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A CHANGING FOCUS OF ANIMAL PERCEPTION—FROM ABILITIES TO PROCLIVITIES

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ABSTRACT: Several methodologies are available to evaluate how animals discriminate and perceive stimuli. These methodologies are described herein, and the kinds of questions that can be addressed with each technique, and its strengths and limitations, are addressed. Detection and discrimination studies are described that measure animal abilities, followed by classification and judgment studies that measure animal proclivities. The choice of methodology is a consideration in experimental design, because the format of the question can direct, and sometimes define the answer. The experiments discussed emphasize that animals have multiple processing modes available to them that they use to classify stimuli. Detection and discrimination experiments may tap into one of those modes, while categorization and judgment experiments may address a different mode. A feature of these experiments is that they reduce the extent to which we view animal perception and cognition as distinct from human perception and cognition.

Traditional animal psychophysical experiments have been concerned with defining the limits of the sensory systems of animals. For example, they have described the minimum amount of acoustic or light energy detectable as a function of frequency, or the smallest difference in frequency or intensity the animal observer can discriminate (see Stebbins, 1970, and Berkeley & Stebbins, 1990, for pertinent reviews). The focus of these experiments has been on what the animal *can do* when pressed to the limits of its sensory resolving capabilities.

Concurrent with the laboratory studies, ethological experiments have been carried out in the field to assay what animals *do* in their natural environment. These experiments have explored how animals behave in response to the rich variety of stimuli and events present in their native habitat (Beecher & Stoddard, 1990; Nelson & Marler,

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1990). The focus of these studies has been to determine how the animal classifies elements of multimodal stimuli.

While both experimental approaches have provided information regarding the sensory, perceptual, and cognitive abilities of many animal species, and while numerous studies using these techniques remain to be done, there have been recent attempts to increase the flexibility of both approaches. Thus, laboratory studies have attempted to explore not only what the animal can do when pressed to the limits of its sensory abilities, but also what the animal does when presented with the option of structuring or classifying stimulus events. Similarly, field efforts have been made to discern how the resolving powers of animals are compromised by the noise inherent in the natural environment. Narins (in press), for example, has made measurements of basic auditory function in the frog, using modified psychophysical techniques, in the natural environment.

This paper discusses animal psychophysical experiments designed to elucidate how animals categorize and organize stimuli (May, Moody, & Stebbins, 1989; Dooling, Brown, Park, & Okanoya, 1990). Detection and discrimination studies, measuring animal *abilities*, are briefly described to give a reference point from which the newer procedures have departed. The limitations of the detection and discrimination methodology, and of field studies, are discussed. We then examine classification and judgment experiments, designed to measure animal *proclivities*. We indicate why these important experiments are particularly difficult to conduct. Finally, we describe the variety of experimental approaches which have been developed to answer classification and judgment questions with animals in the laboratory. Ten to twenty years ago, these approaches were in their infancy. Ten to twenty years from now, we anticipate that new approaches which have emerged from currently used techniques will have enlarged the window through which we can explore the perceptual world of animals.

DETECTION AND DISCRIMINATION EXPERIMENTS IN THE LABORATORY

Most experiments which determine the limits of an animal's sensory capabilities have been similarly designed. Prior to stimulus presentation, the animal performs an observing response, which minimizes activity and optimizes the probability that the animal is attending to the stimulus. In the subsequent presentation of the stimulus, or of a change in the stimulus, the animal performs a reporting response. In positive reinforcement studies, correct detection of the stimulus is followed by food or water, while in avoidance studies, correct detection permits the animal to avoid shock. Premature releases

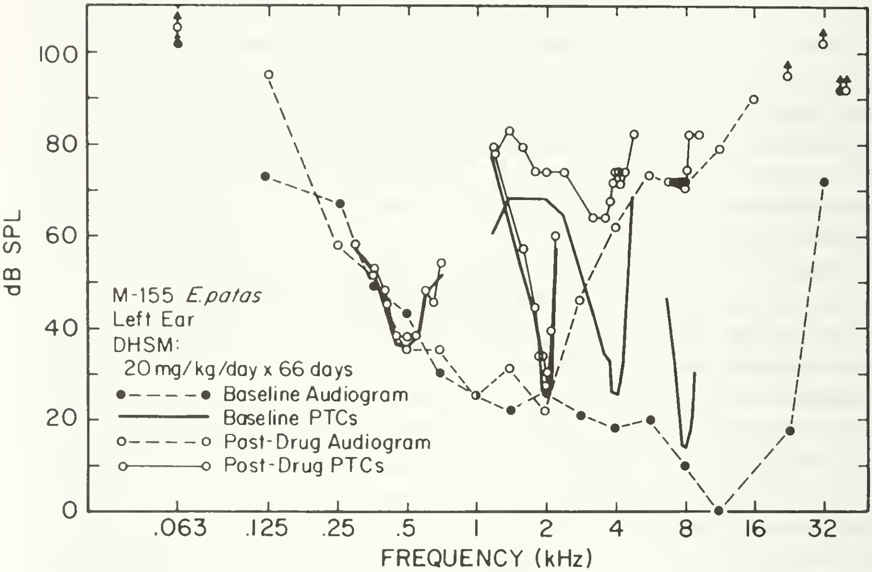

FIGURE 1. A direct comparison of baseline (pre-drug) and post-drug pure-tone threshold curves and psychophysical tuning curves from one patas monkey (*Erythrocebus patas*). These data suggest that the outer hair cell system contributes to frequency tuning in the mammalian cochlea. From "Effects of Outer Hair Cell Loss on the Frequency Selectivity of the Patas Monkey Auditory System," by D.W. Smith, D.B. Moody, W.C. Stebbins, & M.A. Norat, 1987, *Hearing Research, 29*, pp. 125-138. Copyright 1987 by Elsevier Science Publishers BV. Reprinted by permission.

frequency tuning in the mammalian cochlea. Finally, the experimental design employed in these studies can be used prior to conducting experiments which ask how animals classify stimuli, for if they cannot discriminate between the stimuli, they are unlikely to classify them distinctly.

A highlight of these techniques is that they are adaptable to a wide variety of animals, thereby permitting cross-species studies to explore the relationship between structure and function in species whose peripheral sensory systems are distinct. The conditioned suppression technique described above and used by Heffner and Heffner (1985) is a case in point—this methodology has been used to assess absolute auditory thresholds in a wide variety of mammals, including the wood rat (*Neotoma floridana*), least weasel (*Mustela nivalis*), pocket gopher (*Geomys bursarius*), prairie dog (*Cynomys ludovicianus*), cat (*Felis catus*), and guinea pig. A particularly clever adaptation of the operant-conditioning methodology using positive reinforcement was described by Nachtigall (1986), who measured the chemoreceptive abilities of the dolphin. In these experiments, the dolphins bit a plastic plate, through which distilled water with or without a chemical was dispersed into the mouth. Release of the plastic plate in the presence of a chemical, i.e., a correct detection, was reinforced with a fish. Using this procedure, Nachtigall and his colleagues measured threshold levels for the detection of chemicals which humans describe as sour, bitter, salty, and sweet.

In sum, psychophysical techniques have been used in animals with great success to ask detection and discrimination questions. Issues surrounding reinforcement are clear cut: responses made in the presence of the stimulus are reinforced, while other reporting responses are inappropriate. Researchers differ with respect to how false alarms (reporting responses made in the absence of a stimulus) and misses (failures to respond in the presence of a stimulus) should be regarded when calculating threshold; however, the resultant data from these experiments are relatively unambiguous, and are expressed in terms of the threshold for detection or discrimination. The methods employed in these studies are powerful tools for examining the relationship between structure and function both within and between different sensory systems.

PLAYBACK EXPERIMENTS IN THE FIELD

While determining the limits of an animal's sensory capabilities is relatively straightforward, it is much more difficult to discover how an animal makes use of its sensory capabilities, as noted by Hunt (1986), and it is to this type of experiment that we now turn. The traditional locale for these experiments has been the field. Seyfarth, Cheney, and Marler (1980) designed an exemplary experiment to assess how monkeys respond to acoustically distinct species-specific vocalizations. Free-ranging vervet monkeys (*Cercopithecus aethiops*) give acoustically distinct alarm calls to three different species of predators—leopards, eagles, and pythons. To explore if these calls were functionally distinct to the recipient animals, Seyfarth and colleagues played the alarm calls back to monkeys in the absence of the predators, and watched the monkeys' behavior for 10 s before and 10 s after the presentation of each call. They reported that each alarm call precipitated a distinct set of responses—leopard alarm calls were associated with vervets running into the trees; eagle calls caused the animals to take cover; and python calls were followed by the monkeys looking down. These data suggested that the vervets detected differences in the three varieties of alarm calls (reflecting the monkeys' discriminative abilities), and that they categorized the three types of calls as functionally distinct (reflecting the monkeys' natural organizational strategy).

A second example of asking categorization and judgment questions of animals in their natural environment was carried out by Beecher and Stoddard (1990) in playback experiments using several species of swallows as experimental subjects. Young swallows make "signature calls," presumably to facilitate parent-offspring recognition. Beecher and Stoddard asked if cliff swallows (*Hirundo pyrrhonata*), whose nests are in close proximity to each other, and barn swallows (*Hirundo rustica*), whose nests are more distant, are equally adept at recognizing signature calls emitted by their young. They played the signature calls back to the parents after removing the young from the nest, and measured how often the two species of parents correctly identified calls made by their own offspring. The data suggested that parental recognition of the young by the signature call alone is well-developed in the cliff swallow, but not in the barn swallow.

Based on these field data alone, Beecher and Stoddard might have argued that the auditory discriminative abilities of the cliff swallow were superior to those of the barn swallow. To test this hypothesis, these scientists took members of each species into the laboratory and assessed their ability to discriminate between the signature calls of both cliff and barn swallows. The laboratory data indicated that both cliff and barn swallows could discriminate the calls of the two species, while the cliff swallow calls were more discriminable from each other than the barn swallow calls. Based on the laboratory data alone, one might argue that parent-offspring recognition would occur in both cliff and barn swallows in the field. In sum, neither the laboratory nor the field study alone provided a complete picture of the auditory perceptual capabilities of the two species of swallows.

CLASSIFICATION AND JUDGMENT EXPERIMENTS IN THE LABORATORY

Laboratory explorations of how animals structure and categorize their perceptual world can help bridge this gap. While various experimental approaches have been used to ask classification and judgment questions of animals in the laboratory, all have in common the fact that the *contingencies of reinforcement*, that is, the decision regarding when reinforcement should be delivered, are no longer clear. The potential pitfalls engendered by the uncertainty of when to reinforce were discussed by Herrnstein and van Sommers (1962). In a laboratory study, the experimenter must instruct the animal to respond to the stimulus. But if the instructions are given too narrowly, or the responses are too constrained, the animal's answer becomes trivial. A delicate balance must be struck: the experiment must be designed so that more than one answer is possible, while providing the animal with adequate instruction regarding what constitutes a correct response. Care must be exercised to not "teach" the animal the correct (i.e., experimenter-predicted) answer to the question. The next sections of this paper describe several experimental approaches which have been used to ask classification and judgment questions of animals in the laboratory. While the experiments that are discussed are by no means exhaustive, the procedures which are described represent the variety of experimental approaches that have been used to date.

Scaling

Scaling experiments, first conducted with humans, are carried out when the stimulus in question varies along one dimension. The intent is to permit the animal to tell the experimenter how it scales a unidimensional stimulus—for example, if the magnitude of the stimulus is increased geometrically, is there a concomitant geometric increase in the perception of the stimulus by the animal? In designing scaling experiments, animals are instructed to respond at different rates in the presence of the training stimuli, and are reinforced for any responses (or, alternatively, *no* responses when testing is carried out in extinction) made to the novel test stimuli. Critics of scaling experiments suggest that during training, the experimenter builds into the animal the very scale she is trying to determine. An early scaling experiment was conducted by Herrnstein and van Sommers (1962) to assess how pigeons scale light intensity. Pigeons were reinforced with food in the presence of a given intensity of light only if they pecked at a response key at an experimenter-chosen peck rate. During these training sessions, Herrnstein and van Sommers used five intensities of light, and five reinforced rates of response. When behavior was well-established, they tested four novel intensities of light, that logarithmically bisected the interval between successive pairs of training stimuli. The data indicated that the pigeons responded to the test stimuli at rates equal to the geometric means of the training stimuli response rates, suggesting that the subjective brightness scale in the pigeon is a power function of light intensity. While this study may have represented a conceptual breakthrough in the design of animal psychophysical experiments, it was subject to the criticism it was designed to avoid. That is, by reinforcing particular rates of response during training, the experimenters may have dictated too closely the answers the animals should give during testing.

Reaction Time Experiments

A second experimental approach used to estimate sensory scales in animals has measured reaction times (RT). These studies are based

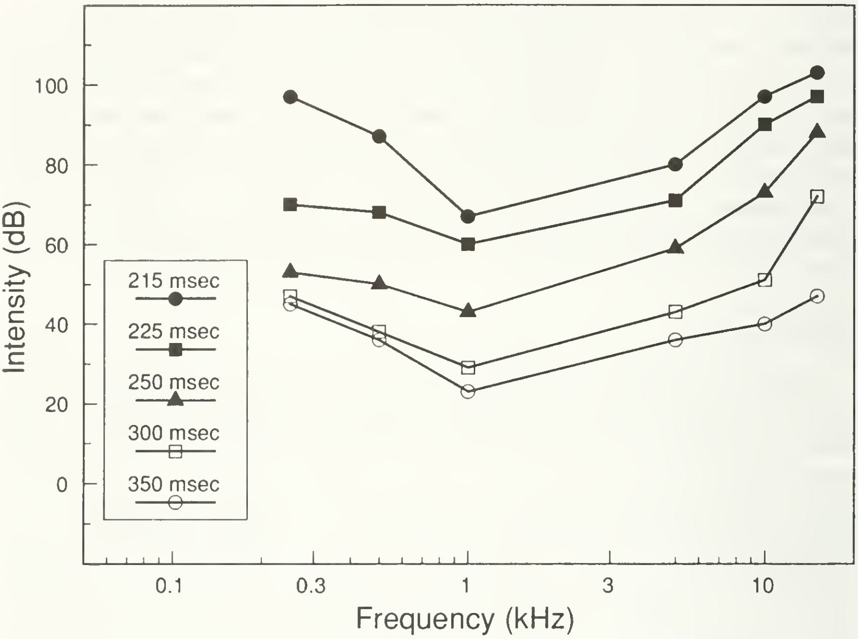

FIGURE 2. Equal loudness contours from one behaviorally-trained crab-eating macaque (*Macaca fascicularis*), where equal loudness was inferred from equal latency contours. Adapted from "Auditory Reaction Time and Derivation of Equal Loudness Contours for the Monkey," by W. C. Stebbins, 1966, *Journal of the Experimental Analysis of Behavior, 9*, pp. 135-142. Copyright 1966 by the Society for the Experimental Analysis of Behavior, Inc. Reprinted by permission.

on the assumption that equal reaction times are measures of equal sensory effect. RT experiments traditionally have been constrained to stimuli which vary in intensity, which severely limited the type of question experimenters could ask of their animals. However, as discussed below, the utility of RT as a tool to explore animal perception has recently increased dramatically by combining it with statistical data analysis techniques, such as multidimensional scaling and cluster analysis (Dooling et al., 1990).

Stebbins (1966) measured equal loudness contours in the monkey using RT as the dependent variable. Figure 2 depicts equal loudness contours for one monkey subject, a crab-eating macaque (*Macaca fascicularis*), where tone intensity is plotted as a function of tone frequency, with each separate function depicting data collected at an equal response latency. Data from humans are similarly configured (Pfingst, Heinz, Kim, & Miller, 1975), reinforcing the hypothesis that equal reaction times in animals measure equal sensory effect.

Generalization Gradient Studies

In generalization gradient experiments, reinforcement is delivered for responses made in the presence of one training stimulus. For example, an animal may be required to make an observing response, and reporting responses are only reinforced when made in the presence of the single training stimulus, such as a pure tone or a photo of a conspecific animal at a particular stage of development. When responding to this one stimulus is well established, generalization testing commences, in which other stimuli along the continuum of interest are presented. Thus, pure tones of different frequencies, or photos of the same animal at different stages of development, are presented. The rate of response to the test stimuli compared to the rate of response to the training stimulus is taken as a measure of the similarity of the stimuli—the greater the difference in response rate, the greater the presumed difference in the stimuli.

The earliest and simplest generalization experiments were conducted in extinction. The purpose of conducting the testing phase of a generalization experiment in extinction is to avoid biasing the animals' responding to the test stimuli. Generalization gradient experiments are not subject to the criticism of scaling experiments—that the experimenter rather than the subject defines the scale to be measured—because only one parameter of the stimulus is reinforced. Further, generalization gradient experiments can assess animal perception along dimensions other than intensity. Mallott and Mallott (1970), for example, trained pigeons to peck at a response disk which had a horizontal line of a fixed length and two vertical end-bars on it. After responding to this training stimulus was well established, they measured response rates to test stimuli. As seen in Figure 3, test stimuli were lines of different length, with either vertical end-bars, like the training stimulus, outward pointing arrowheads on the ends of the lines, or inward pointing arrowheads on the ends of the lines. Using these stimuli, Mallott and Mallott demonstrated that pigeons perceive the Mueller-Lyer illusion in a similar fashion to humans. That is, they found that the pigeons responded at the training stimulus response rate to test stimuli with outward pointing arrowheads only when the length of the test stimulus line was greater than the length of the training stimulus line.

The fact that animals and humans experience illusions similarly suggests that animal perception may share some of the complexities once thought confined to the human perceptual experience. A disadvantage of the generalization technique is that, when the gradients are measured in extinction, their shape changes over time, so that the data must be collected in a single session. Further, the resultant data are often excessively variable.

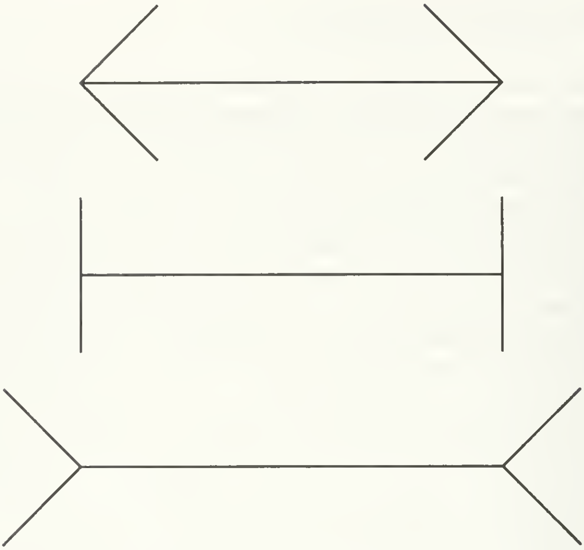

FIGURE 3. Models of the stimuli used by Mallott and Mallott (1970). The middle figure, with a horizontal line and two vertical endbars, represents the training stimulus. All three figures represent test stimuli.

The way in which animals are trained during a generalization study also can influence the shape of the generalization gradient. Jenkins and Harrison (1960, 1962) trained pigeons to peck in the presence of a 1000 Hz tone, and then tested them for their generalization to tones of other frequencies and to silence. They found no generalization gradient; that is, pecking occurred whether the sound was present or not. Does this mean that pigeons cannot discriminate between tones of different frequencies? A second group of pigeons was trained differently; they were reinforced for pecking in the presence of a 1000 Hz tone, but not reinforced for pecking in the presence of silence. When the generalization gradients were assessed in these animals, they were symmetrical against the log of frequency. Finally, a third group of pigeons was reinforced in the presence of a 1000 Hz tone but not in the presence of a 950 Hz tone. The generalization gradients from these animals fell off much more rapidly than either of the first groups. Thus, the structure of the experiment can influence the resultant date, an important point for experimental design considerations which we discuss in more detail below.

Generalization Probe Experiments

An important objection to the generalization gradient procedure, that behavior degenerates when tested in extinction, has been eliminated in recent studies that continue using and reinforcing responses made to training stimuli during testing, while inserting the test stimuli occasionally as unreinforced "probes." As with the other experimental approaches discussed in this section, the intent of these studies is to examine how animals categorize stimuli. During training for a generalization probe experiment, animals are reinforced for responding to stimulus A with response A′ and to stimulus B with response B′. Correct responses are commonly reinforced at a level less than 100% to prepare the subject for the lower level of reinforcement during the testing sessions. This lower level of reinforcement occurs during testing because while the test stimuli are infrequently inserted into the session, responses to these stimuli are neither reinforced nor punished. If reinforcement was maintained at 100% during training, the test stimuli could be clearly identified by the subject during testing, because of the absence of reinforcement following a response to these stimuli. Test stimuli must be inserted infrequently to maintain baseline responding to the training stimuli. The measure of similarity in a probe experiment is how frequently the subject responds to the novel test stimuli as A or as B. Generalization probe experiments result in stable between-subject data, while permitting the experimenter to explore animal perception along many dimensions.

The most severe criticism of this technique is that the experimenter teaches the animal to attend to "unnatural," experimenter-defined categories. Hence, the finding that animals place some novel test stimuli in category A and others in category B may not mean that the experimenter is assessing natural categories formed by the subject, but rather that it reflects that animal's ability to learn to attend to those features of the stimuli which distinguish the categories as defined by the experimenter. Two steps can be taken to mitigate this criticism. First, as discussed below, if species-differences can be demonstrated for category formation, those differences might reflect the fact that the categories are more "natural" for one of the species. Second, if the same categories are formed in experiments that use different methodologies, the confidence in the finding is increased.

The probe technique has been used to explore animal perception in a wide variety of modalities. Herrnstein (1979) used the approach in visual perceptual experiments with pigeons. He trained 4 pigeons to categorize pictures into two groups: those which contained trees, and those which did not. Forty of his training pictures contained trees, and 40 did not. A peck at the response disk in the presence of a tree picture was reinforced with food, while a peck in the absence of a tree picture was not reinforced. After the discrimination was well-established, Herrnstein inserted novel pictures, some containing trees and some not, and found that the discrimination generalized to the new instances with little or no decrement in performance. This experiment preceded numerous explorations of how the pigeon categorizes its visual world. Researchers demonstrated that pigeons could discriminate fish pictures from nonfish pictures (Herrnstein & DeVilliers, 1980), white oak leaves from other leaves (Cerella, 1979), the letter A from the number 2 (Herrnstein, 1984), and birds from mammals (Cook, Wright, & Kendrick, 1990). Using a similar experimental design, chickens displayed individual visual recognition of a particular chicken (Ryan, 1982). These are categorization and judgment experiments; while the subjects learn to categorize the stimuli, within-category discrimination is quite likely possible.

Generalization probe experiments have been conducted in the auditory modality to explore animal perception of both human and animal communication signals. Kuhl and Miller (1978) examined how chinchillas categorize human speech sounds. Data from humans gathered prior to the Kuhl and Miller study indicated that when presented with a graded continuum of speech sounds, humans often do not attend to the gradation, but rather they classify these speech sounds categorically, a phenomenon referred to as categorical perception. Kuhl and Miller's finding, that chinchillas categorize human speech-like stimuli similar to the way humans categorize them, suggested new ways for speech scientists to conceptualize how speech is processed by the mammalian nervous system. Prior to the Kuhl and Miller study, it was assumed that speech sounds were processed at a "phonetic" level which was restricted to the human nervous system. Kuhl and Miller's data suggested that some human speech sounds may have been selected in the course of evolution because they fall into natural categories which are present in other mammalian nervous systems.

We conducted a similar experiment with Japanese macaques (*Macaca fuscata*), using as training stimuli two calls normally produced by Japanese macaques. Both of these calls were called "coo" calls by Green (1975) who recorded them from monkeys in the field. The two coo calls differed primarily with respect to the temporal position within the call of a transition (peak) from a rising to a falling frequency. The calls were selected because they represented two points along a continuum of relative peak position. The calls also were selected because field research indicated that they were functionally distinct. That is, one of these call types, the "smooth-early-high," is used primarily by young animals out of contact with other troop members, while the other call type, the "smooth-late-high," is used mainly by estrus females as a sexual solicitation. After conducting discrimination training using natural calls as the training stimuli, intermediate stimuli were computer-generated and used as probes to determine how the Japanese macaques categorized these stimuli (May, Moody, & Stebbins, 1988, 1989). Data from this probe experiment revealed that the Japanese macaques categorically perceived these species-specific stimuli much like humans and chinchillas categorically perceive human speech sounds.

These data suggest that categorical perception may reflect a mode of processing auditory information common to human and nonhuman listeners. Data from control monkey species that participated in the Japanese macaque vocalization study also indicated that there are species-specific mechanisms for categorizing conspecific vocalizations. When speed of acquisition of the discrimination between smooth-early-high and smooth-late-high coo calls was measured, Japanese macaques excelled compared to control species. As noted earlier, this species difference reinforces the hypothesis that the two categories of coo stimuli constitute particularly salient, “natural” categories to the Japanese macaque.

In any scientific study, experimental design might in part dictate the resultant data, as discussed briefly in the generalization gradient section of this paper. This design consideration was demonstrated in the generalization probe experiments with the Japanese macaques (May et al., 1988, 1989). In the experiment, in which responses to the intermediate test stimuli were neither reinforced nor punished, the data suggested that the smooth-early-high and the smooth-late-high stimuli were categorically perceived as a member of one group or the other, as seen in Figure 4. But in a second experiment, May and colleagues asked if animals could discriminate between these stimuli. In one variant of this procedure, one of the stimuli (the standard) was repeatedly presented; when this stimulus changed to one of the other stimuli along the continuum (the comparison stimulus) and the monkey released the response cylinder, he was reinforced. Now, the animals demonstrated that they could discriminate between all of the stimuli located along the continuum, with only slightly better discrimination behavior at the category boundary, as seen in Figure 4.

These categorical perception data may seem contradictory—is categorical perception an epiphenomenon, or is it a universal mode of perceiving communication signals even from other species? But within this apparent contradiction lies an important distinction in perception—that animals, and humans, have multiple processing modes that they use to classify stimuli. Many people say “hello” when greeted, and human listeners regard all the variations of these acoustically distinct stimuli as having the same meaning. However, these same stimuli are easily discriminated. Similarly, the Japanese macaque data suggest that the psychophysical method used to study acoustic communication in the monkey may strongly influence the processing mode applied to the stimuli. The discrimination procedure

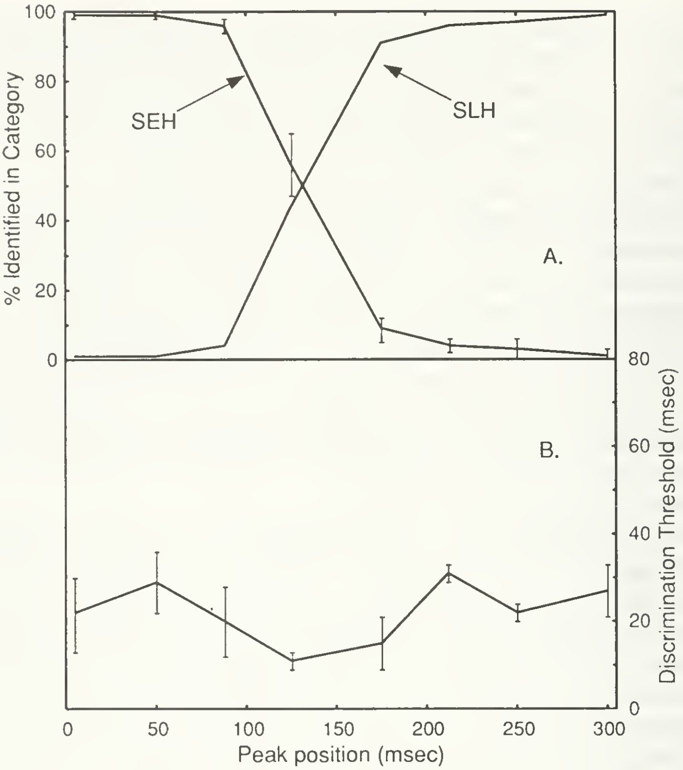

FIGURE 4. A. Identification of synthetic contact "coo" calls by Japanese macaques (*Macaca fuscata*). SEH designates smooth-early-high calls, in which the temporal position of the peak frequency of the call occurred early, while SLH designates smooth-late-high calls, in which the temporal position of the peak frequency of the call occurred late. Data are presented as mean and standard error of the mean for four Japanese macaques. A category boundary, as indicated by the sharp transition in the behavioral response, was observed near the midpoint of the peak position continuum. B. Discrimination thresholds, in ms, for the synthetic vocal stimuli. Data are presented as mean and standard error of the mean for the four Japanese macaques. Data are replotted from "Categorical Perception of Conspecific Communication Sounds by Japanese Macaques, *Macaca fuscata*," by B. May, D.B. Moody, & W.C. Stebbins, 1989, *Journal of the Acoustical Society of America, 85*, pp. 837-847. Copyright 1989 by the Acoustical Society of America. Reprinted by permission.

directed the monkey's attention to small changes in the acoustic dimension of the stimuli, while the probe procedure encouraged phonetic processing while discouraging attention to minor acoustic variations in the stimuli which lacked communicative relevance. The hypothesis that multiple modes are available to animals to process complex stimuli is discussed below.

Multidimensional Scaling

Another technique available to animal psychophysicists which recently has gained increasing acceptance asks animals to perform a simple discrimination task. The data, however, are analyzed with statistical techniques, such as cluster analysis and multidimensional scaling. While these experiments are time-consuming, they permit the experimenter to draw conclusions about how the animals organize stimuli. This procedure has been used to determine how monkeys categorize pictorial stimuli (Hunt, 1986), how pigeons segment visual stimuli which differ along multiple dimensions (Blough & Blough, 1990), and how budgerigars process both simple and complex, species-specific vocalizations (Dooling et al., 1990). These experiments have enriched our understanding of the perceptual proclivities of animals by asking categorization and judgment questions—questions that are difficult to frame using some of the methodologies described above because the format of the question defines the answer. In experiments using these procedures, animals perform an observing response in the presence of a single stimulus, and a reporting response any time the stimulus changes. Either the speed of reporting "stimulus change" (the reaction time), or the frequency of this report (the percentage of correct detections for each stimuli pair), then can be entered into a similarity matrix. Shorter reaction times or a higher percent correct to pairs of stimuli in these experiments indicate that those stimuli are less similar than other pairs of stimuli which take longer to discriminate or are less frequently identified as different. The statistical procedures can be used to evaluate *how* similar the stimuli are by plotting the data in a three-dimensional format presumed to reflect how the animals categorize the stimuli. An advantage of this technique is that the decision regarding when to reinforce a response, the *contingencies of reinforcement* problem addressed earlier, is straightforward—any response made to a pair of stimuli that differ is reinforced. While the methodology encourages the animals to discriminate between stimuli, thereby clarifying the contingencies of reinforcement, the statistical data analysis permits the experimenter to assess categorization. Multidimensional scaling procedures are described in more detail by Dooling et al. (1990); they represent a powerful new technique for conducting future categorization and judgment experiments in the laboratory.

Unconditioned Responses

A final technique available to the experimenter investigating animal perception makes use of unconditioned, "natural" responses. Caution is encouraged in designing and interpreting these experiments, because of the possibility of experimenter bias in determining when a response occurred, and the fact that responses may habituate with time. With this in mind, several carefully controlled studies using unconditioned responses as the dependent variable have enjoyed considerable success in investigating animal perception. Humphrey (1974) and Perrett and Mistlin (1990) explored how monkeys perceive visually presented information. Humphrey examined the amount of time monkeys looked at pictures, and noted that after seeing one picture of a cow, the monkey spent much less time looking at a second picture of a cow, whereas after looking at one picture of a conspecific monkey, other pictures of conspecific monkeys were proportionately more interesting. Perrett and Mistlin reported that stump-tailed macaques (*Macaca arctoides*) gave an appeasement response (teeth chattering and lip smacking) more frequently to pictures of monkey faces making eye contact than to pictures of monkey faces with the eyes averted. These scientists argued that if such untrained responses are provoked consistently more to one type of stimulus than to a second, the ability of the animal to perceive the difference between the stimuli may be inferred.

CONCLUSION

Recent advances in the design of animal psychophysical experiments permit scientists to explore the perceptual world of animals in greater detail—not only to determine the limits of the animals' sensory systems, but also to examine how animals use incoming perceptual information. While these studies have augmented information already available about animal sensation, they also have fundamentally changed the way we regard animal perception. Herrnstein (1984) suggests that the ability to categorize stimuli confers such an evolutionary advantage that it may be universal among all living organisms. Nelson and Marler (1990) discuss in detail the advantages and disadvantages of categorization, when an animal "lumps" stimuli together, versus when it "splits" stimuli into distinct categories. Too much lumping, while rapidly reducing complex information into a small number of categories, may neglect variation critical for an animal's survival. Alternatively, too much splitting renders every experience unique. The distinction we have drawn in this paper, between what animals are capable of, and what they do, is similar to Nelson and Marler's (1990) differentiation of the "just-noticeable-difference" (JND) and the "just-meaningful-difference" (JMD). While the JND has an established definition in both human and animal psychophysics, the JMD is a new term, reflecting the minimal difference between natural stimuli which elicits a measurable difference in the nature or the intensity of a natural response to a particular signal class. Beecher and Stoddard (1990) address the same distinction with yet a different terminology: "discriminable," but "biologically-equivalent" stimuli.

Earlier in this paper, we suggested that organisms have available to them multiple modes of processing complex stimuli. Detection and discrimination experiments may tap into one of those modes, while categorization and judgment experiments may address a different mode. Hulse, Page and Braaten (1990) have suggested that these modes may be arranged hierarchically, such that while one mode is possible, it may function normally as a secondary strategy, with an alternative strategy being the primary processing mode. Earlier, Marler (1982) suggested that there is a species-specific hierarchy of attentional preferences for perceptual cues. The experiments described in this paper are designed to examine these different perceptual strategies; the design of the experiment can dictate which processing mode is selected by the animal. One feature of these experiments is that they reduce the extent to which we view animal perception and cognition as distinct from human perception and cognition. The histories of philosophy and psychology are filled with attempts at distinguishing humans from animals along a variety of dimensions. Once it was assumed that while humans categorize, animals discriminate. Recent laboratory experiments suggest that the difference is in degree rather than in kind.

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of the observing response, or false alarms, are discouraged by following these releases with a time-out from the experiment and from the opportunity to receive reinforcement. A feature of the design of these experiments is that the contingencies of reinforcement are clear—all responses made in the presence of the stimulus, or the stimulus difference, are reinforced. There is no ambiguity here—the stimulus is either present or it is not, and those responses made in its presence are reinforced.

Other studies that have helped define the perceptual abilities of animals have used classically-conditioned responses, pairing a sensory stimulus with shock, and presenting these paired stimuli to a water-deprived animal that is drinking. After a number of paired presentations, the animal will stop drinking during the presentation of the sensory stimulus alone, permitting the experimenter to determine thresholds for detection or discrimination. Heffner and Heffner (1985) have used this conditioned suppression procedure to measure absolute auditory thresholds in a wide variety of animal species. An advantage of these operant and classical conditioning procedures is that unequivocal answers are obtained from the animals; a disadvantage is that only a limited subset of questions can be asked, as noted below.

Using the operant conditioning technique, our laboratory has tested the hearing of several species of Old World monkeys, chinchillas (*Chinchilla langier*) and guinea pigs (*Cavia porcellus*). We have determined audiograms representing the minimum amount of energy detectable as a function of frequency for these three species.

We also have used these techniques to explore the minimum detectable difference in frequency and intensity, and the frequency selectivity of monkeys, chinchillas and guinea pigs at a variety of frequencies and sound pressure levels. All of these experiments have refined our understanding of the limits of the auditory system of the species in question. We have determined the effects of the destruction of various parts of the peripheral auditory system on these measures of auditory perception. In Figure 1, we see psychophysical tuning curves, used as a measure of frequency selectivity, from a patas monkey (*Erythrocebus patas*) before and after the selective loss of cochlear outer hair cells. Psychophysical tuning curves are similar in shape to electrophysiological tuning curves, and are thought to be a psychophysical correlate of the electrophysiological measure. They assess the detectability of a probe tone at 10 dB above threshold and a specific frequency, in the presence of pure tone maskers of different frequencies. These functions are plotted as level of the masker needed to mask the probe tone as a function of masker frequency. As seen in Figure 1, in the absence of the outer hair cells, the psychophysical tuning curves are considerably less sharp than in the presence of these cells, suggesting that the outer hair cell system contributes to