The Representative Animal

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The anthropocentric approach to the study of animal behavior uses representative nonhuman animals to understand human behavior. This approach raises problems concerning the comparison of the behavior of two different species. The datum of behavior analysis is the behavior of humans and representative animal phenotypes. The behavioral phenotype is the product of the ontogeny and phylogeny of each species, and this requires that contributions of genotype as well as behavioral history to experimental performance be considered. Behavior analysis tends to favor the ontogenetic over the phylogenetic component, yet both components are responsible for the performance of each individual animal. This paper raises questions about the role of genotype variables in the use of representative animals to understand human behavior. Examples indicating the role of genotype in human behavior are also discussed. The final section of the paper deals with considerations of genotype in the design of animal experiments.

Key words: animal models, behavioral phenotypes, phylogeny, representative animals

We, however, shall have little interest in the activity of animals markedly different from man, or in those infrahuman activities which throw no light upon *human* [their italics] conduct. (Keller & Schoenfeld, 1950, p. 2)

This quote is from the period in history of animal study that still governs the use of nonhuman forms as behavioral representatives of *Homo sapiens*. This approach requires some consideration of the problems that arise when relating the behavior of one species to that of a second. These problems are seldom discussed in behavior analysis journals, except at the nonfactual or principle level (Blackman, 1983). In contrast, the present discussion is concerned with the empirical problems arising from comparison of the behavior of two organisms. Whether the behavior of 2 subjects is similar is fundamentally an empirical question, but an empirical approach to behavioral similarity, especially when comparing human and nonhuman animal behavior, is relatively rare (Boakes, 1983).

There have been a number of recent papers on the generality of animal studies and the relevance of these studies to un-

derstanding human behavior (e.g., Burkist, Newland, & Sherburn, 1991; Shull & Lawrence, 1991). In fact, there is considerable skepticism that the fruits of the study of animal behavior have materially contributed to the understanding of human behavior (Lowe, 1983). The purposes of this paper are (a) to examine briefly the representative animal approach within an historical context, (b) to consider some of the problems that underlie understanding the behavior of one species by studying the behavior of a second, and (c) to suggest changes in the approach to the study of animal behavior.

The Representative Animal: Historical Considerations

Nonhuman animals have been studied as a way of understanding human behavior at least since the acceptance of Darwin's (1859) theory of evolution and its application to the evolution of mind (Spencer, 1896, p. 453 on; Huxley, 1874). Although the theories of psychological evolution were stated in mentalistic terms that cannot be easily translated into behavioral terms, it was assumed that human mental attributes formed a hierarchy of complexity (e.g., reflexes, instincts, emotions, reasoning, judgment, and volition; Klopfer & Hailman, 1967), each level having evolved from the previous one. Not all attributes were assumed to

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be present or equally developed in each nonhuman species. Romanes (1884) attempted to set up a classification system (analogous to anatomical phylogenies) based on similarities and differences in mental functions among species. The different species were expected to differ from each other and from humans in a manner that allowed them to be placed in a sequence or hierarchy of increasing number of mental attributes, with humans at the high end of the sequence. The application of this approach required behavioral observations over a wide range of different species. Thus, in this approach, the study of animal behavior was directly relevant to understanding human behavior, but by virtue of the behavioral differences among species, no species was representative of any other. The approach failed because of the unreliability of the observational data base and difficulties with behavioral categories, but the idea that behavior is the product of evolution is virtually universally accepted in the biological sciences (Tinbergen, 1972, p. 162).

The observational method was replaced by the experimental method towards the end of the 19th century. The investigation of the animal mind remained the problem (Washburn, 1926), but the stress on attempting to prove the existence of mental evolution tended to vanish. The presence of certain kinds of behavior were assigned a special status as indicators of the presence of various conscious processes, and experimental tasks were designed to investigate such behavior (Terrace, 1984). For example, behavior that could be correctly executed in the absence of the stimulus conditions that determined it was taken to require the presence of an image (e.g., Hunter's 1913, delayed response, without orientation); correct responses to the relation between open doors in the multiple choice apparatus was said to require the use of ideas (Yerkes & Coburn, 1915); and rapid changes in learning curves and single-trial learning were assumed to require insight (Kohler, 1925). This approach to the study of behavior is still used (especially by cognitive psychologists), as il-

lustrated by the idea that sensory preconditioning demands cognitive processes (Dickinson, 1980), and the occurrence of exploratory behavior, in the presence of a mirror, of a chimpanzee with respect to body parts not otherwise visible, indicates self-awareness (Gallop, 1970).

Experiments were carried out using a wide range of different species with primary interest in the behavior of the animal in its own right. For example, Thorndike (1898, 1901) investigated escape from problem boxes, imitation, and go/no-go discriminations in dogs, cats, and monkeys and, in spite of rapid changes in some monkey learning curves, concluded that these animals were no different from cats. Yerkes and his colleagues investigated the behavior of crawfish (Yerkes & Huggins, 1903), crabs (Yerkes, 1902), frogs and toads (Yerkes 1905b), earthworms (Yerkes, 1912a), turtles (Yerkes, 1901), mice (Yerkes, 1907), squirrels (Yoakum, 1909), pigs (Yerkes & Coburn, 1915), and monkeys and apes (Yerkes, 1916), using a variety of experimental techniques.

Although Yerkes was interested in problems of animal mind (Yerkes, 1905a), his experimental papers are objective and detailed descriptions of experimental procedures in which the data are presented for individual animals. The paper on hearing in the frog (Yerkes, 1905b), for example, starts with a field study of the effects of sound on frog behavior. This is followed by an experimental study of effects of sound on hind-leg flexion and the effects of destruction of the ear upon this behavior. The introduction of the paper is concerned entirely with anatomical and other data that indicate that frogs are likely to respond to environmental sounds. The purpose of the paper was to provide data concerning the properties of hearing in frogs. Apart from the use of the mentalistic vernacular in describing the behavior of the animal, there was no speculation concerning the frog's conscious processes or on problems of mental evolution.

Yerkes's interest in basic behavioral processes is illustrated by his paper on

the Yerkes discrimination box (Yerkes, 1912b). Investigators frequently found it difficult to train animals using the discrimination box. Yerkes (1912b) described various techniques (such as fading) for easing such difficulties, the paper being concerned entirely with objective considerations and suggestions. In a blind review it would be difficult to differentiate a Yerkes paper from a Watson paper (see, e.g., Watson & Watson, 1913), and it was a small step from Yerkes to Watson.

Watson, like Yerkes, did not believe in the notion of a representative animal. The laws of the behavior of animals, "the range of responses, and the determination of effective stimuli, of habit formation, must be determined and evaluated in and for themselves, regardless of their generality, or their bearing upon such laws in other forms" (Watson, 1914, p. 27).

Watson's *Introduction to Comparative Psychology* (1914) was the last "behavioristic" book to deal with evolutionary and comparative problems, the need for field observation, and the investigation of a wide range of different species. Following this book, interest in studying different species declined in the United States and the study of learning, with the use of representative animals, became the major focus (Boakes, 1984, p. 235; Dewsbury, 1992). In continental Europe, the ecological and ethological approach to the study of animal behavior outlined in the first half of Watson's (1914) book continued to dominate the field until the present time.

Direct comparison of Watson (1914) and Tinbergen (1951) reveals the near identity of their approaches. For example, Watson (p. 7) and Tinbergen (p. 4) were explicitly objective, rejecting subjective interpretations of behavior. The notion of a representative animal was rejected by Watson (p. 27; see the quote above) and Tinbergen ("In spite of the respect deserved by the interesting work done with rats, one should be a little skeptical of the laboratory rat as a representative of the whole animal kingdom"; p. 11). Both worked in the field, and both considered the field to be the

source of problems and the place where laboratory investigations are tested (Tinbergen, 1951, p. 8; Watson, 1908, 1914, p. 30; Watson & Lashley, 1915). Both were concerned with observational and experimental study of instincts, the ontogeny and phylogeny of behavior, and the correlation of behavior with internal neural and other processes.

Watson (1914, p. 120 on) and Tinbergen (1951, chap. II and IV) stressed the study of behavior as a reaction to external stimuli. Both distinguished between reflexes and instincts. Both carried out field studies and developed descriptions of the complexities of responses in the everyday environment. Both, for example, investigated alarm reactions in certain birds produced by a shadow passing over the field of vision (Tinbergen, 1951, p. 31; Watson, 1914, p. 43). Both stressed the need to investigate the potential capacities of sense organs, both advocating conditioning and discrimination experiments for this purpose. Both were concerned with the social modification of instinctive behavior, and Watson (p. 142 on) discussed the effects of rearing sparrows in isolation, with conspecifics, or with different species, on the development of bird song; he also discussed the various dialects of song of different populations of a given species living in different locations (Conradi, 1905).

The current representative animals are presumed to be representative with respect to each other as well as to humans. Skinner (1938, p. 47) selected the rat as being as similar to man as is consistent with experimental convenience and control. The rat may differ more from humans (e.g., poor vision) than other mammals (dog or ape) that may serve just as well but for the fact that these animals are much less convenient to house and control and more expensive to use. Skinner (1960) used the pigeon in his work on missile guidance during World War II, and this animal became a second representative animal (Ferster & Skinner, 1957, p. 7). Various species of monkeys have also served as representative animals.

The foregoing considerations indicate

that historically there is a clear difference between the earlier and later approaches to the study of animal behavior as a vehicle for understanding human behavior. The classical approach stressed the differences in behavior of different species as a way of understanding the historical development of human behavior. This approach requires the study of a large number of different species. The representative animal approach is orthogonal to the classical approach in that it stresses the similarities among different species and uses a few convenient species to study aspects of human behavior that are not amenable to experimental study for ethical and other reasons.

The Representative Animal Approach: Empirical Considerations

The datum of the experimental analysis of behavior consists of the behavior of phenotypical pigeons, rats, primates, and humans. This behavior is the product of their phylogeny and ontogeny. Behavior analysts generally favor behavioral history as the overriding determiner of behavior (Boakes, 1983, p. 16). However, there is an unequivocal difference in the genotype of two different species, and this would seem to point to a need to, at least, explicitly consider the phylogeny as well as the ontogeny of the species concerned (Emlen, 1973).

Different species. Each species brings a different behavioral phenotype to the experiment. The behavioral phenotype (which includes specific behavioral flexibilities, such as Tinbergen's, 1951, p. 45, "localized learning," or Emlen's, 1973, genetic guidance of learning) may be described by an ethogram. The ethogram reveals the characteristic behavioral interactions that occur between the animal and its everyday environment, behavior that can be seen as defining its "behavioral" environment in von Uexkull's *umwelt* sense (Schleidt, 1985, p. 317). Thus, one species is likely to abstract certain stimulus features from the environment, be subject to particular stimulus filtering, and have a strong tendency to emit a number of characteristic responses (J. M.

Harrison, 1992; Sidman et al., 1982), all of which may be different in a second species. There is a match or fit between the behavioral phenotype and the environment to which the animal is normally exposed (Schleidt, 1985, p. 312).

Behavioral experiments are typically designed to eliminate conspicuous species-specific behavior that might disrupt orderly performance in the experimental task. Thus, Skinner (1938, p. 48) chose the rat over the cat as the representative animal because the former lacks the "strong reflexes" (Skinner referred here to difficulties associated with confinement in cats) that interfere with the experimental procedures. Timberlake (1989) refers to the need for "detuning" the experimental environment to eliminate conspicuous items of species-typical behavior while still obtaining the expected orderly performance. Such detuning is not always successful; in some species the lack of fit between the experimental environment and the behavioral repertoire results in unexpected behavior that may prevent the use of that species in typical experimental procedures. Many well-known examples of this are given in Breland and Breland (1966). Although conspicuous and disruptive items of species-specific behavior may be eliminated from an experiment by eliminating potential sign stimuli (for example), species-specific behavior (including species-specific plasticity) cannot be eliminated by detuning an experiment, because species-specific behavior is all the animal (or human) has. The experimental performance is the result of the interaction between species-specific behavior and the experimental conditions. The apparatus and procedure are normally adjusted to obtain normal orderly performances (to the extent that this is possible in each species; Breland & Breland, 1966). This comes close, as Timberlake (1989) suggests, to deciding that certain procedures produce certain behavior, and then adjusting the apparatus and procedure to produce the "correct" behavior.

The significance of genotype is stressed here to focus on the fact that animal experiments are traditionally designed to study human behavior in a nonhuman

animal. Little need be known about the biological properties of the animal, except those properties that disrupt the experiment, and the results of the experiment will contribute little to the understanding of the natural behavior of the animal. In the event that the behavior of the animal in some experimental task is different from that of the human, the results are wasted in the sense that they make no contribution to understanding the animal in its own right.

Same species. Some of the problems that arise when comparing different species also appear when comparing two members of the same species. One cannot always predict the behavior of one member of a species from the behavior of a second member of the same species. Each member of a given species (apart from monozygotic siblings) possesses a particular sample from the same gene pool as other members, and it is possible that distinctly different phenotypes, due in part to genotype differences, will be found among a group of the animals. The possible role of genotype in behavioral variation is illustrated in many human behavioral studies.

Some people, for example, have blue eyes and others have brown. Likewise, humans are not behaviorally homogeneous. For example, it would be expected that the equivalences found in a conditional discrimination experiment might be quite different in normal and color-blind people if certain hues were used as the experimental stimuli. It is likely that such differences would be attributed to genotype rather than to different individual histories because of what is known about the role of genotype in color blindness (Nathans, Piantanida, Eddy, Shows, & Hogness, 1986).

There is considerable variation among subjects in some human behavioral research. For example, 4 experimentally naive children were studied in a matching-to-sample task (R. J. Harrison & Green, 1990, Experiment 2). One acquired the initial task in 80 trials, 1 acquired it in 192 trials, and 2 failed. One child performed at the 100% correct level in equivalence tests, whereas a 2nd failed

all tests. Again, individual humans show one of two modes of responding on fixed-interval schedules. One mode is characterized by a constant rate of responding with no scallop or postreinforcement pause. The other mode consists of the emission of one or two responses at the end of each interval (Lowe, 1983; Lowe, Harzem, & Bagshaw, 1978). In these examples, unlike the color-blind example, there are no genetic markers to indicate whether there are significant correlations between genotype and experimental performance.

The acceptance of genotype as playing a role in a particular behavioral variation may seem to cut off any further experiments, whereas the acceptance of environmental causes leads to experimental investigation of the causes of the variability (Sidman, 1960, p. 191). However, the real possibility of a genotype component tends to focus interest on the experimental problems raised by this possibility. Variation, for example, is one of the major behavioral characteristics underlying evolution, yet little is known of the role of genotype in behavioral variation.

Descriptions of the everyday behavior of monozygotic twins raised in different environments illustrate forcefully the significance of genotype in human behavior. The behavior manifested in casual interactions with business and other associates is typically thought of as determined by the present environment and behavioral history. However, the everyday behavior of monozygotic twins reared apart showed remarkable similarities when the twins were interviewed apart (Lykken, McGue, Tellegen, & Bouchard, 1992). For example, two women were afraid to enter the acoustic chamber for acoustic measurements and required that the door be left open, and both, when at the beach, insisted on entering the water backwards, and then only up to their knees. Two male twins were found to be a fund of funny stories. Two were gunsmith hobbyists; two women habitually wore seven rings; two men offered the same diagnosis of wheel bearing trouble in a car; two obsessively counted things; two had been

married five times; two were captains of volunteer fire departments; two were fashion designers; and two left love notes around the house for their wives. Two males divorced women named Linda and remarried women named Betty; two found that for years before they met they had vacationed in Florida on the same stretch of beach, driving there in the same model Chevrolet; they both named their sons "James Alan" and they both chain-smoked Salems® with nail-bitten fingers while working in their basement workshops. Such behavioral similarities were seldom found in an equal number of dizygotic twins.

Most people are not twins; hence, there is no pointer to suggest what components of their behavior are dependent upon their genetic makeup, but the behavior of singles must be as controlled by their genes as is that demonstrably controlled in monozygotic twins. In certain cases, such as color vision, the presence of one genetic component produces color blindness and the presence of a second produces normal color vision. However, the genetic components underlying the behavior of the twins reared apart are completely unknown in terms of such basic behavioral variables equivalent to color vision.

Representative Animals and Human Behavior

The selection of a model species to investigate some aspect of human behavior requires that the behavior of the two species is similar in some experimental task. Thus, it appears that one may simply compare the behavior of the two organisms under formally the same conditions. The general method in experimental analysis is to use one of the standard representative species to understand human behavior. For this approach to be useful, it will be necessary from time to time to check whether the animal and human perform the same way in similar tasks. The first step is to determine whether the two species give the same baseline behavior (Nevin, 1982; Pierce & Epling, 1991).

Baseline behavior. Performance in

differential-reinforcement-of-low-rate (DRL) schedules has been investigated in many species, allowing estimates of similarity of baseline behavior of different species (Richelle & Lejeune, 1980). Rats perform efficiently (between one and two responses per reinforcement) on DRL schedules in the normally used range of 10 to 120 s. There is typically a sharp peaked mode of percentage of interresponse-time (IRT) values around (typically just after) the DRL value (Barofsky, 1969; Beasley & Seldeen, 1965; Ferraro, Schoenfeld, & Snapper, 1965; Laties, Weiss, & Weiss, 1969; LeFrancois & Metzger, 1993; Terman, 1974; Zimmerman & Schuster, 1962). Rats also perform well at longer DRL values. For example, 2 rats showed a mode of percentage of IRT values around a DRL value of 4 min (Marcucella, 1974).

In contrast, performance of pigeons on DRL schedules is different (Harzem, 1968; Lowe & Harzem, 1977; Richelle & Lejeune, 1980), rendering it a poor representative animal for the study of rat performance. For DRLs up to about 5 s, pigeons may show two modes in the distribution of the percentage of responses at each IRT. One mode ("bursting") is at very short IRTs, and the second is typically around the DRL value. For DRLs around 10 s, there is variability among subjects, some showing "bursting" and a mode around the DRL value, whereas others show a wide variety of different patterns of the percentage of responses falling at each IRT. The pigeons made between five and about 50 responses per reinforcement. For DRLs above 10 s, there was little evidence of timing at the DRL value. (Powell, 1974; Reynolds, 1964a, 1964b; Richardson, 1973; Richardson & Loughhead, 1974; Schwartz & Williams, 1971). The animals may emit several hundred responses per reinforcement (Richardson & Clark, 1976). The poor performance of pigeons was not due to special properties of pecking, because similar results were obtained with a treadle response (Richardson, 1973).

Comparison of rat and human performance on DRL schedules suggests that the rat may be representative of humans for studying baseline behavior (e.g., Bra-

dy & Conrad, 1960; Dews & Morse, 1958; Hodos, Ross, & Brady, 1962; Weiner, 1969). The rat's performance is also a good predictor of the performance of crows (*Corvus brachyrhynchos*) on DRL schedules from 10 to 120 s (Powell, 1974). The crows made only two to three responses per reinforcement over the entire range of DRL values, and showed the typical mode of percentage of responses per IRT value at a point slightly longer than the DRL value. Pigeons studied in the same experiment made between about seven and 270 responses per reinforcement.

The pigeon, on the other hand, may be a representative of the performance of mice (Richelle & Lejeune, 1980). On a DRL of 30 s, the mice made between 33 and 1,000 responses per reinforcement. For 2 of the mice, the percentage of responses per IRT value declined from a high at the shortest IRT to the longest IRT value. The other 2 mice showed modes at around 15 s.

These data illustrate the behavioral variation among species and the need to study a number of species to find one that is representative of human behavior.

Manipulation of baseline behavior. Similar baseline behavior may depend upon different behavioral processes in each species. Hence, similarity of baseline behavior does not imply that further manipulation of that behavior will have the same effect in the two species concerned. To be useful, the performance of the representative animal must change in the same way as that of the modeled species. This point may be illustrated by reference to work on matching to sample (conditional discriminations).

The effect of matching-to-sample training on the appearance of untrained discriminations (equivalences) has been studied in a number of different species. One interest has centered around the way in which different species respond to novel arrangements of the stimuli following matching-to-sample training (MacKay, 1991). In the following experiments, Iversen (1993) trained rats, Lipkens, Kop, and Matthijs (1988) trained pigeons, Fields, Reeve, Adams, and Verhave (1991) trained adult humans, and Sid-

man et al. (1982) trained rhesus monkeys, baboons, and children in matching-to-sample tasks using (approximately) the same methods. All species performed the baseline behavior at about the same level of correct responses. The performance of the rats indicated that they had acquired specific discriminations that broke down when conditions were changed. The other species were tested using novel arrangements (symmetry probe) in which the sample and comparison stimuli were reversed. The pigeons, rhesus monkeys, and baboons performed at chance level to the test stimuli, whereas the adults and 2 of 3 experimentally naive children performed at or above the 90% correct response level. Only the humans developed the symmetrical relation.

Manipulation of training procedures. Modification of the matching-to-sample training procedures may produce the same baseline behavior described in the previous section, but may produce differences in the effects of subsequent manipulation of the baseline behavior. For example, McIntire, Cleary, and Thompson (1987) reported symmetry and transitivity in two monkeys (*Macaca fascicularis*) after a special training procedure and the use of multiple (six different hues) colored stimuli. Each sample required a specific scheduled response (fixed-ratio 8 or a 3.5-s holding response). If the correct comparison stimulus was selected, the other comparison was turned off. A correct scheduled response to the remaining sample was then required to obtain food. The monkeys required about 6,000 trials to reach the baseline behavior criterion. Both monkeys showed typical equivalence discriminations.

Other special training methods have been developed in attempts to demonstrate other complex behavioral effects in representative animals. For example, pigeons required about 55 sessions to reach a criterion of 80% correct responses on a multiple visual-stimulus discrimination problem (Fersen & Delius, 1989). Four pigeons required about 100 sessions to acquire five visual discriminations to a criterion of 80% correct responses (Fersen, Wynne, Delius, & Staddon, 1991). Two pigeons failed to reach criterion in

this experiment. Two pigeons required about 360 sessions to acquire 152 trial unique series of discriminations (Wright, Cook, Rivera, Sands, & Delius, 1988). Monkeys required 24,000 trials to acquire a same/different concept with visual stimuli (Wright, Santiago, & Sands, 1984). Only 2 of 6 pigeons acquired a symbolic matching-to-sample task (Fersen, Emmerton, & Delius, 1992).

These data raise a number of problems. Some of the animals did not reach the baseline criterion and were eliminated from the study. Thus, the task selected animals into two classes that limited the generality of the experimental results (Wright et al., 1988). The time required to train the animals may exceed the life span of feral animals (Delius, 1992), eliminating generality of results to feral animals. The special training methods were different from the relatively simple methods used with humans. The need for excessive and different training methods, together with the failure to perform when trained approximately the same way as humans, suggest that the representative animals are probably not good models. This doubt may underlie the behavior of equivalence researchers, as indicated by the contents of the 1992 and 1993 issues of the *Journal of the Experimental Analysis of Behavior*. There are 11 studies of equivalence in humans and one in a nonhuman animal. The increase in interest in human research led to an issue of *JEAB* (November 1990) devoted to the analysis of human behavior.

The previous paragraph suggests that it is more useful to study humans than representative animals when investigating some complex human behavior. This does not mean that the representative approach is fundamentally faulty, because it is possible that useful representative species could be found. In the biological sciences it is usual to examine a range of different species until one that possesses the desired property in considerable detail is found. For example, the processes underlying deafness in Waardenburg's syndrome (degeneration of the organ of Corti; Waardenburg, 1951) are almost exactly mimicked by the blue-eyed deaf

white cat. This particular mutant strain of cat is the representative animal for the investigation of this human condition (Tait, 1883; West & Harrison, 1973). However, the amount of work required to find suitable representative species (should they exist) for each property of human behavior points to the advantages of studying humans to investigate human behavioral phenomena.

The Study of Nonhuman Animal Behavior

Behavior is one mechanism by which human and nonhuman animals survive and breed in their everyday environments. Behavioral interaction with the environment is also one of the mechanisms through which genetic selection takes place (Delius, 1985; Johnston, 1985). In human experiments, both subject and experimenter are of the same species and have the same general fit to their social and nonsocial environments. This results, presumably, in the design of experimental environments in which the experimenter could perform and in which the subject is likely to be able to perform because of the same fit to the experimental environment. The fit of nonhuman animals to the environment is different from humans (and is generally unknown). To the extent that it is possible to gauge the fit of the animal's behavior to its environment and to adjust the experimental environment appropriately, human and nonhuman behavioral experiments can address behavior at more nearly the same level. The results of such nonhuman animal experiments may reveal processes not normally encountered and suggest the investigation of these in humans. The results will also be useful in understanding the behavioral fit of the animal to its environment, and will not be lost if the processes do not have a human counterpart. The following section discusses experiments that illustrate the experimental study of animal behavior that may address problems of adjustment to everyday environments.

Acquisition of performance. In many nonhuman animal experiments, training

the subjects may take many hundreds or thousands of trials. It is difficult to believe that animals require large numbers of trials to adjust to new everyday environmental circumstances or that the environment supplies thousands of "natural trials." The failure to train rapidly in traditional experiments may be due to the mismatch between the animal's behavior and the experimental environment. That is, initially the animal brings inappropriate behavior to the experiment. Experimenter-designated correct performance in the task may require the elimination of this initial behavior (resulting from its nonreinforcement) and the emergence of other behavior that happens to fit the reinforcement requirement. It is these processes that produce the typical long training times.

The performance of an animal in an experiment that includes a number of natural features may be different from that found in traditional experiments revealing previously undiscovered behavioral processes. The role of the various natural features in these processes can be analyzed by variation of the incorporated features. The following experiments illustrate this and the point made in the previous paragraph.

The effect of the inclusion of natural features in experiments has been analyzed in auditory stimulus control (Downey & Harrison, 1972; J. M. Harrison, 1981). Sound-producing objects occupy the everyday environment. In the everyday environment the site of the object and the origin of the sound it produces occupy the same location, and appetitive behavioral interactions with the sound source also occur at the origin of the sound. This spatial overlap of origin, object position, and behavioral manipulation of the object is the only kind of (appetitive) interaction that occurs under everyday conditions. There are no instances, for example, in which a sound located at A requires that an object located at B be approached and manipulated. Everyday environments contain many sound-producing objects that produce noisy complex sound fields. Pure tones (long rise-decay sine waves) are sel-

dom found in the field. These are the kinds of environments in which auditory stimulus control occurs naturally. These environmental features were incorporated into the experiments. The sound field in the experimental room produced by the stimulus was of the normal complex type found in everyday environments that contain echo-producing objects and other random sounds. The experimental room was not soundproofed (i.e., it was noisy). Pure-tone sound sources were not used. This is the kind of environment in which auditory stimulus control naturally occurs.

Rats and monkeys were studied under conditions in which the source, origin of the sound, and behavioral interaction were in the same position. The animals were trained in a two-lever go-right/go-left task in which the speakers were mounted adjacent to the levers. Noise bursts, which are readily localized, were presented through either the left or right (in random alternation) speaker in each trial. A response on the lever at the sounding speaker was reinforced and the trial terminated. The sound was novel at the start of discrimination training. The discrimination was acquired in essentially one trial.

Elimination of the various natural features from the experiment revealed the behavioral components of both species that appeared to fit the arrangements of the everyday environment. First, the connection between the position of the origin of the sound and the position of the reinforced response was broken by training animals to respond on the lever remote from the sounding speaker. That is, moving away from the sounding source was reinforced on each trial. With this arrangement, the percentage of correct responses fell to about 10% over the first four discrimination training sessions, and the animals required 20 sessions to reach 90% correct responses (Beecher & Harrison, 1971). Here, the effect of reinforcing a remote lever response was to strengthen the response of going to the sounding speaker rather than strengthening the reinforced response. This effect of reinforcement is advantageous in the

everyday environment because it will take the animal to the sound source and is presumably one factor responsible for the one-trial acquisition in the experiment in which responding on the adjacent lever was reinforced.

The preceding two experiments showed that early in training the animals pressed the lever adjacent to the sounding speaker whether that response or the remote response was reinforced. Because either programming of reinforcement produced the same response, it appears that differential reinforcement of responding on one or the other lever at each trial was unnecessary. Animals were trained on a task in which a response on either lever was reinforced (nondifferential reinforcement; Downey & Harrison, 1972). The animals made 90% to 100% responses to the adjacent lever from the first session on. Nondifferential reinforcement did not generate 50% correct responses, as occurs in many traditional experiments (J. M. Harrison, 1992).

If the speakers were displaced from the levers, and responding on one lever was reinforced when the sound was presented through one speaker, and responding on the second lever was reinforced when the sound was presented through the second speaker, a normal acquisition curve, starting at the 50% correct level and reaching the 90% correct response level after 20 sessions, was obtained (J. M. Harrison, 1992).

These experiments reveal an effect of reinforcement (strengthening the response of approaching the source rather than the reinforced response) that has not been revealed by traditional experiments. The results also indicate that the presence and shape of long acquisition curves are a function of not using the natural adjacent coincidence of source and object. The large number of trials required in the various unnatural arrangements resulted, presumably, from the necessity of reducing the natural approach response to the sound source to a low level and of accommodating this response to allow the correct (nonadjacent) lever to be pressed (J. M. Harrison & Briggs, 1977). Performance in the nat-

ural and unnatural arrangements thus depended upon different processes.

Everyday observation shows that many organisms (including humans) orient to and often approach novel-sounding objects. The status of the object (reinforcer? for example) is initially unknown, and it is just such novel objects to which rapid behavioral adjustment is required. Thus, it might be expected that novel sounds are those that most rapidly acquire control of the animal's behavior. In the go-right/go-left experiments discussed above, it was found that one-trial acquisition was obtained only when the sound was novel at the start of discrimination training (J. M. Harrison, 1981). Exposure to the sound prior to training in the apparatus lengthened acquisition from one trial to one to four sessions.

These experiments illustrate a number of points discussed in this paper. The properties of everyday acoustic environments of surface-dwelling animals, and the constraints these environments place upon the nature of behavioral interactions with sounding objects, have existed over an indefinite time period and are factors that have influenced the evolution of auditory behavior. It is to be expected that over evolutionary time, the animal's behavior has evolved such that it can perform sufficiently well in such environments to survive and breed. To the extent that these acoustic environmental features are incorporated into an experiment, the animal is performing in an environment to which it has a behavioral fit. In this sense, the experiments were carried out at the same fit level as human experiments.

A central finding was that reinforcement of any response in the presence of a sounding object strengthened the response of approaching that object. This effect of reinforcement results in behavior that fits the demands of the everyday environment for a behavioral interaction with the object. This suggests that the special behavioral effect of reinforcement has a strong genotypic component. The same can be said of the rapidity of development of stimulus control by novel-sounding objects. The experiments

showed that when features are varied so as to produce experimental environments that do not exist in the field, acquisition takes many sessions. Some of these arrangements are used in traditional experiments in which they might be referred to as arbitrary arrangements. Acquisition data obtained from such experiments are the result mainly of forcing the species-specific behavior to fit the experimenter-designated behavioral interactions with the experimental environment. In contrast, our experiments were designed to be sensitive to the biological properties of the animal in its own right and attempted to use the animal to study human behavior. Finally, this series of experiments, together with a series of go/no-go experiments (J. M. Harrison, 1992), demonstrated behavioral effects that have not been found in traditional experiments.

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