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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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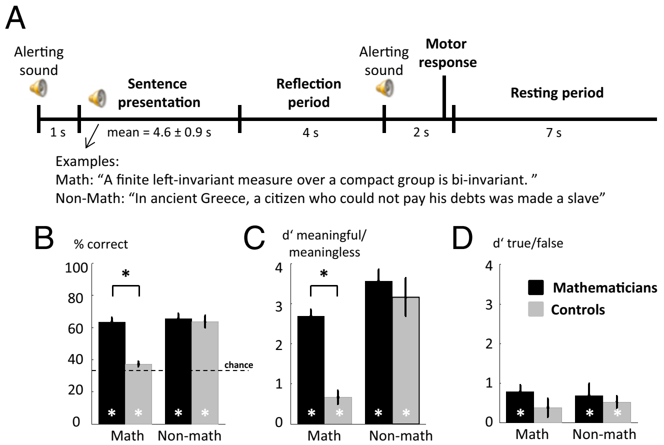

Fig. 1. Main paradigm and behavioral results. (*A*) On each trial, subjects listened to a spoken statement and, 4 s later, classified it as true, false, or meaningless. (*B*) Performance in this task (% correct). (*C* and *D*) Mean d′ values for discrimination of meaningful versus meaningless statements (*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).

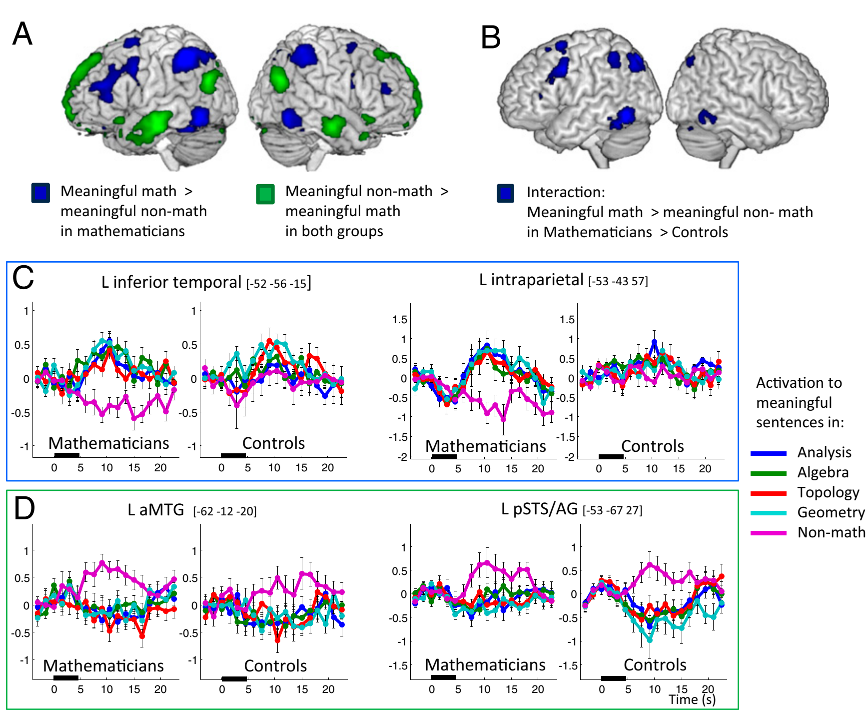

Fig. 2. Distinct brain areas for mathematical expertise and for general semantic knowledge. (*A*) Whole-brain view of areas activated during reflection on mathematical statements (blue) versus general knowledge (green). In this figure and all subsequent figures, brain maps are thresholded at voxel $P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

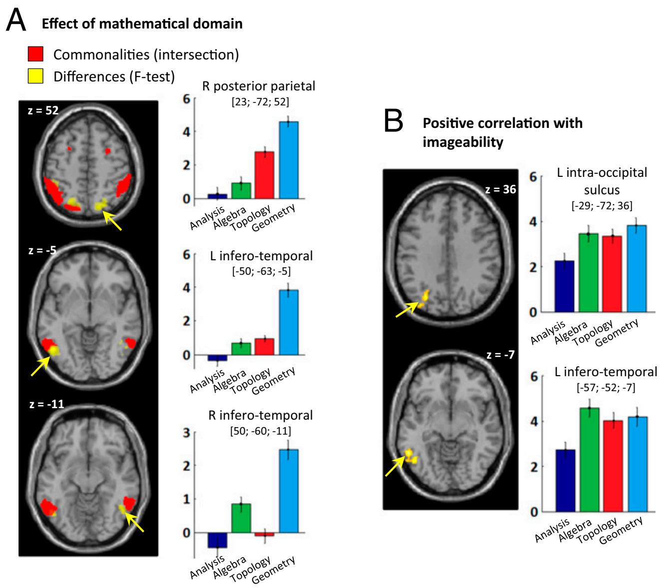

Fig. 3. Variation in brain activation across mathematical problems. (*A*) Cortical sites where responses were common (red) or different (yellow) between analysis, algebra, topology, and geometry. The commonalities of the four mathematical domains were assessed by the intersection of activation maps for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

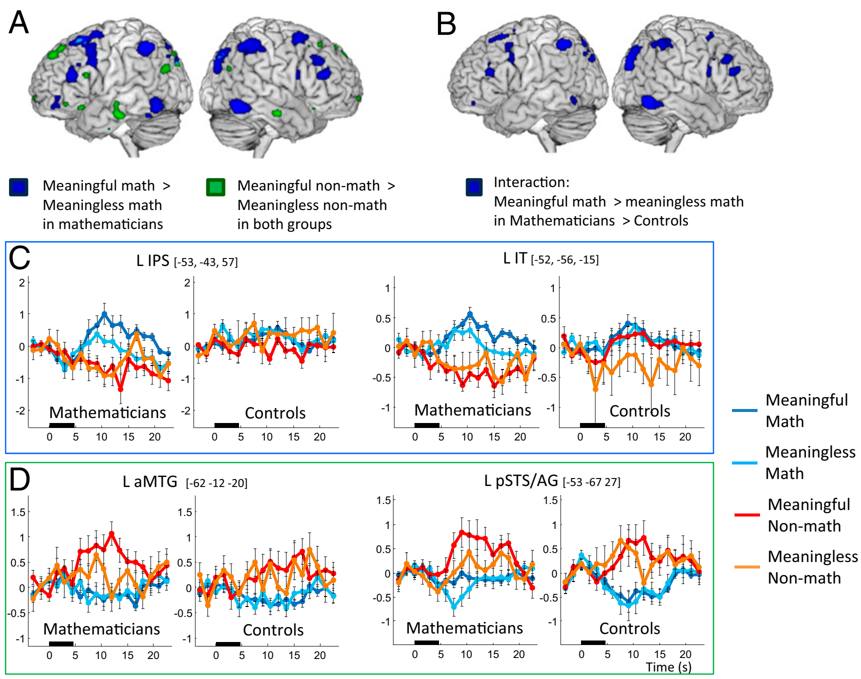

Fig. 4. Math and nonmath semantic effects. (*A*) Whole-brain view of semantic effects (meaningful > meaningless) for math statements in professional mathematicians (blue) and for nonmath statements in both groups (green). (*B*) Mathematical expertise effect: Interaction indicating a large difference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

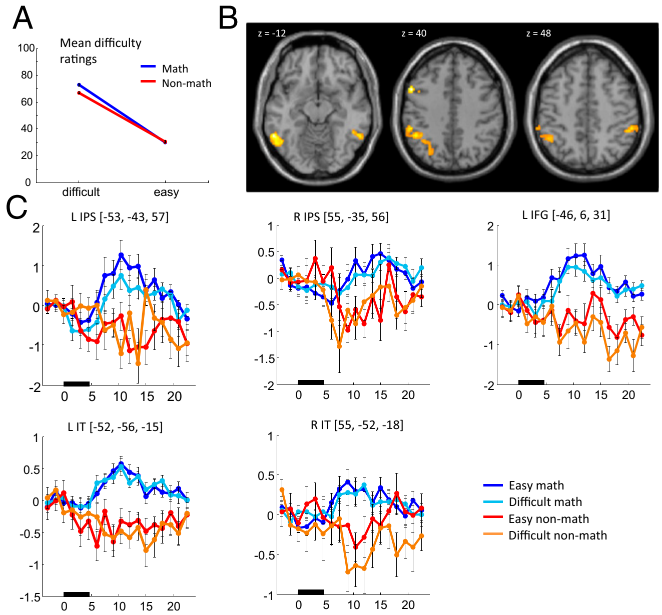

Fig. 5. Control for task difficulty. For each subject, math and nonmath statements were sorted into two levels of difficulty (easy versus difficult) depending on whether their subjective rating was below or above the subject's mean. (*A*) Mean difficulty ratings for easy and difficult math and nonmath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

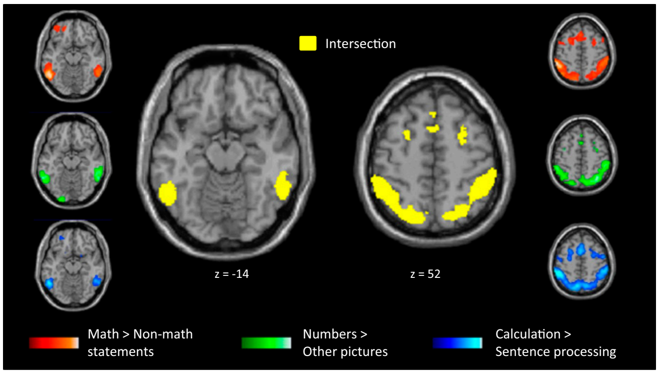

Fig. 6. Overlap of the mathematical expertise network with areas involved in number recognition and arithmetic. Red, contrast of math versus nonmath statements in mathematicians; green, contrast of Arabic numerals versus all other visual stimuli in both mathematicians and controls; blue, contrast of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

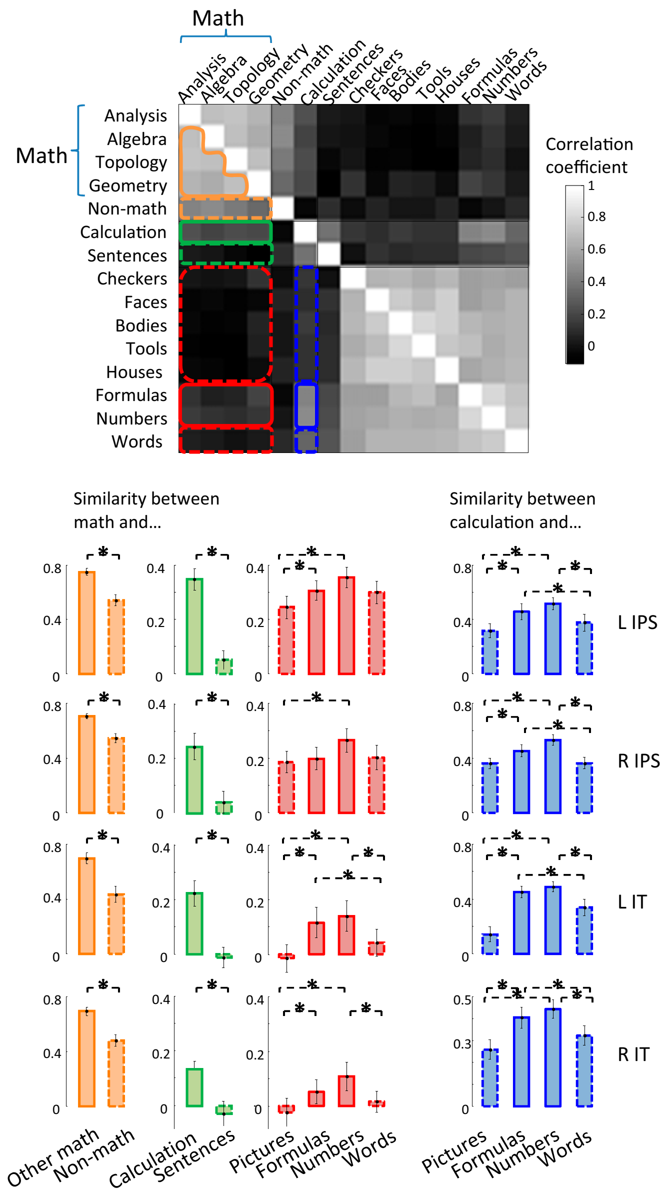

Fig. 7. Representational similarity analysis. (*Top*) Sample similarity matrix in left infero-temporal cortex showing the mean, across subjects, of the correlation between the spatial activation patterns evoked by the 15 experimental conditions of the whole experiment: four domains of math plus nonmath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

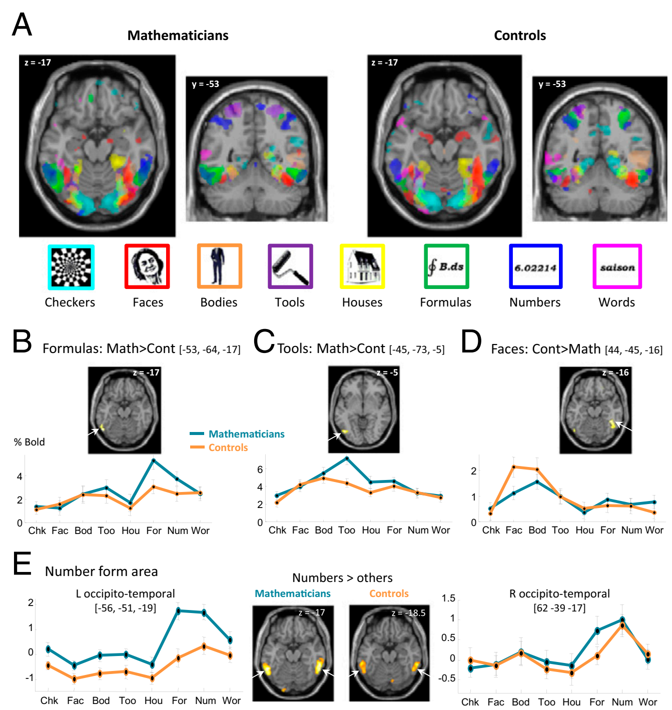

Fig. 8. Effects of mathematical expertise on the ventral visual pathway. (*A*) Mosaic of preferences for different visual categories in ventral visual cortex. Slices show the activation for the contrast of a given category (represented by a specific color) minus all others. (*B* and *C*) A whole-brain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