

mice were tested at 21 days of age and tested again later (9). The four "least susceptible" strains, including the C57B1/6J strain, did not show seizure at the initial acoustic presentation but did so when tested again 7 days later. Fuller and Sjurdsen noted this in their tables but did not discuss it in the text.

These data indicate that this is not a transient sensitization effect; instead, it involves a longer-term neural change—perhaps an increase in auditory sensitivity or a decrease of neural inhibition. Acoustic priming can occur during wakefulness or under anesthesia by ether or sodium pentobarbital (Table 2); this suggests that neither the brainstem reticulum nor a conscious mechanism is involved. Because the C57B1/6J strain is homozygous nondilute (its chromosomes do not carry the mutant genes responsible for a lighter coat pigmentation and reduced liver phenylalanine activity; the dilute condition has been used by some as an analog of the human phenylketonuric mental deficient condition), its susceptibility to audiogenic seizure rules out the dilute genetic locus as a necessary condition for seizures, as some have suggested (10). The priming technique may provide a more useful means of analyzing audiogenic seizures than comparison of strains that differ at many loci does, in that it permits an experimental rather than a correlative approach. Biochemical examinations of primed and nonprimed mice may reveal whether differences in oxidative phosphorylation, concentration of norepinephrine and serotonin in the brain, or liver phenylalanine hydroxylase activity are associated with changes in audiogenic seizure susceptibility. Whether auditory priming affects other behaviors

—chemoconvulsive and electroshock seizures, learning, and emotionality—is still unknown. The phenomenon in this study is analogous in some respects to Lorenz' descriptions of imprinting; both have a critical period early in life during which a relatively brief stimulus can exert a profound, long-lasting effect on later behavior (although acoustic priming may not constitute as natural a situation as that which occurs when a duckling imprints its behavior to the first moving object it sees, accepts it as its mother, and models later behavior after this relationship). This technique may be useful in the investigation of behavioral development and of musicogenic seizures in humans.

KENNETH R. HENRY

*Regional Primate Research Center,
University of Wisconsin,
Madison 53706*

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response during a 30-second trial shows its "degree of certainty" that a reinforced stimulus was present on that trial. From such ratings, existing procedures yield relatively well-defined receiver-operating characteristic (ROC) functions (2).

Three White Carneaux pigeons with a long history of discrimination training were the subjects. Each pigeon, in a darkened chamber, pecked at a plastic disk upon which appeared a bright spot (0.95 cm in diameter). A 250-mm grating monochromator supplied light for this spot through a fiber-optics light guide. The stimulus assumed one of 12 wavelengths (570 to 592 nm in 2-nm steps), each with a half-width dispersion of 6.6 nm. The stimuli were uncorrected for brightness; over this range, brightness probably varied little for the pigeons (see 3).

After several weeks of training, experimental data were collected for 28 days. Each daily session comprised a 2-hour series of 30-second presentations of the stimulus with 3-second dark periods between these presentations. The key also went dark during reinforcement and for 0.6 second after each peck. On some trials, with 582 nm on the key, pecks intermittently brought reinforcement of 3-second access to mixed grain. Such reinforced trials were mixed with unreinforced "test trials" in a semirandom sequence as follows. Each session began with four reinforced trials followed by 13 stimulus sequences presented serially. The 16 stimuli in each sequence included four reinforced trials of 582 nm and 12 test trials in random order, with each test wavelength appearing once. The data below came from responses made in the 12 test trials on the last 12 stimulus series. Although 582 nm was the reinforced stimulus, it also appeared as one of the unreinforced test stimuli. Responses to reinforced trials and to the first complete series each day are omitted from this analysis.

A LINC digital computer (4) controlled the experiment and recorded responses. One reinforcement was delivered, on the average, on each reinforced trial. A peck produced reinforcement only if it followed the preceding peck by an interval least frequently emitted by the pigeon. This schedule is designed to generate a moderate, stable rate of response (5). In two birds, performance over the 28

Stimulus Generalization as Signal Detection in Pigeons

Abstract. Pigeons that were reinforced for pecking at a single-wavelength responded to nearby wavelengths with lower rates. Response rates indicated the pigeons' certainty that the reinforced stimulus was present. The ratings yielded receiver operating characteristic functions that approximated straight lines on a double probability plot.

Modern psychophysics may clarify our thinking about the stimulus control of animal behavior (1). Conversely, animal subjects might supply data necessary to test psychophysical hypotheses. Unfortunately, most experiments with animals are concerned with transient phenomena, whereas psychophysics

deals with the steady state; many animal experiments yield response rates to prolonged stimuli, while psychophysics favors choice responses to brief stimuli. This experiment effects a compromise by putting the response rate of an animal in a form suitable for signal detection analysis. A pigeon's

days was quite stable; the third bird showed a trend toward sharper stimulus control, and so its data were not fully analyzed.

We may consider the test stimuli as signals whose strength increases as their wavelength departs from the reinforced value of 582 nm. The response rate decreases as the bird becomes more certain that the stimulus is not 582 nm. A peck means that the stimulus does not differ from 582 nm. This is the reverse of the usual system, because fewer responses mean detection of a difference. To derive a point on the ROC curves for test stimuli, we reduce the bird's response rate on a given trial to a simple "yes" or "no"; by redefining "yes" and "no" many times, we get many points. For example, we may take ten or fewer pecks to mean "yes, the stimulus differs from 582 nm" and more than ten pecks to mean "no, the stimulus does not differ from 582 nm." We then compute the relative frequency of this "yes" response to 582 nm and to each test wavelength. These values are the abscissa and the ordinate, respectively, of a point on the ROC curve for each test wavelength. The changing of the definition of "yes" to 11 or fewer pecks provides another point on the curve (2).

Data from one bird appear in Fig. 1, A-C. Total response output was precisely controlled by stimulus wavelength (Fig. 1A). The curve is comparable to many wavelength generalization functions, but, because of the differential reinforcement, it is much sharper than curves from the usual transient extinction test (6). Data from the same bird are next plotted according to the rating procedure (Fig. 1B). The functions are well defined, as those derived from human ratings are, and they are somewhat asymmetric with respect to the coordinate axes. Figure 1C reproduces the ROC curves on coordinates scaled according to a normal probability transform; Fig. 1D shows comparable data for the second bird with a stable performance. In theory, if the sensory events underlying the data have a Gaussian distribution, the ROC functions here should be straight lines. They are reasonably straight, but they reflect the asymmetry of Fig. 1B in failing to lie parallel to the diagonal. This failure indicates that the distributions along the two axes have unequal variance.

The form of this experiment is derived from animal studies in generali-

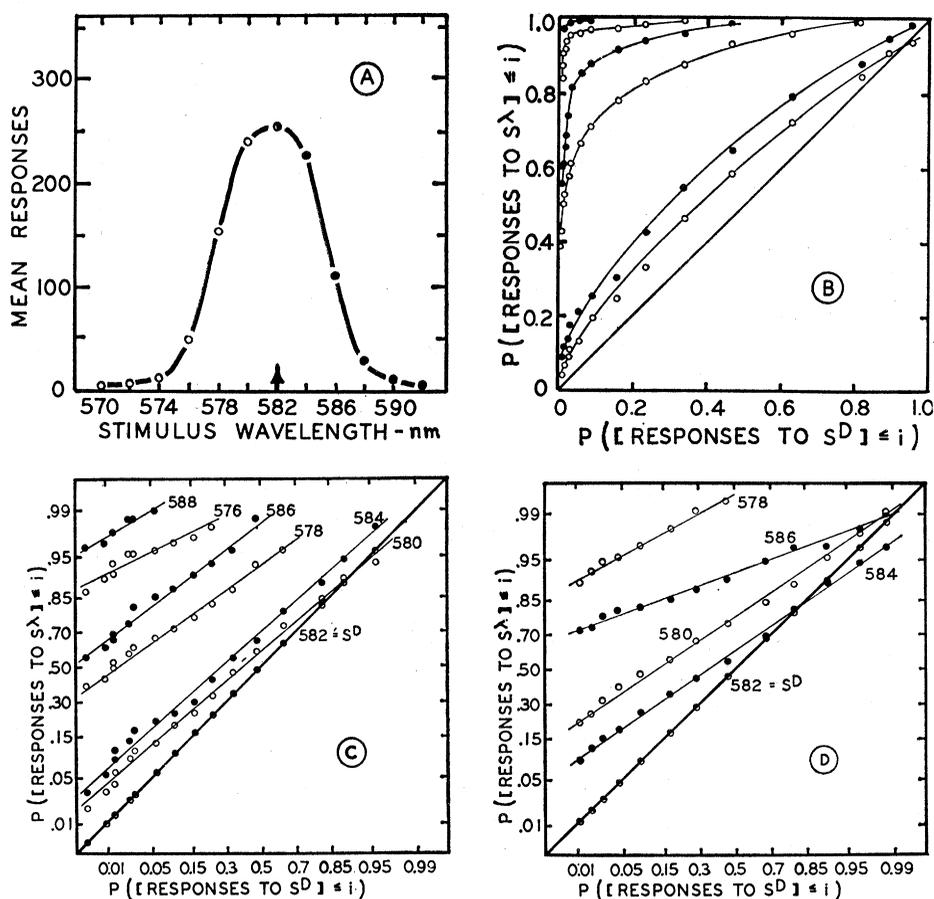


Fig. 1. Data from 28 sessions: (A), (B), and (C) results from one bird, (D) results from a second bird. (A) Generalization gradient around 582 nm, the reinforced wavelength (S^D); (B) ROC functions for the six stimuli nearest 582 nm; (C) same functions plotted on double probability coordinates. (D) Functions comparable to those in (C), but for a second bird. Axes in (B), (C), and (D) represent relative frequencies estimating the probability that a given number (i) of responses or fewer were made to the stimulus in question.

zation; it is perhaps needlessly complex from the point of view of detection theory. For example, the test wavelengths are divided into two classes, one on each side of 582 nm. This probably yields two functionally discrete detection tasks, a conclusion supported by the somewhat different slopes of the ROC functions from the two sides (Fig. 1D). A second complexity is suggested by the common observation that generalization gradients sometimes come to a peak at one or the other side of the reinforced stimulus. One might say that the bird is uncertain not only that a test stimulus is 582 nm, but also that 582 nm is indeed the stimulus being reinforced. This additional uncertainty may account for the fact that the ROC functions for 584 and 580 nm are "too close" to the diagonal in Fig. 1. Signal detectability analysis is valuable for helping to make such aspects of the generalization experiment explicit, though further work is needed to clarify the situation.

Evidently, the generalization gradient, like the usual psychometric function, confounds the subject's "criterion" with its "sensitivity." As in experiments with human subjects, detectability analysis may enable us to measure these factors independently.

DONALD S. BLOUGH

Department of Psychology, Brown University, Providence, Rhode Island

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