Conditioned suppression/avoidance as a procedure for testing hearing in birds: The domestic pigeon's audiogram. However, false positives are easily controlled in the method of conditioned suppression/avoidance, in which a pigeon is trained to peck a key to obtain food and to stop pecking whenever it detects a sound that signals impending electric shock. Here, we describe how to determine psychophysical thresholds in pigeons using a method of conditioned suppression in which avoidable shock is delivered through a bead chain wrapped around the base of a pigeon's wings. The resulting audiogram spans the range from 2 to 8000 Hz; it falls approximately in the middle of the distribution of previous pigeon audiograms and supports the finding of Kreithen and Quine (Journal of Comparative Physiology 129–41, 1979) that pigeons hear infrasound.

Keywords Pigeon · Conditioned suppression · Avoidance conditioning · Psychophysical procedures · Audiogram · Infrasound

Introduction

The comparative study of avian hearing is of particular interest because some species appear to be unusually sensitive to low-frequency sound. However, how widespread this training a pigeon to peck a key to obtain food and to stop (suppress) its pecking whenever it detects a sound that signals impending electric shock. False positives, in this case, are kept low by adjusting the level of the shock and/or by increasing the rate of the reward. Although conditioned suppression has been used to test hearing in a wide above the floor on a tripod. Wire mesh fencing was inserted inside the cage, narrowing the width to 10 cm, which limited a pigeon's movement while allowing it to easily turn around. Because standard pigeon response keys are large and would obstruct the sound field, a response key was constructed using a set of normally open relay contacts with a plastic disk (15-mm diameter, 4 mm thick) containing a green LED embedded in it. The response key was mounted vertically 18 cm above the floor of the cage so that the pigeons could easily peck it to obtain food. The LED embedded in the key was normally on and provided feedback that the key had been depressed by turning off momentarily when a pigeon depressed the key and made contact closure. Access to pigeon food was provided by a solenoid-operated food tray that, when operated, would come up underneath the bottom of the cage in front of the response key so as to allow an animal to eat from it for 1.65 s; the entire feeder mechanism was below the level of the cage floor so that it would not interfere with the sound field.

Finally, electric shock was provided by a shock generator that was connected via alligator clips hanging from the top of the cage to the bead chains worn by the pigeons (for a description of the bead chain procedure for administering shock to pigeons, see Hoffman, 1960; Stein, Hoffman, & Stitt, 1971; for its use on small birds, see Hoffman & Ratner, 1974). The animals were trained and tested using shock levels of 0.14–0.23 ma for a 1-s duration, with the level adjusted for each animal to the lowest level that produced a consistent avoidance response to an obviously audible signal. A 25-W light bulb, placed above and behind the cage, was turned on whenever the shock was on.

Acoustical procedures

Pure tones were generated (Agilent 33220A function generator), attenuated (Coulbourn S85-08 programmable attenuator), and gated on and off (Coulbourn S84-04 rise-fall gate) at zero crossing, with a 20-ms rise–decay for signals above 250 Hz, and 200 ms for lower frequencies. The sine wave for frequencies above 4 Hz was filtered with a bandpass filter (Krohn-Hite 3550) set 1/3 octave above and below the tone's frequency. Finally, the signal was amplified (Crown D-75 amplifier for frequencies above 16 Hz and an Adcom GFA 545 amplifier for lower frequencies), monitored on an oscilloscope, and sent to a loudspeaker: The loudspeakers used were a Motorola KSN1005A piezoelectric speaker for frequencies 4000 to 8000 Hz, a 6-in. RS 2000 Infinity woofer for 250 to 2000 Hz, a Paradigm Servo 15 subwoofer for 8 to 125 Hz, and a TC Sounds Axis 15-in. (38.1-cm) subwoofer in an unported enclosure (65 × 65 × 120 cm) for 2 to 4 Hz and for rechecking thresholds from 8 to 125 Hz. All speakers were placed at least 1 m in front of the test cage. Testing at frequencies below 250 Hz was conducted with and without foam pads under the feet of the tripod on which the test cage was mounted, in order to investigate the possibility that the animals might be detecting vibrations mediated through the cage floor; thresholds did not change when the tripod was placed on foam pads.

The sound pressure level (SPL re 20 µN/m^2) of the stimulus was measured and checked for overtones using a 1-in. (2.54-cm) microphone (Brüel & Kjaer 4145) or a ¼-in. (0.635-cm) microphone (Brüel & Kjaer 4939, calibrated down to 2 Hz), a measuring amplifier (Brüel & Kjaer

frequencies had been tested, the animals were experienced observers, and a threshold could typically be replicated to within 3 dB in a single session; thus, the results can be considered accurate to within ±3 dB. Absolute thresholds for the 15 frequencies, which included obtaining a stable threshold for each frequency for at least three sessions, were completed in 85 sessions.

Surgery

To demonstrate that the conditioned suppression/avoidance procedure is applicable to birds that have been compromised in some way, two pigeons were anesthetized with isoflorane (mixed with oxygen), and their eardrums were ruptured with a double-pronged pick. The animals were then retested to determine whether they could detect tones from 2 to 63 Hz, which would also reveal whether the pigeons' sensation of the low-frequency tones was auditory or vibrotactile in origin.

Results

The audiograms of the pigeons are shown in Fig. 1; four animals were tested at 2, 4, 8, 16, 31.5, 63, 125, 250, 500, 1000, 2000, 4000, 5600, and 8000 Hz, with a fifth animal (pigeon D) being tested at all but 2 and 4 Hz. At a level of 60 dB SPL, the mean audiogram extends from 54 Hz to 6400 Hz, with a best sensitivity of about 14 dB at 1000–4000 Hz. This is the first pigeon audiogram in which thresholds were obtained for the same individuals for frequencies ranging from the infrasonic to their high-frequency upper limit. The close agreement between individual animals suggests that the thresholds are valid.

Pigeons A and E were retested following rupture of their eardrums, a procedure that would be expected to raise thresholds, especially at low frequencies, but not to entirely abolish their hearing. To maintain their performance when they could not hear a tone, blocks of tone trials were alternated with blocks of trials that contained both the tone and a broadband noise. The pigeons did not suppress to tones ranging0.1(to.(09.1(by

The next study attempted to control the false-positive rate by adding an "observing" response and by punishing false positives with an ETO (Stebbins, 1970; Study 4 in Fig. 2). Specifically, pigeons were trained to peck an observing or "ready" key, in order to turn on a tone, and then to peck a "response" key whenever the tone was detected. Although it

Conditioned suppression/avoidance Prior to the present study, Dalton (1967) demonstrated the applicability of conditioned suppression/avoidance for testing hearing in

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