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Conditioned suppression/avoidance as a procedure for testing hearing in birds: The domestic pigeon (*Columba livia*)

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Abstract Although the domestic pigeon is commonly used in learning experiments, it is a notoriously difficult subject in auditory psychophysical experiments, even those in which it need only respond when it detects a sound. This is because pigeons tend to respond in the absence of sound —that is, they have a high false-positive rate—which makes it difficult to determine a 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 129:1–4, 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 sensitivity might be is not known, as few studies in birds have examined their low-frequency hearing (cf. Dooling, Lohr, & Dent, 1985). Although determining the audiogram of some birds presents no special problems, others are so difficult to train on auditory tasks that it has been suggested that a physiological measure, the auditory brainstem response, be used instead (Noirot, Brittan-Powell, & Dooling, 2011). However, the auditory brainstem response is not a good measure of pure-tone behavioral sensitivity, as it depends on the synchronous firing of neurons evoked by brief and impure tones (e.g., Elberling & Don, 2007). Thus, it is important to find a behavioral procedure that works well with a broad range of species, including those species that are difficult to test.

Surprisingly, one of the most difficult birds to train on auditory tasks has been the domestic pigeon. Although pigeons are widely used in studies of learning, they do not perform well on tasks in which they are rewarded for making a response when a sound is presented, because they have a high false-positive rate and often respond in the absence of the sound (e.g., Stebbins, 1970). One approach to reducing their false-positive rate has been to avoid rewarding a pigeon for accidently responding to a subthreshold sound by only rewarding it for responding to obviously audible sounds (e.g., Harrison & Furumoto, 1971). However, this procedure risks training an animal to ignore sounds near threshold. Another approach has been to punish false positives with a short wait or error time out (ETO) before an animal can respond again for food. However the ETOs used with pigeons have tended to be long, with the result that in one case, the animals had to be tested in 12-h overnight sessions (Hienz, Sinnott, & Sachs, 1977).

There is, however, a procedure for testing hearing that allows for effective control of false positives and other errors, and that is the method of conditioned suppression. First used by Dalton (1967), this procedure consists of

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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 variety of mammals (e.g., Heffner & Heffner, 1995), it has never been used on birds by other researchers, perhaps because the procedure used by Dalton administered the shock via surgically implanted electrodes, which was done because birds have no exposed fleshy surfaces on their feet on which to make reliable electrical contact for foot shock.

Recently, we became interested in the hearing abilities of birds, especially as they compare with mammals, and began testing the hearing of pigeons. Although we initially trained the pigeons to respond when they detected a sound, we soon found, as had others, that pigeons have a high false-alarm rate that makes it difficult to obtain reliable thresholds. We then turned to the method of conditioned suppression using avoidable shock, and we found that the pigeons could be easily trained to give reliable thresholds.

This report demonstrates the utility of conditioned suppression in obtaining auditory thresholds in pigeons, and probably in birds generally. The procedure used here differs from the procedure used by Dalton (1967) in several ways. First, the original conditioned suppression procedure used unavoidable shock, whereas our animals were able to passively avoid shock by not responding (suppressing) when a sound was presented, a modification that increases the number of trials that can be given in a session. Second, Dalton administered shock through surgically implanted electrodes wrapped around the pubic bone; we administered the shock noninvasively, through bead chains wrapped around the base of each wing (Hoffman, 1960; Honig & Slivka, 1964). Third, Dalton required pigeons to stop pecking for 20 s; we required pigeons to stop pecking for only 0.3 s, a change that reduced the response cost to the animal, since it could not earn a reward during that time. Finally, we used a different suppression ratio to calculate an animal's performance, one that reduced the raw hit rate by the proportion attributable to false alarms (Heffner & Heffner, 1995).

Method

We used the method of conditioned suppression/avoidance to obtain absolute thresholds on pigeons for pure tones ranging from 2 to 8000 Hz. This consisted of training the birds to peck a key to obtain access to food and to stop pecking when a tone was turned on, in order to avoid electric shock that was delivered through bead chains that the pigeons wore at the base of their wings.

The present procedure is a modification of the original conditioned suppression procedure that we began using many years ago (e.g., Heffner & Masterton, 1970); the change to avoidable shock was one of several modifications that we have made. However, using avoidable shock changes the procedure from classical "conditioned suppression" to an "avoidance" or "discriminated punishment" procedure (e.g., Church, Wooten, & Matthews, 1970; Goodall, 1984). Nevertheless, we have retained "conditioned suppression" in the name while noting that the shock is avoidable, because it distinguishes this procedure from other animal psychophysical procedures, all of which require an animal to *make* a response when it detects a sound (cf. Klump, Dooling, Fay, & Stebbins, 1995). This is a crucial difference: Because ceasing activity or freezing is the natural response of many animals when a stimulus that signals danger is detected, the use of suppression to indicate that an animal has detected a sound simplifies training and accelerates testing. Thus, whereas from a learning standpoint there are important differences between conditioned suppression and discriminated punishment, from the standpoint of animal psychophysical testing, the differences are small, though not unimportant (e.g., there is evidence that using avoidable shock enhances suppression; see Church et al., 1970; Goodall, 1984).

Subjects

Five homing pigeons (*Columba livia*), obtained from a local breeder, were used in this study. The animals were between 3 and 4 years old at the beginning of testing and were housed in cages with access to grit and water. Pigeon food (a grain mixture) was used as a reward, and the animals were weighed daily during testing to ensure that they maintained a healthy body weight. After completion of the audiogram, the eardrums of two of the pigeons were ruptured and the animals were retested, to demonstrate that they were using their ears to detect the low-frequency tones. The use of animals in this study was approved by the University of Toledo Animal Care and Use Committee.

Behavioral apparatus

Testing was conducted in a double-walled sound chamber (IAC Model 1204; Industrial Acoustics Co., Bronx, NY; 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were lined with egg-crate foam, and the floor was carpeted to reduce sound reflections. The equipment used for behavioral control and stimulus generation was located outside the chamber, and the pigeons were monitored over a closed-circuit television. To avoid sound reflections, the pigeons were tested in a cage (50 × 30 × 42 cm) constructed of half-inch (0.127-cm) wire mesh, which was mounted 98 cm 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 $20\,\mu\text{N/m}^2$) 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 2610), and a spectrum analyzer (Zonic A&D 3525 FFT Analyzer). Sound measurements were taken by placing the microphone in the position occupied by a pigeon's head when it was pecking the response key and, for frequencies of 125 Hz and higher, pointing it directly toward the loudspeaker (0° incidence). The Paradigm subwoofer, which was 46 × 55 × 51 cm in dimensions, was placed on the floor of the chamber in front of the test cage; the TC Sounds Axis 15 was placed in front of the cage, turned at 120° so that there was no chance of a pigeon seeing the movement of the speaker diaphragm.

Prior training

Before beginning conditioned suppression, two different procedures were used in an attempt to obtain the pigeons' audiograms without using electric shock.

The first procedure was a two-choice procedure in which the pigeons were trained to peck a center response key to begin a trial and then peck a key to the left if they detected a tone or a key to the right if no tone was detected; correct responses were rewarded with food, and incorrect responses were followed by a short wait or error time out. This procedure had previously worked with blackbirds and cowbirds but had been unsuccessful with pigeons (Hienz et al., 1977). Although we were able to train the pigeons to perform the two-choice discrimination above chance levels, they were unable to consistently maintain 90 % correct, a level needed for threshold testing. Specifically, after 4 months of training, two pigeons were occasionally able to reach 90 % correct for groups of 20 trials; one pigeon never scored higher than 85 % correct; and the other two pigeons rarely performed above chance levels. Therefore, the two-choice procedure was abandoned.

The second nonshock procedure was a go/no-go procedure that consisted of training the pigeons to peck an "observing" key to indicate that they were ready to perform the task, and then to peck a "response" key whenever they detected a sound; in this task, correct detections were rewarded with access to food, whereas false positives were punished with a short wait or error time out (Stebbins, 1970). Although this procedure had been used with pigeons, it required long error time outs and test sessions lasting 12 h

(Hienz et al., 1977). We were able to obtain apparently reasonable thresholds with shorter error time outs and sessions of an hour or less, but the thresholds often varied by as much as 20 dB between individual pigeons, indicating that the results were probably not valid. Therefore, after 5 months of training, we abandoned the go/no-go procedure and turned to the method of conditioned suppression/avoidance that we have used to test hearing in mammals (Heffner & Heffner, 1995).

Conditioned suppression/avoidance

The pigeons were trained to peck the response key to obtain access to food on a variable-ratio schedule of 10 (VR 10). They were then trained to stop pecking whenever a tone was presented in order to avoid a mild electric shock. A session consisted of a series of 2-s trials with a minimum intertrial interval of 1.5 s, following which the next trial was begun when the pigeon pecked the key. Because a trial was initiated by a keypeck, the length of the intertrial interval would exceed 1.5 s if the pigeon stopped to eat a reward or had just received a shock, but it was typically less than 10 s. The VR 10 was in effect during the entire 2-s trial and the intertrial interval. The LED in the key was on during both the trial and the intertrial interval, going off momentarily only when the pigeon pecked the key; thus, the animals pecked continuously throughout the session, stopping only when they detected a tone, received a shock, or the food hopper came up. The response of a pigeon was defined by whether or not it pecked during the last 300 ms of the trial, giving the animal sufficient time to react to the signal. Requiring an animal to suppress pecking for only 300 ms reduced the response cost to the animal and allowed a lower level of shock to maintain good performance. If the pigeon did not peck during this 300-ms period, an avoidance response was recorded. The avoidance response (withholding keypecks) was classified as a "hit" if a tone had been presented, and as a "false alarm" if there had been no tone. Each trial had a 22 % probability of containing a tone.

To reduce the effect of spurious pauses, a trial was not begun until the pigeon pecked the key, which also meant that a tone was only presented when an animal's head was in position in front of the response key. In addition, rewards were never given during a 2-s trial, but only during the intertrial intervals. If a peck during a trial triggered a reward, the reward was withheld until the first peck in the following intertrial interval (a peck during the intertrial interval that triggered a reward did not start a trial); however, if the trial was a tone trial and the pigeon failed to suppress its pecking, the reward was not given.

The pigeons, which had previously been trained to peck the response key for food, were acclimated to pecking with their bead chains connected to the shock leads for three sessions (no sound or shock was presented). The initial suppression training consisted of presenting a salient sound (broadband noise) followed by shock if a pigeon pecked during the last 300 ms of the 2-s trials. The performance of the animals in discriminating noise from silence rose above chance levels ($p < .05$, binomial distribution) within 1–3 sessions (average 1.8 sessions) and reached a corrected hit rate of 95 % or better in 7–11 sessions (average 8.8 sessions). The test sessions typically consisted of 50–100 tone trials (and associated silent trials) and lasted from 30 to 90 min, depending on the individual pigeon and how much food it wished to eat.

Hit and false alarm rates were determined for each block of trials (5–7 tone trials interspersed among 18–25 no-tone trials) for each frequency. The hit rate was corrected for the false-alarm rate so as to produce a performance measure according to the following formula: Performance = Hit Rate – (False-Alarm Rate × Hit Rate) (Heffner & Heffner, 1995), which can also be expressed as Performance = Hit Rate × Correct-Rejection Rate, where Correct-Rejection Rate = 1 – False-Alarm Rate. This measure varies from 0 (*no hits*) to 1 (*100 % hit rate with no false alarms*). Note that this calculation proportionately reduces the hit rate by the false-alarm rate observed for each block of trials in each stimulus condition, rather than by the false-alarm rate averaged for the session as a whole. This was done because false-alarm rates varied within a session, depending on the difficulty of the discrimination.

Absolute thresholds were determined by reducing the amplitude of a tone in successive blocks of trials until the pigeon no longer responded to the tone above the .01 chance level (binomial distribution). Once a preliminary threshold had been obtained, final threshold determination was conducted by presenting blocks of trials in which the amplitudes of the tones of the different blocks were reduced in 5-dB steps extending from 10 dB above to 10 dB below the estimated threshold (the amplitude of the tone within a trial block did not vary). Trial blocks of higher intensities were occasionally given to ensure that an animal's asymptotic performance had not declined. Threshold was defined as the amplitude corresponding to a performance of .50, which was usually determined by interpolation. Threshold testing for a particular frequency was considered complete when the thresholds obtained in at least three different sessions were within 3 dB of each other. After an audiogram had been completed, each threshold was rechecked to ensure reliability.

Threshold testing was begun at 1 kHz, with the pigeons requiring six to eight sessions to reach their lowest threshold (average, seven sessions). The pigeons reached their lowest threshold for the next test frequency (2 kHz) in two to four sessions (average, three sessions), which was typical for the remaining frequencies. However, by the time that all 15 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 ranging from 2 to 63 Hz at the highest intensities that could be produced, although they did suppress to the broadband noise. This demonstrates that an intact ear is necessary for the pigeon to detect very low frequencies and that these thresholds are not likely due to somatosensory responses to vibration. The pigeons' eardrums healed back after 10 days, at which time their thresholds returned to preoperative levels.

Discussion

Comparison with previous pigeon audiograms

Figure 2 illustrates how the present results compare with all of the previous pigeon audiograms except for the low-frequency audiogram of Kreithen and Quine (1979), which is compared separately. Although there is noticeable variation between the different studies, the audiograms generally show that, beginning at the low frequencies, the pigeon's sensitivity gradually increases as frequency is increased, with a region of best sensitivity from 1 to 4 kHz, followed by a rapid decrease in sensitivity to an upper hearing limit of about 8 kHz.

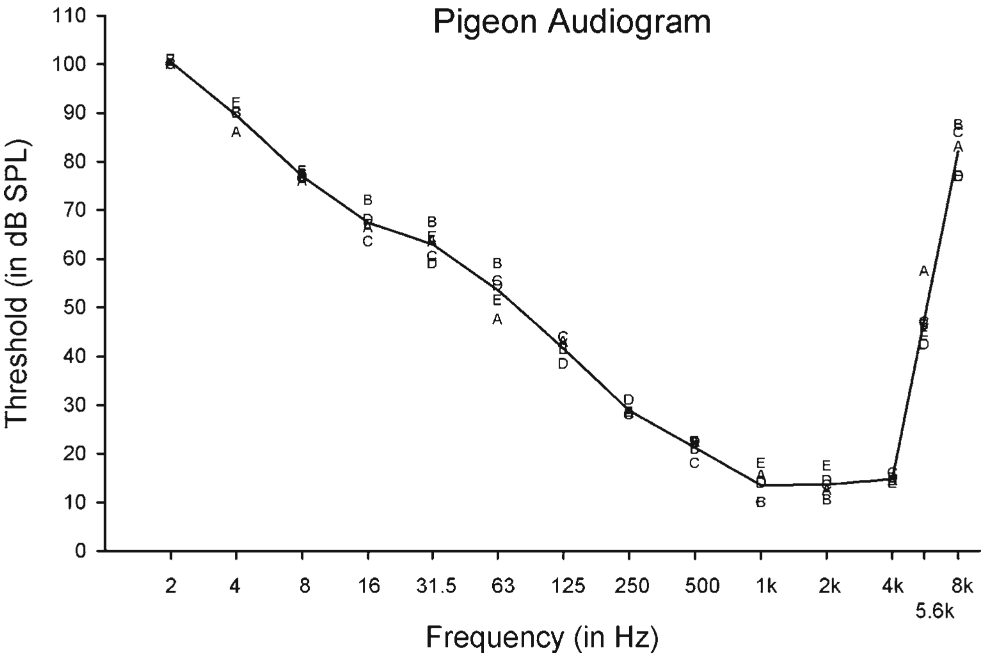

Fig. 1 Audiogram of the pigeon, as determined by conditioned suppression/avoidance. The letters indicate individual pigeons.

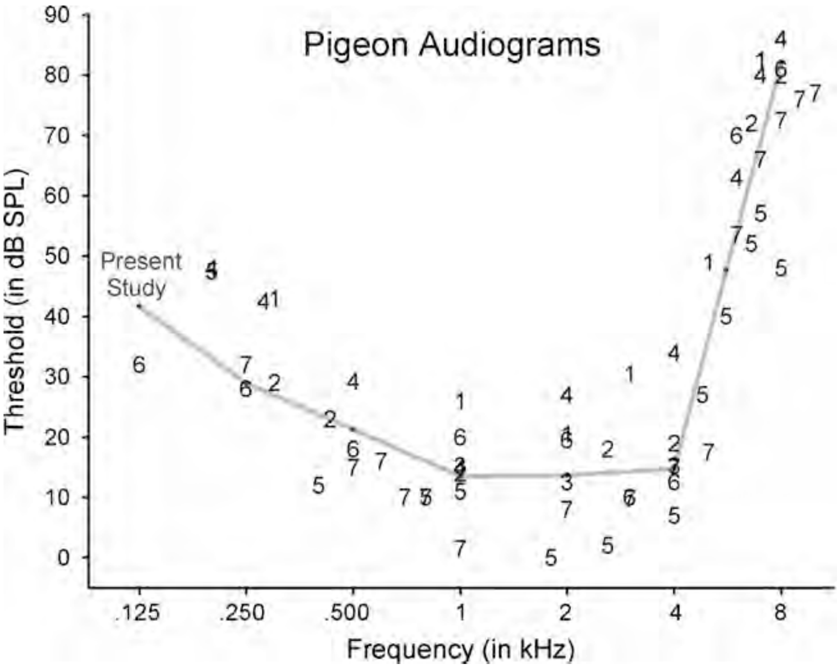

Fig. 2 Comparison of the present audiogram (line) with previously published pigeon audiograms (only the portion of the present audiogram that falls within the range of frequencies tested by the previous studies is shown). Note that the thresholds of the present study fall approximately in the middle of the distribution of previous thresholds. The numbers indicate previous studies: 1, Trainer (1947); 2, Heise (1953); 3, Dalton (1967); 4, Stebbins (1970); 5, Harrison and Furumoto (1971); 6, Hienz et al. (1977); 7, Goerdel-Leich and Schwartzkopff (1984).

There are several of reasons why studies of the same species may report different thresholds. One is the uniformity of the sound field in the vicinity of the animal's head; if an animal is allowed to move around within the sound field, it may not be possible to accurately specify the amplitude of the sound at its ears. In the present study, the sound was only presented when an animal was positioned directly in front of the response key, and the sound field in that location did not vary. Another source of variation is the behavioral procedure, and indeed, a number of the studies in Fig. 2 reported problems with the pigeons responding in the absence of sound—false positives (more on this below). The present study had no problem with false positives. Finally, it is possible that some pigeons might have different thresholds due either to inbred genetics or to abnormalities such as ear mites or middle ear infection. The pigeons in the present study were the result of random breeding, and their ears were inspected and found to be free of any signs of mites or infection.

Figure 3 illustrates how the present results compare with the low-frequency audiogram of Kreithen and Quine (1979). We found that pigeons are indeed sensitive to very low frequencies. As compared with humans tested under the same acoustic conditions (Jackson, Heffner, & Heffner, 1999), the pigeons' better low-frequency hearing emerges for frequencies below 32 Hz. Thus, as first noted by Kreithen and Quine, pigeons do hear infrasound, defined anthropocentrically as low-frequency sounds that are inaudible to humans at intensities exceeding 60 dB SPL.

It can also be seen in Fig. 3 that the thresholds that we obtained are noticeably less sensitive than those of Kreithen and Quine (1979), which may be due to differences in the ways that the two audiograms were conducted. One difference is the way in which a response was defined. Specifically, Kreithen and Quine used heart rate conditioning in which tones were paired with electric shock, with a positive response defined as an increase in heart rate of 12 or more beats per minute; any such definition is necessarily arbitrary, and choosing a different definition of a response would have yielded a different threshold. There is no way to precisely equate thresholds obtained with such a response with those obtained with an operant yes/no response without comparing them in the same animals. A second difference is the attenuation step size; the present study attenuated the sound in 5-dB steps, whereas Kreithen and Quine often used larger step sizes, which would result in slightly lower thresholds (Quine, 1979). Finally, Kreithen and Quine tested their animals in a small pressure box, which makes it difficult to compare their results with those of other animals tested in much larger sound chambers. The pigeons in the present study were tested in the same acoustic conditions used for testing other species, thereby making direct comparisons possible. In comparing human and pigeon thresholds, a recheck of the low-frequency thresholds (125 Hz and lower) of two human observers, conducted at the time that the pigeons were tested, found the same thresholds shown for humans in Fig. 3 (neither observer was able to hear 2 Hz at 105 dB). However, regardless of the differences between the present results and those of Kreithen and Quine, both studies indicate that pigeons have good low-frequency hearing.

Comparison of psychophysical procedures

A recent report on bird hearing stated that some avian species cannot be easily tested behaviorally, in which

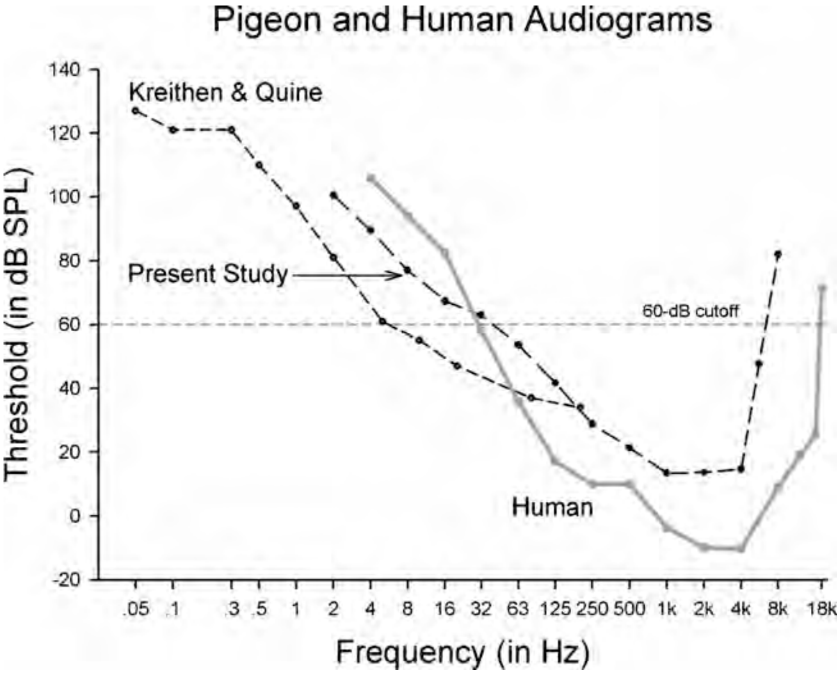

Fig. 3 Comparison of the present audiogram with the low-frequency pigeon audiogram of Kreithen and Quine (1979) and with the human audiogram (Jackson, Heffner, & Heffner, 1999). Although the present audiogram does not show the pigeons to be as sensitive as does that of Kreithen and Quine, it does confirm their previous finding that pigeons have better low-frequency hearing than humans do. Humans, on the other hand, have better sensitivity in their mid-frequency range and are able to hear higher frequencies than pigeons.

case the auditory brainstem response may be substituted (Noirot et al., 2011). Although the authors do not say what species were untestable, a review of the published pigeon audiograms reveals that most investigators have found pigeons to be difficult subjects. Therefore, it is worth reviewing the four procedures used to test pigeon hearing for insight into any critical differences in the methods.

Double-grill box avoidance The earliest pigeon audiogram appeared in an unpublished dissertation, along with the audiograms of six other species of birds (Trainer, 1947; Study 1 in Fig. 2). The pigeons were tested in a double-grill box in which an animal was required to move from one compartment of the box to the other whenever it heard a tone, to avoid electric shock delivered through the floor bars. With regard to the relative difficulty in training, Trainer reported that "In numerous cases, most commonly with the pigeons, extended intervals of up to ten minutes [between trials] were necessary in order to combat extreme nervousness." Apparently, the pigeons had the highest tendency of the seven species to respond in the absence of sound—that is, the highest false-positive rate.

In the double-grill box avoidance procedure, there is no easy way to reduce false positives, as an animal can successfully avoid shock by continuously crossing back and forth between the two compartments. Although false positives can be punished with "counter shock"—that is, shocking an animal when it responds in the absence of sound—our experience is that this is likely to cause an animal's performance to deteriorate to the point at which it completely ceases to respond.

Go/no-go Four pigeon audiograms have been obtained using go/no-go procedures in which an animal is trained to peck a key for food in the presence of a tone and to withhold responding in the tone's absence. In the first go/no-go audiogram, pigeons were required to wait until a tone was presented and then to peck a key at least ten times during a tone interval to receive access to food (Heise, 1953; Study 2 in Fig. 2). To reduce the problem of false positives, the animals were never reinforced when a tone was within 10 dB of threshold, and long silent periods between trials were sometimes given to extinguish responding in the absence of a tone. Nevertheless, of the six pigeons that were used, one was untrainable, and relatively complete audiograms could be obtained on only two of the remaining five animals.

A second study used a go/no-go procedure in which false positives were also controlled by not rewarding keypecks to low-intensity tones (Harrison & Furumoto, 1971). In this study, the pigeons were reinforced with food for pecking a key in the presence of an easily audible tone on a variable-interval schedule. After two months of training, thresholds were obtained by inserting lower intensity tones into a session, but never rewarding keypecks during these tones. The resulting audiogram obtained some of the lowest thresholds of any pigeon audiogram (Study 5 in Fig. 2). The pigeons may have responded to low-intensity tones in the absence of reinforcement because of the extensive training that they received before testing was begun. It is also possible that the low thresholds were the result of using a curve-fitting procedure rather than the actual data points to calculate threshold.

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 was hoped that the observing response would give an animal something to do while waiting for a tone, the animals still had high false-positive rates. Thus, Stebbins noted that "We found the pigeon a recalcitrant subject, as others apparently have, for auditory experimentation."

The last pigeon audiogram to use the go/no-go procedure is of particular interest because it demonstrated how the ability of pigeons to perform auditory detection tasks compares with that of other species (Hienz et al., 1977; Study 6 in Fig. 2). The authors of this study first attempted to use a two-choice procedure in which a pigeon pecked a center key to initiate a trial (a "ready" response) and then pecked a key to its right, if it detected a tone, or a key to its left, if no tone was detected. Although red-wing blackbirds and brown-headed cowbirds learned the task without difficulty, pigeons did not, despite six months of training. As a result, audiograms had to be obtained with a go/no-go procedure similar to that used by Stebbins (1970); however, the animals required such long ETOs for punishing false positives that they had to be tested overnight in 12-h sessions.

In analyzing the difficulties that these studies had with false-positive responses, it may be noted that the response of pigeons on auditory generalization tasks is affected by whether the response key is lit or dark (Honig & Urcuioli, 1981; Rudolph & van Houten, 1977). Specifically, pigeons show a steep generalization gradient to tonal frequency when the response key is dark, but not when it is lighted, indicating that a lighted key is a competing stimulus that can affect a pigeon's response to auditory stimuli. Although this could account for the high false-positive rate found by Harrison and Furumoto (1971), it would not account for Heise's (1953) difficulties, as his response key was an apparently unlit button attached to a microswitch. Nor can it provide a simple explanation for the results of Stebbins (1970) and Hienz et al. (1977), who used an observing key and a response key, both of which were lit. Nevertheless, the effect of lighting the response key on auditory generalization tasks is important to keep in mind when designing auditory tests for pigeons and, perhaps, for other birds.

In summary, the problem of false positives in the go/no-go procedure has been addressed in two ways. One is by never rewarding an animal for responding to low-intensity sounds, which eliminates the possibility that it might be rewarded for responding when it did not detect a tone, but runs the risk of training the animal to ignore low-intensity tones. Another way is to punish false positives with ETOs, although ETOs do not seem to be as aversive to pigeons as they are to other species. However, the go/no-go procedure might work satisfactorily with pigeons if the aversive contingencies were increased by punishing false positives with mild shock.

Heart rate conditioning Two pigeon audiograms have been obtained using classical conditioning of heart rate, in which pairing tones with electric shock causes a pigeon's heart rate to increase whenever it detects a tone. Because a positive response is determined by comparing the heart rate during tone presentation with the heart rate during the silent interval preceding the tone, it is necessary to keep a pigeon's heart rate during the silent intervals from becoming erratic. Accordingly, the level of shock is kept low and the tone trials are infrequent.

The first audiogram to use heart rate conditioning in the pigeon was the low-frequency audiogram by Kreithen and Quine (1979), which paired tones with shock and defined a response as an increase in heart rate of 12 or more beats per minute. To maintain the response, it was necessary to space trials at least 4 min apart and to limit the number of trials that could be given in a session. Although, as noted by Quine (1979), the heart rate response has the advantage of requiring little training, 85 sessions were needed to obtain thresholds for 11 frequencies—this is about the same length of time it took to obtain thresholds for 15 frequencies using conditioned suppression/avoidance.

The authors of the second study that used heart rate conditioning to test pigeon hearing also commented on the need to keep the electric shock "as weak as possible" to avoid disrupting an animal's behavior (Goerdel-Leich & Schwartzkopff, 1984). Although they did not give details about the procedure, the article they cited for their methods described a 5-min pause between shock trials, fewer than 20 shock trials per session, and testing every other day, apparently to prevent the shock from disrupting the pigeons' performances (Shen, 1983). Even these precautions were not always sufficient, as another study found that three of 11 pigeons had to be excluded from a sound localization study either because they could not be conditioned or because they had an irregular heart beat (Lewald, 1989). As can be seen in Fig. 2 (Study 7), the audiogram obtained with this procedure gives some of the lowest thresholds, although this may be because threshold was defined as the lowest intensity that caused an increase in heart rate over baseline ($p < .025$) rather than as the 50 % detection level used by the other studies.

In summary, false positives in heart rate conditioning are controlled by keeping the level of shock low and allowing sufficient time between shock trials, although some animals may still not be testable with this method.

Conditioned suppression/avoidance Prior to the present study, Dalton (1967) demonstrated the applicability of conditioned suppression/avoidance for testing hearing in pigeons by obtaining thresholds for three frequencies (Study 3 in Fig. 2). Dalton noted that pigeons easily learned to suppress keypecking for food when a suprathreshold tone was turned on, showing evidence of learning in the first 2 days of training. False positives in conditioned suppression/avoidance—that is, ceasing to respond in the absence of sound—are controlled two ways. The first is to reduce the level of the shock—which, if too high, will cause a pigeon to stop pecking. The second is to increase the frequency of reward delivery by, for example, changing the variable-ratio schedule from VR 10 to VR 5. Thus, as has been noted, conditioned suppression has "the advantages of aversive control [which controls an animal's propensity to suppress] while the ongoing behavior of the animal [pecking the key] is being maintained on a positive reinforcement schedule" (Smith, 1970; see also Heffner & Heffner, 1995).

In summary, conditioned suppression and conditioned suppression/avoidance have the advantage of allowing fine control over both misses and false alarms by adjusting both the reward and shock levels. The validity of the thresholds obtained is attested by the agreement of thresholds obtained in different laboratories at different times (e.g., Heffner, Heffner, Contos, & Ott, 1994). Indeed, as can be seen in Fig. 2, the average thresholds found by the present study are within 3 dB of the three thresholds obtained by Dalton (1967). Given the ability of conditioned suppression/avoidance to easily provide reliable auditory thresholds for even difficult-to-test birds like pigeons, we see no reason to use physiological estimates of hearing in birds, because such measures do not accurately reflect an animal's behavioral capacities.

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