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The Value of Research in Comparative Cognition

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Most research in the field of comparative cognition has focused on the degree to which cognitive phenomena that have been reported in humans, especially children, can also be demonstrated in other animals. The value of such comparative research has not only been the finding that other animals show behavior that is qualitatively similar to that of humans but because the comparative approach calls for the careful control of variables often confounded with the mechanisms being tested, the comparative approach has identified procedures that may also improve the design of research with humans. The comparative approach has also been used to study the degree to which other animals demonstrate human biases and suboptimal behavior (e.g., commercial gambling). When applied to this field of research, the comparative approach has generally taken the position that human biases thought to be established by complex social and societal mechanisms (e.g., social reinforcement and entertainment) may be more parsimoniously accounted for by simpler mechanisms (i.e., conditioned reinforcement and positive contrast). When explained in terms of these mechanisms, the results have implications for explaining in simpler and more general terms the results of similar research with humans. Thus, comparative psychology tells us not only about the similarities and possible differences in behavior among species but it also may have implications for our understanding of similar behavior in humans.

Comparative cognition is an area of comparative psychology that deals with the relation between the learning of humans and other animals (Beran, Parrish, Perdue, & Washburn, 2014). Traditionally, learning implies changes in behavior governed by Pavlovian and instrumental conditioning, together with primary stimulus generalization, and although cognition implies a broad range of learning processes, it has typically been borrowed from research with humans to suggest an attempt to describe possible internal states or representations that result in the behavior observed. As the description of internal states cannot be observed directly, comparative cognition research often attempts to distinguish between simple associative processes and more complex processes generally attributed to humans. Although the term cognition has been defined in various ways, for the present purposes it will be defined as acquired behavior that cannot be explained by simple associative processes, including stimulus generalization along physical dimensions (Tolman, 1948).

Comparative cognition research begins with the premise that behavior has evolved for the survival and reproductive success of organisms and given the fact that many of the behavioral demands of survival of different organisms have been similar, the processes that underlie those behaviors may be similar as well (Beran et al., 2014). Whether those processes exist in other animals, or even in humans for that matter, is an empirical question but it should not be assumed that they are unique to humans.

The goal of this article is twofold: first to present several examples of research in comparative cognition to determine whether or not they can be accounted for with relatively simple learning mechanisms and second to ask whether contexts in which humans are known to choose suboptimally can also be found in other animals. In the case of human suboptimal choice, if similar behaviors can be demonstrated in other animals, can they be explained by relatively simple learning mechanisms? And if they can, is it possible that the same mechanisms are responsible for similar behavior when it occurs in humans (see e.g., Epstein, Lanza, & Skinner, 1981). Many of the examples described in this article come from research with pigeons. This is in part because extensive research has been conducted with pigeons because of their excellent vision and visual

stimuli are easy to obtain and present. Paradoxically, research on comparative cognition has often studied pigeons because they are so different from humans that if certain cognitive abilities can be demonstrated in pigeons it is likely that they can be found in other species as well.

Methodological Problems

In comparing the learning abilities among animals one encounters the problem of distinguishing differences in cognition from differences in perception (the ability to process sensory stimuli). When compared to humans, many mammals do not have well developed color vision and nocturnal species depend primarily on their auditory and olfactory senses. Species also differ in the kind of responses that they can make. For example, most primates have the ability to respond by grasping objects, whereas other species have more limited ability to make a response (e.g., with a paw or a beak). Bitterman (1975) has suggested an experimental means of bypassing the input-output limitations of species comparisons that he suggests should compensate for differences in sensory capacity, motor responding, and even motivation to participate. 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 (Harlow, 1949). In other words, to what extent can learning facilitate new learning (learning to learn)? For example, an animal may be trained to make a simple discrimination (e.g., between black and white) and then the discrimination may be reversed repeatedly. Then, using the rate of original learning as a baseline, one can determine the degree to which later learning (reversals), presumably involving the same processes, is facilitated. Sometimes an approach that appears to be a logical, however, is not always psychological. The general finding from research with visual discriminations is that monkeys show more improvement with reversals than rats, and rats show more improvement that pigeons. Surprisingly, however, if the discriminations are olfactory, rats show better improvement over reversals than monkeys do with visual discrimination (Slotnick & Katz, 1974). Thus, even with these learning-to-learn measures, it may be difficult to make quantitative comparisons among species. Such findings also suggest that the failure to find evidence that a given species has a particular cognitive ability is not evidence that it does not have such an ability. It may be necessary to use other procedures, modalities, dimensions, or stimulus differences to demonstrate it.

The Problem of "Instructions"

An important problem that often occurs in evaluating the cognitive capacity of animals is distinguishing between what an animal understands the task to be and its ability to perform the task (see Zentall, 1970, 1997). When assessing the cognitive capacity of humans, subjects are typically given instructions about the nature or demands of the task. If humans are asked to learn a list of words and tested for their memory at a later time, they may be instructed to recall as many words they can remember from the list that they learned earlier. Assuming that animals had learned to make a series of responses, it is not clear how they would be given instructions to reproduce the set of responses that they had learned earlier. With animals the context may act as a cue to "do what you did in this context earlier" (Zentall, 1970), but the context may not provide an unambiguous cue.

Attempts to study pigeon working memory for temporal durations provides an interesting example of how one can misinterpret the results of an experiment because of the problem of inadequate "instructions." Pigeons can learn a temporal discrimination in which after a short duration (2 s) stimulus (sample), choice of a red comparison stimulus is correct but after a longer duration (8 s) stimulus, choice of a green comparison

stimulus is correct. When working memory for sample duration is assessed by inserting a delay between the offset of the sample and the onset of the comparison stimuli, unexpected retention functions have been found. As the delay increases, the retention function (probability of being correct) for the long sample declines rapidly, quickly falling below chance, whereas the retention function for the short sample declines hardly at all (see Figure 1a). This finding of divergent retention functions with increasing delay, referred to as the choose-short effect (Spetch & Wilkie, 1983), has been attributed to the subjective shortening of memory for duration as a function of the time since the duration was presented (Spetch & Sinha, 1989). The idea is, as the delay increases, the long duration stimulus would be increasingly remembered as being shorter and at some point would be responded to as if it was the shorter one, whereas the shorter duration stimulus would never be remembered as being longer.

The problem with the subjective shortening account is because the delays are novel events, and typically they are dark intervals, similar in appearance to the time between trials (the intertrial interval), the way animals treat the delay trials may be different from the way their behavior is interpreted. Imagine that the animals interpret the delay as the end of the trial and the appearance of the comparison stimuli as choice on the next trial (that would have occurred without a sample duration). The closest duration to no duration would have to be the short duration, hence a choose short effect and the longer the delay the more certain the pigeon would be that the trial was over.

One way to disambiguate the delay would be to make the intertrial interval distinctive from the dark delay by turning on the houselight. When that has been done, the retention functions have been found to be quite parallel (see Figure 1b; Dorrance, Kaiser, & Zentall, 2000). This finding suggests that the divergent retention functions may result, at least in part, from the ambiguity of the meaning of the novel delays. Confusion between the intertrial interval and the delay can be reduced by using distinctive intertrial intervals and delays but even when distinctive, when trained without delays and tested with delays, the delays are novel and a failure to understand the "meaning" of the delay interval may underestimate the pigeons working memory. That is, during training without a delay the comparison stimuli always appeared immediately after the offset of the sample. When a delay is introduced, the comparison stimuli do not appear when they are expected and it may not be clear to the subject that the task is to try to keep the sample stimulus in memory until the comparisons stimuli appear. To test this hypothesis, Dorrance et al. (2000) trained pigeons on a duration discrimination with delays inserted between the sample and the comparison stimuli from the start of training. Under these conditions the retention functions obtained were quite parallel and more important, they were considerably flatter (the pigeons were more accurate) than were the retention functions found by Spetch and Wilke (1983). Thus, how one tests animals can have an important effect on the assessment of their abilities (see also Zentall, 1970).

In general, whenever the testing conditions are different from the training conditions, one may not obtain a true estimate of the animals' cognitive ability. Thus, if at all possible, one should try to minimize the difference in conditions between training and testing (see e.g., Zentall, Edwards, Moore, & Hogan, 1981).



Figure 1. **Duration-sample matching with delays between the offset of the sample and the onset of the comparison stimuli.** (a) Dark delays, dark intertrial intervals. (b) Dark delays, lit intertrial intervals.

a.

Examples of Cognitive Abilities

Many of the barriers to the assessment of comparative cognition are methodological. In addition to the problems associated with the selection of appropriate stimulus and response for the species, there is the problem of the appropriate interpretation of the results. To illustrate the problems one can encounter with interpretation of results produced by animals I will describe three lines of research that have attempted to identify the underlying cognitive mechanisms by testing them against more mechanistic (stimulus-response) learning plus stimulus generalization based on physical similarity.

Stimulus Class Formation

One of the important characteristics of human cognition is the ability to group objects into categories. Several approaches to category formation in animals have been studied including perceptual classes, equivalence classes, and sameness.

Perceptual classes. Pigeons are remarkably adept at responding selectively to photographs of natural scenes, depending on whether the scene involves a human form (Herrnstein & Loveland, 1964) or trees or water (Herrnstein, Loveland, & Cable, 1976) and those objects need not be anything that they might have actually encountered in their past (e.g., underwater pictures of fish; Herrnstein & deVilliers, 1980). To demonstrate that the animals were actually learning to categorize the exemplars, all of these studies demonstrated that the animals could respond appropriately to new exemplars of the category. Consistent with the formation of perceptual classes, however, it is generally difficult to specify what elements of the concept are used to classify the exemplars.

Equivalence classes. 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 & 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 usually 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 possibly get 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 Table 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 dot) and a horizontal 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 (e.g., red and vertical with the circle). To show that an emergent relation has developed between the red hue and the vertical line and between 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 (see Figure 2; Urcuioli, Zentall, Jackson-Smith, & Steirn, 1989; Wasserman, DeVolder, & Coppage, 1992; Zentall, 1998).

Table 1	
Design of stimulus equivalence experiment (after Urcuioli, Zentall, Jackson-Smith, & Steirn, 1989)	
Phase 1 Training	
Red -> Circle	Green -> Dot
Vertical -> Circle	Horizontal -> Dot
Phase 2 Training	
Red -> Blue	Green -> White
Phase 3 Test	
Vertical -> Blue	Horizontal -> White



Figure 2. Equivalence testing. Following many-to-one training (Red->Circle, Vertical-> Circle, and Green->Dot, Horizontal->Dot) and one-to-one training (Red->Blue, Green->White) pigeons were tested for Vertical-Blue and Horizontal->White associations.

Sameness. The concept of sameness can be described as the recognition that two stimuli are the same. Although evidence of sameness has been found with matching to sample procedures using a small number of stimuli followed by transfer of training to novel stimuli, many animals have a tendency to be somewhat neophobic, a bias that may underestimate the degree of transfer found (Zentall & Hogan, 1974, 1976). Alternatively, one can train with a large number of stimuli and transfer to novel stimuli (Cook & Wasserman, 2006; Katz & Wright, 2006) but possible stimulus generalization from the training stimuli to the test stimuli may at least partially account for the good transfer typically found. Zentall et al. (1981; see also Zentall, Andrews, & Case, in press) developed a procedure with pigeons involving all familiar stimuli with matching and mismatching and found that with matching, replacing the correct comparison but not the incorrect but not the correct comparison disrupted accuracy (see Figure 3). It appears that with both tasks, the pigeons looked for the matching stimulus; if the task was matching, they chose it, if the task was mismatching, they avoided it. Thus, it appears that sameness was the basis for learning both tasks.



Figure 3. **Evidence of a Sameness Concept**. Following matching or mismatching training pigeons were tested with a new (but familiar) stimulus replacing either the correct or the incorrect comparison stimulus (Zentall et al., 1981). Pigeons were trained with color matching and mismatching and either the correct or the incorrect comparison was replaced by a new but familiar color. With both tasks, when a new color replaced the matching comparison accuracy dropped whether it replaced the correct or the incorrect comparison.

Transitive Inference

Transitive inference is a task used by Piaget (1955) to assess the cognitive development of children. When given verbally to children it might take the form: If Alice is taller than Betty, and Betty is taller than Carol, who is taller Alice or Carol? The correct response is thought to involve the inference involving Betty as the mediator and children generally solved this task at about the age of 7 years. Bryant and Trabasso (1971) argued that a five-term version of the task was needed to avoid end-point effects (Alice is taller than someone but Carol never is). Furthermore, they found that younger children could perform well, if the memory aspects of the task were reduced (children did not have to remember the names given to the objects being compared. McGonigle and Chalmers (1977) developed a nonverbal version of the task by presenting pairs of stimuli and reinforcing responding to one member (S+) of each pair: thus, A+B-, B+C-, C+D-, D+E- (the letters stand for arbitrary stimuli that could be colors or shapes) and testing for a preference between B and D (an untrained, non-endpoint pair). They found evidence for transitive inference in monkeys (a preference for B) and others found similar evidence in apes (Gillan, 1981), rats (Davis, 1992), and pigeons (Fersen, Wynne, Delius, & Staddon, 1991).

An alternative, simpler account of the findings was proposed by (Couvillon & Bitterman, 1992) who argued that differences in reinforcement history to the B and D stimuli might account for the test results. But Steirn, Weaver, and Zentall (1995) found no correlation between reinforcement history and the transitive inference effect and Lazareva and Wasserman (2006) further tested this hypothesis by giving pigeons extended training with the D+E- pair and still found a strong preference for B over D.

Another simpler account of the transitive inference effect called the value transfer hypothesis was proposed by Fersen et al. (1991). According to the value transfer hypothesis, whenever a simultaneous discrimination is learned, some of the value that accrues to the positive stimulus transfers to the negative stimulus, in proportion to the value of the positive stimulus. In the transitive inference task, B and C acquire positive value directly via reinforcement in the B+C- and D+E- discriminations, respectively. In addition, they acquire value that transfers from the A+B- and C+D- discriminations, respectively. But given that responses to the A stimulus are always reinforced, whereas responses to the C stimulus are not (when it is paired with the B stimulus), the B stimulus can get more value transfer from A than the D stimulus can get from C. Weaver, Steirn, and Zentall (1997) tested for transitive inference under conditions that equated the presumed transfer from A and C to B, as well as the presumed transfer from C and E to D, by reinforcing responses to A, C, and E only 50% of the time (see Table 2). Under these conditions they still found significant transitive inference, thus making less plausible value transfer as the primary determinant of the transitive inference effect.

Table 2Transitive Inference Design	
Standard Group:	$A_{100} B_0; B_{100} C_0; C_{100} D_0; D_{100} E_0$
Experimental Group:	A50 B0: B100 C50: C50 D0: D100 E50

Note: Subscripts indicate the percentage of reinforcements associated with choice of each stimulus.

Imitation

When one animal copies the behavior of another one might be tempted to consider it to be imitated. Piaget (1952) has suggested, however, that imitation reflects the ability to take the perspective of another (perhaps even to have a theory of mind—knowing what others know). But there are likely to be other mechanisms involved when one organism copies the behavior of another and if one would like to claim a cognitive process of the kind suggested by Piaget, one should try to distinguish it from other mechanisms.

Contagion. Behavioral contagion generally refers to the copying of species typical behavior. That is, it is behavior that does not have to be learned and also will occur in the absence of a social stimulus but it is often triggered by the specific behavior of a member of the same species.

One of the more interesting examples of behavioral contagion in animals has been found with regard to eating behavior (Rajecki, Wilder, Kidd, & Jaeger 1976). In this research, food-deprived chickens were given free access to food until eating stopped (they were presumably sated). When a food deprived conspecific was introduced, the presumably sated chickens showed a significant increase in eating as compared to control chickens that were alone.

The finding of contagious eating behavior has important implications for the assessment imitation in animals. Given the fact that at the time of introduction of the conspecific, the eating behavior does not have to be acquired, it may be inferred that the effect of the conspecific on the sated chicken represents an increase in motivation and an increase in motivation is what is presumed to be responsible for the resumption of eating.

Social facilitation. Social facilitation can be defined as the effect of the mere presence of a conspecific (a member of the same species) on the behavior of the focal animal. Zajonc (1965) reported that the effect of the presence of a conspecific may facilitate or retard performance depending on the nature of the behavior being assessed. According to Zajonc, the presence of a conspecific will generally increase the arousal or motivation of the observing organism and that increased arousal would tend to facilitate ongoing (or well learned) behavior but would tend to retard the acquisition of to-be-learned behavior. Zajonc cited examples from humans in diverse settings, such as running races, working on an assembly line, and taking exams, as well as in other animals. This theory has had some support. On the one hand, Zajonc noted that human performance of well-practiced athletes when competing in the presence of others. On the other hand, when humans performed complex math problems or took difficult tests, the presence of others tended to interfered with performance.

In support of Zajonc's (1965) theory, Zentall and Levine (1972) found that the mere presence of another rat retarded the acquisition of a not-yet-learned lever-press response for reinforcement, relative to the absence of a conspecific, whereas once that response had been well acquired, Levine and Zentall (1974) found that the mere presence of another rat facilitated the performance of a similar lever-press response for reinforcement.

There also appear to be conditions under which the presence of a conspecific can facilitate new learning if that new learning is taking place in a novel, potentially fear-inducing environment. Under such conditions the presence of a conspecific may reduce fear and increase exploratory behavior, leading to faster acquisition of the to-be-learned response (Moore, Byers, & Baron, 1981).

Observational conditioning. Observational conditioning refers to the learned association between an environmental action and a desired consequence. An example might be the case of an observing rats that sees a demonstrator press a lever and soon after a pellet is delivered to the demonstrator. If the observer is more likely to press the lever after such an observation, the behavior of the demonstrator may not be necessary for learning to occur. That is, the movement of the lever followed by pellet delivery, a stimulus-stimulus association (i.e., Pavlovian conditioning), may be sufficient to increase the probability that the observer will press the lever (see Heyes, 1994).

Affordance learning. The affordance of an object is learning what can be done with it. For example, one can learn the affordance of a door knob by seeing someone turn the knob and then pull it, and such observation may increase the likelihood that the observer will open the door. But the same movement of the door knob and the door may facilitate learning without the presence of a demonstrator (imagine an unseen person on the other side of the door turning the knob and pushing the door open). One would not consider learning of this kind (i.e., learning from a "ghost" control) imitation but it may represent a form of cognition that requires mechanisms different from simple associative processes.

True imitation. One can think of imitation as the absence of other forms of social influence and social learning. To separate imitation from those other processes, it is useful to think in terms of the actual behavior of the demonstrator, rather than of the outcome of the demonstrator's behavior. One design that has been effective in separating imitation from these other mechanisms is the two-action procedure. In the two-action procedure, one can identify two behaviors that have the same effect on the environment, such that only the specific behavior of the demonstrator differs between them. With birds as subjects, training demonstrators to either peck at a treadle or step on the treadle and allowing observers to see one or the other behavior should satisfy that criterion (see Figure 4). The correlation between the behavior observed and then the behavior of the observer when given access to the treadle should provide a measure of imitation (Akins & Zentall, 1996; Zentall, Sutton, & Sherburne, 1996).

Suboptimal Choice

The research described earlier was directed at asking what cognitive abilities other animals have. The present section focuses on behavior in humans that logically would be considered suboptimal. Examples that considered are, commercial gambling (in which the investment is almost always more than the return), the choice of less of a good thing over more of a good thing, and the tendency to persist on a choice when changing to a different alternative would be optimal (sunk cost). When studied in humans, the suboptimal choice is typically attributed to complex social processes. In the case of gambling, people typically attribute their losses to the cost of "entertainment." In the case of choice of less over more, people appear to average rather than sum rewards. In the case of sunk cost, the culturally reinforced (but usually mistaken) notion that to change would mean a waste of energy, time, or resources already exerted. If these phenomena are actually culturally determined, then other animals should not show similar effects. If, however, it appears that other animals show them as well, these phenomena are likely to result from simpler learning mechanisms that have been triggered (perhaps inappropriately) by environments conditions.

Gambling. If one gives pigeons a choice between an alternative always gives the pigeon a yellow light (or a blue light) that is always followed by 3 pellets of food or an alternative that 20% of the time gives the pigeons a green light that is always followed by 10 pellets of food but 80% of the time gives the pigeons a red light that is never followed by food (see Figure 5) one finds that the pigeons will strongly prefer the second alternative (Zentall & Stagner, 2011). This suboptimal choice is analogous to human gambling behavior

because there is a low probability of getting a high reward. It appears to result from the failure of the red light to generate a significant aversion to the suboptimal alternative (Laude, Stagner, & Zentall, 2014). To the animal, it appears to be a choice between the value of the color associated with reinforcement following each alternative. That is, it is as if the pigeon views the choice as being between 10 pellets of food and 3 pellets of food.

To test this hypothesis more directly, Smith and Zentall (2016) gave pigeons a choice between an alternative that always provided a yellow light followed by 100% reinforcement and an alternative that 50% of the time provided them with a green light that was always followed by food and 50% of the time provided them with a red light that was never followed by food. In support of the hypothesis that it is the value of the color associated with reinforcement, although the second alternative provided the pigeon with half as much food as the first, the pigeons were generally indifferent between the alternatives (see also Stagner, Laude, & Zentall, 2012).



Figure 4. **Two-action procedure apparatus.** Demonstrator birds were trained to either peck at the treadle or step on the treadle. When observer birds were exposed to the treadle, they showed a significant tendency to use the same response to operate the treadle (Akins & Zentall, 1996; Zentall et al., 1996).

Given that pigeons show choice behavior that is similar to that of problem gamblers, it suggests that gambling behavior may be supported by conditioned reinforcers (stimuli associated with reinforcement) rather than by the probability of reinforcement associated with their choice. Apparently, animals have been selected to approach stimuli associated with reinforcement. In nature approaching conditioned reinforcers is likely to increase the probability of encountering food. With gambling, or this pigeon gambling analog, attraction to the conditioned reinforcer does not increase the probability that it will occur. Interestingly, hungrier pigeons show a greater preference for suboptimal alternatives than only moderately hungry pigeons (Laude, Pattison, & Zentall, 2012). Furthermore, exposure to an enriched environment slows pigeons' attraction to suboptimal alternatives (Pattison, Laude, & Zentall, 2013).



Figure 5. Design of the suboptimal choice experiment. Following Zentall & Stagner (2011).

Less is more. Economists have proposed that humans are rational (e.g., Becker, 1976; Persky, 1995) but Kahneman and Tversky (1979) demonstrated that humans use various heuristics in making decisions and that those decisions are not necessarily rational or optimal. Humans often base decisions on affective heuristics (their subjective feeling). An example of an affective heuristic known as the less is more effect comes from an experiment in which subjects were asked to evaluate a set of dishes (Hsee, 1998). Humans gave greater value to a set of 24 dishes in perfect condition than a larger set of 40 dishes but only 31 of them were in perfect condition. According to Hsee, the overall quality of the set appears to detract from its objective value. Thus, humans may use an averaging heuristic to judge the quality of a set rather than judge its overall value. According to optimal foraging theory (Stephens & Krebs, 1986), animals should not show such a bias because any tendency to prefer an alternative that provides less food over one that provides more food should be selected against. However, there is evidence that a similar preference for less over more occurs in monkeys (Kralik, Xu, Knight, Khan, & Levine, 2012). In these experiments, monkeys showed a preference for a grape over a cucumber slice but would work for both. Yet, when offered a choice between a grape and a grape plus a cucumber slice, they preferred the grape alone. Similar findings were reported by Pattison and Zentall (2014) with dogs, which would eat both cheese and carrots but preferred the cheese. When the dogs were offered a choice between a piece of cheese and a piece of cheese plus a piece of carrot, all of the dogs except one preferred the cheese alone.

A constraint on this general phenomenon was found by Zentall, Laude, Case, and Daniels (2014) with pigeons. They found that normally hungry (24 hrs food restricted) pigeons chose optimally between a preferred

pea and a pea plus a milo seed, whereas less hungry (4 hrs food restricted) pigeons preferred the pea alone. Interestingly, all of the dogs in the Pattison and Zentall (2014) study were companion animals but one of them was adopted as a stray, an animal that was likely to have experienced long periods of hunger, and that was the dog that had chosen optimally. Thus, degree of hunger experienced (but not necessarily at the time of testing) may be a factor in observation of the less is more effect.

Sunk cost. The sunk cost effect, sometimes referred to as the sunk cost fallacy or concord effect, involves the bias to stay with an initially chosen alternative, even though there is a better alternative available (Arkes & Blumer, 1985). The rationale is that one has already invested resources in the first alternative and that investment would go to waste if one switched. Economists have been particularly interested in studying human's tendency to continue to invest in pursuits which seem unlikely to end profitably. Researchers have attributed this suboptimal choice to various social influences. Staw (1981) proposed that it represents an effort to salvage a project and prove that a previous commitment was rational, part of an external justification process, or an adherence to norms of consistency. Brockner (1992) attributed suboptimal sunk cost decisions to an unwillingness to admit a mistake. Novemsky and Kahneman (2005) attributed it to loss aversion, the greater motivation to avoid losses than to achieve gains.

The many reasons given for humans to view sunk costs as a motivation to persist in the face of failure suggest that other animals should be unlikely to show this kind of suboptimal choice. That is, animals should be more likely to switch to a more profitable alternative if given a chance. Navarro and Fantino (2005, Experiment 1) examined the sunk cost effect in pigeons using a procedure in which on each trial there was a 0.50 probability that a small number (10) of pecks would be required for reinforcement and there was a decreasing probability that many more responses (40, 80, or 160) would be required. At any time, the pigeon could choose to start a new trial, thereby potentially getting a trial with a smaller number of pecks to reinforcement. The optimal strategy would be to make 10 pecks or so and if reinforcement did not occur, to start another trial. In fact, pigeons rarely started a new trial but typically persisted until reinforcement was provided. Although the Navarro and Fantino procedure had many of the characteristics of the human sunk cost scenario (i.e., the possibility that persisting might be the better option), Pattison, Zentall, and Watanabe (2012) removed the possibility of uncertainty associated with starting a new trial (i.e., that the outcome could have been worse than persisting). They did this by training pigeons to make a variable number of pecks to a green stimulus on one side key to cause a white stimulus on the center key to appear. A single peck to the white stimulus caused the green stimulus to reappear and a red stimulus to appear on the other side key. For reinforcement, the pigeons could return to pecking the green stimulus to complete 30 pecks or they could switch to the red stimulus and make a fixed number of responses (always 10). Although most of the time switching to the red stimulus would have provided them with food sooner (and with less effort), all of the pigeons preferred to return to pecking the green stimulus. The only exception was on trials in which there were no initial pecks to green and the choice was between 30 pecks to green and 10 pecks to red.

Sunk cost research with animals suggests that the phenomenon need not be related to social influence (e.g., having been taught to always complete a job once started) or to loss aversion. Instead, it may result from a more basic evolutionary process. Although under laboratory conditions switching is almost always better than staying, in nature, the uncertainty and potentially dangerous cost associated with switching may outweigh its benefits. In humans, as well, the unknown cost of switching may contribute to the sense of loss that comes from the feeling that one has left the job unfinished.

Conclusions

Comparative psychology provides a valuable contribution to our general understanding of behavior in the sense that it can identify genetic predispositions and behavioral flexibility important to the survival of the organism. For example, how the organism adapted to changes in the availability of resources, changes in competition for those resources, changes in predatory species and their behavior, and changes in the climate. In recent times an understanding of species' behavioral flexibility has taken on a more immediate concern as humans reduce many natural populations through hunting, habitat reduction, and our contribution to climate change.

The subfield of comparative cognition focuses primarily on the similarities and differences between human behavior and that of other animals and as noted earlier there have been two approaches to these comparisons. The first focuses on the rational cognitive processes that have often been thought to be unique to humans (and perhaps some other primates). Under the best of conditions, comparisons are difficult because of differences in sensory capacity (as well as the nature of the response and motivational differences). We tend to test animals with tasks using sensory modalities that have been found to maximize human cognitive capacity (i.e., sight), whereas other animals are often more sensitive to tasks involving stimuli from other modalities (e.g., dogs' sensitivity to odors).

Less obvious, perhaps, we tend to assume that what we are assessing is cognitive capacity while often capacity is confounded with the rules or instructions of the task. Although ensuring that task instructions do not play a role in underestimating cognitive capacity may be difficult, it is crucial that we appreciate the potential confound in conducting comparative cognitive research (see, e.g., Dorrance et al., 2000).

To illustrate how researchers have approached the assessment of cognitive capacity in animals, I have described three areas of research with animals focusing on human cognitive development, stimulus class, formation, transitive inference, and imitation and shown how research with other animals has brought to light mechanisms that have not typically been acknowledged in the human cognitive literature. A good example is in the area of copying behavior. Although it is typically assumed that when human observers copy the demonstration of a behavior that it involves the cognitively based imitation that Piaget (1952) proposed was present. Animal researchers, however, recognized that behavioral similarity shown between observation and performance could result from simpler mechanisms (e.g., contagion, social facilitation, observational conditioning, or learned affordances). The recognition that simpler processes may be involved when two behaviors match has led to more carefully controlled experiments that have allowed researchers to isolate these simpler mechanisms from the kind of imitation that Piaget had in mind.

The second approach focuses on what might be called irrational or suboptimal behavior that also has been thought to be unique to humans. I described three examples, commercial gambling, the less is more effect, and sunk cost.

When humans engage in commercial gambling (when the expected return on investment is less than one), it is often attributed to a form of entertainment unique to humans. Because animals are hungry, evolution should have selected them to make optimal choices (Stephens & Krebs, 1986). The finding that pigeons too make suboptimal choices under conditions similar to human gambling suggests that entertainment may not be the only motivation that is involved. Once again, research with other animals has important implications for how we interpret human behavior.

Similar conclusions can be drawn from research with the less is more task. The addition of a less preferred food object to a more preferred food object should not diminish the value of the more preferred food but it appears to do so for monkeys and dogs. Furthermore, as discovered with pigeons, the effect appears to depend on how motivated the animal is. Only moderately motivated pigeons appear to be susceptible to this effect.

The sunk cost effect, persistence with one's current goals when logic would suggest that an alternative behavior would have greater value, has been attributed to cultural influence, an overgeneralization of the admonition to avoid waste. But pigeons show sunk cost as well, a finding that suggests it is based on a simpler process unrelated to cultural influence.

Finally, the study of comparative cognition encourages researchers to consider behavior from the perspective of the animal being studied (to the extent that we are able) and in so doing it may enable us to recognize that specialized cognitive capacities may have evolved because of deficits in our ability to survive without them and that those cognitive abilities allowed us to overcome those deficits. In contrast, other animals, those without those deficits, did not require the evolution of those particular cognitive capacities. Thus, our cognitive capacities may represent a way to compensate for a less than ideal way to deal with environmental change and some of the important benefits of the study of comparative psychology are potential insights into the place of humans in the context of other animals.

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