**THE MEASUREMENT OF SENSORY PROCESSES IN
ANIMALS. A REVIEW OF ANIMAL PSYCHOPHYSICS:
THE DESIGN AND CONDUCT OF SENSORY
EXPERIMENTS, EDITED BY WILLIAM C. STEBBINS¹**

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Efforts to measure sensory and perceptual phenomena in non-human species date back at least to the first decade of this century. Rapid improvements in technique, both for the control of sensory stimuli and for the control of behavior by these stimuli, has been paralleled by increases in the amount and especially the quality of this research. W. C. Stebbins' *Animal Psychophysics* impresses the reader with both the sophistication and the variety of experiments that this area is now producing.

Good reasons abound for the study of sensory processes in animals. By relating behavioral data to known anatomy and physiology of a sensory system, by measuring the effects on behavior of specified physiological operations, and by comparing sensory data across species we greatly improve our knowledge of sensory mechanisms. Furthermore, the effort to obtain good psychophysical data forces the experimenter to seek the best possible stimulus control; thus, our understanding of that area is also enhanced.

Traditionally, psychophysics is defined as the study of the relation between stimulus and response; as Stebbins puts it in his introductory chapter, it seeks "... a functional relation between environmental stimuli and behavior." (p. 2). In order to determine such a relation, one must provide a measurable stimulus continuum and a measurable response continuum; yet it is not easy to meet either of these

conditions. The control and measurement of the stimulus is often fraught with problems. Lights that change in wavelength must be constant in luminance; tones that vary in loudness should not change with the subject's head position; and so forth. Equipment is often expensive; the experimenter must fully understand the pitfalls that characterize the stimuli for the modality he has chosen to study.

The measurement of the response can be equally frustrating. The response ideally should be a function of the stimulus only; it should not be affected by such problems as attention, fixation, or reinforcement contingencies irrelevant to the stimulus. Thus, research in animal psychophysics requires skills—or access to skills—both in the control of animal behavior and in sensory psychophysics. Competence in sensory physiology is also useful to the animal psychophysicist if he is interested in anatomical or physiological correlates of his behavioral data. Some of the best chapters in Stebbins' book combine imaginative approaches to the behavioral problems with competent control of the stimulus dimension and informative demonstrations of physiological effects.

The present volume emphasizes methodology. Moreover, the contents are restricted to applications of operant procedures. Many of the authors concern themselves with anatomical or physiological correlates of the behavioral data, but tend to present these results to demonstrate the usefulness of the behavioral techniques. The research is varied and somewhat uneven in quality. In discussing the various contributions, we might organize by sensory modality, by psychophysical method, or by the nature of the psychophysical problem. It seems reasonable to group the chapters as the editor did and to take up the individual contributions in his order.

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The Book

Following Stebbins' introduction, four chapters describe research in auditory psychophysics. The auditory modality has its special problems; the stimulus is difficult to calibrate; pure tones may vary in loudness according to the subject's position; and, since stimuli must be presented successively, the simultaneous forced-choice procedure, so useful in vision, is out of the question. The authors of Chapters 2, 3, and 4, J. I. Dalland, W. C. Stebbins, and G. Gourevitch, respectively, illustrate solutions to some of these problems. They used similar procedures, designed and described with careful attention to problems of training, of maintaining the discrimination, and of calibration. Basically, this procedure required two responses: one that produced the stimulus and one reinforced in the presence of the stimulus. Measures to improve stimulus control included timeouts for incorrect responding and schedules that discouraged responding to temporal rather than auditory cues.

Dalland's research, "The measurement of ultrasonic hearing", had special problems, because his subject was the bat, a species whose operant level evidently is minimal and for which there was little help available from commercially built levers, keys, and chairs. This chapter is almost all methodological, recounting, in perhaps too much detail the rationale and background of the procedures. Evidence for their success takes the form of graphs describing audibility functions. Differences between a behavioral function and one based on cochlear microphonics lead the author to suggest "... hearing sensitivity is not primarily determined at the hair cell level" (p. 25).

Chapters by Stebbins, "Studies of hearing and hearing loss in the monkey", and Gourevitch, "Detectability of tones in quiet and in noise by rats and monkeys", abound with methodological detail and with data. For example, Stebbins discusses the important problem of behavioral stability and the criteria by which it might be assessed in his procedure. Both authors have tried various methods of stimulus presentation, and a graph in the Stebbins chapter shows good agreement among auditory threshold functions yielded by three different psychophysical methods. The effectiveness of Stebbins' method is further attested by impressive data showing effects on audi-

bility of noise and drugs, while histological findings suggest a correspondence between anatomical and behavioral effects. Gourevitch's work concerned problems in auditory masking, and his chapter describes not only absolute thresholds across the frequency spectrum, but also the effects at various frequencies of various bandwidths of masking noise. A section on instrumentation deals specifically with problems of controlled tone presentation and with calibration procedures.

Two chapters discuss the use of conditioned suppression in animal psychophysics. This method appears to be an efficient means of turning out stable psychophysical data and has the additional advantage of yielding a continuous record of "baseline" behavior. The baseline is the rate of an operant response sustained by a reinforcement schedule, variable ratio in the first of these chapters, variable interval in the second. Superimposed on this schedule is the aperiodic presentation of a stimulus that precedes an unavoidable shock by a given time interval. The "response" to that stimulus is a decrease in baseline rate and is known, of course, as conditioned suppression. A stable baseline rate just before stimulus presentation assures the experimenter that apparent stimulus effects are not simply the result of a change in the subject's activity level or his physical position.

Chapter 5, "Psychophysical testing of neurologic mutant mice", by B. A. Ray describes a series of conditioned suppression experiments in which white noise was the principal stimulus and a "tracking" method was used. The neurologically-impaired subjects offered special problems, and Ray describes procedures for their maintenance and testing. The findings, presented in an almost anecdotal fashion, are illustrated by many small, sample graphs indicating the effects of various procedures on various strains of mice. Some of the graphs are confusing, and the reader has to work hard at times to put these findings together in a meaningful fashion. If the individual data are "representative", however, this chapter provides convincing evidence of specifically auditory deficits in certain mutant mouse strains. Histological evidence of cochlear damage indicates the anatomical basis for the hearing loss.

The second chapter on conditioned suppression, J. Smith's "Conditioned suppression as

an animal psychophysical technique", describes experiments involving an interesting variety of subjects and modalities and including studies in the less-usual fields of olfaction and X-ray detection. High inter-subject reliability and the orderliness of the psychophysical functions impress the reader with the effectiveness of the technique. (One graph disturbs this reviewer, however. It shows, for a single pigeon, a "photopic" spectral sensitivity function quite different from much of the published data.) There is more emphasis on data and less on instrumentation and methodological detail here than in many of the contributions. However, Smith does discuss such parameters as conditioned stimulus duration, shock levels, and psychophysical method.

"Tracking" or "titration" procedures were used in much of the research reported in this book. Chapter 7, P. R. Rosenberger's "Response-adjusting stimulus intensity", deals with methodological aspects of these procedures and discusses data treatment. As the author points out, these techniques are particularly well adapted to following a threshold through time because the subject maintains the stimulus in the vicinity of the "threshold" value. A related advantage cited by Rosenberger is efficiency, since there are fewer "wasted" trials in which the stimulus is well above or below threshold. Among the disadvantages of titration schedules mentioned are the relative instability of the subject's performance and the danger that temporal cues rather than test stimulus cues may gain control of behavior. Other discussions (*e.g.*, Frazier and Elliott, 1963) suggest that tracking procedures yield relatively high thresholds. In a critical report, Saslow (1967) suggested how reinforcement contingencies might lead to this effect.

The use of titration schedules in assessing a less well-known sensory modality is the subject of Chapter 8, "The psychophysics of pain and analgesia in animals", by B. Weiss and V. G. Laties. The authors suggest that their technique, in which operant responses decrease the level of continuously delivered shock, provides a more sensitive measure of the pain stimulus than the more standard avoidance procedure. Their data include some parametric effects of the rate at which the shock level rises and the reinforcement schedule of shock reduction. Another set of re-

sults demonstrates drug effects on shock tolerance.

The next set of studies, "Thermal reinforcement and temperature regulation", by H. J. Carlisle mainly concerns the effects of amount of thermal reinforcement in rats and monkeys. The interaction of these effects with cutaneous and hypothalamic measures of temperature is discussed, and there are also sections on instrumentation. (The thermal stimulus is difficult to control; an apparatus recently described by Matthews (1969) might overcome some of the problems described here.)

Both the Carlisle contribution and that of Weiss and Laties differ from the usual psychophysical paradigm. Ordinarily, in a operant psychophysical study, the principal stimulus is a discriminative stimulus, not a drive stimulus as in the Weiss and Laties work or a reinforcer as in the Carlisle experiments. Furthermore, in most psychophysical studies, the discrimination is pushed to a limit through differential reinforcement. In Carlisle's experiments, there was no differential reinforcement, since the reinforcer was, in fact, the stimulus. In the Weiss and Laties work, reinforcement was contingent on the presence of the stimulus (electric shock), since reduction of that stimulus constituted the reinforcing event. However, drive and signal strength were confounded, because the shock served both functions. No doubt both these procedures related to the sensory capacities of the subject. Nonetheless, their relation to the usual discriminability measures is unclear.

Three chapters concern discriminations in the visual modality. All of these experiments used a simultaneous forced-choice procedure, feasible with the visual stimulus and desirable because it eliminates a number of sources of bias. A chapter by M. A. Berkley, "Visual discriminations in the cat", and one by M. Glickstein, S. Barrow, and E. Luschei, "Vision in monkeys with lesion of the striate cortex", describe similar procedures. Berkley discusses in some detail apparatus and procedures for training cats to make form and motion discriminations. This contribution is important because, while cats have provided a great deal of anatomical and physiological data, efficient operant procedures for assessing their behavioral performance have been lacking. Glickstein, *et al.*, describe studies of luminance,

form, and color discriminations in monkeys. Common to both this and the Berkley work is a "fading" technique for measuring effects of lesions. Here, a brightness difference was introduced into a form discrimination problem so that the negative stimulus was initially relatively dim. Correct choices increased the luminance of the negative stimulus, and final performance was assessed in terms of the extent to which the positive and negative stimuli were matched in brightness. Glickstein, *et al.*, conclude that this method may reveal the presence of discriminative capacities that would otherwise seem to have been lost following cortical lesions. The studies described in these two chapters mainly involved discriminations between two stimuli, instead of the more extended functional relations usually sought by the psychophysicist. They do, however, introduce useful methodologies.

D. Yager and S. Thorpe's chapter, "Investigations of goldfish color vision" describes a straightforward procedure that has effectively yielded spectral sensitivity and spectral saturation functions. The subject's task was to make an observing response to illuminate two choice keys and then to press the correct key for food reinforcement. The authors describe the effects of chromatic adaptation on spectral sensitivity, and theoretical treatment of the data in terms of the formulae of Hurvich and Jameson lend meaningfulness to their findings. Thorpe (in press) has reported more data obtained with this technique, and her comparisons of behavioral and electroretinographic data have contributed further information about visual processing in this species. As is true for the cat, effective behavioral techniques for the goldfish are especially useful because of our knowledge of the anatomy and physiology of its visual system.

Several chapters describe the use of reaction time in animal psychophysics. The first of these, D. B. Moody's "Reaction time as an index of sensory function", perhaps exemplifies the ideal contribution to a book of this type. Methodology, including training techniques, procedures for data treatment, and instrumentation, is explained in careful but relevant detail. Moody discusses the rationale for a reaction-time technique and justifies its value with graphs that compare rat and monkey reaction-time data with related human

data. Effects of exposure to loud tones illustrate the sensitivity of this measure.

The following chapter deals with applications of the reaction time technique to problems in neurophysiology. This contribution, by J. M. Miller, in collaboration with J. Kimm, B. Clopton, and E. Fetz, is titled "Sensory neurophysiology and reaction time performance in nonhuman primates". Of interest to the animal psychophysicist here are techniques for obtaining simultaneous behavioral and electrophysiological data on the awake monkey and the comparisons between these measures. The authors have considered, for example, the reaction times for stimuli presented to the eye or ear compared with reaction times for direct stimulation of the brain. They have also compared reaction-time data with the amplitude of an appropriate electrophysiological response. A recent paper by Glickstein (1972) summarizes this and other behavioral and electrophysiological reaction-time work.

A third chapter in this area is R. W. Reynolds' "The use of reaction time in monkeys for the study of information processing". The author discusses here some preliminary efforts to compare "simple" and "disjunctive" reaction times. The method here is like Moody's; the data are sparse, however, and stimulus control rather rough. The value of Reynolds' contribution is perhaps best stated in its title. With the renewal of interest in human reaction-time studies (*e.g.*, Sternberg, 1969), the development of comparable techniques for animals could lead to useful experiments on information processing in "simpler" organisms.

Chapters 16 and 17 deal with the difficult problem of measuring perceptual phenomena in animals. As Stebbins remarks in the introduction, a major problem here is how to reinforce, since there is no "correct" response in a perceptual experiment. T. R. Scott and W. L. Milligan's chapter, "The psychophysical study of visual motion aftereffect in monkeys", describes, lightheartedly at times, an apparently heroic effort to measure the spiral after-effect. Having trained subjects to respond differentially to an expanding or contracting circle, the authors then measured the effect of pre-exposure to a rotating spiral. The reinforcement problem occurred, of course, because the effects of this pre-exposure period

were unknown, and it was necessary to collect test data in extinction. The method described here, as well as the procedure for plotting data, is similar to that described by Heinemann, *et al.*, (1969), who relate this technique to some of the broader problems of psychophysics. Another problem worked out by Scott and Milligan was that of training monkeys to fixate. Methodological description may at times include too much detail in this chapter, but the data are impressive. They represent a successful effort to quantify the after-effect and a convincing demonstration of its disappearance following cortical lesions.

A broader approach to problems in perception is introduced by R. W. Malott and M. K. Malott in "Perception and stimulus generalization". Subdivided into three sections, the chapter begins with some studies of the Müller-Lyer illusion in pigeons. The authors hoped to measure apparent changes in line length in terms of peak shift along a generalization gradient. Although this idea seems reasonable, the data are confusing and not especially convincing. A second section discusses problems of training pigeons in color matching discriminations, where the intent evidently was to test the transposition of matching behavior to new colors. This section also suggests means of combining generalization gradients to predict matching behavior to novel colors, but the authors offer no empirical test of their proposal. A third section suggests a scaling technique in which one stimulus becomes a "measuring stick" for a second. The experiments here used the generalization method to relate a color "continuum" to a line tilt continuum. Again, the data are variable, and the results unclear. Further research along the lines of the last two sections would benefit from more attention both to the physical and the psychological control of the stimulus. For example, Wratten filters, uncorrected for luminance, provided the stimulus colors; these stimuli are unsuitable for most psychophysical research because it is difficult to specify the controlling variables. Furthermore, a psychological scale of color would be necessary to combine gradients as suggested in the second section; yet the specification of such a dimension in terms of line tilt would be inadequate without the psychological scaling of line tilt itself. (D. S. Blough's (1972) discussion of wavelength scaling is pertinent here.) Al-

though this chapter has some interesting ideas, there is a disappointing lack of empirical support.

The final chapter changes focus and is the only contribution that deals with applications of signal-detection theory. The experiments described in this chapter, "On differential stimulation and differential reinforcement" by J. A. Nevin, concern luminance discrimination in rats, but the author's principal interest is in the effects of signal strength and reinforcement contingencies on detectability. In a series of experiments with a procedure similar to Stebbins', Nevin demonstrates, for example, that reinforcement contingencies may interact with signal strength; the differences in detectability between a strong and a weak signal depended on the scheduling of reinforcement in the presence of the two signals. Another experiment suggested that reinforcing false alarms had the same effect on detectability as decreasing signal strength. Nevin's treatment of detectability was in terms of the d' measure, which assumes a particular relation between correct detections and false alarms. The second experiment also included an examination of this relationship and the construction of isosensitivity functions. Although the functions generally fit the detection model, they cover too small a range for detailed conclusions.

Some Problems

A number of problem areas are common to much of the research described in this book. The following paragraphs can do little more than mention some of these and touch on related work.

Nevin's contribution introduced the area of signal-detection theory, which promised applications to animal psychophysics. Some of his work supported this model by suggesting an invariant d' with certain types of bias. However, he also provided unsettling evidence for changes in d' resulting from certain reinforcement contingencies. Among related studies is recent work of Terman and Terman (1972) on auditory intensity discrimination in rats. These authors found that d' remained approximately constant across a range of bias values, but that the more traditional per cent correct measure was affected by bias. This result accords with the predictions of detection theory and is not at odds with the Nevin data,

since the Termans' manipulation of bias (signal probability) was quite different from Nevin's manipulation of reinforcement contingencies. The Termans' work supports the validity of the d' measure, and other authors (e.g., Boneau and Cole, 1967; Heinemann *et al.*, 1969) have also concluded that this is an appropriate approach. The message to the animal psychophysicist, then, is that he must be aware of bias effects. If he wishes to use the d' measure, he may consult a table (Elliott, 1964), or he may use a forced-choice procedure, such as that of Yager and Thorpe. Many of the threshold studies in the present volume did not use the d' measure, however. In such cases, the control of bias is very important and the "thresholds" must be interpreted as relative values.

Reinforcement contingencies constitute another problem common to experiments in animal psychophysics. One role of the reinforcer is to define the "correct" response, a specification that is not obvious for stimuli whose effects are unknown. When testing at weak signal values, for example, the experimenter may simply define as "correct", and thus reinforce, the "signal present" response as long as the signal is physically present. If the signal is below threshold, however, a response in its presence would be a false alarm where the subject was concerned, and reinforcement of this response would appear to change the definition of the correct response. Part of Nevin's research concerned the reinforcement of near-threshold signals, and his data indicate that increasing reinforcement probability increased false alarm rate. (Since it also increased the rate of correct detections, d' remained constant.) From other contributors come methods of avoiding difficulties introduced by reinforcing weak signals. The use of "catch" trials, for example, was common in the auditory work. Here, responding in the absence of the signal was discouraged by introducing time-outs or electric shocks when responses occurred during scheduled occasions without the signal. Some contributors recommended the descending order of stimulus presentation to minimize the number of weak signals used. The Blough tracking method, described by Rosenberger, introduced trials on which the signal really did disappear, and reinforcement was available for correct responses only on those occasions. An analogous problem arises

in the conditioned suppression procedure, where subthreshold stimuli may give rise to "unsignalled" shocks. Ray refers briefly to a finding that a "minimum" number of these events did not affect the data.

The problems of reinforcement are analogous, but may be more difficult in scaling and in some perceptual tasks. Here, the "correct" response is undefinable for a broad class of stimuli; thus, data are often collected in extinction. As the Malotts point out, the generalization task seems appropriate for perceptual studies; its drawback is the variability of the data, which may be based on a relatively small number of trials. In their experiments, for example, the position of the peak of the generalization gradient was a major dependent variable; yet the data were not reliable enough to permit a confident analysis of "peak shift" effects. The use of a maintained discrimination (e.g., P. M. Blough, 1972) technique might help to solve this problem. In studying the Müller-Lyer illusion, for example, the Malotts might have continued to reinforce responses to the training stimulus through the testing period. By mixing unreinforced presentations of test stimuli with occasional reinforced presentations of the training stimulus, they might have maintained responding over a longer period of time, and the resulting function might have been smoother. The impressive data obtained by Scott and Milligan resulted from a variation of this procedure. Here, too, many of the test data were collected in extinction, but unreinforced test trials (following fixation of a rotating spiral) were mixed with reinforced training trials (following fixation of a stationary spiral). Even in these procedures, of course, the subject comes to discriminate between the training and test conditions, and only limited data can be collected.

The problems raised here are basically problems in stimulus control. The animal psychophysicist's goal is to achieve a response measure that is a function solely of the stimulus variable. The detection approach concerns the effects on behavior of non-stimulus cues, which may change the subject's "criterion". Reinforcement contingencies may act as one such source of bias. Other factors affecting stimulus control, such as attention, pre-existing stimulus preferences, and temporal cues have been discussed by Blough (1966) and

Blough and Yager (1972). Techniques to achieve good fixation, both in the visual and the auditory modalities, have been discussed by authors in the present volume. The choice of a psychophysical method also bears on the matter of stimulus control. In threshold work, the animal psychophysicist must often choose between the relative efficiency of working mainly with weak signals and the advantages of including strong signals, whose presence may help to maintain the discrimination. An excellent index of stimulus control is a psychophysical function that relates the response measure to a range of signal strengths. When it is regular and monotonic, this function provides good evidence that the desired stimulus-response relationship has been achieved.

The Stebbins volume contains much data of interest to comparative sensory psychology. As the editor intended, however, its principal value is as a methodological handbook for those who wish to approach these problems psychophysically. In both respects, it should make a valuable addition to many libraries.

REFERENCES

- Blough, D. S. The study of animal sensory processes by operant methods. In W. K. Honig (Ed.), *Operant behavior: areas of research and application*. New York: Appleton-Century-Crofts, 1966. Pp. 345-379.
- Blough, D. S. Recognition by the pigeon of stimuli varying in two dimensions. *Journal of the Experimental Analysis of Behavior*. 1972, 18, 345-367.
- Blough, D. S. and Yager, D. Visual psychophysics in animals. In L. Hurvich and D. Jameson (Eds.), *Visual psychophysics (handbook of sensory physiology)*. Vol. VII/4. Berlin: Springer-Verlag, 1972. Pp. 732-763.
- Blough, P. M. Wavelength generalization and discrimination in the pigeon. *Perception and Psychophysics*, 1972, 12, 342-348.
- Boneau, C. A. and Cole, J. L. Decision theory, the pigeon and the psychophysical function. *Psychological Review*, 1967, 74, 123-135.
- Elliot, P. B. Appendix 1—tables of d' . In J. A. Swets (Ed.), *Signal detection and recognition by human observers*. New York: Wiley, 1964. Pp. 651-684.
- Frazier, L. F. and Elliott, E. W. Size and reliability of frequency-difference threshold determined with operant tracking procedures. *Journal of the Experimental Analysis of Behavior*, 1963, 6, 189-195.
- Glickstein, M. Brain mechanisms in reaction time. *Brain Research*, 1972, 40, 33-37.
- Heinemann, E. G., Avin, E., Sullivan, M. A., and Chase, S. Analysis of stimulus generalization with a psychophysical method. *Journal of Experimental Psychology*, 1969, 80, 215-224.
- Matthews, T. J. A convective thermal controller for behavioral experiments. *Behavior Research Methods and Instrumentation*, 1969, 1, 126-128.
- Saslow, C. A. *Animal psychophysics: an examination of the field*. Report PRP-37N, University of Washington, 1967.
- Sternberg, S. Memory-scanning: mental processes revealed by reaction-time experiments. *American Scientist*, 1969, 57, 421-457.
- Terman, M. and Terman, J. S. Concurrent variation of response bias and sensitivity in an operant-psychophysical test. *Perception and Psychophysics*, 1972, 11, 428-432.
- Thorpe, S. A. The effects of temperature on the psychophysical and electroretinographic spectral sensitivity of the chromatically-adapted goldfish. *Vision Research*, (In press).