



Animal cognition

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The main topics in the study of animal cognition are reviewed with special reference to direct links to human, and in particular developmental, cognitive sciences. The material is organized with regard to the general idea that biological organisms would be endowed with a small set of separable systems of core knowledge, a prominent hypothesis in the current developmental cognitive sciences. Core knowledge systems would serve to represent inanimate physical objects and their mechanical interactions (*natural physics*); numbers with their relationships of ordering, addition, and subtraction (*natural mathematics*); places in the spatial layout with their geometric relationships (*natural geometry*); and animate psychological objects (agents) with their goal-directed actions (*natural psychology*). Some advanced forms of animal cognition, such as episodic-like representations and planning for the future, are also discussed. © 2010 John Wiley & Sons, Ltd. *WIREs Cogn Sci* 2010 1 882–893

INTRODUCTION

Starting from the 1980s, animal cognition emerged as a separate and strikingly interdisciplinary field, comprising traditional comparative psychology and ethology, as well as comparative neuroscience and behavioral ecology (see Refs 1,2 for review). The topic areas investigated nowadays overlap completely with those of human cognitive sciences, spanning studies of abstract concepts, spatial learning and memory, attention, imitation, representation of social relationships, problem solving, and decision making. Interest in the neural bases of cognitive processes in animals is also flourishing, particularly with regard to those capabilities that are uniquely or particularly developed in the human species, such as language or social intelligence,³ and for which evolutionary and neurobiological origins need to be clarified.⁴ The field is so huge that to make any attempt to summarize it is desperately difficult. One way to circumvent such a difficulty would be to organize the material around an overarching hypothesis which is gaining interest and consensus in the cognitive sciences in general and which is also capable of capturing the special link

represented by developmental comparisons between children and animals, which is becoming so prominent in the field of cognitive development. According to this hypothesis, biological organisms would be endowed with a small set of separable systems of core knowledge.^{5,6} Human beings, of course, would also possess incredibly flexible skills and belief systems that are not shared with other animals,⁷ but still these skills and belief systems would be built on the very same core knowledge foundations shared with other animals. Core knowledge systems would serve to represent inanimate physical objects and their mechanical interactions (*natural physics*), numbers with their relationships of ordering, addition and subtraction (*natural mathematics*), places in the spatial layout with their geometric relationships (*natural geometry*), and animate psychological objects (agents) with their goal-directed actions (*natural psychology*). The hypothesis thus contrasts the ideas that cognition would be served by a single general-purpose learning system device or by a myriad of special-purpose systems that would cope with all challenges of a natural environment. Rather, the hypothesis would assume a Kantian stance, according to which learning and acquisition of information would only be made possible by a reduced set of general core systems of inborn *necessary knowledge*.⁸ Human core systems would thus be apparent in young infants, shared by other species, persist in adults, and show little variation by culture, language, or gender. Needless to say, animal cognitive research may represent a benchmark for testing this hypothesis.

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NATURAL PHYSICS

While perceiving the physical world around us and moving about it or deciding what action to take next, we reason about inanimate material objects, grasping and manipulating many concepts underlying the way objects are, behave or interact, and understanding their spatial and temporal relationships. Such fundamental concepts are part of our knowledge and we subconsciously use them to plan our activities. Concepts such as *cohesion*, *continuity*, and *contact* summarize those properties that make objects move as a unit and in the same path or that specify objects' constraints on other objects when they come in contact or interact. All these concepts have been found in human infants and in many nonhuman species; hence, they are undoubtedly shared in the animal kingdom and have been maintained during evolution.⁶

Perceptual segregation and organization seem to be strikingly similar in all species studied, ranging from insects to higher vertebrates. Object boundaries, for instance, represent an essential source of information in visual perception. However, given that in natural scenes objects frequently occlude one another, contours may vanish. Thus, the visual system of animals would be unable to segregate objects if it had been designed to respond only to information directly present within the retinal images. Contour perception requires active organization of visual information to achieve a perceptually coherent representation of the shape of the objects. It has been shown in fact that animals detect boundaries and complete shapes of partially occluded entities, and perceive subjective contours, depth through motion, and a variety of visual illusions (in Ref 2). Such abilities seem to be available with little if any visual learning experience (both human infants and naïve chicks, for instance, when tested early after birth, appear to be predisposed with the same sophisticated set of completion and detection systems^{9,10}), and are supposed to be universal.

Object permanence has been described in several nonhuman species, many being able to retrieve objects after either a single invisible displacement or double invisible displacements (see Ref 11). Infants were believed to appreciate object permanence starting from stage 4 of the sensorimotor period, at around 8 months of age. However, Baillargeon¹² proved that infants as young as three and a half months have a sense of object permanence. After habituation to the sight of an opaque screen describing a 180° back-and-forth flapping motion on a table, infants were shown an object disappearing behind the barrier so that when the moving barrier reached the object, it should have stopped. Instead, when the barrier was experienced to complete the 180° movement falling horizontal

on the table, infants manifested dishabituation, thus revealing the ability to understand that the object behind the barrier continues to exist and possesses some physical properties, such as impenetrability by other material objects. Long before infants can act on this knowledge, they are able to recognize violations and to represent specific physical properties of objects. Objects take up space, are impenetrable, and may provide support to other objects. Nonhuman animals seem to recognize the very same violations as toddlers do. Apes (bonobos, gorillas, and orangutans) have recently been tested successfully in the Baillargeon paradigm, thus pointing to a basic continuity in cognitive processing across species.

Our cognition of the world also comprises unseen forces acting on visible objects. Usually, we easily cogitate on such common and predictable physical forces underpinning physical events: we think about the physical world within a naïve physical theory. What aspects (if any) of such intuitive causal structures are universal across species? The answer is controversial. The first complication pertains to the fact that each species should be sensibly questioned in the appropriate manner. For example, Wolfgang Koehler described how it was difficult for chimpanzees to stack boxes in a pile: as happens for children, it seemed that chimpanzees have difficulties in realizing that the box should not project too much over the previous one, as if they were lacking an adequate comprehension that each box needs an adequate supporting surface preventing the box from falling down. Failure in this task would suggest an incapability in considering gravity. However, more recent work using violation-of-expectancy techniques has shown that when human infants or chimpanzees are presented with possible/impossible supporting events, they show an understanding of what can act as a support and what cannot. Whether this successful performance mirrors a sophisticated or a merely implicit comprehension of unseen gravity force is under scrutiny. Spelke and collaborators¹³ introduced the table task for examining infants. In the solidity version of this paradigm, the subject sees first a shelf alone, then an opaque partition is set in front of it and an object is dropped behind it. After removing the partition, the object is shown either resting on the shelf (possible event: when solid, objects may not penetrate each other) or under it (impossible event); in the gravity version of the same paradigm, no shelf is present in the set-up: the object is shown either floating in midair (impossible event) or resting on the floor (possible event). Infants (3–4 months old) fail in the gravity version of the task supporting the idea that 'solidity' would belong to the core knowledge whereas

'gravity' would develop with experience. However, when faced with a ball dropped down one of a set of three interwoven tubes landing in one of three hiding places, 2-year-old infants showed a gravity bias in their choices. Different species have been evaluated in the same paradigm as toddlers or in modified versions of it: cotton-top tamarins, orangutans, bonobos, gorillas, chimpanzees, and dogs all showing, to some degree, a gravity bias. In another test, rhesus macaques were presented with two containers, one on the top of a table and another under it, and had to choose the landing location of some food dropped behind an opaque screen; monkeys showed a strong gravity bias. Chimpanzees also strongly responded in the direction of gravity when they had to choose the landing location of an object before it was dropped into the tube (i.e., making a prediction). Future research needs to highlight under what circumstances gravity may be an appreciable force to animals. Insights may arrive from studies about the appreciation of weight. Consider a balance beam: its orientation (when not in equilibrium) depends on the presence of an object on either of the two extremities. Looking at this final situation (effect) should make it possible to infer the preceding event, i.e., that an object has been positioned on the side grounded (cause). Hanus and Call¹⁴ tested chimpanzees in such a situation. Animals had to retrieve a food reward that was hidden under one of two opaque cups located at the extremities of a balanced beam ignoring the exact hiding position but determining it on the basis of the orientation of the balance beam when released from its equilibrium. Chimpanzees showed that they possess some understanding of the fact that objects have weight, and chose accordingly.

Animals (including human beings) usually need trials and errors to solve physical problems. It has been shown that even a species of rodent may be taught to use instruments. In a similar vein, the astonishing performance of orangutans that are able to add available water to raise the level of water in a container in order to reach a nut¹⁵ may appear less surprising when it is known that the animals had previous experience of a high level of water in the container. Yet, the story is not so simple. Of course, experience may lead to gaining of information about physical properties (capuchins, who have been shown to be able to choose the effective stone to crack nuts, may act on the stone in order to select the appropriate one¹⁶). However, rats have been proved to correctly represent instrumental actions on the basis of purely observational learning.¹⁷ Rooks tested in the presence of an out-of-reach reward floating in water, which had not had any previous experience with the same test apparatus, appeared to be able to assess and

change the water level, in order to grab the reward, by inserting stones in it.¹⁸ What is challenging here is that this species of corvids usually do not use tools in the wild, and all birds in the experiment were extremely accurate, for instance in using larger stones so as to reach the reward more quickly.

The role of experience in tool-use for understanding physical causation is controversial.¹⁹ Consider research carried out with the so-called *trap-tube task*, introduced by Visalberghi and Limongelli.²⁰ The set-up consists of a transparent tube, open at both ends, in the center of which a nut is placed. On one side or the other of the nut, there is a trap (a holed-box) and the subject is required to retrieve the nut by pushing it in one direction or the other with an available stick. Gravity makes objects fall down whenever a discontinuity is encountered: pushing in the wrong direction would lead to the impossibility of retrieving the reward. Only a few subjects in each group of chimpanzees and capuchin monkeys tested to this purpose learned the task. Subjects who solved this problem were presented with an inverted trap, abolishing in this case the effectiveness of the trap itself since gravity was no longer playing any substantial role. Surprisingly, the animals (chimpanzees, orangutans, and woodpecker finches, a species of tool-user birds) persisted in the use of the same strategy learned during the test with the functional trap, suggesting that they had learned a rule of action without any real appreciation of the causal mechanism involved. Note, however, that human subjects tested in a similar way²¹ also showed persistence in use of the same strategy passing from the normal trap-tube task to the inverted version of it. This clearly casts doubts as to whether failure in the reversed trap-tube task may be considered evidence of lack of causal understanding. Some interesting evidence recently came from research with rooks. Because these birds do not make spontaneous use of tools, in the trap-tube task they were tested in a slightly different manner: the stick was already available in the transparent tube which had this time two trap-boxes: one functional (with one hole on it) and one ineffective (with a lid on the hole). One rook proved able to solve the task. Trying to see whether the ability to solve the task was affected by additional task demands (for instance, the inclusion of a tool), Seed et al.²² recently found that chimpanzees tested with the same paradigm adopted for rooks also solved the task.

One problem with the understanding of physical causation is to what extent the variables intervening in the task are actually appreciated by the animals, for behavior may be coupled to perceptual cues instead of reasoning about invisible forces. Consider an analogy of the trap-tube task: the trap-table task. The subject

has to use a rake-like tool to retrieve an otherwise out-of-reach reward. In one version, the animal may choose between raking in a reward behind a trap and raking in one on a flat surface without a trap; in another version a hole is interposed between the reward and the subject, where they are tested to pull in a direction that avoids the trap. Primates do not always solve the trap-table problem but New Caledonian crows as well as rooks may do it²² and these species of birds may even transfer from the trap-table to the trap-tube and vice versa (whereas apes cannot). Since both tool-user species and non-tool-user species may cope with these physical puzzles, the idea that causal reasoning may depend on the ability to make use of tools seems untenable.

Animals were traditionally thought to be incapable of reasoning about unobservable causal forces; however, the recent evidence shortly summarized here suggests some common phylogenetic origins of the basic capabilities for causal reasoning. Clearly, further comparisons are needed to tackle the issue. The fact that we should be cautious cannot be set aside and we should try to explain the behavior we observe with parsimonious mechanisms rather than extraordinary high-level mental abilities^{19,23} and consider species-specific differences that may be due to different selective pressures on cognition.

NATURAL MATHEMATICS

Adult humans use numbers constantly in their everyday life, in order to make sense, to measure, and to quantify almost every aspect of their environment.²⁴ Doubtless, selected numerical concepts—such as real numbers, algebra, and calculus—are only performed by a subset of humans, while other, basilar, numerical abilities are widespread.²⁵ Even though human mathematical capacities exceed those of nonhuman animals, maybe because of language abilities, several instances of numerical competence in nonverbal creatures have been documented for almost 100 years.

The simplest aspect of number is protonumerosity: the ability to make judgments of size differences between two or more sets, i.e., ‘more than ...’, ‘less than ...’.²⁶ Such an ability would be at the base of efficient foraging strategies: the spontaneous preference for choosing the alternative offering the larger amount of food. Ten-month-old human infants,^{27,28} rhesus monkeys, and even salamanders preferred the larger between small sets made of pieces of food, showing a spontaneous protonumerical ability in the absence of language. Nevertheless, in these experiments, changes in number correlated with changes in quantitative variables (i.e., volume and surface area)

that covary with numerosity, the so-called *continuous variables*.

When the number of elements is contrasted with their overall area or contour length, infants sometimes preferentially rely on the continuous physical extent.^{28,29} However, there are circumstances in which infants rely on numerosity disregarding the continuous physical extent.³⁰ In general, when objects have similar or homogeneous properties^{28,29} or are from a domain in which physical extent is expected to be particularly important (e.g., food, see Ref 28), then infants seem to favor extent over number. When, however, the task requires reaching for individual objects or objects contrasting in color, pattern, or texture,³⁰ then infants seem to respond to number rather than extent. A striking parallel with the results obtained in human infants has been provided in animals. Three-day-old domestic chicks were tested for their sensitivity to number versus continuous physical extent of small sets of artificial objects they had become familiar with (through filial imprinting). When objects used for imprinting and for testing were similar, chicks based their choices on non-numerical variables, selecting the larger stimulus. However, when chicks were reared with objects differing in color, size, and shape and then tested with objects of novel color and shape (but of controlled continuous extent), they chose to associate with the same number of objects they had been reared with. Heterogeneity of the set would therefore force the identification of objects as different and separate individuals, and this would be crucial for computing numerosity of the set, otherwise continuous variables would be used.³¹

Another central aspect of number is the ability to represent ordinal relations, which is based on the comprehension of the principle that by adding one element to a given set, the new set becomes larger than the previous one and yet smaller than the next one up. Eleven-month-old infants are sensitive to the ordinal relations between numerical values while 9-month-old infants succeed only when multiple converging cues to ordinality are available.³² Rhesus monkeys, hamadryas baboons, squirrel monkeys, and brown capuchin monkeys trained to discriminate between numbers from one to four, in ascending order, could then generalize this discrimination to numbers from five to nine. Monkeys trained to respond (in ascending or descending order) to pairs of numerosities (1–9) spontaneously ordered in the same direction new pairs of larger values (i.e., 10, 15, 20, 30) demonstrating that there is no upper limit in such ability.³³

Research has focused also on a different, simpler, and concrete ordinal ability: to identify an object on the basis of its ordinal position in a series of identical

objects. Rats are capable of learning to enter a target tunnel solely on the basis of its ordinal position in an array of 6 or 18. Honeybees are able to find a food source located between the third and the fourth position along a series of four identical, equally spaced landmarks. These insects can also identify the fourth position in a series of five and generalize it to a new series of objects.³⁴ Even 5-day-old domestic chicks are able to identify the third, the fourth, or the sixth positions in a series of 10 identical landmarks, without relying on non-numerical cues.³⁵

The more complex nonverbal numerical ability consists in the manipulation of numerical representations of numbers in simple arithmetic operations such as additions and subtractions. Rhesus monkeys, squirrel monkeys, and chimpanzees following a specific training on symbols representing numbers were able to solve arithmetic operations.

Using the methodology of the violation of expectancy, Wynn²⁷ showed that 5-month-old infants can solve some simple arithmetic operations such as $1 + 1$ and $2 - 1$. In the original study, continuous variables were not controlled for, thus infants might well have attended to the volume, area, or contour length of the objects rather than to their actual number. Wynn's results, however, were then replicated also when continuous variables were at least partially controlled for. Wynn's paradigm was also adapted to test arithmetic reasoning in rhesus monkeys,³⁶ cotton-top tamarins, and lemurs.³⁷ Rhesus monkeys solved the task even when continuous variables were partially controlled for. Using a different paradigm, it was demonstrated that 5-day-old domestic chicks are able to add with and subtract from each other a total of five objects. In free test choices in which sets of three and two objects disappeared each behind one of two opaque identical screens, chicks spontaneously inspected the screen occluding the larger set, and did so even when the continuous variables (total surface area or contour length) had been controlled for. When chicks were presented with subsequent displacements of objects that appeared and disappeared behind the two screens, they successfully kept track of which screen hid the larger number of objects, and did so by performing subsequent additions or subtractions of the objects.³⁸

The evidence currently available suggests that natural number concepts are based on two systems of core knowledge of numerosity which would be spontaneously present and functional in both nonhuman animals and human infants (and would therefore be basically nonlinguistic): a system for representing the exact number of object arrays or events with very small numbers of entities, and a system for representing the approximate cardinal values of large sets of objects

or events.²⁴ Whereas the evidence in animals for the system of exact representation of small numbers is relatively recent, a long tradition of conditioning experiments suggests that animals form representations of large, approximate numerosities and that their representations accord with Weber's Law.²⁵ This means that the difficulty of any given numerical discrimination depends on the ratio of the two numerosities (e.g., 8 and 12 are just as discriminable as 16 and 24, and more easily discriminated than 8 and 10). Such a Weber ratio appears to characterize discrimination of the numerosities of different types of entities: objects, tones, light flashes, and self-generated actions.²⁴

Overall, evidence coming from comparative research has convincingly shown that number cognition, in its full variety of expressions, is widespread in the animal kingdom. Understanding numbers must have provided a precious tool to survival, shaped through natural selection to best suit the needs of the different species.

NATURAL GEOMETRY

Spatial navigation is the 'process of determining and maintaining a course or trajectory from one place to another'.³⁹ When finding, relocating, or avoiding specific places, basic cognitive processes that subtend spatial abilities, such as self- and goal-localization, and route planning are enrolled. The wealth of spatial information all diurnal animals may rely on in order to find their way (coming from all sensory modalities) suggests orientation ability to be a complex function and behavior to be controlled in different ways depending on the specific input considered.¹ Because of the task's demands, these different strategies may be opportunely questioned and, when adopted by the organism, they may be experimentally dissociated to study the basic internal algorithms presumably used to acquire an internal representation (whatever it is) for successful navigation.

Much effort has been devoted in the last three decades to observe animal behavior during free navigation. Idiopathic information is the first source of signals that accounts for accurate navigation of organisms, from insects to mammals. Several species integrate distances and direction of each travel by means of internal, vestibular, and kinaesthetic signals originated by the self-motion (*path integration*). This mechanism is empowered when used in combination with allothetic cues, i.e., external information that serve for an enriched and more detailed representation.⁴⁰ With regard to the so-called *near space*, several different cues can be used to localize a place: single and multiple landmarks of different sensorial domains,

contextual cues, and extended surfaces of enclosed environments.⁴¹ All this learned information may be combined with animals' self-motion in order to have a constantly updated encoding of the actual position. A different strategy is the use of an image-like spatial representation (*snapshot*) taken at relevant locations. By comparing the current sensory input with the stored views and computing the differences among the internal sketches until the snapshots match, insects for instance would be able to retrieve a certain location. However, much evidence has been collected in support of a richer spatial representation being at play even in insects.⁴² In fact, a map-like representation for spatial relations among places and objects—that seems to exist even in organisms like insects—was Tolman's leading proposal that had a quite influential role not just on the way we look at human spatial cognition⁴³ but at animal behavior as well (which would no longer be explained on the exclusive basis of a stimulus–response associative mechanism).

It is controversial whether nonhuman animals do represent space in a completely allocentric, map-like fashion. However, cognition is the natural product of biological activity of the brain, and a comparative approach led to important discoveries on spatial mechanisms. For instance, the hippocampus, a central cerebral area in spatial analysis and synthesis, has been widely investigated.^{44,45} By means of this integrated approach, it has been possible to deepen the understanding of spatial processing. The discovery of neurons in the rat's hippocampus which fire in correspondence to a specific position occupied by the animal, the so-called *place cells*, was interpreted as the neurophysiological foundation for spatial maps. Although appealing, there are still no unequivocal proofs about place cells' presence in diverse species, and the complexity of navigation ability calls for a more elaborate net of neurons to be postulated. Head direction cells, for instance, located outside the hippocampus itself and firing with respect to which way the animal faces, are essential while delineating an effective navigational model.⁴⁶ Another system located in the hippocampal complex is supplied by *grid cells*, which fire in correspondence to regular spatial intervals in the environment, and are located upstream from the place cells. Forming a grid-like structure, these cells may coordinate place cells' activity, allowing information to be continuously updated while the organism is moving around. However, their exact role in coordinating navigation and orientation, including how the inputs are assembled to form a spatial representation of the environment and how the effective neural net is wired, remain unanswered issues for future investigation.⁴⁷ Recently, another class of cells has been added in

the spatial neural circuit: the *border cells*.⁴⁸ First posited in computational models as boundary vector cells,⁴⁹ border cells are assumed to encode obstacles and borders of the surroundings allowing the definition of the perimeter of the environment. Responsible for capturing distances and directions from surfaces, border cells may be instrumental in anchoring grid and place cells' fields activity to a geometric frame of reference. This circuit fits well with a peculiar paradigm, investigated by the geometric module task. All vertebrate species studied while reorienting in a rectangular room showed comparable abilities and a preference in relying on distances, lengths and angles⁴¹ even when other sources of information were available for reorientation (and would have even sufficed alone). Such predominant use of the 'geometry' of the environment seems quite ubiquitous among species, hence predisposed in the brain and already available at birth regardless of direct exposition or learning.⁵⁰ Of course each species in its proper niche may choose an alternative mechanism to solve the same problem; an example would be that ants are shown to be capable of reorientation in the very same geometric module task although presumably with a view-based matching strategy.⁵¹ Here again we see the importance of an integrated analysis for the comprehension of navigational dynamics; that is, also considering many other aspects which are shared by vertebrates. Age-related decrements, for instance, are typical in spatial abilities in our species and similarly can be found in spatial performance of other species.⁵² On the other hand, it has been ascertained that new neurons may be generated throughout the life span of the organism. Neurogenesis takes place in the dentate gyrus of the hippocampus but there are still no unambiguous results that prove a direct relation between neurogenesis and the increasing demands of spatial abilities,⁵³ although recent data are trying to tackle this idea.⁵⁴ The functional role of adult neurogenesis is not yet clear: it has been proposed that new neurons are integrated in preexisting circuits in order to allow the encoding of spatial information. This is a mechanism supposed to hold for food caching behaviors shown by several bird species, in which hippocampal volumetric increase is probably due to neurogenesis or to selective neural recruitment.

NATURAL PSYCHOLOGY (AND OTHER ADVANCED FORMS OF COGNITION)

The very same issues brought up for physical objects (i.e., whether animals show an understanding of the underlying physical forces that guide physical events)

also hold for psychological (intentional) objects. No doubt, animals can predict and anticipate the action of others in many circumstances on the basis of their past experience. However, do they show a real understanding of the goals, perceptions, knowledge, and beliefs underlying other individuals' actions?

In trying to dissect the various components of the abilities of animals as 'natural psychologists', a first issue to consider is whether animals possess mechanisms for recognition of other animated (as distinct from unanimated) objects. Parallel research in newly hatched chicks^{9,55} and human newborns⁸ has showed inborn predispositions to attend to the semirigid pattern of biological motion which is typical of vertebrates. Interestingly, both species respond to some quite general characteristics of biological motion rather than to species-specific properties of motion. This suggests that a predisposition is at work the function of which would be to guide and canalize young animals' attention toward the types of objects that would be more likely to represent social companions in a natural environment, and toward which specific learning mechanisms (such as filial imprinting) should be selectively addressed. The neural mechanisms underlying recognition of biological motion overlap with those involved in perception of basic social signals such as facial expression and gaze direction: 2-year-old infants with autism failed to orient toward point-light displays of biological motion responding instead to purely nonsocial, physical contingencies of the stimulation. Thus, attention to biological motion can be considered as a precursor to the capacity of attributing intentions to others (see also Ref 56 for evidence that other properties of object motion, such as self-propulsion, could be inborn in young animals and form the basis for the distinction between animate and inanimate objects).

In a similar vein, converging evidence from several different species has led to the proposal that some newborn vertebrates, including humans, have visual predispositions to attend to the head region of conspecifics.⁵⁷ Faces are likely to have had great adaptive relevance for many social species. Attention to faces allows animals to identify conspecifics, to recognize specific individuals, to engage in social interaction with them and, in some cases, to obtain information about their intentions, emotions, and attentional or motivational state. Evidence supports the existence of specific biases for the visual processing of faces compared to other objects.⁵⁸

Although some researchers claim that human newborns have domain-relevant preferences for attending to faces, and specific aspects of faces such as direct-gaze, others argued that these effects can be

explained by domain-general biases or by the comparative visibility of stimuli to an underdeveloped visual system such as that of the human baby. A criticism of the work supporting domain-relevant face biases in human newborns is that studies are conducted with newborns of more than a few hours old, raising the possibility that very rapid early learning contributes to some of the effects observed. This criticism has been recently addressed by testing newly hatched visually deprived chicks whose preference for visual stimuli can be assessed prior to any other visual experience with faces.⁵⁷ Parallel studies in infants and chicks showed that spontaneous preferences for looking at a face were apparent in both species with respect to a simultaneously presented noise stimulus that was matched to the face in terms of the component spatial frequencies and color distribution.⁵⁸ The existence of similar visual preferences in the chick and in the human baby supports the idea that equivalent (maybe homologous) routes in the avian and in the primate brain would share a common function.

In humans, eyes play a crucial role in conveying social signals of intentions and dispositions. The communicative function of eyes in animals depends on species and context. Several species show aversive reactions to eyes, associated with antipredatory strategies, and there seem to exist mechanisms to automatically coorient gaze direction with that of conspecifics. However, most species favor the use of head and body orientation as indicators of attention while they find it difficult to use more subtle cues such as gaze following, particularly in cooperative contexts. Interestingly, however, there is evidence that animals may be able to use gaze direction in competitive situations. Again, species differences and context make it difficult to generalize the findings. Jackdaws, which exhibit an eye morphology similar to that of humans, when presented with a preferred food took longer to retrieve the reward when a person was directing his eyes toward the food than when he was looking away, but only when the person was unfamiliar. In a cooperative context, in which a human experimenter provides cues indicating the location of food hidden under one of two containers, jackdaws used cues provided by a familiar person if they were communicatory, i.e., gaze alternation and pointing cues, but not static cues signifying direction of attention toward one container, such as eye-gaze or head orientation. It is noteworthy that apes require intense training to use gaze, head and gaze, or pointing as discriminative cues in object-choice tasks, unless they were strongly 'enculturated'. Dogs and horses, in contrast, performed much better. Free-ranging rhesus monkeys, however, also seem to perform well, providing that they were tested

with cues which are naturally communicative. This suggests that, although domestication and human enculturation may play a significant role in tuning up the capacity to infer intentions from communicative gestures, these factors are not necessary. The suggestion which has been put forward is that species that do not communicate cooperatively cannot use gaze cues in a cooperative context. Jackdaws, which share food and jointly explore the environment, seem to be sensitive to eye movements and pointing cues in cooperative task (differently from chimpanzees, but similarly to rhesus monkeys), but do not respond to the person's direction of attention in a cooperative context, i.e., only active communicatory cues seem to be considered as relevant in a cooperative situation.

After the initial excitement generated by the Premack and Woodruff⁵⁹ original study about chimpanzees' understanding of human goals, there has been increasing skepticism about theory of mind in animals. In particular, the finding by Povinelli and Eddy⁶⁰ that chimpanzees would beg indiscriminately from humans facing them and humans that could not see them (e.g., because of buckets over their heads) raised serious doubts about chimpanzees' or other nonhuman primates' understanding of the psychological states of others. This, however, stands in contrast with evidence that chimpanzees would show tactical deception in natural contexts, and would show evidence of imitation and of withholding information and deceiving. In addition, they show clear evidence of mirror self-recognition. Recent innovative experimental paradigms based on situations closest to the animals' species-typical behavior, such as situations in which chimpanzees must compete, rather than cooperate with others, seem to have switched the balance of evidence. It seems now well attested that apes understand what others intend, what others can see, and what others know. In contrast, no convincing evidence is currently available of false belief understanding in chimpanzees, in spite of several attempts to show it. Whether it may be concluded that false belief understanding in humans is an exclusively human capacity is still uncertain, however. Although the age of emergence of false belief understanding has traditionally been set at around 4–5 years, recent methods based on looking behavior revealed early, probably implicit, understanding of false belief in 15-month-old infants. Preliminary looking behavior studies in apes have produced only suggestive data which need to be pursued further.

Differences with respect to the performances exhibited by monkeys seem to be less clear-cut than previously claimed. Although monkeys do show limitations in tasks such as acquisition of tool-use

by imitation (and other theory of mind-related tasks⁶¹), there is recent evidence that they make use of gaze following, show understanding of perception of others and are capable of distinguishing between human guessers and knowers and of tactical deceiving. The picture that is emerging is that theory of mind does not represent a single mechanism but rather is composed of a set of computational abilities, some of which humans may share with other organisms. Indeed, capacities associated with theory of mind do not seem to be confined to primates. They have been observed in other mammals and in birds as well. Although domestic dogs (*Canis familiaris*) appear to be responsive to human-given gaze cues in object-choice (see above) situations, they do differentiate between different attentional states of humans and communicate selectively to ignorant rather than knowledgeable owners the location of favored items. Corvids outwit competitors for food by withholding information or by enacting misleading attempts.⁶² Ravens follow gaze direction of humans around obstacles. Research carried out with western scrub-jays (*Aphelocoma californica*) is particularly revealing of corvids' abilities. Dally and collaborators allowed jays to hide worms either while they were alone or when another bird was watching, and to recover the hidden items in private later that day. They found that when scrub-jays were allowed to return to their stash, those that had hidden worms under the gaze of a would-be thief moved them to new sites. Birds did not recache the worms they had hidden in private, however. This is not the only strategy scrub-jays use to protect their caches, for when hiding worms in the presence of another bird, jays prefer to cache their meal behind a barrier that blocks their rival's view, suggesting that they may be able to take the visual perspective of another individual. Note, however, that these capacities cannot be confined to corvids, among birds. Bee eaters (*Merops orientalis*, small tropical birds) can appreciate what a predator can or cannot see. These birds were shown to avoid entering their nest in the presence of a human observer. Avoidance was, however, reduced when the observer was located in a position from which it was unable to see the nest, although the two positions were approximately equidistant from the nest, and in both cases the bird could see the observer clearly. This suggests that birds can appreciate the visual perspective of others and make a decision based on the information accessed by the observer.

In general, it seems apparent that all these species face a complex social life with strong affiliative bonds among individuals and dominance relationships, and the argument has been put forward that theory of

mind abilities have evolved as adaptation to specific socioecological challenges, such as competitive foraging for hidden food, or as refinements of behavioral cues associated with recognition of others (e.g., presence of eyes, others' head orientation). In fact, similar arguments have been raised for other sophisticated mental capacities, such as transitive inference. Transitive inference involves using known relationships to deduce unknown ones (e.g., using $A > B$ and $B > C$ to infer $A > C$), and is thus essential to logical reasoning. Originally described as a developmental milestone in children's cognitive development, transitive inference has since been reported in nonhuman primates, rats, birds, and fish. For instance, it has been shown that pinyon jays (*Gymnorhinus cyanocephalus*) draw sophisticated inferences about their own dominance status relative to that of strangers that were observed interacting with known individuals.

Planning about the future is another mental activity that may be observed in socially sophisticated species. Research with western scrub-jays suggested that these birds may be able to plan for future food shortages by adjusting their caching behavior.⁶³ On alternate mornings, scrub-jays were given breakfast in one compartment or were refused breakfast in another, before being allowed free access to food for the rest of the day. On the sixth day of the experiment, in the evening, they were given some food suitable for caching (whole pine nuts). Scrub-jays consistently cached most pine nuts in the tray placed in the 'no breakfast' compartment, anticipating that they would not be fed in the following morning in that compartment. Another experiment showed that the jays were able to plan ahead to provide themselves with a more varied diet. The birds were consistently given either a breakfast of peanuts in one compartment or of dog kibble in the other. When the birds were offered both foods in the evening (and were free to cache them in either compartment), they preferred to cache peanuts in the kibble compartment and vice versa—to make sure they would receive a more interesting breakfast the following morning. Thus, jays spontaneously plan for tomorrow's needs, independently of their current needs. These findings seem to suggest some understanding of future events. Apes have also been reported to plan for the future. Mulcahy and Call⁶⁴ trained bonobos and orangutans to use a certain tool to retrieve a treat from a piece of apparatus. Then the apes were offered a selection of tools, some suitable, some not, at a time when immediate access to the reward was prevented. The apes (and the tool they had chosen) were then led off to another location where they had to wait for 1 h (or, in another experiment, for 14 h) before being returned to the

original room where, if they had selected the correct tool, they could retrieve their treat. Apes successfully chose the correct tool, kept it with them in the waiting room, and then used it to access the reward. Spontaneous planning for future stone throwing has been documented in a 30-year-old chimp from Furuviik Zoo in Sweden,⁶⁵ although a controlled experiment would yet be required to determine the nature of the cognitive processes involved.

Complementary to that of planning for the future is the issue of whether animals have a concept of past events. There is of course evidence that animals possess declarative-like memories as opposed to procedural memories. This has been shown in both mammals and birds, using extended and trials-unique events. For instance, Clayton and Dickinson⁶³ reported experiments in which scrub-jays cached peanuts and kibble in two distinct containers. The relative incentive of food was manipulated by prefeeding on one food immediately before cache recovery. It was found that scrub-jays preferentially searched for the non-pre-fed food, thus showing evidence that they had encoded the what-and-where of the caching event. Scrub-jays, moreover, seem to have a concept of the past, remembering what they have cached, where and also how long ago. Magpies, a relative of the scrub-jay (i.e., another member of the crow family), can also remember which foods they have cached, where and how long ago (they are also the first species of birds in which mirror self-recognition has been documented). Scrub-jays were shown to even keep track of which particular bird was watching when they cached so that they can best protect their caches from knowledgeable potential thieves. Research has begun to test episodic-like (what–where–when) memory in nonhuman animals other than western scrub-jays. Hampton and collaborators⁶⁶ allowed rhesus monkeys to explore a room that contained three foraging sites, two of which were baited and one unbaited. The monkeys also had to learn that all the food was fresh and edible after 1 h, but their preferred food was rotten and therefore inedible after 25 h while the less-preferred food remained edible. Although the monkeys rapidly learned to search first for their preferred food, and to always avoid the empty foraging location, they were unable to reverse their search pattern after the longer delay but instead they revisited those locations that contained their preferred food irrespective of the length of the delay. Thus, unlike the jays, they failed to remember the 'when.' Note, however, that rhesus monkeys do not depend for their survival on burying food for later, and their feeding ecology does not require them to keep track of decay rates as they are

primarily herbivorous. Babb and Crystal⁶⁷ reported evidence that rats remember the what–where–when of specific past events. However, the findings are disputed because Roberts and collaborators⁶⁸ showed that rats could remember the when of an episodic-like memory trace in terms of the relative time elapsed (how long ago) but not in terms of an absolute time of day at which the event occurred. Interestingly, however, Norman and Eacott⁶⁹ showed that rats are able to recollect the object (what) and its location (where) in a particular context (which, rather than when). Clayton and Russell⁷⁰ observed that the ecological validity of the task may be crucial. In fact, rats do appear to remember what happened, where, and how long ago, when tested for the memory of food they have seen previously but not of food they have cached previously.

CONCLUSION

A crucial issue in classical comparative psychology, which persists in modern animal cognition, is that of continuity versus noncontinuity of mental functions between human and nonhuman animals (see e.g., Ref 71). In this review we stressed the core knowledge system foundations that humans share with other organisms. This should not, however, obscure the fact that humans engage in a series of activities that seem to have no obvious equivalent among nonhuman species. Although animals certainly recognize food, only humans engage in cooking and novel cuisine; although animals sometimes build beautiful natural architecture, only humans systematize their

knowledge of constructing buildings in formal architecture and engineering. And, again, although animals teach and, to a limited degree, transmit culture to their offspring, they do not do that using novels and narrative as humans do. There seem to be two ways to explain this state of things. The first is to imagine that there are species-specific uniquely human abilities that could account for uniquely human cognitive feats. In other words, core knowledge systems would be different (maybe only slightly different in some cases) in different species, or maybe there could be some other core knowledge systems available to humans alone other than those we share with nonhuman animals. The empirical evidence we reviewed above does not favor this view. The alternative is to imagine that uniquely human abilities arise from uniquely human combinatorial capacities.⁵ Language, in particular, may be an extraordinarily powerful device for assembling and coordinating the systems of core knowledge.

If this view were correct, when humans form and use concepts that no other species can attain, they do so by assembling a set of building blocks that are shared with the other animals. These building blocks are part of core knowledge. What humans do and nonhumans cannot do (or cannot do to the same degree) is to combine creatively and flexibly the outputs of the different core knowledge systems. Whatever the merits (or the faults) of this hypothesis, it is apparent that scientific research on nonlinguistic species (and prelinguistic infants) is uniquely placed to provide an answer to some of the most enduring and challenging issues about our very human nature.

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