FREQUENCY DL IN THE PIGEON AS DETERMINED BY CONDITIONED SUPPRESSION

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Behavioral studies involving either absolute or differential auditory thresholds on animals have employed avoidance conditioning (Culler, et al., 1935; Elliott, et al., 1960; Trainer, 1946), respondent conditioning (Dworkin, et al., 1940; Tumjanzeff, 1931; Wassiljew, 1933), and operant conditioning (Clack and Harris, 1963; Elliott, et al., 1962; Frazier and Elliott, 1963; Heise, 1953). A major problem with all of these techniques has been interval responding; that is, positive responses by the animal in the absence of the auditory stimulus.

With operant techniques the problem has usually been that the response to the auditory stimulus and the hunger motivated behavior are one and the same. Because of this, at near threshold levels of the stimulus, ambiguity of response often becomes so marked that data must be rejected. Thus, extensive delays may result and long periods of retraining become necessary (Dworkin, et al., 1940; Heise, 1953).

In avoidance conditioning, the response to the auditory stimulus and the avoidance of the aversive stimulus are identical. Thus, as in respondent and operant techniques, the problem of interval responding must be dealt with. In addition, avoidance paradigms may produce behavior problems in the experimental animal. According to Elliott, et al. (1962), a major disadvantage of using avoidance conditioning is that "neurotic" behavior develops in the testing situation. In studies in which threshold is repeatedly determined this neurotic behavior may develop to the extent that reliable thresholds cannot be found.
Recently, Dalton (1967) has shown that a modified version of the conditioned suppression technique (Estes and Skinner, 1941) provides a reliable method for measuring the absolute auditory sensitivity of pigeons. Hendricks (1966) had earlier shown the technique to be both rapid and reliable in obtaining vision flicker thresholds in pigeons.

Conditioned suppression, as a technique for determining sensory thresholds, is based upon the findings of Estes and Skinner (1941) that operant behavior can be suppressed by the pairing of a neutral stimulus such as light or tone with a brief unavoidable electric shock. Conditioned suppression thus permits the advantages of aversive control while maintaining the behavior of the organism on a positive reinforcement schedule. The problems of interval responding are minimized since the hunger motivated behavior and the response to the stimulus are no longer one and the same. The ambiguity at near-threshold levels of the stimulus is greatly reduced.

Since the conditioned suppression technique has been shown to be effective in visual and absolute auditory threshold studies with pigeons, the present experiment was designed to determine whether the technique could be used effectively in measures of auditory difference thresholds. It was felt that DL measures on the pigeon, an animal with relatively poor auditory discriminatory ability (Heise, 1963; Tjumianzeff, 1931; Wassiljew, 1933; Wever and Bray, 1936), should provide a stern test for the technique.

**METHOD**

**Subjects.** Three White Carneau Pigeons were used as subjects. The pigeons were two months of age at the beginning of the study. They were maintained at about 80% of free-feeding body weight throughout the experiments.

**Apparatus.** Figure 1 is a block diagram of the stimulus-producing and -controlling apparatus. The signal from oscillator A served as the reference tone while oscillator B produced the comparison tone. The alternator allowed either tone A or tone B to pass to the electronic switch which pulsed the signal. The pulsed signal then passed through the attenuator to the loudspeaker.

The reference frequency was set by adjusting oscillator A to zero beats with the line frequency and reading directly from the frequency dial.
of the oscillator. Error of the reference tone was less than 1.0% when checked by a Hewlett Packard Model 521C frequency counter. The comparison frequency was calibrated by setting oscillator B to zero beats with oscillator A using a Lissajous figure on scope A for monitoring. Frequency increments were controlled by adjusting the "cycles increment" dial on oscillator B. The frequency increments were within one cycle of the dial reading when monitored on the frequency counter. Scope B was used to monitor the signal (either A or B) which was passing to the loudspeaker. The purity of the signal could be continuously checked in this way and any undesired transients would be readily detected.

The intensity outputs from the two oscillators were matched by adjusting internal attenuators while monitoring with the VU meter. Calibration of the intensity of the auditory signal was accomplished by putting the microphone from an Allison Model 300 audiometer calibration unit in the position of the pigeon's head and noting the sound pressure level (SPL).

In order to minimize the possibility of transients, all switching was done during the "off" phase of the electronic switch. This was accomplished by taking a portion of the audio signal from the electronic switch to an isolation transformer, the output of which fed into an amplifier. The
amplifier boosted the signal sufficiently to operate a normally closed relay. This relay, when closed, allowed a negative pulse to reach the alternator which in turn switched from one oscillator to the other. However, this switching could occur only when the relay was closed, i.e., when no signal was passing through the electronic switch.

When the electronic timer was in the "off" position, the opening and closing of the relay had no effect on the alternator. When the timer was "on", however, each pulse from the electronic switch resulted in the opening and closing of the relay and a switching of the alternator. Thus, when the timer was "off", only signal A passed to the speaker; when the timer was "on", signal B replaced every second pulse of signal A. The electronic timer, therefore, controlled the stimulus presentation.

The instrumentation used in the operant portion of the apparatus consisted of standard electrical switching circuits.

The training box was a plywood chamber 10 in. long, 8 in. wide, and 12 in. high with an aluminum faceplate for key mounting. The key was a standard Harvard Apparatus Co. pigeon key illuminated from behind by a small lamp. A 10 in. loudspeaker formed the top of the box. This large speaker located immediately over the bird’s head assured that the pigeon would be in the sound field even if it moved around somewhat.

The training box was placed inside the test chamber which consisted of two double-walled boxes, one inside the other. These boxes were joined by hoses and ventilation was provided by pulling air through a baffle system on either end of the outside box. Noise levels within the test chamber were below 40 db SPL (lower limits of measuring equipment) when a 200 c/s high-pass filter was placed in the line. Without the filter, the low-frequency noise levels fluctuated up to about 65 db SPL.

Procedure. Difference limens (DLs) for frequency were determined on three pigeons for the frequencies .5, 1, 2, and 4 kc/s. All measures were made with the stimulus at 50 db above normal threshold for the pigeon. Data taken from Dalton (1967) and Heise (1953), were used as the references for normal hearing.

The shaping of the pigeons to peck the key was carried out in the presence of a pulsing 2 kc/s tone from oscillator A. Each pulse had a duration of 200 msec with a 50% duty cycle. Shaping was carried out in
the presence of a 2 kc/s tone because according to Dalton (1967) and Heise (1953) this frequency is the one at which the pigeon's ear is most sensitive.

Training sessions were carried out daily from the time of initial hopper training until completion of threshold data collection. Each training session was 1 hr in duration. Figure 2 shows a sample of a cumulative recording of the responses of one bird after his response rate had stabilized.

After approximately 50 training sessions, a stable response rate had been established on a variable interval 2-min schedule of reinforcement for all three birds. At this point conditioned suppression training was begun by alternating tone B with tone A for a 20-sec period and terminating this alternation of the signals with an electric shock. The shock was delivered through implanted electrodes as described by Azrin (1959). During the training sessions tone B was always higher in frequency than tone A by a factor of at least 0.25.

Fig. 2. A cumulative recorder sample of response baselines just prior to suppression training.

Fig. 3. A cumulative recorder sample of responses showing suppression to a stimulus.
Once suppression training was accomplished, the frequency difference between tones A and B was reduced by lowering tone B until threshold was reached. During this period an intermittent shock was used in order to minimize problems associated with shocking the birds at sub-threshold levels. Using this procedure, it was not necessary to shock on the initial presentation of any new stimulus level. If suppression was evident on the first presentation, subsequent presentations at this level could be terminated with a brief shock. Figure 3 is a portion of the cumulative recording of the responses of one bird showing suppression to the stimulus.

Threshold was taken as the least difference between the two tones at which a suppression ratio of 0.5 or higher was obtained on three of five consecutive presentations. The suppression ratio was calculated by subtracting the per-stimulus response from the pre-stimulus response and dividing the difference by the pre-stimulus response (Hoffman, et al., 1963). The number of responses made during the 20 sec immediately preceding onset of change in the frequency of the stimulus was the pre-stimulus, while the number of responses made during the 20 sec in which the frequency was changing was the per-stimulus response. Using this formula, complete suppression gives a ratio of 1.0, and a pre-stimulus and per-stimulus response which are equal gives a ratio of 0. Electrical impulse counters were used to record pre- and per-stimulus responses.

Sham trials were introduced periodically in order to insure that the birds were not responding to some stimulus other than a frequency difference. The sham runs were carried out with all equipment settings the same as for DL measures except that the two oscillators were set to the same frequency. A minimum of five sham trials were run on each bird at each frequency.

In the threshold data reported in this paper, thresholds are the smallest differences in frequency at which suppression (0.5 or higher on three of five consecutive presentations) could be obtained a minimum of five times. Frequency changes at near-threshold values were in steps of 0.005 times the reference frequency.
RESULTS

Table 1 presents the absolute and relative DLs for frequency obtained in the present study. It is interesting to note that these DLs are approximately ten times larger than, and follow a similar pattern as, the data reported by Shower and Biddulph (1931) for humans. The data also follow the same pattern and are larger by a factor of about three than the best reported data for cats (Elliott, et al., 1960). Figure 4 shows these relations.

<table>
<thead>
<tr>
<th>Bird No.</th>
<th>0.5</th>
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<th>2</th>
<th>4</th>
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<tr>
<td>Mean</td>
<td>21.7</td>
<td>.043</td>
<td>26.7</td>
<td>.027</td>
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</table>

![Fig. 4. Relative DLS for frequency in c/s for humans (Shower and Biddulph, 1931), cats (Elliott, et al., 1960) and for pigeons (present study).](image)

![Fig. 5. Differential thresholds in c/s at frequencies from 0.5–4 kc/s. Triangles represent Bird No. 29, squares Bird No. 31, and circles Bird No. 46. The line represents a Weber fraction of 0.024.](image)
Figure 5 shows the thresholds obtained on the three birds in the present study plotted along a line representing a Weber fraction of 0.024. A striking feature of this figure is the compact nature of these data. The DLs for the three birds were quite similar. Except for 0.5 kc/s the data points fall remarkably close to the predicted line.

The DLs obtained in the present study are not directly comparable to the results of the frequency discrimination studies on pigeons by Tjumjanzeff (1931) and Wassiljew (1933) because of differences in frequencies tested and methods of reporting results. However, generally, the data in the present study would indicate that the pigeon can detect frequency differences of 1/8 to 1/4 the size suggested by the earlier reports.

The amount of time required for suppression training varied from three days for birds No. 29 and 46 to seven days for bird No. 31. After seven to ten days of suppression training, the response patterns of all three birds were stable enough to permit collection of threshold data.

Frequency generalization was good. The birds, while taking three to seven training sessions to establish initial suppression, suppressed in 10 to 20 pairings of the stimulus and shock when a new frequency was introduced. As a result, threshold determination for any given frequency after the first usually required only four to seven test sessions. The entire period from hopper training through data collection took approximately 85 days.

A sham trial consisted of three to five presentations with the two oscillators set to the same frequency. At least five sham trials were run on each bird at each frequency. This means that a minimum of 60 sham trials were run. Of these, none showed suppression (0.5 or higher on three of five presentations).

**DISCUSSION**

*Conditioned Suppression.* Conditioned suppression to auditory frequency difference was not obtained as readily on the pigeons in the present study as was reported by Dalton (1967) for absolute auditory threshold sensitivity, and by Hendricks (1966) for visual flicker threshold. Dalton found evidence of suppression within the first two sessions of stimulus-shock presentations and found suppression ratios to be consistent over the full seven days of conditioned suppression training. Hendricks reported that
evidence of suppression was apparent within the first session of flicker-shock presentations, and that a stable suppression baseline was obtained on all birds by the seventh day of conditioned suppression training.

In the present study, birds No. 29 and 46 first evidenced suppression during the third training session of stimulus-shock presentations while bird No. 31 showed no suppression until the seventh day of training. All three birds required relatively high levels of shock in order to establish suppression. Even after suppression training had been accomplished, it remained somewhat unstable and the birds appeared to lose the stimulus-shock association rather rapidly unless moderate shock levels were maintained.

After about 10 days of suppression training, however, measures of thresholds became quite reliable. While the inconsistent nature of the responses resulted in no F-ΔF differences at which 100% suppression occurred, there was a definite change in responses at sub-threshold levels. Suppression (0.5 or greater on three of five presentations) was not obtained at sub-threshold values on any bird at any frequency. In other words, if suppression was obtained one time at a given stimulus level, it could be obtained five times at that level. Thus, while the birds tended to be somewhat inconsistent in responding to supra-threshold stimuli, they were extremely consistent in not responding to sub-threshold stimuli. This is in line with Hendrick's (1966) observation that at the critical frequency, an abrupt change was observed in the suppression behavior.

A major problem in all behavioral studies is the maintenance of stimulus control of the organism at near-threshold values of the stimulus. If there is a loss of stimulus control it often results in lengthy retraining periods or rejection of data at near-threshold values. Both Hendricks (1966) and Dalton (1967) report excellent maintenance of stimulus control using the conditioned suppression technique. The present study did not show this control to the degree reported by Hendricks and Dalton; however, control was remarkably good. No extensive retraining was necessary, and no data were rejected due to loss of stimulus control.

*Difference Limens.* If Weber's Law may be applied to frequency discriminations, \( \frac{\Delta F}{F} \) should be a constant. Except at 0.5 kc/s, the data obtained in the present study fall rather close to a line describing a Weber
fraction of 0.024 (see Fig. 5). This variation from the Weber fraction at
0.5 kc/s has also been observed in humans by Shower and Diddulph (1931)
who found that at frequencies below 1 kc/s the absolute DL is roughly
constant and above 1 kc/s the relative DL is approximately constant. A
partial explanation for this difference in discrimination for low- and high-
frequency sounds may be related to the two types of frequency analysis
which occur in the cochlea. According to Davis (1961) we should expect
the psychoacoustics of low frequency sounds to be different from the psy-
choacoustics of high-frequency sounds.

SUMMARY
Auditory DLs for frequency were determined on three White Carneaux
pigeons using a modified conditioned suppression technique for training.
The frequencies 0.5, 1, 2, and 4 kc/s were tested by a modified descending
method of limits. The data collected fitted well to a line describing a
Weber fraction of 0.024 except at 0.5 kc/s where a fraction of 0.043 better
described the results. The frequency DL in the pigeon is from 1/8 to 1/4
the size previously reported.

The conditioned suppression technique proved to be a very satis-
factory tool for the collection of differential threshold data on pigeons.
The technique was effective in maintaining stimulus control of the organism
at near-threshold values. Stimulus generalization was good and extended
retraining was not necessary when going from one frequency to the next.

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