Origins of the brain networks for advanced mathematics in expert mathematicians

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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 and others that they are grounded in language competence. To evaluate what brain systems underlie higher mathematics, we scanned professional mathematicians and mathematically naive subjects of equal academic standing as they evaluated the truth of advanced mathematical and nonmathematical 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 nonmathematicians, 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 nonlinguistic brain circuit.

mathematical cognition | semantic judgment | functional MRI

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" (1). Many mathematicians and physicists, however, disagree and insist that mathematical reflection is primarily nonlinguistic—Albert Einstein, for instance, stated: "Words and language, whether written or spoken, do not seem to play any part in my thought processes." (2).

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 nonlinguistic intuitions of space, time, and number (3, 4). Indeed, even infants and uneducated adults with a drastically impoverished language for mathematics may possess abstract protomathematical intuitions of number, space, and time (5, 6). Such "core knowledge" is predictive of later mathematical skills (7–9) and may therefore serve as a foundation for the construction of abstract mathematical concepts (10). Advanced mathematics would arise from core representations of number and space through the drawing of a series of systematic links, analogies, and inductive generalizations (11–14).

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 (10, 15). 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 whereas 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 (16), a circuit already present in infants and even in untrained monkeys (17). Additionally, a bilateral inferior temporal region is activated by the sight of number symbols, such as Arabic numerals, but not by visually similar letters (18). Those regions lie outside of classical language areas, and several functional MRI (fMRI) studies have confirmed a double dissociation between the areas involved in number sense and language (19, 20). Only a small part of our arithmetic knowledge, namely the rote memory for arithmetic facts, encoded in linguistic form (16, 21). The bulk of number comprehension and even algebraic manipulations can remain preserved in patients with global aphasia or semantic dementia (22–24). Contrary to intuition, brain-imaging studies of the processing of nested arithmetic expressions show little or no overlap with language areas (25–27). 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.

Significance

Our work addresses the long-standing issue of the relationship between mathematics and language. By scanning professional mathematicians, we show that high-level mathematical reasoning rests on a set of brain areas that do not overlap with the classical left-hemisphere regions involved in language processing or verbal semantics. Instead, all domains of mathematics we tested (algebra, analysis, geometry, and topology) recruit a bilateral network, of prefrontal, parietal, and inferior temporal regions, which is also activated when mathematicians or nonmathematicians recognize and manipulate numbers mentally. Our results suggest that high-level mathematical thinking makes minimal use of language areas and instead recruits circuits initially involved in space and number. This result may explain why knowledge of number and space, during early childhood, predicts mathematical achievement.

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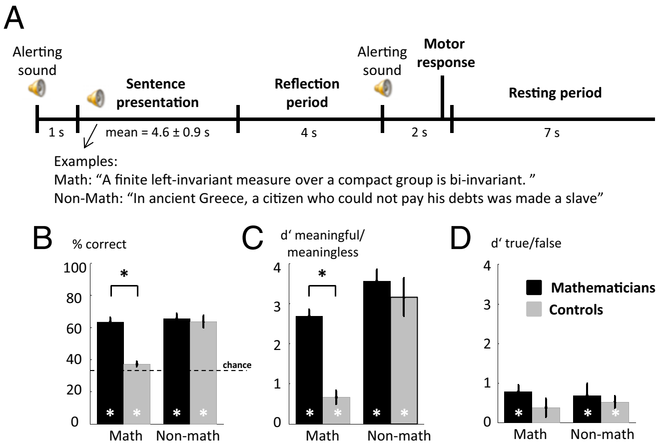

Fig. 1. Main paradigm and behavioral results. (*A*) On each trial, subjects listened to a spoken statement and, 4 s later, classified it as true, false, or meaningless. (*B*) Performance in this task (% correct). (*C* and *D*) Mean d′ values for discrimination of meaningful versus meaningless statements (*C*) and, within meaningful statements, of true versus false statements (*D*). $*P < 0.05$ (Student *t* tests). Error bars represent one SEM.

We collected fMRIs in 15 professional mathematicians and 15 nonmathematician controls of equal academic standing while participants performed fast semantic judgments on mathematical and nonmathematical statements (Fig. 1*A*). On each trial, a short spoken sentence was followed by a 4-s 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, whereas 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 nonmath sentences, matched in length and complexity, probed general knowledge of nature and history. Two additional fMRI runs evaluated sentence processing and calculation (28) and the visual recognition of faces, bodies, tools, houses, numbers, letters, and written mathematical expressions.

Results

Behavior. Math and nonmath problems were well-matched in objective difficulty level because mathematicians performed identically on both (63% and 65% correct) (Fig. 1*B* and *SI Appendix*, *Supplementary Results*). Mathematicians quickly separated the meaningful from the meaningless statements (Fig. 1*C*) (all d′ > 2). Judging the truth value of the meaningful statements was more challenging (d′ < 1), yet mathematicians' performance remained above chance in both conditions (Fig. 1*D*). Control subjects performed well with nonmath statements, achieving the same performance level as mathematicians (64% correct). Unsurprisingly, they fell close to chance level with math (37% correct, chance level = 33%; $P = 0.014$): They managed to perform above chance in detecting which statements were meaningful or meaningless (d′ = 0.67, $P = 0.002$) but could not identify their truth value (d′ = 0.38, n.s.).

Although objective performance on nonmath problems did not differ for mathematicians and controls, their subjective ratings of comprehension, confidence, or difficulty, collected after the fMRI session, revealed that each group felt more comfortable with its respective expertise domain (see *SI Appendix* for details).

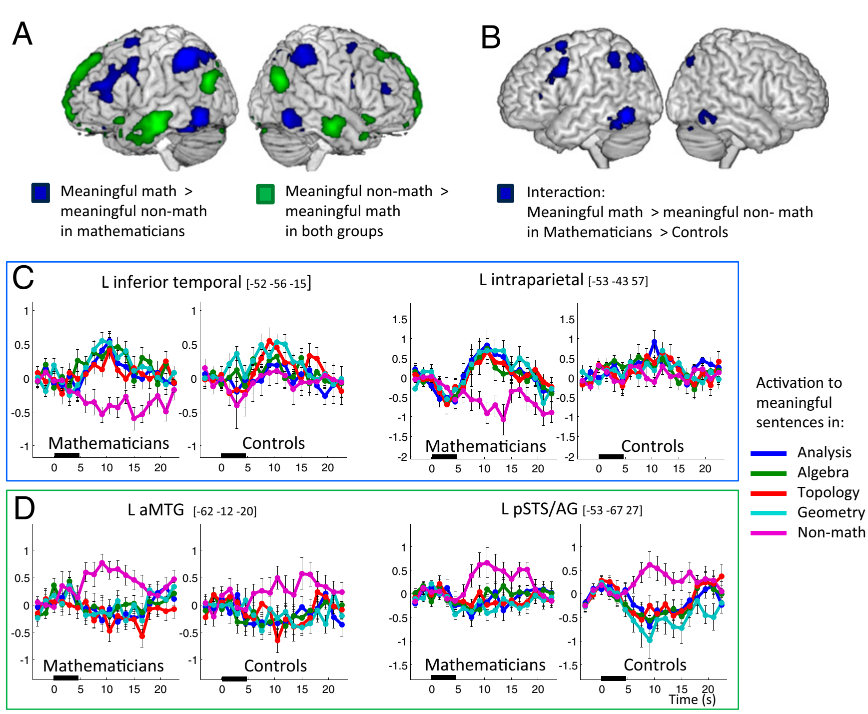

Fig. 2. Distinct brain areas for mathematical expertise and for general semantic knowledge. (*A*) Whole-brain view of areas activated during reflection on mathematical statements (blue) versus general knowledge (green). In this figure and all subsequent figures, brain maps are thresholded at voxel $P < 0.001$, 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.

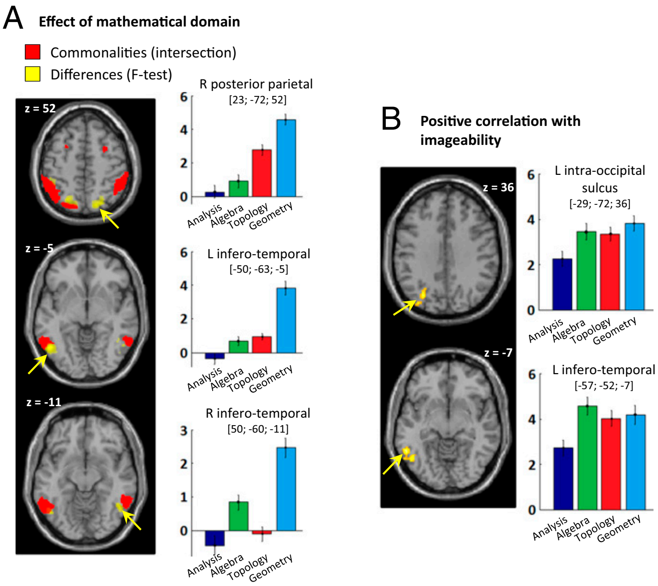

Fig. 3. Variation in brain activation across mathematical problems. (*A*) Cortical sites where responses were common (red) or different (yellow) between analysis, algebra, topology, and geometry. The commonalities of the four mathematical domains were assessed by the intersection of activation maps for 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.

fMRI Activations Associated with Mathematical Reflection. Within the group of professional mathematicians, we first searched for greater activations to math than to nonmath 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 (Fig. 2 and *SI Appendix*, Table S1). All four domains of mathematics activated those regions, as revealed by a significant intersection of activations to each domain (Fig. 3*A*) (each at $P < 0.001$). The only detectable differences among problems were a small additional activation in posterior IT and IPS for geometry relative to nongeometry problems, and an increased activity in left IT and intraoccipital sulcus for problems subjectively rated as easier to visualize (Fig. 3 and *SI Appendix*, *Supplementary Results* and Table S2).

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 s (Fig. 2*C* and *SI Appendix*, Fig. S1). Contrariwise, for nonmathematical statements, a slow deactivation was seen (Fig. 2*C*). Thus, this network was strongly activated by all domains of mathematics but remained inactive during reflection on matched nonmathematical problems. Furthermore, an interaction with group (math > nonmath × mathematicians > controls) showed that this activation pattern was unique to subjects with mathematical expertise (Fig. 2*B* and *SI Appendix*, Table S1). In control subjects, the math > nonmath contrast yielded a different set of regions that overlapped with the sites activated by meaningless nonmath statements (*SI Appendix*, Fig. S2 and Table S1), suggesting that math statements sounded like gibberish to nonmathematicians.

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 above results. In mathematicians, activation was stronger in bilateral IPS, IT, and PFC for meaningful than for meaningless math statements (Fig. 4*A* and *SI Appendix*, Table S1), with the latter inducing only a transient activation in most areas (Fig. 4*C*, no activation at all in right IPS, and *SI Appendix*, Fig. S3). The same contrast yielded no significant difference in controls, resulting in a significant group × meaningfulness interaction in the same brain regions (Fig. 4*B* and *SI Appendix*, Table S1).

Controls for Task Difficulty. The activations observed during mathematical reflection overlap with a set of areas that have been termed the "multiple demand system" (29). Those regions are active during a variety of cognitive tasks that involve executive control and task difficulty (30). It is therefore important to evaluate whether our results can be imputed to a greater task difficulty for math relative to nonmath statements. As noted in the behavioral section, objective task difficulty, as assessed by percent correct, was not different for math and nonmath statements within the mathematicians, and for nonmath 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 nonmath 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 nonmath; $t = 2.4$, $P = 0.03$). 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 nonmath statements (subjective difficulty = 53.9 ± 2.8 for meaningful math, versus 49.4 ± 4.7 for meaningful nonmath; $t = 0.8$, $P = 0.5$). In other words, the small difference in subjective difficulty (math > nonmath) 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. However, when we excluded the meaningless statements from the fMRI analysis, the difference in brain activation between math and nonmath statements remained and was in fact larger for meaningful than for meaningless statements (Figs. 2 and 4).

Second, to directly evaluate the impact of difficulty on the observed brain networks, within each subject, we sorted the meaningful math and nonmath statements into two levels of subjective difficulty (easy or difficult: i.e., below or above the subject's mean of the corresponding category). As expected, the easiest math statements were rated as much easier than the difficult nonmath statements (Fig. 5*A*). Despite this difference, the contrast of meaningful easy math > meaningful difficult nonmath again revealed the same sites as the ones that were activated for the standard math > nonmath contrast (Fig. 5*B*). Thus, those sites were activated even during simple mathematical reflection, and their greater activation for math than for nonmath occurred irrespective of task difficulty. Indeed, the time course of fMRI signals in the five main regions identified by the math > nonmath contrast (Fig. 5*C*) showed no effect of difficulty. This result was confirmed by the contrast of difficult > easy math and difficult > easy nonmath, which revealed no significant sites. Similar results were obtained when problems were sorted by objective performance (*SI Appendix*, Fig. S4).

Dissociation with the Areas Activated During Nonmathematical Reflection. We next examined which regions were activated by nonmath statements. Pooling across the two groups, areas activated bilaterally by nonmath > math reflection included the inferior

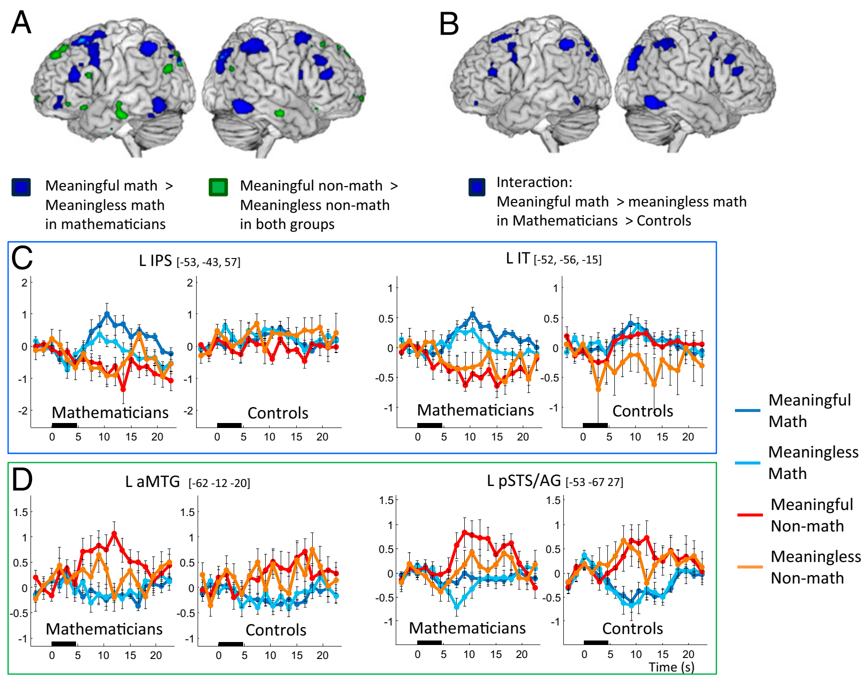

Fig. 4. Math and nonmath semantic effects. (*A*) Whole-brain view of semantic effects (meaningful > meaningless) for math statements in professional mathematicians (blue) and for nonmath statements in both groups (green). (*B*) Mathematical expertise effect: Interaction indicating a large difference 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*, Figs. S3 and S6 for additional areas).

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 area (BA) 47], an extended sector of mesial prefrontal cortex (PFC) (mesial parts of BA 9, 10, and 11), and cerebellum Crus I (Fig. 2*A* and *SI Appendix*, Fig. S5 and Table S3), consistent with previous studies of semantic networks (19, 31). The majority of these regions showed no difference between groups (*SI Appendix*, Table S3). Their time course indicated a significant activation just after nonmath statements and a systematic deactivation to all four types of math statements (Fig. 2*D*). The contrast meaningful > meaningless nonmath statements, which provides an orthogonal means of identifying general-knowledge semantics, pointed to virtually the same sites (Fig. 4*A* and *SI Appendix*, Table S3) and did not differ across groups (*SI Appendix*, Fig. S6 and Table S3).

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 nonmath, was tested formally through the appropriate interactions: i.e., (meaningful – meaningless math) – (meaningful – meaningless nonmath) and the opposite contrast (*SI Appendix*, Table S4). Stronger activations for meaningful math were again seen in bilateral IT, bilateral IPS, right posterior superior frontal, and left lateral IFG/middle frontal gyrus (MFG) whereas stronger activations for meaningful nonmath were in right posterior superior temporal sulcus (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 nonmath (Fig. 4*A* and *SI Appendix*, Tables S1 and 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.

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 (32) 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 (33). We then used an independent functional localizer (28) 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. All regions were activated during sentence presentation (*SI Appendix*, Fig. S7), either identically across conditions, or more for nonmath than for math and/or for controls than for mathematicians (*SI Appendix*, Table S5). Thus, if anything, mathematics called less upon those language regions than did general semantic reasoning. Whole-brain imaging confirmed a near-complete spatial separation of areas activated by mathematical judgments and by sentence processing (*SI Appendix*, Fig. S8). A very small area of overlap could be seen in the left dorsal Brodmann area 44 (*SI Appendix*, Fig. S8*B*), an area also singled out in previous reports (34) and which should certainly be further investigated in future research. Note, however, that this small overlap was present only in smoothed group images and failed to reach significance in higher resolution single-subject results (*SI Appendix*, Table S5).

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 nonmath reflection in mathematicians, with the activations

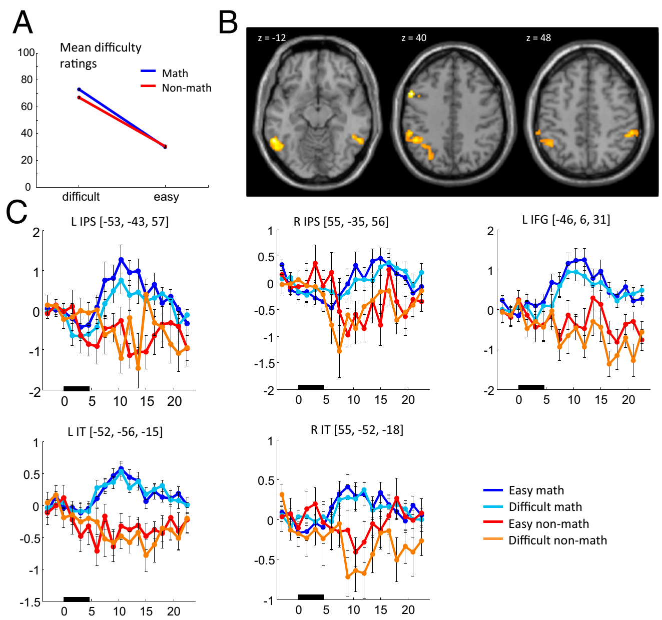

Fig. 5. Control for task difficulty. For each subject, math and nonmath statements were sorted into two levels of difficulty (easy versus difficult) depending on whether their subjective rating was below or above the subject's mean. (*A*) Mean difficulty ratings for easy and difficult math and nonmath 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 *SI Appendix*, Fig. S1).

evoked either by calculation relative to sentence processing (28) 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 (Fig. 6). Remarkably, those activations overlapped entirely with the regions activated by higher level mathematics in mathematicians only (Fig. 6).

Our mathematical statements carefully avoided any direct mention of numbers or arithmetic facts (*SI 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 (*SI Appendix*, Fig. S9 and 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.

Because group-level overlap of activation can arise artificially from intersubject averaging, we next turned to more sensitive within-subject analyses. First, within each of four regions of interest (left and right IPS and IT) identified from an independent calculation localizer (28), 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, nonmath reflection and nonsymbolic pictures) (*SI Appendix*, 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. For each subject, we first computed the matrix of correlations between the activations evoked by each of the experimental conditions (Fig. 7, *Top*). We then compared the correlation coefficients across matched cells of this matrix. The results revealed, first, that, in bilateral IPS and IT, 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 nonmath statements. Second, the activation during mathematical reflection was better correlated with the activation evoked by simple arithmetical problem solving than with the activation evoked by nonnumerical 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 nonsymbolic pictures or by written words (in bilateral IT only). Finally, in all four regions, the activation during simple calculation was better correlated with the activation evoked by numbers or formulas, than with the activation evoked by nonsymbolic pictures or written words (all Ps < 0.05) (Fig. 7, *Bottom* and *SI Appendix*, Table S7; see *SI Appendix*, *Supplementary Results* for results in additional regions).

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.

Activations During the Sentence-Listening Period. We also analyzed activations during sentence listening, before the reflection period. Our conclusions remained largely unchanged (see *SI Appendix*, *Supplementary Results* and Fig. S10 for details). Two additional effects emerged only during sentence presentation. First, a group × problem type interaction revealed a striking group difference in the bilateral head of the caudate nucleus (*SI Appendix*, Fig. 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 nonmath statements. Thus, the engagement of this subcortical region, which is known to participate in motivation and executive attention, shifted radically toward the subject's preferred domain. Second, another group difference concerned the left angular gyrus. It was

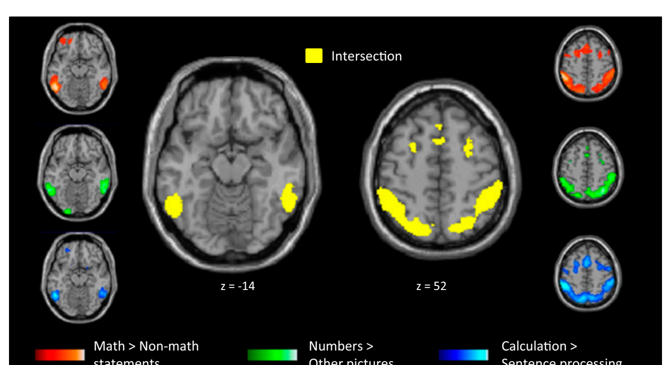

Fig. 6. Overlap of the mathematical expertise network with areas involved in number recognition and arithmetic. Red, contrast of math versus nonmath statements in mathematicians; green, contrast of Arabic numerals versus all other visual stimuli in both mathematicians and controls; blue, contrast of single-digit calculation versus sentence processing in the localizer run, again in both groups; yellow, intersection of those three activation maps (each at $P < 0.001$).

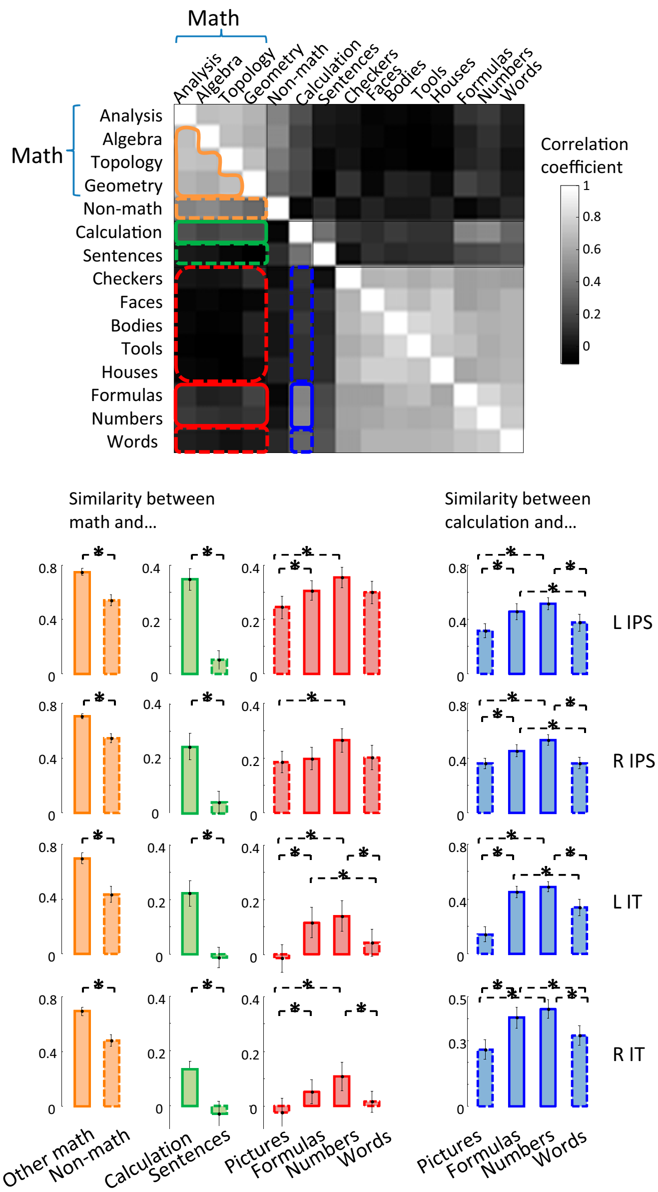

Fig. 7. Representational similarity analysis. (*Top*) Sample similarity matrix in left infero-temporal cortex showing the mean, across subjects, of the correlation between the spatial activation patterns evoked by the 15 experimental conditions of the whole experiment: four domains of math plus nonmath 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.

deactivated by meaningless compared with meaningful general-knowledge statements in both groups, as previously reported (32, 35). However, in mathematicians only, it also showed a greater activation for meaningful than for meaningless math (*SI Appendix*, Fig. S12). Thus, mathematical expertise enables the left angular gyrus, which is engaged in sentence-level semantic integration (35, 36), to extend this function to mathematical statements. Importantly, this contribution is only transient, restricted to the sentence comprehension period, because this area was deactivated during mathematical reflection.

Differences Between Mathematicians and Controls in Ventral Visual Cortex. Because 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 occipitotemporal preferences for one category of visual stimuli over all others (Fig. 8*A* and *SI Appendix*, Table S8). Those regions included the right-hemispheric fusiform face area (FFA), bilateral parahippocampal place areas (PPAs), bilateral extrastriate body areas (EBAs), bilateral lateral occipital cortices for tools (LOCs), 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 (VNFAs) (18, 37). 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) (Fig. 8*B*). Single-

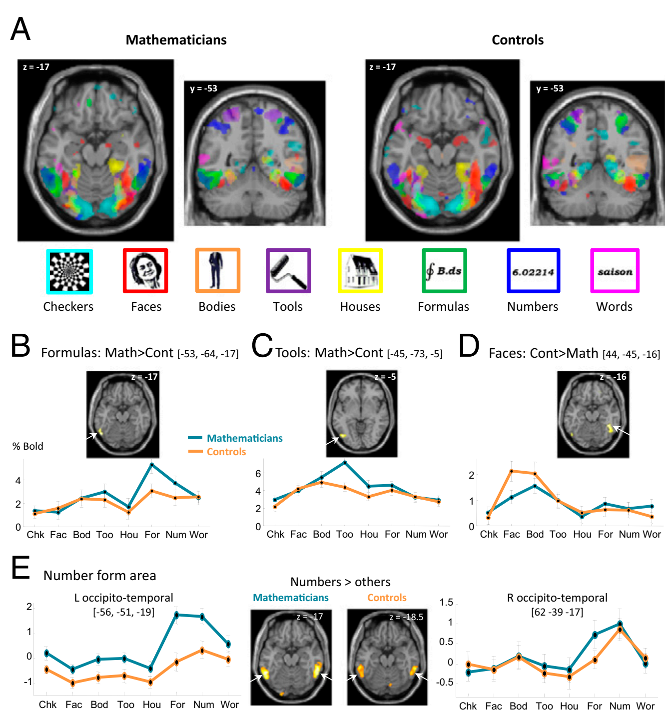

Fig. 8. Effects of mathematical expertise on the ventral visual pathway. (*A*) Mosaic of preferences for different visual categories in ventral visual cortex. Slices show the activation for the contrast of a given category (represented by a specific color) minus all others. (*B* and *C*) A whole-brain 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.

subject ROI analyses verified that this effect was not simply due to greater variance in anatomical localization in controls compared with mathematicians, but to a genuine increase in the volume of bilateral IT cortex activated by mathematical formulas (*SI Appendix*, 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 that have been previously related to IT and IPS regions (26). Just as reading expertise massively enhances the left ventral visual response to written letter strings (38), 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 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 > nonsymbolic 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, $t = 2.72$, $P = 0.01$) (Fig. 8*E*). 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 (38), we also examined face processing in our mathematicians. Although 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, $t = 4.72$) (Fig. 8*D*). 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, $t = 5.12$) (Fig. 8*C*). These intriguing differences must be considered with caution because their behavioral impact and causal link to mathematical training remains presently unknown.

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 nonmathematical 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 (*SI Appendix*, Table S7). In particular, bilateral ventral inferior temporal areas corresponding to the visual number form area (18, 37) 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 toward letters and away from faces (38–40).

Our findings shed light on the roots of mathematical abilities. Some authors have argued that mathematics rests on a recent and specifically human ability for language and syntax (1) whereas others have hypothesized that it is a cultural construction grounded upon evolutionary ancient representations of space, time, and number (3, 4, 12). In our task, language areas were activated only transiently during the presentation of auditory statements, whether mathematical or nonmathematical. 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 (16) and contain neurons tuned to numerical quantities (17). Bilateral inferior temporal regions have been termed "visual number form areas" (VNFAs) because they activate to written Arabic numerals much more than to letter strings or other pictures (18, 37). The VNFAs were previously difficult to detect with fMRI because they lie close to a zone of fMRI signal loss (18). 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.

Although we investigated, within our subjects, only 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 (41, 42). Indeed, representations of cardinal number, ordinal knowledge, and spatial extent overlap in parietal cortex (43, 44). 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 (12).

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 nonmathematicians also revealed a dissociation between mathematical and syntactic knowledge (19, 22, 26, 45). 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 (10). 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 (29) active in many effortful problem-solving tasks (30) and dissociable from language-related areas (46). Some have suggested that these regions form a "general problem solving" or "general purpose network" active in all effortful cognitive tasks (47). 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 nonmathematical semantic knowledge. In fact, the easiest mathematical problems caused more activation than the most difficult nonmathematical problems (Fig. 5), and even meaningless mathematical problems caused more activation than meaningful general-knowledge problems (Fig. 4). Second, other studies have found a dissociation between tightly matched conditions of linguistic versus logical or arithmetical problem solving (19, 48). 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 nonmath reasoning, meaningful and meaningless math, etc.). As an additional control, we also presented the same stimuli to a gender- and age-matched group of nonmathematically 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 (49). 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 seems to be a plausible candidate that should be tested in further work.

The regions we observed also fit with the sites showing increased gray matter in mathematicians relative to control subjects of equal academic standing (50). During elementary problem-solving tasks, fronto-parietal activations at locations similar to ours were enhanced in mathematically gifted subjects (51). Interindividual variations in this network predict corresponding variations in fluid intelligence (29, 52), 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 (53–55).

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 prelinguistic number skills and later mathematical skills, whereby intuitive number sense predicts subsequent mathematical scores at school (7–9, 56) and, conversely, mathematical education enhances the precision of the nonverbal approximate number system (57). Educational research also provides ample correlational and interventional evidence suggesting that early visuospatial and numerical skills can predict later performance in mathematics. The present results provide a putative brain mechanism through which such links may arise.

Methods

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

Professional mathematicians were full-time researchers and/or professors of mathematics. All had a PhD in mathematics and/or had passed the French national examination called "aggregation," which is the last qualification examination 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 as follows: literature ($n = 3$), history ($n = 3$), philosophy ($n = 1$), linguistics ($n = 2$), antiquity ($n = 1$), graphic arts and theater ($n = 3$), 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 (Comité de Protection des Personnes, Hôpital de Bicêtre).

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 (see *SI Appendix* for details).

Auditory Runs. Subjects were presented with 72 mathematical statements (18 in each of the fields of analysis, algebra, topology, and geometry) and 18 nonmathematical statements. Within each category, 6 statements were true, 6 were false, and 6 were meaningless. All meaningless statements (in math or nonmath) were grammatically correct but consisted in meaningless associations of words extracted from unrelated meaningful statements. All meaningful statements bore upon nontrivial facts that 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 *SI Appendix*.

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, nonmath = 12.6, $t = 0.24$, $P = 0.81$), and duration (mean duration in seconds: math = 4.70, nonmath = 4.22, $t = 1.93$, $P = 0.056$).

The experiment was divided into six runs of 15 statements each, which included one exemplar of each subcategory 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. After auditory presentation, a fixed-duration reflection period (4 s) 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 s, 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-s resting period (Fig. 1*A*).

Localizer Scan. This 5-min fMRI scan is described in detail elsewhere (20). For present purposes, only two contrasts were used: language processing (sentence reading plus sentence listening relative to rest) and mental calculation (mental processing of simple subtraction problems, such as $7 - 2$, presented visually or auditorily, and contrasted to the processing of nonnumerical visual or auditory sentences of equivalent duration and complexity).

Post-MRI Questionnaire. Immediately after fMRI, all of the statements that had been presented during fMRI were reexamined in the same order. For each of them, participants were asked to rate the following: 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.

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) (58) [multiband factor = 4, Grappa factor = 2, 80 interleaved axial slices, 1.5-mm thickness and 1.5-mm isotropic in-plane resolution, matrix = 128×128, repetition time (RT) = 1,500 ms, echo time (ET) = 32 ms].

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

A two-level analysis was then implemented in SPM8 software. For each participant, fMRI images were high-pass filtered at 128 s. Then, time series from visual runs were modeled by regressors obtained by convolution of the eight categories of pictures plus the button presses with the canonical SPM8 hemodynamic response function (HRF) and its time derivative. Data from the auditory runs were modeled 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 postsentence reflection period) or evaluating the impact of a continuous variable, such as subjective difficulty, on a subset of sentences. Regressors of noninterest included the six movement parameters for each run. Within each auditory run, two additional regressors of noninterest 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 $P < 0.001$.

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Supplementary materials for

Origins of the brain networks for advanced mathematics in expert mathematicians

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Contents:

Visual stimuli details

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 = π). 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.

Supplementary results

Behavioral results in auditory runs

Results are presented in figure 1B in the main text. With mathematical statements, mathematicians performed way above chance level (63.6 ± 2.8 % [mean ± standard error]; chance = 33.3%; Student's t test, $t = 11.3$ $p < 0.001$), while control subjects were just above chance (37.4 ± 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 ± 3.1 %, $t = 10.6$, $p < 0.001$; controls: 63.7 ± 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 ($t = 0.5$, $p = 0.6$).

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 ($d'_{math} = 2.68 \pm 0.18$, $t = 15.9$, $p < 0.001$; $d'_{non\text{-}math} = 3.56 \pm 0.28$, $t = 13.0$, $p < 0.001$). 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 ($d'_{non\text{-}math} = 3.16 \pm 0.47$, $t = 6.99$, 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 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 ($d'_{non\text{-}math} = 0.68 \pm 0.31$, $t = 2.30$, $p = 0.04$). Controls did not show a significantly positive d-prime for mathematics but they did for non-mathematics ($d'_{math} = 0.38 \pm 0.23$, $t = 1.72$, $p = 0.11$; $d'_{non\text{-}math} = 0.52 \pm 0.15$, $t = 3.48$, $p = 0.004$). 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 1D).

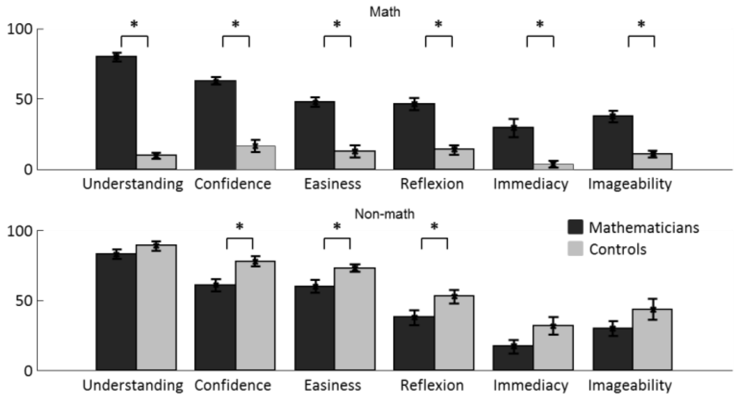
In summary, mathematicians performed equally well with both types of sentences. Within the allotted time period of 4 seconds, they managed to discriminate meaningful mathematical statements from meaningless ones, as well as to distinguish true statements from false ones. Controls only managed to understand 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.

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: $F(1)=0.18$, $p=0.67$; category: $F(6)=0.29$, $p=0.94$; interaction group x category: $F(6)=0.69$, $p=0.66$). An ANOVA on reaction time showed equivalent results (group: $F(1)=1.63$, $p=0.20$; category: $F(6)=0.67$, $p=0.67$; interaction group x category: $F(6)=0.54$, $p=0.78$). 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 ($t = 0.83$, $p = 0.41$).

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). 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.



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.

Variation in brain activation across mathematical problems

Figure 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 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).

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 3B).

Activation to mathematical statements in control subjects without mathematical expertise

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).

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.

ROI analyses in language-related areas

Additional analyses were performed in seven regions of interest (ROIs) that had been previous identified as related to language processing. They included the six cortical left-hemispheric ROIs previously reported by Pallier et al. (1) as involved in the constituent structure of sentences: temporal pole (TP), anterior superior temporal sulcus (aSTS), posterior superior temporal sulcus (pSTS), temporo-parietal junction (TPj), inferior frontal gyrus pars orbitalis (IFGorb), and inferior frontal gyrus pars triangularis (IFGtri) (the left putamen, present in Pallier et al, was not included here because we could not identify active voxels during language processing in this region in every subject). We added the cyto-architectonically defined left Brodmann area 44 (2).

Within each region, for each subject, we first used a separate functional localizer (3) to identify voxels activated by sentences (spoken or written) relative to rest (voxel p<0.001 uncorrected). We then averaged the responses in these subject-specific voxels across participants, and performed statistical t-tests across conditions. 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.

RSA analyses in math-related areas

First, thanks to independent localizer scans performed in a different cohort of 83 subjects, 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.

At subject level, within each of these 13 regions, 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 7). 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 inferior temporal regions, activation to mathematical reflection was significantly more correlated to activation to math-related visual conditions (formulas and numbers recognition) than to corresponding visual control conditions (non-symbolic pictures viewing or words recognition). 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).

Moreover, left and right IPS and IT exhibited a strong correlation of activations to simple calculation and visual formula or number recognition, stronger than the correlation of activations to calculation and non-symbolic pictures or words (all p*s* < 0.027 uncorrected, 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).

Activations during sentence presentation

We replicated the contrasts reported in the main text, but now analyzing the period of sentence presentation (with regressors proportional to sentence duration). 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).

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).

Remarkably, the head of the caudate nucleus activated for math > non-math in mathematicians and for non-math > math in control subjects, thus revealing a systematic engagement for the subject's main domain of predilection. 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). Plots of temporal profiles of fMRI signals for math and non-math stimuli over the whole regions of interest, separately for the two groups, are shown in figure S11.

We then studied the contrast of meaningful > meaningless non-math during sentence presentation. The most important cluster was found in the left angular gyrus, 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).

Finally, in mathematicians, bilateral angular gyri (left: -48, -60, 16, t = 5.52; right: 44, -79, 22, t = 4.35), 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) revealed greater activation for meaningful than meaningless math. 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 (1, 4, 5), 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.

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Supplementary figures

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). Plots show the fMRI signal (mean +/- 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.

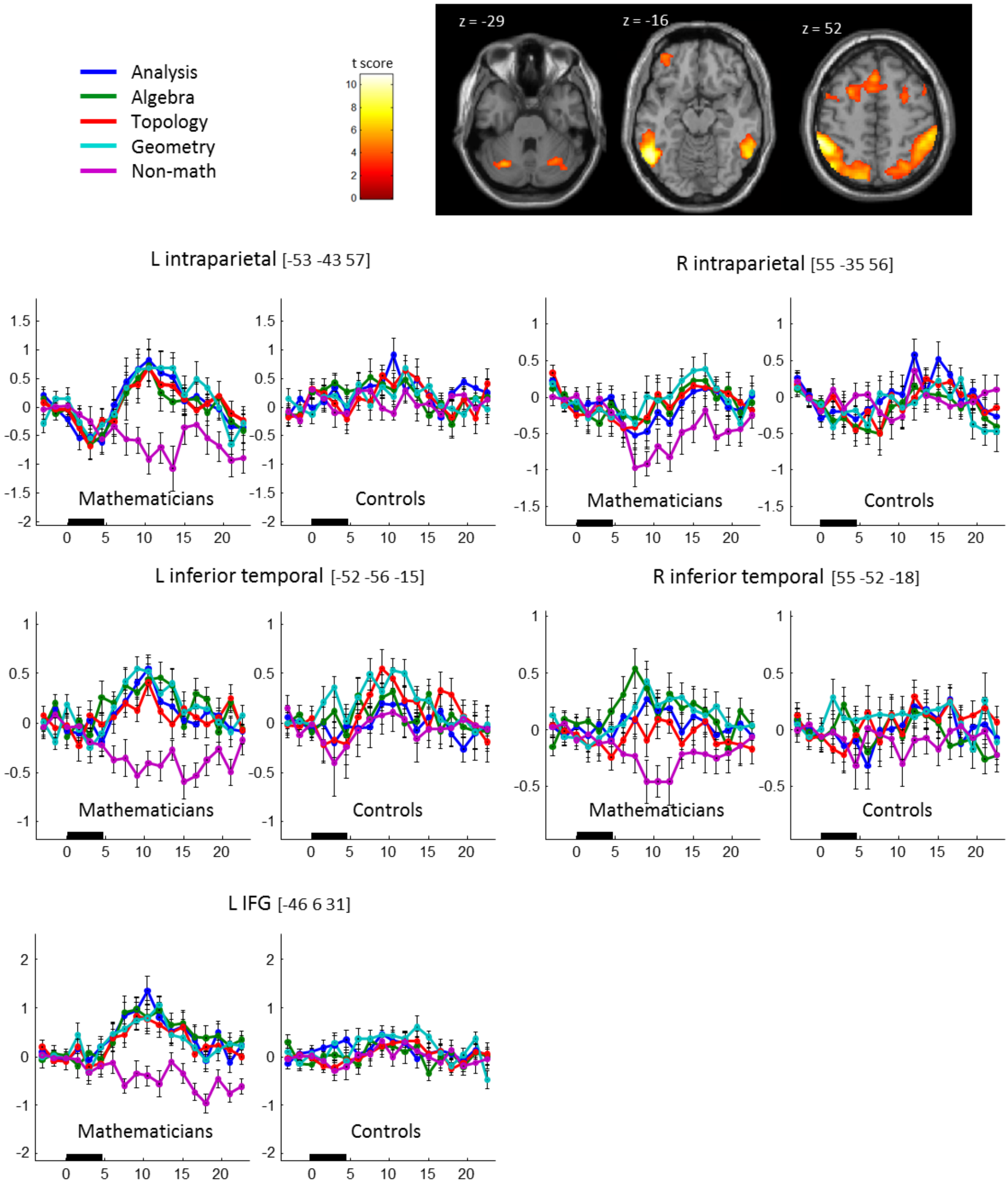


Figure S2. Brain areas showing a difference math > non-math in control subjects

(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.

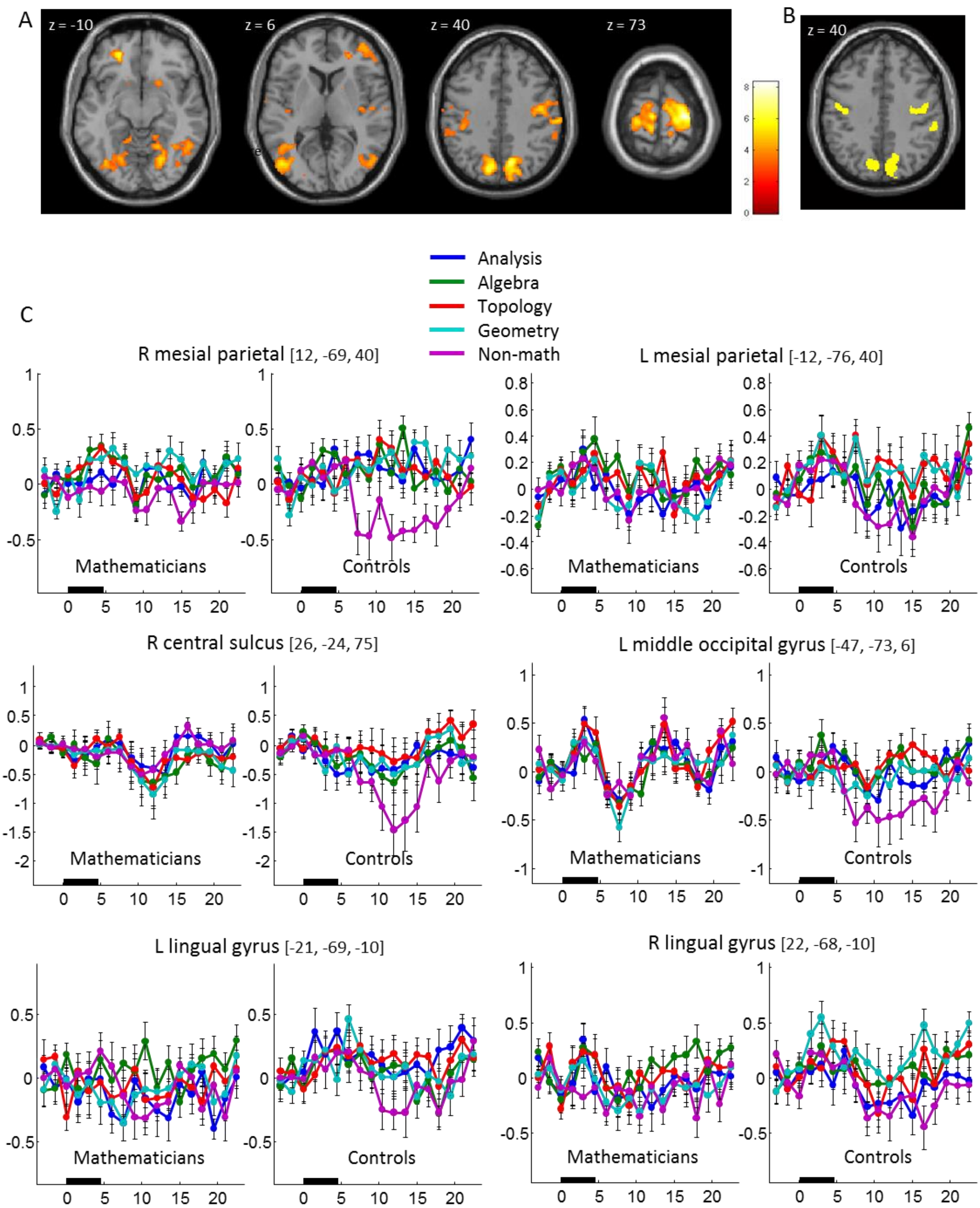


Figure S3. Activation profiles for meaningful and meaningless statements in brain areas responsive to mathematical statements.

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).

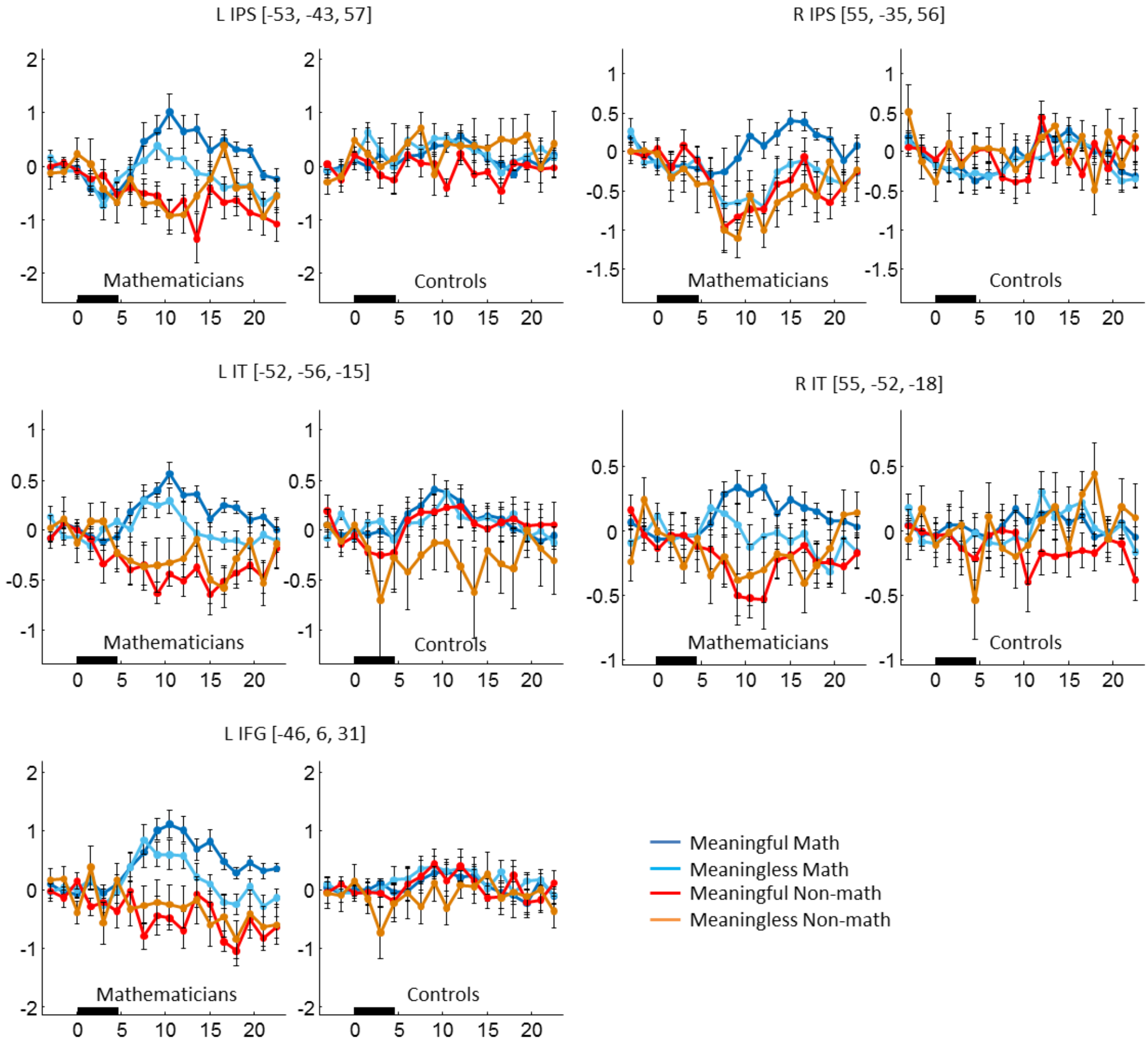


Figure S4. Control for task difficulty

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).

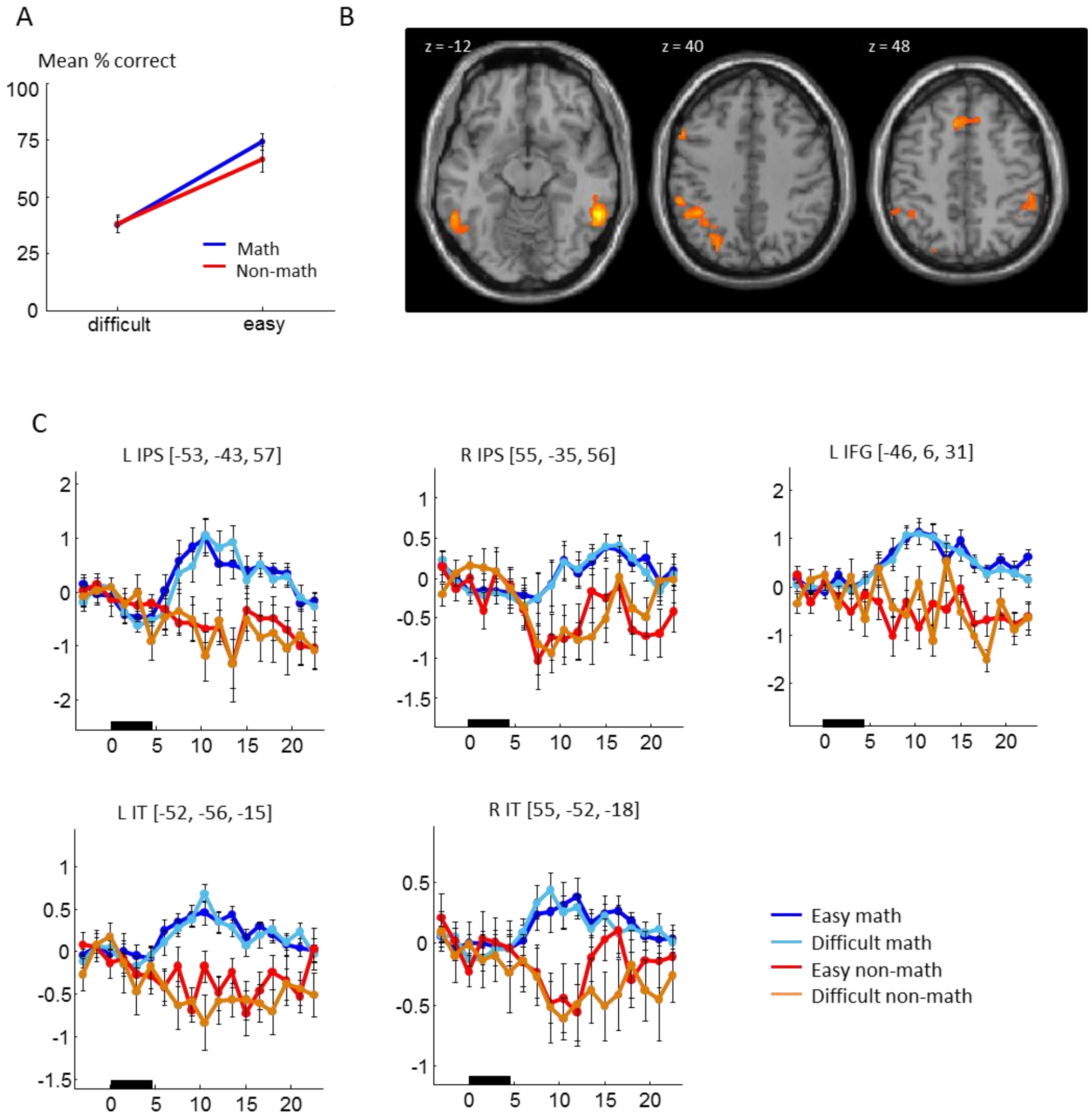


Figure S5. Activation profiles within areas of the general-knowledge network

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.

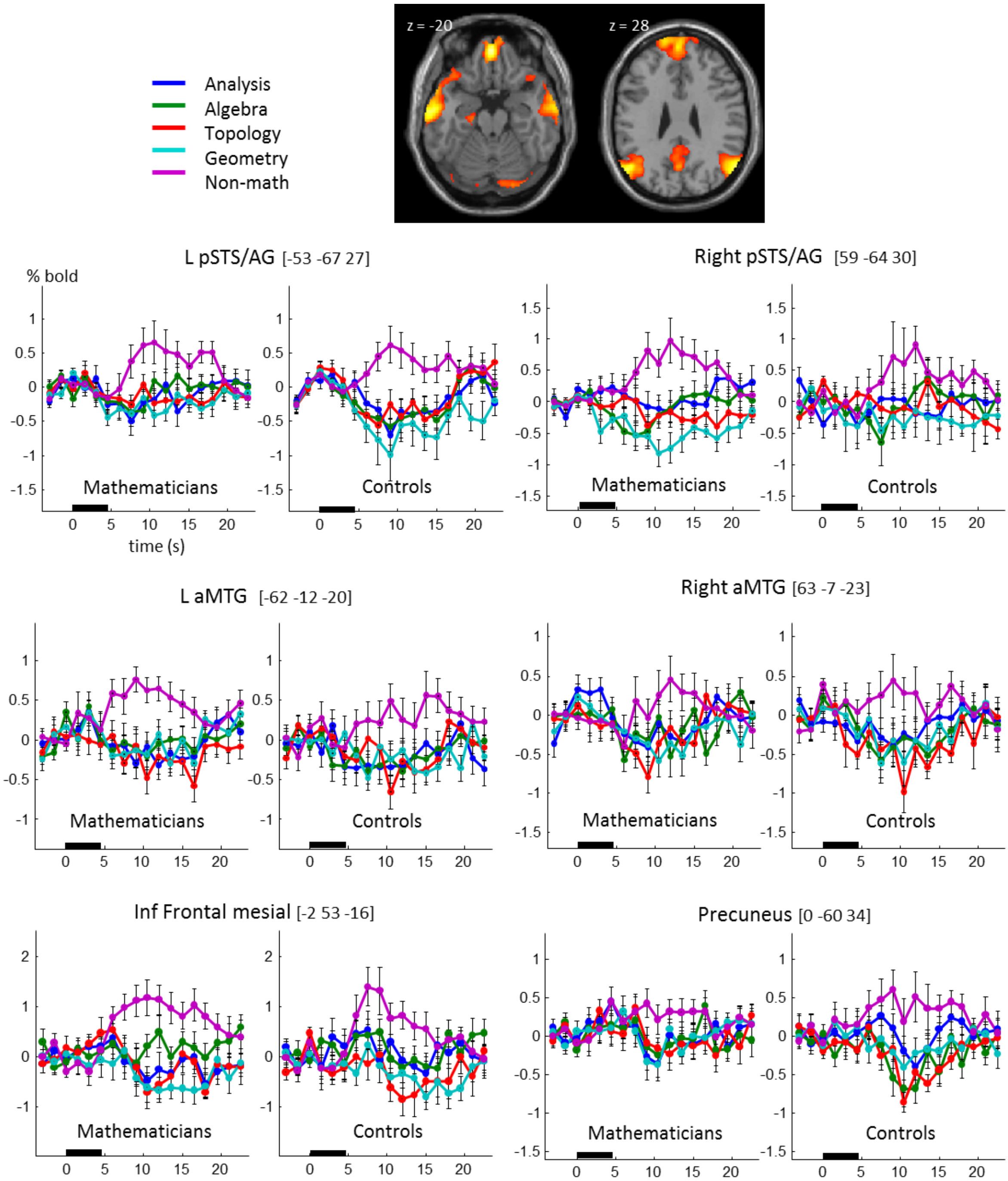


Figure S6. Activation profiles for meaningful and meaningless statements in brain areas mainly responsive to non-mathematical statements during the reflection period

Plots at the peaks of the 6 main regions identified in the contrast of non-math > math in both groups during the reflection period.

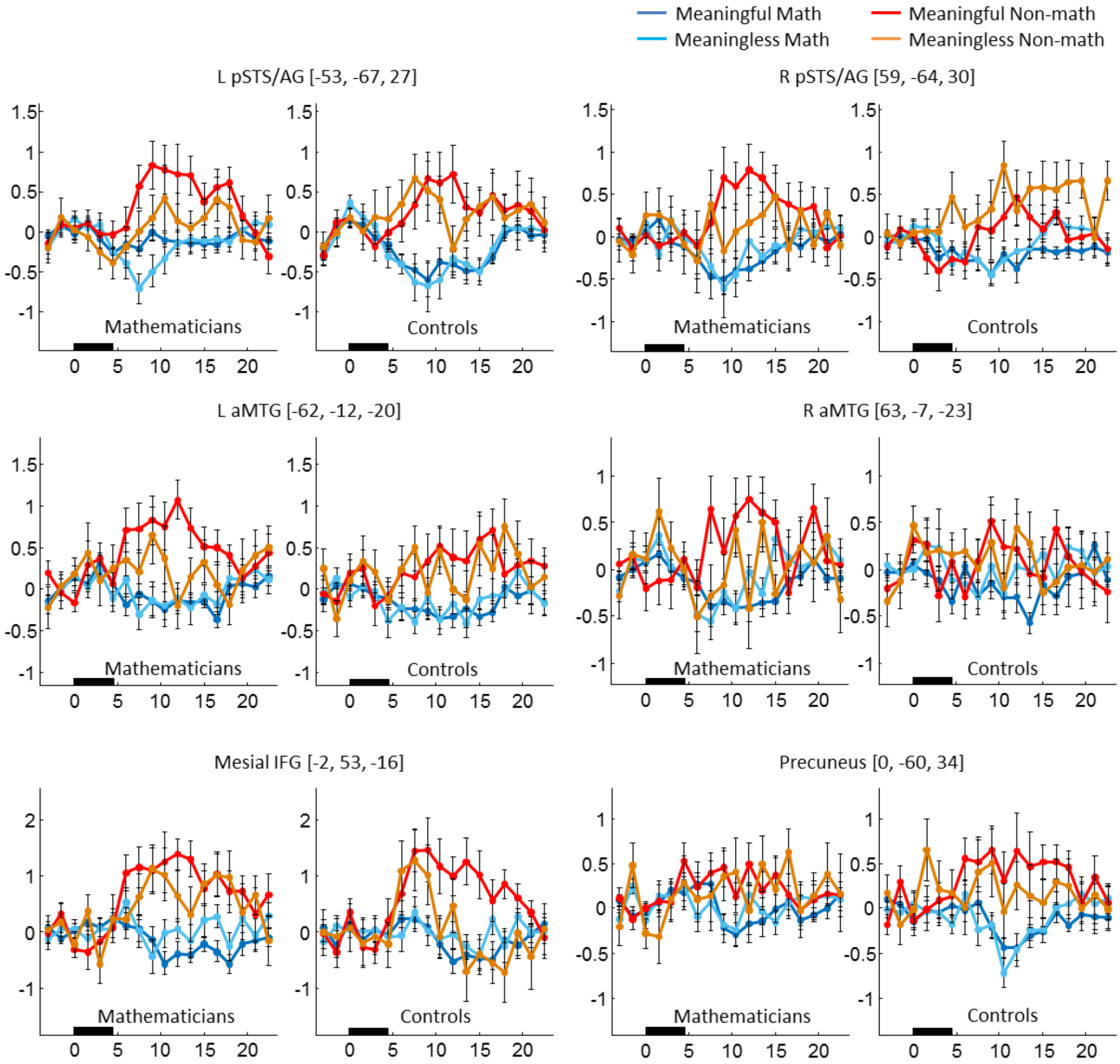


Figure S7. Activation evoked by mathematical and non-mathematical statements in classical language-related regions

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).

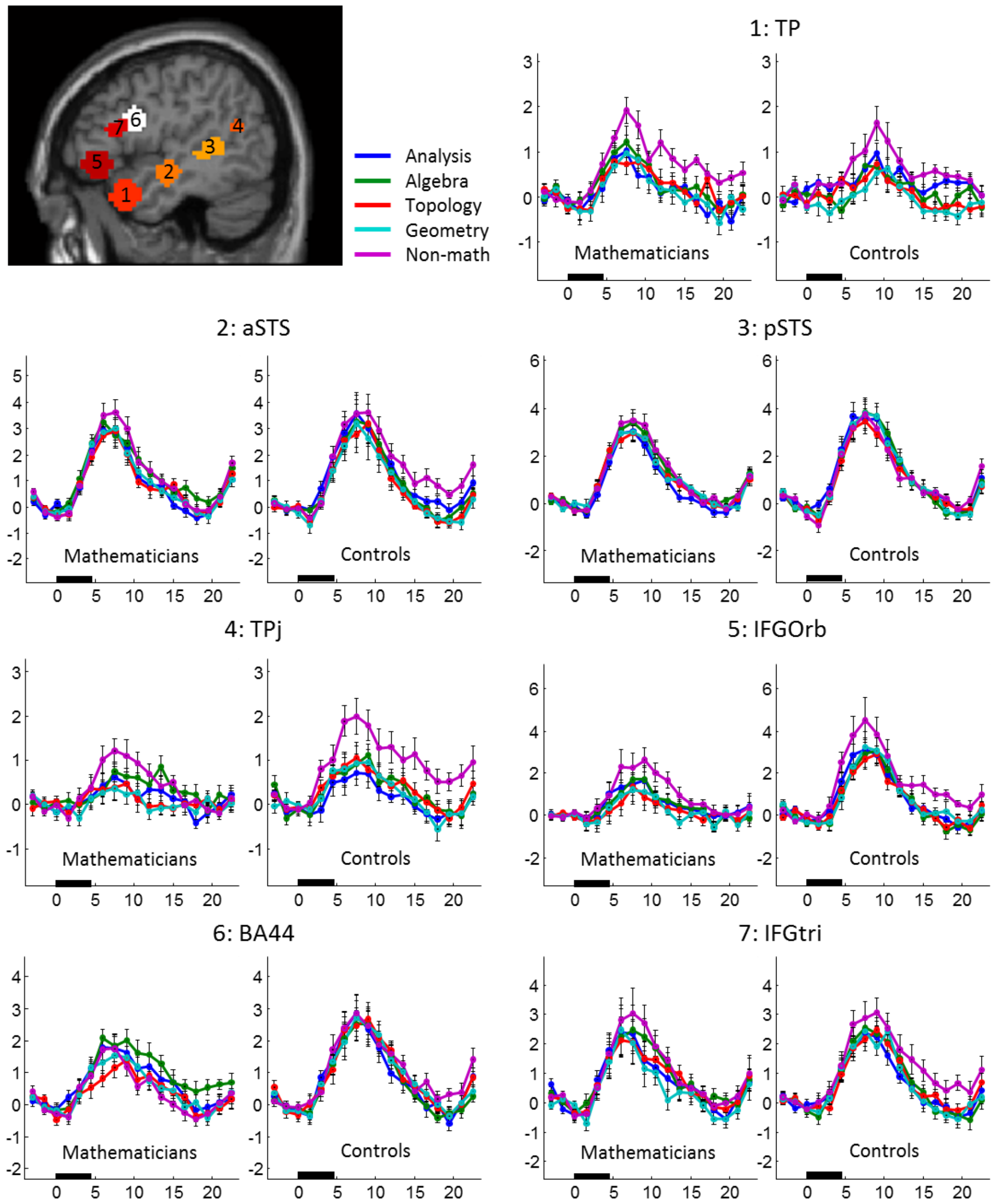


Figure S8. Spatial relationship between the math and language networks

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.

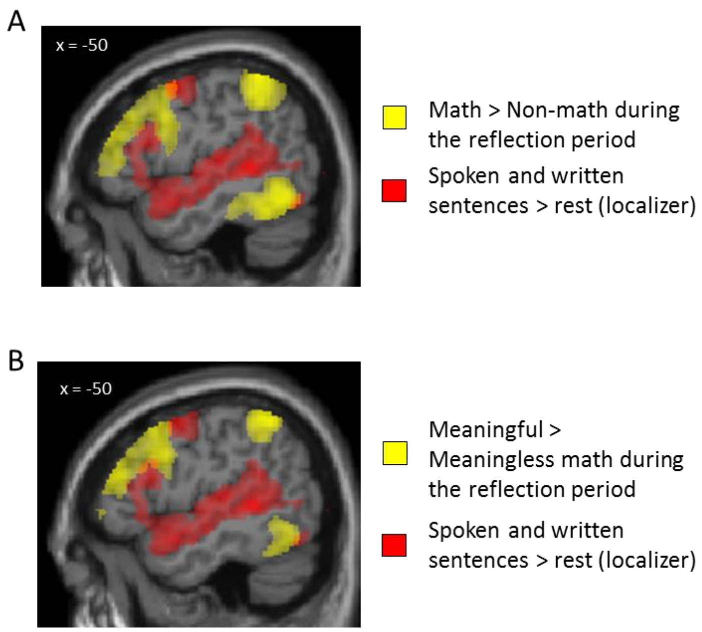


Figure S9. Activation for math > non-math in mathematicians, after removal of sentences containing occasional reference to numbers

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.

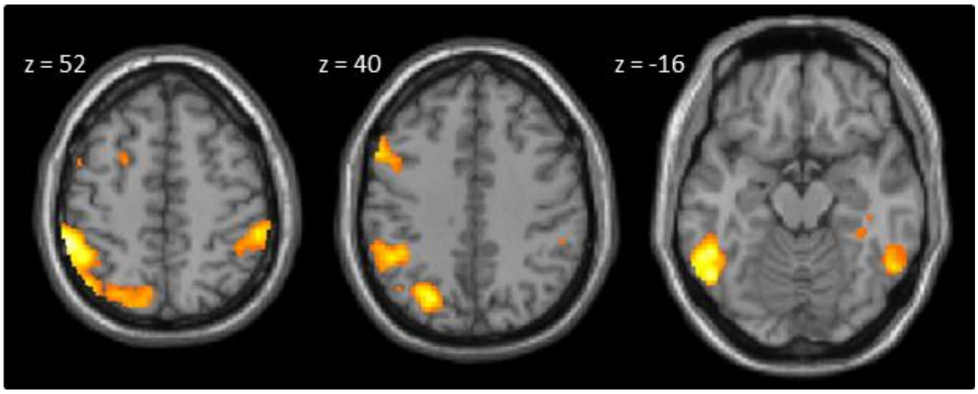


Figure S10. Superposition of the math > non-math contrasts in mathematicians during statement presentation and during the subsequent reflection period

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.

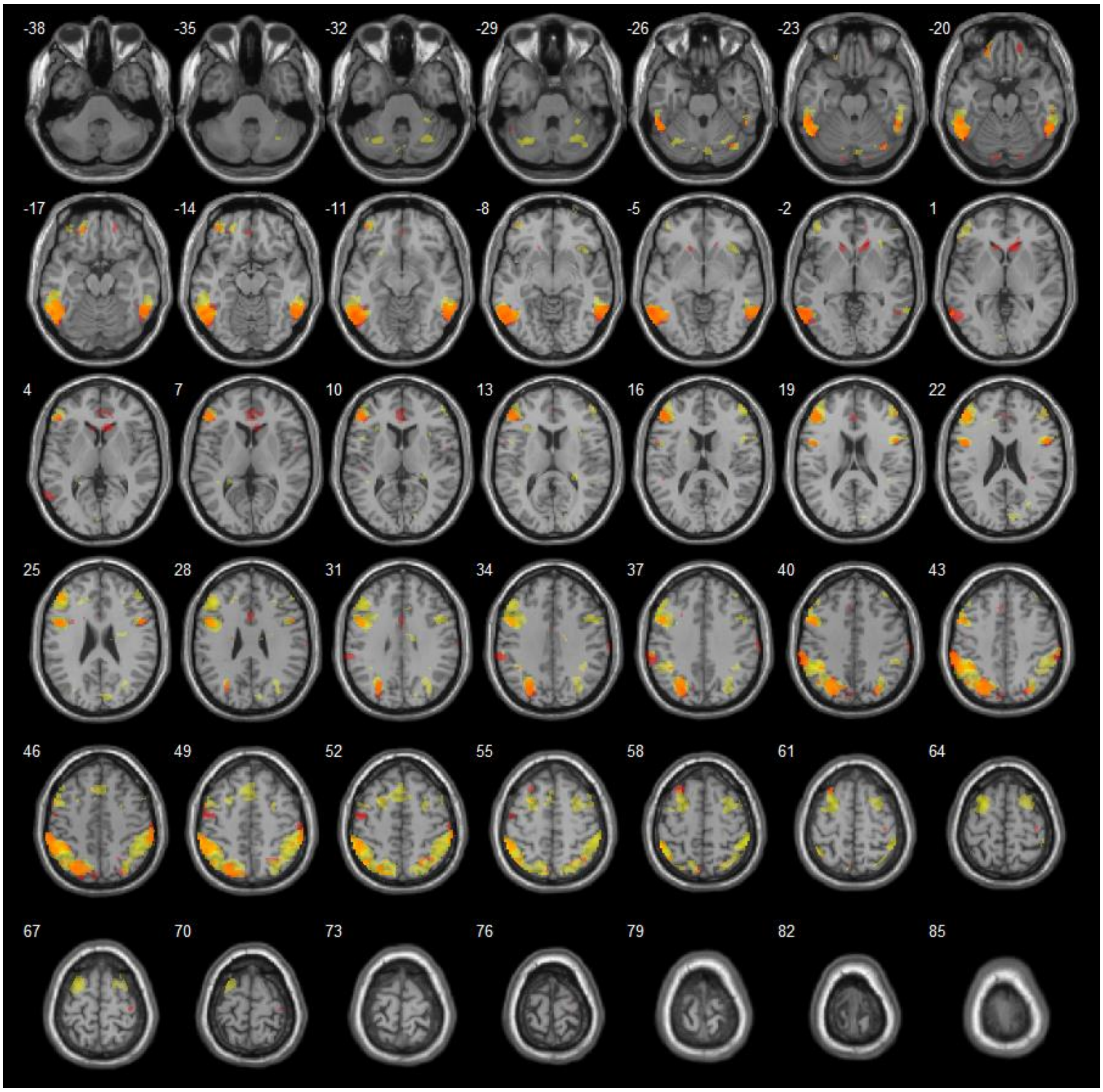


Figure S11. Interaction between group and problem type during statement presentation in the head of the caudate nucleus

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.

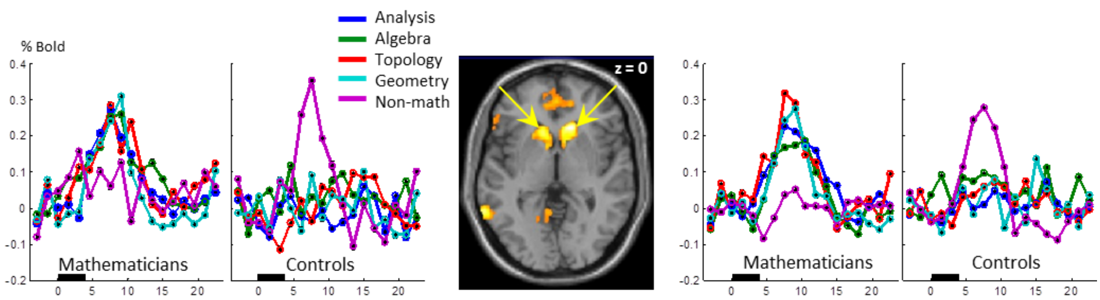
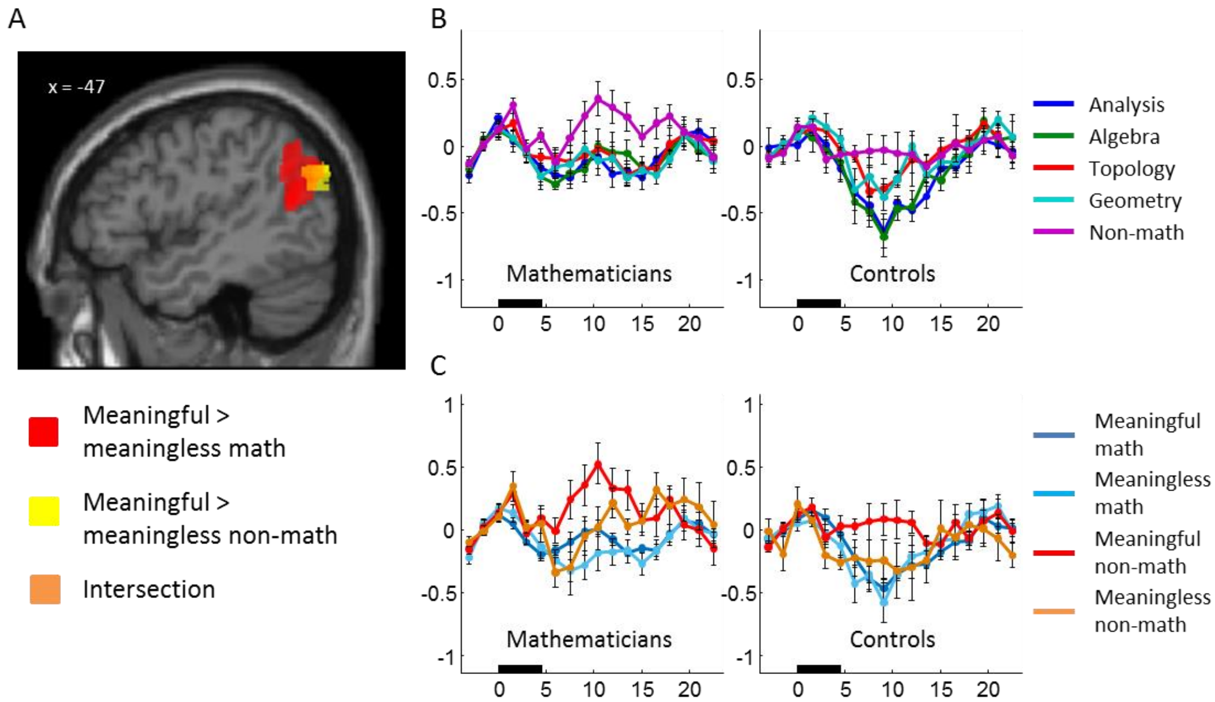


Figure S12. Transient effect of meaningful versus meaningless statements during sentence presentation in the angular gyrus.

(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.



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/ BA13	-	-	-	-	-	-	-	-	-38	-19	12	5.47	-	-	-	-	-	-	-	-	-	-	-	-
R insula/ BA13	-	-	-	-	-	-	-	-	40	-14	2	4.96	-	-	-	-	-	-	-	-	-	-	-	-
L Putamen	-	-	-	-	-	-	-	-	-14	18	-2	4.86	-	-	-	-	-	-	-	-	-	-	-	-
R Putamen	-	-	-	-	-	-	-	-	18	16	-2	4.85	-	-	-	-	-	-	-	-	-	-	-	-

Table S2. Activation peaks unique to a mathematical domain in mathematicians

Mathematicians	Analysis > other domains				Algebra > other domains				Topology > other domains				Geometry > other domains			
	x	y	z	t	x	y	z	t	x	y	z	t	x	y	z	t
Mesial frontal orbital	-2	65	-1	4.49	-	-	-	-	-	-	-	-	-	-	-	-
L middle frontal gyrus	-	-	-	-	-	-	-	-	-50	13	27	4.23	-	-	-	-
L inferior temporal	-	-	-	-	-	-	-	-	-	-	-	-	-50	-63	-5	6.39
R inferior temporal	-	-	-	-	-	-	-	-	-	-	-	-	50	-58	-14	5.8
R superior parietal	-	-	-	-	-	-	-	-	-	-	-	-	18	-72	52	5.05
L superior parietal	-	-	-	-	-	-	-	-	-	-	-	-	-23	-66	52	4.94
L supra marginal gyrus	-	-	-	-	-	-	-	-	-	-	-	-	-65	-30	37	4.32
L inferior parietal	-	-	-	-	-	-	-	-	-	-	-	-	-42	-37	42	4.22
R intra occipital sulcus	-	-	-	-	-	-	-	-	-	-	-	-	42	-81	21	5.02

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 FGOrb / 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 in 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 > math*non-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 > math*sentence	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 > math * non-symbolic pictures	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 * numbers > 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 > math * words	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 > math * words	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 > calculation * non-symbolic pictures	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 > calculation * non-symbolic pictures	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

Appendix. List of mathematical and non-mathematical statements

List of mathematical and non-mathematical statements

1 Analysis

1.1 True :

Statement 1. The Fourier series expansion of a continuous and piecewise $\mathcal{C}^1$ function f converges pointwise to f.

Statement 2. Any locally polynomial function from $\mathbb{R}$ to $\mathbb{R}$ 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 $p \geqslant 1$.

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

1.2 False :

Statement 7. The spaces 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 $\mathrm{L}^\infty(\mathbb{R})$ is $\mathrm{L}^1(\mathbb{R})$.

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 Heaviside function admits a Taylor expansion in L^p.

Statement 14. The space $\mathrm{L}^1(\mathbb{R}^n)$ 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 $p \notin \{1, \infty\}$.

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 exists 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 subgroups.

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 exists 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 exists 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 inifinite 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. Evey 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 axe over the eccentricity.

Statement 58. The set of points that are equidistant from two given disjoint lines of $\mathbb{R}^3$ is an 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 tangent 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.