Symposium on Animal Cognition

THE EXPERIMENTAL ANALYSIS OF COGNITION IN ANIMALS

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Abstract—*The origins and current status of comparative cognitive psychology are examined. Great strides have been made in the last 20 years, but two problems are identified as obstacles to future progress. One is the very limited number of species studied by comparative cognitive psychologists. The second is the conflict between the increasing use of complex stimulus discriminations and the need for precise stimulus control in animal experiments. An expanded examination of more species as selected by phylogenetic and ecological considerations and an unwavering demand for the experimental identification of the controlling features of complex discriminations are suggested as solutions to these difficulties.*

It is now widely recognized that substantial changes have occurred in the last 20 years in how we think about the mechanisms underlying animal behavior. The first fruits of this change were seen in the edited volume *Cognitive Processes in Animal Behavior* (Hulse, Fowler, & Honig, 1978). This book contained a wide-ranging collection of new findings, reformulations of old questions, and programmatic summaries that fashioned a new focus to the comparative study of psychological mechanisms in animals—from its almost exclusive focus on learning to a considerably broader examination of cognitive processes in general. Thus, the modern comparative study of cognition seeks to understand how animals encode, transform, compute, and manipulate symbolic representations of the real world's spatial, temporal, and causal texture for the purposes of adaptively organizing their behavior.

The most important catalyst for this

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transformation can be traced directly to the information processing revolution that similarly altered the investigation of human learning and memory (Gardner, 1985). The character of this change can be illustrated simply by comparing older reflexive analyses of classical conditioning (Kimble, 1961) with more contemporary perspectives, in which action is based on the information content of the conditioned stimulus and its perceived causal relation to the unconditioned stimulus (Dickinson, 1980; Mackintosh, 1983; Rescorla, 1988). Once viewed as reflecting the simplest form of learning, this conditioning paradigm has now become one of the primary means for studying stimulus and interevent representations in animals (see almost any issue of the *Journal of Experimental Psychology* (JEP): *Animal Behavior Processes*).

An important, but clearly secondary, influence on the development of the study of animal cognition can be traced to the fields of ethology and behavioral ecology. Their concerns with the ecological and evolutionary foundations of animal behavior were first manifested in the constraints-on-learning literature (Hinde & Stevenson-Hinde, 1973; Seligman & Hager, 1972), but have now expanded to other areas of learning and cognitive research with animals. Although the idea is not always acted upon, it is now widely recognized that knowledge of the ecology and adaptive functions of an animal's behavior is an important element in understanding the animal's underlying cognitive organization (Bolles & Beecher, 1988; Kamil & Sargent, 1981; Roitblat, 1987).

This modern synthesis of animal learning, cognitive science, and behavioral ecology has enormously expanded the breadth, nature, and sophistication of the psychological issues studied in animals. Here again, compare the contents of a traditional animal-learning textbook with the contents of a textbook focused on animal cognition (Kesner & Olton,

1990; Pearce, 1987; Roitblat, 1987). As its vitality is increasingly well documented and recognized (Church, this issue; Domjan, 1987; Gallistel, 1990; Roitblat, Bever, & Terrace, 1984; Terrace, this issue; Wasserman, this issue; Yoerg, in press), any further description of this new conceptual framework, or affirmation of its value, would serve little purpose.

It is more propitious instead to address two of the more prominent obstacles still facing researchers operating within this perspective. The first centers on the different strategies used by psychologists in selecting and comparing different animals. My comments on this problem are brief, as its fundamental issues and theoretical positions are so well articulated in the other articles in this Special Section. More time is spent examining a second important problem, one which revolves around the inherent conflict between the requirements for precise stimulus control and description in animal research and the increasing use of highly complex discriminative stimuli and testing situations in animal cognition studies.

SPECIES SELECTION IN COMPARATIVE PSYCHOLOGY

Comparative investigations of cognition contribute important and unique information to several important psychological topics. For instance, animal studies remain the best way to explore the relations between the cognitive and neural mechanisms of behavior (Kesner & Olton, 1990) and for discovering and establishing the taxonomic distribution and function of different, potentially divergent, cognitive structures and processes. And animal studies are our only means for studying the evolution of behavior, the mind, and their underlying mechanisms. In addressing these questions, the generalist and ecological approaches (Riley & Langley, this issue) have been the most prominent comparative research

strategies. The generalist approach has concentrated on a few taxonomically distant focus animals (rats, pigeons, and monkeys) in order to understand the general processes shared among species (Bitterman, 1965, 1975; Rilling & Neiworth, 1986; Skinner, 1938; Thorndike, 1911), while the ecological approach has concentrated on a variety of more closely related species to better understand the cognitive mechanisms of specific adaptive behaviors and their ecological determinants (Johnston, 1981; Kamil, 1988; Shettleworth, 1972, this issue).

The generalist approach has been and remains the more frequently employed strategy, despite the important information to be gained from more ecologically motivated comparisons. Its continued popularity is due in part to the fresh wind of human cognitive psychology invigorating many of our research programs, and its convenient fit to our established laboratory practices. Part of cognitive psychology's recent influence has been to shift the nature of the questions investigated with animals to problems more closely related to those previously investigated in humans. One very positive result of this shift has been a growing set of fertile new comparisons of human, rat, pigeon, and monkey cognitive processes within the same or directly comparable experimental and conceptual frameworks (Allan & Blough, 1989; Blough, 1979, 1984; Church, this issue; Cook, 1992b; Cook, Wright, & Sands, 1991; Terrace, this issue; Wasserman, this issue; Wright, Santiago, Sands, Kendrick, & Cook, 1985). In large part, the generalists' traditional concentration on these particular species allowed this new activity, as the extensive background information already collected and available about these animals permitted the immediate, direct, and profitable examination and use of contemporary cognitive theories and procedures with these animals.

This strategy's limited repertoire of species—accounting for over 88% of the animal reports in JEP during the last 50 years—has not been as helpful with questions concerned with the evolution of cognitive processes, the influence of ecological factors, or how cognitive processes might be used by animals on an everyday, or nightly, basis. No other comparative science, from anatomy (Radinsky, 1987) to ornithology (Gill, 1990),

restricts itself in this peculiar way. Given the more than 9,000 species of birds, for instance, our reliance on the noble pigeon to be the psychological representative of this phylogenetic class is surely fraught with scientific peril.

The solution to this problem is clear: A broader range and greater number of animal species need to be examined by psychologists (hardly new news! Beach, 1950; Bitterman, 1965; Hodos & Campbell, 1969; Lockard, 1971). As the wholesale and arbitrary addition of more species is inefficient and unadvisable, a number of researchers have advocated the increased use of the ecological approach (Johnston, 1981; Kamil, 1988; Shettleworth, 1972; see Shettleworth, this issue, for good examples of this approach). The use of this approach makes very good sense, as new species are chosen with care—based on a combination of ecological considerations, phylogenetic status, or other special features of their behavior. The generalist approach has been an efficient first step, and will remain a productive strategy for comparative cognitive research for quite some time. But its restrictive study leaves important questions about the evolution, distribution, ecological determinants, and functional significance of animal cognitive mechanisms unanswered. These questions require examining a greater number of species representing different phylogenetic groups and ecological niches. The ecological approach is the best extant framework for guiding these new selections. Together, the parallel use of both strategies should make for a powerful and complementary alliance for the future investigation of animal cognition.

THE CONFLICT BETWEEN STIMULUS CONTROL AND COMPLEXITY

One of the most fundamental concerns in comparative psychology is the nature of the stimulus controlling an animal's behavior. Traditionally, only a few simple unidimensional stimuli (jeweled lights, colored pecking keys, tones and clickers; see Balsam, 1988) have been used in animal experiments in an effort to define and control these stimuli precisely. The obvious virtue of this ap-

proach lies in the simplicity of such stimuli and the ease with which their relations can be manipulated and identified. It is for this very reason that the classical conditioning paradigm has become a preferred vehicle for studying animal cognition.

This reliance on simple stimuli may also have been a significant barrier to our completely understanding animal cognitive processes. For instance, simple stimuli do not possess the configural or emergent attributes of the more complicated object stimuli and categories that compose the natural world. Therefore, our restricted experimental situations may not have permitted our animals to display the full scope and power of their cognitive abilities. This realization, and the recent infusion of modern cognitive theories and techniques, has resulted in the increasing use of more complex and "realistic" visual and spatial stimuli in testing animals over the last 20 years. One of the most prominent examples of this shift is the frequent use of colored slide photographs of natural objects as discriminative stimuli (Terrace, this issue; Wasserman, this issue). In studies of categorical discrimination, for example, these complex pictorial stimuli seem to have been instrumental in revealing previously unknown conceptual abilities in pigeons (Herrnstein, Loveland, & Cable, 1976; Wasserman, this issue; Wright, Cook, Rivera, Sands, & Delius, 1988).

Despite the fascinating new findings often accompanying this increased complexity, there is a serious drawback to this approach. It lies in the difficulty of isolating and identifying the specific controlling features of such complex stimuli. Without this essential information, the appropriate interpretation of a particular finding can be made significantly more difficult or impossible to determine. A classic example of this problem, and its nefarious subtlety, is Siegel's (1967) ingenious reanalysis of Lawrence's (1949) experiments on acquired distinctiveness of cues. In that case, a more detailed examination of the specific stimuli controlling the rats' behavior indicated that Lawrence's results could be accounted for by traditional means, and without recourse to attentional mechanisms. It is possible that some of our field's more interesting new results could suffer sim-

Experimental Analysis of Animal Cognition

ilar fates, when and if the proper experiments decomposing their complex discriminative stimuli are conducted.

While the potential problems arising from this increased complexity are widely recognized, many experiments are still conducted without the requisite control or analysis of the stimulus—especially in research on animal spatial cognition. The early research on the radial maze task, for instance, clearly demonstrated that it was extramaze cues surrounding the maze that controlled the rats' choice behavior (Kraemer, Gilbert, & Innis, 1983; Olton, 1978; Zoladek & Roberts, 1978). But for the vast majority of radial maze research, this critical stimulus environment remains the unappraised standard laboratory room, often described only as being "rich" in extramaze cues, and with a tone more suggestive of this as an asset than a liability. With a few notable exceptions (Brown, 1992; Cheng, 1986; Leonard & McNaughton, 1990; Suzuki, Augerinos, & Black, 1980), surprisingly little research has been directed at investigating how these multiple complex cues and their relations are actually represented and utilized by the rats. Without this kind of explicit analysis, understanding the processes underlying spatial navigation and memory in rats seems a remote possibility.

One reason this problem persists lies in the great difficulty of systematically decomposing an animal's response to complex stimuli. Recently, I completed a lengthy series of experiments examining the features used by pigeons in discriminating complex line drawings of birds and mammals. These pigeons had learned earlier to discriminate these two natural categories quite readily (Cook, Wright, & Kendrick, 1990). I then varied the original line drawings in terms of a number of different qualities in an attempt to locate the attributes critical to this discrimination (brightness, number of legs, orientation, figure–ground relation, relative proportion of real animals in composite "animals," arrangement of body parts, etc.). I found the birds could discriminate the two categories reliably based on a number of features. The next step in this type of stimulus dissection would require determining how these multiple features are hierarchically related, weighted, and integrated by the pi-

geons. The almost Sisyphian nature of this task recommends a different strategy be used to resolve the inherent conflict between control and complexity.

One potential solution lies not in the simple or complex extremes, but in a middle ground—use of artificially constructed, multidimensional stimuli of more intermediate intricacy. This strategy takes best advantage of the precise laboratory control intrinsic to synthetic stimuli and combines it with the potential theoretical benefits of more complex stimuli. Furthermore, this strategy has become considerably more feasible with the recent advent of computer-generated and -presented stimuli in animal research.

My work on the avian perception and

processing of textured stimuli is a good example of this kind of approach (Cook, 1992a, 1992b, 1992c, in press). Visual textures are multidimensional patterns in which distinct global regions are derived from the perceptual grouping of smaller component elements. Some examples of the different kinds of texture stimuli that I have recently tested with pigeons are shown in Figure 1. One of the strengths of this research is that these computer-generated, artificial stimuli are moderately complex, by virtue of their multielement, multidimensional, and hierarchical properties, but still allow total control over their generation, manipulation, and analysis as a result of their manufactured design. This capacity to manage precisely the visual and informa-

FEATURE - COLOR

CONJUNCTIVE
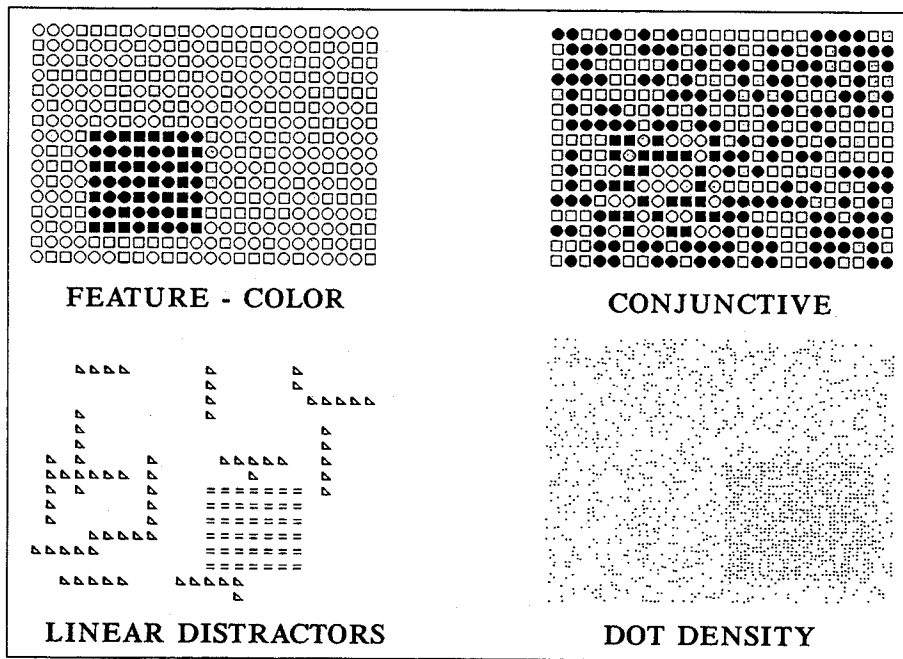
LINEAR DISTRACTORS

DOT DENSITY

Fig. 1. Examples of four stimuli used in comparative tests of perception in pigeons and humans. The pigeons respond for food reinforcement by indicating with their beaks where the small target region is located in each display. The top two stimuli are examples of feature and conjunctive displays. Each is based on four elements composed from two shapes (square and circle in this example) and two colors (depicted as black and gray), but each is organized in a different manner. The target and distractor regions of feature displays differ consistently in either color (shown) or shape (not shown), whereas conjunctive displays are formed by joint mixtures of these two dimensions (target = black squares and gray circles). Both pigeons and humans are better at discriminating feature displays than conjunctive displays. The bottom left display shows an example of a target region surrounded by linear arrangements of distractor elements. Pigeons are less accurate with such displays than with ones in which the same distractors are randomly distributed (not shown). The textured regions of the bottom right display are composed exclusively of small dots that must be globally integrated for the accurate visual discrimination of the different regions. Like humans, pigeons find textured regions differing in dot density easier to discriminate than those differing only in the spacing of their dots (not shown).

tional content of these displays, pixel by pixel if necessary, has permitted many of the important findings of this research.

In humans, texture stimuli seem to reveal straightforwardly many of the earliest and most fundamental operations of the perceptual system (Beck, 1982; Grossberg & Mingolla, 1985; Julesz, 1981; Marr, 1982). The effortless nature of human texture discrimination has suggested that its underlying grouping mechanisms are located early in the stream of visual processing and are parallel and preattentive in character. Textured stimuli seemed an excellent starting point for examining the basic mechanisms of visual cognition in birds.

Avian visual cognition is of considerable psychological interest because the demands of muscle-powered flight require both modest size and acute vision, and in response, birds have evolved small visual nervous systems that are both powerful and efficient. This naturally occurring combination of small size and power is something of a puzzle, however, given our current thinking about the computational complexity of visual processing (Arbib & Hanson, 1987; Fischler & Firschein, 1987; Landy & Movshon, 1991). Hence, a program to compare the mechanisms of avian visual perception with those of mammals and of computers programmed for pattern recognition follows quite naturally.

In my texture discrimination experiments, the pigeons are tested for their ability to discriminate the different textural regions of displays like those depicted in Figure 1. I measure how accurately and quickly the pigeons can locate and peck at the small, odd target region in each computer display, resulting in food reinforcement. Pecking responses are detected by an infrared touchscreen that surrounds the computer screen. These experiments have suggested that pigeons perceive and process textured stimuli in a manner that seems to parallel human perception and processing. For example, Treisman has found in both visual search and texture segregation tasks that humans can discriminate feature displays more quickly than conjunctive displays (Treisman & Gelade, 1980). The regions of textured feature displays differ consistently in only one dimension (color or shape), while conjunctive displays require the joint processing of both

dimensions (color and shape) in order to respond correctly. Pigeons likewise find feature displays easier to discriminate visually than conjunctive displays (see Fig. 1; Cook, 1992b). The fact that both species have the same difficulty in segregating these textured stimuli perceptually suggests a similar organization to their processes for combining dimensional information.

Other experiments have suggested that the emergent visual discontinuities at the boundaries between textural regions are also critical to the pigeons' discrimination of such displays (Cook, in press). For instance, target regions surrounded by linear arrangements of distractors produce greater interference in performance than displays in which the same distractors are randomly distributed. I have also found that pigeons respond to dotted texture stimuli much as humans do (Cook & Sanders, 1990; Julesz, 1981), with regions differing in dot density being easier to discriminate than those differing only in the spacing of their component dots. Together, these findings suggest that the avian mechanisms for visually grouping textured elements into perceptual regions have many functional similarities, and perhaps a common structural organization, to the mechanisms found in mammals.

The utility of such structured synthetic stimuli for bridging the gap between simple colored patches and complex object photographs seems highly promising. It would be easy, for example, to program textured stimuli to form distinct clusters of related stimuli, making in essence artificial categories. The component features of these categories (color, shape, size, location, brightness, element distribution, and proportion) could then be varied experimentally in terms of their structure, variability, degree of correlation, and relevance to reinforcement in order to test competing theories of categorization in animals. Unlike pictures of objects from naturally occurring categories, such manufactured categories could be easily manipulated and their controlling features experimentally identified. Despite the strong and intuitive attraction of more realistic stimulus materials, a comparable degree of control is simply not possible. One of animal learning's traditional strengths was its attention to stimulus control, a heri-

tage not to be forgotten as we expand our testing of animals using more complex and cognitively interesting stimuli.

As does any human social activity, science shows distinct trends and fashions. The recent growth in cognitive interpretations of animal behavior reflects both their power and utility, but perhaps a certain trendiness as well. While our field's cognitive revolution has broadened its scientific horizons, one other fundamental principle should not be forgotten—Morgan's (1984) canon. Simply paraphrased, it says that in no case should we interpret an animal's action as the outcome of a complex cognitive mechanism if a simpler one will do. Given the permanently foreign nature of our subjects' mental life, premature cognitive explanations will only hurt our pursuit. It is of the utmost importance that rigorous evidence and substantial caution guide any such explanations of animal behavior.

Overall, the contemporary study of cognition in animals has made considerable strides in the last 20 years. Its detailed laboratory comparisons of the cognitive mechanisms of rats, pigeons, monkeys, and humans have been very successful and valuable, and should be continued. To achieve a true comparative psychology of cognition, however, we will need to start examining the behavior of more species, chosen by sound biological principles. If we start to exploit this intrinsic and unique quality of our subject matter, then perhaps our new field can stop being the weather vane, blown by the winds of human cognitive science, and instead increasingly become a more significant partner in the pursuit of a mutual goal—understanding the mechanisms of behavior in both human and nonhuman species.

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