Animal cognition

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Washoe, a female common chimpanzee, was the first non-human to learn to communicate using American Sign Language, as part of a research experiment on animal language acquisition.

Animal cognition describes the mental capacities of animals and its study. It has developed out of comparative psychology, including the study of animal conditioning and learning, but has also been strongly influenced by research in ethology, behavioral ecology, and evolutionary psychology. The alternative name cognitive ethology is therefore sometimes used; much of what used to be considered under the title of *animal intelligence* is now thought of under this heading.[1]

Research has examined animal cognition in mammals (especially primates, cetaceans, elephants, dogs, cats, horses,[2][3] raccoons and rodents), birds (including parrots, corvids and pigeons), reptiles (lizards and snakes), fish and invertebrates (including cephalopods, spiders and insects).[1]

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Historical background

Animal cognition from anecdote to laboratory

The behavior of non-human animals has captivated human imagination from antiquity, and over the centuries many writers have speculated about the animal mind, or its absence, as Descartes would have it.[4] Speculation about animal intelligence gradually yielded to scientific study after Darwin placed humans and animals on a continuum, although Darwin's largely anecdotal approach to the topic would not pass scientific muster later on.[5] Unsatisfied with the anecdotal method of Darwin and his protégé J. G. Romanes,[6] E. L. Thorndike brought animal behavior into the laboratory for objective scrutiny. Thorndike's careful observations of the escape of cats, dogs, and chicks from puzzle boxes led him to conclude that intelligent behavior may be compounded of simple associations and that inference to animal reason, insight, or consciousness is unnecessary and misleading.[7] At about the same time, I. P. Pavlov began his seminal studies of conditioned reflexes in dogs. Pavlov quickly abandoned attempts to infer canine mental processes; such attempts, he said, led only to disagreement and confusion. He was, however, willing to propose unseen physiological processes that might explain his observations.[8]

The behavioristic half-century

The work of Thorndike, Pavlov and a little later of the outspoken behaviorist John B. Watson[9] set the direction of much research on animal behavior for more than half a century. During this time there was considerable progress in understanding simple associations; notably, around 1930 the differences between Thorndike's instrumental (or operant) conditioning and Pavlov's classical (or Pavlovian) conditioning were clarified, first by Miller and Kanorski, and then by B. F. Skinner.[10][11] Many experiments on conditioning followed; they generated some complex theories,[12] but they made little or no reference to intervening mental processes. Probably the most explicit dismissal of the idea that mental processes control behavior was the radical behaviorism of Skinner. This view seeks to explain behavior, including "private events" like mental images, solely by reference to the environmental contingencies impinging on the human or animal.[13]

Despite the predominantly behaviorist orientation of research before 1960, the rejection of mental processes in animals was not universal during those years. Influential exceptions included, for example, Wolfgang Köhler and his insightful chimpanzees[14] and Edward Tolman whose proposed cognitive map was a significant contribution to subsequent cognitive research in both humans and animals.[15]

The cognitive revolution

Beginning around 1960, a "cognitive revolution" in research on humans[16] gradually spurred a similar transformation of research with animals. Inference to processes not directly observable became acceptable and then commonplace. An important proponent of this shift in thinking was Donald O. Hebb, who argued that "mind" is simply a name for processes in the head that control complex behavior, and that it is both necessary and possible to infer those processes from behavior.[17] Animals came to be seen as "goal seeking agents that acquire, store, retrieve, and internally process information at many levels of cognitive complexity.".[18] However, it is interesting to note that many cognitive experiments with animals made, and still make, ingenious use of conditioning methods pioneered by Thorndike and Pavlov.[19]

The scientific status of "consciousness" in animals continues to be hotly debated. Serious consideration of conscious thought in animals has been advocated by some (e.g., Donald Griffin),[20] but the larger research community has been notably cool to such suggestions.[21]

Methods

The acceleration of research on animal cognition in the last 50 years has led to a rapid expansion in the variety of species studied and methods employed. The remarkable behavior of large-brained animals such as primates and cetacea has claimed special attention, but all sorts of mammals large and small, birds, fish, ants, bees, and others have been brought into the laboratory or observed in carefully controlled field studies. In the laboratory, animals push levers, pull strings, dig for food, swim in water mazes, or respond to images on computer screens in discrimination, attention, memory, and categorization experiments.[19] Careful field studies explore memory for food caches, navigation by stars, communication, tool use, identification of conspecifics, and many other matters. Studies often focus on the behavior of animals in their natural environments and discuss the putative function of the behavior for the propagation and survival of the species. These developments reflect an increased cross-fertilization from related fields such as ethology and behavioral biology. Also, contributions from behavioral neuroscience are beginning to clarify the physiological substrate of some inferred mental process.

Several long term research projects have captured a good deal of attention. These include ape-language experiments such as the Washoe project and project Nim. Other animal projects include Irene Pepperberg's extended series of studies with the African gray parrot Alex, Louis Herman's work with bottlenosed dolphins, and studies of long-term memory in pigeons in which birds were shown to remember pictures for periods of several years.

Some researchers have made effective use of a Piagetian methodology, taking tasks which human children are known to master at different stages of development, and investigating which of them can be performed by particular species. Others have been inspired by concerns for animal welfare and the management of domestic species: for example Temple Grandin has harnessed her unique expertise in animal welfare and the ethical treatment of farm livestock to highlight underlying similarities between humans and other animals.[22] From a methodological point of view, one of the main risks in this sort of work is anthropomorphism, the tendency to interpret an animal's behavior in terms of human feelings, thoughts, and motivations.[1]

Research questions

Human and animal cognition have much in common, and this is reflected in the research summarized below; most of the headings found here might also appear in an article on human cognition. Of course, research in the two also differs in important respects. Notably, much research with humans either studies or involves language, and much research with animals is related directly or indirectly to behaviors important to survival in natural settings. Following are summaries of some of the major areas of research in animal cognition.

The common chimpanzee can use tools. This individual is using a stick to get food.

Perception

Like humans, non-human animals process information from eyes, ears, and other sensory organs to perceive the environment. Perceptual processes have been studied in many species, with results that are often similar to those in humans. Equally interesting are those perceptual processes that differ from, or go beyond those found in humans, such as echolocation in bats and dolphins, motion detection by skin receptors in fish, and extraordinary visual acuity, motion sensitivity and ability to see ultraviolet light in some birds.[23]

Attention

Much of what is happening in the world at any moment is irrelevant to current behavior. Attention refers to mental processes that select relevant information, inhibit irrelevant information, and switch among these as the situation demands.[24] Often the selective process is tuned before relevant information appears; such expectation makes for rapid selection of key stimuli when they become available. A large body of research has explored the way attention and expectation affect the behavior of non-human animals, and much of this work suggests that attention operates in birds, mammals and reptiles in much the same way that it does in humans.[25]

The following paragraphs contain brief accounts of several experiments. These are intended to give the reader a bit of the flavor of research on attention, but they barely scratch the surface, and readers should consult the references for descriptions of many other experiments. Also, one must interpret putative "attentional" effects with caution, because they can often be accounted for in several different ways. For example, lack of response to a current stimulus might reflect inattention, but it might also reflect lack of motivation, or result from past learning that suppresses response to that stimulus or promotes an alternative response. Most experiments include control conditions intended to exclude as many alternative interpretations as possible.

Selective learning

Animals trained to discriminate between two stimuli, say black versus white, can be said to attend to the "brightness dimension," but this says little about whether this dimension is selected in preference to others.

More enlightenment comes from experiments that allow the animal to choose from several alternatives. For example, several studies have shown that performance is better on, for example, a color discrimination (e.g. blue vs green) after the animal has learned another color discrimination (e.g. red vs orange) than it is after training on a different dimension such as an X shape versus and O shape. The reverse effect happens after training on forms. Thus, the earlier learning appears to affect which dimension, color or form, the animal will attend to.[26]

Other experiments have shown that after animals have learned to respond to one aspect of the environment responsiveness to other aspects is suppressed. In "blocking", for example, an animal is conditioned to respond to one stimulus ("A") by pairing that stimulus with reward or punishment. After the animal responds consistently to A, a second stimulus ("B") accompanies A on additional training trials. Later tests with the B stimulus alone elicit little response, suggesting that learning about B has been blocked by prior learning about A .[27] This result supports the hypothesis that stimuli are neglected if they fail to provide new information. Thus, in the experiment just cited, the animal failed to attend to B because B added no information to that supplied by A. If true, this interpretation is an important insight into attentional processing, but this conclusion remains uncertain because blocking and several related phenomena can be explained by models of conditioning that do not invoke attention.[28]

Divided attention

Casual observation suggests that attention is a limited resource and is not all-or-none: the more attention is devoted to one aspect or dimension of the environment, the less is available for others.[29] In preparing a meal you may divide your attention among a number of things, but a sudden spill may distract you from a falling souffle. A number of experiments have studied this sort of thing in animals. For example, in one experiment, a tone and a light came on simultaneously. The pigeon subjects gained reward only by choosing the correct combination of the two dimensions (a high pitch together with a yellow light). The birds did fairly well at this task, presumably by dividing attention between the two dimensions. When only one of the stimulus dimensions varied, while the other was held at its rewarded value, discrimination improved on the variable stimulus, and later tests showed that discrimination had also gotten worse on the alternative stimulus dimension.[30] These outcomes are consistent with the idea that attention is a limited resource that can be more or less focused among incoming stimuli.

Visual search and attentional priming

As noted above, attention functions to select information that is of special use to the animal. Visual search typically calls for this sort of selection, and search tasks have been used extensively in both humans and animals to determine the characteristics of attentional selection and the factors that control it.

Experimental research on visual search in animals was initially prompted by field observations published by Luc Tinbergen (1960).[31] Tinbergen observed that birds are selective when foraging for insects. For example, he found that birds tended to catch the same type of insect repeatedly even though several types were available. Tinbergen suggested that this prey selection was caused by an attentional bias that improved detection of one type of insect while suppressing detection of others. This "attentional priming" is commonly said to result from a pretrial activation of a mental representation of the attended object, which Tinbergen called a "searching image."

Tinbergen's field observations on priming have been supported by a number of experiments. For example, Pietrewicz and Kamil (1977, 1979)[32][33] presented blue jays with pictures of tree trunks upon which rested either a moth of species A, a moth of species B, or no moth at all. The birds were rewarded for pecks at a picture showing a moth. Crucially, the probability with which a particular species of moth was detected was higher after repeated trials with that species (e.g. A, A, A,...) than it was after a mixture of trials (e.g. A, B, B, A, B, A, A...). These results suggest again that sequential encounters with an object can establish an attentional predisposition to see the object.

Another way to produce attentional priming in search is to provide an advance signal that is associated with the target. For example, if you hear a song sparrow you may be predisposed to detect a song sparrow in a shrub, or among other birds. A number of experiments have reproduced this effect in animal subjects.[34][35]

Still other experiments have explored nature of stimulus factors that affect the speed and accuracy of visual search. For example, the time taken to find a single target increases as the number of items in the visual field increases. This rise in RT is steep if the distracters are similar to the target, less steep if they are dissimilar, and may not occur if the distracters are very different in from the target in form or color.[36]

Concepts and categories

Fundamental but difficult to define, the concept of "concept" was discussed for hundreds of years by philosophers before it became a focus of psychological study. Concepts enable humans and animals to organize the world into functional groups; the groups may be composed of perceptually similar objects or events, diverse things that have a common function, relationships such as same versus different, or relations among relations such as analogies.[37] Extensive discussions on these matters together with many references may be found in Shettleworth (2010)[1] Wasserman and Zentall (2006)[19] and in Zentall *et al.* (2008). The latter is freely available online[38]

Methods

Most work on animal concepts has been done with visual stimuli, which can easily be constructed and presented in great variety, but auditory and other stimuli have been used as well.[39] Pigeons have been widely used, for they have excellent vision and are readily conditioned to respond to visual targets; other birds and a number of other animals have been studied as well.[1] In a typical experiment, a bird or other animal confronts a computer monitor on which a large number of pictures appear one by one, and the subject gets a reward for pecking or touching a picture of a category item and no reward for non-category items. Alternatively, a subject may be offered a choice between two or more pictures. Many experiments end with the presentation of items never seen before; successful sorting of these items shows that the animal has not simply learned many specific stimulus-response associations. A related method, sometimes used to study relational concepts, is matching-to-sample. In this task an animal sees one stimulus and then chooses between two or more alternatives, one of which is the same as the first; the animal is then rewarded for choosing the matching stimulus.[1][19][38]

Perceptual categories

Perceptual categorization is said to occur when a person or animal responds in a similar way to a range of stimuli that share common features. For example, a squirrel climbs a tree when it sees Rex, Shep, or Trixie, which suggests that it categorizes all three as something to avoid. This sorting of instances into groups is crucial to survival. Among other things, an animal must categorize if it is to apply learning about one object (e.g. Rex bit me) to new instances of that category (dogs may bite).[1][19][38]

Natural categories

Many animals readily classify objects by perceived differences in form or color. For example, bees or pigeons quickly learn to choose any red object and reject any green object if red leads to reward and green does not. Seemingly much more difficult is an animal's ability to categorize natural objects that vary a great deal in color and form even while belonging to the same group. In a classic study, Richard J. Herrnstein trained pigeons to respond to the presence or absence of human beings in photographs.[40] The birds readily learned to peck photos that contained partial or full views of humans and to avoid pecking photos with no human, despite great differences in the form, size, and color of both the humans displayed and in the non-human pictures. In follow-up studies, pigeons categorized other natural objects (e.g. trees) and after training they were able without reward to sort photos they had not seen before .[41][42] Similar work has been done with natural auditory categories, for example, bird songs.[43] Honeybees (*Apis mellifera*) are able to form concepts of "up" and "down".[44]

Functional or associative categories

Perceptually unrelated stimuli may come to be responded to as members of a class if they have a common use or lead to common consequences. An oft-cited study by Vaughan (1988) provides an example.[45] Vaughan divided a large set of unrelated pictures into two arbitrary sets, A and B. Pigeons got food for pecking at pictures in set A but not for pecks at pictures in set B. After they had learned this task fairly well, the outcome was reversed: items in set B led to food and items in set A did not. Then the outcome was reversed again, and then again, and so on. Vaughan found that after 20 or more reversals, associating reward with a few pictures in one set caused the birds to respond to the other pictures in that set without further reward, as if they were thinking "if these pictures in set A bring food, the others in set A must also bring food." That is, the birds now categorized the pictures in each set as functionally equivalent. Several other procedures have yielded similar results.[1][38]

Relational or abstract categories

When tested in a simple stimulus matching-to-sample task (described above) many animals readily learn specific item combinations, such as "touch red if the sample is red, touch green if the sample is green." But this does not demonstrate that they distinguish between "same" and "different" as general concepts. Better evidence is provided if, after training, an animal successfully makes a choice that matches a novel sample that it has never seen before. Monkeys and chimpanzees do learn to do this, as do pigeons if they are given a great deal of practice with many different stimuli. However, because the sample is presented first, successful matching might mean that the animal is simply choosing the most recently seen "familiar" item rather than the conceptually "same" item. A number of studies have attempted to distinguish these possibilities, with mixed results.[1][38]

Rule learning

The use of rules has sometimes been considered an ability restricted to humans, but a number of experiments have shown evidence of simple rule learning in primates[46] and also in other animals. Much of the evidence has come from studies of sequence learning in which the "rule" consists of the order in which a series of events occurs. Rule use is shown if the animal learns to discriminate different orders of events and transfers this discrimination to new events arranged in the same order. For example, Murphy *et al.* (2008)[47] trained rats to discriminate between visual sequences. For one group ABA and BAB were rewarded, where A="bright light" and B="dim light." Other stimulus triplets were not rewarded. The rats learned the visual sequence, although both bright and dim lights were equally associated with reward. More importantly, in a second experiment with auditory stimuli, rats responded correctly to sequences of novel stimuli that were arranged in the same order as those previously learned. Similar sequence learning has been demonstrated in birds and other animals as well.[48]

Memory

The categories that have been developed to analyze human memory (short term memory, long term memory, working memory) have been applied to the study of animal memory, and some of the phenomena characteristic of human short term memory (e.g. the serial position effect) have been detected in animals, particularly monkeys.[49] However most progress has been made in the analysis of spatial memory; some of this work has sought to clarify the physiological basis of spatial memory and the role of the hippocampus; other work has explored the spatial memory of scatter-hoarder animals such as Clark's Nutcracker, certain jays, tits and certain squirrels, whose ecological niches require them to remember the locations of thousands of caches,[1][50] often following radical changes in the environment.

Memory has been widely investigated in foraging honeybees, *Apis mellifera*, which use both transient short-term working memory that is non-feeder specific and a feeder specific long-term reference memory.[51][52][53] Memory induced in a free-flying honeybee by a single learning trial lasts for days and, by three learning trials, for a lifetime.[54] Slugs, *Limax flavus*, have a short-term memory of approximately 1 min and long-term memory of 1 month.[55]

Methods

As in humans, research with animals distinguishes between "working" or "short-term" memory from "reference" or long-term memory. Tests of working memory evaluate memory for events that happened in the recent past, usually within the last few seconds or minutes. Tests of reference memory evaluate memory for regularities such as "pressing a lever brings food" or "children give me peanuts."

Habituation

This is one of the simplest tests for memory spanning a short time interval. The test compares an animal's response to a stimulus or event on one occasion to its response on a previous occasion. If the second response differs consistently from the first, the animal must have remembered something about the first, unless some other factor such as motivation, sensory sensitivity, or the test stimulus has changed.

Delayed response

Delayed response tasks are among the most useful methods used to study short-term memory in animals. Dating from research by Hunter (1913), the animal was shown a stimulus, such as a picture or a colored light, and a few seconds or minutes later the animal had to choose among alternative stimuli. In Hunter's studies, for example, a light appeared briefly in one of three goal boxes and then later the animal was allowed to choose among the boxes, finding food behind the one that had been lighted.[56] Most research has been done with some variation of the "delayed matching-to-sample" task. For example, in the initial study with this task, a pigeon was presented with a flickering or steady light. Then, a few seconds later, two pecking keys were illuminated, one with a steady light and one with a flickering light. The bird got food if it pecked the key that matched the original stimulus.[57]

A commonly-used variation of the matching-to-sample task requires the animal to use the initial stimulus to control a later choice between different stimuli. For example, if the initial stimulus is a black circle, the animal learns to choose "red" after the delay; if it is a black square, the correct choice is "green". Ingenious variations of this method have been used to explore many aspects of memory, including forgetting due to interference and memory for multiple items.[1]

Radial arm maze

The radial arm maze is used to test memory for spatial location and to determine the mental processes by which location is determined. In a radial maze test, an animal is placed on a small platform from which paths lead in various directions to goal boxes; the animal finds food in one or more goal boxes. Having found food in a box, the animal must return to the central platform. The maze may be used to test both reference and working memory. Suppose, for example, that over a number of sessions the same 4 arms of an 8-arm maze always lead to food. If in a later test session the animal goes to a box that has never been baited, this indicates a failure of reference memory. On the other hand, if the animal goes to a box that it has already emptied during the same test session, this indicates a failure of working memory. Various confounding factors, such as odor cues, are carefully controlled in such experiments.[58]

Water maze

The water maze is used to test an animal's memory for spatial location and to discover how an animal is able to determine locations. Typically the maze is circular tank filled with water that has been made milky so that it is opaque. Located somewhere in the maze is small platform placed just below the surface of the water. When placed in the tank, the animal swims around until it finds and climbs up on the platform. With practice the animal finds the platform more and more quickly. Reference memory is assessed by removing the platform and observing the relative amount of time the animal spends swimming in the area where the platform had been located. Visual and other cues in and around the tank may be varied to assess the animal's reliance on landmarks and the geometric relations among them.[59]

Spatial cognition

Whether an animal ranges over a territory of measured in square kilometers or square meters, its survival typically depends on its ability to do such things as find a food source and then return to its nest. Sometimes such a task can be performed rather simply, for example by following a chemical trail. Typically, however, the animal must somehow acquire and use information about locations, directions, and distances. The following paragraphs outline some of the ways that animals do this.[1][60]

- **Beacons** Animals often learn what their nest or other goal looks like, and if it is within sight they may simply move toward it; it is said to serve as a "beacon".
- **Landmarks** When an animal is unable to see its goal, it may learn the appearance of nearby objects and use these landmarks as guides. Researchers working with birds and bees have demonstrated this by moving prominent objects in the vicinity of nest sites, causing returning foragers to hunt for their nest in a new location.[1]
- **Dead reckoning** Dead reckoning, also known as "path integration," is the process of computing one's position by starting from a known location and keeping track of the distances and directions subsequently traveled. Classic experiments have shown that the desert ant keeps track of its position in this way as it wanders for many meters searching for food. Though it travels in a randomly twisted path, it heads straight home when it finds food. However, if the ant is picked up and released some meters to the east, for example, it heads for a location displaced by the same amount to the east of its home nest.
- **Cognitive maps** Some animals appear to construct a cognitive map of their surroundings, meaning that they acquire and use information that enables them to compute how far and in what direction to go to get from one location to another. Such a map-like representation is thought to be used, for example, when an animal goes directly from one food source to another even though its previous experience has involved only travel between each source and home.[1][61] Research in this area [60] has also explored such topics as the use of geometric properties of the environment by rats and pigeons, and the ability of rats to represent a spatial pattern in either radial arm mazes or water mazes. Spatial cognition is sometimes explored in visual search experiments in which a human or animal searches the environment for a particular object.
- **Detour behaviour** Some animals appear to have advanced understanding of their spatial environment and will not take the most direct route if this confers an advantage to them, for example when a predator can remain hidden from prey it is stalking. Some jumping spiders choose to take an indirect

route to prey rather than the most direct route, thereby indicating flexibility in behaviour and route planning, and possibly insight learning.[62]

Long-distance navigation; homing

Many animals travel hundreds or thousands of miles in seasonal migrations or returns to breeding grounds. They may be guided by the sun, the stars, the polarization of light, magnetic cues, olfactory cues, winds, or a combination of these.

It has been hypothesized that animals such as apes and wolves are good at spatial cognition because this skill is necessary for survival. This ability may have eroded somewhat in dogs because humans have provided necessities such as food and shelter during some 15,000 years of domestication.[63][64][65]

Timing

Time of day: Circadian rhythms

The behavior of most animals is synchronized with the earth's daily light-dark cycle. Thus, many animals are active during the day, others are active at night, still others near dawn and dusk. Though one might think that these "circadian rhythms" are controlled simply by the presence or absence of light, nearly every animal that has been studied has been shown to have a "biological clock" that yields cycles of activity even when the animal is in constant illumination or darkness.[1] Circadian rhythms are so automatic and fundamental to living things — they occur even in plants[66] - that they are usually discussed separately from cognitive processes, and the reader is referred to the main article (Circadian rhythms) for further information.

Interval timing

Survival often depends on an animal's ability to time intervals. For example, rufous hummingbirds feed on the nectar of flowers, and they often return to the same flower, but only after the flower had had enough time to replenish its supply of nectar. In one experiment hummingbirds fed on artificial flowers that quickly emptied of nectar but were refilled at some fixed time (e.g. twenty minutes) later. The birds learned to come back to the flowers at about the right time, learning the refill rates of up to eight separate flowers and remembering how long ago they had visited each one.[67]

The details of interval timing have been studied in a number of species. One of the most common methods is the "peak procedure". In a typical experiment, a rat in an operant chamber presses a lever for food. A light comes on, a lever-press brings a food pellet at a fixed later time, say 10 seconds, and then the light goes off. Timing is measured during occasional test trials on which no food is presented and the light stays on. On these test trials the rat presses the lever more and more until about 10 sec and then, when no food comes, gradually stops pressing. The time at which the rat presses most on these test trials is taken to be its estimate of the payoff time.

Experiments using the peak procedure and other methods have shown that animals can time short intervals quite exactly, can time more than one event at once, and can integrate time with spatial and other cues. Such tests have also been used for quantitative tests of theories of animal timing, though no one theory has yet gained unanimous agreement.[1]

Tool and weapon use

Because tool use is traditionally assumed to be a uniquely human trait, discussion of the cognitive underpinnings of animal tool use very often includes consideration of insight and comparisons of the overall intelligence and brain size. There is also considerable debate about what constitutes a "tool". A wide range of animals is considered to use tools including mammals, birds, fish, cephalopods and insects.

Mammals

Tool use has been reported many times in both wild and captive primates, particularly the great apes. The use of tools by primates is varied and includes hunting (mammals, invertebrates, fish), collecting honey, processing food (nuts, fruits, vegetables and seeds), collecting water, weapons and shelter. Research in 2007 shows that chimpanzees in the Fongoli savannah sharpen sticks to use as spears when hunting, considered the first evidence of systematic use of weapons in a species other than humans.[68] Other mammals that spontaneously use tools in the wild and captive include elephants, bears, cetaceans, sea otters and mongooses.

Series of photographs showing a bonobo fishing for termites.

A bonobo inserting a stick into a termite mound

The bonobo starts "fishing" for the termites

The bonobo withdraws the stick and begins eating the termites

The bonobo eats the termites extracted with the tool

Birds

Several species of birds have been recorded as using tools in the wild including Warblers, Parrots, Egyptian Vultures, Brown-headed Nuthatches, Gulls and Owls. One species examined extensively under laboratory conditions is the New Caledonian crow. One individual called “Betty”, spontaneously made a wire tool to solve a novel problem in the laboratory and attracted considerable attention. She was being tested to see whether she would select a wire hook rather than a straight wire to pull a little bucket of meat out of a well. Betty tried poking the straight wire at the meat. After a series of failures with this direct approach, she withdrew the wire and began directing it at the bottom of the well, which was secured to its base with duct tape. The wire soon became stuck, whereupon Betty pulled it sideways, bending it and unsticking it. She then inserted the hook into the well and extracted the meat. In all but one of 10 subsequent trials with only straight wire provided, she also made and used a hook in the same manner, but not before trying the straight wire first.[69][70] Some other species of birds, such as the woodpecker finch of the Galapagos Islands, use particular tools as an essential part of their foraging behavior. However, these behaviors are often quite inflexible and cannot be applied effectively in new situations. Several species of corvids have also been trained to use tools in controlled experiments, or use bread crumbs for bait-fishing.[71] A great many species of birds build nests with a wide range of complexities. Nest-building behaviour fulfils the criteria of some definitions of "tool-use", but not others.

Fish

Several species of wrasses have been observed using rocks as anvils to crack bivalve (scallops, urchins and clams) shells. It was first filmed [2] (http://scienceblog.com/48078/video-show-tool-use-by-a-fish/) in an orange-dotted tuskfish (*Choerodon anchorago*) in 2009 by Giacomo Bernardi. The fish fans sand to unearth the bivalve, takes it into its mouth, swims several metres to a rock which it uses as an anvil by smashing the mollusc apart with sideward thrashes of the head. This behaviour has been recorded in a blackspot tuskfish (*Choerodon schoenleinii*) on Australia's Great Barrier Reef, yellowhead wrasse (*Halichoeres garnoti*) in Florida and a six-bar wrasse (*Thalassoma hardwicke*) in an aquarium setting. These species are at opposite ends of the phylogenetic tree in this family, so this behaviour may be a deep-seated trait in all wrasses.[72]

Invertebrates

Some cephalopods are known to use coconut shells for protection or camouflage.[73]

Ants of the species *Conomyrma bicolor* pick up stones and other small objects with their mandibles and drop them down the vertical entrances of rival colonies, allowing workers to forage for food without competition.[74]

Reasoning and problem solving

Closely related to tool use is the study of reasoning and problem solving. It has been observed that the manner in which chimpanzees solve problems, such as that of retrieving bananas positioned out of reach, is not through trial-and-error. Instead, they were observed to proceed in a manner that was "unwaveringly purposeful."[75]

It is clear that animals of quite a range of species are capable of solving a range of problems that are argued to involve abstract reasoning;[76] modern research has tended to show that the performances of Wolfgang Köhler's chimpanzees, who could achieve spontaneous solutions to problems without training, were by no means unique to that species, and that apparently similar behavior can be found in animals usually thought of as much less intelligent, if appropriate training is given.[77] Causal reasoning has also been observed in rooks and New Caledonian crows.[78][79]

Language

The modeling of human language in animals is known as animal language research. In addition to the ape-language experiments mentioned above, there have also been more or less successful attempts to teach language or language-like behavior to some non-primate species, including parrots and great spotted woodpeckers. Arguing from his own results with the animal Nim Chimpsky and his analysis of others results, Herbert Terrace criticized the idea that chimps can produce new sentences.[80] Shortly thereafter Louis Herman published research on artificial language comprehension in the bottlenosed dolphin. (Herman, Richards, & Wolz, 1984). Though this sort of research has been controversial, especially among cognitive linguists, many researchers agree that many animals can understand the meaning of individual words, and some may understand simple sentences and syntactic variations, but there is little evidence that any animal can produce new strings of symbols that correspond to new sentences.[1]

Consciousness

The sense in which animals can be said to have consciousness or a self-concept has been hotly debated; it is often referred to as the debate over animal minds. The best known research technique in this area is the mirror test devised by Gordon G. Gallup, in which an animal's skin is marked in some way while it is asleep or sedated, and it is then allowed to see its reflection in a mirror; if the animal spontaneously directs grooming behavior towards the mark, that is taken as an indication that it is aware of itself. Self-awareness, by this criterion, has been reported for chimpanzees and also for other great apes, the European magpie,[81] some cetaceans and a solitary elephant, but not for monkeys. The mirror test has attracted controversy among some researchers because it is entirely focused on vision, the primary sense in humans, while other species rely more heavily on other senses such as the olfactory sense in dogs.

It has been suggested that metacognition in some animals provides some evidence for cognitive self-awareness.[82] The great apes, dolphins, and rhesus monkeys have demonstrated the ability to monitor their own mental states and use an "I don't know" response to avoid answering difficult questions. A 2007 study has provided some evidence for metacognition in rats,[83][84] although this interpretation has been questioned.[85][86] These species might also be aware of the strength of their memories. Unlike the mirror test, which relies primarily on body images and bodily self-awareness, uncertainty monitoring paradigms are focused on the kinds of mental states that might be linked to mental self-awareness.


Mirror test with a baboon

A different approach to determine whether a non-human animal is conscious derives from passive speech research with a macaw (see Arielle). Some researchers propose that by passively listening to an animal's voluntary speech, it is possible to learn about the thoughts of another creature and to determine that the speaker is conscious. This type of research was originally used to investigate a child's crib speech by Weir (1962) and in investigations of early speech in children by Greenfield and others (1976). With speech-capable birds, the methods of passive-speech research open a new avenue for investigation.

In July, 2012 during the "Consciousness in Human and Nonhuman Animals" conference in Cambridge a group of scientists announced and signed a declaration with the following conclusions:

> Convergent evidence indicates that non-human animals have the neuroanatomical, neurochemical, and neurophysiological substrates of conscious states along with the capacity to exhibit intentional behaviors. Consequently, the weight of evidence indicates that humans are not unique in possessing the neurological substrates that generate consciousness. Non-human animals, including all mammals and birds, and many other creatures, including octopuses, also possess these neurological substrates.[87]

Animal insight

Along with consciousness comes insight. Do animals have that “outside-the-box” or the “Aha! experience", sometimes called the Eureka effect? That thinking process that helps them solve everyday problems and help them to adapt in the outside world. Some may argue that this is called instinct, but insight is different. Wolfgang Köhler is usually credited with introducing the concept of insight into the psychological world.[70] Köhler worked with apes that became masters of solving puzzles he gave them. Köhler followed Edward Thorndike's theory that animals solve problems gradually, first finding success through a process of trial and error and slowly becoming more skillful. Köhler came to disagree with this theory saying, “Thorndike's animals could only escape by chance at first because their structure did not permit other kinds of situations.”[70] More recently, it has been shown that Asian elephants (*Elephas maximus*) may exhibit insightful problem solving. A male was observed moving a box to a position where it could be stood upon to reach food that had been deliberately hung out of reach.[88]

Contemporary studies of human insight address the cognitive and neural mechanisms underlying problem-solving behavior that fit this definition. In the case of animals, this usually means associative learning. Because we cannot simply ask animals about their “aha” experiences we should define insightful behavior in terms of processes such as mental trial and error or casual understanding.[70]

Numeracy

Some animals are capable of distinguishing between different amounts and rudimentary counting. Elephants have been known to perform simple arithmetic, and rhesus monkeys and pigeons, in some sense, can count.[89][90][91] Ants are able to use quantitative values and transmit this information.[92][93] For instance, ants of several species are able to estimate quite precisely numbers of encounters with members of other colonies on their feeding territories.[94][95] Numeracy has been described in the yellow mealworm beetle (*Tenebrio molitor*)[96] and the honeybee.[97]

Western lowland gorillas given the choice between two food trays demonstrated the ability to choose the tray with more food items at a rate higher than chance after training.[98] In a similar task, chimpanzees chose the option with larger amount of food.[99] Salamanders given a choice between two displays with differing amounts of fruit flies, used as a food reward, reliably choose the display with more flies, as shown in a particular experiment.[100]

Other experiments have been conducted that show animals' abilities to differentiate between non-food quantities. American black bears demonstrated quantity differentiation abilities in a task with a computer screen. The bears were trained to touch a computer monitor with a paw or nose to choose a quantity of dots in one of two boxes on the screen. Each bear was trained with reinforcement to pick a larger or smaller amount. During training, the bears were rewarded with food for a correct response. All bears performed better than what random error predicted on the trials with static, non-moving dots, indicating that they could differentiate between the two quantities. The bears choosing correctly in congruent (number of dots coincided with area of the dots) and incongruent (number of dots did not coincide with area of the dots) trials suggests that they were indeed choosing between quantities that appeared on the screen, not just a larger or smaller retinal image, which would indicate they are only judging size.[101]

Bottlenose dolphins have shown the ability to choose an array with fewer dots compared to one with more dots. Experimenters set up two boards showing various numbers of dots in a poolside setup. The dolphins were initially trained to choose the board with the fewer number of dots. This was done by rewarding the dolphin when it chose the board with the fewer number of dots. In the experimental trials, two boards were set up, and the dolphin would emerge from the water and point to one board. The dolphins chose the arrays with fewer dots at a rate much larger than chance, indicating they can differentiate between quantities.[102] A particular grey parrot, after training, has shown the ability to differentiate between the numbers zero through six using vocalizations. After number and vocalization training, this was done by asking the parrot how many objects there were in a display. The parrot was able to identify the correct amount at a rate higher than chance.[103] Angelfish, when put in an unfamiliar environment will group together with conspecifics, an action named shoaling. Given the choice between two groups of differing size, the angelfish will choose the larger of the two groups. This can be seen with a discrimination ratio of 2:1 or greater, such that, as long as one group has at least twice the fish as another group, it will join the larger one.[104]

Monitor lizards have been shown to be capable of numeracy, and some species can distinguish among numbers up to six.[105]

Cognitive bias

A cognitive bias is a pattern of deviation in judgment, whereby inferences about other animals and situations may be drawn in an illogical fashion.[106] Individuals create their own "subjective social reality" from their perception of the input.[107] It refers to the question "Is the glass half empty or half full?", used as an indicator of optimism or pessimism. To test this in animals, an individual is trained to anticipate that stimulus A, e.g. a 20 Hz tone, precedes a positive event, e.g. highly desired food is delivered when a lever is pressed by the animal. The same individual is trained to anticipate that stimulus B, e.g. a 10 Hz tone, precedes a negative event, e.g. bland food is delivered when the animal presses a lever. The animal is then tested by being played an intermediate stimulus C, e.g. a 15 Hz tone, and observing whether the animal presses the lever associated with the positive or negative reward, thereby indicating whether the animal is in a positive or negative mood. This might be influenced by, for example, the type of housing the animal is kept in.[108]


Is the glass half empty or half full?

Using this approach, it has been found that rats which are subjected to either handling or playful, experimenter-administered manual stimulation (tickling) showed different responses to the intermediate stimulus: rats exposed to tickling were more optimistic.[109] The authors stated that they had demonstrated "...for the first time a link between the directly measured positive affective state and decision making under uncertainty in an animal model."

Cognitive biases have been shown in a wide range of species including rats, dogs, rhesus macaques, sheep, chicks, starlings and honeybees.[109]

Biological constraints


Hedgehogs instinctively roll into a ball when threatened, making them unsuitable for studies on aversion avoidance

The instincts of an animal are considered in the interpretation of experiments on animal cognition. For example, dogs and rats easily learn to avoid an electric shock from the floor by moving to another part of the experimental chamber when they hear a tone preceding the shock. However, hedgehogs fail to learn this avoidance behavior. Whilst this might seem to show an inability to learn, the hedgehog's instinctive reaction to a threat is to curl up into a ball, a response that interferes with possible escape behavior in this situation.

Instinctive drift is another biological constraint that can influence interpretation of animal cognition studies. Instinctive drift is the tendency of an animal to revert to instinctive behaviors that can interfere with learned responses. The concept originated with Keller and Marian Breland when they taught a raccoon to put coins into a box. The raccoon drifted to its instinctive behavior of rubbing the coins with its paws, as it would do when foraging for food.[110]

An animal is able to process and respond to stimuli limited by the brain size. Simple animals like most invertebrates have very limited brains, and also show simple and/or repetitive behaviour. Vertebrates, particularly mammals, have larger brains and more complex behaviour. Brain size is therefore sometimes considered to be linked to cognition. The size of both brains and animals varying considerably, a formula called the encephalization quotient (EC) was developed by H.J. Jerison in the late 1960s.[111] The EC is in the form of a curve, where animals with encephalization above the curve are expected to have more spare capacity for cognition, and those below less spare capacity available that average for an animal of the same size. The formula for the curve varies, but an empirical fitting of the formula to a sample of mammals gives $Ew(brain) = 0.12w(body)^{2/3}$.[112] While the formula gives a very basic idea of the potential cognitive complexity an animal might be expected to show, the formula is based on data only from mammals and should be applied to other animals with extreme caution. For some of the other vertebrate classes, the power of 3/4 rather than 2/3 is sometimes used, and for many groups of invertebrates, the formula may give no meaningful results.

Cognitive faculty by species

A common image is the *scala naturae*, the ladder of nature on which animals of different species occupy successively higher rungs, with humans typically at the top.[113]

A more fruitful approach has been to recognize that different animals may have different kinds of cognitive processes, which are better understood in terms of the ways in which they are cognitively adapted to their different ecological niches, than by positing any kind of hierarchy. (See Shettleworth (1998), Reznikova (2007).)

One question that can be asked coherently is how far different species are intelligent in the same ways as humans are, i.e., are their cognitive processes similar to ours. Not surprisingly, our closest biological relatives, the great apes, tend to do best on such an assessment. Among the birds, corvids and parrots have typically been found to perform well. Some octopodes have also been shown to exhibit a number of higher-level skills such as tool use,[114] but the amount of research on cephalopod intelligence is still limited.

Baboons have been shown to be capable of recognizing words.[115][116][117]

See also

- Anthropomorphism
- Cetacean intelligence
- Deception in animals
- Dog intelligence
- Cognitive abilities

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- Animal Cognition (http://plato.stanford.edu/entries/cognition-animal) entry by Kristin Andrews in the *Stanford Encyclopedia of Philosophy*
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- Center for Avian Cognition (http://digitalcommons.unl.edu/bioscaviancog/) University of Nebraska (Alan Kamil, Alan Bond)

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