

Research

Core systems of geometry in animal minds

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Research on humans from birth to maturity converges with research on diverse animals to reveal foundational cognitive systems in human and animal minds. The present article focuses on two such systems of geometry. One system represents places in the navigable environment by recording the distance and direction of the navigator from surrounding, extended surfaces. The other system represents objects by detecting the shapes of small-scale forms. These two systems show common signatures across animals, suggesting that they evolved in distant ancestral species. As children master symbolic systems such as maps and language, they come productively to combine representations from the two core systems of geometry in uniquely human ways; these combinations may give rise to abstract geometric intuitions. Studies of the ontogenetic and phylogenetic sources of abstract geometry therefore are illuminating of both human and animal cognition. Research on animals brings simpler model systems and richer empirical methods to bear on the analysis of abstract concepts in human minds. In return, research on humans, relating core cognitive capacities to symbolic abilities, sheds light on the content of representations in animal minds.

Keywords: cognitive development; animal cognition; navigation; geometry

1. CORE COGNITIVE SYSTEMS IN ANIMAL MINDS

For well over 2000 years, studies of higher cognition have focused primarily on capacities that are unique to humans, such as language and geometrical intuitions. Debates about the nature and sources of these capacities continue to the present day, however, and progress in resolving them pales by contrast with the progress achieved in understanding the perceptual capacities that humans share with other animals. This contrast highlights problems faced by attempts to study higher cognition in any species, and it hints at a solution to those problems.

The modern study of perception began with research on humans, who experimented on themselves to probe the physical events that evoke conscious experiences of colour, tone or motion. The power of these ‘psychophysical experiments’ was greatly enhanced, however, by parallel research on animals. Studies of perception in humans and in other animals were mutually illuminating: while human psychophysical findings guided research on animal perceptual systems, animal research shed light on the development and architecture of those systems, using methods of controlled rearing, neurophysiology and (more recently) genetics. Research from evolutionary biology and computer science enriched both sets of insights, by shedding light on the computational problems that visual systems evolved to solve.

The study of higher cognition has not experienced the same synergies. Indeed, attempts to use human conscious experience as a guide to animal research often lead to blind alleys, because human intuition is a poor source of insights into animal minds. This failure stems, we suggest, from three prominent differences between perceptual systems, on one hand, and higher cognitive systems on the other. First, perceptual systems show strong continuity over development, but systems of abstract knowledge, such as natural number, Euclidean geometry or morality, undergo qualitative developmental changes. Second, perceptual systems are substantially alike in all cultures, but systems of abstract concepts are more variable: their development depends on a complex interplay of intrinsic growth processes and culture-specific achievements. Third, fully abstract concepts are expressed through systems of symbols that are unique to our species. The intuitive concepts of mature scientists therefore may distort attempts to understand animal minds.

Despite these obstacles, we propose that higher cognition in humans and animals indeed can be studied by the methods that have emerged from synergistic research on perception. We hypothesize that uniquely human cognitive achievements build on systems that humans share with other animals: *core systems* that evolved before the emergence of our species. The internal functioning of these systems depends on principles and processes that are distinctly non-intuitive. Nevertheless, human intuitions about space, number, morality and other abstract concepts emerge from the use of symbols, especially language, to combine productively the representations that core systems

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deliver. If this proposal is correct, psychologists and biologists can discover the sources of our abstract ideas through interdisciplinary studies of the sort that bolstered our understanding of human perceptual experience. Because uniquely human abstract concepts change both over development and across cultures, however, research must look primarily to the behaviour of animals and young children, rather than to the intuitions of human experimenters, for insight into the core cognitive capacities of human and animal minds.

2. NATURAL GEOMETRY

Here, we develop this hypothesis by focusing on the domain of Euclidean geometry and its fundamental relations of *distance*, *angle* and *direction*. Euclidean concepts have three striking properties. First, they are extremely simple: just five postulates, together with some axioms of logic, suffice to specify all the properties of points, lines and forms. Second, they are exceedingly useful: almost all human cultural accomplishments depend on these concepts, from the measurement of space and time to the pursuit of science, technology and the arts. Third, the objects of Euclidean geometry go beyond the limits of perception and action: points are so small they have no size and so cannot be detected by any physical device; lines are so long they cannot be fully seen or traversed.

For these reasons, research on spatial cognition has a long and rich history. The behaviour of animals navigating through laboratory mazes or natural environments has been a topic of study in experimental psychology and behavioural biology since the emergence of those fields. With the development of neurophysiology, both navigation and form perception became popular topics for research on the neural systems guiding behaviour. Nevertheless, debates over the nature and sources of geometrical concepts and representations continue to the present day, and attempts to elucidate these concepts often meet with controversy. The study of cognitive maps in animals and humans provides an instructive example.

3. COGNITIVE MAPS

Tolman [1] proposed that animals navigate through novel environments by forming mental representations with four key properties of external, symbolic maps: they are unitary, enduring, observer-free (and hence usable from any location) and Euclidean. The cognitive map hypothesis proved a fruitful guide to research on the neural mechanisms of navigation [2] and to computational theories of those mechanisms in animals from insects to humans [3]. Nevertheless, research on diverse animals now suggests that the representations guiding navigation do not have these properties. Both animal and human navigation depend on multiple representations, each with its own properties and limits [4]. Some of these representations are momentary and tied to particular viewpoints [5]. Above all, the representations of the paths taken by navigating animals and humans are not Euclidean.

Evidence that navigation depends on non-Euclidean representations came first from studies of insects [5], but striking recent evidence comes from research on humans navigating in immersive virtual environments [6]. College students were allowed to learn the structure of a maze of hedges containing stable landmarks, much as did Tolman's rats. After exploring a maze and discovering the landmark objects along its paths, participants were instructed to move from one landmark to another. In one condition, each location in the maze was locally Euclidean but its overall structure was not, for it contained two 'wormholes' that radically altered its global geometry. Remarkably, students in this condition never discovered the wormholes, and they learned to navigate the maze as effectively as those in an otherwise matched, Euclidean condition. Students' spatial learning evidently did not result in the construction of a Euclidean map.

These findings suggest that the representations guiding human navigation are remarkably impervious to education in geometry or to culture-specific experiences with maps. Although intuition suggests that we form internalized maps of our surroundings, the findings hint that intuition, perhaps shaped by experience with real maps, is a poor guide for studies of the basic navigation systems not only of ants or rats, but of our own species. Studies of navigation in non-human animals may be a better source of insights into human spatial cognition.

4. NAVIGATING BY THE DISTANCES AND DIRECTIONS OF EXTENDED SURFACES

Research on animals provides evidence for at least two systems guiding human navigation: a system for representing the distances and directions of large-scale, extended surfaces and a system for representing landmark objects and surface markings. We consider each system in turn.

Cheng & Gallistel [7,8] discovered that disoriented animals recover their sense of place by analysing the shape of the surrounding layout. When hungry rats, who had previously observed the location of now-buried food, were disoriented in a rectangular enclosure, they dug for food reliably at the two locations consistent with the enclosure's shape (figure 1*a*). Without training, rats tended not to use landmarks (such as a wall of a distinctive brightness or a corner panel with a distinctive geometrical pattern) to break the room's symmetry. With training, rats used landmarks to distinguish between the correct and opposite locations, both in Cheng's original experiments and in further studies [11]. Nevertheless, rats' behaviour prior to digging suggested that the processes of using layout geometry and landmark objects were distinct. Disoriented rats first responded to the enclosure's geometry and headed for one of the two locations with equal frequency. Then they checked nearby landmarks and proceeded to dig if the correct landmarks were present. Recent experiments provide evidence for the same search patterns in ants [9] (figure 1*b*). While the nature of the processes underlying this behaviour is debated (see below), navigation in both species depends on

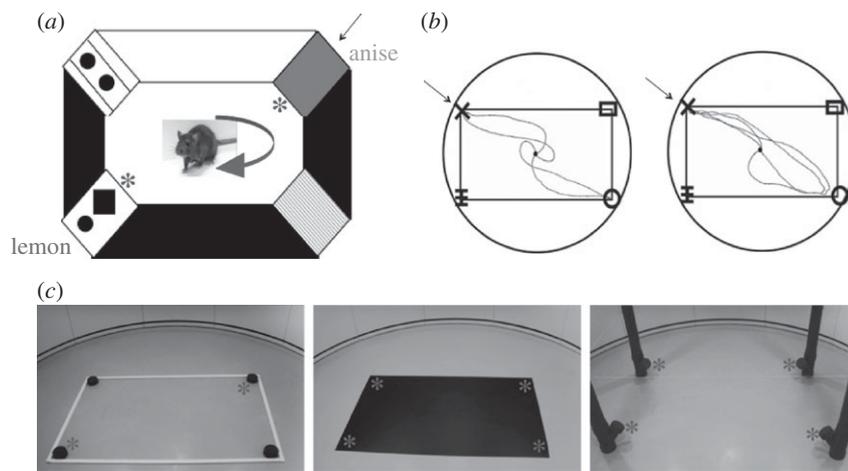


Figure 1. Schematic, overhead view of displays for studies of reorientation in (a) rats (after [8]), (b) ants (after [9]) and (c) young children (after [10]). Arrows indicate the target location (respectively, buried food, the favoured exit from the chamber or a hidden toy). Asterisks indicate the search locations in (a,c); in (b), lines indicate the paths of ants tested with no training and exits at all four corners (left) or with training and a single exit (right). (a) Untrained rats dug for food either in the correct location or in the geometrically congruent, opposite location, ignoring the two-dimensional form and brightness cues that distinguished these locations. (b) Untrained ants performed similarly, but trained ants engaged a two-step search strategy: after approaching the correct or opposite exit with equal frequency, they continued forward if the correct form cue was present and reversed direction otherwise. (c) Untrained children confined their search to the correct and congruent opposite corners when tested in a circular arena with a central rectangular structure that differed minimally from the surrounding ground in height and brightness (left). In contrast, children ignored this geometrical structure and searched the four corners equally when the rectangle was defined by a maximal difference in brightness and no difference in height (centre), or by four free-standing columns at its corners, enclosed by twine so as to constrain children's exploration (right).

distinct representations of the large-scale layout and small-scale landmarks that interact to influence behaviour [11].

Human adults show a different search pattern: after disorientation in a rectangular room with one distinctively coloured wall, college students directly located the unique corner. Young children, in contrast, showed the same search pattern as untrained rats and ants, searching the correct and opposite corners with equal frequency [12]. Children also used landmarks to guide their search, when the landmarks were direct cues to a hidden object's location [13] and when they were large and highly salient [14]. In that case, children's search patterns indicated that the process of navigating by the landmark was distinct from the process of reorienting by the shape of the room, as in rats and ants.

Further evidence for two separate processes of navigating by enclosure geometry and by landmark objects comes from studies of human adults tested under conditions that place demands on language and working memory. When adults were disoriented in a rectangular room with one coloured wall while performing a demanding verbal task, they consistently reoriented by the shape of the enclosure. In contrast, their use of the coloured wall depended on initial task instructions. Adults who were not forewarned about the task searched the correct and opposite corners equally, showing no effect of the coloured wall [15]. Those who were forewarned, in contrast, used the wall to narrow their choice to the correct corner [16]. The effects of task instruction on human adults resemble the effects of training on ants and rats.

Further insights into the representations guiding reorientation have emerged from neurophysiological

studies of navigating rats. Individual neurons in the hippocampus and surrounding cortex were found to be active when a rat stood at a particular distance and direction from one or more of the extended surfaces in the environment [17–19]. These cells respond to the positions of extended surfaces but not to the colours or textures of those surfaces [20] or to the locations of freestanding objects [18].

Burgess and his collaborators extended these findings to human adults performing a virtual navigation task. Adults were asked to reposition a known target in a virtual environment after the environment disappeared and then reappeared at a different perspective (akin to disorientation). Adults learned to locate the target object relative to both the extended surface and the landmark in the virtual environment, but the two types of learning engaged different neural and cognitive systems. Learning in relation to landmarks was based on processes of reinforcement learning, whereas learning in relation to extended surfaces occurred automatically [4]; the two types of learning were associated with activity in the same two brain systems as in rats [21].

These findings provide evidence for homologous mechanisms of navigation in humans and rats. In recent experiments, this homology has been documented in exquisite detail [22,23]. The findings also provide insights into the behaviour of both species after disorientation. Full disorientation is a rare event in nature, and so humans and other animals do not normally prepare for it in advance by attentively encoding the positions of significant objects in relation to their surroundings. When untrained animals or children are disoriented, therefore, they typically reorient only by the environmental information that they

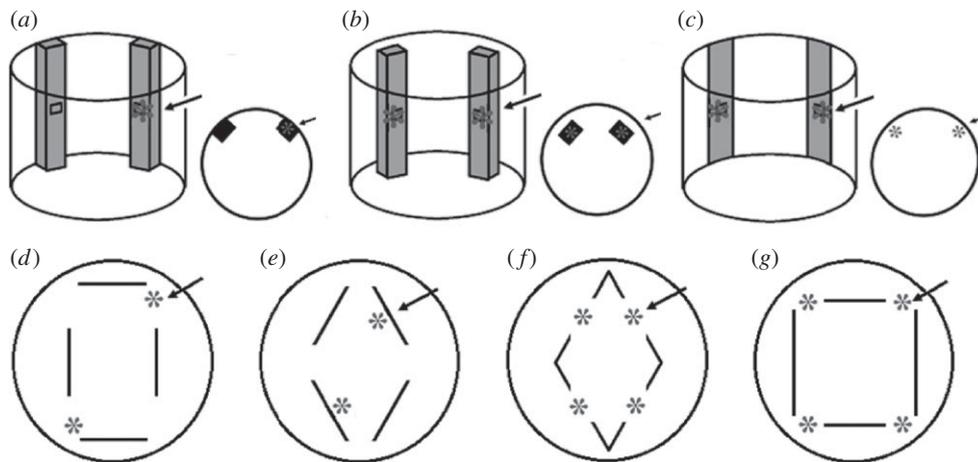


Figure 2. Depiction of the displays for studies of reorientation in untrained children tested in a cylindrical enclosure with two tall columns [25] (*a–c*; side view on left, overhead view on right), or four extended surfaces or corner objects [27] (*d–g*; overhead view). Arrows indicate the target location; asterisks indicate children's search locations. When columns were placed flush against the enclosing cylindrical wall (*a*), children confined their search to the single location specified by the geometry of this extended surface layout. When columns were free-standing (*b*) or were replaced by flat patches of the same colour and contrast (*c*), children ignored this geometry and searched equally at the correct column and its featurally identical twin. When the four surfaces were equal in length but placed at different distances or orientations so as to form a fragmented rectangle (*d*) or rhombus (*e*), children confined their search to the correct and the geometrically congruent opposite locations: they were guided by surface distance and orientation despite the absence of distinctive surface lengths or corner angles. In contrast, when the surfaces differed in length (*f*) or angle (*g*) but their distances were equated, children searched equally at the four locations with the same distance relations, ignoring the differences in length or angle.

encode automatically: the distances and directions of extended surfaces. After appropriate training or instruction, however, animals and humans engage attention to encode the relation of significant objects to landmarks.

If separate systems serve to represent extended surfaces and landmark objects, what counts as an object, and what counts as an extended surface? Studies of reorientation in young children address this question. When a rectangular arena of variable height was placed in the centre of a uniform cylindrical chamber, children used its shape to reorient not only when the enclosure was tall enough to block their view of the surroundings, but also when it was small enough to look or step over [24], and even when it protruded only slightly off the ground [10]. In contrast, children failed to reorient by a rectangular pattern of flat lines or contours on the ground or by a rectangular array of large, freestanding columns [10,24] (figure 1*c*). When two columns were placed asymmetrically within the cylindrical room, children reoriented by the columns when they stood flush against the walls. When the columns were freestanding or flattened, however, children used them as direct landmarks [25] (figure 2*a–c*). Reorientation therefore depends on the shape of the layout of extended surfaces that are continuous with the array's borders. Recent research confirms these conclusions in chicks, who also reorient by subtle three-dimensional perturbations of the extended surface layout but not by two-dimensional patterns or arrays of columns [26].

A further question concerns the types of geometric information that children and animals extract from the surface layout. In rectangular arrays, target locations can be specified by directional relationships between walls differing either in length (e.g. a corner with a

longer wall on the left) or in distance (e.g. a corner with a closer wall on the left). Studies of children [27] provide evidence for reorientation by distance but not length (figure 2*d–f*), in accord with findings from neurophysiological studies of rats [17]. In most environments, surfaces also differ in orientation or slope, and they meet at corners, cliffs or other junctions. Both pigeons and human adults reorient by surface slope or orientation [28,29], but children fail to reorient by corner angles [27] (figure 2*g*). The reorientation system therefore captures some but not all of the geometrical properties of extended surface layouts.

Although early experiments tested children and animals in highly elongated rectangular enclosures, young children reorient effectively in rectangular enclosures whose walls differ only slightly in distance [30,31] (figure 3*a*). This high sensitivity may account for otherwise puzzling effects of surface brightness and patterning on navigating children and animals. For example, both children and mice fail to reorient in square rooms whose alternating walls are covered with different patterns (such as crosses versus circles or circles versus no pattern) but successfully reorient in square rooms whose alternating walls are covered with the same pattern at two scales [32,33]. In children, pattern scaling influences perceived surface distances [31]. Nevertheless, there are limits to distance perception [30,31]. A recent study showing successful use of geometric information in symmetric but not asymmetric enclosures [34] may reflect limitations on the number and degree of subtle distance relations that children detect and remember [27].

In the above research, studies of children shed light on a long-standing controversy in animal navigation: do navigating animals respond to geometric properties of the three-dimensional surface layout, or do they

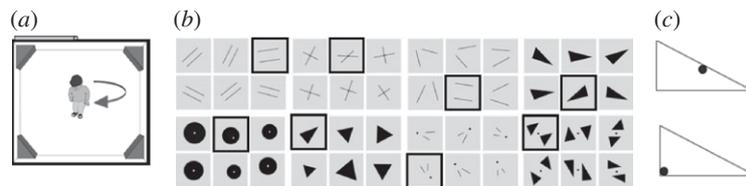


Figure 3. Example displays for a study of interrelationships between performance on tests of (a) reorientation by subtly rectangular enclosures, (b) visual form analysis and (c) map-based navigation to surfaces (top) or corners (bottom). In (a), children searched for a sticker after they were disoriented in a room whose walls differed subtly in length by ratios of 6 : 7, 24 : 27 (shown here) or 12 : 13. In (b), children were presented with six forms, one of which differed from the others with respect to length, angle, parallelism/alignment or sense/symmetry (from left to right). Children's task was to indicate the outlier (outlined in black; after [30]). In (c), children stood inside a three-dimensional triangular enclosure with three purple bowls placed at either the centre of its walls or at its corners, centred within a cylindrical room. They viewed a map depicting an overhead view of the enclosure and room at one-tenth the size and variable orientation relative to the enclosure. Children were told to place an object in the room at a location indicated by a single purple dot on the map (after [30]). Performance on the reorientation and form analysis tasks was uncorrelated, but reorientation accuracy predicted map-based navigation to surfaces, and form analysis accuracy predicted map-based navigation to corners.

mimic such responses through mechanisms operating only on two-dimensional images of the layout [35]? Recent computational studies reveal that simple matching processes, applied to panoramic images of the environment, can account for the findings from studies of reorientation in rectangular enclosures with high walls [36–38]. These models cannot, however, account for the abilities of children and chicks to reorient in subtly geometric environments [10,26] or in square environments whose patterning creates an illusory impression of depth [31–33]. Although the surface layout representation guiding reorientation is not fully Euclidean (because it fails to capture relationships of length and angle), it does capture aspects of the environment's three-dimensional structure.

Human children cannot be tested in reorientation tasks until they begin to locomote independently, in the second year of life. Because the mechanisms of reorientation are so similar in other vertebrates, however, controlled rearing experiments on model animals can test for effects of experience on the developing propensity to reorient by layout geometry. In one series of experiments, separate groups of chicks were reared either in a geometrically rich environment or in a homogeneous, cylindrical environment, and then they were disoriented in a rectangular room. On the very first reorientation trial, chicks in the two groups showed reliable and equal abilities to reorient by the shape of the environment [39]. Further studies of fish and mice replicated this finding, while also providing evidence for experience-dependent abilities to navigate by landmarks [40,41]. Converging evidence for innate representations of layout geometry comes from neurophysiological experiments on infant rats, tested at the onset of independent locomotion [42,43].

In summary, humans and animals navigate by a system for representing aspects of the geometry of the extended surface layout. This system arises in animals with no prior experience navigating in a geometrically structured environment, and it operates automatically, in a manner that is largely impervious to variations in attention. The system incorporates information about the positions of extended three-dimensional surfaces that are continuous with the ground surface, but not about the positions of free-standing objects or surface

markings. Finally, the system captures some geometric properties with high resolution (surface distances and directions) but fails to capture other properties (surface lengths or corner angles).

Studies of robot navigation reveal the computational advantages of such a system. Systems for simultaneous localization (of the self) and mapping (of the environment) face three problems (see [44] for review). First, navigable environments often contain confusable objects: one corridor or forest clearing may look much like another. Second, environments change their appearance when objects are displaced or surface markings are obscured. Third, environments tend to be cluttered with objects, and a navigator who represents these objects must retain and process large bodies of data. All three problems are reduced if the navigator can disregard the objects and surface markings in the environment and represent only the large-scale three-dimensional structure of its extended surfaces. In natural environments, these surfaces rarely have symmetries that create false correspondences. Barring earthquakes, moreover, these surfaces do not move. Because extended surfaces tend to be smooth at most locations, they can be represented economically: only a few points suffice to specify surface distance, direction and curvature. These computational properties may explain why a system for navigating by extended surfaces emerged in distant ancestral species and has been preserved over subsequent evolution.

5. RECOGNIZING THE SHAPES OF VISUAL FORMS

Nevertheless, this layout representation is not the sole potential source of Euclidean geometry. Animals and humans also recognize objects and patterns on the basis of their shapes. This ability has been investigated intensely for a century, in diverse animals, including insects [45], birds [46], rodents [47], monkeys [48] and humans in diverse cultures [49–51]. Studies using neurophysiological methods have probed the architecture of visual form analysis in animals, yielding findings that later were confirmed and extended by research using non-invasive neuroimaging in humans [52,53]. Moreover, the nature and limits of experience effects on the development of form perception have

been probed through studies of controlled-reared animals [54], newborn human infants [55] and older children with a delayed onset of pattern vision [56,57].

Converging findings from all these strands of research provide evidence that animals from insects to humans recognize objects primarily on the basis of their shapes, regardless of task demands [58]. Object recognition depends on a system of visual form analysis that builds shape representations with three properties (see [59] for review and discussion). First, representations of visual forms are scale-invariant over a considerable range: they fail to capture information about the absolute lengths of parts or distances of one part from another. Second, these representations are sense-invariant: they fail to capture the distinction between a form and its mirror image. Third, shape representations capture the relationships of *length* and *angle* that distinguish one shape from another. All these properties are evident in behavioural studies of human infants, who generalize across the same shape presented at different sizes or in two mirror image variants, and who discriminate between shapes that differ in the angular size of their corners or in the relative lengths of their sides [60]. These properties continue to be evident in behavioural studies of human adults, who detect relationships of length and angle across figures more easily than relationships of symmetry and sense [51,59] (figure 3*b*).

In all these respects, the core geometric representations guiding form analysis differ from core geometric representations guiding navigation. Indeed, the two sets of representations are nearly complementary. Whereas the core navigation system applies best to large three-dimensional arrays, the core form analysis system applies best to small two-dimensional patterns. The core navigation system captures absolute distance and sense (distinguishing between corners whose nearer wall is on the left versus right) but not relative length or angle; the core form analysis system does the reverse. The core navigation system is engaged when animals navigate, independently of attention; the core form analysis system is engaged when animals attend to a specific object or environmental location. Might these two systems together serve as sources for uniquely human, abstract geometry?

6. CORE KNOWLEDGE AND GEOMETRICAL INTUITION

Neither core system, considered alone, could account for mature human geometrical intuitions, because each system is limited in ways that explicit geometric concepts and intuitions are not. This observation raises two distinct possibilities. First, the geometrical representations guiding navigation and object recognition may be irrelevant to the development of abstract geometry: although abilities to navigate and recognize objects can be described by psychologists and biologists using concepts of abstract geometry, attributing knowledge of those concepts to navigating children and animals may be as mistaken as attributing concepts of ellipses to orbiting planets. Second, the representations guiding navigation and object recognition may combine to form mature, abstract geometrical

concepts and intuitions. In the latter case, concepts of formal geometry would not merely describe the behaviour of children and animals; they would capture aspects of the content of the representations in child and animal minds.

Although trained animals from ants to rats can learn to associate particular visual forms or other features to particular environmental locations [9,11,61], the productive system of Euclidean geometry appears to be unique to humans. Thus, research on human cognitive development can distinguish these two possibilities. Recent research provides evidence that systematic, intuitive reasoning about the Euclidean properties of dimensionless points, one-dimensional lines and triangles emerges universally in humans over the ages of 6–12 years [62]. Over the same time period, children come to master the skill of navigating by a special kind of symbolic device: a purely geometric map. When 6-year-old children are shown a flat map depicting an overhead view of a simple surface layout (for example, a long and short flat surface meeting at a right angle, and depicted on the map by an L-shaped form), they use relative lengths and angles on the map to locate positions in the three-dimensional array, but they fail to use sense relations and confuse corners with a shorter side on the left versus right [63]. Research using similar methods and displays with children of different ages revealed a developmental progression from 2.5 years to adolescence, with the youngest children navigating primarily by distance relationships [64,65] and the oldest navigating by distance, angle and sense [51].

Do these abilities depend on the two core systems of geometry? Research can approach this question by investigating relationships between children's performance on symbolic map tasks and their performance on tasks tapping the core systems of navigation and form analysis. In one experiment [30], children aged 4–5 years were given a test of reorientation in three subtly rectangular enclosures (figure 3*a*), a test of visual form analysis (figure 3*b*), and two tests of navigation by geometric maps within a triangular enclosure, focusing on relationships of distance or angle (figure 3*c*). Simple correlations between children's performance on these different tasks were evaluated.

Performance on the reorientation and form analysis tasks was independent: children who were especially sensitive to the shape of the rectangular chamber were no more sensitive than other children to the shapes of visual forms. This negative finding suggests that spatial ability is not a unitary attribute for children: the two core systems of geometry are distinct. Contrasting with this negative finding were two positive ones. Children who performed better on the reorientation task also navigated better on the version of the map task focusing on distance (but not angle). Moreover, children who performed better on the test of visual form analysis navigated better on the version of the map task focusing on angle (but not distance). Thus, each of the core systems that children share with animals was related, in a distinct way, to performance on the uniquely human, symbolic task of navigating by geometric maps. These findings suggest that symbolic devices such as maps could serve to

combine information from the two core systems of geometry.

The ability to combine information from these core systems also may depend on a second, uniquely human symbolic system: natural language. Between 5 and 8 years of age, children's behaviour in reorientation tasks undergoes a qualitative change: instead of navigating separately by the shape of the environment and the position of a distinctive landmark, children begin to combine representations of surface layouts and landmark objects productively, so as to locate directly an object hidden at a particular distance and direction from a landmark [66,67]. This change occurs when children begin systematically to produce spatial expressions, including the terms *left* and *right* [66,68]. A recent study of adult speakers of an emerging language suggests that the acquisition of spatial language plays a causal role in the emergence of this new navigational pattern [69].

Nicaraguan sign language (NSL) began to develop when a new school for the deaf brought together students with no prior exposure to a conventional language. Over successive cohorts of students, the language became increasingly systematic. In particular, speakers from later cohorts were more likely than earlier-cohort speakers to adopt a consistent spatial frame of reference for the terms *left* and *right*. To test for effects of this and other differences in the language of earlier- and later-cohort speakers, adult speakers of NSL were given the reorientation test in a rectangular room with one coloured wall, as well as a second spatial memory task involving a small rotating box; then the consistency of their language was assessed. Later-cohort speakers outperformed earlier-cohort speakers on both non-linguistic spatial tasks. Across cohorts, moreover, the ability to combine the room shape and landmark information in the reorientation task, but not in the box task, was correlated with the systematicity of use of the terms *left* and *right*, and not with any other language measure. Thus, the ability to combine layout representations and landmarks, required only by the reorientation task, was specifically impaired in adults whose prior language exposure led to inconsistent use of expressions containing the terms *left* and *right* [69]. This finding accords with the hypothesis that language supports uniquely human navigational abilities by allowing human navigators to combine productively the geometric representations that they share with other animals.

This research on human map use, language and species-unique spatial concepts sheds light, we believe, on the geometrical representations of animals as well as humans. It provides evidence that the representations of spatial layouts and object shapes that are shared by humans and animals truly have geometrical content, for they are reflected in our symbols and support our geometrical intuitions. Many questions remain concerning both the nature of these core representations and the processes by which humans harness them to construct systems of formal mathematics. Coordinated research on non-human animals, human children and human adults, with methods targeting multiple levels of analysis, may serve to address those questions.

7. CORE SYSTEMS IN HUMAN AND ANIMAL MINDS

In summary, research on non-human animals, young children and adults with varying access to maps or language, converge to provide evidence for two core systems of geometry. These systems are limited in the entities to which they apply (large-scale surface layouts versus small-scale objects and forms), in the tasks that elicit them (navigation versus object recognition), and in the types of geometric information that they capture (distance and direction versus length and angle). Thus far, comparative studies reveal the same signature limits across species, providing opportunities for conjoint research on humans and other animals to elucidate the computational and neural properties of these systems and to probe the roles of genes and experience in their development.

In this domain, studies of animals have yielded significant insights into human minds. Controlled rearing studies of chicks address questions that cannot be answered by research on humans, concerning the role of experience with a geometrically structured world on the development of navigation. Neurophysiological studies of rats similarly address questions that are difficult to answer by other means, concerning the neural circuitry that underlies navigation abilities. Above all, studies of animals, whose spatial behaviour is observed in natural contexts and studied at multiple levels of analysis, are a source of testable hypotheses that would never arise if human experimenters consulted only their intuitions. Thus, animal research is especially valuable as a guide to understanding the highly surprising properties of the core systems of geometry.

Just as importantly, studies of humans bring insights into animal minds. These insights depend on a final property of core systems: they provide at least part of the foundations for uniquely human, explicit and symbolic systems. In the case of geometry, studies of young children suggest that each of the two core systems relates to a different aspect of children's early attempts to navigate by symbolic maps. Moreover, studies of human adults with limited spatial language suggest that humans use language, our pre-eminent symbol system, to combine representations from the core systems of geometry. Thus, concepts with geometrical content may arise from cognitive systems that are shared by human and animal minds.

Beyond the domain of geometry, the search for the sources of uniquely human, abstract concepts provides evidence for other systems of core knowledge shared by animals. The uniquely human system of natural number concepts has been traced to a core system for representing one to three objects in parallel, and to a core system for representing approximate numerical magnitudes with ratio-limited precision [70]. Like the two core systems of geometry, these systems show common limits in children and animals, they are functional at birth, and they are associated with specific, distinct brain systems. Both these systems contribute to preschool children's learning of verbal counting [71], and at least one of them—the approximate number system—contributes to school-aged children's mastery of symbolic arithmetic [72,73].

These findings address long-standing debates over the existence of numerical concepts in animal minds.

More tentatively, research on human infants is beginning to suggest that uniquely human social and moral concepts depend on a core system for representing agents and their actions as goal-directed [74], efficient [75] and causally efficacious [76], as well as a core system for representing social beings and their interrelations as mutual and reciprocal [77]. The search for these systems in non-human animals is underway. If they are found, then studies of animals may shed light on what are arguably the most distinctive characteristics of human minds. Like Euclidean geometry and natural number, uniquely human social and moral concepts may arise from the productive combination of representations from ancient systems for predicting future actions and modulating social exchanges.

If these suggestions are correct, then synergistic studies of humans and other animals may shed light on some of the deepest questions concerning the nature of mind and knowledge. Intuition and observation suggest that a vast chasm separates our own minds from those of any other animal. Only humans are capable of studying our own minds, using methods from psychophysics and neuroscience to deepen our self-understanding. Only humans create and use external symbols both to communicate our concepts to one another and to combine distinct concepts productively to form new systems of knowledge. Beneath these differences, however, are cognitive systems that humans share with other animals, and that provide the foundations for all knowledge. Detailed study of these systems, probing both the extent and the limits to their homologies across different animal species, promises new insights into human and animal minds.

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