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STIMULUS CONTROL OF HEART RATE BY AUDITORY FREQUENCY AND AUDITORY PATTERN IN PIGEONS[1]

A new method was used to investigate auditory discrimination in pigeons. Basically, the method involves the repeated presentation of one stimulus preceding the single presentation of a different stimulus that is followed by shock. Stimulus control is assessed by the increase in heart rate that accompanies the presentation of the second stimulus. In Experiment 1, the efficiency of the method was explored by determining the frequency difference thresholds of pigeons at 500, 1000, 2000, and 4000 Hz. Weber fractions comparable to those reported in an earlier study using the conditioned suppression method were obtained. Experiment 2 demonstrated that, contrary to results of earlier studies, auditory temporal patterns can exercise differential stimulus control in pigeons. One stimulus consisted of the presentation (once per second) of a 1000-Hz pure tone of 150 msec duration followed by a 2000-Hz pure tone of equal duration; the other was the same except for the reversed order of the frequency components. Results indicated that the frequency pattern and not the loudness pattern of the stimuli was the cue controlling heart-rate changes.

Vocalizations appear to be used as cues for species and individual recognition in doves and pigeons and play an important part in their social communications (Beer, 1970). This ethological evidence seems to demand that these species be capable of auditory pattern discrimination, since the main distinguishing characteristic of the calls is their temporal patterning. However, while studies on the ontogeny of avian calls have produced evidence of excellent tone-pattern discrimination for a number of bird species (Konishi and Nottebohm, 1969), they have failed to do the same for doves (Nottebohm and Nottebohm, 1971). Krasnegor (1971) found differential control over key-pecking behavior of pigeons when the stimuli were two tones differing in frequency, but was unable to obtain such control when the stimuli were two tone patterns. Previously, similar attempts of our own also failed to demonstrate stimulus control with auditory patterns.

The present paper, however, illustrates stimulus control with auditory patterns. More specifically, Experiment 1 describes a new technique for investigating stimulus control using tone frequency. Experiment 2 utilized this technique to demonstrate stimulus control using auditory patterns.

EXPERIMENT 1

METHOD

Subjects and Apparatus

Two pigeons (*Columba livia*) served as subjects. Their electrocardiogram (EKG) was recorded by using stainless-steel hypodermic needles as the electrodes. They were inserted into the superficial layers of the skin by lifting a feather and inserting the needle through the resulting fold. This procedure produced no signs of pain in the subject. To ensure retention, small corks were impaled on the tips of the needles. Two such electrodes were placed close to the axilla rostrally from the wings; two additional needles, placed just anterior to the legs, served both as indifferent and as shock electrodes. The subjects were wrapped lightly with a length of cloth strip so that vigorous wing movement was impossible. Their legs were also bound together to prevent their scratching at the electrodes or wires. This pro-

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cedure slightly impeded breathing, and thus depressed the baseline heart rate, but *changes* in heart rate (that were of interest in this study) were still very apparent.

Testing was conducted in a ventilated, sound-attenuating chamber measuring 60 by 60 by 60 cm. The walls of the chamber were 7 cm thick and were constructed from polystyrene and acoustic tiles between plywood layers. The subject was placed, on its back at a 45° angle, in a foam rubber "cradle" 5 cm beneath the 10-cm speaker (Radiospares Longthrow) that delivered the tone stimuli. This arrangement minimized struggling; electrode contact was unaffected by the remaining small movements.

The EKG was amplified differentially with an Alvar Rega 8 EEG amplifier and then fed into a monostable trigger, which in turn activated a reed relay for each heart-beat response. Both the EKG and the relay closure were monitored with a Tektronix 502 oscilloscope. Tone stimuli were produced by two transistorized Weinbridge oscillators of our own construction, amplified with a Grason-Stadler sound amplifier (Model 902A). Sound intensities measured with the microphone of a Dawe 1400E sound level meter (using the C weighting circuit) placed where the subject's head was normally located were 75 ± 3 dB (re: $20\mu N/m^2$), allowing for the slight head movements of the subject. The frequency settings were monitored with a Racal timer-counter (Model SA 535). The fidelity was established by placing a Grampian DP 456 H microphone at the position of the subject's head and feeding the signal into an Aim TFO 129 tunable filter and Tectronix 502 oscilloscope. The total harmonic distortion was less than 2% at all standard frequencies.

Procedure

A session consisted of a 5- to 10-min adaptation period followed by 240 trials. A trial was a 10-sec tone. A 30-sec intertrial interval followed each trial. The trials were grouped into 40 blocks of six trials. During the first five trials of a block, the "standard" tone (for that particular session) was always presented. The sixth trial in a block was the presentation of one of four "comparison" tones. It was followed by a 0.1-sec electric shock pulse of 3 mA intensity (from a Grason Stadler source). Five standard trials were presented again before the next comparison trial. The heart rate was recorded on the fifth standard trial in each block and on the subsequent comparison trial. This was accomplished by feeding the signal (resulting from the relay closure for each heart beat) through a Grason-Stadler multiple class time analyzer (Model #E3950A) and noting the distribution of interbeat intervals.

Table 1 lists the standard and the corresponding comparison tones used. Each subject was given two sessions with each standard; thus, the total number of presentations for each standard-comparison combination was 20 for each subject. The order of presentation of comparison tones was random within each group of four blocks of trials.

Table 1

The standard tone frequencies (Hz) and each corresponding comparison frequency. Both subjects received a total of 20 exposures to each combination.

Standard Tones (Hz)	*Comparison Tones (Hz)*			
	C1	*C2*	*C3*	*C4*
500	500	512	525	550
1000	1000	1012	1025	1050
2000	2000	2025	2050	2100
4000	4000	4050	4100	4200

RESULTS AND DISCUSSION

The raw data, expressed in beats per minute during each 10-sec trial, are shown in Figures 1 and 2. The solid lines represent heart rate during the fifth (standard) trial of each block and the dotted lines show the heart rate during the subsequent, sixth (comparison) trial of that block. For purposes of clarity, the data for each standard-comparison combination are presented separately for each session. Thus, for example, Subject #1's first session with the 500-Hz standard is found in the top row (labelled Stan = 500) of Figure 1 (top); the 40 blocks of six trials for that (and every) session are visually separated according to the comparison stimuli (*i.e.,* C1, C2, C3, or C4 as noted in Table 1).

It is immediately clear that the standard and comparison rates differed little on the C1 blocks of trials for almost all sessions. If anything, heart rate during the comparison trial was lower than during the previous standard trial, *e.g.,* see Figure 2 (top), C1 blocks for the 2000-Hz standard session. Such a continued de-

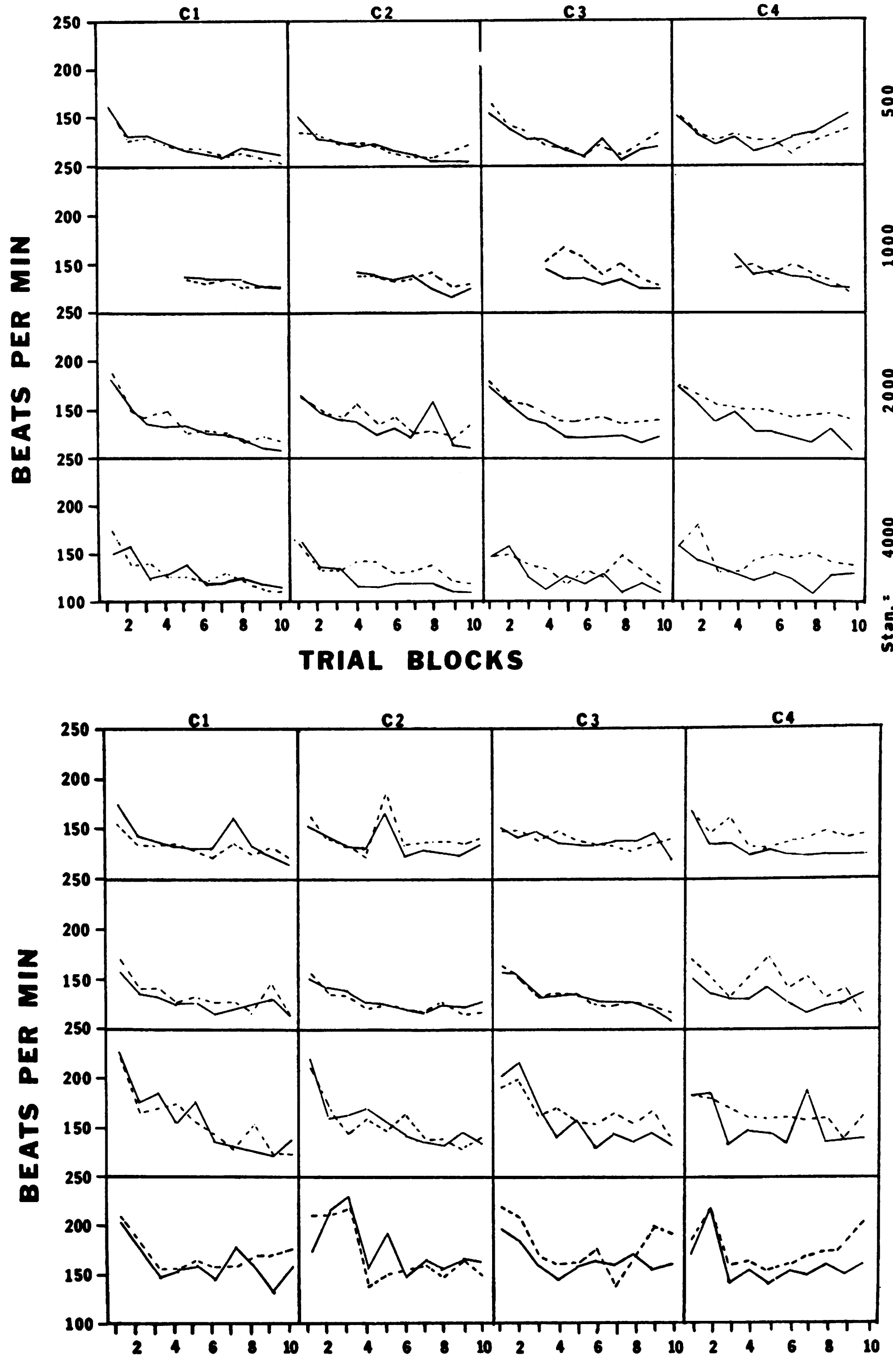
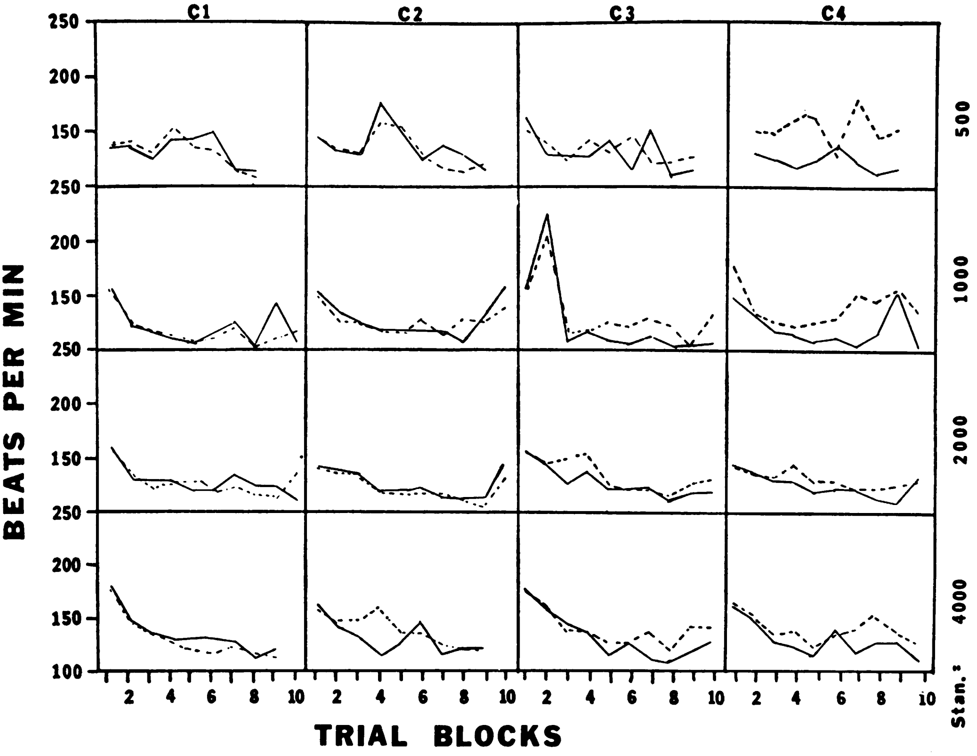


Fig. 1. Raw data in beats per minute as a function of blocks of trials for Subject #1 in Session 1 (top) and Session 2 (bottom). Solid line represents the response to the fifth standard stimulus while the dotted line indicates the response to the subsequent comparison stimulus.



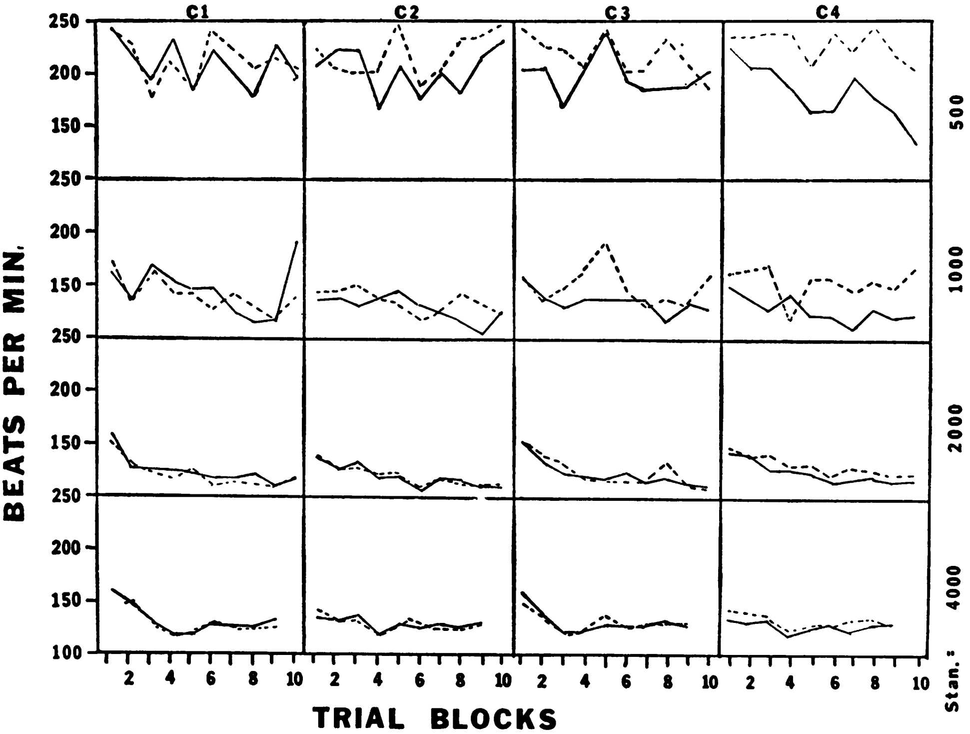


Fig. 2. Raw data in beats per minute as a function of blocks of trials for Subject #3 in Session 1 (top) and Session 2 (bottom). Solid line represents the response to the fifth standard stimulus while the dotted line indicates the response to the subsequent comparison stimulus.

crease in heart rate, of course, is not surprising, since the C1 frequency was always equal to the standard frequency.

In contrast, as the comparison frequency became increasingly different from the standard frequency (C2 through C4), the heart rate during the comparison trial was elevated. This clear evidence of stimulus control is most noticeable for the C4 comparisons, although the trend is found on C2 and C3 blocks too. For example, Subject #1's first session with a 2000-Hz standard (Figure 1 top) illustrates discrimination between the 2000-Hz standard and both the C3 (2050 Hz) and C4 (2100 Hz) comparisons. In each case, heart rate during the comparison trial was higher than during the preceding standard trial.

The basic finding, then, was that heart rate was generally higher on comparison trials (relative to the preceding standard trial). The consistency and magnitude of these response differences reflects the difference in frequency between the standard and comparison tones. To confirm this result, the data were pooled over subjects and sessions. Table 2 shows the percentage of trials for which the heart rate during the comparison tone was higher than during the standard tone. A 50% level indicates no stimulus control (*i.e.,* heart rate on the comparison trial varied randomly with respect to rate on the preceding standard trial). A higher percentage indicates a consistently higher rate during the comparison tone, and thus an increase in the degree of stimulus control.

Table 2 indicates little discrimination for the C1 and C2 comparison tones. However, stimulus control increased for more discrepant comparison tones. For example, the mean total percentage of trials on which the heart rate during the C4 comparisons exceeded the heart rate during the standard was 84.4%. Table 2 (bottom row) supports this fact by showing that the mean percentage level differed significantly from chance for the C3 and C4 comparisons but not for the C1 and C2 comparison tones.

Table 2

Percentage trial blocks on which the heart rate during the comparison tone was greater than during the preceding standard tone.

Standard Tones	*Comparison Tones*			
	C1	*C2*	*C3*	*C4*
500	44.4	63.1	66.6	83.8
1000	55.5	45.9	67.5	89.2
2000	46.1	52.5	77.5	77.5
4000	45.9	50.0	66.6	87.2
Mean	47.9	52.8	69.5	84.4
z	.49 N.S.	.72 N.S.	4.90 $p < 0.001$	8.49 $p < 0.001$

The percentages in Table 2 were used to compute a difference limen for each standard. The limen was defined as the point on the frequency continuum at which a heart-rate increase (on the comparison trial relative to the preceding standard trial) was found on 75% of the trials. The mean percentage of comparison trials showing an increase was first converted to a standard score. The four scores for each standard were then fit with a straight line (least-squares method). The difference limen (in Hz) was taken as the frequency occurring at 0.67 standard units (75%) minus zero standard units (50%). Thus, the difference limen represents the average minimum *increment* in frequency required to produce a heart-rate increase on 75% of the trials. A similar procedure has been used to assess reinforcement parameters (Campbell, 1955, 1956; Tarpy, 1969*a*, *b*).

The difference thresholds are illustrated in Figure 3 (solid line, left ordinate). The values increased from about 43 Hz for the 500-Hz standard to about 100 Hz at the 4000-Hz standard frequency. The relative function, ΔF/F, shows that the discrimination at the three higher standard frequencies was nearly the same (dotted line, right ordinate). For those frequencies, the Weber fraction was between

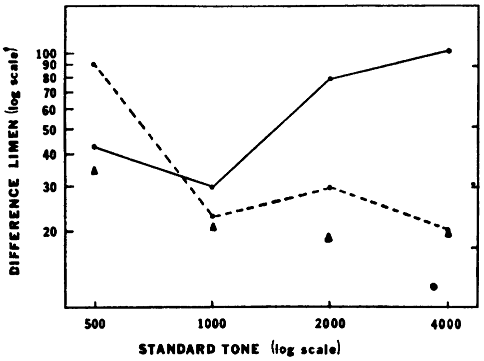


Fig. 3. Difference limen in Hz (solid line—left ordinate) and Weber fractions (dotted line—right ordinate) as a function of the standard frequency. Weber fractions from the Price *et al.* (1967) study are shown by triangles.

2.5% and 4.0%. However, for the 500-Hz standard frequency, the fraction was about 8.0%.

These data can be compared to the results obtained by Price, Dalton, and Smith (1967) who used a completely different technique, namely conditioned suppression. Pigeons were trained to peck a key with food reinforcement on a variable-interval schedule until a steady pecking rate was established. For the auditory discrimination training, the pigeons pecked during a standard tone that was interspersed with brief periods during which a comparison tone plus shock were presented. After repeated exposure to this condition, responding was suppressed as soon as a discriminable tone was presented.

Price *et al.* defined a difference limen as the frequency difference between the standard and the comparison tone that yielded suppression of pecking on 50% of the presentations. The Weber fractions they obtained, shown in Figure 3 (triangles), agree reasonably well with those found in the present study, except for the disparity at 500 Hz. Despite these similarities, the method and parameters in the Price *et al.* study differed appreciably from those used in the present study, making strict comparison impossible.

It is important to note that the present data were obtained in only 16 sessions, although there is clear evidence for discrimination in the *first* session for both subjects. Price *et al.* gave no information regarding the time it took to obtain their data, but their experiments must have extended over a considerable period of time. The present technique therefore appears to have a distinct advantage when compared with the procedures currently used in animal psychophysical research (Stebbins, 1970).

In conclusion, this technique does clearly indicate stimulus control. In this experiment, tone frequency was the controlling factor because no differential response was observed when the comparison frequency equalled the standard frequency (C1 trials). Although this method works, our understanding of the underlying mechanisms is incomplete. We believe that the heart-rate response to discriminable comparison tones was largely an unconditioned heart-rate increase due to the relative novelty of the comparison tone, and thus similar to the effect reported by Cohen and MacDonald (1971). The brief shock following each comparison tone heightened this generalized "emotional" response. The comparison tone-shock combination probably also produced conditioning (see Cohen and Durkovic, 1966), but this can only at best have been a partial component because totally novel tones, not used during any session, elicited a heart-rate increase in each subject when presented at the end of the last training session.

EXPERIMENT 2

Experiment 1 demonstrated a technique for establishing stimulus control. The purpose of Experiment 2 was to determine if pigeons could discriminate tone patterns.

METHOD

Subjects

Two male and one female pigeons (*Columba livia*), each about 2 yr old, served.

Apparatus

The apparatus was basically the same as in Experiment 1. The tone patterns were produced with the aid of two program-controlled, transient-suppressing, transistorized, audio-signal switches of conventional design and our own construction. There were two auditory patterns: one was a 1-kHz pure tone of 150 msec duration followed by a 2-kHz pure tone of equal duration; the other one was the reverse sequence. The amplitude envelope of the tone components was trapezoidal and the rise and fall times of the leading and trailing edges were 10 msec. The harmonic distortion of the tones at the pigeon's ear was less than 2%. Both tone components were set to give an 80-dB (re $20\mu N/cm^2$) sound intensity at the pigeon's ear. According to Trainer (1946) and Heise (1953), the pigeon's sensitivity is approximately the same for the two frequencies used, and thus setting the two components to the same intensity should match them for pigeon loudness.

Procedure

Four sessions were given to each pigeon. In two of these sessions, the high/low pitch pattern was used as a standard stimulus, and the low/high pattern as comparison stimulus, whereas in the other two this was reversed. The sequence of these two types of sessions was random and different for each pigeon.

Fifty blocks of six trials were given. Trials, lasting 10 sec, were separated by 30-sec intertrial intervals. During the first five trials of each block, the standard tone pattern was repeated once every second. The baseline heart rate was recorded during the fifth trial. Depending on a Gellerman sequence, the tone pattern presented on the sixth trial, again once every second, was either the standard pattern (25 trials in a session) or the comparison pattern (25 trials in a session). The comparison tone trials were always followed by a 1-mA shock of 0.1 sec duration; the standard tone trials were never followed by shock. In these latter details, the procedure differed somewhat from that used in Experiment 1. Preliminary experiments indicated that 1-mA shocks were as effective as the higher intensity shocks used in Experiment 1 and suggested also that the exclusive association of shocks with the comparison tone pattern might improve the attainment of differential stimulus control.

Three control sessions were held, one with each pigeon. They were designed to exclude the possibility that extraneous, unintended cues might be responsible for the control of behavior. The same procedure as in the experimental session was followed except that (in a given session) either one or the other of the two tone patterns mentioned above was presented throughout the session. The sixth trial was sometimes followed by shock ("comparison" trial), sometimes not ("standard" trial), but there were no intentional auditory cues that could differentially control the pigeon's heart rate.

Results and Discussion

The focus of the present experiment was on the final stimulus control, and not on its acquisition. Nevertheless, some data on acquisition are also presented. The heart-rate changes, *i.e.*, increases or decreases in number of beats from the baseline fifth trials to the critical sixth trials for randomly chosen but typical sessions, are indicated in Figure 4. These data are presented separately for standard and comparison trials. Comparison trials yielded somewhat variable heart-rate differences, but most of them were increases. Standard trials yielded smaller, less variable differences that often were decreases. Which of the two tone patterns was used as standard and which as comparison stimulus did not make a discernible difference.

Figure 4 also shows a similar plot for one control session. Both "comparison" and "standard" trials yielded heart-rate changes of similar amplitude and no consistently different sign.

Figure 5 presents the mean heart-rate changes averaged for all 12 experimental sessions as a function of blocks of trials. This figure illustrates the acquisition of stimulus control and suggests that stimulus control was nearly maximal by the end of the first 10 blocks of a session.

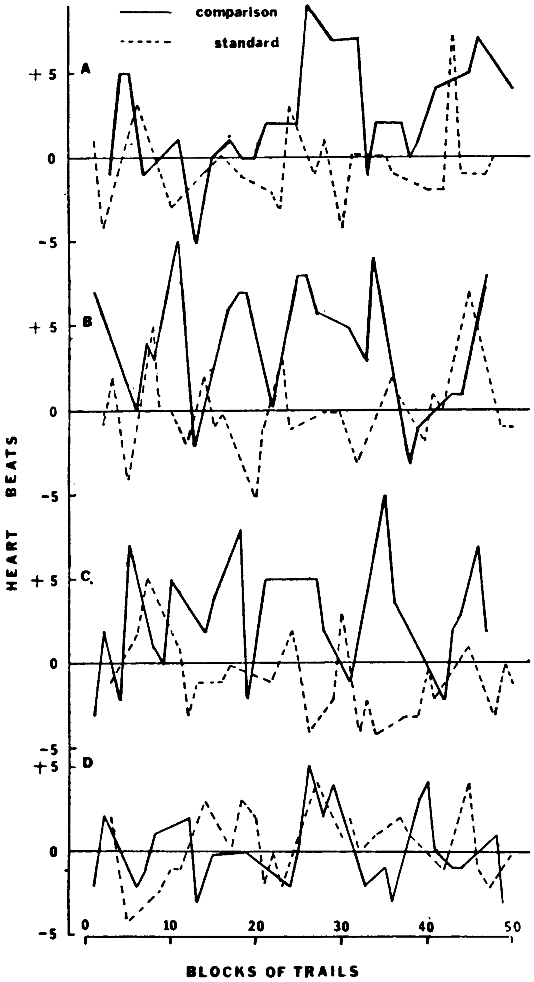


Fig. 4. Heart-rate changes as a function of blocks of trials. Three experimental and one control session are illustrated. A: Bird C, Session 1, 2000/1000 Hz standard stimulus (no shock), 1000/2000 Hz comparison stimulus (followed by shock). B: Bird A, Session 3, 1000/2000 Hz standard stimulus, 2000/1000 Hz comparison stimulus. C: Bird A, Session 4, 2000/1000 Hz standard stimulus, 1000/2000 Hz comparison stimulus. D: Bird A, control session, 2000/1000 Hz "standard" and "comparison" stimulus.

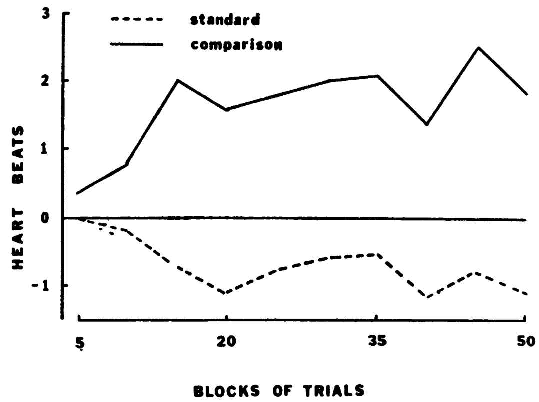


Fig. 5. Mean heart-rate changes as a function of consecutive groups of five blocks in a session. Averages from all 12 experimental sessions.

For all subjects, the experimental sessions were irregularly spaced with intervals as short as one day or as long as six days. Thus, the improvement in stimulus control over sessions is difficult to assess. However, some evidence is provided in Figure 6. The differential stimulus control attained in a session is best indexed overall by the difference between the mean heart-rate changes on standard and comparison trials. Figure 6 shows averages of these differences for all subjects as a function of the sequence of sessions. It is clear that there was some improvement in stimulus control from one session to the next.

As pointed out earlier, the primary purpose of the experiment was to demonstrate that terminal stimulus control by patterned auditory stimuli can be obtained in pigeons. Since acquisition seems largely complete after the first 10 blocks of trials of each session and the improvement over sessions is not very marked, asymptotic stimulus control was assessed by considering the last 40 blocks of each and all sessions.

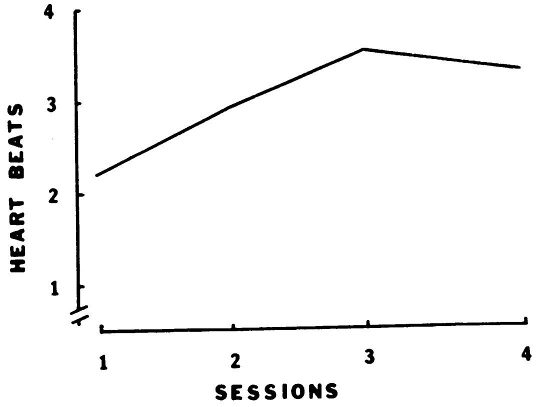


Fig. 6. Mean heart-rate differences between standard and comparison trials as a function of the four consecutive experimental sessions with the three pigeons.

Figure 7 illustrates the distributions of the mean heart-rate changes in all experimental sessions for the standard and comparison trials. Since the baseline heart rate for all subjects was about 30 beats per 10 sec, an *approximate* percentage scale based on this rate is also given in Figure 7. The two distributions are virtually segregated: the comparison pattern produced consistent heart-rate increases, whereas the standard pattern produced reliable heart-rate decreases.

These decrements associated with standard trials require comment. Since in these trials the stimulus was identical to that presented during the baseline trials, one might have expected no systematic heart-rate changes. That they did occur might be due to either a continuing decay of heart rate following the increase produced by the last shock, a continuing habituation to the standard stimulus, or conditioned inhibition associated with the fact that the standard trials were always either 6, 12, or 18 trials after the last comparison trial plus shock.

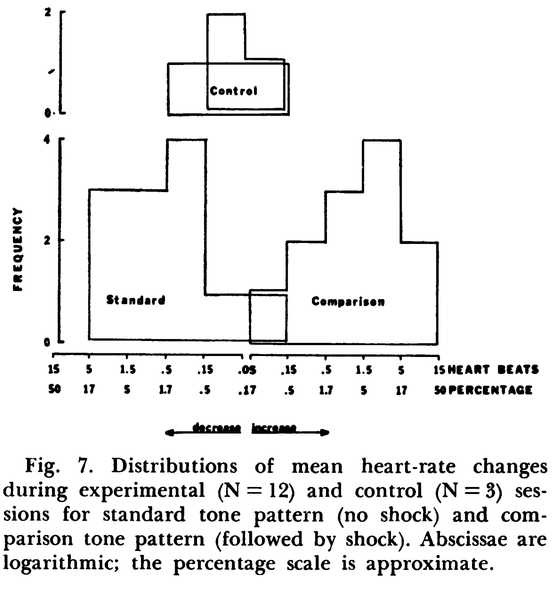


Fig. 7. Distributions of mean heart-rate changes during experimental (N = 12) and control (N = 3) sessions for standard tone pattern (no shock) and comparison tone pattern (followed by shock). Abscissae are logarithmic; the percentage scale is approximate.

The mean heart-rate changes for the standard trials represent matched controls for the heart-rate changes on the comparison trials. The difference between the paired means was calculated for each session. The distribution of these 12 differences with an approximate percentage scale is shown in Figure 8. The differences are consistently positive, *i.e.,* in every session the comparison pattern caused an increase of heart rate as compared to the standard pattern. These differences were significant by a Wilcoxon test at the $p < 0.001$ level.

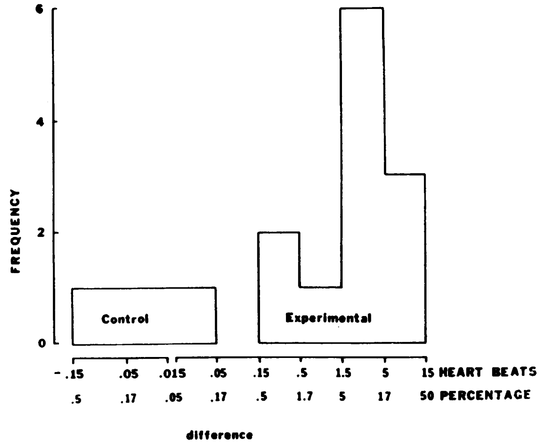


Fig. 8. Distribution of mean heart-rate differences between standard and comparison tone pattern trials for 12 experimental and three control sessions. Abscissae are logarithmic; the percentage scale is approximate.

The distributions of the mean heart-rate changes obtained during the control sessions are shown in the upper part of Figure 7. "Comparison" trials were followed by shock, whereas the "standard" trials were not. However, the tone pattern was identical for both. Average heart-rate increases and decreases were small and a Mann-Whitney test did not show a significant difference between "standard" and "comparison" trials.

The differences between the "standard" and "comparison" heart-rate scores for the control sessions are small and of varying sign, as can be seen in Figure 8. Comparison of this distribution with that obtained in the experimental sessions by a Mann-Whitney test yielded a $p < 0.02$. This clearly shows that the differential control over the heart rate was exerted by the two auditory patterns, and not by uncontrolled, spurious cues.

Although an attempt was made to match the component tones of the patterns to equal loudness for pigeons, the success of this attempt is not certain. It is possible that the stimuli could have controlled behavior through their loudness patterning. To check for this possibility, in one session with each pigeon, the effect of loudness as a cue was minimized by varying (in a random fashion) the intensity of one of the frequency components over the range of ±5 dB throughout the session. This procedure did not affect the control over the heart rate. The distributions of the heart-rate changes for the three subjects were significant as found previously ($p < 0.001$, Mann-Whitney). These results suggest further that the auditory patterns exerted control on the basis of their frequency patterning alone.

GENERAL DISCUSSION

The results establish beyond doubt that auditory patterns can be used to achieve differential control over a behavior in pigeons. Thus, these birds are capable of discriminating sounds by their temporal patterning, as one would expect from ethological evidence (Beer, 1970) but not from previous experimental analysis (Krasnegor, 1971). Moreover, the results suggest that the control can be exerted by the frequency patterning alone, that is, in the absence of any consistent loudness pattern. The arduous task of exploring the range of auditory patterns capable of such stimulus control still remains; an investigation into the minimum temporal duration of pattern components would be of great interest in view of the remarkably fine temporal structure of many avian vocalizations. Regarding the frequency difference thresholds of pigeons, the present results broadly confirm the estimates obtained with a different method of analysis by earlier investigators (Price *et al.,* 1967).

These studies suggest also that the stimulus control technique we utilized may be one of general usefulness in animal psychophysical research. At least compared with the other techniques that have been used in auditory discrimination research with pigeons, ours is far more rapid in demonstrating differential stimulus control. In the particular case of auditory pattern stimuli, it did so where earlier protracted efforts with more conventional procedures had failed. Since the experiments reported were not specifically aimed at clarifying the nature of the stimulus control achieved, our understanding of this is quite incomplete. A number of different processes could possibly be involved, and experiments designed to clarify this issue might well contribute to the development of more effective variants of the procedure.

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