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ORIGINAL PAPER

Budgerigars (*Melopsittacus undulatus*) do not hear infrasound: the audiogram from 8 Hz to 10 kHz

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Abstract The pure-tone thresholds of three budgerigars were determined from 8 Hz to 10 kHz. At a level of 60 dB sound pressure level (re 20 μN/m^2), their hearing range extends 6.6 octaves from 77 Hz to 7.6 kHz, with a best sensitivity of 1.1 dB at 3 kHz. Unlike pigeons and chickens, budgerigars do not have better low-frequency hearing than humans. This difference implies anatomical, physiological, and ecological differences between birds that hear infrasound (so far, pigeons and chickens) and those that do not (budgerigars).

Keywords Parakeet · Audiogram · Infrasound · Pigeon · Chicken

Introduction

An interesting feature of avian hearing is that some birds are able to hear low-frequency sounds that are inaudible to humans, that is, they hear infrasound. This was first demonstrated by Kreithen and Quine (1979) for the homing pigeon, a discovery that was replicated 30 years later (Heffner et al. 2013) but not explored further until recently. The explanation given by Kreithen and Quine (1979) for the infrasound ability of homing pigeons is that they use it for navigation, a hypothesis that remains popular (e.g., Hagstrum and Manley 2015). However, we recently found that domestic chickens are not only able to hear infrasound, but are more sensitive to it than pigeons (Hill et al. 2014). Because neither the domestic chicken, nor its wild ancestor, the red Jungle Fowl, are capable of more than very limited flight; it appears that there must be another reason for birds to hear very low frequencies.

In attempting to determine why some birds hear infrasound, it is of interest to compare low-frequency hearing in birds that vary in habitat and ancestry. Although audiograms for more than 40 species of birds have been published (Dooling 2002), all but two of those (pigeon and chicken) are limited to the bird's mid- and high-frequency hearing range with the result that nothing is known about the ability of other birds to hear low frequencies. Thus, the purpose of this study was to extend our knowledge of low-frequency hearing in birds by determining the complete audiogram of the budgerigar, a bird commonly used in auditory research (e.g., see the studies cited by Dent et al. 2016). As we show, the budgerigar does not hear infrasound, indicating that infrasound sensitivity is a characteristic of some, but not all birds. Understanding this difference could be useful for understanding the mechanisms underlying low-frequency hearing in general and the selective pressures that influence it.

Methods

Absolute thresholds for three budgerigars for pure tones ranging from 8 to 10,000 Hz were determined using a go/no-go procedure with a "ready" response. An animal pecked a key to begin a trial (the ready response) and was rewarded with access to food for either pecking the key again if no sound was presented or for not pecking the key if a sound was presented. During training and initial testing, pecking in the presence of a tone was followed with a brief electric shock delivered through bead chains around

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the base of their wings. The equipment and general procedure are similar to those used elsewhere (Heffner et al. 2013; Hill et al. 2014).

Animals

One male budgerigar (designated P2) and two females (designated P1 and P3) were obtained from a local supplier and were approximately 6 months old when testing began. They were group housed in a bird cage with free access to water. They were fed pelleted budgerigar food (ZuPreem Natural Diet Bird Food Parakeet and ZuPreem Fruitblend Small Keet Food) and the animals were weighed before each test session to monitor their health and deprivation level. Because the animals could not sustain themselves with a single daily feeding, they were tested twice daily, first in the morning beginning around 8 AM and then in the evening beginning around 6 PM.

Behavioral apparatus

Testing was conducted in a double-walled sound chamber (IAC model 1204; Industrial Acoustics Co., Bronx, NY, USA; 2.55 × 2.75 × 2.05 m), the walls and ceiling of which were lined with eggcrate foam and the floor carpeted to reduce sound reflections. The budgerigars were tested in a cage (21 cm × 11.5 cm × 13.5 cm) constructed of half-inch (1.27 cm) vinyl-coated hardware cloth that was mounted 90 cm above the floor on a tripod. A response key was constructed using a plastic disk (1.5 cm diameter, 1.5 mm thick) with a red LED embedded in it. The response key was mounted vertically 5.5 cm above the floor of the cage and the LED was momentarily turned off when the key was pecked. Access to food was provided by a solenoid-operated food tray, that when operated, came up underneath the bottom of the cage (in front of the response key) to allow the budgerigar to eat from it for 1 s; the entire feeder mechanism was below the level of the cage floor so that it would not interfere with the sound field.

Electric shock was produced by a Coulbourn constant current shock generator that was connected via alligator clips hanging from the top of the cage to bead chains around the base of a budgerigar's wings [for a description of the bead chain procedure, see Hoffman (1960) and Stein et al. (1971)]. The animals were trained and tested using a shock level of 0.2 mA, 1.5-s duration, which was the lowest level that the generator could produce. A 25-W light bulb, mounted above the loudspeaker that produced the test tones, was turned on at the end of a tone trial either as the shock was being delivered or when it would have been delivered had the animal not stopped pecking. Once the birds had learned to consistently withhold pecking when an audible signal was presented, the shock was discontinued as it was not necessary to produce good performance. However, the light bulb was still momentarily turned on at the end of a tone trial, and thus served as confirmation that a tone had indeed been presented.

Acoustical procedures

Pure tones were generated with a function generator (Agilent 33220A), gated on and off at zero crossing (Coulbourn S84-04 rise-fall gate), attenuated (Coulbourn S85-08 attenuator), filtered (Krohn-Hite 3550 band-pass filter set 1/3 octave above and below the tone's frequency), and amplified (Crown D-75 amplifier). The tones were gated 900 ms on, 100 ms off for 2 s (2 pulses) with a rise-fall time of 50 ms for tones of 8–250 Hz and 20 ms for higher frequencies.

The loudspeakers used were a TC Sounds Axis 15-in (38.1 cm) subwoofer in an unported enclosure (65 × 65 × 120 cm) for 8–63 Hz, a Paradigm Servo 15 subwoofer for 16 and 32 Hz, a 12-in (30.5 cm) woofer for 63–500 Hz, an Infinity RS 2000 for 1–4 kHz, and a Motorola piezoelectric tweeter for frequencies from 5.6 to 10 kHz. All speakers were placed at least 1 m from the front of the test cage.

The sound pressure level (SPL re 20 $\mu N/m^2$) of the stimulus was measured and checked for overtones using a 1-inch (2.54-cm) microphone (Brüel & Kjaer 4145) or a ¼-inch (0.635 cm) microphone (Brüel & Kjaer 4939), 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 budgerigar's head when it was pecking the response key and pointing it directly ahead toward the loudspeaker [for details of the sound measurement, see Hill et al. (2014)]. The background noise level in the sound chamber was relatively low; although modern buildings often have significant low-frequency noise produced by the heating-ventilating-air conditioning system, our laboratory is located in a building constructed in 1929 for which the air handling equipment is located in an external room. No background noise could be detected in the double-walled IAC test chamber from 500 Hz to 10 kHz using the above sound measuring equipment and the 1/3-octave filter. Low-level noise could be detected at lower frequencies and was as follows: 12 dB at 250 Hz, 18 dB at 125 Hz, 34 dB at 63 Hz, 45 dB at 32 Hz, 40 dB at 16 Hz, and 41 dB at 8 Hz. As will be seen in the results, these levels were well below the animals' thresholds, and thus could not have affected the thresholds.

Behavioral procedure

The budgerigars were first trained to peck the response key to obtain access to food for 1 s. Next they were trained to peck the key during 2-s trials in which no sound was presented ("silent" trials), but not during trials in which a tone was present ("tone" trials)—in other words, tones signaled danger, and silence signaled safety, an arrangement similar to our conditioned suppression/avoidance procedure (Heffner et al. 2013). This was done by rewarding an animal at the end of a trial with food both when it pecked during a silent trial and when it did *not* peck during a tone trial, thereby rewarding both hits and correct rejections. During training and initial testing, an animal received a mild shock if it pecked during a tone trial.

A session consisted of a series of 2-s trials, each with an intertrial interval of no less than 1.0 s. Because each trial was initiated by a key peck, the length of the intertrial interval exceeded 1.0 s if the bird stopped to eat a reward or had just received a shock, but was typically less than 10 s. The response of an animal was defined by whether or not it pecked during the last 300 ms of the trial, giving the animal sufficient time to react to a tone. If the budgerigar did not peck during this 300-ms period, an avoidance response was recorded. The avoidance response (withholding key pecks) 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 24 % probability of containing a tone. An animal gained access to food at the end of a trial if it had made a correct response, that is, if it pecked during a silent trial (correct rejection) or if it stopped key pecking during a tone trial (hit). Pecking during the last 300 ms of a tone trial was scored as a "miss". The number of trials varied from session to session depending on the amount of food the animals had gotten in the previous session or how much food they had gotten during the weekend when they were on free feed. Examining ten sessions of a randomly chosen week showed an average of 108 trials per session of which 82 were no-tone trials and 26 were tone trials.

A trial did not begin until the budgerigar pecked the key, which meant that a tone was only presented when an animal's head was in position in front of the response key. Test sessions typically lasted from 30 to 60 min depending on the individual bird and how much food it wished to eat.

Hit and false alarm rates were determined for each block of tone and associated silent trials. The hit rate was corrected for the false alarm rate to produce a performance measure according to the following formula: Performance = hit rate − (false alarm rate × hit rate) (Heffner and Heffner 1995). This measure proportionally reduces the hit rate by the false alarm rate and varies from 0 (no hits) to 1 (100 % hit rate with no false alarms).

Absolute thresholds were determined by presenting tone trials at suprathreshold intensities and then reducing the amplitude in 10- and then 5-dB steps until the budgerigar no longer responded to the tone above the 0.01 chance level; at that point, the amplitude of the tone was varied to obtain a final threshold determination for that session. Threshold was defined as the amplitude corresponding to a performance of 0.50, 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 stable (neither systematically increasing nor decreasing) and within 3 dB of each other.

Threshold testing was begun at 1 kHz, progressing to the higher frequencies, and then systematically moving to the lower frequencies beginning with 500 Hz. The animals were tested at 1 kHz for 18–22 sessions to ensure that they had learned the task and that their thresholds had stabilized. Subsequent testing required between three and seven sessions to obtain stable thresholds that were within 3 dB of each other. Because of our special interest in their low-frequency hearing, the thresholds from 8 to 63 Hz were double checked by returning to them after another frequency had been tested. Finally, their 1 kHz threshold was rechecked after testing was complete and found to be unchanged.

Results

As shown in Table 1, the absolute thresholds of the three budgerigars are generally in good agreement with each other, although P2 was sometimes less sensitive than the other two animals, especially at frequencies below 125 Hz. The budgerigar's 60-dB hearing range extends from 77 Hz to 7.6 kHz, a range of 6.6 octaves. Unlike nearly all mammals, but like most other birds, budgerigars are unable to hear above 10 kHz (Heffner and Heffner 2008).

Table 1 Individual and average pure-tone thresholds of three budgerigars (P1, P2, and P3)

Frequency (Hz)	P1 (female)	P2 (male)	P3 (female)	Mean
8	90	103	97	96.7
16	85.3	97.7	88.2	90.4
32	74.3	80.8	76.3	77.1
63	64	70.5	66	66.8
125	49.8	50.8	48.2	49.6
250	31	30.5	29.3	30.3
500	18.5	24.7	19.3	20.8
1k	7.8	10.5	7.5	8.6
2k	3.3	0.3	2	1.9
3k	1.2	0.7	1.5	1.1
4k	6	4	3.8	4.6
5.6k	16.5	15.3	17.3	16.4
8k	67.3	69.5	67.7	68.2
10k	82.3	85.2	80.8	82.8

In a previous study of chicken hearing, it was noted that the chickens required extra training before their final thresholds for frequencies below 64 Hz emerged, an observation that suggested that they perceived those frequencies differently than the high frequencies on which they were trained (Hill et al. 2014). With this in mind, we carefully observed the budgerigars' thresholds as testing moved to the low frequencies. We did not find that their behavior changed in any way or that they required extra training before their low-frequency thresholds stabilized, suggesting that they perceived the lower frequencies in the same way as they perceived the higher frequencies. This suggests that there may be a qualitative difference between the ears of budgerigars and those of pigeons and chickens in the way in which they sense low-frequency sounds.

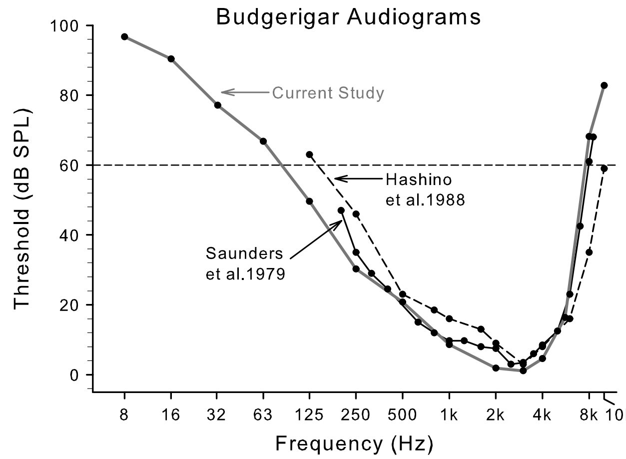

Fig. 1 Comparison of the budgerigar thresholds obtained in this study with those obtained by Hashino et al. (1988) and Saunders et al. (1979). SPL is the sound pressure level re 20 μN/m^2. Horizontal dashed line indicates the 60-dB sound pressure level

Discussion

Comparing budgerigar audiograms

Although pure-tone thresholds of budgerigars have been determined in at least ten different studies, none of those tested frequencies lower than 125 Hz (Dooling 1973; Saunders and Dooling 1974; Dooling and Saunders 1975; Saunders et al. 1978, 1979; Saunders and Pallone 1980; Okanoya and Dooling 1987; Hashino et al. 1988; Hashino and Sokabe 1989; Farabaugh et al. 1998). Figure 1 compares the current audiogram with two earlier audiograms, chosen because they covered a wide frequency range and were obtained in different laboratories. As can be seen, the three audiograms are in close agreement, with the current audiogram being in slightly better agreement with that of Saunders et al. (1979). However, the differences between the audiograms are small and not of theoretical import, demonstrating that behavioral audiograms obtained in different laboratories using different procedures, and conducted decades apart can give equivalent results if the animals are carefully trained and the sound field is well controlled.

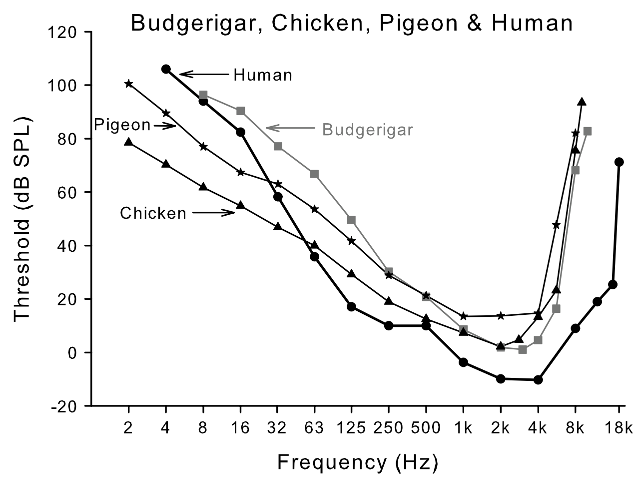

Fig. 2 Audiogram of the budgerigar from this study compared with the audiograms of humans (Jackson et al. 1999), pigeons (Heffner et al. 2013), and the domestic chicken (Hill et al. 2014). Budgerigars do not hear infrasound. SPL is the sound pressure level re 20 μN/m^2

Budgerigars do not hear infrasound

The main purpose of this study was to determine whether budgerigars hear infrasound, which is anthropocentrically defined as sound below the low-frequency hearing ability of humans. Note that there are at least two ways to define infrasonic hearing. One is to define it as the ability to hear sound below 20 Hz, which is the nominal low-frequency hearing limit of humans (e.g., Bedard and Georges 2000). However, this is an arbitrary definition because, as shown in Fig. 2, humans can hear several octaves below 20 Hz. Another way is to define it as the ability to hear low-frequency sounds that are inaudible to humans because we lack sufficient sensitivity. It is this later definition that we use because we want to know if there are low-frequency sounds that animals can hear that we cannot, and if so, why they hear them.

Among mammals, humans have relatively good low-frequency hearing and only elephants and cattle are known to hear lower (Heffner and Heffner 1982, 1983). Of the other two species of birds whose low-frequency hearing has been behaviorally determined, the pigeon and the domestic chicken, both can detect infrasound (Heffner et al. 2013; Hill et al. 2014). However, as illustrated in Fig. 2, budgerigars do not have better low-frequency hearing than humans, and therefore, by definition, do not hear infrasound.

It appears, then, that unlike high-frequency hearing in birds, which varies by less than an octave, their low-frequency hearing ability varies over a range of several octaves with some birds able to hear infrasound while others cannot. Moreover, the observation that chickens required extra training before their final thresholds for frequencies below 64 Hz emerged suggests that they may use a different modality to perceive low-frequency sound (Hill et al. 2014). This suggests the possibility of anatomical and/or physiological differences between the ears of birds that hear infrasound (such as chickens and pigeons), as opposed to those that do not (budgerigars and, presumably some other birds). However, at this time, the sample of birds whose low-frequency sensitivity is known is so small (three) that we cannot speculate on either a morphological or ecological basis for the remarkable differences in low-frequency hearing so far observed. Thus, an understanding of low-frequency hearing in birds awaits a determination of the hearing abilities of species that differ in such factors as size, ear morphology, evolutionary lineage, and ecological lifestyle.

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