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fetious virus in siRNA-transfected cells (Fig. 4, D and E). Thus, F11L-mediated inhibition of RhoA signaling is required for both vaccinia morphogenesis and infection-induced cell motility. Our observations may also explain, at least in part, why MVA, which lacks functional F11L, is unable to replicate in most cell types in culture (7–9). They also offer molecular insights into the mechanism by which vaccinia induces cell migration (5, 6). One can envisage that migration of an infected cell will increase the efficiency of virus spread because extracellular virus particles associated with the plasma membrane, which are responsible for direct cell to cell spread, will come into contact with more neighboring noninfected cells than they would if the infected cell were static.

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Supporting Online Material

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Materials and Methods

Figs. S1 to S6

Movies S1 to S4

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Core Knowledge of Geometry in an Amazonian Indigene Group

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Does geometry constitute a core set of intuitions present in all humans, regardless of their language or schooling? We used two nonverbal tests to probe the conceptual primitives of geometry in the Mundurukú, an isolated Amazonian indigene group. Mundurukú children and adults spontaneously made use of basic geometric concepts such as points, lines, parallelism, or right angles to detect intruders in simple pictures, and they used distance, angle, and sense relationships in geometrical maps to locate hidden objects. Our results provide evidence for geometrical intuitions in the absence of schooling, experience with graphic symbols or maps, or a rich language of geometrical terms.

Through natural selection, our mind has adapted to the conditions of the external world, [...] it has adopted the geometry most advantageous to our species; or, in other words, the most convenient.

—Henri Poincaré, *La Science et l'Hypothèse*

Euclidean geometry is one of the deepest and oldest products of human reason, but its foundations remain elusive. Many of its propositions—that two points determine a line, or that three orthogonal axes localize a point—are judged to be self-evident (1, 2) and yet have been questioned on the basis of logical argument, physical theory, or experiment [(3–5)]; for a historical review, see (6)]. Here we ask whether the conceptual principles

of geometry are inherent in the human mind, by studying the spontaneous geometrical knowledge of the Mundurukú, an Amazonian indigene group (7). The present data were collected by one of us (P.P.) during a field trip in 2004–2005 to remote sites along the Cururu river. Most of the children and adults who took part in our experiments inhabit scattered, isolated villages and have little or no schooling, rulers, compasses, or maps. Furthermore, the Mundurukú language has few words dedicated to arithmetical, geometrical, or spatial concepts, although a variety of metaphors are spontaneously used (see Supporting Online Material for a list).

Our first test [inspired from (8)] was designed to probe the Mundurukú's intuitive comprehension of the basic concepts of geometry, including points, lines, parallelism, figures, congruence, and symmetry (9). For each such concept, we designed an array of six images, five of which instantiated the desired concept while the remaining one violated it (Fig. 1). The participants were asked, in their language, to point to the “weird” or “ugly” one. Care was taken to minimize cues other than the desired conceptual relation that could be used to

identify the target. For instance, if the desired concept was “trapezoid,” the target was a non-trapezoidal quadrilateral whose size and orientation fell within the range of variation of the other five trapezoids. There are many ways in which the participants could have selected an odd picture out of the six, including size, orientation, or personal preference. If the Mundurukú share with us the conceptual primitives of geometry, however, they should infer the intended geometrical concept behind each array and therefore select the discrepant image.

All participants, even those aged 6, performed well above the chance level of 16.6% (average 66.8% correct, minimum 44.2% correct, $P < 0.001$). Performance was higher than chance in all but 6 of the 45 slides ($P \ll 0.001$) and was indistinguishable for Mundurukú adults and children. There was no significant influence of the bilingualism or schooling exhibited by some of the participants (9). As shown in Fig. 1, the Mundurukú succeeded remarkably well with the core concepts of topology (e.g., connectedness), Euclidean geometry (e.g., line, point, parallelism, and right angle), and basic geometrical figures (e.g., square, triangle, and circle). They experienced more difficulty, but still achieved higher-than-chance performance, in detecting symmetries and metric properties (e.g., equidistance of points). They performed poorly only in two domains: a series of slides assessing geometrical transformations, for instance, by depicting two triangles in a mirror-symmetry relation; and another two slides in which the intruder shape was a randomly oriented mirror image of the other shapes. Interestingly, both types of slides require a mental transformation of one shape into another, followed by a second-order judgment about the nature of this transformation. It is possible that geometrical transformations are inherently more difficult mathematical

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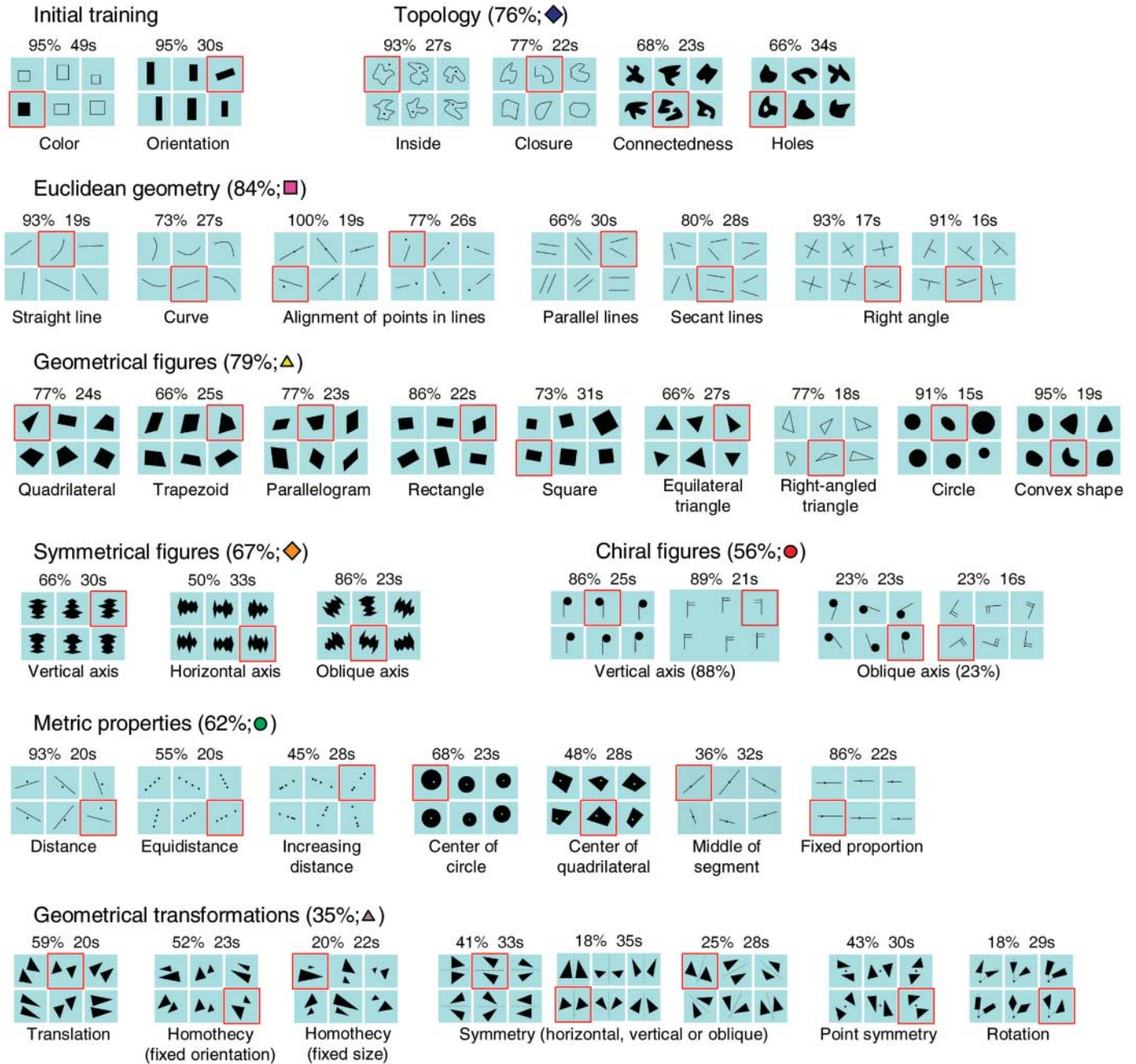


Fig. 1. Performance of Mundurukú participants in a multiple-choice test of the core concepts of geometry, rearranged in hierarchical order. In each slide, five images instantiate a specific concept indicated below, whereas the sixth (surrounded in red) violates it. The percentage of participants choosing the correct intruder is shown on top of each slide.

Chance level is 16.6% correct; 28% correct corresponds to $P < 0.05$, and 35% correct to $P < 0.001$. Mean response times (in seconds) are also indicated. For each category of concept, the averaged percentage of correct answers is shown along with a color symbol used to refer to individual test items in Fig. 3.

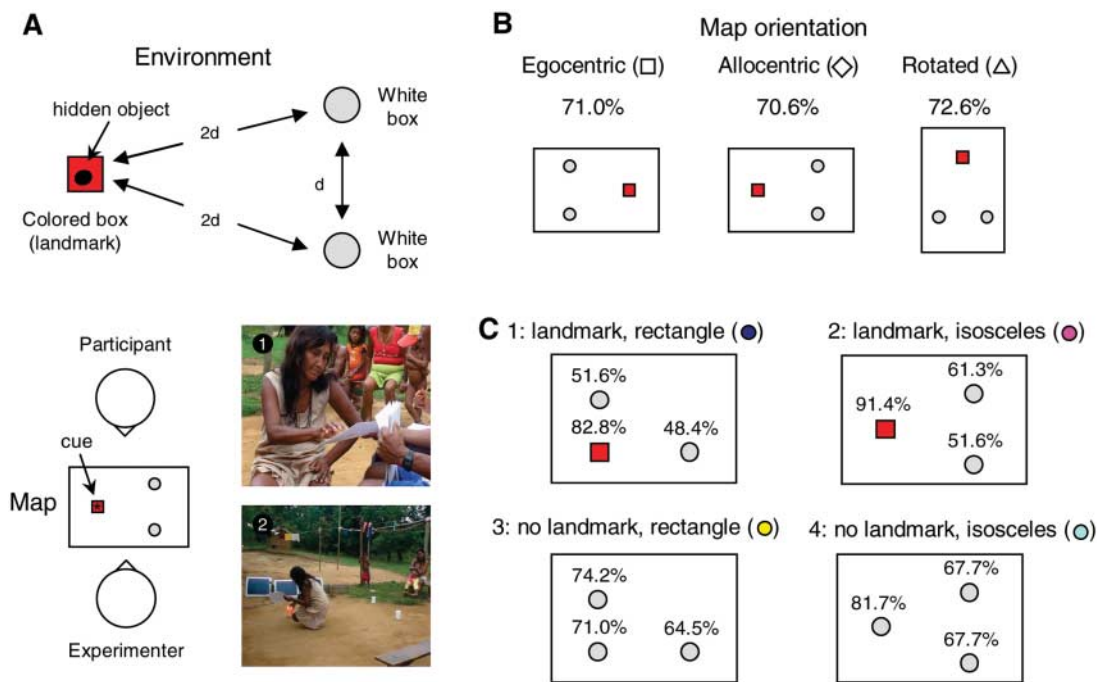
concepts. Alternatively, such transformations may be more difficult to detect in static images.

To assess the generality of the patterns of difficulty of our images, we also tested American children and adults. An analysis of variance with factors of age (children or adults) and culture (Mundurukú or American) revealed effects of age ($P < 10^{-6}$), culture ($P < 10^{-5}$), and their interaction ($P = 0.0002$). As shown in Fig. 3A, the performance of Mundurukú children and adults was identical to that of

American children, whereas the performance of American adults was significantly higher. Indeed, we observed a well-defined profile of difficulty common to both cultures. Across the 45 slides, the mean performance of the Mundurukú children correlated closely with that of the American children ($r^2 = 61.8\%$, $P < 10^{-9}$). In this regression, the intercept and the slope were nonsignificantly different from 0 and 1, respectively, confirming that performance was highly similar in both cultures (Fig.

3B). Furthermore, despite their vastly different cultures and levels of schooling, Mundurukú and American adults also showed a shared profile of difficulty ($r^2 = 49.4\%$, $P < 10^{-7}$), although American adults performed at a higher overall level (Fig. 3C). This reproducible ordering of error rates does not support Piaget's hypothesis of a developmental and cultural progression from topology to projective and Euclidean geometry (10), but rather suggests that geometrical intuition cuts across all of

Fig. 2. Performance of Mundurukú participants in the map test. (A) Schematic representation of the spatial layout of the experiment. On each trial, the participant was shown a “map” representing the location of three boxes, one of which contained a cue symbolizing a hidden object. Then he or she turned around and searched for the hidden object (distance $d \approx 1.5$ m). (B) Performance in the three map orientations. The map and the environment could be aligned as seen from the top (allocentric condition), aligned relative to the participant before and after turning (egocentric condition), or nonaligned (90° rotation condition). (C) Performance at each location in the four successive blocks of the experiment. The symbols in (B) and the colors in (C) are used to refer to individual test items in Fig. 3.



these domains. In summary, uneducated adults from an isolated culture, as well as young children from the same culture or from a Western culture, exhibit a shared competence for basic geometrical concepts.

Although the multiple-choice test was designed so that the target picture could only be identified once the relevant geometrical property had been grasped, it could be argued that the test requires solely a visual judgment of dissimilarity among closely similar images. We argue, however, that judgments of visual similarity do not merely result from superficial sensory computations, but reflect deep properties of cognitive architecture (11). Geometrical intuitions, in the final analysis, may rest on a spontaneous imposition of stable conceptual relations onto variable and imperfect sensory data, a process well captured by the multiple-choice test. Nevertheless, we sought to replicate and extend our findings in a second task that would demonstrate more directly the use of abstract geometrical knowledge and its transfer across widely different contexts.

Etymologically, “geo-metry” is the science of measuring the Earth. Geometrical concepts first were used to measure and chart the length, area, and shape of land surfaces. To investigate whether the Mundurukú spontaneously understand and use geometry in this sense, we designed an abstract map test. Three boxes or cans were arranged in a right-angled or isosceles triangle, and an object was hidden in one of them (9) (Fig. 2). With his or her back to this array, each participant was presented with a sheet of paper in which square and circular symbols represented the three containers, and a star on one of the forms marked the location of

the hidden object. This “map” preserved the two-dimensional geometrical relationships between the objects, as viewed from above, except for scale. The orientation of the map relative to the array varied across trials, so that only the geometrical relationships among the forms specified the hidden object’s location. By recording where each participant first searched for the object, we evaluated whether participants could relate the geometrical information on the map to the geometrical relations in the environment, over changes in orientation, an ~ 10 -fold change in size, and a change from two dimensions to three.

The map test is likely to be entirely novel to the Mundurukú. Although they live in widely dispersed villages between which they navigate by boat or foot, and although they also manipulate tools, build baskets, craft necklaces and bracelets, sculpt symbolic miniatures, and are renowned for their elaborate traditional face- and body-painting schemes, the Mundurukú do not typically possess maps or spontaneously draw pictures of their houses, villages, or environment. Across several trips to the Mundurukú territory, we occasionally observed spontaneous activities such as the drawing of circles on the ground to represent villages. These drawings were coarse, however, and failed to preserve metric information about the angles and distances between the referents. Our map test, by contrast, could not be accomplished without attending to metric information.

Overall, the participants’ success rate averaged 71%, which was well above the chance level of 33.3% (across subjects, $P < 0.0001$). Performance did not differ between children (73.3% correct) and adults (70.4% correct; both $P <$

0.0001 relative to chance). There was also no effect of map orientation (Fig. 2B): Performance with allocentric, egocentric, and rotated maps did not differ ($F < 1$) and was always significantly above chance, suggesting that participants either extracted the geometrical relationships directly or performed a mental rotation so as to align the map with the environment.

An interesting insight into the cues used by the participants came from an analysis of the evolution of their performance. During training, and in the first half of testing, one of the hiding locations was a red box quite distinct from the other hiding locations (white cans) and depicted as a red square on the map. Although performance did not differ overall as a function of presence or absence of this landmark ($F < 1$), there was a significant landmark by object location interaction ($P < 0.0001$), as well as a triple interaction with age ($P = 0.003$), indicating that the effect of the landmark on search patterns was more pronounced in adults. During the first two experimental blocks in which the red box was present, participants performed well when the object was placed at this landmark location (87.1% correct) but less well when the object was placed in one of the other two unmarked locations (54.3% correct). An analysis of errors indicated that, in the latter case, they avoided the landmark location (only 9.1% of responses) but tended frequently to select the wrong nonmarked location (36.6% of responses). Still, participants chose the incorrect, unmarked location less frequently than the correct one ($P < 0.003$ on a t test comparing the two nonmarked locations), thus providing evidence for sensitivity to purely geometrical information.

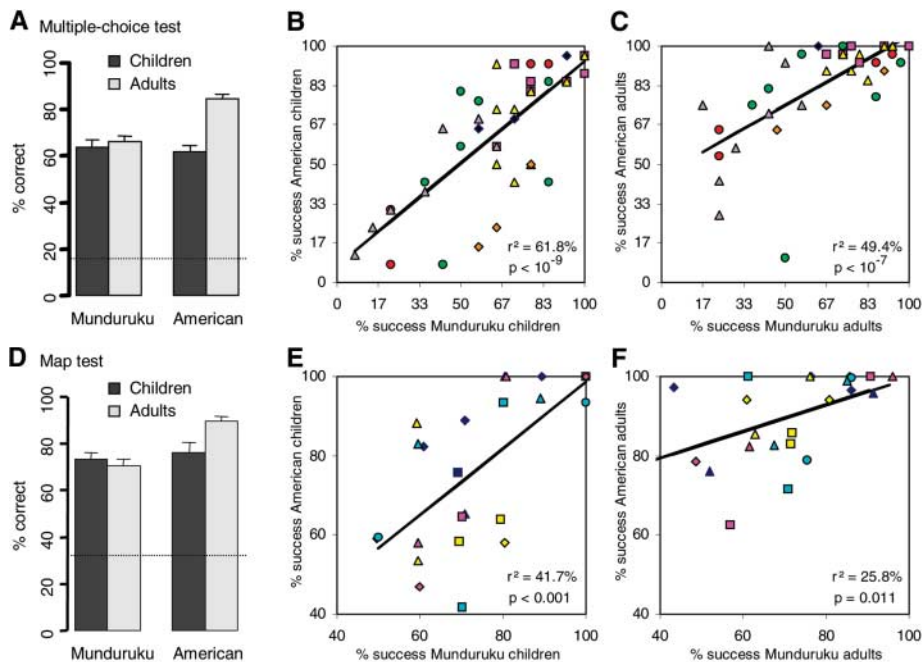


Fig. 3. Comparison of the geometrical performance of Mundurukú and American participants. (A to C) Multiple-choice test; (D to F) map test. (A) and (D) show the percent success averaged across participants and test items, as a function of age and culture (horizontal line = chance level; vertical bar = standard error). (B), (C), (E), and (F) show the correlation of performance level across test items, separately for children and adults. Each symbol represents average performance in response to a given test item. In (B) and (C), the symbol shapes and colors refer to the categories of slides defined in Fig. 1. In (E) and (F), symbol shapes refer to map orientation and color to map layout, as defined in Fig. 2. In both cases, r^2 and P values indicate the significance of the observed linear correlation in performance across the two cultures.

Geometrically driven behavior became much more evident in the trials in which the landmark was absent, such that only the geometrical relationships between the circles and cans specified the position of the hidden object. In this situation, performance was high on average (72.0% correct) and far exceeded chance level at all locations and with both triangular configurations (all P values < 0.0003). In the final block with an isosceles configuration, performance was good even at the two symmetrical locations of the isosceles triangle (67.7% correct). The Mundurukú therefore were able to use sense relationships, as well as distance or angle, to relate the map to the environment.

For direct comparison, we also tested educated American children and adults in this map task (Fig. 3D). All of the above effects were replicated. An analysis of variance revealed effects of age ($P = 0.043$), culture ($P < 10^{-4}$), and their interaction ($P = 0.013$). As in the multiple-choice test, the Mundurukú children and adults performed at a level indistinguishable from that of American children, whereas the American adults performed significantly better. Nevertheless, even the latter group made some errors, and we observed high correlations between the performance profiles of American and Mundurukú participants across the test items, both within children and within adults (Fig. 3, E and F). Those results again point to a

shared pattern of core geometrical knowledge despite increases in absolute performance levels in the educated American adults.

Studies of the universality of human geometrical knowledge have a long history. As chronicled by Plato in the *Meno* (~380 B.C.), Socrates probed the geometrical intuitions of an uneducated slave in a Greek household, leading him, through a series of questions, to discover relations between the areas of squares drawn in the sand. He concluded of the slave that “his soul must have always possessed this knowledge” (12). Nevertheless, the slave shared a language with educated Greeks, likely was familiar with pictures and other products of Greek culture, and revealed his intuitions by engaging in a conversation about lines, areas, and number. Our experiments, in contrast, provide evidence that geometrical knowledge arises in humans independently of instruction, experience with maps or measurement devices, or mastery of a sophisticated geometrical language. This conclusion is consistent with paleoanthropological evidence (13) and with previous demonstrations of a right-hemisphere competence for nonverbal tests of geometry in split-brain patients (8). Further research is needed to establish to what extent this core knowledge is shared with other animal species (14, 15) and whether it is available even in infancy or is acquired progressively during the first years of life (4, 10, 16–18). There is little

doubt that geometrical knowledge can be substantially enriched by cultural inventions such as maps (19), mathematical tools (3, 4, 6), or the geometrical terms of language (18, 20–25). Beneath this fringe of cultural variability, however, the spontaneous understanding of geometrical concepts and maps by this remote human community provides evidence that core geometrical knowledge, like basic arithmetic (7, 26), is a universal constituent of the human mind (11).

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