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AUDITORY SENSITIVITY AND EQUAL LOUDNESS IN THE SQUIRREL MONKEY (SAIMIRI SCIUREUS)[1]

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The effects of the type of reinforcer on auditory sensitivity and equal-loudness data were determined in the squirrel monkey. The monkeys, restrained and provided with earphones, were conditioned to depress and hold a bar down in the presence of a stimulus light and then to terminate the holding response after onset of a tone. In Experiment 1, the specified behavior sequence postponed electric shock; in Experiment 2, a food reinforcer was dependent on bar release during the tone. The shape of the auditory sensitivity function and the acuity level at each frequency were the same for the two procedures. The audible frequency range extended from below 0.125 kHz (lowest frequency used) to 46 kHz. Sensitivity was maximum at 8 kHz. Latency of bar release following tone onset served as the basic data for constructing a family of equal-loudness contours. The type of reinforcer appeared not to be a determinant of either the shape of individual loudness contours or the pattern of family of equal-loudness functions. At the lower sound-pressure levels, the equal-loudness contours closely paralleled the threshold curves. At more-intense levels, the contours tended to flatten and depend less on frequency.

The importance of a reinforcer *per se* to the behavioral analysis of sensory function in the nonhuman subject is well established (Blough, 1966; Blough and Yager, 1972; Stebbins, 1970*b*). However, the issue of which is the more effectual type of reinforcer—an aversive or an appetitive stimulus—is the subject of much discussion based on inconclusive empirical evidence.

One view receiving considerable support (Bragg and Dreher, 1969; Clack and Herman, 1963; Mitchell, Gillette, Vernon, and Herman, 1970; Mitchell, Vernon, and Herman, 1971) was advanced by Harris (1943). Harris compared the effectiveness of his aversive control technique with an appetitive procedure used by Wendt (1934) and concluded that aversive stimuli provide a more efficient means of conditioning behavior and collecting reliable data. A counterargument that is increasingly gaining favor (Stebbins, 1970*a;* Stebbins, 1971) is based on difficulties encountered with shock-avoidance procedures. Stebbins (1970*a*) surmised that behavior instability during threshold testing (and, consequently, large data variability) stems from administering electric shock on occasions when the subject fails to respond to a nonaudible stimulus. The present study measured auditory sensitivity and equal loudness in the squirrel monkey and compared functions obtained with aversive and appetitive techniques.

EXPERIMENT I: DISCRIMINATED AVOIDANCE PROCEDURE

METHOD

Subjects

Four mature male squirrel monkeys (*Saimiri sciureus*) (Animals 1, 2, 4, and 5) with no experimental history, ranging in weight from 0.6 to 1.0 kg, were housed individually in open mesh cages (45.7 by 81.3 by 61.0 cm) where they had free access to food and water.

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Apparatus

Experimental sessions were conducted in a double-walled, electrically shielded and sound-deadened room (Industrial Acoustics Company, IAC Model 1201-A) with individual monkeys restrained in a modified version of the primate chair (Figure 1) developed by Moody, Stebbins, and Miller (1970). A blue-colored lens transilluminated with a 24-V dc bulb (6 W) was attached to the restraining unit 12 cm from the subject at eye level. A response bar, secured to the chair at waist level, required a force of 80 g (0.8 N) with the arm fully extended for operation. The aversive stimulus consisted of a 60-Hz ac pulse delivered to the monkey through 0.64-cm aluminum rods that provided support for the feet. Animals 1 and 2 received a 5-mA (rms) shock of 1-sec duration. A 3-mA (rms), 0.5-sec shock was administered to Animal 4, and a 5-mA (rms), 0.3-sec shock was presented to Animal 5. Shock was generated by a noncommercial constant-current stimulator and de-

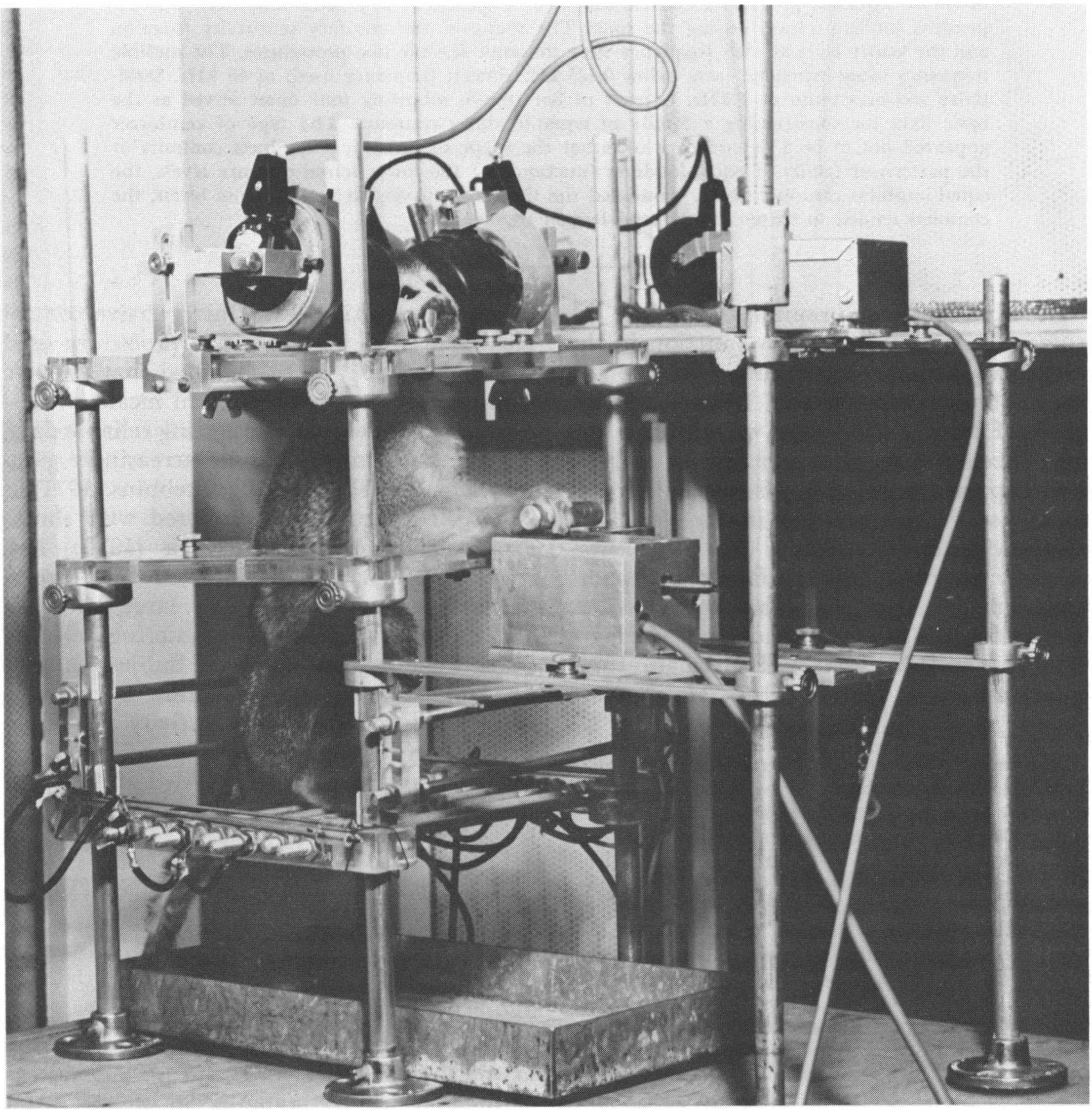

Fig. 1. Photograph of a squirrel monkey restrained in the primate chair during a discriminated avoidance session. A closed sound system is provided by the pair of earphone-couplers enclosing the subject's ears. The animal is holding the bar down after onset of the cue light, which is attached to a supporting rod at eye level.

livered to the electrodes through a 100 k-ohm series resistance.

Pure tones were presented binaurally through an earphone system similar to that described by Moody *et al.* (1970). It was necessary to interpose a coupler (5 by 5 by 2.5 cm) made of soft rubber between each earphone and the head to provide a closed sound system. In addition, this arrangement served to fixate the head and orient the body toward the visual cue and operandum (Figure 1). During experimental sessions, the acoustic system consisted of the serial arrangement of an audio oscillator, a decade attenuator, a noncommercial tone switch (rise and decay time of 10 msec, on/off ratio of 120 dB), and the earphones.

Aperiodically during the study, sound pressure (re: 2×10^{-4} dyne/cm^2) and harmonic distortion were determined for the earphones (Permoflux—PDR-600) at each frequency (0.125 to 32 kHz in octave steps and 40 and 46 kHz for the threshold functions; 0.250 to 32 kHz in octave steps for the equal-loudness contours) used in the experiment. To obtain these measurements, a 0.25-in. condenser microphone (cartridge type 4136, Brüel and Kjaer) was passed through the wall of the coupler to a position opposite the auditory canal of a nonexperimental squirrel monkey tranquilized intramuscularly with phencyclidine (Sernylan, 2 mg/kg). A cathode follower (type 265, Brüel and Kjaer), power supply (type 2301, Brüel and Kjaer), and an automated wave analyzer (General Radio, type 1900-A) with a graphic level recorder (General Radio, type 1521-B) were in series with the condenser microphone. The frequency response curves of the two earphones were not more than 5 dB apart at any given frequency. The harmonic distortion was no greater than 0.01 at 1.0 V rms (the maximum voltage used).

The experimental conditions were arranged with solid-state digital logic (BRS-Foringer). In addition, an on-line computer (PDP-8) and a programmable attenuator were used to collect the reaction-time data from which the equal-loudness measures were derived. These data were recorded in milliseconds on punched paper tape for off-line computations.

Procedure

The discriminated avoidance procedure (Figure 2) was adapted from a reaction-time procedure that required an appetitive reinforcer (Stebbins, 1966). After onset of the cue light, the subject was required to depress the bar and hold it down until the tone occurred (Figure 2A) 0.5 to 4.5 sec later (mean time of 2.5 sec). Bar release terminated the trial and initiated a 15-sec intertrial interval. To maintain behavior, a brief electric shock followed by a 3.0-sec intertrial interval was dependent on two departures from this sequence: (1) bar-release latency to the tone greater than 1 sec (Figure 2B); (2) bar release before tone onset (Figure 2C). Also, whenever bar-press delay exceeded 2.0 sec after cue-light onset, shock was administered and remained on until a bar-press response occurred (Figure 2D). Responding during the intertrial interval produced no scheduled consequences.

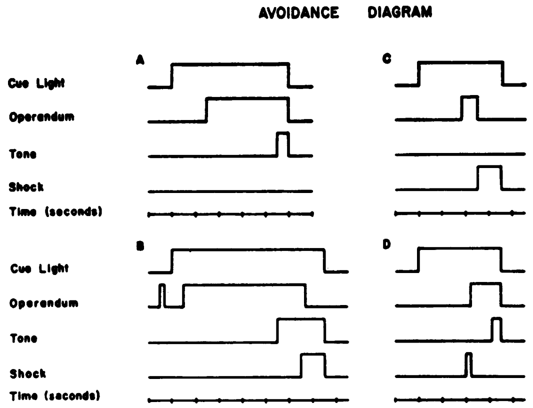

Fig. 2. Four schematic diagrams illustrating the interrelationships among the cue light, responding, and aversive stimulus under the discriminated avoidance procedure.

The psychophysical method of constant stimuli was combined with the behavior procedure to collect auditory sensitivity data. A warm-up period preceded each session of threshold testing. During this period, the intensity was varied (including no-tone) over 10 trials at one frequency. The frequency was varied across sessions. For each threshold determination, four stimuli in 10-dB increments were presented in mixed order. Each stimulus was presented for 10 trials. If bar release occurred within 1 sec after tone onset, electric shock was postponed, and a correct response was recorded. If the bar was held down for 1 sec during the tone, shock was administered, and an incorrect response was recorded. A complete auditory sensitivity function of 12 frequencies in octave steps was obtained in each 2-hr session.

Equal-loudness contours were derived from response-latency data (Cattell, 1902; Chocholle, 1940; Stebbins, 1966). To achieve minimal response latencies to the tone, the 1-sec bar-holding limitation was replaced with a limited hold that varied over a range of 100 to 500 msec (a mean of 300 msec) across trials. Once the behavior had stabilized, the 1-sec limited hold was re-introduced for 70% of the trials. These two limited holds were presented in random order across trials, and reaction-time data were collected only when the 1-sec limited hold was in effect. Latency-intensity functions were obtained over a frequency range of 0.25 to 32 kHz in octave steps. Data were obtained at each of three frequencies in a 4-hr session. For each latency-intensity function, six intensity levels at 10-dB intervals were presented in random order. Each stimulus was presented over 30 to 40 trials. A complete set of auditory threshold and equal-loudness data was obtained from only two subjects (Animals 1 and 5).

RESULTS

Auditory Sensitivity

Absolute threshold was defined as the intensity level to which a correct response to the tone occurred 50% of the time. The first four consecutive sessions in which threshold values did not differ by more than 5 dB were used in determining the maximum sensitivity level at each frequency tested. The median threshold of the last three sessions was used to plot sound pressure against frequency in Figure 3. These criteria were generally met with four to 19 determinations at each frequency.

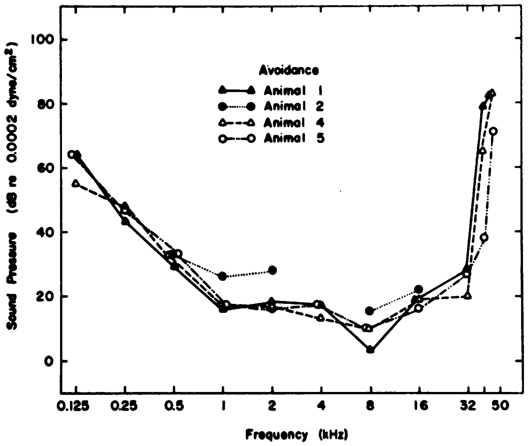

Fig. 3. Auditory sensitivity functions obtained for four subjects with the discriminated avoidance procedure. The minimal audible sound-pressure level is plotted against frequency.

Equal Loudness

A set of latency-intensity functions is shown for one animal in Figure 4. These reaction-time curves extended over a frequency range of 0.25 to 32 kHz in octave steps. The relatively small dynamic range of hearing at the extremes of the audibility range of *Saimiri* prevented inclusion of data for 0.125, 40, and 46 kHz. Each curve is a composite of two sets of data, with one interposing the other at equal intervals of 5 dB. The medians and quartiles for each set were obtained from the combined data of two consecutive sessions.

The lines of best fit for the reaction-time data in Figure 4 were determined by visual estimation and by applying Equation 1:

$$L = a + cI^n, \qquad (1)$$

where L is the response latency, a is the asymptote and has the effect of raising or lowering the entire curve, c positions the curve along the abscissa and gives the apparent effect of altering the curvature, I is the intensity in decibels (re: 2×10^{-4} dyne/cm^2), and since n is negative, the function is hyperbolic.

The family of equal-loudness functions derived from the latency-intensity curves illustrated in Figure 4 is shown in Figure 5. Each equal-loudness contour was defined in terms of the interpolated sound-pressure levels across frequency that corresponded to a given latency value. These data represent equal loudness along a broad extent of the dynamic range of hearing. Since the median reaction times to the more-intense tones were shorter, the contours are arranged from top to bottom in order of increasing latency criterion values. The auditory sensitivity function is included as the lower-most curve.

EXPERIMENT 2: APPETITIVE PROCEDURE

METHOD

Subjects

Two of the squirrel monkeys from Experiment 1 (Animals 4 and 5) were maintained at

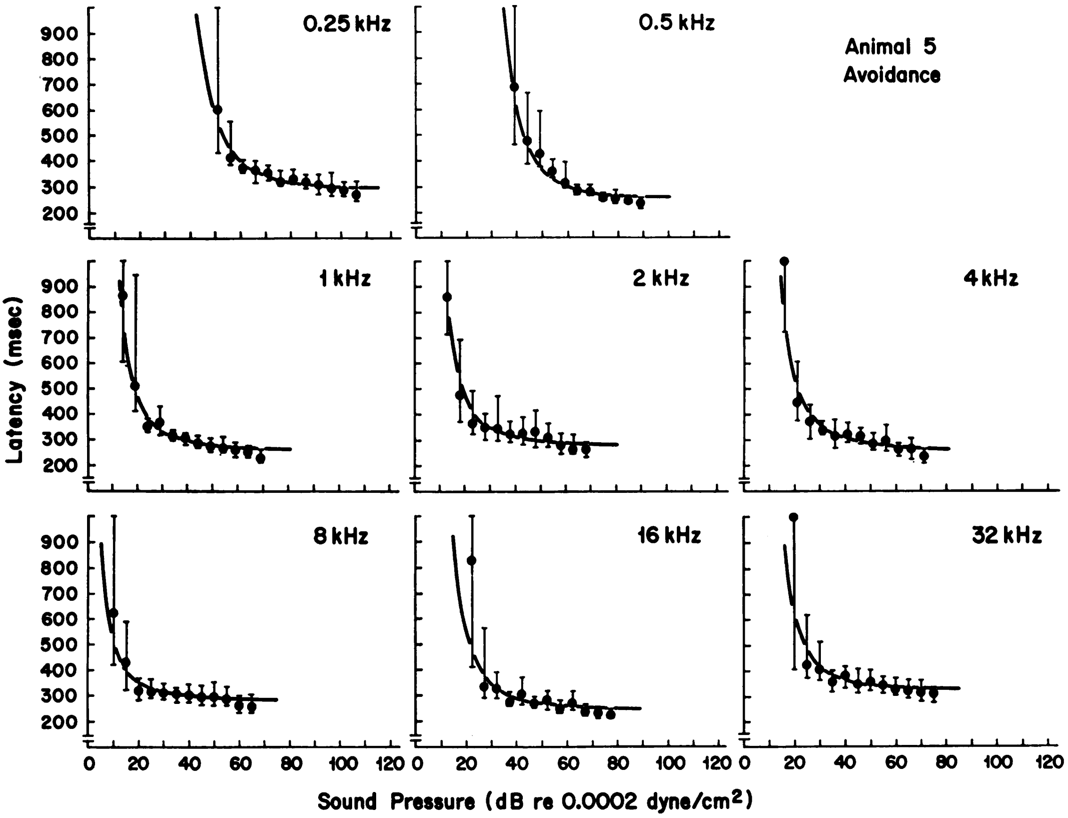

Fig. 4. Latency-intensity data obtained for one animal at several frequencies with the discriminated avoidance procedure. Median latency of bar release to the tone is plotted against sound pressure. The interquartile range for each data point is represented by the vertical line drawn through that data point.

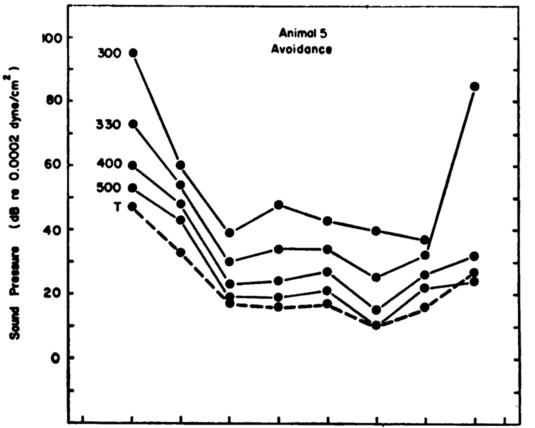

Fig. 5. A family of equal-loudness contours derived from the latency-intensity functions shown in Figure 4. Sound pressure is plotted against frequency. Latency criterion is indicated to the left of each contour. The absolute threshold function (T) is redrawn from Figure 3.

75% to 85% of free-feeding weights and were 22-hr food-deprived before each experimental session.

Apparatus

The restraining apparatus, scheduling equipment, and acoustical system were the same as those used in Experiment 1 with two important differences. First, a food-delivery system was substituted for the electric-shock generator. The food dispenser (Gerbrands, model D) and delivery tube were positioned to assure immediate presentation of the reinforcer at the subject's mouth. The reinforcer consisted of 45-mg whole diet banana-flavored food pellets (P. J. Noyes). Second, an electronic counter (Hewlett-Packard, model 523DR) and a digital printer (Hewlett-Packard, model 560A) replaced the on-line computer and paper-tape punch for the recording of response latencies (in milliseconds).

Procedure

The reinforcement contingencies were analogous to those described for the aversive control procedure in Experiment 1 (compare Figures 2 and 6). The subject was required to press the bar down in the presence of the cue light and to continue holding it down until tone onset (Figure 6A) 0.5 to 4.5 sec later (mean time of 2.5 sec). Bar release terminated the trial and initiated a 4-sec intertrial interval. The desired behavior was maintained by making the food reinforcer dependent on latencies shorter than 1 sec (Figures 6A and 6C). In addition, a timeout event (termination of the trial followed by a 15-sec intertrial interval) followed each bar release that occurred before tone onset (Figure 6B) and each prolonged holding response (beyond 1 sec) to the tone (Figure 6C). Delayed bar press to the cue light (Figure 6D) and intertrial interval responding had no scheduled consequences.

The psychophysical technique described in Experiment 1 was combined with the present behavioral procedure to measure auditory sensitivity. If bar release occurred within 1 sec after tone onset, a correct response was recorded and food was delivered. If the bar was held down for 1 sec during the tone, an incorrect response was recorded, the reinforcer was withheld, and the subsequent trial was postponed for 15 sec. Absolute threshold determinations were obtained for four to six frequencies in a 1- to 2-hr session. The frequencies ranged from 0.125 to 32 kHz in octave steps and 40 and 46 kHz.

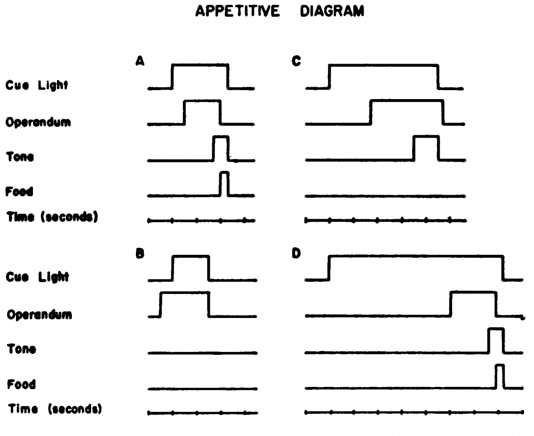

Fig. 6. Four schematic diagrams illustrating the interrelationships among the cue light, responding, and reinforcer under the appetitive procedure.

As in Experiment 1, latency-intensity functions were used as the basic data to generate a family of equal-loudness contours. Preliminary findings (Green, 1971) suggested an alternative to the procedure used in Experiment 1 to achieve minimal response latencies to the tone and to maintain behavioral control while collecting data. The method of successive reductions in the limited hold was adapted from a technique developed by Miller, Glickstein, and Stebbins (1966) and used by Stebbins (1966) in an investigation of equal loudness in the macaque. This consisted of decreasing the 1-sec bar-holding limitation to the tone in successive intervals of 100 msec until a duration of 300 msec was attained. Once the behavior had stabilized, the 1-sec limited hold was re-introduced, and reaction-time data were collected over a frequency range of 0.125 to 32 kHz in octave steps and 40 and 46 kHz. With the exception of the extreme upper and lower frequencies, six tones separated by 15-dB intervals were chosen to collect data for each latency-intensity function. The smaller dynamic range of the squirrel monkey at the extremes of the audibility range permitted a 10-dB separation and/or a smaller number of stimuli. Each stimulus was presented randomly for 30 trials. Data were obtained at one frequency in a 1- to 2-hr session. A complete set of auditory threshold and equal-loudness data were obtained from only one (Animal 4) of the two monkeys.

RESULTS

Auditory Sensitivity

As in Experiment 1, the point of maximum auditory sensitivity was defined in terms of the sound pressure corresponding to the 50% response level. The auditory threshold function for Animal 4 is represented by the appetitive curve in Figure 7. Each data point was determined by the first four consecutive sessions in which the individual threshold values did not differ by more than 5 dB. The median threshold of the last three sessions at each frequency was used to construct the audibility curve. Four to seven threshold determinations at each frequency were necessary to meet these criteria. The curve labelled avoidance was redrawn from Figure 3 for comparison.

Equal Loudness

Latency-intensity data are shown for Animal 4 in Figure 8. Median latency was plotted

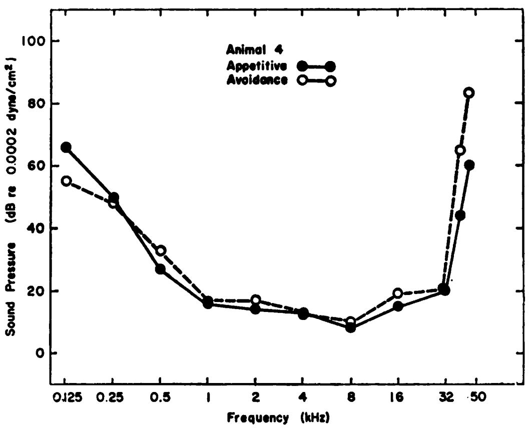

Fig. 7. Auditory threshold data for one animal. The data for the function with the filled data points were obtained under the appetitive procedure. The unfilled data points represent data obtained under the aversive control procedure, and are redrawn from Figure 3 for comparison.

against sound pressure. The frequencies are identical to those shown in Figure 7 for the auditory sensitivity curves. Each function is composed of data points from two successive sessions at equal intervals in an alternating sequence. The line of best fit was determined visually and by applying Equation 1.

The method of equal latency was used to produce the sound pressure-frequency plot illustrated in Figure 9 for Animal 4. Each individual loudness contour was derived from the smooth curves (Figure 8) by determining the stimulus level at each frequency necessary to produce a given latency criterion. The latency criterion value is indicated to the left of each curve, and the lower-most function is the absolute threshold curve for the same subject.

DISCUSSION

The primary objective of the present research was to determine whether auditory sensitivity and equal-loudness data obtained with behavioral procedures depend upon the nature of the reinforcer. Many investigators (Bragg and Dreher, 1969; Clack and Herman, 1963; Harris, 1943) are of the opinion that data obtained when the reinforcer is an aversive stimulus are more reliable than those obtained when the reinforcer is an appetitive stimulus; other experimenters (Stebbins, 1970*a*, Stebbins, 1971) hold the opposite view.

The present findings failed to support either position. No difference was found between auditory threshold functions obtained with an aversive stimulus and those obtained with an appetitive stimulus. Although a modest difference was observed in the latency-intensity data for the two reinforcement systems (a greater sound pressure was required with the positive reinforcer), the difference was not of sufficient magnitude to produce discrepancies in the equal-loudness contours. The shape of corresponding loudness contours and the pattern of the family of equal-loudness functions was not significantly different for the two behavior procedures.

These results suggest that sensory data are not influenced by the type of reinforcer used to maintain behavior during testing. The procedural difficulties and data discrepancies reported in other studies may have been a function of the reinforcement contingencies and behavior stability criteria, rather than stemming from inherent properties of the reinforcer. Further, the equal-loudness findings are consistent with Moody's (1970) contention that the absolute value of a median response latency is irrelevant to the derived equal-latency function. Moody argued that the critical factor consists of holding all variables constant except the test stimulus when collecting response-latency data.

The auditory capacity of the squirrel monkey may be compared to that of other nonhuman primates. Auditory threshold data are available for only seven (Dalton, 1968; Elder, 1934; Farrer and Prim, 1965; Fujita and Elliott, 1965; Seiden, 1958; Wendt, 1934) of the 31 genera of simiae, and equal-loudness data have been described for only one species (Stebbins, 1966). Data describing the audible frequency range of the nonhuman primate are incomplete. Of the seven genera examined, the upper limit was determined for only *Callithrix* (Seiden, 1958), *Macaca* (Stebbins, Green, and Miller, 1966), and *Pan* (Farrer and Prim, 1965), and there has been no attempt to measure the lower end of the continuum. If placed in a phylogenetic context, the present data for the upper frequency cutoff (46 kHz) in the squirrel monkey, together with previous findings, suggest that high-frequency hearing is essentially the same in the New and Old World monkey (about 40 to 45 kHz) and that high-frequency receptivity is substantially lower in

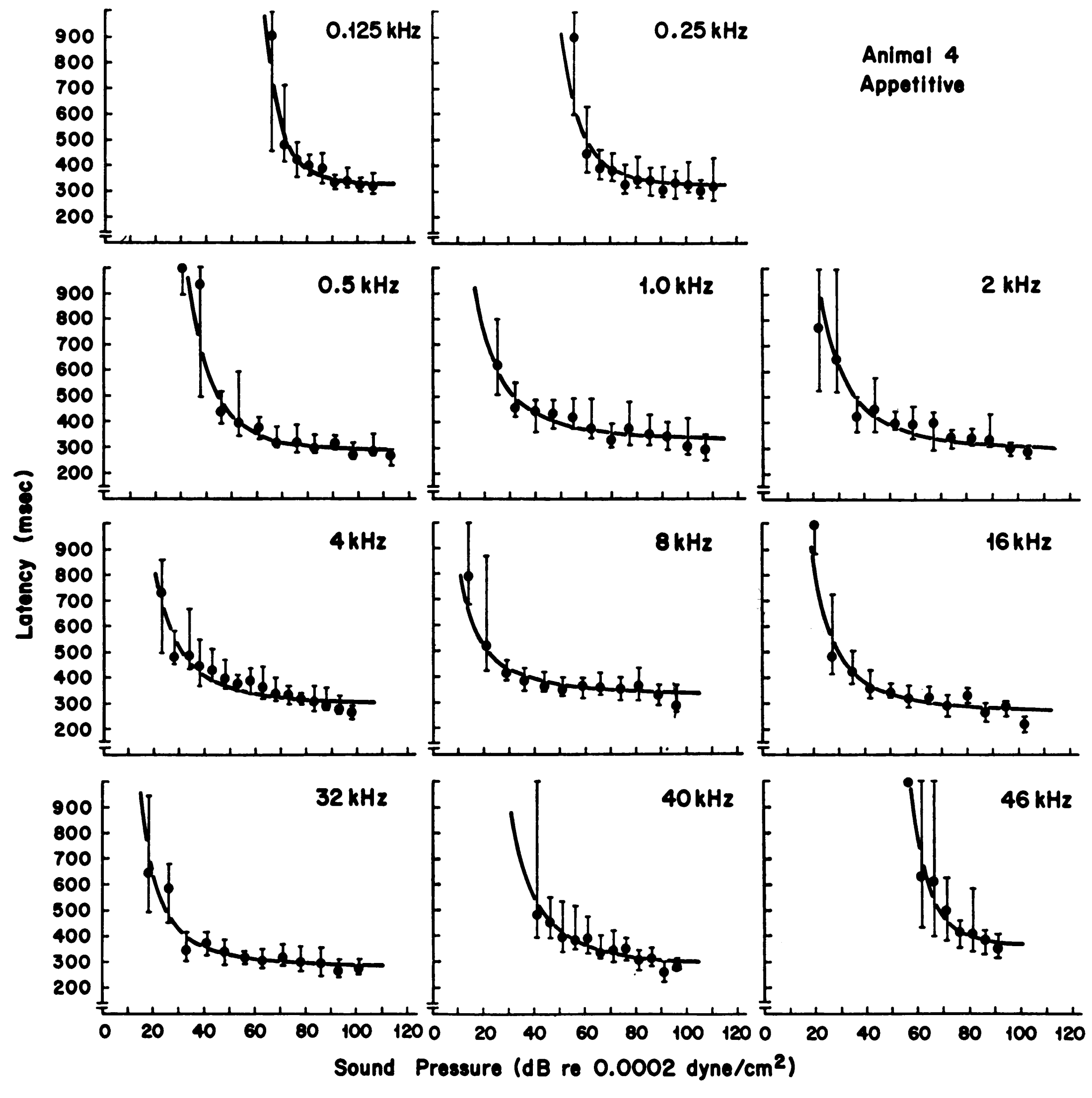

Fig. 8. Latency-intensity data obtained for one animal with the appetitive procedure. The frequencies are the same as those used in the collection of data for the auditory threshold functions shown in Figure 7. Median latency of bar release to the tone is plotted against sound pressure. The interquartile range for each data point is represented by the vertical line drawn through that data point.

the ape (20 to 25 kHz). With respect to the general configuration of the threshold function, the present data agree with other findings, in that there is a continual decrease in sensitivity for frequencies below 1 kHz and above 8 kHz. The change is less abrupt at the lower end of the curve. One important difference in the present data consisted of the smoothness of the middle portion of the function. Previous data indicated that the mid-range frequency response of the nonhuman primate is characterized by an abrupt decrease ("dip" in curve) in sensitivity at one or more frequencies. Other data from the squirrel monkey (Fujita and Elliott, 1965) suggest that this discrepancy is subject- and/or procedure-related, rather than a species characteristic. The best frequency of 8 kHz was consistent with previous findings for the nonhuman primate.

The pattern of the family of equal-loudness functions for the squirrel monkey may be compared with related data obtained with similar reaction-time procedures from the human (Chocholle, 1940) and the macaque (Stebbins,

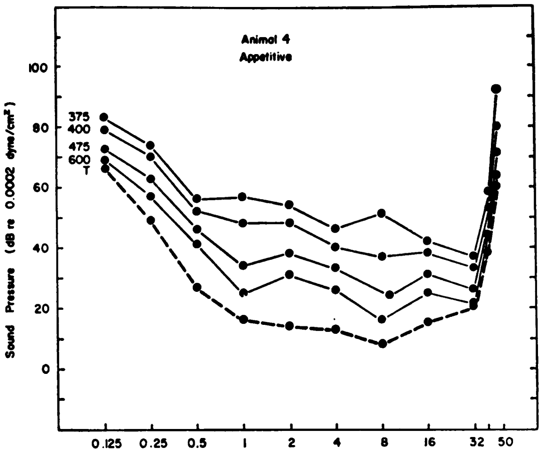

Fig. 9. A family of equal-loudness contours derived from the latency-intensity functions shown in Figure 8. Sound pressure is plotted against frequency. Latency criterion is indicated to the left of each contour. The absolute threshold function (T) is redrawn from Figure 7.

1966). For the squirrel monkey and the human, the lower equal-loudness contours parallel the auditory sensitivity function. When the macaque threshold function, published separately by Stebbins *et al.* (1966), is plotted on the same graph as the macaque equal-loudness functions, a discrepancy is seen. With the exception of data points at 1 kHz, equal-loudness contours corresponding to low sound-pressure levels are displaced significantly above the threshold function. Saslow (1972) attributed this discrepancy between the human and macaque data to the greater behavioral control provided by verbal instructions in comparison to that offered by nonverbal reinforcement contingencies. But it is more likely that the difference may be accounted for in terms of the point-to-point plot of the data, frequency selection (only two frequencies in the mid-range), and the particular set of latency criteria used to determine the family of equal-loudness contours, since the appetitive procedure in the present study used essentially the same set of reinforcement contingencies. Also, the steady-state behavior in the present study did not differ significantly from that reported by Stebbins. The equal-loudness data for these three primates are in good agreement at the more intense sound-pressure levels. The curves tend to flatten as they become less dependent on frequency.

In conclusion, the present experiments demonstrated that auditory threshold and equal-loudness data are invariant with respect to the type of reinforcer used to maintain the specified behavior. The results support the use of reaction-time data to measure equal loudness. In addition, they amplify and extend the generality of the view that human psychophysical techniques may be used in conjunction with a set of reinforcement contingencies to estimate quantitative differences in the perception of stimuli by nonhuman subjects.

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