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Humans tend to have an anthropocentric view of intelligence that views them at the top and quite often animals that look like us close behind. Although the notion of an evolutionary scale with humans at the top is popularly held, it is also self-serving. We tend to overvalue our problem-solving ability, our capacity to modify our environment, and our ability to communicate with each other. Conversely, we tend to undervalue the exceptional sensory skills of other animals, for example, the tracking and drug-detecting ability of dogs; the navigational abilities of homing pigeons, whales, and monarch butterflies; and the ability of birds of prey to detect the minute movement of a small animal on the ground far below them. The role of our intelligence in the domination of our species over others seems obvious, but in the broader perspective of evolutionary success, as measured by the number of surviving members of a species, intelligence, as a general characteristic, correlates somewhat negatively with most measures of evolutionary success. Consider the relatively small numbers of our closest relatives, the great apes, compared with the large numbers of physiologically simpler insects, bacteria, and viruses. And it is estimated that if a massive disaster were to occur (e.g., if the Earth

were hit by a large asteroid or suffered a self-inflicted nuclear disaster), many simpler organisms would likely survive much better than large intelligent animals like us.

From a purely biological perspective, the ideal survival machine is a simple, one-celled, organism (e.g., the amoeba) that has survived as a species in one of two ways. Either it has needed to undergo little change in morphology or behavior for millions of years because it exists in a remarkably stable (predictable) environment, in which case there has been little need for change, or if its environment does change, it relies on natural selection by means of very rapid reproduction and mutation (e.g., bacteria and viruses). This ability to reproduce quickly and often, ensures the survival of many of these organisms (albeit not necessarily in the same form) even in the event of a major catastrophe. Many other organisms whose rate of reproduction has not been able to keep up with relatively rapid changes in the environment have relied on the ability to modify their behavior during their lifetime. Intelligence, in its simplest form, can be thought of as the flexibility endowed by our genes that allows organisms to adjust their behavior to relatively rapidly changing environments. For some animals, a stable supply of a highly specific food may be predictable (e.g., eucalyptus leaves for the koala or bamboo leaves for the giant panda)—at least until recently. For most animals, however, environments are much less predictable, and their

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predisposed eating preferences have had to be much more flexible. For still other animals, the environment is sufficiently unpredictable that it is impossible for them to be predisposed to know (by genetic means) what food will be available (consider the varied diet of the city-dwelling rat). For these animals to survive, more general (abstract) rules must be available. Rules about what to eat may not be based on the sight or taste of what is ingested but on its consequences. Instead of instructing the animal to eat eucalyptus leaves or to eat a certain class of seeds, these genes instruct the animal that if it feels sick after eating a new food, it should avoid eating more of that food. Such general rules allow for the behavioral flexibility that we call learning.

But there is a price to pay for this added flexibility. The animal must sometimes suffer the consequences of eating something bad. If the novel food is poisonous, the animal may not survive to use its newfound knowledge. The creation and maintenance of a nervous system capable of such learning represents a cost as well. For many animals, the benefits of the capacity for simple associative learning outweigh the cost, but for some animals, the negative consequences of trial and error learning are sufficiently costly that simple learning rules are not enough.

Some animals have found ways to reduce this cost. Rats, which live in highly unpredictable environments, have evolved the ability to learn, in a single experience, the consequences of eating a small amount of a novel food, even when those consequences are experienced hours after the food was ingested (Garcia and Koelling 1966). Rats also have developed the ability to transmit food preferences socially. If a rat experiences the smell of a novel food on the breath of another rat, it will prefer food with that smell over another equally novel food (Galef 1988), and it may also be able to assess the consequences to the other rat of having eaten a novel food (Kuan and Colwill 1997).

But what if this degree of flexibility in learning is still not enough to allow for survival? In the case of humans, for example, our poorly developed sense of smell, our relatively poorly developed gross motor response (e.g., slow

running speed), and our relative physical weakness may not have allowed us to hunt competitively with other predators (e.g., large cats). The competition with other animals for food must have come about slowly enough for us to develop weapons and tools, complex forms of communication (language), and complex social structure (allowing for cooperation, teamwork, and reciprocity). According to this view, although our intellect appears to have given us a clear advantage over other animals, its evolution is likely to have emerged because of our relative weakness in other areas. Other animals have compensated for their weaknesses by developing strengths in nonintellectual areas (e.g., the snail compensates for its lack of rapid mobility by building a protective shell around itself). Discussions of animal intelligence often assume, inappropriately, that intelligence is inherently good. In our case, it has turned out to be generally true (at least to the present). For us, intelligence has had a runaway effect on our ability to adapt to change (an effect that Dawkins 1976 calls hypergamy), which has allowed us to produce radical changes in our environment. However, from a biological perspective, in general, intelligence can be viewed as making the best out of a bad situation, or producing a complex solution to problems that other species have often solved in simpler ways. As we evaluate the various intellectual capacities of nonhuman animals, let us try to keep in mind that they have survived quite well (until recently) without the need for our complex intellectual skills.

The Comparative Approach: Two Caveats

First, most people have a vague idea of the relative intelligence of animals. As a general rule, those species that are more like us physically are judged to be more intelligent. But we must be careful in making such judgments because we humans are the ones who are defining intelligent behavior. We make up the rules and the testing procedures, and those tests may be biased in favor of our particular capacities. Isn't it interesting that

animals that are more similar to us, that have similar sensory, motor, and motivational systems, just happen to be judged as more intelligent?

Bitterman (1975) has suggested that a relational view of animal learning can be used to correct for peripheral differences in sensory capacity and motor coordination. He suggests that rather than looking for differences in the rate at which different species can learn, we might look at differences, for example, in an animal's ability to learn from the experience of learning. In other words, to what extent can learning facilitate new learning (learning to learn)? Then, using the rate of original learning as a baseline, one can determine the degree to which later learning, presumably involving the same processes, is facilitated. However, this approach is not always possible, and we must be aware that our assessment may be biased by the use of testing procedures not well suited for the species we are studying.

Second, we must guard against the opposite bias—the tendency to interpret behavior as intelligent because of its similarity to intelligent human behavior. In evaluating research addressing the cognitive capacity of animals, we should adopt C. Lloyd Morgan's (1894) position that it is not necessary to interpret behavior as complex (more cognitive) if a simpler (less cognitive) account will suffice. This is the principle of parsimony. Thus, higher-level cognitive interpretations should always be contrasted with simpler, contiguity- and contingency-based, associative-learning accounts. I will start with several classical issues concerned with the nature of learning and intelligence in animals, move to more complex behavior thought to be uniquely human, and end with examples of presumably complex behavior that are likely to be based on simpler predisposed processes.

This review will focus primarily on the flexible behavior of nonprimates because the cognitive behavior of primates is covered elsewhere in this volume, and thus, it will not address several areas of research that have been conducted uniquely with primates, such as analogical reasoning, conservation of volume and mass, language, perspective taking, theory of mind, and deception.

Absolute Versus Relational Learning

One of the most basic cognitive functions involves not being bound to the absolute properties of a stimulus. Although Hull (1943) claimed that learning involves solely the absolute properties of a stimulus, he proposed that animals will appear to respond relationally because they will respond similarly to similar stimuli, a process known as stimulus generalization. Spence (1937) elaborated on this theory by proposing that discrimination learning establishes predictable gradients of excitation (approach) and inhibition (avoidance) that summate algebraically. And this theory of generalization gradient summation can account for a number of phenomena that were formerly explained as relational learning (see Riley 1968). The fact that one sees little discussion of this issue in the modern literature suggests that animals are capable of using either the absolute or relative properties of a stimulus in making discriminations.

Learning to Learn

Can an animal use prior learning to facilitate new learning? That is, can animals learn to learn? If an animal learns a simple discrimination between two stimuli (an S+, to which responses are reinforced, and an S-, to which responses are extinguished) and then, following acquisition, the discrimination is reversed (the S+ becomes S- and the S- becomes S+), and then reversed again, repeatedly, are successive reversals learned faster than earlier reversals? Animals trained on such a serial-reversal task often show improvement within a few reversals, and the rate of improvement can be used as a measure of learning to learn. For example, rats show more improvement than pigeons, and pigeons show more improvement than gold fish (Bitterman and Mackintosh 1969). Mackintosh (1969) attributes these differences in serial-reversal learning to the differential ability of these species to maintain attention to the relevant dimension and ignore irrelevant dimensions.

A different approach to learning to learn is to look for improvement in the rate at which discriminations involving new stimuli are learned. This phenomenon, known as learning set (Harlow 1949), has been studied primarily using visual discriminations with monkeys, but good evidence for such effects has also been found with olfactory discriminations with rats (Slotnick and Katz 1974). In the limit, learning of a new discrimination, or of a reversal, can occur in a single trial. When it does, it is referred to as a win-stay-lose-shift strategy because stimulus choice is completely controlled by the consequences of choice on the preceding trial. One means of developing such a strategy is to learn to forget the consequences of trials prior to the immediately preceding trial. In fact, research has shown that memory for the specific characteristics of the stimuli from prior discriminations does decline as the number of discriminations learned increases (Meyer 1971). Thus, animals approach optimal learning by learning to ignore the effects of all but the most recent experience.

Stimulus Class Formation

Perceptual Classes

Pigeons are remarkably adept at responding selectively to photographs of natural scenes, depending on whether the scene involves a human form (Herrnstein and Loveland 1964) or trees or water (Herrnstein et al. 1976) and those objects need not be anything that they might have actually encountered in their past (e.g., underwater pictures of fish; Herrnstein and deVilliers 1980). To demonstrate that the pigeons do not simply memorize a list of pictures and their appropriate responses, Herrnstein et al. showed that the pigeons would respond appropriately to new examples of the positive and negative stimulus sets.

What is interesting about perceptual classes is that it is difficult to specify what features humans or pigeons use to discriminate members from nonmembers of the perceptual class. However, examination of the kinds of errors made can tell us about the attributes that were used to categorize

the exemplars and the similarities in the underlying processes for different species. For example, pigeons make errors similar to those of young children (e.g., they often erroneously assign a picture of a bunch of celery or an ivy-covered wall to the category “tree”).

Equivalence Relations

The emergent relations that may arise when arbitrary, initially unrelated stimuli are associated with the same response are often referred to as functional equivalence because they belong to a common stimulus class (see Zentall and Smeets 1996). The best example of equivalence relations in humans is that aspect of language known as semantics—the use of symbols (words) to stand for objects, actions, and attributes. What makes these relations so powerful is what one learns about one member of the stimulus class (i.e., a word) will transfer to others (i.e., the object that it represents). Thus, a child can be told about the varied behavior of dogs (sometimes friendly but not always) without having to actually experience them (and getting bitten). Thus, stimuli that belong to the same stimulus class can be thought of as having the same meaning. The most common procedure for demonstrating the development of functional equivalence in animals involves training on two conditional discriminations. In the first, for example, a red hue (sample) signals that a response to a circle will be reinforced (but not a response to a dot), and a green hue signals that a response to a dot will be reinforced (but not a response to a circle; see Fig. 16.1). In the second conditional discrimination, a vertical line signals that a response to the circle will be reinforced (but not a response to the dot), and a horizontal line signals that a response to the dot will be reinforced (but not a response to the circle). Thus, the red hue and vertical line can be described as meaning *choose the circle* and the green hue and horizontal line as *choose the dot*. This procedure has been referred to as many-to-one matching because training involves the association of two samples with the same comparison stimulus. To show that an emergent relation has developed between the red hue and the vertical

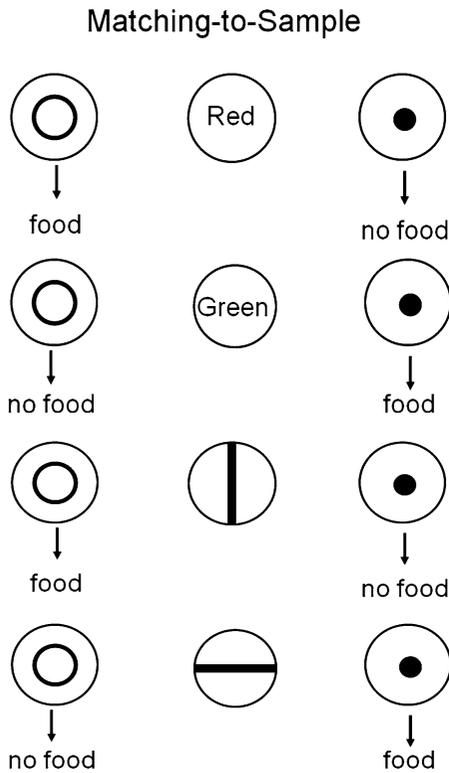


Fig. 16.1 Many-to-one matching training used to show that pigeons will learn that *red* and *vertical* (as well as *green* and *horizontal*) “mean the same thing.” If *red* and *green* samples are now associated with new comparison stimuli, *blue* and *white*, respectively, there is evidence that *vertical* and *horizontal* lines are also associated with the *blue* and *white* stimuli, respectively

line and between the green hue and the horizontal line, one can train new associations between one pair of the original samples (e.g., the red and green hues) and a new pair of comparison stimuli (e.g., blue and white hues, respectively). Then on test trials, one can show that emergent relations have developed when, without further training, an animal chooses the blue hue when the sample is a vertical line and chooses the white hue when the sample is a horizontal line (Urcuioli et al. 1989; Wasserman et al. 1992; Zentall 1998).

Although pigeons are not capable of language learning, the ability of small-brained organisms like pigeons to develop arbitrary stimulus classes, the main characteristic of symbolic representation, suggests that this capacity is much more pervasive than once thought.

Memory Strategies

The task most often used to study memory in animals is delayed matching-to-sample, in which following acquisition of matching-to-sample, a delay is inserted between the offset of the sample and the onset of the comparison stimuli (Roberts and Grant 1976). However, the retention functions typically found with this procedure generally greatly underestimate the animal’s memory capacity for two reasons. First, in many studies, the novel delay interval is quite similar in appearance to the time between trials. This leads to an ambiguity in the meaning of the delay. When the delay interval and the intertrial interval are made distinctive, the retention functions obtained often provide a very different picture of the animal’s memory (Sherburne et al. 1998). Second, the novelty of the delays may result in a generalization decrement that is confounded with memory loss. When pigeons are trained with delays, considerably better memory has been found (Dorrance et al. 2000). Of more interest in the assessment of animal intelligence is an animal’s ability to actively affect its memory.

Prospective Processes

Traditionally, animal memory has been viewed as a rather passive process. According to this view, sensory events can leave a trace that may control responding even when the event is no longer present (Roberts and Grant 1976). However, there is evidence that animals can also actively translate or code the representation of a presented stimulus into an expectation of a yet-to-be-presented event (Honig and Thompson 1982). What does it mean to have an expectation of a future event? Imagine a delayed matching task in which vertical- and horizontal-line samples are mapped onto red and green comparison stimuli. During the delay, one can imagine that some representation of the just seen sample stimulus would be remembered. But it is also possible that the sample is translated into a response intention to select one of the comparison stimuli. The ability to use expectations, or prospective coding processes, has important implications

for the cognitive capacities of animals. If the expectation of a stimulus, response, or outcome can serve as an effective cue for comparison choice, it suggests that animals may be capable of exerting active control over memory, and in particular, it may suggest they have the capacity for active planning.

The notion of expectancy as an active purposive process can be attributed to Tolman (1932). Although one can say that a dog salivates when it hears a bell because it expects food to be placed in its mouth, the demonstration that an expectation can serve as a discriminative stimulus (i.e., as the basis for making a choice) suggests that the expectancy has additional cognitive properties.

The Differential Outcome Effect If a conditional discrimination or matching task is designed such that a correct response following one sample results in one kind of outcome (e.g., food) and following the other sample results in a different kind of outcome (e.g., water), one can show that acquisition of the conditional discrimination is faster (Trapold 1970) and retention is better when a delay is inserted between the conditional and choice stimuli (Peterson et al. 1980). Furthermore, there is evidence from transfer-of-training experiments that in the absence of other cues, outcome anticipations can serve as sufficient cues for comparison choice. That is, if the original samples are replaced by other stimuli associated with the same differential outcomes, positive transfer has been found (Edwards et al. 1982; Peterson 1984). This line of research indicates that presentation of a sample creates an expectation of a particular kind of outcome and that expectation alone can then serve as the basis for comparison choice. In most cases, the differential outcomes have differential hedonic value (e.g., a high probability of food versus a low probability of food), and it is possible that outcome anticipation can elicit differential emotional states in the animal. But there is also evidence that nondifferentially hedonic events such as the anticipation of a particular neutral stimulus can affect response accuracy (Kelly and Grant 2001; Miller et al. 2009; Williams et al. 1990).

Planning Ahead One of the hallmarks of human cognitive behavior is our ability to consciously plan for the future. Although animals sometimes appear to plan for the future (birds build nests; rats hoard food), these behaviors are likely to be under genetic control. That is, animals do it but it is not likely to be with the expectation of later use. Alternatively, what appears to be future planning just may be the ability to delay reinforcement. To distinguish between planning for the future and learning with a long delay of reinforcement, Suddendorf and Corballis (1997) have suggested that the behavior indicative of planning must occur in the absence of the relevant motivation. Roberts (2002) reported the absence of planning by monkeys. After they had eaten a portion of their daily allotment of food, they threw out of their cage whatever food remained but then requested more food later in the day. However, convincing evidence for planning was reported by Raby et al. (2007). Western scrub jays, which cache food for future use, learned that unpredictably, they would either spend the night in a compartment in which in the morning they would find one kind of food (peanuts) or in a compartment in which they would find a different kind of food (kibble). On test trials, the night before, they were allowed to eat and cache food in either compartment. When they were given peanuts, they tended to cache them in the kibble compartment, and when they were given kibble, they tended to cache them in the peanut compartment (i.e., they cached the food in the compartment in which they would not find that particular food in the morning).

Directed (Intentional) Forgetting

The notion of directed or intentional forgetting is borrowed from human memory research. It implies that memory is an active rather than a passive (automatic) process. Presumably, following presentation, items that human participants are instructed to forget may not be well stored or maintained in memory and, thus, should not be well retained. In a directed forgetting task with animals, for example,

pigeons are trained on a matching task, and then a delay of a fixed duration is introduced between the sample and the comparisons. On remember trials, during the delay, the pigeons are cued that there will be a test of sample memory, whereas on forget trials, the pigeons are cued that there will be no test of sample memory. On selected probe trials, the forget cue is presented, but there is a test of sample memory. Matching accuracy on these probe trials is generally below that of remember trials on which there was an expected test of sample memory (Grant 1981). But this design confounds differential motivation on remember and forget trials with sample memory effects because food can be obtained only on remember trials. In a more complex design that controls for motivational effects and that better approximates the human directed forgetting procedure by allowing the animal to reallocate its memory from the sample to an alternative memory on forget trials in training, better evidence for directed forgetting in pigeons has been demonstrated (Roper et al. 1995). Thus, under certain conditions, it appears that animals do have at least some active control over memory processes.

Episodic Memory

Human memory can be identified by the kinds of processes presumed to be involved. Procedural memory involves memory for actions (e.g., riding a bicycle), and it has been assumed that most learned behavior by animals involves this kind of memory. Human declarative memory is assumed to be more cognitive because it involves memory for facts (semantic memory) and memory of personal experiences (episodic memory). Although animals cannot typically describe factual information, their conditional rule-based learning can be thought of as a kind of semantic memory (e.g., if the sample is red, choose the vertical line; if the sample is green, choose the horizontal line). But do animals have episodic memory? Can they retrieve personal experiences or do they simply remember the rules.

Tulving (1972) proposed that an episodic memory should include the what, where, and when of an experience. Clayton and Dickinson (1999) showed that western scrub jays that cached peanuts and wax worms (what) on one side or the other of an ice cube tray (where) learned that their preferred wax worms would be edible after one day but after four days only the peanut would be edible (when; see also Babb and Crystal 2006, for a similar finding with rats). But it can be argued that it is insufficient to retrieve the what, where, and when of an episode because those have been explicitly trained (i.e., they are likely to be semantic or rule-based memories). Instead, better evidence for episodic memory would come from the finding that animals can retrieve information about a past episode when there is no expectation that they will be requested to do so in the future (Zentall et al. 2001). That is, imagine that pigeons are first trained to report the location where they recently pecked (instructions) and then they are trained on an unrelated conditional discrimination in which choice of a vertical line was correct when the sample was blue and choice of the horizontal line was correct when the sample was yellow. Singer and Zentall (2007) found that on probe trials on which following a vertical- or horizontal-line comparison response the pigeons were asked unexpectedly to report the location that they had pecked, they reliably did so. Thus, by either criterion (what-where-when or responding to an unexpected question), pigeons show some evidence of episodic-like memory.

Navigation

Compared to many animals, humans have relatively poor navigational skills. Consider how dependent we are on external supports such as compasses, maps, and more recently global positioning devices. Many animals (e.g., migrating whales, birds, monarch butterflies) can navigate over many hundreds of miles using magnetic fields, chemical gradients, and star patterns. And homing pigeons use a number of these navigational systems including landmarks consisting of

natural and man-made geographic features (Lipp et al. 2004).

However, many humans have the ability to imagine a route that they will take and even to imagine how to get to a familiar destination by a novel path. This ability, known as cognitive mapping, consists of mentally knitting together landmarks one has experienced, such that the relation among them can be used to determine a novel path to arrive at a goal. Landmarks are needed to form a cognitive map, but they should not be necessary to use it. Can animals form a cognitive map?

Before trying to answer this question, we need to make an important distinction. Some animals have the remarkable ability to navigate in the absence of landmarks or other external cues. This ability, known as path integration (or dead reckoning), involves the representation of direction and distance one has traveled from a starting point. Desert ants are particularly adept at path integration as can be shown not only by the direct path that they take to return to their nest after a foraging trip but also by the systematic error incurred if they are displaced just before they attempt to return home (Collette and Graham 2004). The distinction between path integration and cognitive mapping has been a point of controversy. However, under conditions that cannot be accounted for with either landmark use or path integration, there is evidence for the development of a simple cognitive map in rats (Singer et al. 2007) and dogs (Chapuis and Varlet 1987).

Counting

The term numerical competence is often used in animal research because the more common term, counting, carries with it the surplus meaning that accompanies the human verbal labels given to numbers. That this distinction is an arbitrary one, based on limitations of response (output) capacity rather than conceptual ability, is suggested by Pepperberg's (1987) work with generalized verbal number use in an African gray parrot.

An excellent review of the animal counting literature is provided by Davis and Memmott (1982), who conclude that "although counting is

obtainable in infra humans, its occurrence requires considerable environmental support" (Davis and Memmott, p. 566). In contrast, Capaldi (1993) concludes that under the right conditions, animals count routinely. In simple but elegant experiments, Capaldi and Miller (1988) demonstrated that following training, rats can anticipate whether they will get fed or not for running down an alley depending solely on the number of successive times they have run down that alley and found food or the absence of food on successive earlier trials.

The difference in the conclusions reached by Davis and Memmott (1982) and by Capaldi and Miller (1988) has general implications for the study of intelligence in animals (including humans). The context in which one looks for a particular capacity may determine whether one will find evidence for it. As noted earlier, because we, as human experimenters, devise the tasks that serve as the basis for the assessment of intelligence, we must be sensitive to the possibility that these tasks may not be optimal for eliciting the behavior we are assessing. That is, much of our view of the evolutionary scale of intelligence may be biased in this way by species differences in sensory, response, and motivational factors.

Reasoning

Reasoning can be thought of as a class of cognitive behavior for which correct responding on test trials requires an inference based on incomplete experience. Although, for obvious reasons, most research on reasoning in animals has been done with higher primates (e.g., chimpanzees), there is evidence that some reasoning-like behavior can be demonstrated in a variety of species.

In its simplest form, the transitive inference task can be described as follows: if A is greater than B ($A > B$), and B is greater than C ($B > C$), then it can be inferred that $A > C$ (where the letters A, B, and C represent arbitrary stimuli). Correct responding on this relational learning task requires that an inference be made about the relation between A and C that can only be derived from the two original propositions. To avoid

potential problems with end-point effects that could produce a spurious nonrelational solution (i.e., A is always greater, and C is never greater), experimental research typically uses a task that involves four propositions: $A > B$, $B > C$, $C > D$, and $D > E$, and the test involves the choice between B and D, each of which is sometimes greater and sometimes lesser.

When humans are tested for transitive inference, the use of language allows for the propositions to be completely relational. Relative size may be assigned to individuals identified only by name (e.g., given that Anne is taller than Betty, and Betty is taller than Carol, who is taller, Anne or Carol?). With animals, however, there is no way to present such relational propositions without also presenting the actual stimuli. And if the stimuli differ in observable value (e.g., size), then a correct response can be made without the need to make an inference.

McGonigle and Chalmers (1977) suggested that a nonverbal relational form of the task could be represented by simple simultaneous discriminations in which one stimulus is associated with reinforcement (+) and the other is not (-). $A > B$ can be represented as $A + B -$, $B > C$ as $B + C -$, and so on. With four propositions, an animal would be exposed to $A + B -$, $B + C -$, $C + D -$, and $D + E -$. A is always positive and E is always negative, but B and D, stimuli that were never paired during training, would share similar reinforcement histories. If animals order the stimuli from A is best to E is worst, then B should be preferred over D.

Findings consistent with transitive inference have been reported in research with species as diverse as chimpanzees (Gillan 1981), rats (Davis 1992), and pigeons (Fersen et al. 1991). Although some have argued that these results can be accounted for without postulating that an inference has been made (Couvillon and Bitterman 1992; Fersen et al. 1991; Steirn et al. 1995), transitive inference effects have been found when these presumably simpler mechanisms have been controlled (Lazareva and Wasserman 2006; Weaver et al. 1997). Thus, although it is not clear what mechanism produces it, pigeons clearly show transitive choice that is not produced by differential reinforcement history or differential

value that transfers from the positive to the negative stimulus in a simultaneous discrimination.

Taking the Perspective of Others

An organism can take the perspective of another when it demonstrates an understanding of what the other may know. For example, when Susan sees a hidden object moved to a second hidden location after Billy has left the room and Susan understands that Billy will probably look for the object in the first location rather than second, we would say that Susan can take the perspective of Billy or she has a theory of mind because she understands that Billy doesn't know that the object has been moved (see Frye 1993). To demonstrate perspective taking in an animal is a bit more complex because, in the absence of language, theory of mind must be inferred from other behavior (see, e.g., Hare et al. 2001).

Self-recognition

Recognition of the similarity between ourselves and other humans would seem to facilitate perspective taking. If we can recognize ourselves in a mirror, we can see that we are similar to others of our species. Gallup (1970) has shown that not only will chimpanzees exposed to a mirror use it for grooming, but if their face is marked while they are anesthetized, they will use the mirror to explore the mark visually and tactually (i.e., they pass the mark test). Furthermore, both prior experience with the mirror and the presence of the mirror following marking appear to be necessary for mark exploration to occur. Mirror-directed mark exploration appears to occur generally in the great apes (orangutans and perhaps also in gorillas) but not in monkeys even with extensive mirror experience (Gallup and Suarez 1991). However, using the mark test, there is some evidence of self-recognition in dolphins (Reiss and Marino 2001), elephants (Plotnik et al. 2006), and magpies (Prior et al. 2008). Thus, self-recognition appears to occur in several nonprimate species thought to show other kinds of cognitive skills.

Imitation

A more direct form of perspective taking involves the capacity to imitate another (Piaget 1951), especially opaque imitation for which the observer cannot see itself perform the response (e.g., clasping one's hands behind one's back). But evidence for true imitative learning requires that one rule out (or control for) other sources of facilitated learning following observation (see Whiten and Ham 1992; Zentall 1996, 2012). A design that appears to control for artifactual sources of facilitated learning following observation is the two-action procedure based on a method developed by Dawson and Foss (1965). For example, imitation is said to occur if observers, exposed to a demonstrator performing a response in one of two behaviorally different ways, perform the response with the same behavior as their demonstrator. Akins and Zentall (1996) trained Japanese quail demonstrators to either step on a treadle or peck the treadle for food reinforcement. When observer quail were exposed to one or the other demonstrator, they matched the behavior of their demonstrator with a high probability (see also Zentall et al. 1996, for similar evidence with pigeons). Furthermore, there is some evidence that pigeons can imitate a sequence of two responses, operating a treadle (by stepping or pecking) and pushing a screen (to the left or to the right; Nguyen et al. 2005), an example of what Byrne and Russon (1998) refer to as program-level imitation.

If Piaget is correct, the ability to imitate requires the ability to take the perspective of another. But children do not develop the ability to take the perspective of another until they are 5–7 years old, yet they are able to imitate others at a much earlier age. Furthermore, if pigeons and Japanese quail can imitate, it is unlikely that they do so by taking the perspective of the demonstrator, in the sense that Piaget implied. Thus, although cognitively interesting, imitation may not provide evidence for the kind of cognitive behavior implied by perspective taking.

What Animals Can Tell Us About Human Reasoning

I have saved for last the discussion of several lines of research with animals directed to biases and heuristics characteristic of humans that appear to be somewhat irrational or at least suboptimal. The results of these studies are important, not so much because of their implications for animals, but primarily for their implications for how we interpret human behavior. That is, if other animals have these same biases, then the basis for those biases does not depend on language or human culture as is sometimes proposed.

Cognitive Dissonance

One of these biases has to do with a phenomenon extensively studied in humans called cognitive dissonance. Cognitive dissonance is the discomfort that comes when there is a discrepancy between one's beliefs and one's behavior. For example, if one believes that one should tell the truth, one is likely to feel dissonance on occasions when one fails to do so. That dissonance may be resolved by deciding that there are some conditions under which lying is appropriate or the person lied to may have deserved it. Cognitive dissonance presumably comes about because of a need to be consistent or to avoid being labeled a hypocrite. Does this represent a kind of social intelligence? And if so, would nonhuman animals show a similar effect? But how would one go about asking this question of animals?

One approach involves a version of cognitive dissonance called justification of effort (Aronson and Mills 1959). In their study, undergraduates, who underwent an unpleasant initiation to become part of a group, reported that they wanted to join the group more than those who underwent a less unpleasant initiation. It is assumed that those individuals who underwent an unpleasant initiation gave more value to membership in the group to justify undergoing the unpleasantness.

The justification of effort design allows for a direct test of cognitive dissonance in animals. For example, if on some trials a pigeon has to work hard to receive signal A that says food is coming and on other trials the pigeon does not have to work hard to receive signal B that says the same food is coming, will the pigeon show a preference for signal A over signal B? Several studies have shown that they will (e.g., Clement et al. 2000; Kacelnik and Marsh 2002). But is this cognitive dissonance? Do animals need to justify to themselves why they worked harder for one signal than the other?

Alternatively, we have suggested that this choice behavior results from the contrast between the relatively negative emotional state of the organism at the end of the effort and upon presentation of the signal (Zentall and Singer 2007). That difference would be greater when more effort was involved. Thus, the subjective value of the signal for reinforcement might be judged to be greater. Contrast provides a more parsimonious account of the pigeons' choice behavior. Could contrast also be involved in the similar behavior shown by humans? This possibility should be examined by social psychologists.

Maladaptive Gambling Behavior

Humans often gamble (e.g., play the lottery) even though the odds against winning are very high. This behavior may be attributable to an inaccurate assessment of the probability of winning, perhaps resulting in part from public announcements of the winners but not the losers (an availability heuristic). Would animals show a similar kind of maladaptive gambling behavior? According to optimal foraging theory, they should not because such inappropriate behavior should have been selected against by evolution. Furthermore, if the choice is to have any meaning for the animal, it would have to have experienced the probability associated with winning (reinforcement) and that should reduce the likelihood that the animal would not be able to assess the probability of winning and losing. However, we

have recently found conditions under which pigeons will prefer an average of 2 pellets of food over a predictable 3 pellets of food (Zentall and Stagner 2011). The procedure is as follows: If the pigeon chooses the left alternative, on 20 % of the trials, a green stimulus appears and is followed by 10 pellets of food. The remainder of the time it chooses the left alternative; a red stimulus appears and is never followed by food. Thus, on average the pigeon receives 2 pellets of food for choosing that alternative. If the pigeon chooses the right alternative, it received either a blue or a yellow stimulus but in either can it receives 3 pellets of food. Curiously, the pigeons prefer the left alternative overwhelmingly over the right alternative, and they do so in spite of the fact that they would get 50 % more food for choosing the right alternative.

This result suggests that gambling behavior is likely to have a simple biological basis, and although social and cognitive factors may contribute to human gambling behavior, the underlying mechanism is likely to be simpler. The mechanisms responsible for this suboptimal behavior appear to involve the enhanced effect of the signal for the large magnitude of reinforcer (the 10-pellet "jackpot") and the reduced effect of the signal for nonreinforcement with training (Stagner et al. 2012). This account appears to be consistent with research with humans that has found that gamblers overvalue wins in spite of their low probability of occurrence and they give too little negative value to their losses in spite of their high probability of occurrence (Blanco et al. 2000).

Sunk Cost

The sunk cost effect occurs when one allows an amount of money, time, or other resource already invested to affect one's decision to invest more resources. For example, one may sit through a film that one does not like because to leave would be to waste one's investment of the price of the ticket. But in so doing, one is spending additional resources, one's time, and there is no way to recoup the money already invested. Similarly,

one may choose to continue with a failing business because of the past investment one has made in it. This phenomenon comes under the general rubric of prospect theory (Kahneman and Tversky 1979) which suggests that humans will take greater risks to avoid a loss than to obtain a gain. The question is to what extent does this behavior stem from the cultural tenet to avoid wasting resources and to complete what one starts. If one could show that animals show the same behavior, it would suggest that sunk cost is a general phenomenon that has basic behavioral origins.

In fact, evidence for sunk cost has been found in pigeons (Navarro and Fantino 2005; Pattison et al. 2012). For example, pigeons learn that pecking a green light requires 30 pecks, whereas pecking a red light requires only 10 pecks. They then learn that after pecking the green light a number of times (that varied from trial to trial), they would be able to choose to continue with the green light (to complete the 30 pecks) or switch to the red light for which 10 pecks were required. Results indicated that the pigeons often choose to return to the green light even when 20 more pecks are required. Thus, pigeons show a sunk cost effect that is very similar to that shown by humans. Why pigeons show the sunk cost effect is not clear. One can speculate that it arises from the fact that in nature switching to a different patch often involves uncertainty, some travel time, and possible danger, but one can certainly conclude that culture and language are not necessary components.

When Less Is More

When humans are asked to judge the value of a set of objects of excellent quality, they often give it higher value than those same objects with the addition of some objects of lesser quality (Hsee 1998). This bias is an example of the affect heuristic in which it appears that the average quality of a set is used to determine the value of the set rather than the quantity of items in the set. The phenomenon has become known as a less is more effect. It has been found when humans are asked

to judge the value of sets of dishes and sets of baseball cards (Hsee 1998), and it also has been found when academics are asked to judge the quality of a curriculum vita (Hayes 1983). For example, a vita with three publications in excellent journals is judged better than one with the same three publications in excellent journals plus six more in lesser quality journals.

Recent evidence suggests that even pigeons are susceptible to this bias. We found that pigeons will work for dried peas and dried milo seeds, but when given a choice between the two, they prefer the peas. However, when they are given a choice between a pea and a pea together with a milo seed, they prefer the pea alone (Zentall et al. 2013). Apparently, the pigeons too are averaging the high-quality pea with the lower-quality milo seed and value the pair less than the pea by itself (see also Kralik et al. 2012). The basis of this bias may originate in the need to make rapid decisions, presumably because of intense competition from conspecifics and the possibility of predation, and they use it in the laboratory even when speed is not a factor. Once again, the fact that other animals show this suboptimal choice indicates that the bias is probably not dependent on human cultural influence.

Conclusions

The broad range of positive research findings that have come from investigating the cognitive abilities of animals suggests that many of the “special capacities” attributed to humans may be more quantitative than qualitative. In the case of many cognitive learning tasks, once we learn how to ask the question appropriately (i.e., in a way that is accommodating to the animal), we may often be surprised with the capacity of animals to use complex relations.

In evaluating the animal (and human) intelligence literature, we should be sensitive to both overestimation of capacity (what appears to be higher-level functioning in animals that can be accounted for more parsimoniously at a lower level; see Zentall 1993) and underestimation of capacity (our bias to present animals with tasks

convenient to our human sensory, response, and motivational systems). Underestimation can also come from the difficulty in providing animals with task instructions as one can quite easily do with humans (see Zentall 1997). The accurate assessment of animal intelligence will require vigilance, on the one hand, to evaluate cognitive functioning against simpler accounts and, on the other hand, to determine the conditions that will maximally elicit the animal's cognitive capacity.

The study of human biases by examining animals for the presence of similar phenomena in animals can also help us to determine that simpler mechanisms are involved. Thus, the study of animal intelligence can inform us not only of the cognitive abilities of animals but also can suggest the bases of certain human phenomena thought to have complex social origins.

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