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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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Because neither the domestic chicken, nor its w4r its w4r incfanm

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 notec that the chickens required extra training before their na thresholds for frequencies below 64 Hz emerged, an obse vation that suggested that they perceived those frequenci 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 the low frequencies. We did not nd that their behavior changed in any way or that they required extra training before their low-frequency thresholds stabilized, sugges ing that they perceived the lower frequencies in the sam way as they perceived the higher frequencies. This sugges that there may be a qualitative difference between the ea of budgerigars and those of pigeons and chickens in the way in which they sense low-frequency sounds.

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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 eld is well controlled.

Budgerigars do not hear infrasound

The main purpose of this study was to determine whether budgerigars hear infrasound, which is anthropocentrically de ned as sound below the low-frequency hearing ability of humans. Note that there are at least two ways to de ne infrasonic hearing. One is to de ne 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 de nition because, as shown in Fig. 2, humans can hear several octaves below 20 Hz. Another way is to de ne it as the ability to hear low-frequency sounds that are inaudible to humans because we lack suf cient sensitivity. It is this later de nition 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 de nition, do not hear infrasound.