then, time series from experiment 1 and experiment 2 were modelled separately. For both experiments, time series was modelled using a single regressor per statement, with a kernel corresponding to statement presentation plus the mean reaction time for that subject. We then defined subject-specific contrasts by comparing the activation evoked by two subsets of sentences during the reflection period. Regressors of non-interest included the six movement parameters for each run. Within each auditory run, additional regressors of non-interest were added to model activation to the auditory beeps and to the button presses.

For the second-level group analysis, individual contrast images for each of the experimental conditions relative to rest were smoothed with an isotropic Gaussian filter of 5 mm FWHM, and entered into a second-level whole-brain ANOVA with stimulus category as within-subject factor. All brain activation results are reported with a clusterwise threshold of $p < 0.05$ corrected for multiple comparisons across the whole brain, using an uncorrected voxelwise threshold of $p < 0.001$.

8. Supplementary materials

Figure and table S1. Comparison of each mathematical category with nonmath statements and principal peaks

Flat maps and table of principal peaks showing the reproducibility of activation to each category of math statements (red) versus nonmath statements (yellow).



	rote facts > nonmath				algebra > nonmath				trigo > nonmath				complex > nonmath				geometry > nonmath			
	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t
L IPS	-60	-34	46	12.04	-57	-36	48	15.03	-57	-36	48	11.71	-56	-36	49	12.36	-57	-34	48	11.89
R IPS	48	-37	48	11.02	48	-37	48	12.58	48	-39	49	10.57	47	-37	48	10.57	59	-25	46	11.84
L IT	-56	-51	-22	9.36	-54	-51	-22	11.35	-54	-51	-22	10.14	-57	-57	-11	10.70	-56	-57	-10	10.33
R IT	56	-52	-17	9.15	56	-52	-17	9.68	56	-52	-16	9.49	56	-52	-17	10.63	56	-52	-16	9.35
L IFG	-39	41	18	6.36	-39	40	19	7.32	-38	40	18	6.35	-47	43	19	5.91	-44	37	18	6.40
R IFG	45	41	18	7.09	44	40	19	6.48	45	47	13	7.06	51	41	19	6.38	50	41	21	6.11
L MFG	-50	10	39	6.34	-50	10	37	6.73	-50	10	36	6.22	-48	8	34	6.94	-48	7	33	7.54
R MFG	50	11	28	6.89	47	8	25	7.06	44	10	33	5.74	48	8	24	6.35	50	8	25	6.46

Figure S2. Average beta estimates over 6 language regions (TP, aSTS, pSTS, TPJ, IFGOrb and IFGTri), sorted in ascending order.

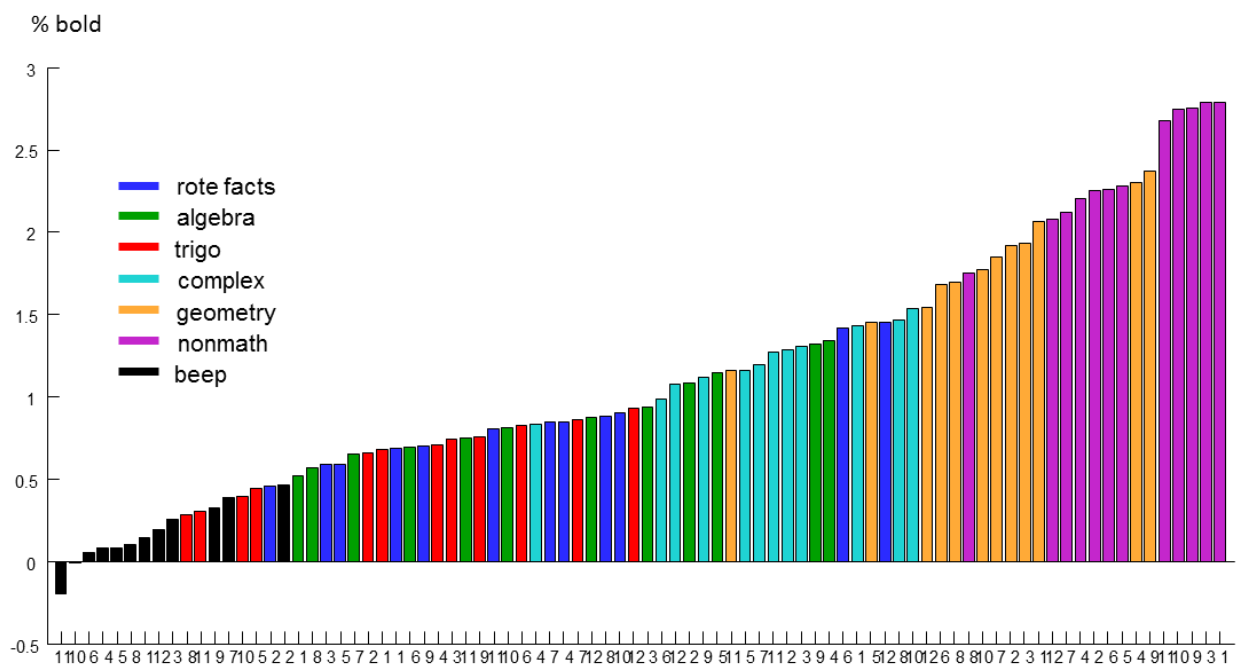


Figure S3. Average beta estimates over 4 math-responsive regions (bilateral IPS and IT), sorted in ascending order.

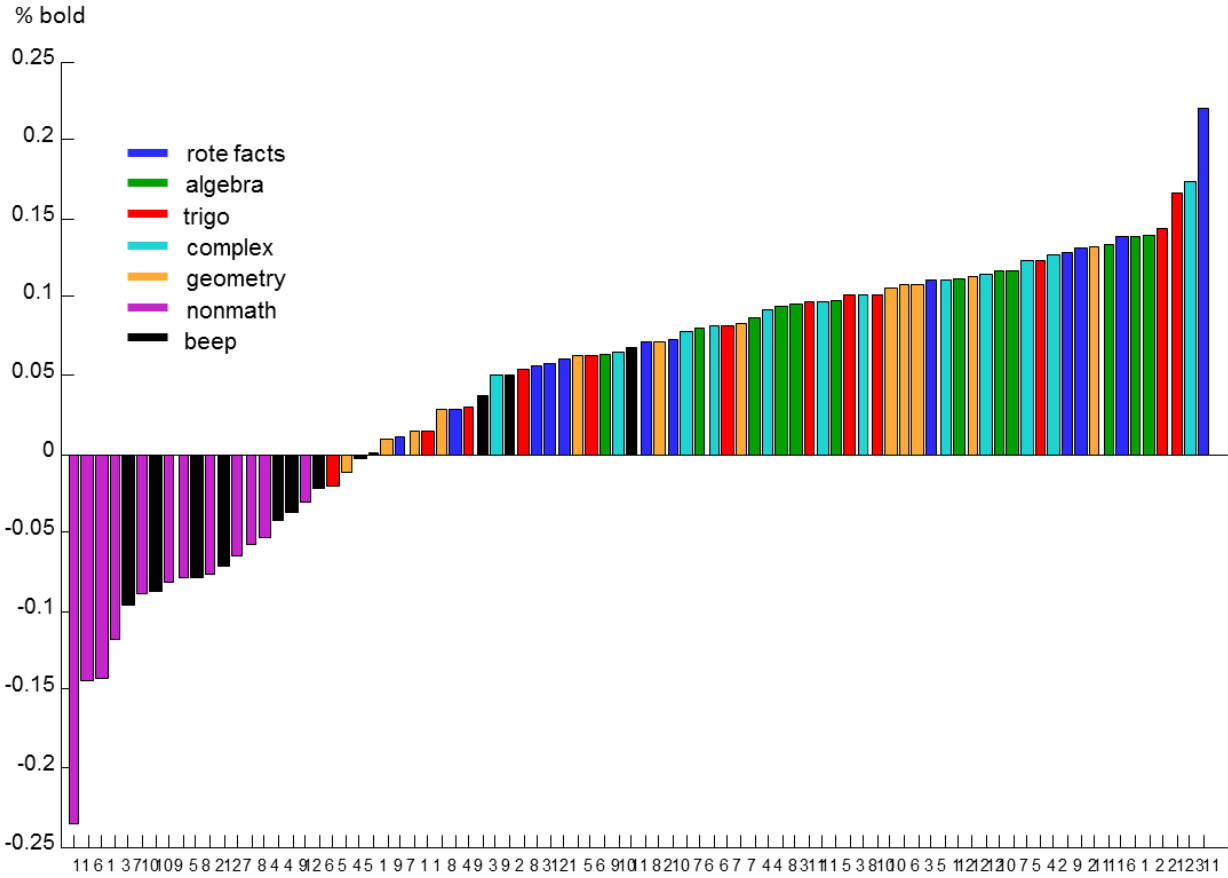
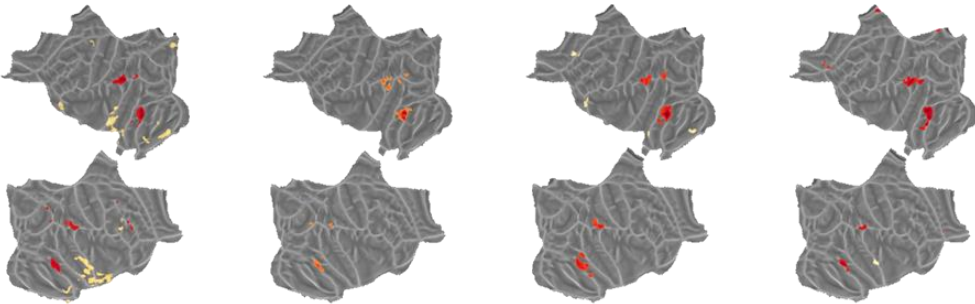


Figure and table S4. Comparison of mathematical and nonmath statements within each category and principal peaks

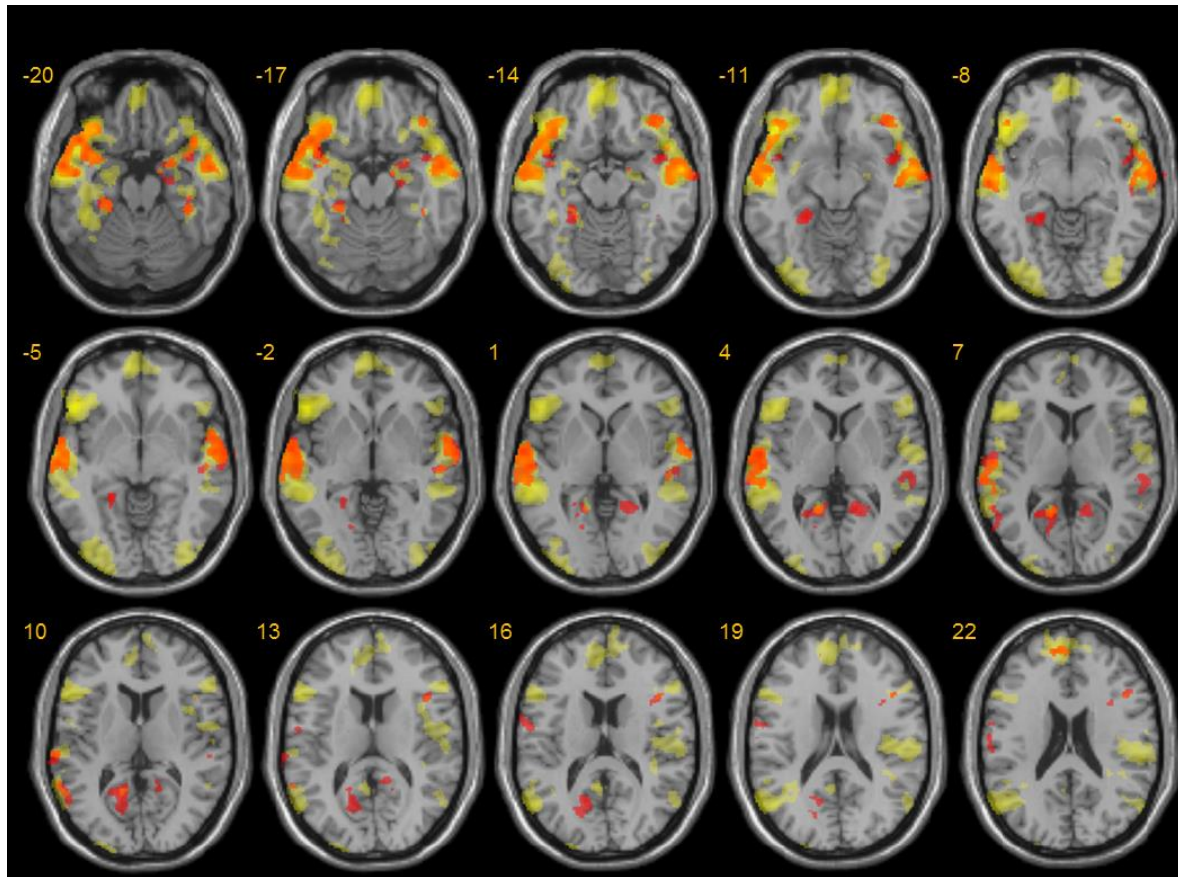
Flat maps and table of principal peaks showing the reproducibility of activation to math statements (red) versus nonmath statements (yellow) in each category.



	declarative math > nonmath				quantifier math > nonmath				negative math > nonmath				negative quantifier math > nonmath			
	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t
L IT	-59	-60	-10	6.97	-54	-55	-14	7.33	-57	-57	-14	7.83	-57	-57	-7	6.89
R IT	63	-58	-10	6.71	57	-49	-22	4.89	62	-58	-10	6.27	57	-52	-16	5.63
L IPS	-51	-48	48	6.07	-56	-40	46	5.08	-60	-33	43	5.80	-53	-48	46	6.3
R IPS	45	-39	46	5.51	50	-43	43	5.07	47	-42	48	6.57	60	-28	48	5

Figure S5. Comparison of activation to nonmath statements in both experiments

Succession of axial slices assessing the overlap of the contrasts of nonmath > math statements between experiment 1 (yellow) and experiment 2 (red). While nonmath statements from both experiments elicit similar activation in primary auditory regions, nonmath statements from experiment 1 elicit additional activation in bilateral angular gyri and mesial frontal regions.



- Nonmath > math in experiment 1
- Nonmath > math in experiment 2

Figure S6. Average beta estimates over 4 math-responsive regions (bilateral IPS and IT), sorted in ascending order.

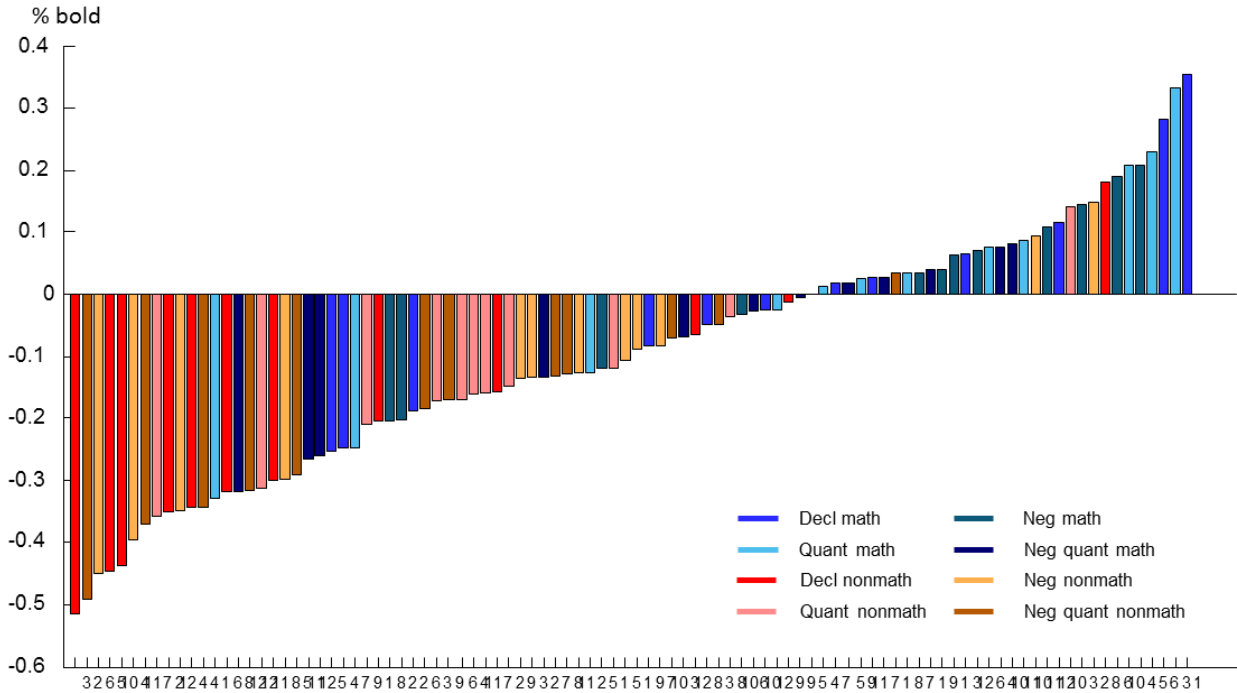
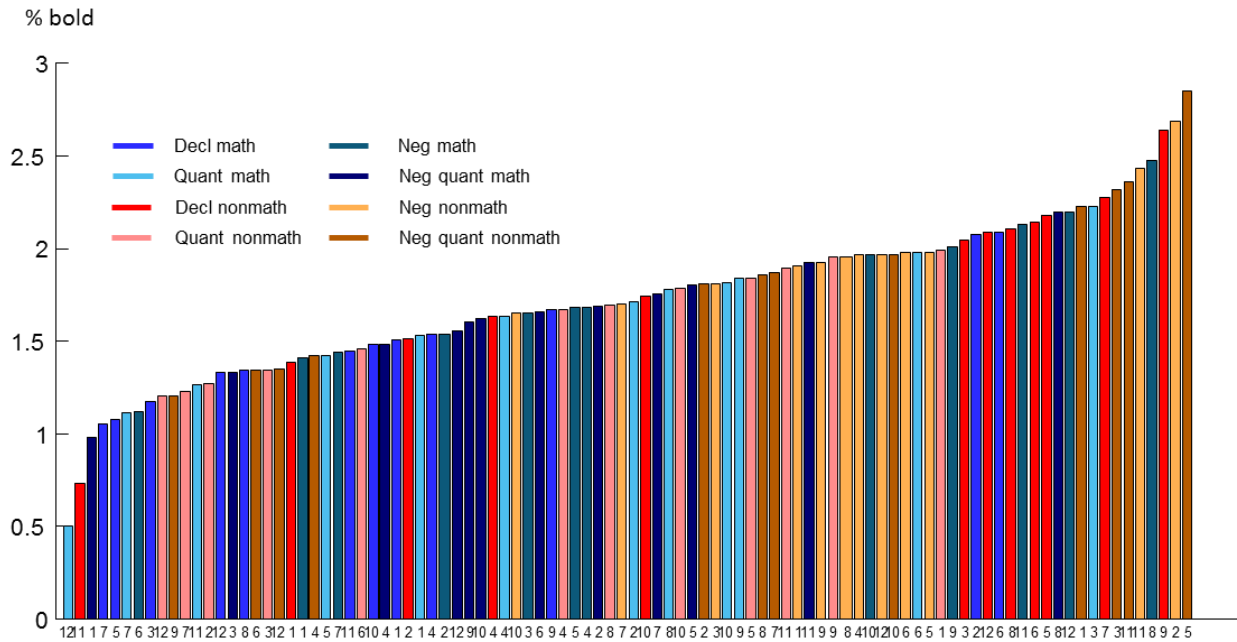


Figure S7. Average beta estimates over 6 language regions (TP, aSTS, pSTS, TPJ, IFGOrb and IFGTri), sorted in ascending order.



Annex 1: list of statements used in experiment 1 (in French)

1. Rote facts

1.1. True

$$(a+b)^2 = a^2 + b^2 + 2ab$$

$$(a+b)(a-b) = a^2 - b^2$$

$$\cos(a+b) = \cos a \cos b - \sin a \sin b$$

$$\sin(a-b) = \sin a \cos b - \cos a \sin b$$

$$\cos(2a) = \cos^2 a - \sin^2 a$$

$$\cos^2 a + \sin^2 a = 1$$

1.2. False

$$(a-b)^2 = 2(a^2+b^2)$$

$$(a+b)^3 = a^3+b^3+1$$

$$\cos(a-b) = \sin a \cos b + \cos a \sin b$$

$$\sin(a+b) = \cos a \cos b + \sin a \sin b$$

$$\cos^2 a + \sin^2 a = \pi$$

$$\sin(2a) = 1 - \cos^2 a$$

2. Algebra

2.1. True

$$(x+2)^2 = x^2 + 4 + 4x$$

$$(3-x)^2 = 9 + x^2 - 6x$$

$$(x-1)(x+1) = x^2 - 1$$

$$(y+1)^2 + (y-1)^2 = 2y^2 + 2$$

$$(1-2y)^2 = 1 + 4y^2 - 4y$$

$$(3y+1)(3y-1) = 9y^2 - 1$$

2.2. False

$$(x+4)^2 - (x-4)^2 = x^2 + 16$$

$$(3x+1)^2 = 9x^2 + 1 + 3x$$

$$(2x-3)(2x+3) = 2x^2 - 3$$

$$(y+1)^2 = y^2 + y + 1$$

$$(y-2)^2 = y^2 + 4 + 4y$$

$$(y-3)(y+3) = y^2 + 9$$

3. Trigonometry

3.1. True

$$\sin(x+3\pi/2) = -\cos x$$

$$\cos(x+3\pi) = -\cos x$$

$$\cos(x+\pi) = -\cos x$$

$$\cos(x-\pi/2) = \sin x$$

$$\cos(x+\pi/2) = -\sin x$$

$$\sin(x-\pi) = -\sin x$$

3.2. False

$$\cos(x-3\pi/2) = \sin x$$

$$\cos(x+3\pi) = -\cos x$$

$$\sin(x-3\pi) = \cos x$$

$$\sin(x+\pi) = \sin x$$

$$\sin(x-\pi/2) = \cos x$$

$$\cos(x-\pi) = \cos x$$

4. Complex numbers

4.1. True

$$\operatorname{Re}(e^{i\pi/2}) = 0.$$

$$\operatorname{Im}(e^{i\pi/4}) = \sqrt{2}/2.$$

$\operatorname{Re}(e^{i\pi/4}) = \operatorname{Im}(e^{i\pi/4})$. (Les parties réelle et imaginaire de $e^{i\pi/4}$ sont égales).

$$\sqrt{2} \cdot e^{i\pi/4} = 1 + i$$

L'angle entre 1 et $1+i$ est égal à $\pi/4$.

L'angle entre 1 et i est égal à $\pi/2$.

4.2. False

$$\operatorname{Re}(e^{3i\pi/4}) = 1.$$

$$\operatorname{Im}(e^{i\pi/3}) = 1/3.$$

$$\operatorname{Re}(e^{i\pi/3}) = \operatorname{Im}(e^{2i\pi/3}).$$

$$\operatorname{Im}(i \cdot e^{i\pi/4}) = \sqrt{2}.$$

L'angle entre $1+i$ et -1 est égal à $\pi/4$.

L'angle entre $1-i$ et i est égal à $3\pi/2$.

5. Geometry

5.1. True

Un losange qui n'est pas un carré ne possède pas de cercle circonscrit.

Dans un triangle équilatéral, l'ellipse tangente au milieu des côtés est un cercle.

La rotation d'une droite autour d'un axe non-parallèle engendre un cône.

Les points dont la somme des distances à deux points est constante forment une ellipse.

Un triangle équilatéral se divise en deux triangles rectangles.

La section d'un cône par un plan parallèle à l'axe du cône est une hyperbole

5.2. False

L'intersection d'une sphère et d'un plan est toujours un point.

On peut paver un hexagone régulier par 4 triangles équilatéraux.

Il existe exactement 3 patrons différents pour un cube.

La révolution d'un cercle autour d'une droite engendre un hyperboloïde.

La section d'un cylindre par un plan est toujours une droite.

Les points équidistants d'un cercle et d'un point extérieur au cercle forment une droite.

6. Non-math

6.1. True

Le pointillisme est un style qui utilise des traits de pinceau visibles.

Une acropole est une citadelle construite sur les hauteurs d'une cité grecque antique.

Le blues est un genre musical dérivé des chants de travail des esclaves noirs.

Le vibrato est une modulation périodique du son d'une note de musique.

La pantomime est fondée sur l'attitude et le geste, sans recours à la parole.

Un texte burlesque est caractérisé par l'emploi de termes familiers voire vulgaires.

6.2. False

La Nouvelle Vague est un mouvement du cinéma des années 2000.

L'Oulipo est un genre musical qui date de la Renaissance.

Un roman épistolaire est un récit qu'une personne fait de sa propre existence.

Le rock'n'roll est un genre musical caractérisé par un tempo lent.

Un Harpagon est une personne caractérisée par sa bienveillance.

Une vanité est un type de nature morte qui évoque la beauté de la nature.

Annex 2 : list of statements used in experiment 2

		Math	Nonmath
Declarative	True	<p>La fonction sinus est périodique.</p> <p>L'ensemble \mathbb{R} est un corps.</p> <p>L'ensemble des entiers est dénombrable.</p> <p>Les relations d'équivalence sont symétriques.</p> <p>Les parties compactes sont fermées.</p> <p>Les cercles sont des ellipses.</p>	<p>Le fruit du figuier est sucré.</p> <p>La montagne Pelée est un volcan.</p> <p>La grotte de Lascaux est préhistorique.</p> <p>Les épines des cactus sont douloureuses.</p> <p>Les bus londoniens sont rouges.</p> <p>Les babouins sont des primates.</p>
	False	<p>La fonction logarithme est définie sur tout \mathbb{R}.</p> <p>Le nombre d'or est un entier.</p> <p>La somme des $\frac{1}{n}$ est convergente.</p> <p>Les fonctions en escalier sont continues.</p> <p>Les rotations de l'espace sont commutatives.</p> <p>Les ensembles discrets sont connexes.</p>	<p>Le fruit du fraisier est récolté en hiver.</p> <p>La noix de coco est une épice.</p> <p>L'eau des lagons est jaune.</p> <p>Les fables de La Fontaine sont post-modernes.</p> <p>Les fruits de la passion sont salés.</p> <p>Les bois fossiles sont flexibles.</p>
Quantifiers	True	<p>True :</p> <p>Certaines quadriques sont des cônes.</p> <p>Certains nombres réels sont des fractions.</p> <p>Certaines médianes sont des bissectrices.</p> <p>Certaines matrices sont diagonalisables.</p> <p>Certains polynômes sont quadratiques.</p> <p>Certains polygones sont convexes.</p>	<p>True :</p> <p>Certains mammifères sont des cétacés.</p> <p>Certains récits antiques sont des épopées.</p> <p>Certains courants marins sont chauds.</p> <p>Certains romans sont autobiographiques.</p> <p>Certains volcans sont explosifs.</p> <p>Certains reptiles sont insectivores.</p>

	False	<p>Certains pentagones sont des rectangles.</p> <p>Certains plans sont de courbure positive.</p> <p>Certaines fonctions affines sont hyperboliques.</p> <p>Certains nombres rationnels sont transcendants.</p> <p>Certains hyperboloïdes sont bornés.</p> <p>Certains triangles sont des parallélogrammes.</p>	<p>Certains scarabées sont des crustacés.</p> <p>Certains rosiers sont des plantes bulbeuses.</p> <p>Certains éléphants sont des félins.</p> <p>Certaines îles tropicales sont glaciales.</p> <p>Certains écureuils sont carnivores.</p> <p>Certains chiens sont des rongeurs.</p>
Negation	True	<p>La fonction cosinus n'est pas monotone.</p> <p>Le nombre π n'est pas rationnel.</p> <p>La fonction exponentielle n'est pas constante.</p> <p>Les fonctions quadratiques ne sont pas bijectives.</p> <p>Les carrés ne sont pas des coniques.</p> <p>Les hyperboloïdes ne sont pas connexes.</p>	<p>Le bois mouillé n'est pas inflammable.</p> <p>La mer Baltique n'est pas chaude.</p> <p>La forêt amazonienne n'est pas désertique.</p> <p>Le lapin de garenne n'est pas agressif.</p> <p>Les grenouilles ne sont pas des insectes.</p> <p>Les algues vertes ne sont pas des plantes.</p>
	False	<p>Le nombre i n'est pas imaginaire pur.</p> <p>L'ensemble des translations n'est pas un groupe.</p> <p>Le groupe des translations n'est pas commutatif.</p> <p>Les tangentes ne sont pas des droites.</p> <p>Les suites convergentes ne sont pas bornées.</p> <p>Le bord d'un fermé n'est pas vide.</p>	<p>La fleur d'oranger n'est pas parfumée.</p> <p>Le système républicain n'est pas une démocratie.</p> <p>L'atome d'uranium n'est pas radioactif.</p> <p>Les tigres ne sont pas carnivores.</p> <p>Les cigognes ne sont pas des échassiers.</p> <p>Le vin rouge n'est pas alcoolisé.</p>

Quantifier + negation	True	<p>Certaines fonctions ne sont pas dérivables.</p> <p>Certains nombres entiers ne sont pas premiers.</p> <p>Certaines matrices ne sont pas inversibles.</p> <p>Certaines fonctions ne sont pas mesurables.</p> <p>Certains ensembles infinis ne sont pas dénombrables.</p> <p>Certaines suites géométriques ne sont pas divergentes.</p>	<p>Certaines plantes ne sont pas grasses.</p> <p>Certains légumes verts ne sont pas bons à manger.</p> <p>Certains romans ne sont pas publiés.</p> <p>Certains fruits ne sont pas comestibles.</p> <p>Certains contes philosophiques ne sont pas enfantins.</p> <p>Certaines plantes vertes ne sont pas grimpantes.</p>
	False	<p>Certains losanges ne sont pas des quadrilatères.</p> <p>Certaines fonctions dérivables ne sont pas continues.</p> <p>Certaines relations d'ordre ne sont pas transitives.</p> <p>Certaines boules ne sont pas convexes.</p> <p>Certaines séries de Fourier ne sont pas périodiques.</p> <p>Certaines fonctions bijectives ne sont pas injectives.</p>	<p>Certains pingouins ne sont pas des oiseaux.</p> <p>Certains poissons de rivière ne sont pas vertébrés.</p> <p>Certains nénuphars ne sont pas des plantes aquatiques.</p> <p>Certains ruminants ne sont pas herbivores.</p> <p>Certains fruits exotiques ne sont pas sucrés.</p> <p>Certains volcans d'Auvergne ne sont pas éteints.</p>

Chapter 3. On the role of visual experience in mathematical development: Evidence from blind mathematicians

1. Introduction to the article

In the first chapter, we have seen that mathematical statements imageability correlates with activation in left intra-occipital sulcus and in left infero-temporal gyrus. In the second chapter, we have observed that problems related to trigonometry and complex numbers, that required visualization, elicited additional activation in occipital cortex, along the calcarine sulcus. These results support the idea that visual processing may underpin mathematical reflection.

In the present chapter, we assess the role of visual experience in the development of brain circuits involved in mathematical processing, thanks to the exceptional participation of three blind professional mathematicians to a fMRI study that took up the paradigms used in previous chapters.

2. Abstract

Advanced mathematical reasoning, regardless of domain or difficulty, activates a reproducible set of bilateral brain areas including intraparietal, inferior temporal and dorsal prefrontal cortex. The respective roles of genetics, experience and education in the development of this math-responsive network, however, remain unresolved. Here, we investigate the role of visual experience by studying the exceptional case of three professional mathematicians who were blind from birth ($n=1$) or became blind during childhood ($n=2$). Subjects were scanned with fMRI while they judged the truth value of spoken mathematical and nonmathematical statements. Blind mathematicians activated the classical network of math-related areas during mathematical reflection, similar to that found in a group of sighted professional mathematicians. Thus, brain networks for advanced mathematical reasoning can develop in the absence of visual experience. Additional activations were found in occipital cortex, even in late blind individuals, suggesting that either mental imagery or a more radical repurposing of visual cortex may occur in blind mathematicians.

3. Introduction

Humans exhibit a unique ability for advanced mathematical thought. This ability seems to be rooted in evolutionarily ancient non-verbal systems for numbers and geometry that all humans

possess from birth and share with other animal species. Indeed, human adults with or without full access to education, young infants, and a variety of non-human animal species all share a capacity to estimate numerosity from visual or auditory sets and to perform arithmetical operations over these quantities (Feigenson et al., 2004; Gilmore et al., 2010, 2007; Izard et al., 2009; Pica et al., 2004). Similarly, they are endowed with basic geometrical skills (Dehaene et al., 2006; Lee and Spelke, 2008; Spelke and Lee, 2012). Recent work has suggested that formal mathematics builds upon this core set of non-verbal proto-mathematical abilities. Behaviorally, some studies have revealed a correlation between the accuracy of the primitive approximate number system and math achievement at schools (Feigenson et al., 2013; Halberda et al., 2008; Libertus, 2015; Piazza et al., 2013; Starr, 2015). In geometry, it has been suggested that non-symbolic knowledge of geometry predicts the ability to use symbolic geometrical cues in 4-year-old children (Dillon et al., 2013). Furthermore, neuroimaging studies of advanced mathematical reflection (Amalric and Dehaene, 2016; Monti et al., 2012) and deductive inference (Monti et al., 2007) have revealed that the neural substrate for advanced formal mathematics strongly overlaps regions involved in basic numerical and spatial abilities (Daitch et al., 2016; Husain and Nachev, 2007; Nieder and Dehaene, 2009; Shum et al., 2013).

However, the mechanisms by which formal mathematics emerges from proto-mathematical systems for numbers and space remain unknown. A possibility is that mathematical representations are rooted in visuospatial thinking and develop through visual experience. This hypothesis transpires in many mathematicians' introspective reports on their invention processes. For instance, Albert Einstein wrote to fellow mathematician Jacques Hadamard that "[t]he psychological 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" (Hadamard, 1945). Support for this "visual" hypothesis can be found in several recent findings. In (Stoianov and Zorzi, 2012), a deep learning network trained with visual arrays containing different numbers of objects spontaneously developed representations of numerosity similar to those identified in monkeys (Nieder, 2005). Some studies also suggest that numerosity is an early visual feature whose extraction is grounded, at least in part, on a form of texture perception (Burr and Ross, 2008; Morgan et al., 2014). At a more abstract level, it has been suggested that the perception of specific features in our environment, such as symmetries or angles, shapes our basic understanding of geometry (Giaquinto, 2005; Howe and Purves, 2005). Visual processing has also proven to be relevant to mathematical problem solving, especially in the domain of algebra where the covert "movements" involved in resolving equations were found to interact with actual motion (Goldstone et al., 2010; Landy et al., 2008).

Neuroimaging studies of mathematical processing are also compatible with the hypothesis of a visual support. In fact, the brain regions involved in mathematical reflection, regardless of domain (arithmetic, analysis, algebra, topology or geometry) or problem difficulty (Amalric and Dehaene, 2016; Dehaene et al., 2003; Monti et al., 2012), include the bilateral intraparietal sulci (IPS) and bilateral infero-temporal regions. The latter are located just lateral to the ventral visual pathway and overlap with the recently discovered “Visual number form areas” (VNFA) (Shum et al., 2013) that systematically activate to the visual presentation of Arabic numerals. Moreover, in (Amalric and Dehaene, 2016), during mathematical reflection, participants’ ratings of imageability of highly-advanced mathematical statements correlated with brain activity in a left occipito-temporal region close to the VNFA. As for the parietal lobe, it is known to be involved in visually guided eye and hand movements, but is also activated conjointly with frontal eye fields during mental arithmetical problems (Knops et al., 2009). It also intervenes in mental rotation (Culham and Kanwisher, 2001; O’Boyle et al., 2005).

One major issue for a visual origin of mathematical abilities, however, lies in the fact that mathematical knowledge also develops in the blind (Landau et al., 1981; Abboud et al., 2015; Kanjlia et al., 2016). The so-called “visual” number form area may, in fact, be activated in congenitally blind subjects when numerals are presented auditorily via visual-to-auditory sensory substitution (Abboud et al., 2015). Blind subjects may even become professional mathematicians, although this is much less documented scientifically (Jackson, 2002). There are actually many examples of famous blind mathematicians in the history of mathematics, such as Leonhard Euler who was blind during the two last decades of his life, or Nicholas Saunderson who went blind in his first year and yet became the Lucasian professor of Mathematics at Cambridge University. In fact, blind mathematicians can be top-of-the-class geometers, like the French mathematician Bernard Morin who first constructed a sphere eversion, topologists such as the famous Russian mathematician Pontryagin, or analysts like the American mathematician Lawrence Baggett.

Two alternative hypotheses may account for the existence of talented blind mathematicians. The first one assumes that blind mathematicians learn mathematics by compensating through other modalities. In this case, the same behavioral outcome – high-level mathematics – would arise from very different cerebral substrates (e.g. areas involved in auditory or tactile processing). The second hypothesis assumes that mathematical activity is in fact based on highly abstract representations which are amodal rather than primarily visual. Several findings indeed suggest that the mental representation of numbers consists of highly abstract entities that can be accessed indifferently from visual, auditory or tactile input (Piazza et al., 2006; Riggs et al., 2006; Tokita et al., 2013). There is also evidence of integration of numerical information presented in two different modalities in newborns

(Izard et al., 2009), in 6-month old infants (Feigenson, 2011), in children (Barth et al., 2005), in human adults (Barth et al., 2003) and in monkeys (Jordan et al., 2008, 2005).

Recently, Kanjlia et al. (2016) used fMRI to investigate the brain mechanisms of mental arithmetic in the blind. Congenitally blind adults were asked to decide whether two equations (e.g. $7 - 2 = x$; $6 - 1 = x$) had the same result. The results indicated that (1) they performed similarly to blindfolded sighted participants and (2) they activated a classical bilateral fronto-parietal network, very similar to what was observed in sighted subjects, the only difference being an additional activity in occipital cortex. These findings show that numerical thinking can develop in the absence of visual experience and is rooted in typical number-related brain circuits, therefore lending support to our second hypothesis.

Many mathematicians, however, argue that simple numerical knowledge may not be representative of the broader field of mathematics, which encompasses domains such as geometry or topology which might conceivably depend on visual experience. Here, we intended to bring some light to bear on this topic through neuroimaging studies of advanced mathematical concepts (rather than the basic arithmetic studied by Kanjlia et al., 2016) in three exceptional cases of blind professional mathematicians. Those subjects accepted to participate in two fMRI experiments similar to our prior work (Amalric and Dehaene, 2016). During fMRI, they were asked to quickly evaluate the truth value of various auditory mathematical and nonmathematical statements with high-level content.

Note that, although our fMRI images were acquired in adults and therefore reflected the end point of a long developmental process, they should still be informative on the role of visual experience in mathematical development. This is because, amongst our three participants, one was blind from birth and all had become blind before the age of 11, and therefore acquired high-level mathematical concepts in the absence of visual experience. If visual experience plays a dominant role in shaping cerebral representations of advanced mathematical concepts, then different brain regions should activate in the blind compared to sighted mathematicians. In this case, even the two blind mathematicians who have developed basic mathematical knowledge while they could still see may recruit different brain regions for advanced mathematical concepts. On the contrary, if mathematical representations develop independently of visual experience, then the same brain regions should activate during mathematical reflection irrespective of blindness. Finally, if occipital cortex can be recycled (Dehaene and Cohen, 2007) or re-used in blind subjects, as previously observed for instance by Kanjlia et al. (2016) for arithmetic and by (Bedny et al., 2011) for language processing, then we might expect an additional activation of occipital cortex in blind subjects.

4. Methods

4.1. Participants

Three blind mathematicians and 20 sighted mathematicians participated in this study. The latter were all professional mathematicians, i.e. full-time researchers and/or professors in mathematics. For more details regarding the subjects who participated in the first experiment ($n=15$), see (Amalric and Dehaene, 2016). The second experiment ($n=14$) comprised 5 subjects who already participated in experiment 1 and 9 new subjects with equivalent academic background. All experiments were approved by the regional ethical committee for biomedical research, and subjects gave informed consent after they read or heard (in case of the blind) consent information.

4.2. Description of the blind participants

Subject A, a 46-year-old male, progressively became blind over a period extending from 3 to 10 years of age, because of optic nerve damage arising from a neurological impairment that also caused facial hemiplegia. He nevertheless followed regular schooling and exhibited precocious mathematical skills. Notably, he explained that mathematical Braille was not well adapted to mathematical lessons in high school, so that he had to do mathematics only mentally. He is now teaching arithmetic and geometry in a top-ranking French university. Surprisingly perhaps, he declared having strong number-color synesthesia to this present day.

Subject B, a 54-year-old male, became blind at the age of 11 as a combined result of glaucoma and Marfan syndrome, a genetic disorder of connective tissue that commonly affects the eyes by inducing lens dislocation. He is a prominent mathematician, essentially known for a major breakthrough in the domain of contact geometry. Like subject A, subject B reported a vivid number-color synesthesia.

Subject C, a 36-year-old male, is congenitally blind due to bilateral anophthalmia. He followed typical university training in mathematics and computer sciences, and defended a PhD thesis on Lambda calculus. He now works as a research engineer in a French computer science laboratory.

4.3. Experiment 1

Participants were presented, in semi-random order, with spoken mathematical statements that belonged to analysis, algebra, topology and geometry, and to non-mathematical statements. Within each category, 6 statements were true, 6 were false, and 6 were meaningless. All meaningful statements bore upon non-trivial facts which required logical reflection. Immediately after fMRI, a paper questionnaire allowed to reexamine all statements in the same order. For each of them, participants were asked to rate, on a scale from 0 to 7, several subjective features such as their

confidence in their answer or the “imageability” of the statements. Blind participants were read each question by the experimenter and responded orally.

4.4. Experiment 2

Participants were exposed to a simpler set of spoken mathematical and non-mathematical statements than in experiment 1. Each statement was either true or false. One category of mathematical statements consisting in canonical algebraic identities and trigonometric formulae was likely to be known by heart. Another category consisted in algebraic equations. The three remaining categories (trigonometry, complex numbers, and geometry) required to visualize a simple mathematical fact concerning the trigonometric circle, the complex plane, or geometrical shapes. Finally, non-mathematical statements were declarative facts about music, painting, literature or movies. Series of pure tone beeps with the same average duration as the statements were also presented as a control for the presence of auditory activation. When the last beep had a higher pitch than the others, subjects were asked to respond “true”, and “false” otherwise. This experiment was divided into 7 runs of 12 statements each, including at least one exemplar of each sub-category.

All statements were recorded using Audacity by a female native French speaker who was familiar with mathematical concepts. Within each experiment, statements from the different categories were matched in syntactic construction, number of syllables and duration.

4.5. Procedure

In both experiments, the only display on screen was a fixation cross on a black background, which sighted participants had to fixate continuously. Each trial started with a beep and a color change of the fixation cross (which turned to red), announcing the onset of the statement. In experiment 1, participants were given a fixed reflection period of 4 seconds following auditory presentation. In experiment 2, they were asked to answer as quickly as they could. In the latter case, a maximum of 2.5 seconds was left for the reflection and the response. In both experiments, the response period started and ended with a beep, and was signaled by the fixation cross turning to green. In experiment 1, subjects gave their evaluation of the sentence (true, false, or meaningless) by pressing one of three corresponding buttons held in the right hand. In experiment 2, they pressed the button held in the right hand for true, and held in the left hand for false. Each trial ended with a 7-second resting period (figure 3.1).

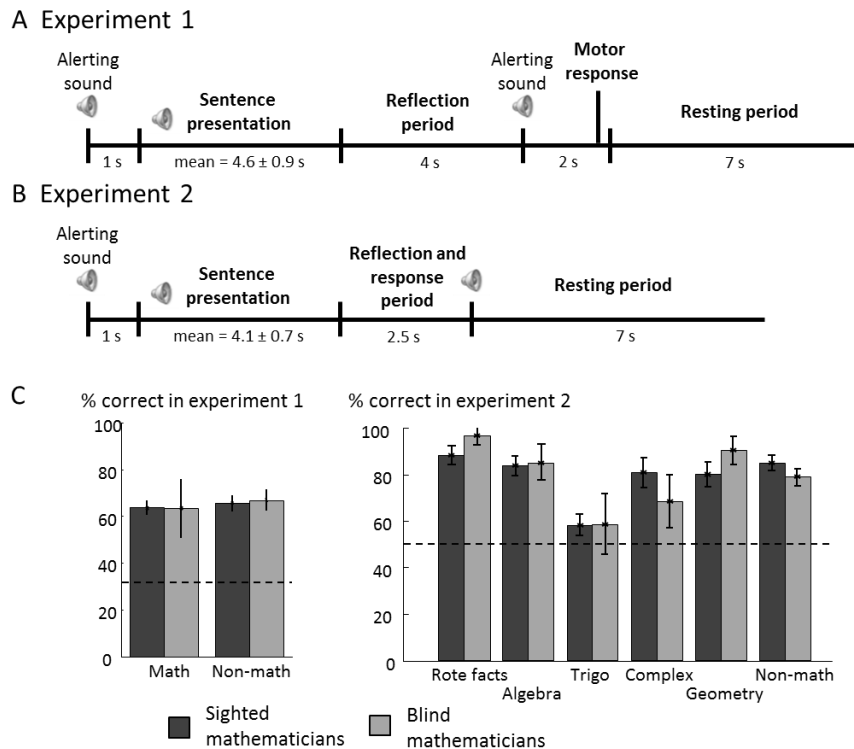


Figure 3.1. Experimental paradigms and behavioral results. (A) In experiment 1, auditory math and nonmath statements were announced by a beep and followed by a 4s reflection period. Another beep announced the 2s response period during which subjects were asked to press one of three buttons placed in right hand to indicate whether they judged the statement as true, false, or meaningless. A resting period of 7s ended each trial. (B) Experiment 2 was similar to experiment 1 except that math and nonmath statements were simpler so that subjects were asked for a speeded response during a single 2.5s period ending with a beep. (C) The two bar plots represent the percentage of correct responses in experiments 1 and 2 (bars = one standard error of the mean). On average, sighted and blind mathematicians performed virtually identically. Dashed lines represent the chance level (33.3% in experiment 1, 50% in experiment 2).

4.6. fMRI data acquisition and analysis

We used two 3-Tesla whole body systems (Siemens Trio and Prisma) with high-resolution multiband imaging sequences developed by the Center for Magnetic Resonance Research (CMRR) (Xu et al., 2013) (multiband factor = 4, Grappa factor = 2, 80 interleaved axial slices, 1.5 mm thickness and 1.5 mm isotropic in-plane resolution, matrix = 128x128, TR = 1500 ms, TE = 32 ms). For sighted mathematicians, a 32 channel head-coil was used for experiment 1 and a 64 channel head-coil for experiment 2. All three blind mathematicians were scanned with a 32 channel head-coil.

Using SPM8 software, functional images were first corrected for slice timing, realigned, normalized to the standard MNI brain space, and spatially smoothed with an isotropic Gaussian filter of 2 mm FWHM. A two-level analysis was then implemented in SPM8. For each participant, fMRI images were high-pass filtered at 128s. Then, time series from experiment 1 and experiment 2 were modelled separately. For experiment 1, two regressors were defined for each sentence, one capturing the activation to the sentence itself (kernel = sentence duration) and the other capturing

the activation during reflection (kernel = reflection duration). For experiment 2, time series was modelled using a single regressor per statement, with a kernel corresponding to statement presentation plus the mean reaction time for that subject. We then defined subject-specific contrasts by comparing the activation evoked by two subsets of sentences during the reflection period. We also used subjective imageability ratings of math statements to compute a normalized and centered SPM contrast. Regressors of non-interest included the six movement parameters for each run. Within each auditory run, additional regressors of non-interest were added to model activation to the alert signals and to the button presses.

For the second-level group analysis, individual contrast images for each of the experimental conditions relative to rest were smoothed with an isotropic Gaussian filter of 5 mm FWHM, and entered into a second-level whole-brain ANOVA with stimulus category as within-subject factor. All brain activation results are reported with a clusterwise threshold of $p < 0.05$ corrected for multiple comparisons across the whole brain, using an uncorrected voxelwise threshold of $p < 0.001$. Individual and averaged time courses of activation were plotted after averaging over spheres of 6 mm centered on the principal peaks of activation observed in the contrast of math versus nonmath statements when pooling across both experiments.

5. Results

5.1. Experiment 1: advanced mathematical statements

In a first experiment, participants were presented with the difficult mathematical and nonmathematical statements used in (Amalric and Dehaene, 2016) and had to judge whether they were true, false or meaningless. After fMRI, they were presented again with all statements and were asked to give ratings about various aspects of these statements, including their “imageability” (see Amalric and Dehaene, 2016, for a full description of the Methods). Within the group of sighted mathematicians, we had previously found that bilateral intraparietal sulci (IPS), bilateral inferior temporal regions (IT), and bilateral sites in dorsolateral, superior and mesial prefrontal cortex (PFC) showed greater activation to meaningful math than to meaningful nonmath judgements during the reflection period, regardless of the mathematical domain or the perceived difficulty (figure 3.2A, for more details, see (Amalric and Dehaene, 2016)).

Behaviorally, an ANOVA with group and problem type as factors revealed no significant main effect of group ($F(1,16) = 0.005$, $p = 0.95$) or math domain ($F(3,48) = 0.93$, $p = 0.43$), nor a group by domain interaction ($F(3,48) = 2.65$, $p = 0.059$). Subject A answered correctly to 66.7% of the math statements and 62.5% of the nonmath statements, which is very similar to the group of sighted mathematicians (math: 63%, nonmath: 65%). Subject B responded correctly to 78.6% of math

statements and 73.3% of nonmath statements, which is slightly but not significantly above the average of our previous group of 15 sighted professional mathematicians. Subject C found experiment 1 challenging: he succeeded only with 44.4% of math statements, compared to 64.3% of nonmath statements.

For subject A, examination of the contrast of meaningful math versus meaningful nonmath during the reflection period revealed activation in bilateral IPS, IT, mesial and inferior PFC (figure 3.2C, table S1). The time course of activation in representative areas of this math-responsive network showed that the fMRI signal increased for all four domains of math, while nonmath statements induced a slow deactivation (figure 3.2F). Additional activation was observed in bilateral occipital cortex (figures 3.2C, 4, table S1). Virtually the same activation was observed when comparing meaningful versus meaningless mathematical statements. Subject A's average imageability rating equaled 42.7% for math statements and 10.3% for nonmath statements. This imageability rating correlated with activation in bilateral middle frontal gyri (BA6), occipital cortex along the calcarine sulci and more dorsal occipital sites, and at several parietal foci (table S3).

For subject B, math reflection induced more activation than nonmath reflection in several bilateral parietal, occipito-parietal and occipital sites, in bilateral IT regions, as well as in bilateral prefrontal foci (figure 3.2D, table S1). Again, similar activation was observed when examining the contrast of meaningful versus meaningless math judgments. Global imageability rating equaled 29.2% for math statements, and 13.5% for nonmath statements. Imageability rating for math statements correlated with activation in bilateral occipital cortices, including at the junction with the precuneus, and bilateral superior frontal sulci (table S3).

Despite subject C's difficulties with math problems, there was small but significant activation elicited by mathematical reflection more than nonmathematical reflection in a few bilateral occipito-parietal and occipital foci, in right IPS and right MFG (figure 3.2E, table S1). Subject C reported no mental imagery in this experiment, therefore preventing us from studying the correlation of imageability with brain activation.

These results suggest that activations observed in each individual blind mathematician and in the group of sighted mathematicians were similar apart from an occasional additional activation in occipital cortex. This conclusion was confirmed by a group analysis comparing 15 sighted versus 3 blind mathematicians. The main effect of math > nonmath in the blind again revealed a parieto-occipital network, plus bilateral activation in inferior temporal regions (figure 3.2B). There was a

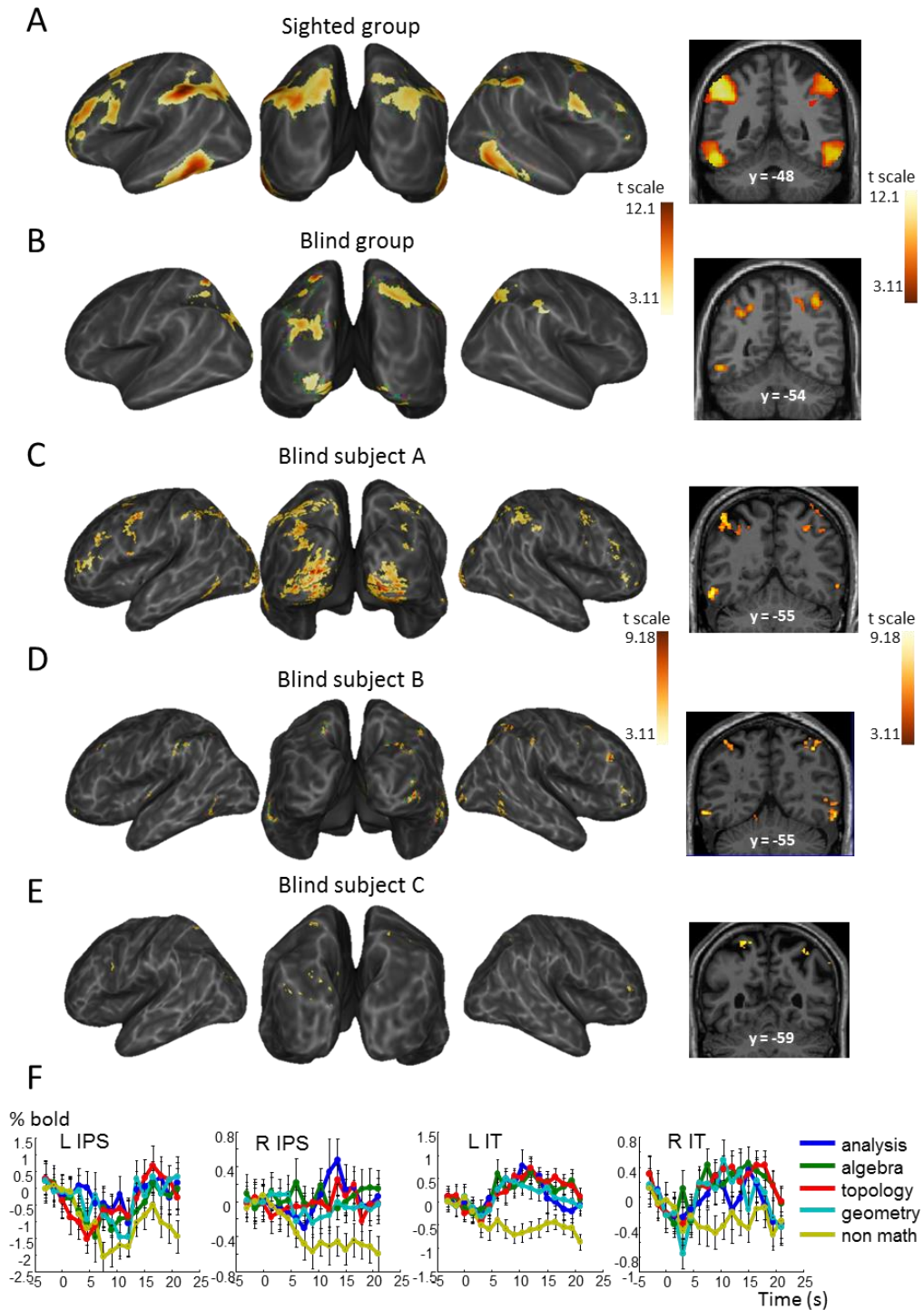


Figure 3.2. Math-responsive network in blind and sighted mathematicians in experiment 1. Whole-brain inflated maps and coronal slice showing the contrast of meaningful math versus meaningful nonmath reflection in 15 sighted mathematicians (A), 3 blind mathematicians (B), and each blind subject individually (C-E). Contrast maps are display at $p_{unc} < 0.001$ uncorrected at the voxel level, and $p_{FDR} < 0.05$ corrected for multiple comparisons at the cluster level. (F) Average time course of the fMRI signal in subjects A, B and C in representative areas of activation: bilateral intraparietal sulci (IPS) and inferior temporal (IT) regions. Note: explore these data yourself at http://www.unicog.org/webdemo/Amalric_oct2016/

significant intersection of the math > nonmath networks in sighted and blind mathematicians in bilateral intraparietal sulci and inferior temporal cortices. The interaction with group, searching for

greater activation to mathematics in blind than in sighted mathematicians (Blind > Sighted x math > nonmath), revealed activation exclusively in left occipital cortex (figure 3.4). A symmetrical activation was seen in the right hemisphere when relaxing the cluster-wise threshold ($p < 0.05$ uncorrected). Examination of fMRI signal for subject A revealed that even if both math and nonmath reflection activated those occipital regions, activation remained transient for nonmath statements (figure 3.4).

5.2. Experiment 2. Simpler mathematical facts

We sought to replicate those results in a second experiment focusing on simpler mathematics. Statements were either true or false and consisted in well-known mathematical facts such as classical algebraic identities (e.g. “ $(a+b)^2$ equals a^2+b^2+2ab ”) or trigonometric formulae (“ $\cos(a+b)$ equals $\cos(a)\cos(b)-\sin(a)\sin(b)$ ”), algebraic equations (“ $(z-1)^2$ equals $z^2 - 2z + 1$ ”), trigonometric equations (“ $\sin(x+\pi)$ equals $-\sin(x)$ ”), complex number properties (“the angle between i and $1+i$ equals $\pi/4$ ”), and non-metric Euclidean geometry (“Any equilateral triangle can be divided into two right triangles”). These were compared to declarative nonmathematical facts about art (“Pantomime relies on attitude and gesture, without speaking”). Auditory controls consisting of series of beeps were also presented.

Overall performance for math statements reached 78.6% correct in both groups of sighted and blind mathematicians, thus confirming that the statements were simpler than in experiment 1. For example, ~90% of classical algebraic identities (called rote facts in figure 3.1) were correctly classified, as were ~84% of algebraic equations. Trigonometric formulae were the most difficult, with an average performance of 58.1% correct. Complex number properties were quite easy for sighted mathematicians (80.6%), and subjects A and B (75% and 80%), but appeared to be harder for subject C (50%). If anything, geometrical statements were responded slightly better by blind mathematicians (respective correct rates: 100%, 87.5% and 83.3%) than by sighted mathematicians (79.9 %). Overall, however, an ANOVA with group and problem type as factors revealed no significant main effect of group ($F(1,15) = 0.07$, $p = 0.80$) nor a group by type interaction ($F(4,60) = 1.46$, $p = 0.23$).

In fMRI, within the group of sighted mathematicians, extensive activations were again elicited by math more than by nonmath statements in bilateral IPS, bilateral IT regions, bilateral superior, and middle frontal regions (Brodmann areas 9 and 46) (figure 3.3A, table S2). These results, which will be detailed in another publication, indicate that the classical mathematical network is highly reproducible even when simple and well-known mathematical facts are used.

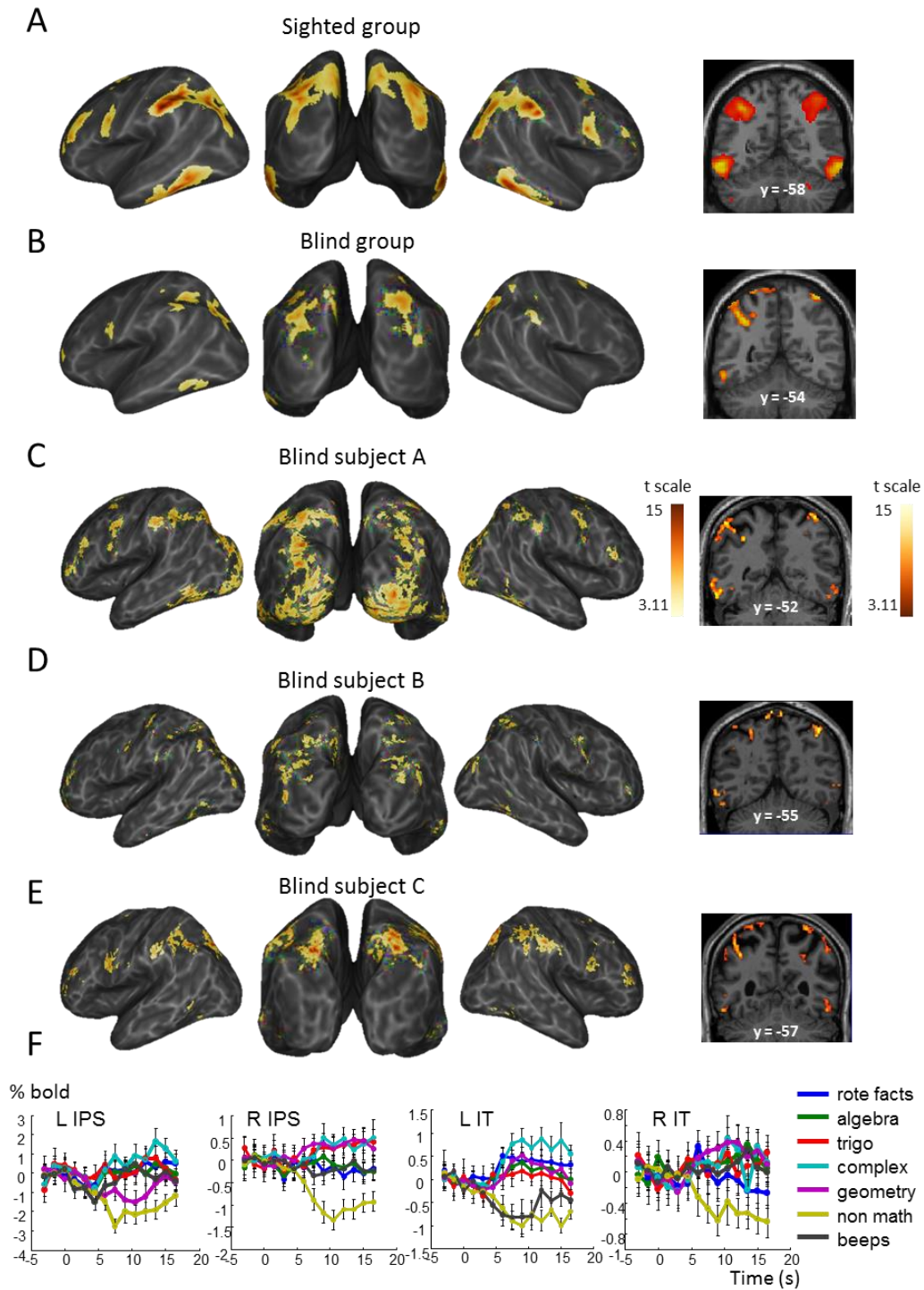


Figure 3.3. Math-responsive network in blind and sighted mathematicians in experiment 2. Same format as figure 3.2.

In blind subject A, the contrast of math versus nonmath statements again revealed activation in bilateral IPS and bilateral IT and bilateral MFG (BA 9), plus activation in a left occipito-parietal region and bilateral lateral occipital foci (figure 3.3C, table S2). Examination of the time course of activation in bilateral IPS and IT also revealed a sharp and sustained activation for all categories of math, a slow deactivation for declarative nonmath facts, and no activation for auditory control beeps (figure 3.3F).

For subject B, the same contrast revealed activation in various bilateral parietal and occipital sites, bilateral IT regions, and some bilateral middle prefrontal foci (figure 3.3D, table S2).

For subject C, math statements, relative to nonmath statements, elicited more activation in bilateral IPS, IT, MFG (BA 9 and BA46), plus one occipital focus near the calcarine sulcus (figure 3.3E, table S2). Examination of the time course of activation in bilateral IPS and IT also revealed a sharp and sustained activation for all categories of math, a slow deactivation for declarative nonmath facts, and no activation for auditory control beeps. We note here that, while complex statements from experiment 1 did not elicit any mental imagery in subject C, he informally reported vivid mental imagery for trigonometry, complex numbers and geometrical statements in this experiment.

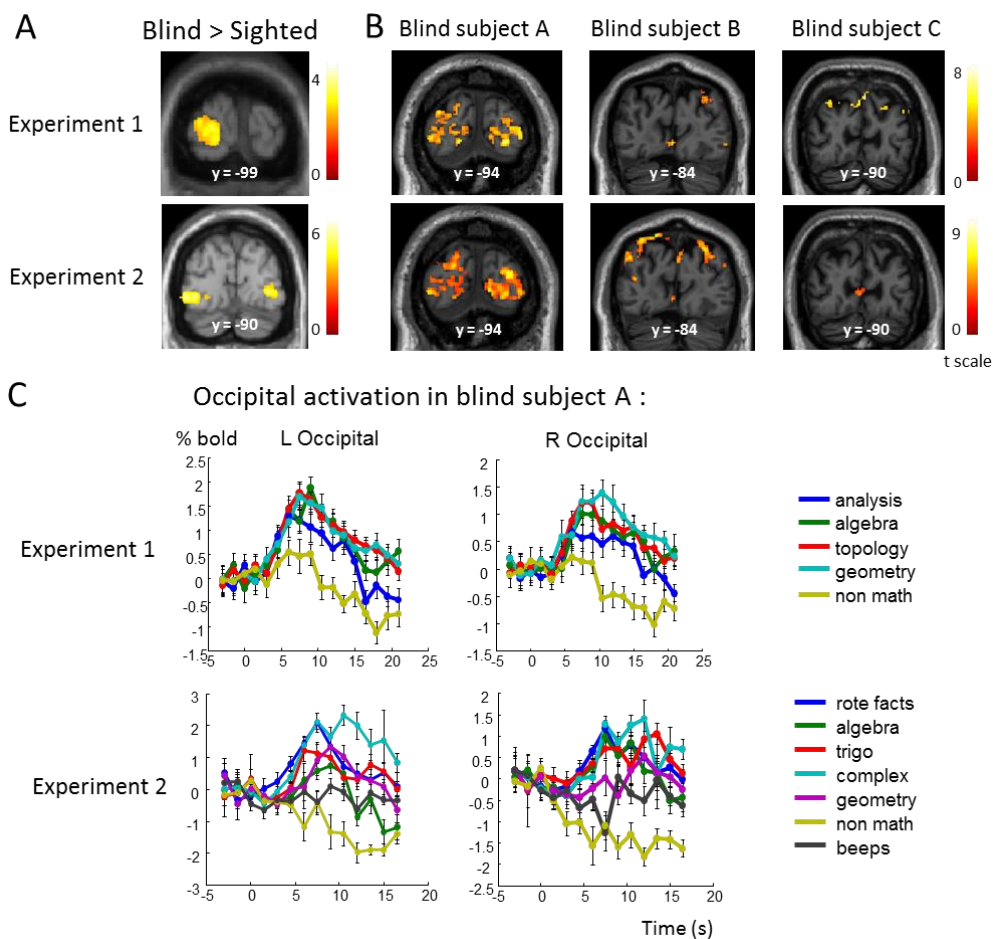


Figure 3.4. Additional occipital activation elicited by math in blind mathematicians. (A) Occipital coronal slices showing the interaction of group (Blind>Sighted) and statement type (math>non-math) in experiment 1 (top panel) and experiment 2 (bottom panel). (B) Occipital coronal slices show the activation elicited by math>nonmath in each blind subject and each experiment. (C) Temporal profile of activation in left and right occipital cortices in subject A in each experiment.

At the group level, pooling over our three blind mathematicians, math versus nonmath problems elicited activation in bilateral IPS, occipito-parietal junction, left IT regions and left MFG (figure 3.3B). There was again a significant intersection of the math > nonmath networks in sighted and blind mathematicians in bilateral intraparietal sulci, left inferior temporal cortex and MFG (BA9).

The only group difference between blind and sighted mathematicians during the resolution of math problems more than during the resolution of nonmath problems, was located in two bilateral occipital regions located close to but slightly anterior and inferior to the left occipital region identified in experiment 1 (figure 3.4). Examination of the fMRI signal over time in these regions revealed a profile of activation similar to the one observed in the rest of the math-responsive network: a fast activation for all types of math problems and no activation or even a slow deactivation for nonmath problems and the auditory control condition.

6. Discussion

In two high-resolution fMRI experiments contrasting math versus nonmath reflection, we observed in blind mathematicians a consistent and systematic activation of the math-responsive network that we had previously identified in sighted professional mathematicians (Amalric and Dehaene, 2016). Indeed, bilateral intraparietal, inferior temporal and dorsal prefrontal sites were activated in both experiments in the group of sighted mathematicians as well as in each individual blind mathematician. The only exception was in experiment 1 for subject C who exhibited very little activation. This negative finding may be due to the fact that subject C received less math training than the others and found experiment 1 harder. In experiment 2, however, subject C exhibited activations to simpler math statements in a set of areas that were very similar to the network exhibited in the sighted group and in subjects A and B.

Previous studies have shown that the parietal lobe, involved in mathematical skills, also houses a diversity of areas for visuospatial functions such as orienting of visual gaze and attention, visually guided hand movements, mental rotation of objects, or the maintenance of visuospatial information in working memory (Hubbard et al., 2005; Husain and Nachev, 2007; Simon et al., 2002). Similarly, inferior temporal activation during mathematical reflection has previously been linked to the recognition of visual Arabic numerals (Shum et al., 2013) and visually presented mathematical expressions (Amalric and Dehaene, 2016). Nevertheless, the present results, together with similar prior findings on number recognition and calculation in blind subjects (Abboud et al., 2015; Kanjlia et al., 2016) refute the hypothesis of a link between mathematical expertise and visual experience. Instead, they suggest that cortical representations of advanced mathematics, involving the IPS and inferior temporal regions as essential nodes, can develop independently of visual experience.

It may seem surprising that all blind participants exhibited activation in bilateral inferior temporal regions that have been described as the visual number form areas (VNFA), because these areas have been reported to be specifically responsive to written Arabic numerals (Shum et al., 2013). However, a similar activation was observed using sight-to-sound sensory substitution in

congenitally blind individuals trained to hear colored-shapes and asked to interpret the shapes I, V, and X as Roman numerals (Abboud et al., 2015). Our result thus supports the idea that the VNFA encodes mathematical symbols and concepts in an abstract way, regardless of any specific sensory modality. Indeed, we found that this area is also responsive to written mathematical formulas in professional mathematicians (Amalric and Dehaene, 2016). A recent intracranial study indicates that this region contains distinct but intermingled sites sensitive to Arabic numerals and to calculation itself (Daitch et al., 2016). Thus, the contribution of this region to mathematics appears to be much broader than its label suggests, and it is probably only because of difficulties in imaging this temporal region with fMRI that this region was not previously considered as a core region for number sense.

The behavioral performance of sighted and blind mathematicians did not provide any evidence that training via nonvisual modalities gives blind individuals any specific advantage or disadvantage in mathematical processing compared to sighted individuals. Indeed, unlike in (Castronovo and Seron, 2007b) where blind participants performed better in numerosity estimation than sighted subjects, blind individuals in our tasks did not judge the truth value of mathematical statements significantly better than sighted participants. However, we examined only the endpoint of mathematical training in adults, and our findings do not preclude the possibility that differences in mathematical skills and conceptual understanding would be observed during development.

Turning to brain-imaging results, a comparison of blind and sighted participants in our experiments revealed an additional activation in the occipital cortex of blind mathematicians while they were thinking about math problems. This finding is compatible with many recent observations that blindness does not lead to a lack of activity of “visual” cortex during tactile or auditory tasks (Bedny et al., 2011; Raz et al., 2005). In particular, a similar activation of occipital cortex has recently been observed during mental calculation (Kanjlia et al., 2016). To the best of our knowledge, however, this is the first time that occipital activation is observed in an activity as abstract and high-level as professional mathematics.

We note in passing that, in our study, the amount and location of occipital activation differed among the three blind mathematicians. While an extensive activation was seen in bilateral occipital cortex in subject A, who became blind between the age of 3 and 10, smaller clusters of activation in right occipital cortex and in the calcarine sulcus were observed in subject B (who became blind at the age of 11), and only very small but significant activation was seen in the calcarine sulcus in subject C (who was congenitally blind). The latter observation may seem surprising given that extensive occipital activation was found in congenitally blind adults performing mental arithmetic (Kanjlia et al., 2016). Our results do not agree either with studies showing greater occipital activation to auditory verbal tasks in early-blind than in late-blind people (Bedny et al., 2012; Burton, 2003). Note

however that all our participants became blind before ages that usually mark the limit between early and late blindness, i.e. 14 (Cohen et al., 1999; Wan et al., 2010) or 16 (Sadato et al., 2002). Some studies have also suggested that the visual cortex is recruited at a level that depends on performance (Amedi et al., 2008, 2003). However, again, this claim does not seem to apply to the present study, given that subject B performed slightly better than subject A but showed less activation in occipital cortex. It is important to note that the apparent contradiction between our results and previous studies does not necessarily question their findings, which were extracted from group analysis. Indeed, it would be bold to draw any conclusions regarding the causes of the observed differences in occipital activation in only three subjects whose individual histories differed massively in the onset and the cause of blindness (optic nerve damage, glaucoma, and anophthalmia).

How can we account for the additional occipital activation in blind participants compared to sighted subjects? We might first speculate that they entertained a form of mental imagery. Indeed, subject A, who exhibited the most extensive occipital activation, also reported a great amount of imageability during math in experiment 1. Furthermore, the two participants who were not congenitally blind reported number-color synesthesia. Subject C also reported that statements dealing with trigonometry or geometry elicited vivid mental imagery. Similar reports of mental imagery have already been discussed in blind individuals during mental rotation of objects (Arditi et al., 1988), drawing (Amedi et al., 2008), or Braille reading (Striem-Amit et al., 2012). There is nothing contradictory in the possibility that blind subjects develop sufficient intuitions of what vision is as to end up forming and manipulating mental images. Indeed, Denis Diderot, in his celebrated Letter on the Blind (1749), already noted how

“Saunderson was extremely successful as professor of mathematics at the University of Cambridge. He gave lessons in optics, he lectured on the nature of light and colors, he explained the theory of vision; he wrote on the properties of lenses, the phenomena of the rainbow, and many other subjects connected with sight and its organ.”

The mental imagery hypothesis, however, conflicts with the fact that occipital activations were absent in sighted participants, even though they too reported high levels of imageability. Since the amount of occipital activation varied across blind participants, even though they all performed similarly in experiment 2, one may doubt the necessity of mental imagery for mathematical processing. Indeed, the mathematical concepts that we studied here are likely to be encoded in an abstract manner, thus allowing blind individuals to manipulate them through nonvisual representations. According to this view, vision could simply be the preferred or the most “advantageous” (Poincaré, 1902) modality by which to convey mathematical information in sighted

people. This hypothesis is compatible with studies showing that visual features are relevant to mathematical understanding (Goldstone et al., 2010; Stoianov and Zorzi, 2012).

An alternative to the mental imagery hypothesis, therefore, is that the occipital activation reflects “neuronal recycling” (Dehaene and Cohen, 2007), i.e. a repurposing of part of the visual cortex towards a related function which would be useful to mathematical processing. Indeed, activation in occipital cortices of blind individuals overlap with areas that, in sighted individuals, are heavily influenced by top-down visual attention (Martínez et al., 1999) and include retinotopic maps or topographically organized visual areas that may constitute a topographic buffer (Kosslyn, 2005) depicting shapes (Vinberg and Grill-Spector, 2008). Such retinotopic maps might therefore be particularly appropriate to support the mental manipulation of geometrical shapes or spatial diagrams that are central to mathematics, regardless of the modality in which they are initially conveyed.

Finally, a third account of the occipital activation may also be proposed, namely a radical reorientation of visual cortex for a completely novel use, unrelated to the normal role of this region in forming retinotopic maps and processing shapes. Indeed, several studies have shown that occipital cortex may be also activated in congenitally blind individuals during nonmathematical tasks such as sentence processing and verbal working memory, with a profile similar to the one observed in Broca’s area (Amedi et al., 2003; Bedny et al., 2011; Lane et al., 2015; Röder et al., 2002). It is hard to see what kind of visual imagery or neuronal recycling could explain these language-related occipital activations. Rather, it seems plausible that a broad form of plasticity, particularly in the developing brain, could lead to a radical repurposing of occipital cortices towards high-level cognitive functions, including mathematical thinking. This radical plasticity hypothesis, however, would still need to explain the recent observation that, in the blind, distinct and reproducible sectors of occipital cortex are allocated to number-related and language-related functions, whose resting-state activity patterns correlate respectively with the frontoparietal number network and the left-hemispheric language network (Kanjlia et al., 2016). This result, suggesting that pre-existing connectivity to distant areas may account for the specialization of occipital cortex in the blind, is in agreement with the neuronal recycling hypothesis (Hannagan et al., 2015). We acknowledge that, at present, our observations are simply insufficient to convincingly distinguish among those three interpretations of occipital activation during mathematical processing in the blind.

Regarding our original question, however, the results are unambiguous in supporting the hypothesis that visual experience is not necessary for the development of a normal cerebral representation of advanced mathematical concepts. Given that the activation during mathematical judgments overlapped with regions classically involved in the mental representation of space and

number, in both sighted and blind subjects, our results are compatible with the hypothesis that advanced mathematics builds upon abstract and amodal systems for number and space, which can develop in the absence of visual experience.

7. Supplementary information

Table S1 – Peaks of activation to meaningful math versus meaningful nonmath in experiment 1

	meaningful math > nonmath																			
	Blind subject A				Blind subject B				Blind subject C				Blind subjects				Sighted subjects			
	X	y	z	t	x	y	z	t	x	y	z	t	x	Y	z	t	x	y	z	t
L IT	-57	-55	-14	7.48	-60	-55	-10	6.01									-53	-57	-16	10.40
R IT	60	-57	-5	5.41	60	-61	-5	5.52									52	-52	-19	7.50
L IPS	-45	-57	54	8.27	-57	-34	36	6.11					-45	-57	54	4.92	-53	-43	57	10.90
R IPS	50	-36	57	5.90	41	-54	49	6.88	54	-43	60	4.80	54	-37	48	4.28	50	-36	56	7.30
L occipito-parietal									-23	-82	31	4.99	-27	-76	48	6.34				
R occipito-parietal					38	-91	4	5.96	24	-70	58	5.47	29	-64	48	5.17				
R calcarine	18	-99	-7	8.89	0	-84	-5	5.82												
L Mid Occipital	-21	-102	3	9.19									-35	-90	-5	4.20				
L Cuneus									3	-90	33	5.84								
R Cuneus									14	-94	27	4.51								
L SFS																	-24	8	64	7.11
R SFS																	32	5	56	4.97
L MFG (BA9)	-29	8	48	6.04	-24	17	67	5.71									-47	7	31	8.21
R MFG (BA9/BA10)	45	11	55	6.98													50	10	21	6.03
L MFG (BA46)	-51	25	36	8.11													-44	31	27	7.81
R MFG (BA46)	50	28	24	5.05	48	28	31	6.80	45	41	16	5.00					50	47	16	6.74
R IFG	50	46	9	5.79	53	43	9	5.99												

Table S2 – Peaks of activation to meaningful math versus meaningful nonmath in experiment 2

	Math > Nonmath																			
	Blind subject A				Blind subject B				Blind subject C				Blind subjects				Sighted subjects			
	X	y	z	t	x	y	z	t	x	y	z	t	X	y	z	t	x	y	z	t
L IT	-56	-55	-13	10.0	-47	-61	-1	7.12	-56	-55	-16	6.86	-56	-55	-11	5.71	-54	-49	-23	12.0
R IT	60	-57	-7	7.31	57	-51	-17	6.55	53	-66	-4	6.79					56	-51	-16	12.2
L IPS	-51	-49	57	7.83	-44	-57	42	5.87	-48	-45	55	10.4	-48	-45	54	6.97	-56	-36	49	16.1
R IPS	48	-36	55	8.97	42	-55	55	7.49	50	-42	57	11.0	42	-49	64	7.35	48	-39	48	12.8
L occipito-parietal	-26	-79	27	9.97	-8	-78	42	9	-24	-76	49	11.9	-26	-78	49	9.22	-30	-84	31	7.24

R occipito-parietal					27	-76	42	6.22	30	-69	45	11.5	29	-63	45	8.03	45	-75	28	7.22
R Mid Occipital/ Calcarine	23	-88	6	8.98					0	-82	-2	5.11								
L Mid Occipital	-20	-97	1	7.42	-33	-87	12	7.17	-8	-91	-5	3.93								
L SFS																	-26	-4	58	6.45
R SFS									24	5	67	7.98					29	5	61	6.62
L MFG (BA9)	-26	8	46	7.08					-51	8	24	8.53	-48	8	34	6.06	-50	8	36	8.76
R MFG (BA9/BA10)	50	5	42	9.00	59	13	31	6.2	54	16	42	10.3					50	8	25	8.50
L MFG (BA46)	-53	32	18	10.4	-36	55	10	8.86	-45	41	21	10.2					-45	34	33	7.81
R MFG (BA46)									42	47	16	9.86					50	41	21	8.07
L IFG													-28	55	7	4.53				

Table S3 – Correlation between activation and statements imageability in experiment 1

	Correlation between activation and statements imageability							
	Blind subject A				Blind subject B			
	x	y	z	t	x	y	z	t
L inf parietal lobule	-42	-55	51	5.38				
R inf parietal lobule	56	-52	46	5.7				
L parietal sup	-36	-61	61	4.84				
R parietal sup	29	-69	60	5.94				
L Occ sup/precuneus	-30	-78	40	6.12				
R Occ sup/precuneus					27	-76	42	5.98
L precuneus	-12	-76	54	6.26				
R Cuneus					2	-79	30	4.95
L Calcarine	-13	-99	-7	4.72				
R Calcarine	15	-100	-7	6.03				
L middle occipital					-38	-85	30	5.24
R middle occipital					41	-82	25	5.35
L MFG (BA6)	-36	14	61	7.52				
R MFG (BA6)	45	13	57	6.56				
L SFS					-23	17	69	5.09
R SFS					29	13	69	5.48

Chapter 4. The language of geometry: Fast comprehension of geometrical primitives and rules in human adults and preschoolers

1. Introduction to the article

In previous chapters, we have shown that mathematical and general nonmathematical semantics call upon two separate brain circuits. In this last chapter, we finally ask whether such dissociation also occurs at the level of syntax. In other words, we investigate the existence of an elementary mathematical language, independent of natural spoken language, would support the comprehension of mathematical principles even in the absence of education and without a dedicated lexicon.

To address this issue, we chose the domain of basic geometry that is known to be highly intuitive, and tested whether a “language of thought” made of geometrical primitives and combinatorial rules could account for humans’ behavior in a novel task also designed for the occasion. This original, completely non-linguistic paradigm required subjects to watch the beginning of a sequence of spatial locations on an octagon, extract the underlying regularities, use them to predict future locations and finally recall the whole sequence.

2. Abstract

During language processing, humans form complex embedded representations from sequential inputs. Here, we ask whether a “geometrical language” with recursive embedding also underlies the human ability to encode sequences of spatial locations. We introduce a novel paradigm in which subjects are exposed to a sequence of spatial locations on an octagon, and are asked to predict future locations. The sequences vary in complexity according to a well-defined language comprising elementary primitives and recursive rules. A detailed analysis of error patterns indicates that primitives of symmetry and rotation are spontaneously detected and used by adults, preschoolers, and adult members of an indigene group in the Amazon, the Mundurucu, who have a restricted numerical and geometrical lexicon and limited access to schooling. Furthermore, subjects readily combine these geometrical primitives into hierarchically organized expressions. By evaluating a large set of such combinations, we obtained a first view of the language needed to account for the representation of visuospatial sequences in humans, and conclude that they encode visuospatial sequences by minimizing the complexity of the structured expressions that capture them.

3. Introduction

In the past decades, studies of sequence learning have outlined one possible mechanism by which complex mental representations are constructed out of simpler primitives: the human ability to extract complex nested structures from sequential inputs (Dehaene et al., 2015). While non-human primates fail to show any systematicity in language learning (Yang, 2013), humans seem to be innately endowed with a quick grasp of complex embedded rules. At 8 months of age already, infants presented with a brief sequence of syllables readily extract recurrent 3-syllabic words (Kabdebon et al., 2015; Saffran et al., 1996), and by 12 months they understand how these words combine to form larger structures (Saffran and Wilson, 2003). A similar ability to group consecutive items according to abstract regularities has also been demonstrated during the learning of visuomotor sequences by adults (Restle, 1970; Sakai et al., 2003). Children and adults are also able to learn more abstract algebraic rules such as “AAB” (a repetition of any two items followed by a third one) (Marcela Peña et al., 2002; Marcus et al., 1999). This capacity for abstract rule learning seems to be enhanced in humans and to rely on inferior prefrontal cortex (“Broca’s area”) (Bahlmann et al., 2008; Wang et al., 2015). Furthermore, different but neighboring sectors of inferior prefrontal cortex appear to be used for linguistic and for mathematical rules (Amalric and Dehaene, 2016; Monti et al., 2012). The question therefore arises whether a capacity for the internal representation and manipulation of nested sequences also underlies the acquisition of mathematics. While there have been several studies of artificial language learning ((Fitch and Friederici, 2012; Friederici et al., 2002; Gómez et al., 2000; Marcus et al., 1999; Saffran et al., 1996); see (Pothos, 2007) for a review), there have been comparatively fewer studies of the acquisition of mathematical structures. Our aim here is to introduce a novel experimental paradigm to study the acquisition of elementary structures in the domain of geometry, with the ultimate goal of probing whether this ability presents some features that are uniquely developed in the human species (for a similar approach, see (M. D. Martins et al., 2014; M. J. Martins et al., 2014)).

Several recent studies have suggested that even uneducated humans possess proto-mathematical intuitions of geometry. Indeed, human abilities to navigate the environment and to recognize geometrical shapes appear to develop early (Landau et al., 1981; Lee et al., 2012), are shared with many different animal species (Cheng, 1986; Chiandetti and Vallortigara, 2007; Spelke and Lee, 2012), and rely on a precocious knowledge of geometrical notions like distance, direction, length, or angle (Dillon et al., 2013; Dillon and Spelke, 2015). Even adults who lack school education and whose language has an impoverished vocabulary for geometry, rely on abstract geometrical cues when processing shapes and maps (Dehaene et al., 2006; Izard et al., 2011a). In analogy with the domain of numbers (Gilmore et al., 2010; Halberda et al., 2008), it seems reasonable to hypothesize

that these basic geometrical intuitions may serve as foundation for more abstract ideas (Dehaene et al., 2008; Lakoff and Núñez, 2000; Spelke et al., 2010). However, the mechanisms that lead to the formation of advanced mathematical concepts from simpler ones still remain unknown.

In the present paper, we propose to formalize the human sensitivity to mathematical rules as the availability of a “language of thought” (Fodor, 1975) that allows the formation of complex representations from a small repertoire of primitives. Following Fodor’s ideas, such a language should comprise a limited set of atomic elements (“lexicon”) that can be combined into more complex representations thanks to a set of formal combinatorial rules (Fodor, 1983, 1975; Romano et al., 2013). Such an approach has already proved relevant to model human conceptual learning (Goodman et al., 2015; Piantadosi et al., 2016, 2012). In the specific case of spatial learning, Yildirim et al. (Yildirim and Jacobs, 2015) introduced a compositional language for spatial sequences, including a cursor, a set a basic commands to move it, “goto” loops, and recursion. They show that this language could capture the behavior of human adults in categorizing auditory or visual spatio-temporal sequences drawn out of seven locations arranged around a circle. Yildirim et al. showed that their language could account for the transfer of abstract sequence knowledge from the visual to the auditory modality (and vice-versa). However, their language did not model the participants’ understanding of geometry. Geometrical primitives such as symmetry were unnecessary for their purposes, since the spatial sequences were drawn from 7 locations on the circle and therefore did not form regular geometrical shapes (unlike the present work). Only a handful of researchers have explicitly focused on geometrical learning. Coding languages such as LOGO, a language in which a child learns to give directional instructions to a turtle walking across a page, have been used to produce regular geometrical patterns (Solomon and Papert, 1976). Following Chomsky’s ideas, Leyton introduced a generative grammar that partially captures the human perception of geometrically regular static shapes (Leyton, 2001, 1988). These research programs, however, either lacked empirical testing or were designed for educational purposes, and they did not systematically probe the human acquisition of geometrical sequences.

Lying at the intersection of those previous efforts, the present work introduces a simple formal language composed of geometrical primitives and combinatorial rules that suffice to describe the symmetries of a regular octagon. We ask whether humans can use such primitives and combine them in order to encode regularities of variable degree of complexity in spatial sequences. By analyzing the speed and ease with which human adults and children detect and memorize geometrical structures, we show that our language provides an adequate description of the representation that humans use to encode spatial sequences. By testing their capacity to anticipate the rest of the sequence, even before it has been fully presented, we examine how quickly human

adults and children learn such combinatorial rules. By testing a variety of sequences, we probed the complexity of the rules that can be acquired. Using these data, we outline a theory of rule complexity consistent with human behavior.

3.1. Language

We designed a formal language capable of describing, in a compact manner, all sequences of movements on a regular octagon. The set of primitive instructions is shown in figure 4.1A and includes rotations, axial and point symmetries. Each of these instructions captures a possible transition from one location on the octagon to another. We denote them as 0 (stay at the same location), +1 (next element clockwise), +2 (second element clockwise), +3 (third element clockwise), -1, -2, -3, H (horizontal symmetry), V (vertical symmetry), P (rotational symmetry, equivalent to +4), A and B (symmetries around diagonal axes).

From these primitives, a sequence can then be generated by simple concatenation (e.g. the expression +2 +2 +2 +2 generates a square). Although any sequence can be encoded in this manner, we will provide evidence that humans detect and encode regular sequences in a much more compressed form. Thus, we also assume that the “language of thought” includes instructions for repeating operations. For instance, the sequence +2 +2 +2 +2 may be encoded as $[+2]^4$, i.e. four repetitions of +2). The language also allows for a more complex form of “repetition with variation”, as when drawing a first square, and then a second one rotated by one dot : the corresponding expression is denoted $[[+2]^4]^{2<+1>}$, where $[+2]^4$ encodes the square and $[]^{2<+1>}$ repeats it twice with an offset of +1 in the starting point. Appendix S1 presents a formal syntax and semantics of this minimal language for geometry.

In most languages, many equivalent expressions provide the same output. Here, for instance, the same square can be captured as +2 +2 +2 +2, $[+2]^4$, $[+2]^3 +2$, etc. We therefore assume that subjects apply Occam’s razor and attempt to select the most parsimonious expression that accounts for the observed sequence. The concept of Kolmogorov complexity, a notion from algorithmic information theory, provides a natural mathematical framework for these ideas (Li and Vitanyi, 2013; Romano et al., 2013). This framework defines the complexity of a given sequence as the length of the shortest expression capable of producing it in a Turing-complete language, (i.e. any reasonable programming language).

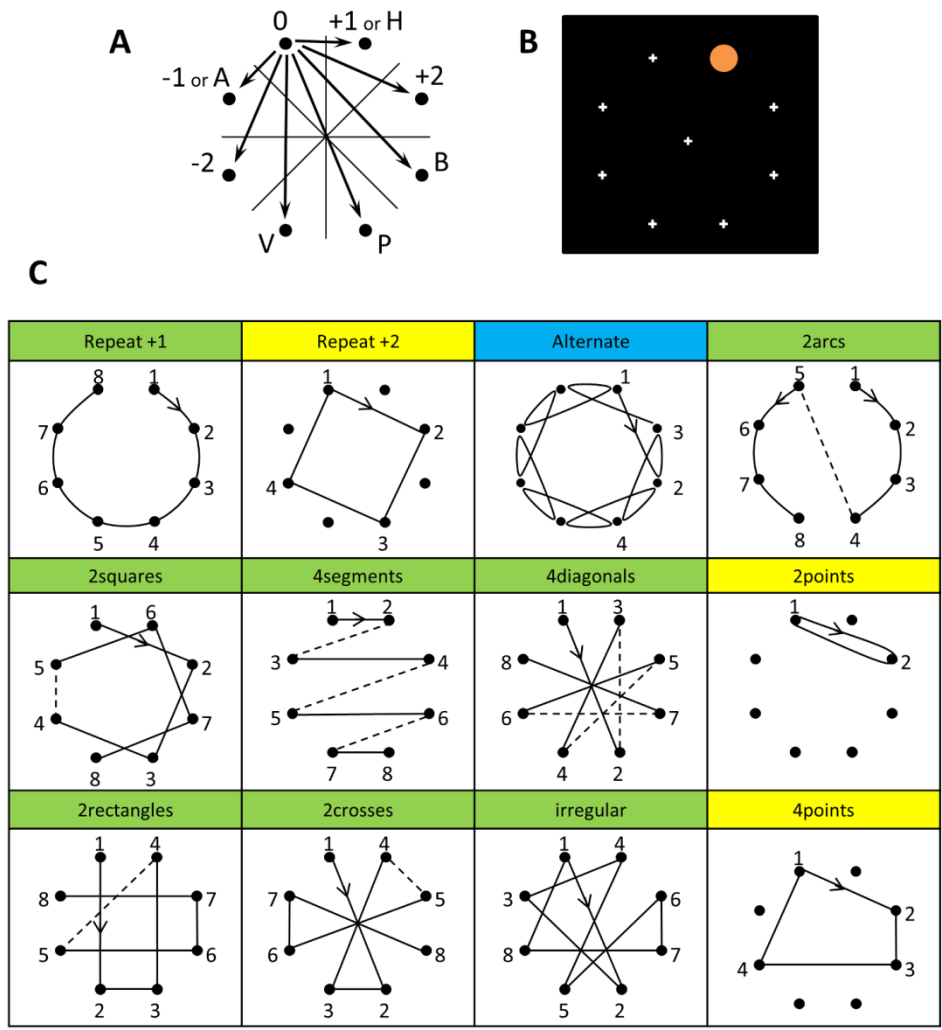


Figure 4.1. Paradigm. (A) Basic geometrical rules used to create sequences: rotations (+1, +2, -1, -2), axial symmetries (H:horizontal, V: vertical, A,B: oblique) and rotational symmetry (P). From one location of the octagon, each of the 7 others can be reached by the application of one or more primitives. (B) Screenshot from experiment 1. The orange dot appears at successive locations on the octagon, and subjects are asked to predict the next location. (C) Examples of sequences presented to French adults (blue), kids and Mundurucu adults (yellow), or both (green).

Unfortunately, a classic result in algorithmic information theory is that, for any Turing-complete language, Kolmogorov complexity is not computable. Even for simple languages, Kolmogorov complexity is often difficult to compute in practice, because it involves examining, for each sequence, all the programs that compute it, a search that typically grows exponentially with the size of the sequence. Different methods have been developed to approximate Kolmogorov complexity. One idea is to approximate it using standard file compressors such as Lempel-Ziv. Such approach was used e.g. in (Cilibiasi and Vitányi, 2005) to cluster large documents via a definition of universal distance. File compressors behave well in relatively large texts but fail to provide any significant compression when the input is a very small text devoid of repetitions, such as the spatial sequences of 8 locations that we used here. In our case, we thus defined a new language capable of detecting specific geometrical patterns in such short sequences. To quantify sequence complexity,

we used the notion of “minimal description length” which is closely related to Kolmogorov complexity (Grunwald, 2004) (for other uses of information theory and minimal description length in psychology, see e.g. (Bradmetz and Mathy, 2006; Feldman, 2003, 2000; Hochberg and McAlister, 1953; Mathy et al., 2016; Mathy and Feldman, 2012; Piantadosi et al., 2016)). From now on, we call “complexity” of a spatial sequence x , denoted $K(x)$, the length of the shortest expression(s) in our language that reproduces it. The corresponding psychological assumption, that we put to a test in our experiments, is that human participants attempt to “compress” the spatial sequence mentally, i.e. to minimize the memory cost by identifying the simplest (shortest) mental expression that allows them to store the sequence.

We make the simplest possible assumptions regarding expression length (see appendix for details). In essence, (1) each additional primitive instruction adds a fixed cost; (2) repeating a set of instructions n times adds a cost proportional to $\log(n)$ to the instructions to be repeated; (3) the relative size of those two costs is such that even a single repetition reduces the size of an expression (thus, the expression “[+2]²” is more compressed than the equivalent “+2 +2”).

3.2. Stimulus sequences

In all experiments below, our general aim was to (1) probe human memory for spatial sequences on the octagon and (2) examine whether human behavior could be captured by our formal language and our definition of complexity. To this aim, we first generated all the 5040 sequences of length 8 that could be generated on the octagon, beginning in the same origin and without repetition of any specific location. We then computed their complexity (K) in the above language, quantifying their degree of geometrical regularity. Finally, we selected sequences that spanned a broad range of geometrical primitives and regularities. All sequences used in experiments 1-4 are shown in figure 4.1C. We now detail them:

- The most complex sequences ($K = 16$), called “irregular”, consisted in a serial presentation of all 8 locations in a fixed order with no apparent regularity. Such sequences could also be called “incompressible” because their minimal description consists in a mere list of successive transitions between locations, without any compression afforded by repetition. Our language comprised 768 such maximal-complexity sequences. For any given subject, one of them was chosen randomly. In order to probe sequence memory, it was then repeated a second time, for a total of 16 locations.
- At the other extreme, the sequence called “repeat” ($K=5$) contained a single repeated primitive (either +1 or -1), and thus consisted in a simple clockwise or counterclockwise progression.

- The “alternate” sequence ($K = 7$) was constructed by applying alternatively two steps in one direction (either +2 or -2), and one step in the opposite direction (respectively -1 or +1). Thus, this sequence involved no nesting, but a mere repetition of two instructions.

Other sequences contained two embedded levels of regularity: a lower level where instructions built a geometrical shape (e.g. a square), and a higher level at which the shape was repeated with a global transformation (e.g. the square was rotated):

- The “2squares” sequence ($K = 8$) was constructed by applying three times the rule +2, thus drawing a square, and then restarting with a rotated starting point, which was defined by applying the rule +1 or -1 to the previous starting point.
- The “2arcs” sequence ($K = 8$), consisted in three applications of the rule +1 (thus drawing an arc of four successive points), then globally flipping this figure using an axial symmetry in order to complete it with the four remaining locations.
- The “4segments” sequence ($K = 7$) consisted in first drawing a segment by applying an axial symmetry, then translating it four times by shifting its starting point. This sequence resulted in a succession of four parallel segments connected by a zigzag shape (see figure 4.1C).
- The “4diagonals” sequence ($K = 7$) was constructed similarly through the repeated application of rotational symmetry to four consecutive starting points.

Finally, two sequences contained three embedded levels of regularity.

- The “2rectangles” sequence ($K = 10$) consisted in an initial segment on which a global axial symmetry was applied (thus tracing a rectangle, see figure 4.1C), and then a +2 rotation that transposed this shape to the remaining four points.
- The “2crosses” sequence ($K = 7$), similarly, started with a rotational symmetry (diagonal segment), which was then transformed by an axial symmetry (thus tracing a cross, see figure 4.1C), and then a +2 rotation that transposed it to the remaining four points.

In experiments 2-4, to evaluate memory span, we added two sequences that spanned only a subset of the 8 locations. These were irregular sequences with respectively 2 and 4 locations (called “2points” [$K = 6$] and “4points” [$K = 9$]).

4. Experiment 1

4.1. Methods

4.1.1. Ethics statement

Experiments were approved by the regional ethical committee (Comité de Protection des Personnes, Hôpital de Bicêtre), and participants gave informed consent.

4.1.2. Participants

Participants were 23 French adults (12 female, mean age = 26.6, age range = 20 – 46) with college-level education.

4.1.3. Procedure

The experiment was organized in short blocks. In each block, subjects were presented with a specific sequence of spatial locations, which they were asked to continue. The eight possible locations, forming a symmetrical octagon, were constantly visible on the computer screen (figure 4.1B). On a given trial, the locations forming the beginning of the chosen sequence were flashed sequentially, and then the sequence stopped. The subject's task was to guess the next location by clicking on it. As long as the subject clicked on the correct location, he was asked to continue with the next one. In case of an error, the sequence was restarted from the beginning: the entire sequence of locations was flashed again, the mistake was corrected, and the subject was again asked to predict the next location. For each sequence, the procedure was initiated by showing only the first two items. Thus, starting with the 3rd location in the sequence, subjects were given a single opportunity to venture a guess at each step. In order to introduce the task, participants were always presented first with a "repeat" sequence of clockwise or counterclockwise rotating locations. The order of subsequent sequences was randomized.

4.1.4. Stimuli

On each block, a spatial sequence consisting in a succession of 16 locations was presented by successively flashing these locations. These sequences are shown in blue and green labels in figure 4.1C. In total, each participant was presented with two "repeat", two "alternate" and two "2squares", each spanning the two directions of rotation around the octagon. Two "2arcs", four "4segments" and one "4diagonals" were also presented in order to test the comprehension of all four axial symmetries and rotational symmetry. In these cases, the direction of rotation was randomized. One exemplar of "2rectangles" and one of "2crosses" were also randomly selected. Finally, two irregular sequences were picked randomly among the 768 sequences of maximal complexity. The starting point of each sequence was picked randomly among the subset of eight locations of the octagon that preserved the global shape.

4.1.5. Statistical analysis

The data consisted in a discrete measure of performance (correct or error) for each subject, each sequence item, and each ordinal position from 3rd to 16th. Because those data were discrete (even after averaging performance over a subset of sequences or ordinal data points), we used Friedman's non-parametric test for paired data (a non-parametric test similar to a parametric repeated-measures ANOVA). When necessary, we used a Bonferroni correction for multiple comparisons (across 14 data points for educated adults, 8 data points for other subjects). To quantify

the evolution of performance over time, we calculated for each subject the Spearman's rank correlation of error rates with ordinal position, and compared the mean correlation coefficient to 0 using a Student t-test. When the evolution of performance over time was evaluated on a small number of ordinal positions (3 or 5, as happens in experiments 2-4), we used Friedman's test for multiple conditions. Finally, whenever we needed to compare performance between groups of subjects on a specific condition (e.g. adults and children, as will arise in experiment 2), given that we had discrete measures (correct or error), we used Fisher's exact test when the number of measures per subject was 1 or 2; and the Wilcoxon rank-sum test for independent samples whenever comparing the means of 3 or more conditions.

Specific planned comparisons were performed in order to finely probe the understanding of hierarchical sequence structure. For example, in "4segments", the even data points correspond to the application of the 1st-level, shallower level of regularity (axial symmetry), while the odd data points result from a change of starting point, and thus represent a deeper, 2nd-level regularity that involves a non-adjacent temporal dependency (subjects must remember the starting point of a sub-sequence of 2 items). Consequently, comparing performance on such data points provides information about the representation of nested rules in our paradigm.

4.2. Results

As a baseline, we first examined the performance with "irregular" 8-item sequences, which contained no obvious geometrical regularity. The evolution of average performance across the two successive repetitions is shown as a background gray curve in all panels of figure 4.2. The mean error rate decreased across trials (mean rank correlation of error rate with ordinal position: $\rho = -0.51 \pm 0.05$, Student t-test: $t_{22} = 10.3$, $p < 7.10^{-10}$). This improvement could be decomposed into two contributions: rote memory and anticipation. First, performance was better in the second half of each block, i.e. during the repetition of the sequence, than in the first half, when the sequence was introduced, indicating rote memory (Friedman test: $F = 15.7$, $p < 10^{-4}$; point-by-point comparisons revealed a significant difference at all but the last location, $p_s < 0.05$). Second, performance improved even within the first half, even before the full sequence had been presented (anticipation; $r = -0.4 \pm 0.08$, Student t-test: $t_{22} = 5.1$, $p < 4.10^{-5}$). This finding indicates that subjects took advantage of the fact that the 8 locations were sampled without replacement, thus narrowing the choice of remaining locations. Yet memory for past locations was not perfect, as shown by the fact that performance on data points 7 and 8 remained worse than the chance level expected if subjects perfectly avoided past locations (respectively $85 \pm 6\%$ vs 50% ; and $54 \pm 8\%$ vs 0% errors; One-Sample Wilcoxon Signed Rank Tests: both $p_s < 0.001$).

Irregular sequences served as a baseline with which to compare other regular sequences. In every regular sequence, the mean error rate was significantly lower than in the irregular baseline (“repeat”: $2.5 \pm 0.9\%$; “alternate”: $25.5 \pm 4\%$; “2arcs”: $15 \pm 1.4\%$; “2squares”: $23.5 \pm 3.7\%$; “4segments”: $15 \pm 1.4\%$; “4diagonals”: $27 \pm 4\%$; “2rectangles”: $38 \pm 3.2\%$; “2crosses”: $27.5 \pm 3.2\%$; “irregular”: $59.5 \pm 3.8\%$; Friedman tests, all p s < 0.001). Moreover, in every case, participants performed significantly better than baseline even before the full presentation of the 8-item sequence (averaged error rate of data points 6-8 for “repeat”: 0% ; “alternate”: $19.6 \pm 6.1\%$; “2arcs”: $8 \pm 2.1\%$; “2squares”: $16.7 \pm 5\%$; “4segments”: $4 \pm 2\%$; “4diagonals”: $17.4 \pm 4.7\%$; “2rectangles”: $33.3 \pm 5.2\%$; “2crosses”: 18.8 ± 5.2 ; and “irregular”: $69.6 \pm 3.8\%$; all p s $< 10^{-4}$).

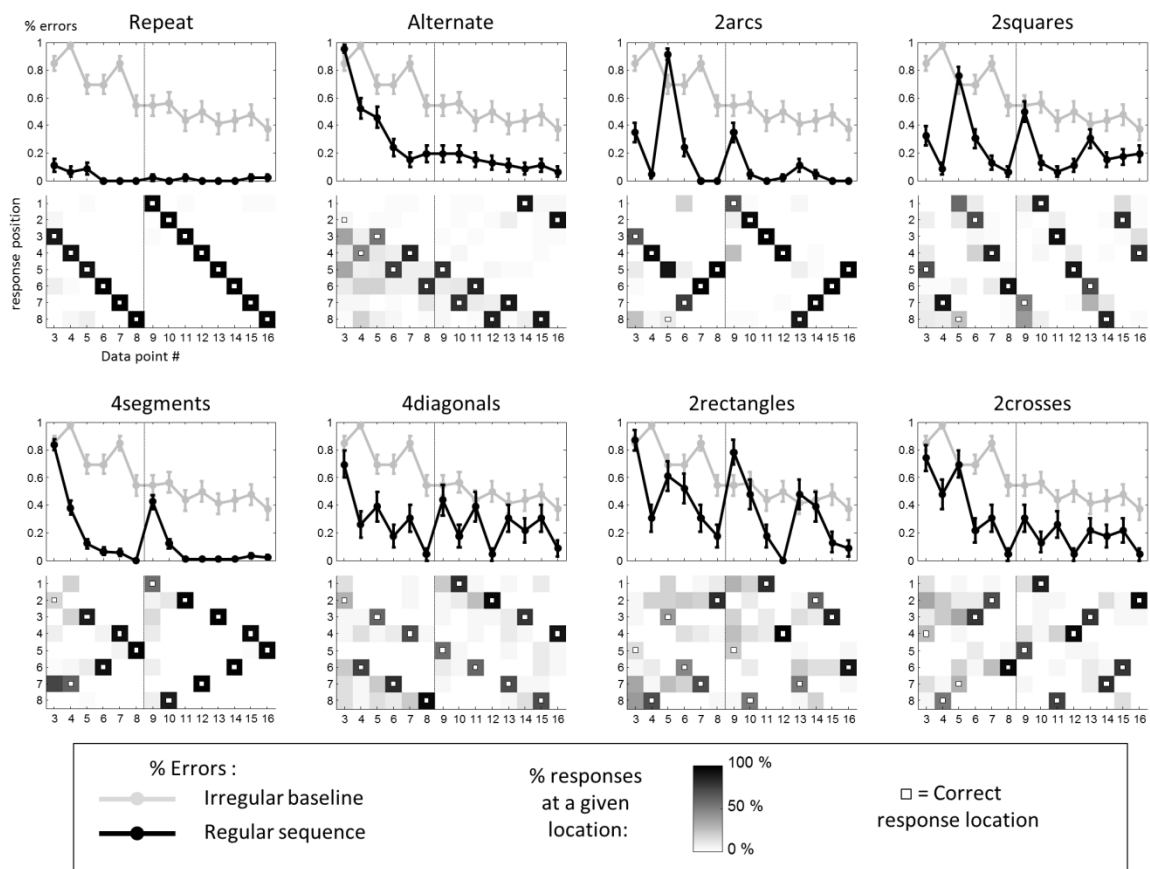


Figure 4.2. Performance of adult participants in experiment 1. Top panels show the evolution of error rate across successive steps (data points 3–16 in adults) for each regular sequence (error bars = 1 SEM). The gray curve in the background shows the error rate for irregular sequences, which serve as a baseline. Bottom panels show the percentage of responses at a given location for each data point. White dots indicate the correct location. Vertical dashed lines mark the transition between the two 8-item subsequences that constitute the full 16-item sequences.

Thus, sequence regularity facilitated both rote memory and anticipation. Crucially, as predicted, these effects were captured by our measure of complexity: the mean error rate was highly correlated with K across sequences (for all data points: Spearman’s $\rho = 0.75 \pm 0.04$, Student t -test: $t_{22} = 21$, $p < 10^{-11}$; for data points 6-8: $\rho = 0.73 \pm 0.04$, $t_{22} = 21$, $p < 10^{-9}$, figure 4.3A). Furthermore,

complexity in our language gave a better account of adults' behavior than alternative encoding strategies which did not use geometrical features such as rotations and symmetries, but used only the distance between successive locations. We computed two variants of sequence complexity devoid of geometrical content: the normalized jump length, measuring the average distance between locations in a sequence, averaged over the number of jumps; and complexity in a degraded language where the primitives were only ± 1 , ± 2 , ± 3 , $+4$, and repetition (figure S1). In both cases, obvious outliers were observed (e.g. the complexity for "4segments" in the second case reached the maximum value of 16, which is inconsistent with the data). Moreover, correlations of those measures with total error rate were significantly lower than those obtained with the full language (normalized jump length $\rho = 0.60 \pm 0.03$, $t(44) = 3.23$, $p = 0.003$; complexity in degraded language: $\rho = 0.51 \pm 0.03$, $t(44) = 4.88$, $p < 10^{-4}$).

We then examined the pattern of errors in each regular sequence. Unsurprisingly, for the "repeat" sequence, which only consisted in the repeated application of the $+1$ or -1 rule, all error rates verged on 0 and were far below the baseline (all p s < 0.001 corrected). The fact that subjects were already able to complete the sequence after seeing only the first two items suggests that they quickly recognized and applied the primitives $+1$ and -1 , and treated repetition as a default assumption.

For "alternate", after a systematic error at the 3rd data point (error rate = 95 %), the error rate continuously decreased over the first half of the sequence (mean correlation coefficient: $\rho = -0.68 \pm 0.06$, Student t-test: $t = 11.8$, $p < 5.10^{-11}$) and dropped to $15 \pm 6\%$ at the 7th data point. Even though "alternate" induced more errors than "repeat" (overall: $F = 23$, $p < 10^{-6}$), performance was significantly better than "irregular" (all p s < 0.05 corrected, except at the 3rd and the 5th data points). Thus, although "alternate" was more difficult than "repeat", participants were able to identify and combine the rules $+1$ and $+2$.

For "2arcs" and "2squares", performance profiles were similar. At all data points except the 5th, 9th, 13th and 16th, error rates were significantly below the baseline (all p s < 0.05 corrected). The data points with high performance correspond to the application of the lowest-level rule ($+1$ for "2arcs" and $+2$ for "2squares"), therefore providing evidence that this superficial rule was quickly learned. On the contrary, data points 5, 9 and 13, corresponding to the application of the higher-level rule, exhibited more errors than their neighbors (Friedman test: $F = 23$, $p = 2.10^{-6}$). At data point 5, the error rate was not significantly below the irregular baseline in "2squares", and it was even worse than baseline in "2arcs" (error rate at 5th data point in "irregular": $70 \pm 6\%$; "2arcs": $91 \pm 4\%$, $F = 6.23$, $p = 0.013$; "2squares": $76 \pm 8\%$, $F = 0.69$, $p = 0.41$). Errors at this point consisted primarily in the continued application of the lower-level rule. Importantly, however, performance on data point 5, 9

and 13 improved over time (“2arcs”: Friedman test: $F = 37, p < 9.10^{-9}$; “2squares”: $F = 18.6, p < 9.10^{-5}$), and error rates at data points 13 fell significantly below baseline in “2arcs” ($p < 0.05$ corrected), indicating that subjects eventually learned both 1st and 2nd-level rules.

For “4segments”, error rate fell significantly below baseline for all data points (all $ps < 0.001$ corrected), except points 3 and 9. Within each block of 8 items, error rate decreased quickly and continuously to 0 (rank correlations for the 1st half: $\rho = -0.82 \pm 0.02, t_{22} = 36.4, p < 0.001$; and the 2nd half: $\rho = -0.62 \pm 0.04, t_{22} = 15.8, p = 2.10^{-13}$). These results suggest that the 1st and 2nd-level rules forming the “4segment” sequence were easily identified and applied. Separate analyses indicated that the mean error rate was similar for horizontal, vertical, and oblique symmetries (vertical: $11.5 \pm 1.6\%$; horizontal: $16.1 \pm 2.8\%$; oblique: $16.8 \pm 2.1\%$ and $15.5 \pm 2.5\%$; Friedman test for differences between the four types of symmetries: $F = 4.3, n.s.$). Thus, adult participants easily identified all axial symmetries.

The performance in “4diagonals” indicated that rotational symmetry was harder to identify than other symmetries (comparison of “4diagonals” and “4segments”; respectively $27.3 \pm 4\%$ vs $15 \pm 1.4\%$ errors, $F = 7.3, p = 0.007$). A saw tooth pattern (figure 4.2) indicated that even data points had systematically lower error rates than odd ones (Friedman test: $F = 18, p < 3.10^{-5}$), suggesting that the application of rotational symmetry (1st-level rule) was easier than that of the rotation of the starting point (2nd-level rule). Even data points exhibited error rates significantly lower than baseline (all $ps < 0.02, ps < 0.001$ corrected except for data points 10, 14 and 16). On the contrary, odd data points exhibited no difference with baseline, again suggesting that the 2nd-level rule was harder to understand than the 1st-level one. Nevertheless, there was a small but significant improvement over time on both odd and even data points (rank correlation for odd data points: $\rho = -0.4 \pm 0.07, t = 5.5, p < 2.10^{-5}$; rank correlation for even data points: $\rho = -0.39 \pm 0.06, t = 7.32, p < 6.10^{-11}$).

In “2 rectangles”, like in “2squares”, data points 5, 9 and 13 corresponded to the application of the deepest (3rd-level) rule. None of these exhibited an error rate lower than the baseline (data point 5: $60.9 \pm 10.6\%$ vs $69.6 \pm 6.2\%$, $F = 0.28, p = 0.6$; data point 9: $78.2 \pm 9\%$ vs $54.3 \pm 8.5\%$, $F = 4, p = 0.046$; data point 13: $47.8 \pm 10.9\%$ vs $41.3 \pm 9.5\%$, $F = 0.69, p = 0.4$), and there was no improvement over time (Friedman test: $F = 4.1, p = 0.13$), suggesting that participants did not manage to understand how the starting point of the rectangle changed. At the immediately subsequent data points 6, 10 and 14, that corresponded to the construction of the first side of the rectangle, performance improved compared to points 5, 9 and 13 (respectively $46 \pm 7\%$ vs $62 \pm 5\%$ errors, $F = 2.88, p = 0.089$), although it was still not significantly lower than baseline ($Fs < 0.5, ps > 0.4$). At subsequent points (7, 8, 11, 12, and 15, 16), the error rate further improved ($14 \pm 4\%$ errors, Friedman comparison with 3rd-level rule: $F = 22, p < 3.10^{-6}$) and became significantly lower than

baseline (all p s < 0.05 corrected), indicating that the 1st and 2nd-level rules that allowed to complete the rectangle were systematically learned.

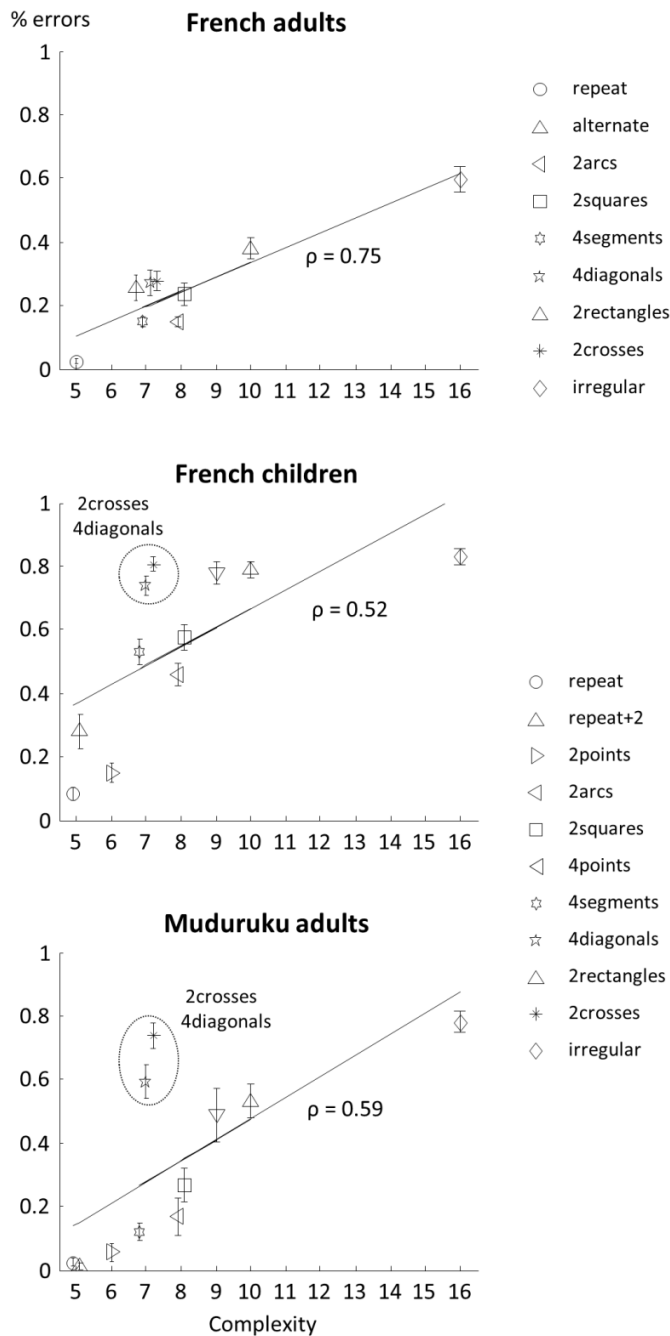


Figure 4.3. Complexity predicts error rates. For each sequence, the y axis represents the mean error rate, and the x axis the sequence complexity, as measured by minimal description length. Panels show data from French adults (top, experiment 1), preschool children (middle, pooling over experiments 2 and 3), and Munduruku teenagers and adults (bottom, experiment 4). For each group, a regression line is also plotted and the Spearman's correlation coefficient is displayed. In French children and Munduruku adults, the "4diagonals" and "2crosses" are clear outliers—as explained in the main text, the regression can be improved by assuming that their "language of thought" does not include rotational symmetry P.

Finally, for "2crosses", the performance profile resembled that of "4diagonals": on even data points, the error rate was systematically lower than the baseline (all p s < 0.03 corrected except at the 14th data point) and globally lower than the error rate on odd data points ($F = 10.7$, $p = 0.001$), indicating that participants easily identified the most superficial rule. Additional evidence for a 3-tiered organization was observed. The error rate was significantly higher on data points 5, 9 and 13,

corresponding to the starting point of the cross (3rd-level rule, 41 ± 7% errors) than on data points 7, 11 and 15, corresponding to the starting point of the second branch of the cross (2nd-level rule 26.1 ± 7% errors, Friedman comparison between 2nd and 3rd levels: $F = 4.45$, $p = 0.035$). No such difference was seen between data points 5, 9, 13 and 7, 11, 15 in “4diagonals” ($F = 1.9$, $p = 0.17$). On data point 7, 11 and 15, the error rate was in turn significantly higher than on subsequent data points 8, 12 and 16, corresponding to the completion of the cross (1st-level rule, 4.35 ± 3.3% errors, Friedman comparison between 1st and 2nd levels: $F = 5.33$, $p = 0.021$). On data points 6, 10 and 14, corresponding to the construction of the first branch of the cross (17.4 ± 5.2% errors, the error rate was also significantly lower than on data points 5, 9 and 13 ($F = 9.3$, $p = 0.002$). Finally, on data points 3, 5, 11 and 15, the error rate was not significantly lower than the baseline. In summary, 2nd and 3rd levels rules, though eventually learnt, were harder to grasp than the 1st level rule.

4.3. Discussion

Adults were able to detect various geometrical regularities and to quickly generalize on the basis of only a few items, before seeing the entire sequence. They correctly prolonged every sequence and erred precisely at the points where past clues did not allow them to guess the requested rule (data point 3 in “alternate”, “4segments”, “4diagonals”, “2rectangles” and “2crosses”; data point 5 in “2arcs”, “2squares”, “2rectangles” and “2crosses”, and data point 9 in “4segments”). In most such cases, systematic errors indicated that subjects systematically continued to apply the lower-level rule. For example, in “2squares”, participants got used to a succession of +2 rules and kept applying it at the 5th data point. In other cases where the previous points formed a sub-sequence that seemed to come to an end (e.g. after the first “4points” in “2rectangles” and “2crosses”, or after the first 8 points in “4segments”), participants failed because they could not guess how to restart.

Aside from these predictable errors, our results indicated that all regular sequences were better learnt than the irregular baseline, with error rates increasing essentially monotonically with complexity. This finding indicates that geometrical regularity is a major determinant of visuo-spatial memory in our task. Indeed, geometrical regularities allowed participants to memorize sequences of 8 items and beyond that would have otherwise exceeded their working memory capacity (as exemplified by the persistence of errors in the “irregular” baseline).

Participants’ performance provided clear indications of the type of regularities that they were able to identify. All the primitives that we hypothesized were easily recognized by adult subjects: +1/-1 (successor), +2/-2, and all axial and point symmetries (as indicated by superior performance on even data points of “4segments” and “4diagonals” sequences). Furthermore, participants also identified additional embedded levels of regularity. Performance with “2arcs”,

“2squares”, “4segments” and “4diagonals” sequences provided evidence for a fast learning of the most superficial rule and its repetition. 2nd and 3rd-level rules were harder to learn, as suggested by (1) the slower decrease of error rates for 2nd level than for 1st level, and (2) the persistence of errors over time at data points corresponding to the 3rd-level rule in “4diagonals”, “2rectangles”, “2crosses”. By construction, evidence in support of those deeper levels is presented with reduced frequency compared to the 1st-level rule – for instance in “2arcs” and “2squares”, the 2nd-level rule applies only to one trial in four. However, sequences such as “4diagonals” and “2crosses”, where 1st- and 2nd-level rules apply with the same frequency (every other trial), the 2nd-level rule still induced more errors than the 1st-level rule. Those results therefore suggest that deeper hierarchical levels are genuinely harder to learn, probably because they involve non-adjacent temporal dependencies: in “2arcs” or “2squares”, for instance, the 2nd-level rule applies to the initial point of a length-4 sub-sequence. Another compounding factor may be spatial distance across space. The “4diagonals” or “2crosses”, in which the distance between odd locations is almost maximum, yielded the maximum error rates.

Altogether, these findings indicated that adult participants easily identified elementary primitives of symmetry and rotation, and promptly understood the hierarchical organization of regular sequences. However, such performance is perhaps unsurprising giving that our subjects were young adults with college-level education. In experiment 2, we asked whether preschoolers, who have not yet received formal education, also grasped geometrical rules.

5. Experiment 2

5.1. Methods

5.1.1. Participants

24 preschoolers were tested (minimal age = 5.33, max = 6.29, mean = 5.83 ± 0.05). The experimental apparatus was installed at school, in a quiet room that was not the usual classroom. Children came one by one to play the game.

5.1.2. Procedure

To render the experiment more attractive for young children, we replaced the flashing dots with pictures of animals, one for each sequence. Children were asked to look carefully at how each animal moved. They were told that animals were playful: they appeared at one place, and then hid at another. Children were asked to catch them by pointing at the next location where they thought that they might appear. The experimenter then clicked on the designated target. To shorten the experiment, we divided each trial into two subsequences of 8 items. Children saw the first five locations of a sequence and had to point to the next three. Then, after a short break, they saw the

first three locations of the same sequence and had to point to the next five. Like in adults' experiment, whenever kids pointed to the wrong location, the program automatically restarted from the beginning of the trial, went on to correct the error, and asked for a guess of the next location.

5.1.3. Stimuli

The sequences were essentially the same as in experiment 1 (yellow and green labels in figure 4.1C). Only the sequence "alternate", which was difficult even for adults, was replaced by a sequence that allowed us to test directly for kids' understanding of the basic rule +2. This sequence consisted in the successive application of the rule +2 (called "repeat+2"). To explicitly measure working memory span, we also introduced two additional baselines, i.e. irregular sequences with only 4 and 2 locations (called "4points" and "2points"). Finally, to reduce the duration of the experiment, we presented only a single exemplar of each sequence category. The only exception was the "4segments" sequence, which was presented 4 times in order to test all 4 axial symmetries.

5.2. Results

We first analyzed performance on the "irregular" baselines with 8, 4 and 2 items. When 8 locations devoid of any geometrical regularity were presented, the error rate was very high ($80 \pm 2\%$ errors in average). Yet notably, as for adults, the performance improved over time (Spearman's rank correlation over the two presentations: $\rho = -0.41 \pm 0.04$, Student t-test: $t_{23} = 10.4$, $p < 4.10^{-10}$). Surprisingly, no such a pattern of error was observed for "4points" in which the error rate remained at a sustained level during the whole trial (minimum error rate: $75 \pm 9\%$). There was no significant improvement neither in the first presentation phase, nor in the second (Friedman's test on 1st and 2nd phases: $F_s = 0.29$; 3.2 ; $ps > 0.5$). However, error rates for "2points" significantly differed from "irregular" (from data points 7 to 16, all $ps < 0.01$ corrected) and significantly decreased over the first phase ($F = 19.7$, $p = 10^{-4}$). Thus, measured with our method, children's visual memory span for irregular sequences fell between 2 and 4.

For most of the regular sequences, the mean error rate was significantly lower than the "irregular" baseline (Friedman's tests: all $ps < 0.002$ either across 1st and 2nd phases or for 1st phase only): "repeat" (across 1st and 2nd phases: $6 \pm 2\%$ errors; on 1st phase only: $13 \pm 5\%$), "repeat+2" (1st and 2nd phases: $24 \pm 7\%$; 1st phase only: $33 \pm 9\%$), "2arcs" ($39 \pm 5\%$; $49 \pm 6\%$), "2squares" ($53 \pm 6\%$; $51 \pm 8\%$) and "4segments" ($50 \pm 5\%$; $54 \pm 5\%$). However, such a performance was not seen for "4diagonals" ($73 \pm 4\%$ errors), "2rectangles" ($79 \pm 3\%$ errors), "2crosses" ($81 \pm 3\%$ errors), for which mean error rates did not differ from baseline (all $ps > 0.07$).

As with adults, we found that preschoolers' overall mean error rate was predicted by the complexity of the sequences (at all data points: Spearman's $\rho = 0.52 \pm 0.02$, Student t-test: $t_{23} = 21$, p

$< 10^{-9}$; at data points 6-8: $\rho = 0.41 \pm 0.03$, $t_{23} = 11$, $p < 10^{-5}$, Figure 4.3B), even though the correlation was lower than in experiment 1 ($t_{46} = 5$, $p < 10^{-5}$).

Examination of individual sequences shown in figure 4.4 revealed that, for “repeat”, all error rates dropped quickly to 0 and were far below the baseline (all $ps < 8.10^{-4}$ corrected), indicating that children quickly recognized and applied the primitives +1 and -1. The same conclusion was reached for the primitives +2 and -2 in “repeat+2”, in which all error rates were significantly lower than baseline (Friedman test: all $ps < 0.05$ corrected), continuously decreased over the 1st phase ($F = 8.4$, $p = 0.15$) and stayed close to 0 over the 2nd phase.

As for adults, performance profiles were similar for “2arcs” and “2squares”. Error rates were below baseline at most of the data points (“2arcs”: all $ps < 0.05$ corrected except at data points 6, 7 and 13; “2squares”: $ps < 0.05$ corrected at data points 6, 12 and 16). These results therefore provide evidence that the superficial rule (+1 for “2arcs” and +2 for “2squares”) was quickly learned, while the application of the higher-level rule, at the 13th data point, induced more errors (Friedman test of comparison between the 13th data point its neighbors : $F = 23$, $p = 2.10^{-6}$). At this particular data point, 67% of children simply continued to apply the 1st-level rule in “2arcs” and 54% in “2squares”.

For “4segments”, error rate was significantly below the baseline at almost all data points (Friedman test: all $ps < 0.05$ corrected at data points 6, 7, 12, 13 and 15) and decreased continuously within each presentation phase (1st phase: $F = 12.4$, $p = 0.002$; 2nd phase : $F = 11.9$, $p < 0.02$). Separate analyses indicated that the mean error rate was similar for horizontal, vertical, and oblique symmetries (vertical: $46 \pm 7\%$ errors; horizontal: $42 \pm 6\%$; oblique: $55 \pm 7\%$ and $58 \pm 6\%$; Friedman test for differences between the four types of symmetries: $F = 4.9$, n.s.). Thus, all axial symmetries forming the 1st level of the “4segments” sequences were correctly identified and applied. Moreover, at odd data points of “4segments”, which correspond to the application of the 2nd-level rule, performance was significantly better than baseline (all $ps < 0.05$ corrected), therefore indicating that children also discovered the 2nd-level rules.

For “4diagonals”, error rate was not significantly below baseline neither at even data points, corresponding to the application of the 1st-level rule, i.e. rotational symmetry, nor at odd data points, corresponding to the application of the 2nd-level rule (all $ps > 0.1$). This result suggests that rotational symmetry was more challenging than axial symmetries for 5-year-old children.

Finally, for “2rectangles” and “2crosses” that contain 3 embedded levels of rules, none of the data points showed an error rate significantly lower than the baseline (all $ps > 0.1$). These rules seemed to be beyond the grasp of our children.

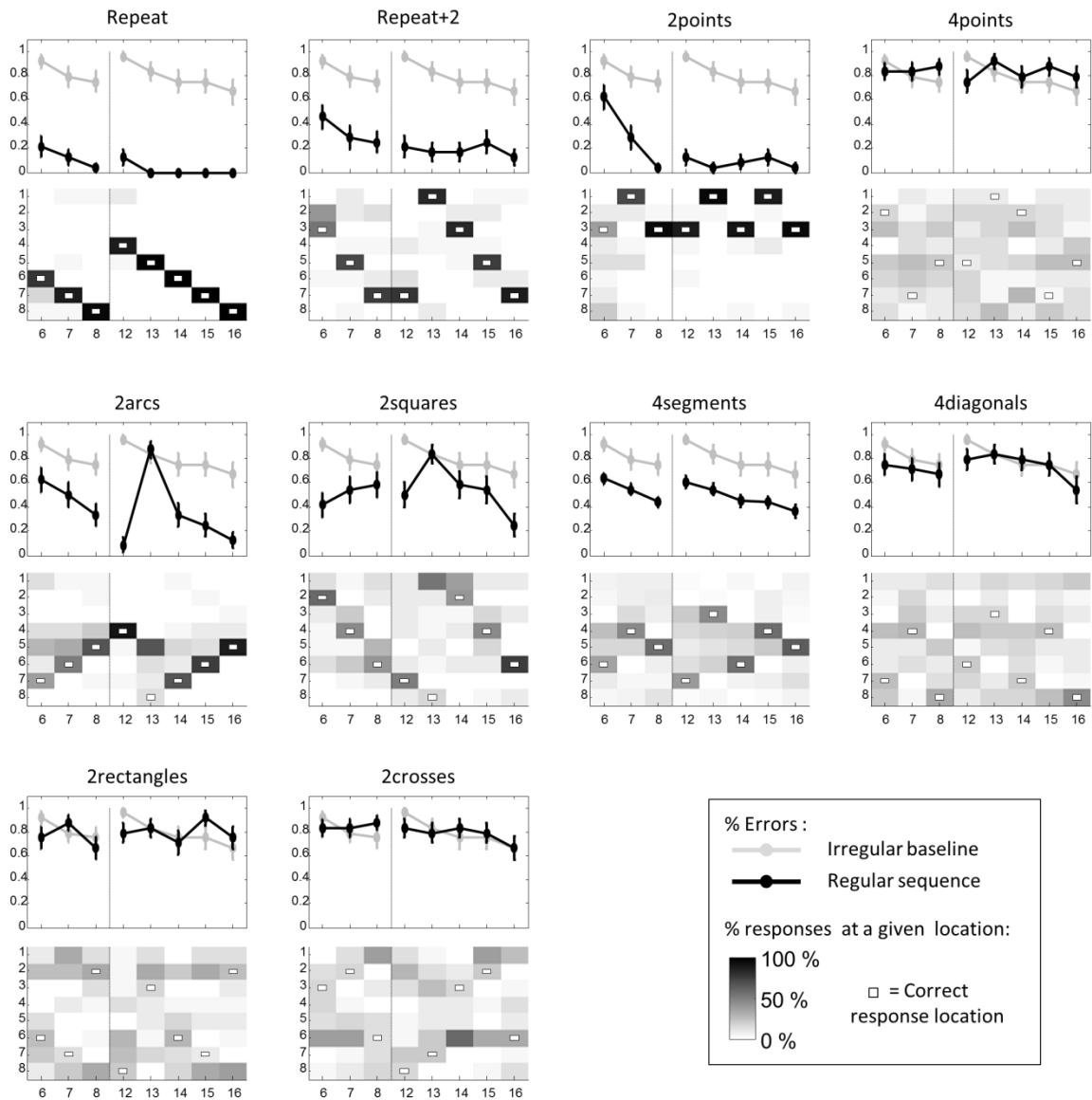


Figure 4.4. Performance of preschool children in experiment 2. Same format as figure 4.2. In children, only data points 6 to 8 and 12 to 16 were collected. Vertical dashed lines indicate the transition between the first and the second presentations of the 8-item sequences.

5.3. Discussion

Kids experienced more difficulty than adults, but their answers still provided evidence for a quick understanding of most geometrical primitives: they mastered +1 and +2 operations as well as axial symmetries, and only failed with rotational symmetry. Their behavior with the category “4segments” demonstrated that they could detect embedded regularities, yet they failed with more complex embeddings that defined the changes in the starting point of arcs, squares, rectangles or crosses. It thus seems that a reduced language, with fewer primitives and shallower embeddings, is needed to capture children’s performance. In the final section, we will provide a formal model of this idea.

One possibility is that children failed to detect sequential dependencies that exceeded their spatial working memory span. Performance on the “4points”irregular sequence suggested that their spatial memory span was below 4, while the “2arcs”, “2squares”, “2rectangles” and “2crosses” sequences involved dependencies spanning over 4 locations. This limitation could also explain the errors children made in “4diagonals”: even if they partially understood what the regularity was, they remained confused about distant locations.

An alternative explanation for the children’s failures is the sequences were not repeated long enough. Indeed, the simplifications that we introduced implied that children were presented with fewer sequence repetitions than adults. This is because, when subjects failed, the entire sequence was repeated, and there was more opportunity for failing in the adults than in the children’s version of the experiment. For instance, when kids were asked to guess the 13th location of a sequence, they had had at most 3 occasions to grasp the corresponding regularity on previous trials, while adults had up to 7 such occasions (assuming they frequently failed on previous trials). To address this issue, in experiment 3 we presented children with two complete previews of each sequence before the test phase started.

6. Experiment 3

6.1. Methods

6.1.1. Participants

Participants were 23 5-year-old children (minimal age = 4.67, max = 5.85, mean = 5.41 ± 0.07), tested at school during school-day.

6.1.2. Stimuli and procedure

The experiment was identical to experiment 2, except that each block started with two full viewings of the corresponding 8-location sequence, while the child was merely instructed to attend carefully. This provided an opportunity to memorize the sequence before the testing phase began.

6.2. Results

In spite of the additional training, the children’s results remained virtually unchanged (figure 4.5). Comparisons of experiments 2 and 3, at each data point of each category, indeed revealed no significant improvement.

In details, the mean error rate remained very high for “irregular” (86 ± 3%) and “4points” (73 ± 6%) sequences, and there was no significant improvement of performance neither in the first phase, nor in the second phase (“irregular”: 1st phase : F = 1.4, p = 0.5; 2nd phase : F = 0.83, p = 0.9; “4points” : 1st phase : F = 0.5, p = 0.78; 2nd phase : F = 1.17, p = 0.88). In “2points”, mean error rate

equaled $13 \pm 4\%$, and at all data points, error rate significantly differed from “irregular” (all $ps < 0.006$ corrected).

Again, for “repeat”, “repeat+2”, “2arcs”, and “4segments”, the mean error rate was significantly lower than baseline (Friedman test: all $ps < 0.007$): “repeat” (across 1st and 2nd stage: $10 \pm 3\%$ errors; on 1st stage only: $19 \pm 6\%$ errors), “repeat+2” ($32 \pm 8\%$; $39 \pm 9\%$ errors), “2arcs” ($55 \pm 6\%$; $52 \pm 9\%$ errors), and “4segments” ($56 \pm 6\%$; $61 \pm 7\%$ errors). In this experiment, the mean performance in “2squares” (overall error: $68 \pm 6\%$; 1st stage: $71 \pm 8\%$ errors) did not differ from baseline ($F = 2$, n.s). “4diagonals” ($78 \pm 4\%$; $80 \pm 6\%$ errors), “2rectangles” ($83 \pm 4\%$; $81 \pm 6\%$ errors), “2crosses” ($82 \pm 3\%$; $80 \pm 5\%$ errors), remained more challenging for children, with mean error rates not different from baseline (all $ps > 0.15$).

We again found a positive correlation between the mean error rate and the complexity of the sequences (at all data points: Spearman’s $\rho = 0.52 \pm 0.02$, Student t-test: $t_{22} = 19$, $p < 10^{-8}$; at data points 6-8: $\rho = 0.41 \pm 0.04$, $t_{22} = 10$, $p < 10^{-4}$). Again, the correlation was weaker in children than in adults ($t_{45} = 5$, $p < 2.10^{-5}$). Pooling across experiments 2 and 3, we found a global correlation between error rate and complexity equal to 0.51 ± 0.02 ($t_{46} = 23$, $p < 10^{-12}$), again significantly weaker than in adults ($t_{69} = 5.8$, $p < 10^{-6}$).

As in experiment 2, error rates on “repeat”, “repeat+2” and “4segments” were significantly better than baseline, and performance significantly improved over time, thus confirming that children were able to detect and use the primitive rules +1, +2 and axial symmetries (“repeat”: all $ps < 0.007$ corrected; improvement for 1st and 2nd stages: $F_s = 5.4$; 11.6 ; $ps < 0.05$; “repeat+2”: all $ps < 0.022$ corrected except at the 6th data point; improvement for 1st and 2nd stages: $F_s = 9$; 11.2 ; $ps < 0.03$; “4segments”: all $ps < 0.05$ corrected except at data points 6, 7 and 12; improvement for 1st and 2nd stages: $F_s = 8.9$; 15.6 ; $ps < 0.02$). As in experiment 2, children’ results on “4segments” were not influenced by the type of axial symmetry (vertical: $50 \pm 8\%$ errors; horizontal: $57 \pm 7\%$; oblique: $66 \pm 7\%$ and $56 \pm 8\%$; Friedman test for differences between the four types of symmetries: $F = 2.5$, n.s.). Error rate on “4diagonals” was not significantly better than baseline (all $ps > 0.1$), indicating that children again experienced more difficulty with rotational symmetry.

As in experiments 1 and 2, “2arcs” and “2squares” showed similar error patterns. “2arcs” provided evidence for the comprehension of the superficial rule: error rate was significantly below baseline at data points 8, 15 and 16 ($ps < 0.05$ corrected) and there was a significant improvement of performance over the 2nd stage ($F = 17.8$, $p < 0.002$). For “2squares”, error rate was not significantly below baseline, but there was a tendency at data points 8, 15 and 16 ($ps < 0.02$ uncorrected). As in

experiment 2, error rate at the 13th data point of “2arcs” and “2squares” was at baseline level ($p > 0.2$).

Finally, no evidence of learning was found in “2rectangles” and “2crosses”, for which error rate was not different from baseline (all $p > 0.2$) and no performance improvement was observed ($p > 0.3$).

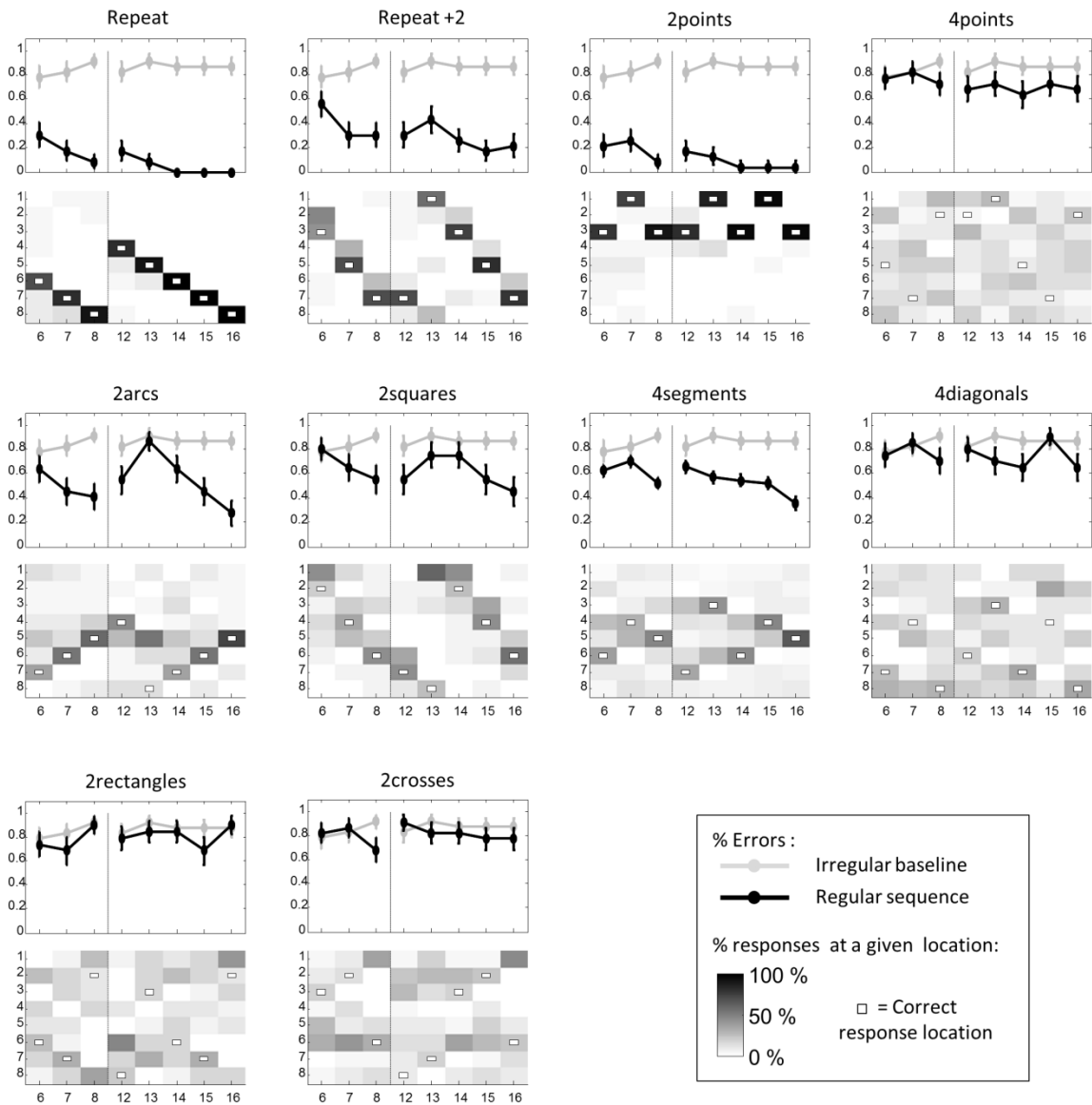


Figure 4.5. Performance of preschool children in experiment 3. Same format as figure 4.4.

6.3. Discussion

In spite of two additional viewings of the complete sequence, experiment 3 fully replicated experiment 2, thus affording several conclusions. First, +1, +2, and axial symmetries are geometrical primitives in children. Second, preschoolers are sensitive to embedded regularities in the “4segments” sequence. Third, under the present conditions, they fail to grasp more complex

embedded regularities. Previewing the sequences did not influence performance, suggesting that the latter conclusion cannot be attributed to a lack of exposure to sufficient evidence.

The difficulties that 5-year-old children experienced with rotational symmetry and with complex embedding could arise from several factors, including age and lack of education. In order to separate those factors, we thus performed a fourth experiment where we tested Amazon Indians (teenagers and young adults) with little or no access to education.

7. Experiment 4

7.1. Methods

7.1.1. Participants

During two field trips in 2014 and 2015, one of us (P.P.) collected behavioral data in Wariri, an isolated village of the upper Cururu region of the Munduruku main territory, located on the Anipiri River. 20 Mundurukus volunteered for this experiment: 14 teenagers (age range 10-14, mean = 12 ± 0.4) and 6 adults (age range 30-67, mean = 46 ± 6.6). As in many other villages of the Munduruku main territory, inhabitants of the Wariri village, including our volunteers, have poor and restricted access to schooling and have a very partial command of Portuguese. Munduruku language is quite impoverished in number words and Euclidean geometrical terms (Dehaene et al., 2008, 2006). Still, previous research has shown that Mundurukus are able to grasp sophisticated concepts of number and space in an approximate and nonverbal manner (Dehaene et al., 2008, 2006; Izard et al., 2011b; Pica et al., 2004).

7.1.2. Stimuli and procedure

Munduruku subjects found the adult version of the task exceedingly dull and could not be persuaded to complete it, so we substituted the shorter but analogous children's version. The design was thus exactly the same as experiment 3 with children.

7.2. Results

For "irregular", the mean error rate equaled $78 \pm 3\%$ and we observed a small but significant decrease in error rate in the second phase ($\rho = -0.25$, $p = 0.035$), indicating rote learning of the succession of positions. This ability to learn positions was confirmed by performance on the "4points" sequence, with a mean error rate of $49 \pm 8\%$, and error rates significantly below baseline at data points 6 and 12 ($ps < 0.013$ corrected). Participants also quickly grasped the sequence "2points", with a mean error rate of $5.6 \pm 2.8\%$, and an error rate below the baseline from the beginning to the end of the trial (all $ps < 0.013$ corrected).

For all regular sequences, except "2crosses", the mean error rate was significantly lower than baseline (Friedman test: all $ps < 0.003$): "repeat" (across 1st and 2nd stage: $2.5 \pm 1.2\%$ errors; on 1st

stage only: $5 \pm 2.8\%$ errors), “repeat+2” ($1.3 \pm 0.9\%$; $1.7 \pm 1.7\%$ errors), “2arcs” ($16.9 \pm 5.9\%$; $23.3 \pm 8.6\%$ errors), “2squares” ($26.9 \pm 5.4\%$; $18.3 \pm 6.8\%$ errors), “4segments” ($12.1 \pm 2.8\%$; $16.1 \pm 3.6\%$ errors), “4diagonals” ($59.4 \pm 5.3\%$; $55 \pm 6.2\%$ errors) and “2rectangles” ($53.1 \pm 5.3\%$; $51.7 \pm 6.3\%$ errors). However, the mean performance in “2crosses” ($78.1 \pm 3.2\%$; $78.3 \pm 5.7\%$ errors) did not differ from baseline ($F = 0.29$, n.s.).

We again found a positive correlation of the mean error rate with the complexity of the sequences (at all data points: Spearman’s $\rho = 0.59 \pm 0.02$, Student t-test: $t_{19} = 28$, $p < 10^{-12}$; at data points 6-8: $\rho = 0.51 \pm 0.05$, $t_{19} = 11$, $p < 10^{-5}$, Figure 4.3C). In this group of teenagers and adults Mundurucus, the correlation was weaker than in adults’ group ($t_{41} = 3.71$, $p < 0.001$), but slightly greater than the correlation observed in both groups of children ($t_{66} = 2.00$, $p = 0.05$).

Munduruku teenagers and adults quickly detected and used the rules +1, +2 and all axial symmetries, as shown in figure 4.6 by error rates on “repeat”, “repeat+2”, and “4segments”, that were below the baseline (“repeat”: $p_s < 0.008$ corrected; “repeat+2”: $p_s < 0.004$ corrected; “4segments”: $p_s < 0.037$ corrected except at the 15th data point). The mean error rate was similar for horizontal, vertical, and oblique symmetries (vertical: $7.5 \pm 3.3\%$ errors; horizontal: $25.6 \pm 8.4\%$; oblique: $9.4 \pm 3.5\%$ and $11.6 \pm 6.6\%$; Friedman test for differences between the four types of symmetries: $F = 3.4$, n.s.). It is less clear, however, that participants were fully able to detect and use rotational symmetry, as performance with “4diagonals” was not significantly better than the baseline, but there was a tendency at data points 6, 8 and 14 ($p_s < 0.04$ uncorrected).

“2arcs” and “2squares” again showed similar error patterns, suggesting that participants were able to understand both superficial and deep rules. For “2arcs”, error rate was significantly below baseline at all data points (shallower rule at points 6-8, 12, 14-16: all $p_s < 0.018$ corrected; deeper rule at point 13: $p = 0.031$ corrected). For “2squares”, error rate was significantly below baseline at all data points except the 13th and 16th (all $p_s < 0.037$ corrected).

On “2rectangles”, the error rate was significantly below the baseline at the 12th data point ($p = 0.013$ corrected), indicating that some features of this three-levels sequence were grasped by participants. “2crosses” was more challenging, and the Munduruku never managed to perform better than baseline.

Interestingly, whenever there was a difference, Munduruku teenagers and adults systematically performed better than French children and worse than French adults.

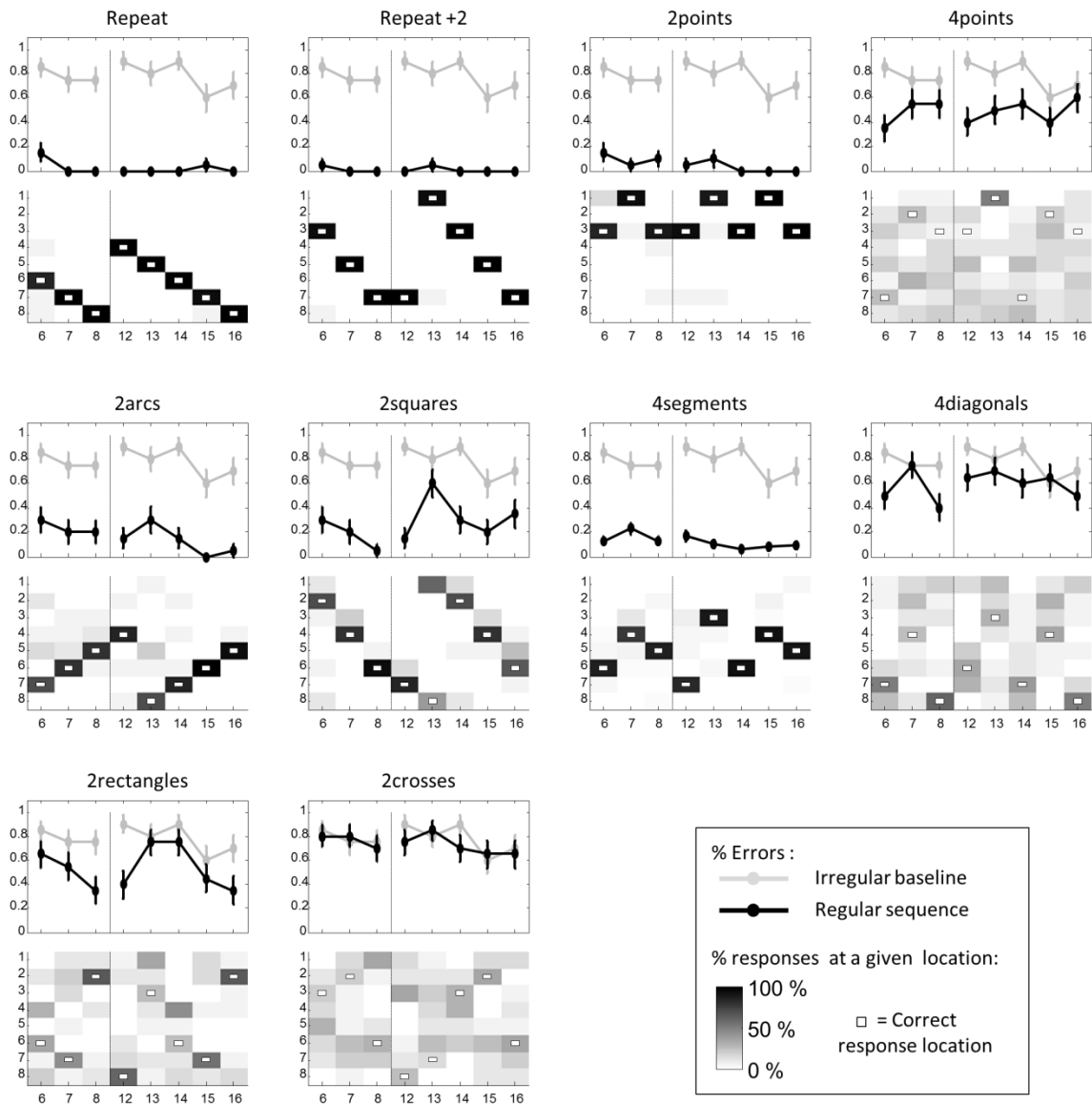


Figure 4.6. Performance of Mundurucu participants in experiment 4. Same format as figure 4.4.

7.3. Discussion

Mundurucu teenagers and adults, although having a limited access to schooling, performed at a level close to French adults, their answers providing evidence for a quick understanding of most of the geometrical primitive rules (+1, +2 and axial symmetries), and for an ability to detect different levels of embedded regularities. Only rotational symmetry was not clearly detected, perhaps explaining their poor performance on “2crosses”. All in all, the results suggest that geometrical primitives and their combinations are available to human adults and teenagers after minimal experience, even in the absence of formal education.

8. Detailed fitting of the “language of geometry” model

The above data indicate that adults quickly infer an internal representation of an unfolding geometrical sequence and use it to predict what comes next. Our experiment is predicated upon the

hypothesis that this representation takes the form of a “language of thought” (Fodor, 1975; Romano et al., 2013) : a set of precise primitive instructions that can be combined into complex expressions that faithfully capture the observed geometrical sequence. The language that we proposed supposes that 2 squares or 2 arcs can be compactly represented by two nested repetitions, and 2 rectangles or 2 crosses by 3 nested repetitions. At the same time, plausibly, it does not attribute a compact form to complex sequences where humans do not detect any specific regularity. Overall, those hypotheses seem to be correct inasmuch as complexity is a good predictor of error rates. In the present section, we go one step further and ask whether the language predicts, in a quantitative manner, why and when errors arise.

8.1. Model description

To predict sequence continuation behavior, we may assume that at any given moment, subjects hold on to the simplest possible hypothesis concerning the current sequence, and use this hypothesis to predict the next items. Formally, after observing the first n items in a sequence (hereafter the “prefix”), subjects identify the shortest expression compatible with this prefix, and then compute the continuation of this expression.

Because actual performance presented some degree of stochasticity, we also introduced what seems to be a natural source of noise in this model. Our proposal is that, as the length of an expression increases, the probability that the subject fails to properly estimate its length increases. We model this by assuming that program length is evaluated with a degree of randomness, i.e. additive Gaussian noise with standard deviation σ (constant across all sequences). Moreover, to avoid a systematically perfect performance at the last data point, we assumed that the model can only compute expressions up to a certain complexity. Here, we set a maximal capacity to $K_{\max} = 12$. Whenever a prefix implies an expression with $K > 12$, the algorithm selects a response at chance.

The initial sequence (S) comprises the first two locations shown to the subject. From this point, the model constructs the sequence by adding one location at a time until it reaches 8, following the pseudo-algorithm below (Figure S2):

While Number of locations < 8 :

- 1) Consider all programs that generate sequences of 8 locations and share the prefix S .
- 2) Estimate the length of those programs, assuming that this estimation has Gaussian noise given by the free parameter σ .
- 3) Choose the sequence S' whose prefix matches S and which has complexity $K(S')$. If there is more than one such sequence, choose randomly between them.

4) If $K(S') \leq K_{max}$, then generate as a prediction the next location predicted by sequence S' ; otherwise, generate a prediction at random.

8.2. Fits to adults' data

To evaluate the fit of the model to the data, we only considered the 8 sequences that were used in all groups and involved no repetition of the 8 locations. The model captured in a very robust manner, independently of parameter values, the most salient aspects of the data (figure 4.7). First, it shows different degrees of performance for each sequence in agreement with the data: close to perfect performance for the repeat sequence, close to chance performance for the irregular sequences, and an intermediate progression for other sequences. The model also captures an overall trend for improving performance as the sequence progresses and, crucially, each of the local drops in performance that arise at specific points within each sequence. Indeed, the model fully accounts for the precise time points at which they occur (odd-numbered time points 3, 5 and sometimes 7, as explained in the results section).

To obtain those results, the only free parameter of the model, σ , was fit by minimizing the mean square errors (MSE) across all time points and all sequences. For each value of σ we performed 300 runs and calculated the average performance of the model for each position of the sequence. This analysis revealed a very clear minimum for $\sigma=2$ (figure S3). For reference, we compared this with the MSE of the simplest possible fit, consisting in a constant level of performance, distinct for each sequence (for a total of 8 parameters). Within a broad range of noise (including the noiseless model with $\sigma=0$) the language-of-geometry model, with its single degree of freedom, performed better than this 8-parameter model. As shown in figure S3, even the performance of the noiseless model, while more discrete than the real data, captures the main aspects of our results.

8.3. Fits to children's data

Our model captures, without any fine parameter tuning, the nonlinear performance functions exhibited by educated adults, by assuming that they use all of the primitives available in our language. Young children or uneducated adults, however, may not master the full language of geometry.

We thus examined, first, which transformation of the model could account for the children's data. We started by fitting the parameter σ , again using 300 independent runs for each value of σ . This analysis showed that no amount of noise could fit the data adequately. This was confirmed quantitatively (MSE for all noise values were greater than 0.3) and also from visual inspection which revealed a pattern very different from the data (figure 4.7). Notably, even for the best fit, performance was massively underestimated for low-complexity sequences such as repeat or 2arcs, while being massively over-estimated for high-complexity sequences such as 2rectangles or 2crosses.

We next examined the hypothesis that children may have additional sources of noise. Specifically, we supplied the model with an additional source of noise in the execution of each program. We assumed that the model could generate a random response (an execution error) with a probability given by a second parameter σ_2 . These two sources of noise had different effects on the simulated data. Yet, even with the inclusion of this additional noise parameter, the model still performed very poorly. Indeed, MSE values were greater than 0.18 for the full set of parameters, and the best fits were achieved with a very high execution noise, which resulted in an ability to predict the fine-grained structure of errors: the model performed in a highly unstructured manner, with a low and flat performance within and across sequences (figure S4).

As a third step, instead of implementing a noisy version of the full language, we assumed that children might use a subset of the language. For instance, their mental programs might lack some of the primitive instructions, or might not be able to express deep levels of nested repetitions. Based on the above results, we examined a semantically and syntactically restricted language devoid of (a) rotational symmetry primitive P (b) the ability to encode nested repetitions: while the original language allows for “repetitions of repetitions”, e.g. to encode the 2squares sequence, we assumed that young children may only be able to encode a single level of repetition. For simplicity, we do not report here a full exploration of other possible sub-languages, which yielded no better fit.

We further assumed that the use of those two resources is probabilistic. This assumption was meant to capture variability both within subjects (e.g. a child may understand nesting and yet fail to use it on some trial) as well as between subjects (some children may not be capable of encoding nested structures). Accordingly, the original model (with single parameter σ) was supplemented with two additional parameters: p_{NEST} , the probability of using nested sequences with repetitions of repetitions, and p_P , the probability of using instruction P.

Our model, in this version, cannot distinguish between these alternatives. We do show below an analysis of correlations that shows that children that perform poorly in a sequence that uses the P instruction also tend to have bad performance in other sequences that use the P instruction. This suggests that, to a certain degree, there is variability in the population of young children in the degree of consolidation of their language of geometry.

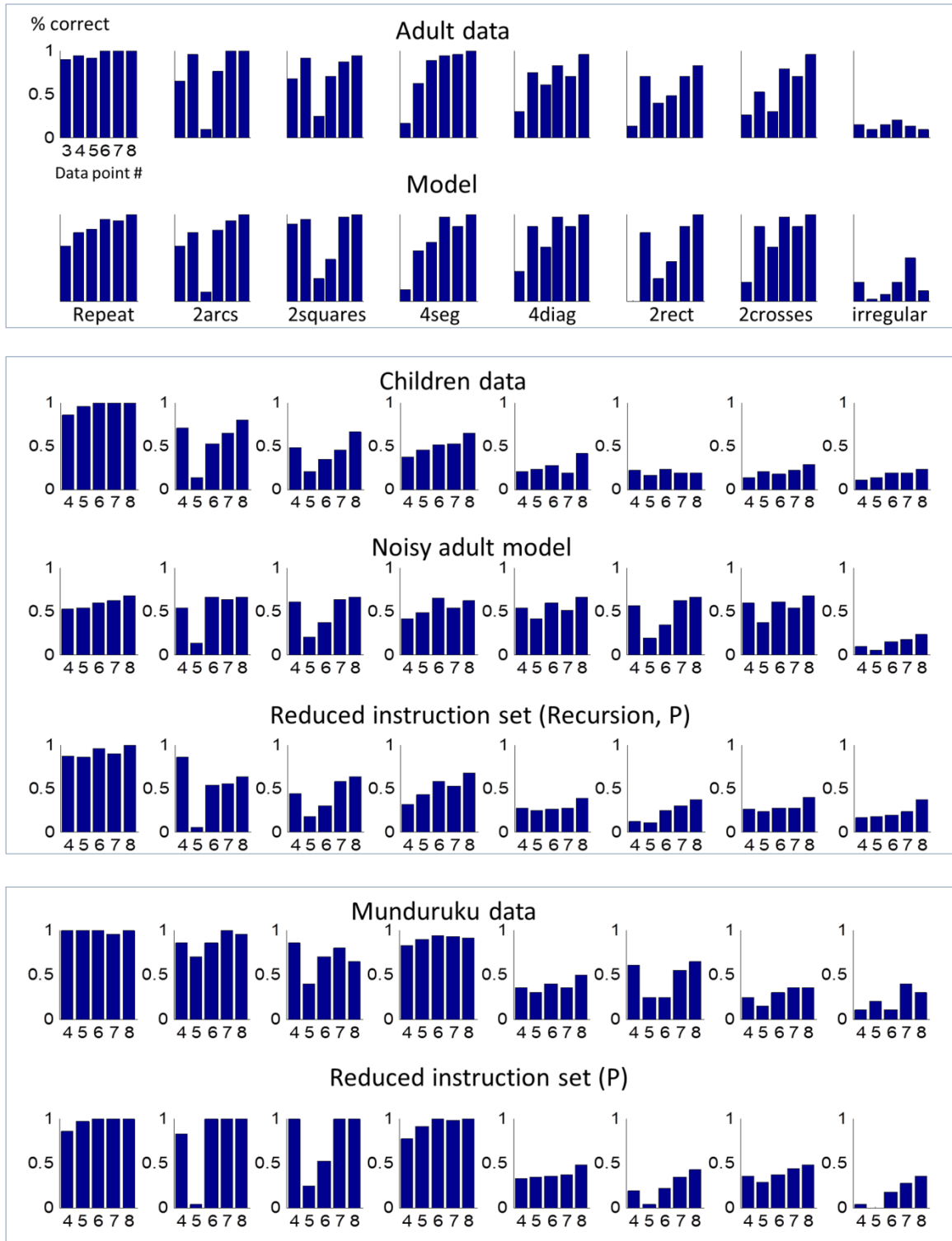


Figure 4.7. Model fits to subjects' data. Comparisons of the correct rates exhibited in completing regular and “irregular” sequences by French adults (top), preschool children (middle) and Munduruku teenagers and adults (bottom) with the performance of our model in its full version (for French adults—top), then in a noisy version (for children—middle), and finally in a version that includes a reduced instruction set (for children—middle; and Mundurukus—bottom).

To fit the data, we performed 300 independent runs of the model for a fixed level of $\sigma=3$ and without program execution noise ($\sigma_2 = 0$). For each run we generated two random variables that determined, with probabilities p_{NEST} and p_P respectively, if all sequences that used nesting or the

instruction P had their complexity set to the maximum value of $K=12$. This is equivalent to stating that any expression using these resources exceeds K_{\max} and hence cannot be used to extract regularities (note that the alternative, which would have been to recompute all complexities K for the language with reduced instruction set, was not available because the language without the instruction P cannot generate the full set of sequences).

Varying p_{NEST} and p_P showed that:

1) The best performance is achieved for values $p_{NEST}=0.14$ and $p_P=0.18$, which captures the children's performance in great detail (figure 4.7). These are relatively low values indicating that for the majority of children and/or trials, these resources are indeed not used to extract regularities.

2) While these values are low, a language entirely lacking these resources fits the data quite poorly, showing near-chance performance for all sequences, except for the simplest repetition of +1. (Figure S5, Panel marked "Full Reduced Instruction set")

3) Removing the instruction P but allowing all levels of nesting, results in a very different pattern of performance, with near-perfect performance for 4 out of the 8 sequences (figure S5, panel marked "No instruction P, normal nesting")

8.4. Fits to Munduruku data

As with children, the noisy version of the full model could not account for the data ($MSE > 0.19$ for the best fit). The analysis varying p_{NEST} and p_P showed that:

1) The best performance is achieved for values $p_{NEST}=0.54$ and $p_P=0.26$ (figure S6). Note that both values, especially p_{NEST} , are higher than those obtained for young children.

2) As with the young children, a language which never uses nesting or P (i.e. with $p_{NEST}=0$ and $p_P=0$) cannot account for the data, as its performance is close to chance for all sequences, except for the simplest repetition of +1. (Figure S6, Panel Full Reduced Instructions)

3) However, compared to young children, a simplified version of the full model, removing only the instruction P but allowing all levels of nesting, results in an acceptable fit, very similar to the best fit. In fact, a plot of the value of MSE for varying probabilities (figure S6, color matrix) shows that the fit varies little over a broad region that includes high values of p_{NEST} . Thus, compared to children, simply lowering the probability of using P resulted in an accurate description of the Munduruku data (figure 4.7).

9. Discussion

The aim of our research was to evaluate whether the human memory for spatial sequences provides evidence for (1) an understanding of simple geometrical primitives in both educated and uneducated humans, (2) a capacity to combine those primitives into complex embedded expressions, and (3) a notion of sequence complexity based on minimum description length. We discuss those aspects in turn.

9.1. Geometrical primitives

The findings from four experiments suggest that simple rotations (equivalent to the rules ± 1 , and ± 2) and vertical, horizontal and oblique symmetries were all detected and quickly used by human adults with various cultural backgrounds and 5-year-old children. These results are consistent with previous work highlighting the importance of the detection of symmetries in shape perception (Giaquinto, 2005; Leyton, 1988; Machilsen et al., 2009; Pizlo et al., 2010; Westphal-Fitch et al., 2012) or in spatial navigation (Cheng, 1986; Lee and Spelke, 2008). The primitive operations postulated in our language (± 1 , ± 2 , axial and rotational symmetries) may form part of the “core knowledge” of mathematics which is thought to be shared by all humans (Izard et al., 2011a). In Plato’s *Meno* (~ 380 B.C.) (*Meno* by Plato, n.d.), Socrates, after interrogating an uneducated Greek slave on the area of various squares drawn in the sand, already concluded that “his soul must have always possessed [the] knowledge” (for a recent replication, see (Goldin et al., 2011)). Recent evidence has confirmed the existence of core geometrical knowledge shared with other animal species and available in early infancy (Cheng, 1986; Lee et al., 2012; Lourenco and Huttenlocher, 2008; Spelke and Lee, 2012; Vallortigara et al., 2009). In particular, previous research with American and Mundurucu adults and children led to the conclusion that they all exhibit a shared competence for various concepts of topology, Euclidean geometry, and basic geometrical figures (Dehaene et al., 2006; Izard et al., 2011b).

It could be argued that the present language mixes purely geometrical properties (axial and rotational symmetries) with other arithmetic (+1, +2, +3) and abstract algebraic features (repetition). However, such a mixture is probably indispensable if we consider that geometry is a branch of mathematics concerned with questions of shape, size, relative position of figures, and the properties of space. Integers, although conceivably part of a distinct system of arithmetic, are indispensable to capture even basic geometrical concepts such as “square” or “triangle”. Numbers and space are tightly intertwined concepts, and the metaphor of numbers as a measure of space (which is the etymology of “geo-metry”) played a foundational role in the history of mathematics from Pythagoras and Euclid to Descartes and Hilbert. Mathematics is a unified discipline in which it is difficult to

delineate the boundaries between geometry and other domains, and the present language reflects this simple fact.

Interestingly, previous behavioral studies also concluded that symmetries and other geometrical transformations were more difficult for Mundurucu adults, Mundurucu children or American children than for educated American adults (Dehaene et al., 2006). The present results are in agreement with this conclusion, inasmuch as (1) axial symmetries induced more errors for Mundurucu than for French adults and even more errors for French preschoolers than for Mundurucu and French adults together; (2) rotational symmetry was quickly detected by French adults, but not by French preschoolers or Mundurucu adults; (3) combinatorial rules that consisted in a global symmetry or rotation of a geometrical shape (e.g. in “2arcs” or “2squares”), were harder to detect for Mundurucu than for French adults and even harder for French preschoolers than for Mundurucu and French adults together.

One might argue that children and Mundurucus’ failure to detect rotational symmetry might be due to a greater movement distance in “4diagonals” than in “4segments”. However, this argument is made less plausible given that the successive distances between points 4, 5 and 6 of the “4segments” and “4diagonals” sequences are exactly the same, and yet the error rates are lower in “4segments” than in “4diagonals”. This observation suggests that distance had a much lesser influence, if any, than the capacity to encode rotational symmetry. It seems that rotational symmetry is inherently a more difficult mathematical concept. Nevertheless, our model simulations suggest that it was not entirely lacking in Mundurucu or in children, but merely probabilistically absent in some trials and/or some children.

9.2. Embedded expressions

Our findings also suggest that human subjects were able to detect most of the embedded expressions we used to define our visuospatial sequences. In details, all subjects easily detected simple repetition (repeat sequence) as well as the concatenation of two instructions underlying the alternate and “2points” sequences. Evidence for repetition with variation was also found in all groups of subjects. In particular, educated adults easily detected and encoded a systematic change in the starting point of a geometrical shape (e.g. “2squares”), or a global transformation applied to the whole shape (e.g. “2arcs”). In Mundurucu, the application of these combinatorial rules was more challenging, but still led to a significant level of success. Finally, 5-year-old children performance on “4segments” tended to show that they were able to apply a repetition with a change in the starting point, and their performance on “2arcs” suggested that they were also able to apply a global symmetry.

The analysis of error patterns provided direct evidence for hierarchical embedding. Superficial rules were acquired more quickly and induced fewer errors than deeper rules. In French and Mundurucu adults, the quantitative error patterns, peaking at odd-numbered time points 3, 5 and 7, were consistent with a single level of embedding for “repeat”, “repeat+2” and “alternate”; two levels of embedding for “2arcs”, “2squares”, “4segments” and “4diagonals”; and three levels of embedding for “2rectangles” and “2crosses”.

These findings thus suggest that subjects spontaneously detected the recurrence of low-level subsequences that shared a common instruction, and then combined them into hierarchically organized expressions. Those conclusions agree with those made in another domain by Kotovsky and Simon (Kotovsky and Simon, 1973): when learning a series of letters, adults first detected the periodic recurrence of some letters, then used it to infer higher-order rules. These authors showed that the postulation of a hierarchical organization of rules was crucial in capturing the subjects’ behavior.

Moreover, the good performance achieved by subjects on time points 6, 7 and 8, even before the entire sequence had been presented, indicates that they quickly inferred an internal representation of the sequence and used it to predict the next locations. This is consistent with works led by Restle in the 70’s (Restle, 1973, 1972, 1970; Restle and Burnside, 1972), in which he showed that adults, when asked to anticipate or track the positions of a series of flashes, easily grouped consecutive items in what he called “runs” (e.g. 1-2-3, where numbers refer to ordinal positions) or “trills” (e.g. 1-2-1-2) and used these regularities to predict the next locations. Restle’s research showed that adults progressively learned how to combine “runs” and “trills” by building a mental tree structure that encoded the sequence of flashes they had been presented with (Restle, 1973, 1972, 1970; Restle and Burnside, 1972).

Our experiments 2 and 3 showed that 5-year-old children experienced difficulties in understanding complex sequences, either involving rotational symmetry or the use of multiple nested calls to the “repeat” instruction. The latter finding, using temporal spatial sequences, can be related to research on the perception of static spatial patterns in childhood (M. D. Martins et al., 2014). Using fractals, Martins et al. tested 7-8 year-old and 9-10 year-old’s ability to represent recursive rules (generating additional hierarchical levels) versus iterative rules (inserting additional items within an existing hierarchical level). They concluded that all children could detect iterative rules, but only fourth graders (9-10 years-old) were able to detect recursive rules.

Collectively, those results suggest an influence of age or education level on the ability to understand hierarchically organized geometrical rules. Crucially, however, Mundurucu teenagers and

adults, who lacked school-based education, performed better than children on sequences with 2 or 3 levels of embedding. Indeed, their results could be accounted for solely by the absence of rotational symmetry. This finding suggests that schooling may not be necessary for the development of the ability to understand nested rules. With age, it seems that a geometrical language with embedding arises even in the absence of formal schooling. In fact, even in young children, the failure with complex sequences need not be due to a lack of understanding of nested structures, but could arise from limitations in working memory, inasmuch as the detection of such sequences requires a visual memory span of at least four. Indeed, even in the absence of any regularity, children failed in memorizing an irregular sequence of length 4, suggesting that their visuo-spatial memory span was below this critical value. Further work will be needed to assess whether children would succeed with nested structures if the working memory load was alleviated.

9.3. Minimal description length as a predictor of spatial memory

We defined the theoretical complexity of a sequence as the length of the shortest expression capable of generating it (following Kolmogorov's ideas (Li and Vitanyi, 2013) and the minimum description length principle (Grunwald, 2004)). In educated adults, this measure of complexity was an excellent predictor of the mean error rate (figure 7), suggesting that it provides a good approximation of the internal representational complexity of spatial sequences. Such a relationship is in accordance with previous works on conceptual learning. Feldman (Feldman, 2000), following earlier work by Shepard, Hovland and Jenkins (Shepard et al., 1961), showed that the description length of Boolean concepts captured the difficulty that humans experienced in learning these concepts. Minimal description length was also successfully used by Bradmetz and Mathy (Bradmetz and Mathy, 2006) to model the response times of human adults in a task requiring conceptual learning of classification rules. Moreover, Mathy and Feldman (Mathy and Feldman, 2012) found that minimal description length was positively correlated with the memorability of a sequence of digits. Our findings confirm that minimal description length provides a reasonable approach to adult sequence learning capacity. For children and Mundurucu subjects, a language with reduced instruction set led to similar conclusions.

In passing, we note that there is a near-complete equivalence between the present Kolmogorov-complexity approach and Bayesian model-selection approaches to sequence learning (Feldman, 2000; Yildirim and Jacobs, 2015). In (Feldman, 2000), internal models are first assigned a prior probability proportional to their complexity, and then this probability is increased or decreased depending on how well each model accounts for the incoming data or, on the contrary, generates a prediction error. This is tantamount to selecting the simplest program that accounts for the observed data, as we do here. In (Yildirim and Jacobs, 2015), the multi-sensory representations of visual or

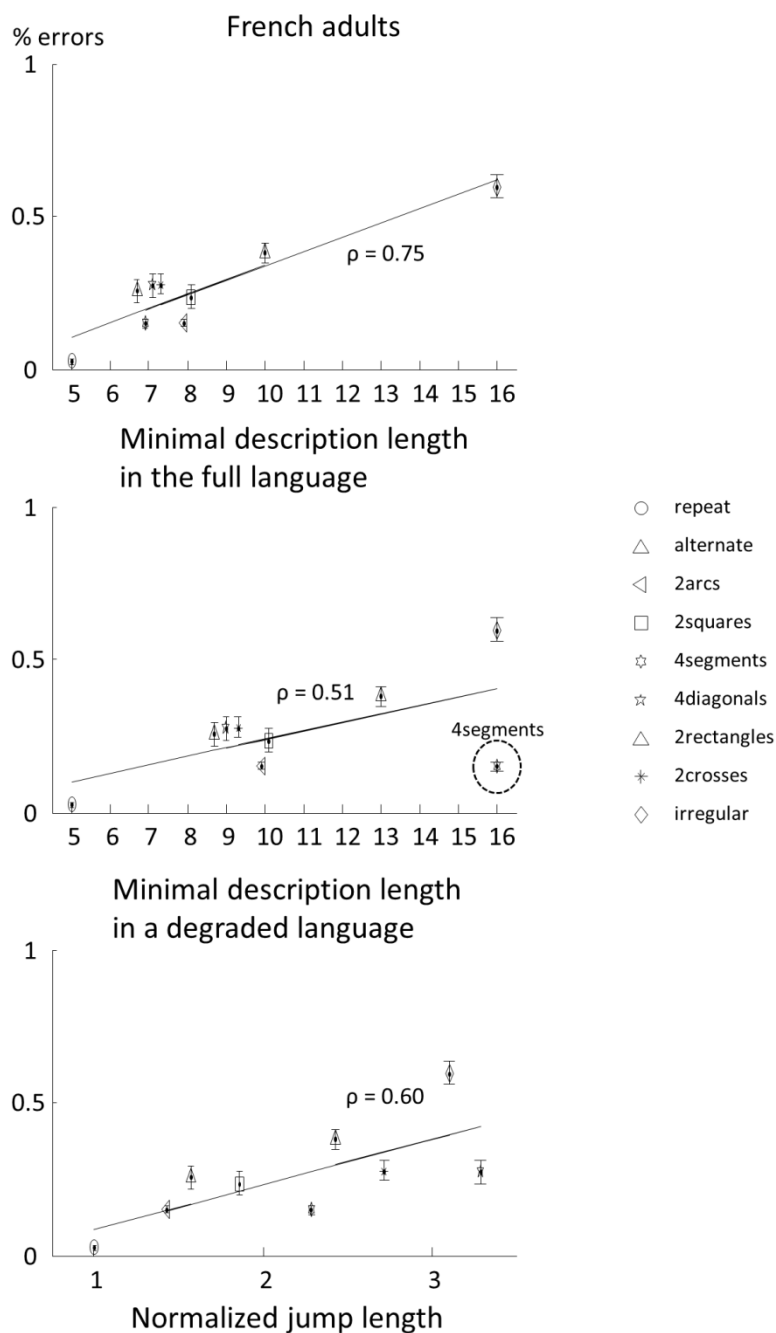
auditory sequences of locations around a circle were modeled as computer programs. These programs were formalized using a probabilistic context-free grammar, and learnt via Bayesian inference. Similar to our work, the prior distribution favored the simplest, shortest programs. We also note that the spatial language using in ref. 40 was closely related to ours (including instructions “next” and “prev” similar to our +1 and -1, loops and recursion). Crucially, however, it lacked geometrical primitives such as horizontal or vertical symmetry that the present work suggests are essential to capture the organization of more complex spatial sequences.

We end by pointing to several limitations of this work. Our model rests on a narrow language that should not be taken as a complete description of “core geometry”. Many additional primitives, both geometrical (e.g. right-angle, parallelism, triangle, distance...) and non-geometrical (e.g. integer sequences) would need to be added to capture the full range of core human intuitions (Dehaene et al., 2006). A particularity of our language resides in the fact that each location is defined relatively to preceding ones thanks to the application of a given geometrical rule. While this choice allowed for a simple definition of complexity, it also resulted in the fact that some simple geometrical shapes could not be easily captured. For instance, in the current language, a circle or an equilateral triangle could not be described. In the future, the present methodology should be extended in order to fully characterize the range of sequences, shapes and scenes that humans readily consider as “geometrically simple”.

10. Supporting information

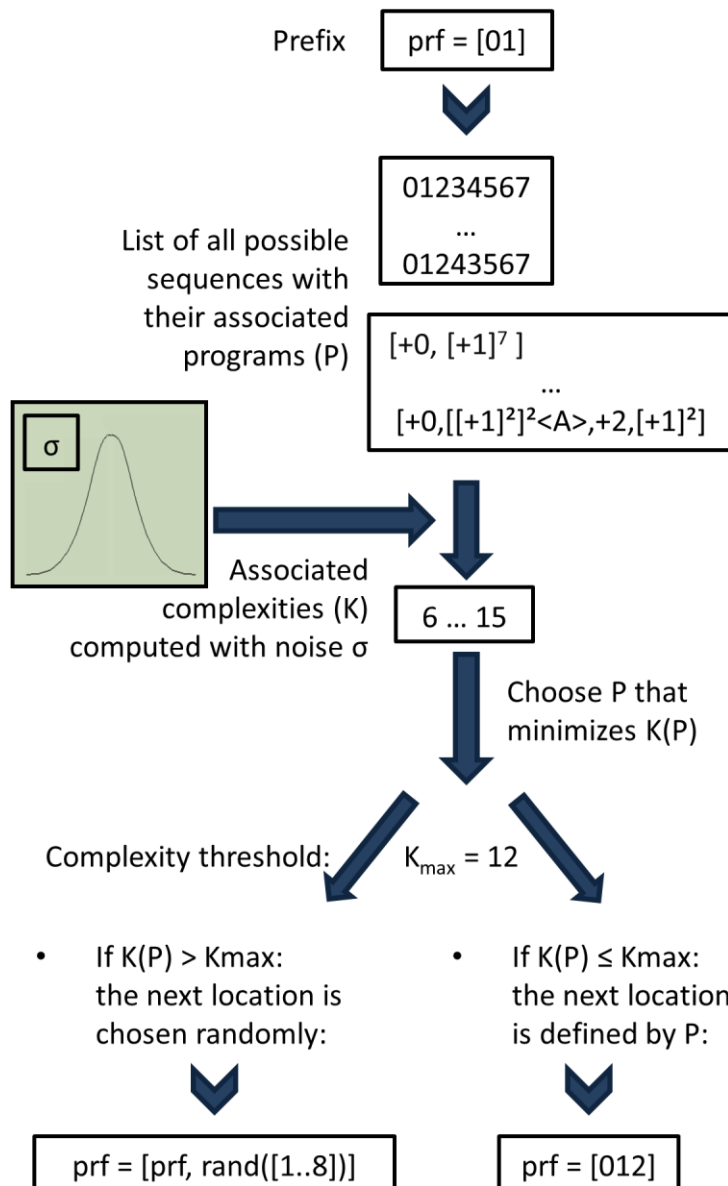
S1 Fig. Comparison of different potential predictors of error rates.

For each sequence, the y axis represents the mean error rate of French adults, and the x axis the sequence complexity, as measured by complexity computed in the full language (top), complexity computed in a degraded language including only the rules ± 1 , ± 2 , ± 3 , ± 4 and repetitions without symmetries (middle), and the normalized jump length of a sequence (bottom). Regression lines are also plotted and Spearman's correlation coefficients are displayed. The middle and bottom plots reveal clear outliers.



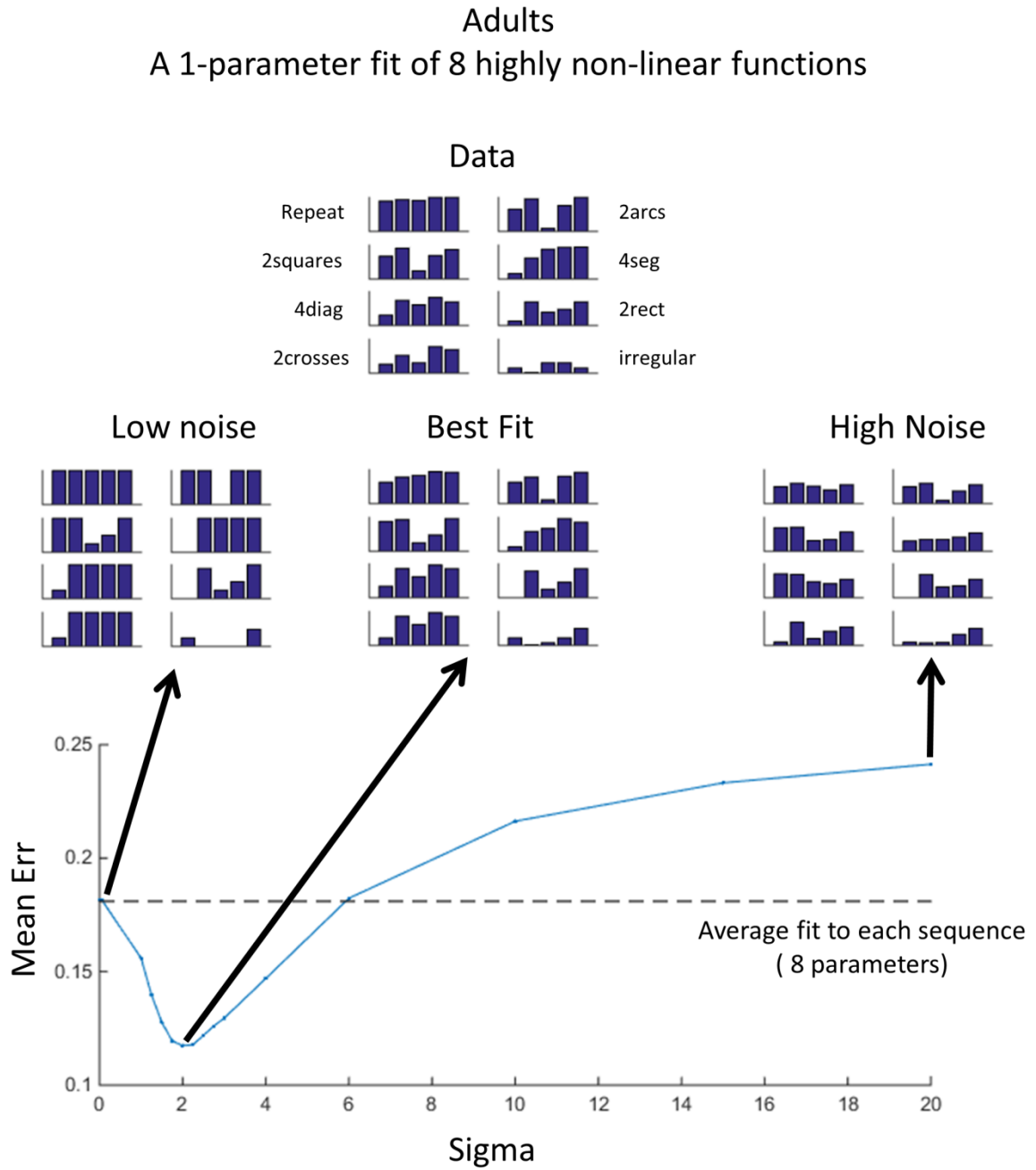
S2 Fig. Model description.

Starting from prefix prf, the algorithm lists all possible sequences and their associated programs P in our language, computes their associated complexity K(P) introducing Gaussian noise, then chooses the program that minimizes K(P), and completes the prefix prf with the next location either defined by P if K(P) does not exceed the complexity threshold Kmax, or chosen randomly if K(P) is greater than Kmax.



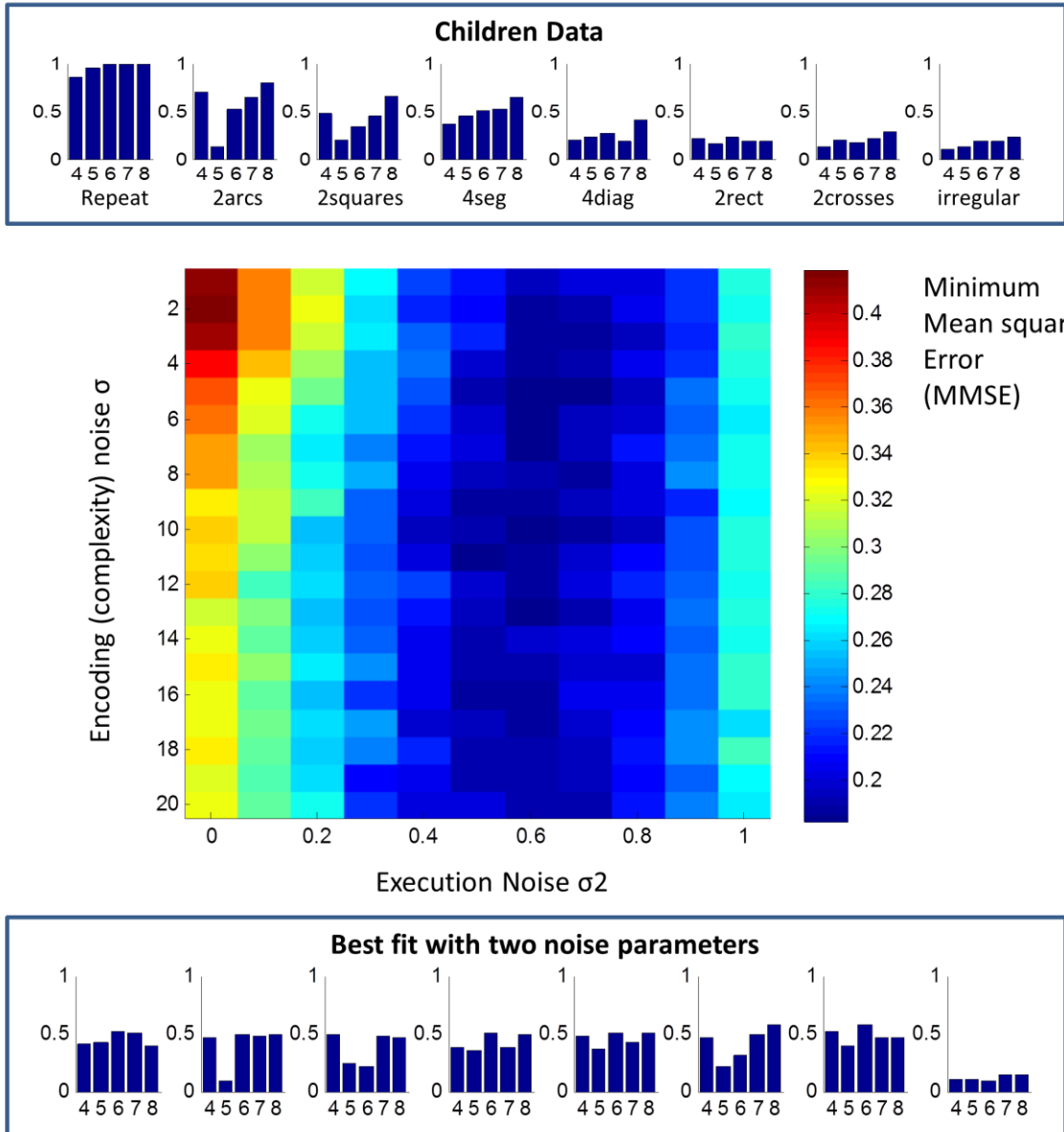
S3 Fig. Fit of the data for varying values of σ .

Even for low values of noise, the model identifies the pattern of performance throughout the sequences (compare to the top panel showing the data for adults).



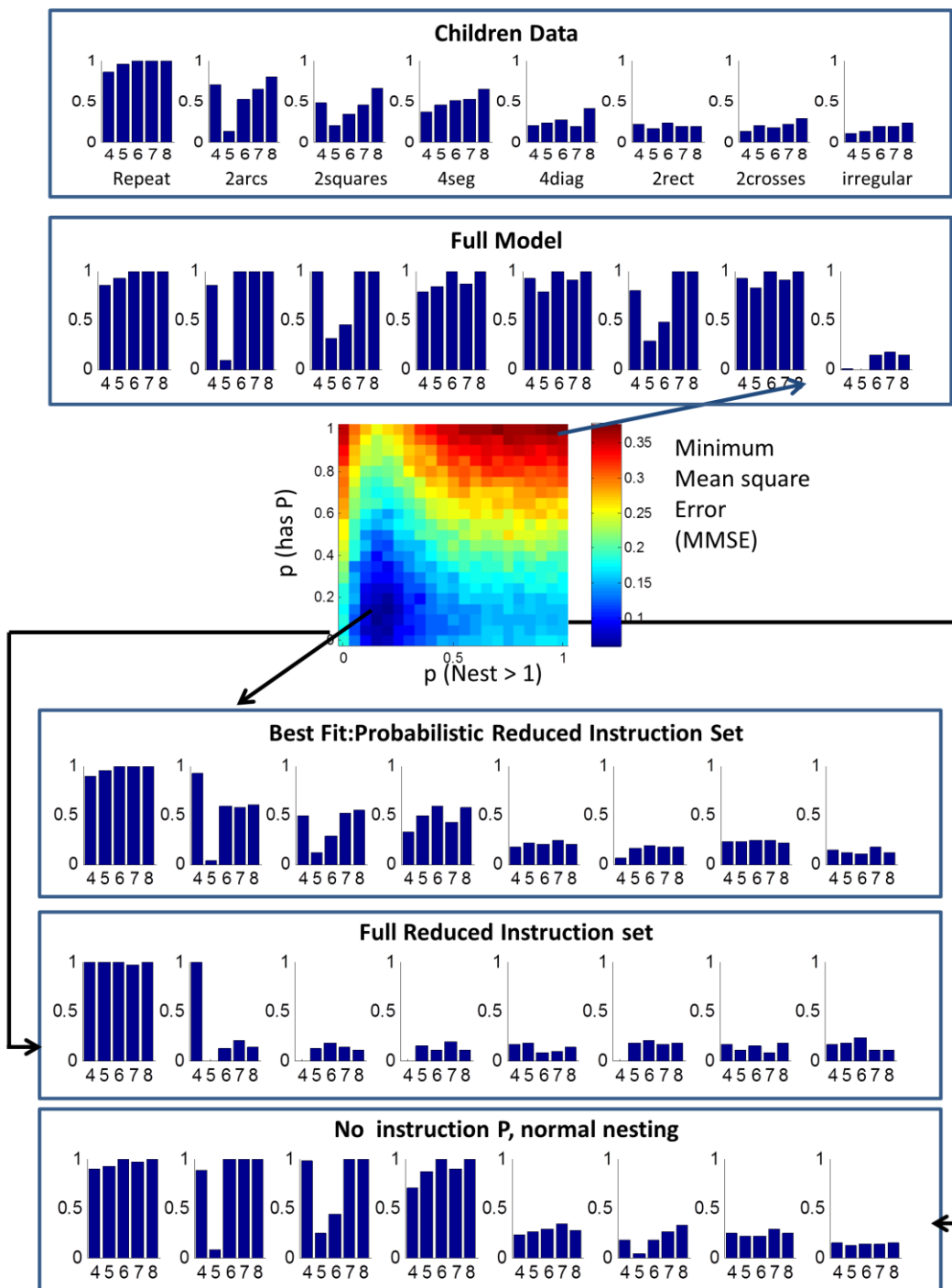
S4 Fig. Fit of children's data using a noisy version of the adult geometrical language.

The top panel shows the observed performance in preschoolers for each sequence. The matrix in the middle shows the minimum mean square error (MMSE), i.e. the quality of the fit, as a function of the amplitude of the noise in encoding σ and execution σ_2 . Even the best-fitting model with these two noise parameters (bottom) shows a performance very different to the data, with almost equal performance for all sequences.



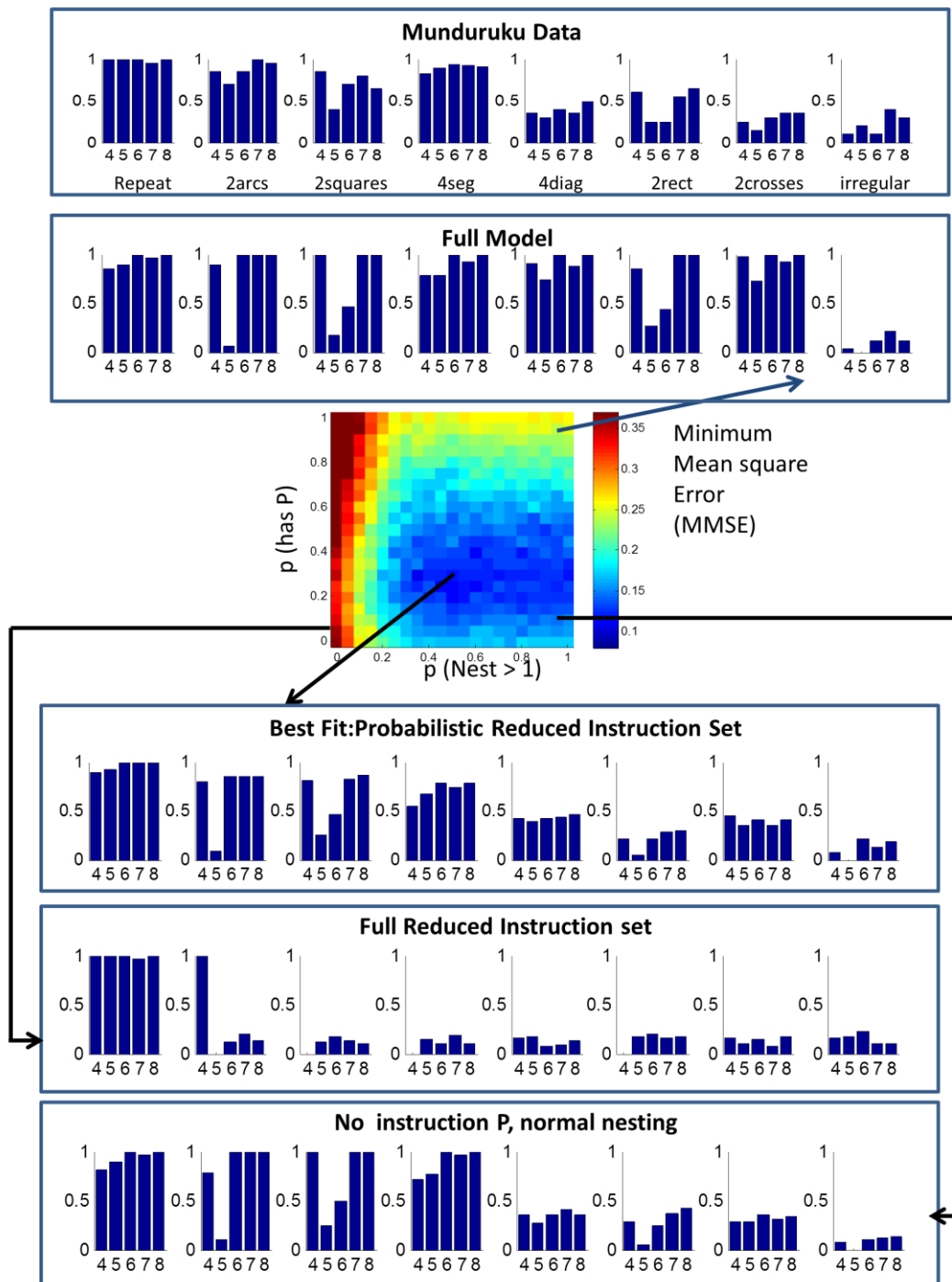
S5 Fig. Comparison of different fits of children's data.

Children data (top panel) is not well described by the adult geometrical model (second panel from the top). The matrix in the center shows the quality of the fit as a function of the probability p_P of having the P instruction (+4) and the probability p_{Nest} of having Nest > 1 in the language. The data is best captured by a model with low values of P and Nest >1 (third panel). However, when making these probabilities equal to zero (fourth panel) the model describes the data very poorly. Similarity, a model allowing for full nesting while fitting p_P (fifth panel) inappropriately predicts near-perfect performance for the first four sequences.



S6 Fig. Comparison of different fits of Mundurucus' data.

Mundurucus' data (top panel) is not well described by the full model (second panel from the top). The image in the center shows the quality of the fit as a function of the probability of having the P instruction (+4) and the probability of having nested repetitions in the language. The data is best captured by a model with low but non-zero values of p_P and p_{Nest} (third panel). Letting these probabilities equal to zero (fourth panel) leads to a model that describes the data very poorly. A model with full nesting, fitting only p_P (fifth panel), results in a fit comparable to the best fit.



General Discussion

1. Main findings summary

Although precise results obtained in each study have already been summarized in their dedicated chapters, I propose here a brief overview of principal findings.

We have identified a math-responsive network in the brain, including bilateral intra-parietal sulci and inferior temporal regions, activated regardless of math domain, problem difficulty or visual experience. Additional activations were observed in the dorsal prefrontal cortex depending on efforts deployed to understand and solve the problem and in the occipital cortex whenever solving problems required some visualization. This brain circuit noticeably dissociates from 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. On the contrary, the math-responsive circuit overlaps with regions typically involved in number and space processing. These results thus support the idea that formal mathematics build upon proto-mathematical intuitions of number and space. First bits of evidence have also suggested that the human acquisition of geometrical rules relies on their compression to minimal description length in a recursive language of thought, some sort of “mathematical language” independent of natural spoken language.

2. Neuronal recycling of evolutionarily ancient areas

Within the math-responsive network, two bilateral regions were consistently activated by mathematical reflection: the intraparietal sulci and the lateral inferior temporal gyri. These regions might constitute a core system of mathematical processing in the brain.

2.1. Intraparietal sulcus

The intraparietal sulcus (IPS) is historically the first region identified by neuroimaging studies that supports numerical processing. First, IPS contains neurons tuned to quantities in monkeys (Nieder, 2005). 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 (Libertus et al., 2008) or near-infrared spectroscopy (Hyde et al., 2010). Adaption effect then progressively appears in the left IPS with age (Ansari and Dhital, 2006). Finally,

bilateral IPS has been shown to be involved in adults in all numerical tasks – comparison, estimation, calculation – approximate or exact, symbolic or nonsymbolic.

IPS thus appears to be the principal basis of numerical processing in the brain. Does this mean that our findings in chapter 1 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 nonmathematical reflection, sentence listening, face or words recognition.

We also note, as suggested in the paragraph 1.2.2 of the present introduction, that IPS and neighboring regions have proved to be engaged in spatial and geometrical processing (Culham and Kanwisher, 2001; Gauthier and Wassenhove, 2016; Husain and Nachev, 2007; Simon et al., 2002; Tzagarakis et al., 2009).

Chapters 1, 2 and 3 report consistent activation in IPS for all types of advanced mathematical problems. These findings support the idea that high-level mathematics “recycles” brain areas involved in simpler numerical and spatial processing.

2.2. Inferior temporal gyri

First, note that the engagement of bilateral inferior temporal gyri in numerical processing was first hypothesized in triple-code model (Dehaene, 1992), which postulated bidirectional exchanges between these regions (representing the visual number form of Arabic digits) and the intraparietal sulcus (representing quantity and other aspects of number meaning). Shum et al. (2013), using electrophysiological signals recorded from surface and depth electrodes in epilepsy patients, were the first to demonstrate the bilateral involvement of inferior temporal 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” (Dehaene et al., 2010) and other category-specific regions of the ventral visual stream (Kanwisher and Dilks, 2012).

Probably because of recurrent signal loss in this part of the brain, it is only recently that such regions have been observed in fMRI (Amalric and Dehaene, 2016; Grotheer et al., 2016; Yeo et al., 2017).

Our results, however, challenge the triple-code model. While IT regions were thought to recognize the visual form of numbers, we now see that they can also activate in the complete absence of visual stimuli (Chapters 1 and 2), and whenever blind mathematicians are thinking about abstract concepts (Chapter 3). The latter result is in line with previous findings suggesting that these regions were activated in congenitally blind adults trained to recognize roman numbers versus letters using a visual-to-music sensory-substitution device (Abboud et al., 2015) or doing simple arithmetic (Kanjlia et al., 2016).

Furthermore, inferior temporal regions do not activate only during the visual recognition of numbers, but also during calculation (Daitch et al., 2016; Pinheiro-Chagas et al., submitted) (figure 5.1) and during advanced mathematical reflection in professional mathematicians (Chapter 1). Daitch et al. (2016) report how different sectors of inferior temporal 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 (1) inferior temporal activity is modulated by problem difficulty (Pinheiro-Chagas et al., submitted); (2) number-active sites in ventral temporal regions exhibit a response pattern similar to and simultaneous with math-active parietal regions during elementary calculation (Daitch et al., 2016).

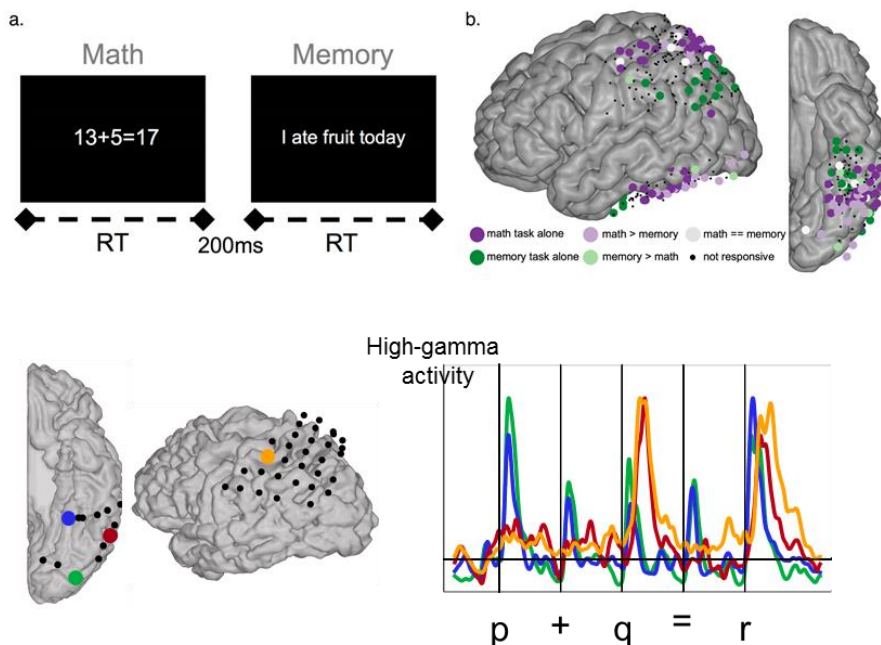


Figure 5.1. Intracranial evidence for a cortical network involved in mental arithmetic. (Top) Parietal and ventrolateral temporal electrodes responding to math (purple) versus verbal memory (green) tasks. (Bottom) High-frequency broadband time course in math-active sites within four anatomical regions in an exemplar subject ((Daitch et al., 2016); Copyright 2016 National Academy of Sciences).

For semantics, it has been suggested that left MTG/ITG/fusiform gyrus “may be a principal site for storage of perceptual information about objects and their attributes” (Binder et al., 2009). By extension, we suggest that lateral IT regions might also be a site for storage of information about the attributes of mathematical concepts.

2.3. Frontal regions

Finally, we note that the math-responsive regions identified in chapter 1 also included bilateral frontal regions. Interestingly, this frontal activation became weaker as the statements became easier (in chapter 2), suggesting that frontal cortex was primarily called upon during intense and prolonged mathematical reflection. Indeed, dorsolateral prefrontal cortex has now proved to be sensitive to verbal memory load increases (Narayanan et al., 2005) and spatial working memory (Curtis, 2006). These observations tend to support the idea that frontal regions are not part of the core math-related network in the brain, but constitute a set of support areas, involved whenever mathematical information needs to be maintained in memory in order to perform semantic decision.

Activation in frontal regions is also really close to frontal eye fields that have proved to be involved in mental arithmetic (Knops et al., 2009; Schneider et al., 2012). This observation could also suggest that more difficult math statements in chapter 1 involved more eye movements than simpler math statements in chapter 2. However, our data are insufficient to confirm this hypothesis.

3. Is there a mathematical language distinct from natural spoken language?

Our findings, together with converging evidence from several domains of cognitive science, support the idea that the ability to understand the “language of mathematics” dissociates from other aspects of linguistic or semantic processing. The studies reported in the present chapters suggest that the behavioral 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 general 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.

3.1. Dissociated syntaxes

In mathematics, at least two domains are endowed with an apparent syntax: algebra and logic. In the case of algebra, Friedrich and Friederici (2009) have shown that the syntactic processing of

mathematical formulas involved a fronto-parietal network but did not elicit activation in Broca's area. Such results have been confirmed by Maruyama et al. (2012) who have recently revealed that parsing algebraic expressions involve brain regions that lay outside of the classical language network. Only a weak but significant effect of expression complexity was seen in IFGTri, IFGOrb and pSTS. These results therefore suggested that algebraic syntax is largely distinct from linguistic syntax. Now regarding logical syntax, brain circuits underlying parsing of logical propositions has, to our knowledge, never been investigated and needs further study. For now, some evidence has emerged suggesting that domain-general deductive inference does not call upon language areas (Monti and Osherson, 2012). Moreover, in chapter 2, main effect of quantifiers was found in right angular gyrus, a region that is not traditionally associated with syntactical processing.

Finally, we have seen in chapter 4 that it is possible to formalize the mechanisms of sequential geometrical learning as a formal language of thought, with a specific syntax based on primitive rules and combinatorial principles. To assess which brain regions encode such nested rules, and whether they share the same neural substrates as language processing, Liping Wang and I have adapted the paradigm presented in chapter 4 to fMRI testing. We have presented 20 participants with the geometrical sequences used in chapter 4 plus sequences controlling for the effect of memory demand. While participants underwent fMRI scanning, we asked them to sequentially saccade to each target as fast and accurately as possible and monitored whether their eyes anticipated the next location. In each block, a fixed sequence of 8 items was repeated four times. From block to block, each category of sequence was presented with variability in its starting point, so that participants could not immediately recognize it, but could infer its organization after a few items. First, to uncover brain regions associated with rule-based encoding of spatial sequences, we searched for brain activity positively correlated with sequences complexity that quantified their degree of external geometrical regularity. After controlling for the activity due to saccade distance and memory demand, we found that complexity correlated with activation in bilateral MFG (figure 5.2). We then examined brain activation that correlated with gaze-anticipation of spatial locations that, in turn, reflected subjects' internal representation of unfolding sequences. We thus measured the anticipation difference between the 5th target (corresponding to second-level rules) and the mean of the indexes of the 3rd and 7th targets (corresponding to first-level rules), and after controlling for the effect of complexity, we showed that anticipation values correlated with activation in the right dorsolateral-prefrontal cortex (DLPFC) (figure 5.2).

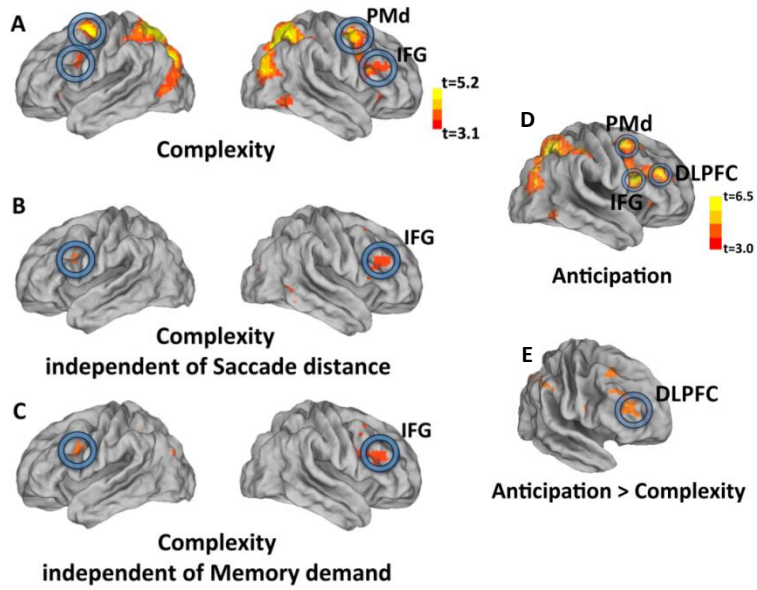


Figure 5.2. Brain activation to sequence complexity and anticipation of nested structures. (A) Lateral views of the brain showing significant correlations with the complexity of each sequence ($p < 0.05$ FDR, spatial extent > 10). (B) + (C) Brain areas showing a significant complexity effect independent of saccade distance (B) and memory demand (C), by masking all voxels above threshold ($p < 0.001$ uncorrected; “exclusive masking”) respectively by the brain maps of saccade distance and memory demand (i.e. the contrast of “4points” versus “2points”) ($p < 0.001$, FDR corrected). (D) Brain regions showing significant correlation with subjects’ anticipation of nested structures ($p < 0.05$ FDR, spatial extent > 10). (E) Areas showing activation to nested structure independent of the effect of complexity, masking all voxels above threshold ($p < 0.001$ uncorrected; “exclusive masking”) activated by the brain map of complexity effect ($p < 0.001$, FDR corrected).

Furthermore, we examined the relation of areas responsive to spatial nested-structure with the language and arithmetic calculation areas that were identified in the same participants using an independent localizer (Pinel et al., 2007). At group level, the areas responsive to nested-structure largely overlapped with the regions involved in calculation (figure 5.3B), but not with the brain areas involved in sentence processing (figure 5.3B). To confirm these findings, we turned to a more sensitive analysis, using the functional localizer to identify participant-specific voxels activated respectively during sentence processing within 6 left-hemispheric regions of interest (ROIs) and mental calculation within 7 ROIs that were respectively selected from previous studies of language constituent structure (Pallier et al., 2011) and mathematical thinking (chapter 1). We then extracted the beta estimates of each spatial sequence from these voxels, and showed again that math-responsive voxels (figure 5.3D) but not language-responsive voxels (figure 5.3C) were significantly activated to the most of spatial sequences.

In summary, this fMRI experiment tends to show that processing the syntax of a simple “language of geometry” that humans are endowed with dispenses with classical language areas but rather recruits fronto-parietal regions known to be involved in mathematical processing. Note that complete results from this experiment will be detailed in further publication (Wang et al., in prep).

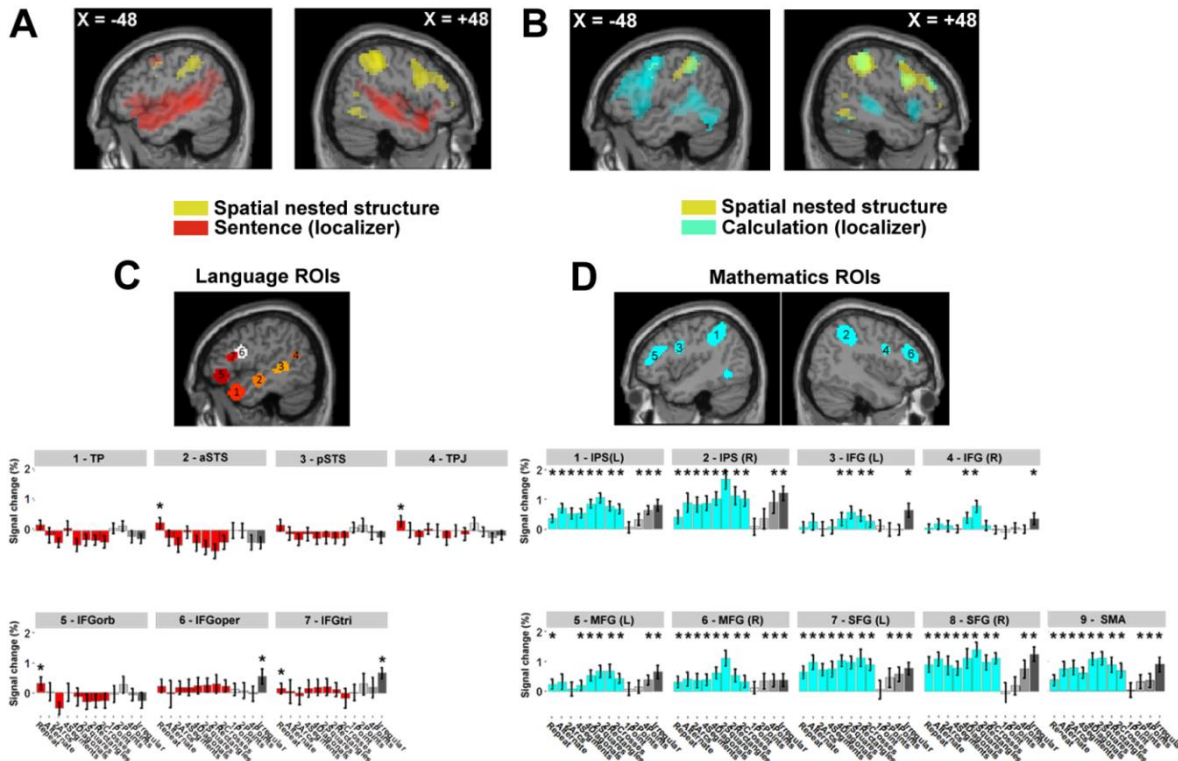


Figure 5.3. Spatial relation of the spatial nested-structure to the fMRI localizer for language and mathematics. (A, B) Sagittal slices showing the contrasts of sentence processing (red) and calculation (cyan) relative to rest during a functional localizer as long as the effect of anticipation to the spatial nested structure (yellow). Nearly no brain areas showed overlapping activity between the nested structure and language network (A), but large common regions displayed responses to both nested structure effect and mathematical calculation in frontal and parietal areas (B). Within each subject, best voxels responsive to sentence listening and calculation ($p_s < 0.001$, uncorrected) were identified. Brain activations in these subject-specific language-responsive (C) voxels within six region-of-interest (ROIs, 1-TP, 2-aSTS, 3-pSTS, 4-TPJ, 5-IFGorb, 6-IFGoper and 7-IFGtri) and math-responsive (D) voxels within nine ROIs (1-IPS(L), 2-IPS(R), 3-IFG(L), 4-IFG(R), 5-MFG(L), 6-MFG(R), 7-SFG(L), 8-SFG(R) and 9-SMA) were plotted for each sequence. Activations in mathematic-responsive ROIs were significant for most of spatial sequences, but not in language-responsive ROIs. (*: $p_s < 0.05$ corrected).

3.2. Fundamental semantic dissociation in the brain

The experiments reported in chapters 1, 2 and 3 required subjects to (1) listen to statements, (2) parse their syntax, (3) retrieve words semantic, (4) combine syntax and word semantic to evaluate the statements' meaning, and (5) make a semantic decision about the statements' truth value. To assess the semantic dissociation between math and nonmath, we will therefore focus on brain activation during phases (3), (4) and (5). In our first experiment (Chapter 1), we observed an early activation of intraparietal (IPS) and inferior temporal (IT) regions during math statements presentation only in mathematicians who could understand, but not in controls who nevertheless knew that statements were about math. Then, we observed a drop of activation in IPS and IT regions when mathematicians identified meaningless math statements, while activation remained sustained during semantical decision

on meaningful statements. On the contrary, nonmath statements elicited activation in bilateral temporal pole (TP) and anterior middle temporal gyri (aMTG), that coincide with regions classically involved in the semantic processing of words or sentences (Binder, 2016). These findings suggest that lexical semantics rapidly recruits regions that partly differ depending on content: IPS and IT for math, for nonmath, and that semantical decision is achieved using essentially the same regions that process the statements' meaning. Data from experiments 2 and 3 (Chapter 2) confirmed such dissociation. Indeed, we have shown that some mathematical statements (algebraic rote facts, algebraic calculation, trigonometry and complex numbers) barely activated language areas, while nonmathematical statements never activated math-responsive regions.

Our results also find support in new data-driven analysis methods that have recently been applied in order to clarify how different cortical sectors contribute to the semantic processing of words (Huth et al., 2016). 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 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. On the contrary, social and relational words were particularly represented at

various specialized sites along the superior and middle temporal region and the inferior frontal gyrus (figure 5.4). 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 (Huth et al., 2016).

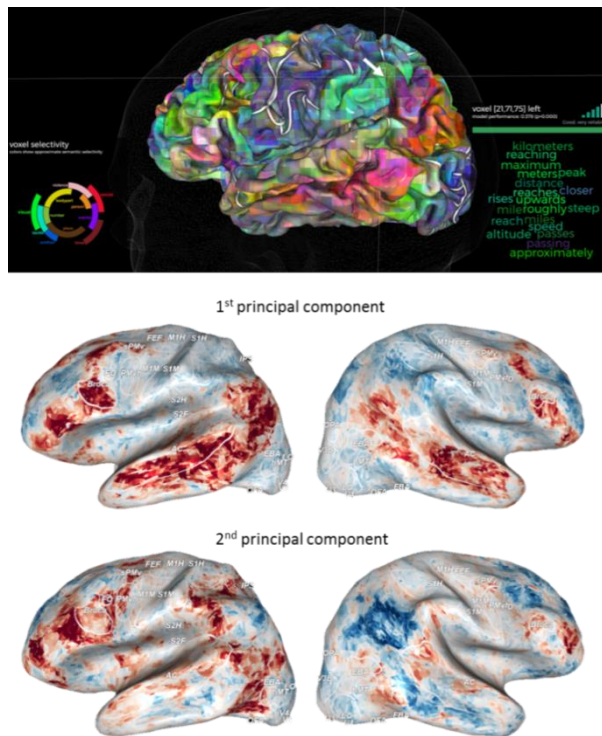


Figure 5.4. Brain activation elicited by word categories contained in naturalistic narrative stories. (Top) snapshot from the explorer proposed by the Gallant lab (<http://gallantlab.org/huth2016/>), showing a parietal site sensitive to various quantity- and math-related concepts. (Bottom) Brain maps of the first and second principal components of cerebral activation to narrative stories (image courtesy of Alexander Huth and Jack Gallant).

3.3. Connections between math- and language-responsive networks

We finally note 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 (Chapter 1). The triple-code model (Dehaene, 1992) also postulated bidirectional exchanges between the intraparietal sulcus and the left-hemispheric language system, including the left angular gyrus (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 angular gyrus. This activation was lower for mathematical than for nonmathematical 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 angular gyrus in the contrast for meaningful compared to meaningless statements, both within math and nonmath domains (see figure S12 in chapter 1). This finding agrees with previous suggestions that the angular gyrus might be involved in the semantic integration of individual words or concepts (Price et al., 2015). Surprisingly, however, rote algebraic facts did not activate the angular gyrus more than other mathematical statements in our second experiment, but continued to activate the classical math network. Prior findings indicated that the angular gyrus might be involved in the retrieval of verbal numerical facts such as multiplication facts (Delazer et al., 2005; Ischebeck et al., 2006), but the present results suggest that algebraic identities may not be stored in the same format.

4. General perspectives

4.1. Is mathematical learning also independent of linguistic abilities?

Our studies allowed concluding that advanced mathematical reflection on concepts encoded for a long time does not rely on verbal representations. In other words, reflection on already learnt mathematical concepts does not seem to rely on language processes – but is it also the case during learning? At present, the mechanisms by which advanced mathematical concepts are learnt still remain unknown. While a dominant view suggests that the basic mathematical intuitions of number, space and time that all human possess may serve as foundations for the construction of more advanced mathematical concepts, linguistic symbols may still play a role in the process by which basic intuitions are integrated with each other. In particular, in classrooms, where mathematical concepts are taught

explicitly thanks to words and sentences, is it also true that mathematical learning dispenses with language?

To address this issue, further investigation of how students are learning mathematics in classroom settings would be needed. One could take inspiration from recent naturalistic neuroimaging studies that measured neural responses spontaneously elicited by real-world stimuli (Cantlon and Li, 2013; Huth et al., 2016) and use stimuli and tasks that parallel classroom exposure as closely as possible.

4.2. What is the nature of mathematical activities?

Our fMRI findings raise many questions regarding the operational definition and intrinsic characteristics of the fields of “mathematics” and “language” that activate those two gross circuits. 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 (Duncan, 2010), as well as in domain-general logical, inferential or relational reasoning (Goel, 2004; Goel and Dolan, 2001; Monti et al., 2009). Even reflection on physics concepts such as “energy” or “wavelength” elicits partially similar activations (Mason and Just, 2016). Nevertheless, the hypothesis of a domain-general “multiple demand” system (Duncan, 2010) does not fit with the observation that this network fails to activate during equally flexible and long-lasting reflection on non-math-related concepts (Amalric and Dehaene, 2016). 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 (Kitcher, 1984).

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 (Dehaene et al., 1999; Pica et al., 2004; Spelke and Tsivkin, 2001). 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 (Dastjerdi et al., 2013; Huth et al., 2016). 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.

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