

DISCRIMINATION OF AUDITORY INTENSITIES BY RATS¹

MICHAEL TERMAN

BROWN UNIVERSITY

Rats were trained to press one of two keys when a standard intensity value of a 4.0-kHz sine tone (70 or 100 db *re* 2×10^{-4} microbar) was presented from a centrally located loudspeaker. Pressing the other key was reinforced when comparison intensity values (as much as 30 db less than the standard value) were presented. The animals initiated tone presentations by breaking a light beam at the rear of the chamber. Correct choices produced brain-stimulation reinforcement, and errors produced a timeout. A procedure designed by Jenkins was used to partial out choice data under potential control of sequential cues in the stimulus series. When the standard-comparison intensity difference was varied, the rats showed similar psychometric functions despite wide differences in response bias (relative position preference). A signal detection analysis showed that response biases for individual animals remained fairly consistent during psychophysical testing. The trend of decreasing choice accuracy at small intensity differences was described by the cumulative normal probability function. The similarity of psychometric functions obtained with 70- and 100-db standards supported Weber's law. There was some evidence that response latencies were controlled by intensity differences even when choice behavior was undifferentiated.

The recent development of operant-psychophysical methods points to the usefulness of discrete choice measures in the analysis of stimulus control (*cf.* Mentzer, 1966; Moskowitz and Kitzes, 1966; Terman and Kling, 1968; Stubbs, 1968). Adaptations of classical human psychophysical methods have produced comparable results from fish, pigeon, rat, and primate subjects. Such data have proved useful in choosing appropriate stimulus values for discrimination experiments (*e.g.*, Nevin, 1967; Terman, 1968) as well as providing a behavioral basis for the study of animal sensory functions (*e.g.*, De Valois, 1965; Blough and Yager, *in press*).

The present experiment used the extensive data available from long-term studies on single animal subjects for analyses of choice behavior during psychophysical testing. An attempt was made to delineate response-bias and

discriminability factors (suggested by signal detection theory) in an operant-psychophysical procedure that afforded explicit specification of reinforcement (or payoff) variables. A visual luminance discriminability test procedure (Terman and Kling, 1968) was adapted for the presentation of auditory intensities, and sine tone stimuli were chosen to allow a direct comparison of a discriminability estimate with the two-value discrimination acquisition data of Pierrel, Sherman, Blue, and Hegge (1970). Brain-stimulation reinforcement was used to suit a psychophysical design that demanded hundreds of massed trials and stable response patterns. The analysis of choice patterns required a conditional choice measure, reflecting response accuracy in the presence of standard and comparison tones independently. Concurrent measurement of latencies permitted contrasting of a time-based measure of stimulus control with the dichotomous choice data.

METHOD

Subjects

Three male albino rats of the Charles River CD strain were fed 20 g of Purina Rat Chow per day and given unlimited access to water, assuring a slow but steady weight gain throughout the experiment.

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Apparatus

The experimental compartment was constructed of clear Plexiglas side and rear walls, with an aluminum front wall, and measured 13 by 9.5 by 19.5 in. (0.33 by 0.24 by 0.49 m). Two Gerbrands pigeon keys were mounted symmetrically on the front (0.24-m) wall, 40 mm from the grid floor and 50 mm from each side wall. The keys were dimly (and equally) transilluminated by incandescent lamps throughout the session.

A central stimulus light with a 25-mm diameter white lens was mounted on the front wall, 100 mm from the floor, with a bronze food cup (not used in this experiment) inserted below it. A photocell was mounted on one side wall 40 mm above the floor, and 40 mm from the rear wall, and a light source was focused on the photocell from the other side of the box.

The compartment was placed inside a ventilated, sound-attenuating chamber, with a dim houselight that was on throughout each session. A pulley-swivel mercury commutator (Berkley and Kling, 1967) was attached to the ceiling to prevent twisting of the flexible electrode leads when the animal turned or made sudden movements. Brain stimulations consisted of 0.5-sec trains of 60-Hz sine waves, taken from an isolation transformer, stepped down by a variable transformer and adjusted by a potentiometer. An oscilloscope was used to monitor brain stimulation current by measuring the voltage drop across a fixed resistor in series with the animal. The current was set at 200 microamperes (peak to peak) for all subjects, which maintained rapid responding.

The auditory stimuli were generated by a Hewlett-Packard 200AB sine wave oscillator, set at a frequency of 4.0 kHz. A University 4401 tweeter was mounted on the ceiling of the sound-attenuating chamber, above the photocell beam at the rear of the experimental compartment. Auditory stimulus intensity was calibrated by placing the remote microphone of a General Radio 1551-B sound level meter (fast speed, "A" weighting scale) directly beneath the speaker at the approximate position of the rat's head. The unattenuated output of the oscillator was set at either 100 or 70 db ($re 2 \times 10^{-4}$ microbar). Variation in intensity throughout the compartment was less than 2 db. By use of a Daven T-734 deci-

bel attenuator, comparison tones as much as 30 db less intense than the standard values could be presented. The outputs of the oscillator and attenuator were connected to separate Raysistor CK1104 photoelectric switches, which were individually controlled by relays in an adjacent room. Once passed by the photoelectric switches, the electrical signals were adjusted by matching transformers and sent to the loudspeaker.

The experimental events were recorded by a Massey-Dickinson data acquisition system, and binary codes were punched on a Tally 401 paper tape perforator. Time codes for every experimental event were recorded with 0.1-sec resolution. The punched tape data were later transferred to a LINC-8 computer using a DEC high-speed photoelectric tape reader. Computer programs were then used to reduce and analyze the data.

Procedure

Electrode implantation and histology. The animals were anesthetized with an oxygen-halothane mixture delivered by a Forreger SA-10 small animal anesthesia apparatus. Bipolar stainless steel electrodes of 0.254-mm diameter (Plastic Products MS303) were aimed at the region of the hypothalamus with the aid of a stereotaxic instrument. The electrodes were secured to the skull by stainless steel screws and dental cement. After the experiment, the animals were sacrificed and perfused with saline and neutral-buffered formalin solutions. The brains were washed in water, dehydrated in alcohol solutions, embedded in celloidin, sectioned and stained. Electrode tips were localized in the following areas, with the aid of König and Klippel's (1963) stereotaxic atlas: Rat T16, *nucleus periventricularis (hypothalami)*; Rat V15, *commisura supraoptica dorsalis, pars ventralis*; Rat V16, *fasciculus medialis prosencephali*.

Nondifferential pretraining. The animals had previously been trained to bar press with brain-stimulation reinforcement in a single-bar compartment. In pretraining, pressing either response key in the experimental compartment was initially shaped. In the presence of the center stimulus light, the experimenter broke a switch in parallel with the photocell, which turned off the light and initiated a 30-sec auditory stimulus presentation during which 100- or 70-db tones were presented

equally often. A response to either key within 30 sec of tone onset produced a 0.5-sec train of brain stimulation, terminated the tone, and turned on the center light. To shape the free-operant chain, the next tone was presented as soon as the center light came on, but as the animals learned to press quickly, tone onset was delayed until they made some movement toward the rear of the chamber. Gradually, the animals were trained to approach the rear of the chamber in the presence of the center light, to break the photocell beam, and thus to set up the next tone presentation independent of the experimenter.

Discrimination training. After several pre-training sessions, the discrimination contingencies were introduced. A response on the left key was reinforced in the presence of the 100-db tone, and a response on the right key produced a 30-sec timeout. The opposite contingencies were in effect during presentation of the 70-db tone. After reinforcement or timeout, the center light turned on and the animal could initiate the next trial. During a timeout the tone was terminated, the center light remained off, and no response had any scheduled consequence. Daily 4-hr sessions were given each animal until high-accuracy levels of discriminative performance were achieved (greater than 95% correct choice over an entire session).

In discrimination training sessions for Rat T16 a Gellermann series was used to schedule the two intensity values, allowing up to three consecutive presentations of a given value, and insuring that the two intensities would each be presented five times in a block of 10 trials. A Fellows series (Fellows, 1967) was subsequently used for Rats V15 and V16; this series has been reported to reduce the adventitious reinforcement of various "hypothesis"-type behaviors incompatible with the acquisition of stimulus control. In the Fellows series, a maximum of three consecutive presentations of a given stimulus value is also scheduled, and the two intensities are each presented six times in a block of 12 trials. Progression through both the Gellermann and Fellows series occurred without regard for the outcome of the previous trial (a "noncorrection" procedure).

Psychophysical testing. The procedural sequence for psychophysical testing is given in Table 1. Each session presented two auditory intensity values (standard and comparison).

Table 1
Psychophysical Test Sequence

Test No.	Standard Intensity	Direction of Intensity Difference	Rats
1 ^a	100 db ^b	Decreasing	T16
2	100 db	Decreasing	T16, V15, V16
3	70 db	Decreasing	T16, V15, V16
4	100 db	Decreasing	T16, V15, V16
5	100 db	Increasing	T16, V15, V16
6	100 db	Decreasing	T16, V15
7	100 db	Increasing	T16, V15

^aTest 1 employed a Gellermann series; subsequent tests all used a Jenkins series.

^bre 2×10^{-4} microbar.

On standard trials (louder tone) the left key was correct, and on comparison trials (softer tone) the right key was correct. The standard was held constant throughout a given test sequence, while the comparison was varied from session to session in discrete steps. For tests with the 100-db standard, the comparison intensities ranged from 80 to 100 db (70 to 100 db in Tests 1 and 2). For Test 3, with the 70-db standard, comparisons ranged from 50 to 70 db. In a typical sequence of test sessions the intensity difference between standard and comparison tones was decreased in the following order: 20, 15, 10, 7, 5, 3, 2, 1, and 0 db. When a test sequence was run with increasing intensity differences this order was reversed. The animals were retrained at large standard-comparison differences before each decreasing test sequence was begun. A given intensity difference was occasionally maintained for several sessions when response patterns appeared unstable.

Following Test 1, which used a Gellermann series for Rat T16, a stimulus series designed by Jenkins (1965), described in the Results, was adopted. Daily 4-hr sessions were run in Tests 1 and 2, with the animals often completing more than 1000 trials. Tests 3 to 7 were run with 500 trials per session, and multiple sessions per day as time permitted. The first 100 trials of each session were discarded to eliminate transient warm-up effects, and 200 even-numbered trials on the Jenkins series (*cf.* Results) were recorded for data analysis.

RESULTS

Choice Measures

Rat T16 was run in Test 1 with the 100-db standard, using an order of decreasing inten-

sity differences, with standard and comparison values presented according to the Gellermann series. In addition to the mean per cent correct curve shown in Fig. 1 (upper-left panel) the data have been dichotomized into conditional components, independently reflecting choice accuracy on trials when the standard or comparison tone was presented (and when a response on the left or right key was reinforced, respectively). Nearly errorless responding was maintained as the comparison value was increased from 70 to 80 db, with greater than 95% mean correct choice. Further increases in comparison intensity resulted in decreases in discriminative accuracy. At 99 db, the mean function reached 58% correct choice, and accuracy showed no further decrease when the standard and comparison values were made physically equal at 100 db. Thus, the animal continued to show some differential behavior with respect to the scheduled reinforcement contingencies, although differential auditory stimulation was absent.

The two conditional components of the mean per cent correct curve reveal radically contrasting relations to decreasing intensity differences. When the comparison tone was presented, regardless of its value, the animal almost always responded correctly by pressing the right key. In contrast, accuracy in the presence of the standard tone decreased rapidly at small intensity differences. At the final 100-db comparison value, the animal reached a level of 20% correct choice in the presence of the standard tone. The contrasting trends of the two conditional components of the psychometric function may be conveniently described as an increase in position preference with decreasing intensity differences. The animal emitted more responses on the right key as the problem become more difficult.

The maintenance of differential control by the scheduled contingencies, in the absence of any physical stimulus difference (resulting in terminal accuracy of 58% correct), presents a major difficulty in applying a psychophysical

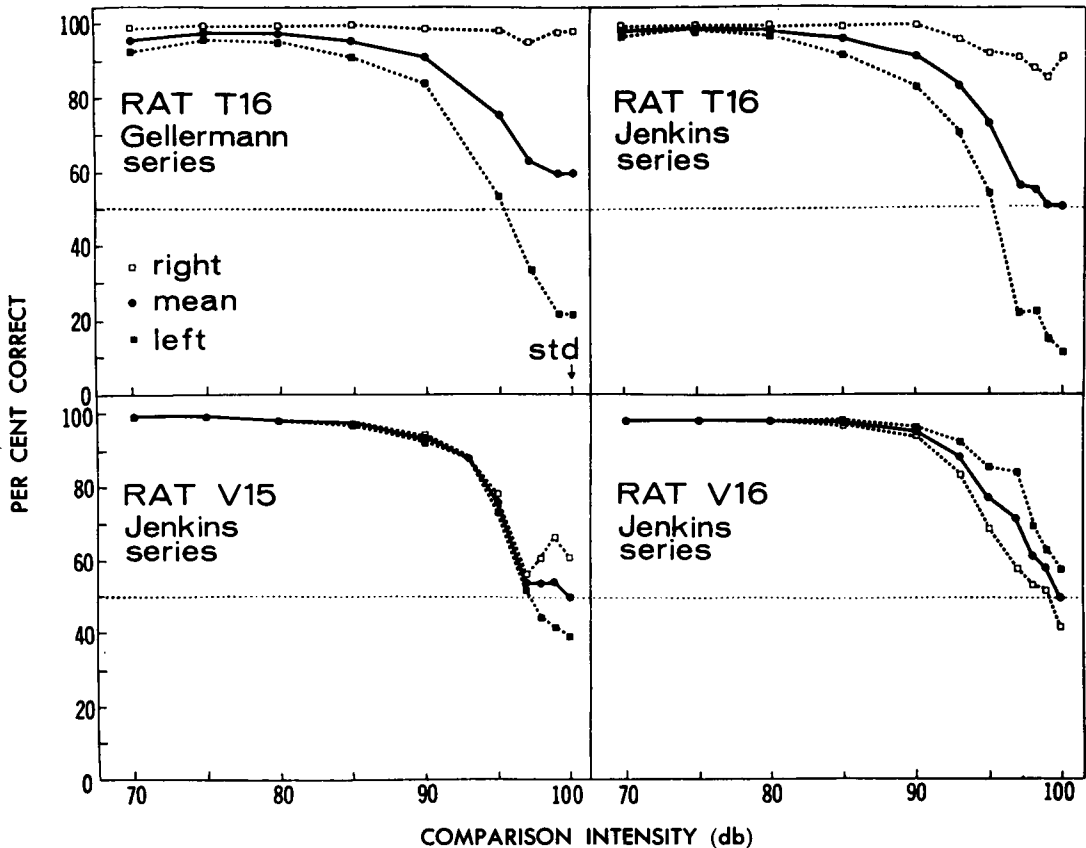


Fig. 1. Per cent correct choice as a function of comparison intensity (100-db standard). Conditional components of the mean functions reflect accuracy on standard trials (left-key correct) and comparison trials (right-key correct).

interpretation to these data. The source of differential control was found to lie in the Gellermann series, as illustrated in Fig. 2. Each of the 30 steps of the Gellermann series occupies one ordinal position on the abscissa. The data were taken from the final 100-db comparison session, when the standard and comparison values were identical. Per cent correct choice scores were computed on the basis of 20 runs through the 30-step series, a sampling of 600 trials taken from the middle of the 4-hr session. Given two consecutive reinforcements, the frequency of a correct response on the nonpreferred left key ranged from 40 to 80%. On the one occasion in the series that three comparison trials were consecutively presented, response accuracy (on the preferred right key) dropped to 80% correct after a run of two reinforcements, while the next standard trial resulted in 15% correct choice. On all other standard trials the frequency of a correct response was 0%. Thus, the sequence of outcomes acted as a discriminative stimulus for switching keys. The animal did not learn the Gellermann series *per se*, or its response accuracy on standard trials would

have exceeded 0% correct, on at least some of the nine occasions in the series where the non-preferred left key was correct but did not follow a run of reinforcements on the preferred right key. (Examination of the Fellows series used in discrimination training for Rats V15 and V16 reveals the same sequential cues as the Gellermann series, and thus it was also judged inappropriate for psychophysical testing.)

Jenkins (1965) suggested that sequences of reinforcement and nonreinforcement may serve a discriminative function in single-response situations. The present experiment demonstrates sequential control in a two-choice situation, and the stimulus series designed by Jenkins to control for such an effect can be appropriately applied. In the Jenkins series, odd-numbered trials present standard (*s*) and comparison (*c*) tones in a regular single-alternation pattern (*scscscscsc . . .*), while even-numbered trials present a randomized series of standard and comparison tones. Accuracy estimates are taken from the even-numbered trials exclusively, if there is any evidence that the animal learns the single-alter-

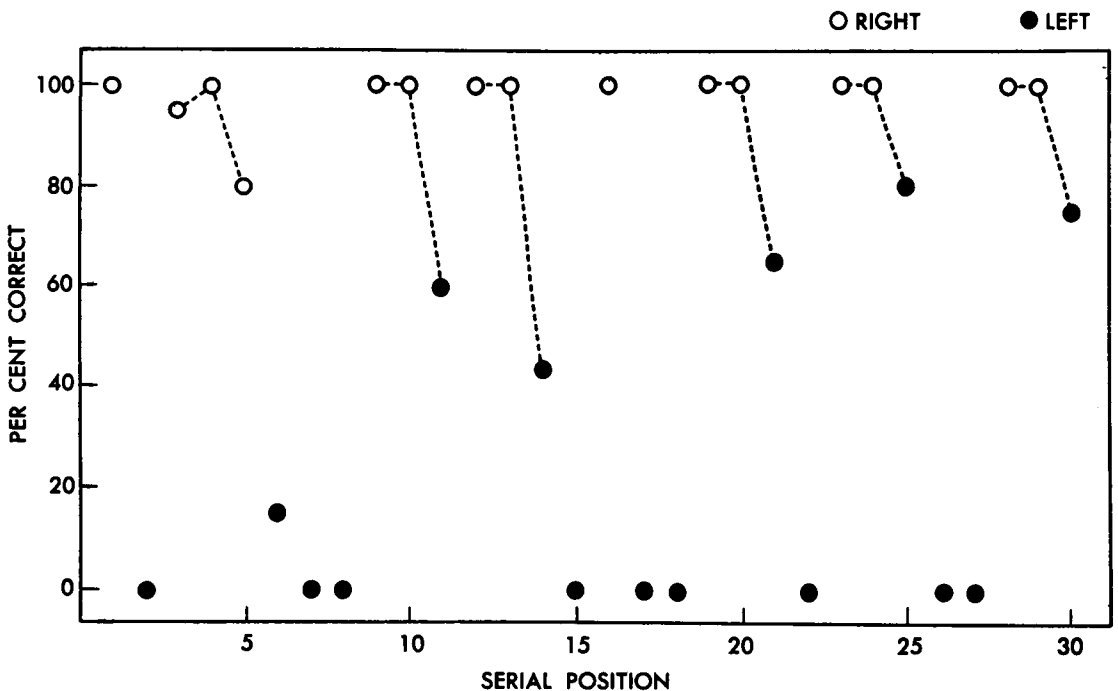


Fig. 2. Per cent correct choice as a function of serial position in the 30-step Gellermann series for Rat T16, when both standard and comparison values equalled 100 db. Closed circles represent standard trials (left-key correct) and open circles represent comparison trials (right-key correct). Dashed lines connect groups of three trials where trials 1 and 2 produced reinforcement when the right key was pressed.

nation rule for odd-numbered trials, or learns to switch from the preferred to the nonpreferred key after a run of three reinforcements. (The latter strategy will yield greater than 50% of available reinforcements, but the "extras" will always be earned on odd-numbered trials, which are partialled out.) A Jenkins series was subsequently used for all psychophysical tests, with the Fellows series interpolated between the odd-numbered trials, as specified in Table 2.

Table 2

Series of Standard and Comparison Presentations*

<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>
<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>
<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>
<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>
<i>s</i>	<i>s</i>	<i>c</i>	<i>s</i>	<i>s</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>	<i>c</i>	<i>c</i>	<i>s</i>

*Read across rows, top to bottom. Odd-numbered trials (italicized) follow a single-alternation order; even-numbered trials follow a Fellows (1967) semi-random order. Data are taken from even-numbered trials exclusively (*cf.* Jenkins, 1965).

Using the Jenkins series in Test 2, the intensity sequence of Test 1 was repeated for Rat T16, and the data are shown in Fig. 1 (upper-right panel). The mean psychometric function reached approximately 50% correct choice in the 99- and 100-db comparison sessions. As in the Gellermann series, an orderly increase in position preference was observed (as reflected by the increasing separation of the conditional component curves), although this test resulted in more errors on comparison trials (preferred right key correct).

Test 2 results for Rats V15 and V16 are also plotted in Fig. 1. Both animals showed an orderly decrease in discriminative accuracy as the intensity difference was reduced, with mean per cent correct curves very similar to Rat T16's. However, the conditional component curves for the three animals reveal marked variations in the patterns of position preference. Rat V15 did not show appreciable position preference (as measured by the diver-

gence in conditional component curves) until its accuracy approached 50% correct at the 97-db comparison value. In the 3-db region below the standard, this animal showed an increasing preference for the right key, although it never reached the magnitude of Rat T16's right-key preference. Rat V16 showed a clear left-key preference as soon as its accuracy started to decrease at the 90-db comparison value. In contrast to Rat T16, however, the conditional component curves did not show consistently increasing divergence as a function of difficulty. The variation in conditional component curves between animals, coupled by the similarity of the mean psychometric functions, suggests that the particular response biases shown by the animals during psychophysical testing have no appreciable effect on discriminative accuracy levels.

A signal detection analysis (*cf.* Green and Swets, 1966) may express response bias phenomena more succinctly than the simultaneous comparison of conditional accuracy functions. In this animal experiment, the two response keys may be thought to parallel the human verbal responses "yes" and "no"; however, which response is designated "yes" or "no" is arbitrary. If left-key responses are reinforced in the presence of the standard, and right-key responses are reinforced in the presence of the comparison, one might say that the animal correctly identifies a difference from the standard when it presses the right key in the presence of the comparison. If this latter event is termed a "hit", it follows that right-key responses in the presence of the standard would be termed "false alarms", left-key responses in the presence of the standard would be termed "correct rejections", and left-key responses in the presence of the comparison would be termed "misses". With equal positive payoff for hits and correct rejections (the reinforcer), and equal negative payoff for false alarms and misses (the timeout), the payoff matrix is held constant and symmetrical throughout the experiment.

The relation between hits [$p(\text{right}|\text{comparison})$] and false alarms [$p(\text{right}|\text{standard})$] for Test 2 is shown in Fig. 3. The data correspond to the psychometric functions previously described. When the intensity difference between standard and comparison is large, the data points for all three animals congregate in the upper-left corner of the correlation plot, indi-

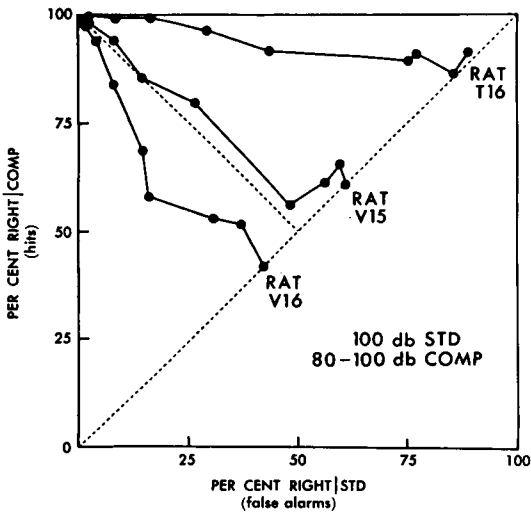


Fig. 3. Isobias functions for a test series with 100-db standard. Hit rate is estimated by the relative frequency of response on the right key in the presence of the comparison; false-alarm rate is estimated by the relative frequency of response on the right key in the presence of the standard.

cating high hit rates and low false-alarm rates. As the intensity difference is reduced, the data points for each animal gradually approach the major diagonal, defining individual "isobias functions" (cf. Galanter, 1966). Each animal's isobias function can be reasonably well described by a straight line connecting high-accuracy points in the upper-left corner to chance-level points on the major diagonal. In the absence of any position preference, the data points would fall along the minor diagonal. If "bias" refers to the degree that one response is favored over the other regardless of stimulus differences, one can say that Rat V16 displayed a moderate bias toward the left key, Rat V15 displayed a very small bias toward the right key, and Rat T16 displayed a strong bias toward the right key.

The straight-line description of the isobias function suggests that the animals maintained a consistent ratio of false alarms to misses as the discrimination problem became more difficult. Such a bias ratio is plotted as a function of comparison intensity in Fig. 4 for the three

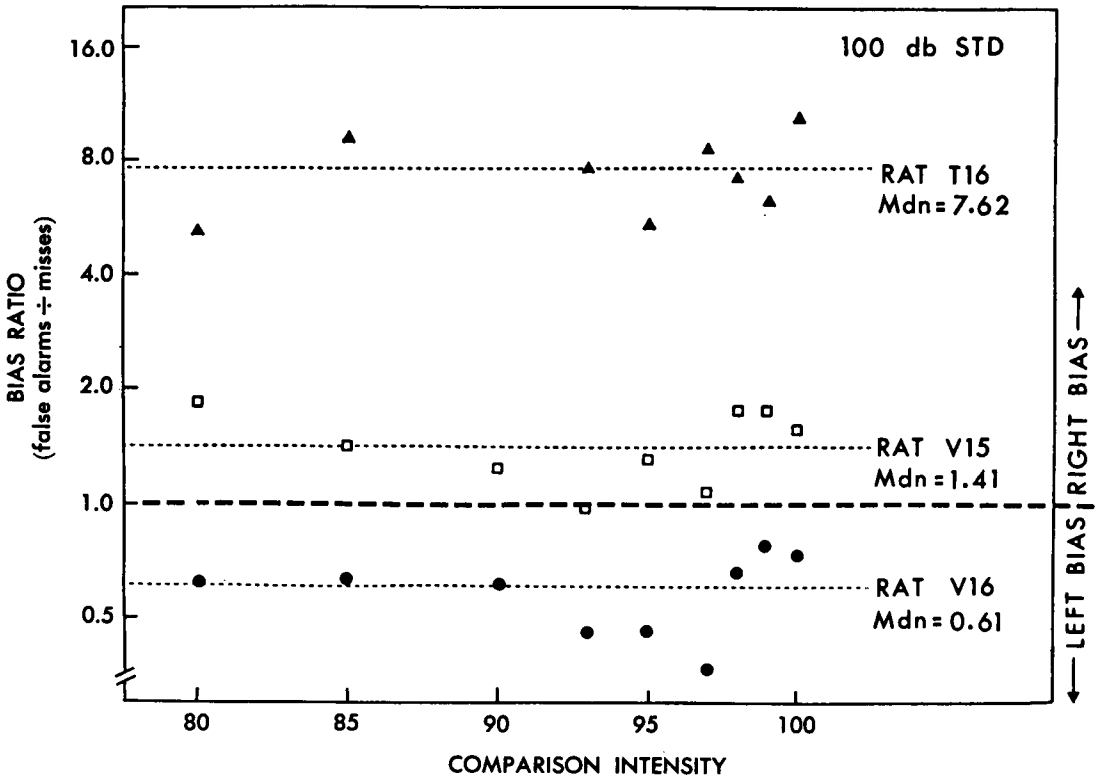


Fig. 4. The ratio of false alarms to misses as a function of comparison intensity. A left-key bias is reflected by ratios of less than 1.0; a right-key bias is reflected by ratios of greater than 1.0.

isobias functions discussed above. When the ratio equals 1.0, both types of errors are emitted with equal frequency, and data points on the isobias function would fall along the minor diagonal. A ratio greater than 1.0 indicates bias toward the right key; a ratio less than 1.0 indicates bias toward the left key. The lower limit of the ratio is zero, corresponding to an absolute left-key preference; the upper limit is plus infinity, corresponding to an absolute right-key preference. Since the scale values are nonlinear (with the range of right-key bias ratios greatly exceeding that of left-key bias ratios), the ordinate in Fig. 4 uses logarithmic spacing. The bias ratio was computed for each point on the isobias function for the three rats, and the median value for each set of points is represented by a thin dashed line. The points for each rat are scattered about the median value; there is no systematic trend away from the median value with increasing problem difficulty.

Signal detection theory suggests that discriminability estimates should employ a "bias-free" measure, because the per cent correct measure is distorted by strong biases. If the underlying sensory distributions for standard and comparison tones are assumed to be normal and of equal variance (*cf.* Green and Swets, 1966), the d' scale for yes-no experiments (Swets, 1964) would provide a detectability measure independent of contamination by biasing factors. To verify the assumptions about the underlying distributions empirically, it is necessary to generate isosensitivity curves by varying a subject's bias at equal stimulus differences; if, on a normalized correlation plot of hits and false alarms, the isosensitivity curves are linear and parallel to the major diagonal, the assumptions are supported. Response bias was not manipulated at equal stimulus differences in the present experiment, and it therefore cannot be demonstrated that the d' scale provides a valid bias-free index of discriminability in this situation. However, a plot of d' as a function of comparison intensity for Test 2 results (shown in Fig. 5) reveals close agreement among three subjects that varied substantially in degree and direction of bias. The mean d' function for the three rats is closely representative of each individual, and resembles the classic psychometric ogive.

Another bias-free index of discriminability

that requires no assumptions about underlying sensory distributions is the area under the isosensitivity curve, but this statistic is not available without explicit manipulations of response bias. Given no further information on the validity of the d' model, it would seem appropriate to retain the per cent correct measure in describing discriminability, recognizing that a strong response bias may depress the value of per cent correct. It should be noted, however, that such a decrease is bound to be slight and well within the range of variability for replication of a psychometric function. Irwin and Terman (1970) have shown that a subject responding with a 5:1 ratio of false alarms to misses would show a maximum decrease of about 4% correct, given the validity of the d' model. Indeed, there is close agreement among the mean per cent correct psychometric functions shown for the three subjects in Fig. 1.

The trend of decreasing accuracy with decreasing stimulus differences provides a more complete description of discriminability than single-value "threshold" estimates (such as the 75% correct point found by interpolation on the psychometric function). The trend has often been summarized by normalizing per cent correct values and obtaining a straight-line fit to the region of decreasing stimulus control (Terman and Kling, 1968; Engen, *in press*). Since the straight-line fit is determined by all the points on the psychometric function, the slope (or standard deviation) provides a summary threshold statistic. In Fig. 6, straight lines were visually fitted to the transformed scores for Test 2. Data points were omitted from this analysis when they fell in the range of 70- to 85-db comparison values, outside the region of rapidly decreasing choice accuracy, as well as when they fell past the "point of subjective equality" (where choice accuracy reached 50% correct). In both regions, the slope of the psychometric function falls to zero, for choice accuracy is asymptotically high or low. The slope (or standard deviation) of the functions is measured by the decibel difference between the point of subjective equality (where $z = 0$) and an intermediate accuracy level near 84% correct (where $z = 1.0$). In classical threshold analyses (*cf.* Engen, *in press*) it is often said that discriminability is finer the steeper the slope (or the smaller the standard deviation), relative to the point of subjective

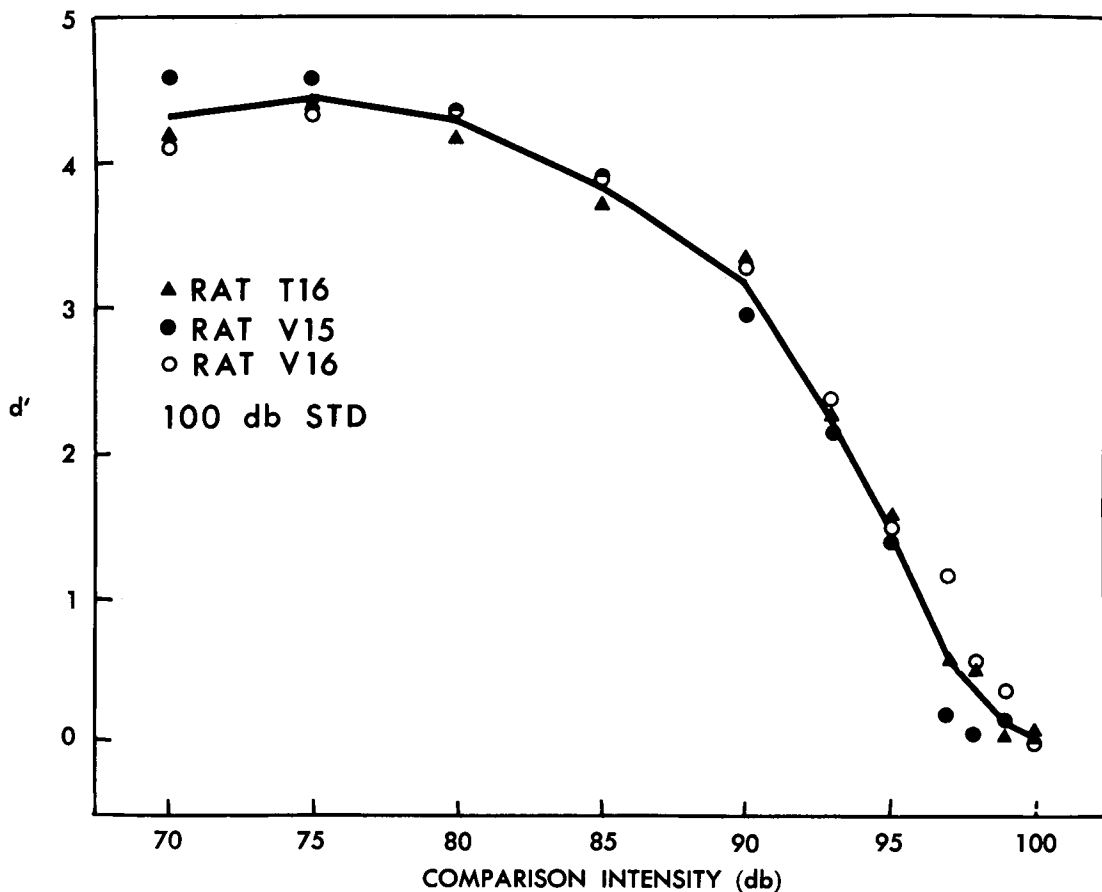


Fig. 5. Signal detectability (d') as a function of comparison intensity. The straight line connects the mean for three rats.

equality. In Fig. 6, Rat V15 shows the lowest standard deviation of 5.0 db, followed by Rat V16 with 6.2 db and Rat T16 with 6.6 db (mean = 5.9 db). It can also be said that discriminability is finer when the intensity difference required to produce a given accuracy level is minimized, relative to the point of physical equality of standard and comparison. The decibel difference required to maintain 75% correct choice (*cf.* Fig. 6) provides such a measure. Rat V16 required 4.2 db, followed by Rat T16 with 5.1 db, and Rat V15 with 5.5 db (mean = 4.9 db). Using this threshold estimate, the animals are ordered quite differently than the slopes of their psychometric functions would suggest, due to individual variations in the range between the points of subjective and physical equality. It is interesting that the animal with the greatest response bias (Rat T16, *cf.* Fig. 4) did not require the greatest intensity difference of the

three animals to maintain a given level of per cent correct choice.

Since the per cent correct measure describes similar psychometric functions for animals with substantial differences in response bias, discriminability can be assessed across subjects as a function of stimulus variables (*e.g.*, position on the continuum of intensity) and procedural variables (*e.g.*, the direction of change in standard-comparison differences). A comparison was made of psychometric functions obtained when 70- and 100-db standards were used (Tests 3 and 4), as shown in Fig. 7. There are no consistent differences in discriminability as a function of continuum position, across subjects. Differences between curves for individual animals are small, and fall within the range of variability for replication of a single function. The data support a Weber formulation of auditory difference threshold in this region of the intensity continuum: equal log

differences in sound pressure produce equally fine discriminative performance.

When the 100-db standard was used, but the comparison intensity was either gradually raised from 80 db (Test 4) or lowered from 100 db (Test 5), consistent differences were obtained in the psychometric functions, across animals (Fig. 8). When the sequence of increasing standard-comparison intensity differences was used, the region of chance performance above the point of subjective equality was extended and performance was poorer at intermediate intensity values, contrasted with the sequence of decreasing standard-comparison differences. However, for both sequences the upper asymptotic levels of accuracy were similar, indicating that at wide stimulus differences there was no decrement in stimulus control attributable to the intensity sequence. It should be noted that a repetition of this procedure for two of the animals (Tests 6 and 7) resulted in equally fine discriminative performance with increasing or decreasing stimulus differences (data for Rat T16 are included in Fig. 8). Apparently, further training eliminated the series effect.

Latency Measures

For every choice an animal makes, we can measure a preceding response latency, defined as the time between stimulus onset (upon breaking the photocell beam) and the first key press. With two choice alternatives and two discriminative stimuli, four classes of latency may occur that correspond to the hits, false alarms, correct rejections, and misses of signal-detection analysis. If latencies differentiate with respect to stimulus values, knowledge of choice latency may be used to predict choice outcome or to provide evidence of stimulus control when choices are undifferentiated.

In Fig. 9, latency distributions are shown for Rat V15 for the nondifferential pretraining procedure, when all key presses were made on its preferred right key. In addition to relative frequency plots, conditional response probability distributions are presented, using a latencies per opportunity estimate adapted from Anger's (1956) treatment of inter-response-time probabilities. Although the relative frequency distributions for the two intensities overlap considerably, the animal tended

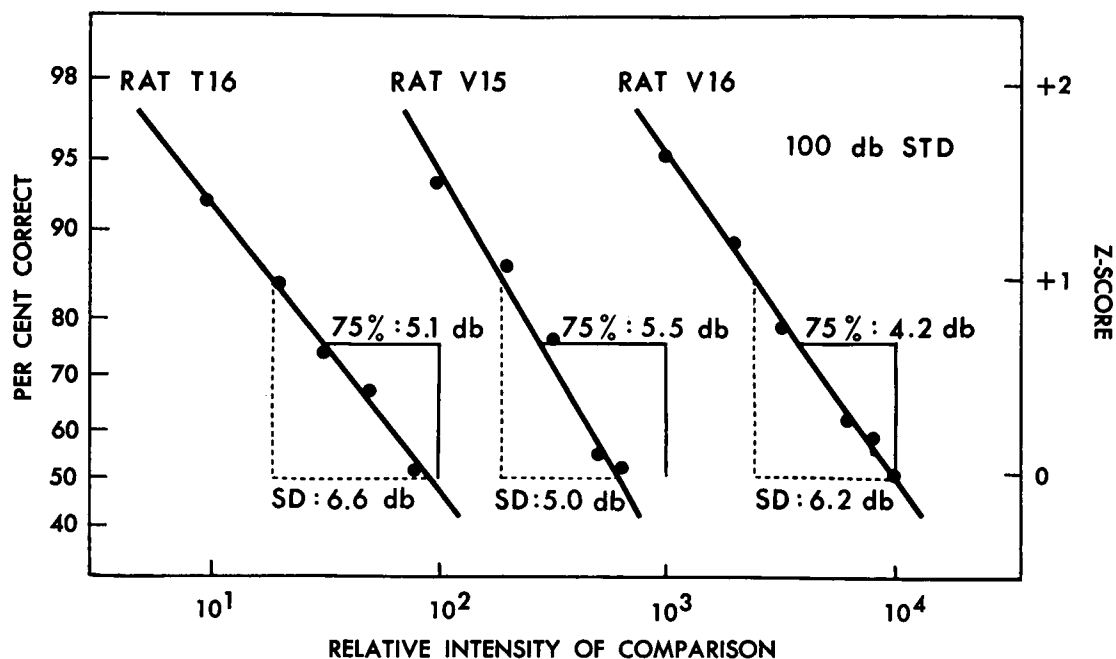


Fig. 6. Normal probability plots of choice accuracy as a function of the relative intensity of the comparison. Mean per cent correct choice scores are plotted in probability scale, and corresponding standard deviation values (z-scores) are shown on the right ordinate. The curves are displaced by one log unit on the abscissa. The SD and 75% correct choice levels provide two indices of discriminability.

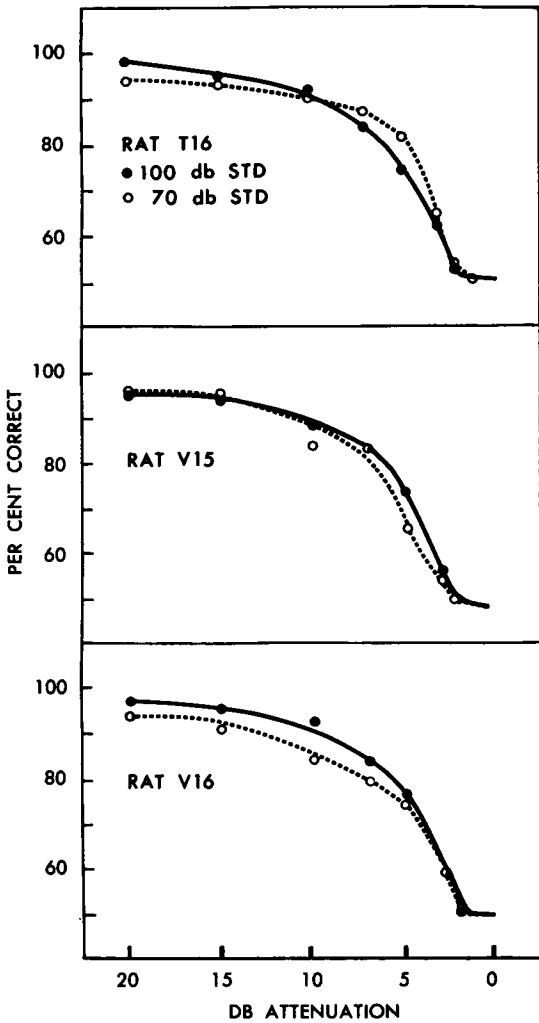


Fig. 7. Per cent correct choice as a function of decibel attenuation of the comparison, for 70- and 100-db standards.

to respond more rapidly in the presence of the more intense tone (100 db). Similar results were obtained for the other two animals. The relation between latency and auditory intensity can be stated most clearly in terms of conditional response probability (latencies per opportunity): in the presence of the more intense stimulus it is more probable for the animal to respond at any given moment after stimulus presentation than in the presence of the less intense stimulus. Hull (1949) labelled such effects "stimulus intensity dynamism". It is clear that differential control of operant behavior was obtained in this experiment before differential reinforcement; analysis of choice laten-

cies after discrimination training must take the "dynamism effect" into account.

In nondifferential pretraining, an animal almost always adopts a strong position preference; its responses are not divided randomly between the two keys, but one key is chosen over the other on nearly every trial. Thus, latency distributions in nondifferential pretraining reflect only the one response alternative that is emitted in the presence of the two stimuli. After discrimination training at wide stimulus difference, correct responses are emitted on both keys, and there are very few errors. Thus, two latency classes predominate: R_L latencies for the standard (S_L) and R_R latencies for the comparison (S_R).

As the stimulus difference is decreased during psychophysical testing, errors occur on both keys in addition to correct responses, and it is possible to compare all four latency classes. Sample latency distributions are shown in Fig. 10 for the three animals in a session with a 3-db intensity difference (Test 4 for Rats T16 and V16; Test 6 for Rat V15). A comparison of latencies terminating in a particular response ($R_R|S_R$ vs. $R_R|S_L$; $R_L|S_L$ vs. $R_L|S_R$) may shed light on the analysis of stimulus control during psychophysical testing. For all three subjects, given that a choice was in error ($R_L|S_R$ or $R_R|S_L$), it was likely to be preceded by a slightly longer latency than for the corresponding correct response ($R_L|S_L$ or $R_R|S_R$, respectively). It can thus be said that the animal pauses before making an error. A "pause" is defined as a depression in latencies per opportunity in the short-latency region; in the long-latency region, a crossover in the distributions most often occurs, with errors showing higher latencies per opportunity. In signal-detection theory a hit and false alarm represent the "same response" given to different stimuli. Even though the occurrence of an error at small stimulus differences suggests the absence of stimulus control, the present data indicate that equivalent choice responses may still be differentiated by their latencies.

If latencies during psychophysical testing showed a dynamism effect (as they did during nondifferential pretraining at 30-db difference), shorter latencies would be emitted to the louder tone (the 100-db standard). Examination of Fig. 10 indicates that this interpretation is possible only for correct rejection ($R_L|S_L$) and miss ($R_L|S_R$) latencies. Since hit

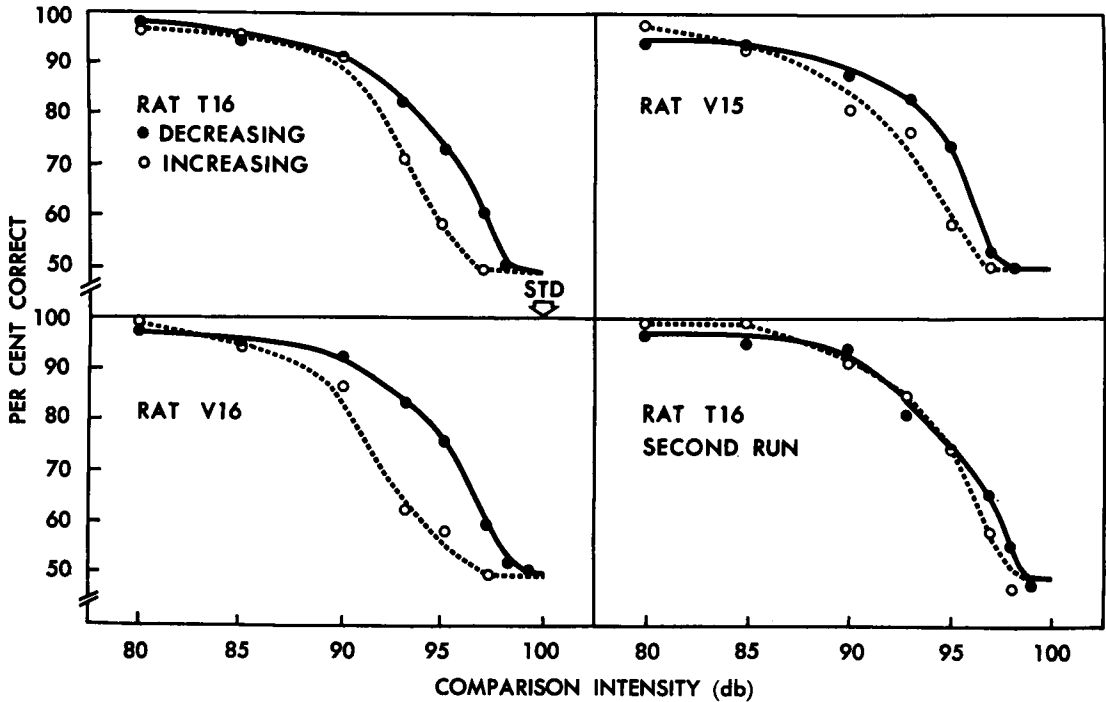


Fig. 8. Per cent correct choice as a function of comparison intensity (100-db standard), for test series with decreasing or increasing intensity differences, including replication data for Rat T16.

($R_R|S_R$) latencies tend to be shorter than false alarm ($R_R|S_L$) latencies, even though they are emitted in the presence of the softer tone (the 97-db comparison), the latency differential cannot be attributed to dynamism. Indeed, it seems unlikely that a dynamism effect would persist at such a small (3 db) intensity difference.

As noted in a previous experiment (Terman and Kling, 1968), it is common for an animal to persist in running toward its preferred key on every trial and then to switch sides before making a response on the nonpreferred key. For a strongly biased animal, switching sides would result in generally longer latencies for responses to the nonpreferred key, regardless of stimulus intensity. For example, Rat T16 (with a strong right-key preference) showed shorter R_R than R_L latencies, for both correct and incorrect choices. When position preferences were not so strong (*cf.* Rats V15 and V16) the latencies per opportunity distributions for the left and right keys still showed differential trends, although latencies to the preferred key were not uniformly shorter. The particular topography of key-approach behavior (*e.g.*, switching sides, turning left or

right) would seem to interact with choice accuracy in determining discrimination latency.

DISCUSSION

The control of choice behavior by auditory intensities was shown to be modulated by the intensity difference of successively presented standard and comparison tones. Psychophysical analyses could be applied when extraneous control of choice behavior by sequential cues in the stimulus series was partialled out by use of Jenkins' (1965) design. The psychometric functions were similar across animals that differed markedly in degree of response bias. These functions differed in detail from those obtained previously in a visual luminance experiment (Terman and Kling, 1968), although in both experiments choice behavior in the region of decreasing stimulus control fit a normal probability model (*cf.* Engen, *in press*). In the present experiment, asymptotic accuracy at wide intensity differences reached approximately 95% correct choice, while the luminance functions all reached 99 or 100% correct choice. The reduction in control by the auditory stimuli may be attributable to the

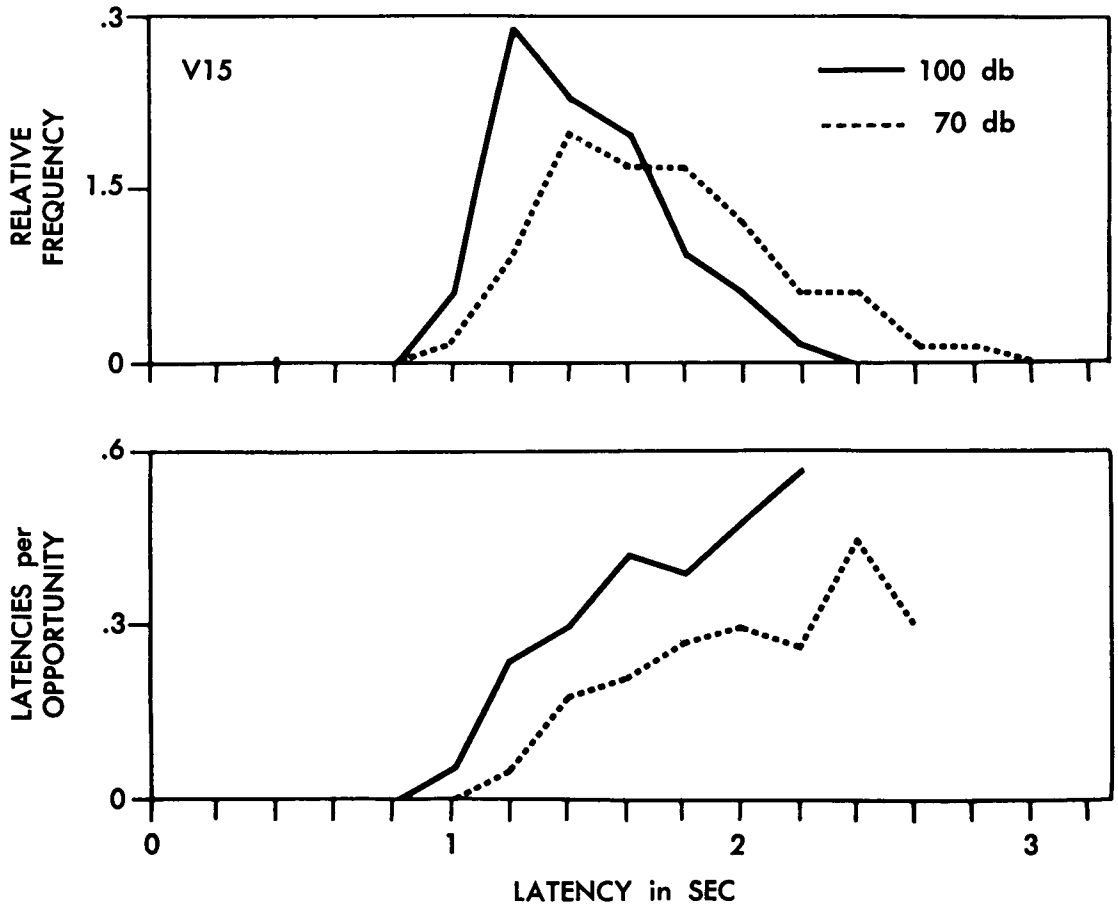


Fig. 9. Relative frequency and latencies per opportunity distributions during nondifferential pretraining, for Rat V15.

method of "free-field" presentation, where there is no arranged spatial correlation between the auditory stimulus source and the two response keys. In our previous luminance experiment, the discriminanda were simultaneously presented behind two response keys, so that the rat responded to the stimuli, while in the auditory situation the keys were equally illuminated at all times, and the stimuli were successively presented from a centrally located loudspeaker. Woodworth and Schlosberg (1954) suggested that spatial correlation between visual stimuli and responses facilitates discrimination acquisition. Heinemann and Rudolph (1963) found flattened gradients of visual stimulus control when the correlation of visual stimulus and response loci was reduced. In addition to response-locus factors, the temporal distinction between simultaneous and successive stimulus presentation procedures may be of importance in determining dis-

crimination accuracy. Signal-detection theory (Green and Swets, 1966) predicts finer discriminability in forced-choice procedures (which present both standard and comparison on each trial) than yes-no procedures (which present only one of the stimuli on each trial). In animal learning experiments, however, there is no clear consensus on acquisition rates under successive and simultaneous procedures (*cf.* Grice, 1949; Spence, 1952; Teas and Bitterman, 1952).

Auditory choice accuracy often reached chance level (approximately 50% correct) a few decibels before equality of the standard and comparison intensities was reached, resulting in a region of nondifferential choice between the points of subjective and physical equality. This effect is not commonly obtained in classical method-of-constant-stimuli experiments, for in the human experimental procedure the observer is allowed to report both

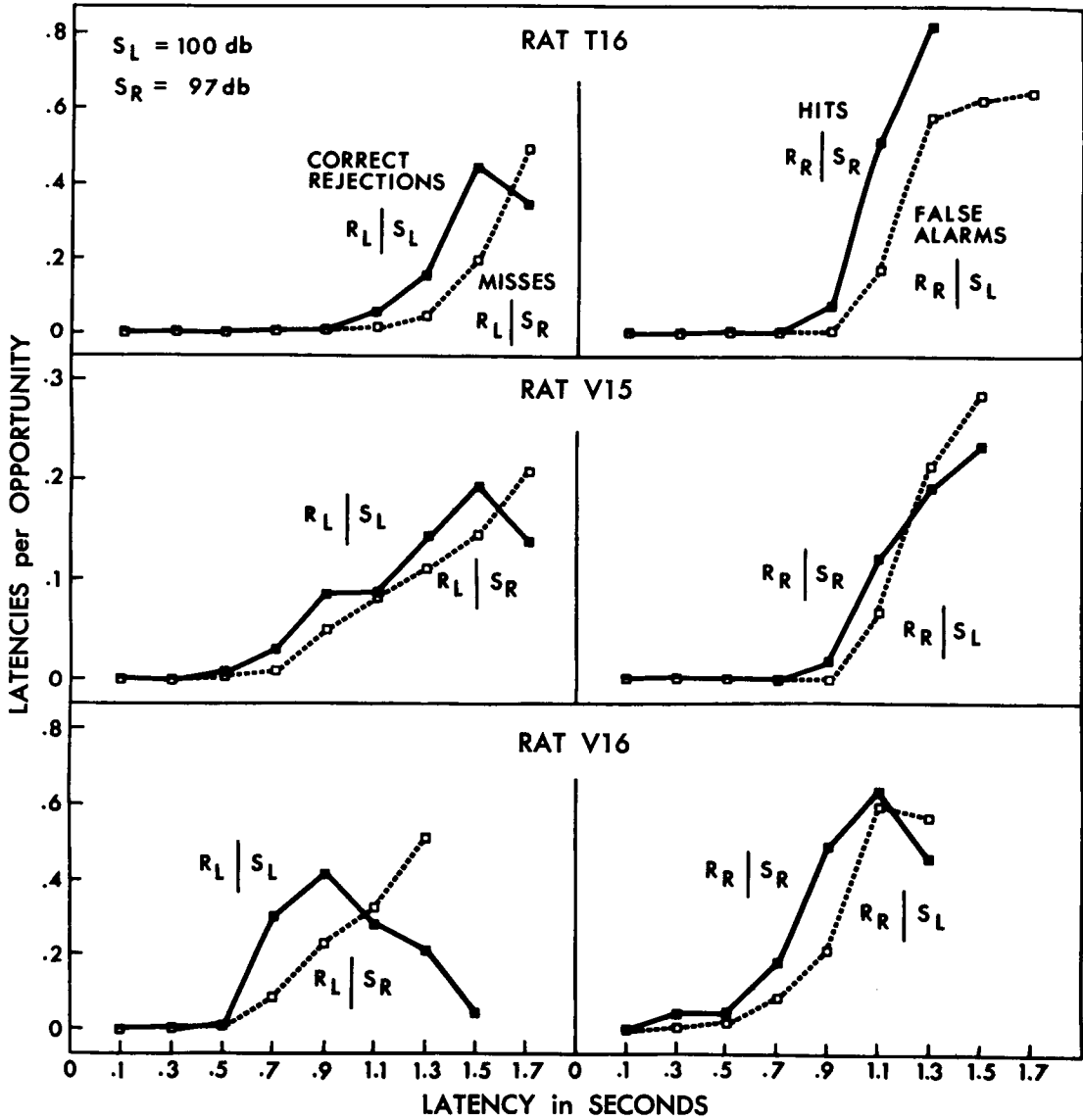


Fig. 10. Latencies per opportunity distributions for four latency classes during a period of low choice accuracy at 3-db standard-comparison difference. The ordinate scale is chosen for each animal to provide optimal data visibility; Rat V15, which showed generally longer latencies, is given a greatly expanded probability scale.

“greater than” and “lesser than” outcomes. Stimuli near physical equality ordinarily produce many reports of both “greater than” and “lesser than” in the constant-stimuli design. The present procedure did not allow the rat to “report” a “greater than” outcome, imposing, in effect, a 50% lower limit on the psychometric function. Further, it seems likely that the region beyond the point of subjective equality would be less pronounced in experiments where the animal can respond to the

stimulus, as in most visual discrimination procedures. Our luminance discriminability functions (Terman and Kling, 1968), for example, did not show such a region.

The results suggest that behavioral indices of discriminability are equally fine for animals with and without strong response biases. The degree of response bias, which becomes increasingly apparent at small intensity differences, is summarized by the correlation plot of hits and false alarms in Fig. 3. The animals remained

in relatively stable states of "isobias" as the problem became more difficult, failing to support the general impression that animals' position preferences are variable and unpredictable from session to session. If position preferences fluctuated nonsystematically as the intensity difference was decreased, the data points for individual subjects would be scattered throughout the entire space above the major diagonal. We have defined the stability of bias as the invariance of the ratio of false alarms to misses. An alternative bias index, proposed by Hodos (in press), implies that such invariance reveals a shift in the subject's signal detection "criterion" with increasing problem difficulty.

Throughout this experiment, the payoff matrix was symmetrical and identical across intensity values. In human experiments, symmetrical payoff matrices are used to minimize response biases (Green and Swets, 1966). Yet the animals in the present experiment maintained consistent between-subjects differences in degree and direction of response bias, even after extended training. A strong bias may be maintained as a superstitious chain: animals are often observed to approach the preferred key on every trial, later switching to the non-preferred key when appropriate. Extreme biases may allow the animal to come under control of sequential cues in the stimulus series (by obtaining runs of reinforcements on a preferred key and then switching), thus earning greater than 50% of available reinforcements in the absence of any stimulus differences. Although the Jenkins series partials out this factor on recorded trials, it is not eliminated. On several occasions, Rat T16 earned greater than 50% reinforcement on odd-numbered trials (when a switch after three reinforcements on the preferred key always would be reinforced), while responses on the even-numbered trials were at chance level.

The equivalence of the psychometric functions for 70- and 100-db standards (Fig. 7) makes it difficult to attribute the corresponding discrimination acquisition data of Pierrel *et al.* (1970) to a discriminability deficit at 70 db. In their experiment, 10-db differences in a 4.0-kHz sine tone were used as the stimuli in a multiple variable-interval extinction schedule, in which the more intense tone was correlated with variable-interval segments and the less intense tone was correlated with extinction

segments. The emergence of a differential response pattern in the two segments was much slower for a group of rats run with a 70-60 db intensity pair than for a group run with a 100-90 db intensity pair. Further, asymptotic performance was inferior for the 70-60 db group, due to greater responding in the extinction segment of the multiple schedule. Pierrel *et al.* (1970) suggest that a psychological distance (or "loudness") factor may be responsible for the performance deficit with low intensities, in the absence of a discriminability difference. Perhaps the group contrasts in their experiment would diminish if a punishment contingency were substituted for the extinction segment, in analogy to the timeout contingency for errors used in the present experiment.

Choice accuracy was partly determined by the direction of changes in comparison value, as illustrated by the psychometric functions obtained with increasing or decreasing stimulus differences (Fig. 8). Series effects in human psychophysics have been attributed to "habituation" or "anticipation" in method-of-limits experiments, where a rapid sequence of intensity values is presented. For example, the subject may persist in reporting "no stimulus" when the intensity is raised from subthreshold values. Although the present procedure used orderly sequences of comparison intensity change, large blocks of trials were given per session with a single intensity difference, with choice accuracy averaged over each block, more closely approximating the classical method of constant stimuli. It is possible that the decreased choice accuracy obtained with the sequence of increasing stimulus differences reflected an "habituation" effect, or loss of attention following sessions at zero or minimal stimulus difference. Indeed, one would expect a decrement in stimulus control after such testing, for the stimuli have lost their discriminative function and the paradigm is reduced to a 0.5 probability learning procedure. It is interesting that further training at large stimulus differences eliminated the choice accuracy decrement in a replication procedure. Since psychophysical tests generally attempt to reduce nondifferential responding to its limit, a series of decreasing stimulus differences is recommended for finer discriminability estimates. Similar recommendations have been made for training animals on diffi-

cult discriminations (Schlosberg and Solomon, 1943; Lawrence, 1952; Terrace, 1966).

The determinants of response latency in two-choice experiments are complex, but the data suggest that this measure may be more sensitive to stimulus differences than the choice measure. In discrimination acquisition, latencies commonly differentiate before the appearance of accurate choice behavior (Terman and Kling, 1968; Terman, 1968). In nondifferential pretraining, the animals in the present experiment showed shorter latencies in the presence of the more intense tone (stimulus intensity dynamism; cf. Fig. 9) although there was no differentiation of choice. In the discriminability test, an animal tends to respond more slowly before making an error. If responses on a single key (e.g., hits and false alarms) can be distinguished by their latencies, it would seem important to integrate such data with discriminability estimates based on choice. Time-based variables, such as latency, may prove more sensitive to minimal stimulus differences than the discrete choice data that form the basis of threshold psychophysics.

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