


Hearing in Indian peafowl (*Pavo cristatus*): sensitivity to infrasound

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re-tested. Finally, the tympanic membranes were punctured at the end of the study and low-frequency sensitivity again tested as a final control.

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The method of conditioned suppression/avoidance was used to obtain absolute thresholds for the Indian peafowl for pure tones ranging from 4 Hz to 10 kHz. The peafowl were trained to continuously peck a key to obtain access to food at regular intervals, then to suppress pecking in the presence of a tone to avoid a mild electric shock. Suppressing pecking when a tone was presented indicated that the bird had detected the sound and it was rewarded with access to food. If the bird continued pecking during a tone, a mild electric shock was delivered.

Subjects

Three Indian peafowl *Pavo cristatus* obtained from a local breeder, one male (labeled A) and two females (labeled B and C), were used in this study. They were group-housed in a room with free access to water. Chicken food (Purina Layena Crumbles) was used as a reward and the animals were weighed daily (when on test) to monitor their health and deprivational status. All birds were 9 months old at the beginning of testing. At the time of crest removal, they were 21 months old and both birds were just sexually mature with the male beginning to display his train and the females beginning to lay eggs. The male crest consisted of 21 feathers, average 5.76 cm length, the female crest had 18 feathers, average length 4.6 cm. These lengths are within the range reported for adults (Kane et al. 2018).

Behavioral apparatus

Testing was conducted in a double-walled sound chamber (Industrial Acoustic Co., model 1204; 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 peafowl were tested in a cage (100 × 55 × 85 cm) constructed of hardware cloth (2.54 × 5.08 cm) and mounted on four wooden supports (5.08 × 10.16 cm), raising the base of the cage 45 cm above the floor of the sound chamber. The bottom of the cage was lined with two layers of thick carpeting (approx. 2.5 cm) to further reduce substrate-borne vibrations.

A contact switch, consisting of a clear plastic disk (3 cm diameter, 1 mm thick) with an embedded red LED served as the response key. This key was mounted at the front of the cage, 66 cm above the cage floor. The lighted LED was momentarily switched on when the key was pecked,

providing feedback to the bird. Access to chicken food was provided by a solenoid-controlled food hopper that, when operated, would come up at the bottom of the cage to allow the peafowl to feed for 3 s. The entire feeder mechanism was placed 53 cm below the response key so that it would not interfere with the sound field.

Electric shock (Coulbourn Regulated Animal Shocker, model E13-14) was delivered via leads hanging from the top of the cage to bead chains around the base of the peafowl's wings. (For a description of the bead chain application, see He ner et al. 2013, Ho man 1960, and Stein et al. 1971.) The birds were trained and tested using shock levels (0.2–0.6 mA, 1.5-s duration) that were individually adjusted to the lowest level that produced a consistent suppression response to an obviously audible signal. The shock was defined as mild, because the peafowl never developed a fear of the response key and readily returned to pecking the key after the shock had been delivered. A 25-W light bulb, placed above the loudspeaker, was turned on concurrently with the shock.

Acoustical procedures

Pure tones were generated and gated on and off at zero cross-

systematically increasing nor decreasing) and within 3 dB of each other. Threshold testing began at 4 kHz and progressed higher to 10 kHz, then down through lower frequencies to 4 Hz and finally replicating all frequencies back up to 9 kHz.

Crest removal

The peafowl's crest and associated filoplumes (the fine mechanosensitive feathers at the base of the larger crest feathers) have been reported to resonate at a narrow range of frequencies between 19.2 and 32.4 Hz (Kane et al. 2018). To investigate whether this vibrotactile stimulus might contribute to their responses to frequencies in this range, additional thresholds were determined for the male (A) and one female (C) peafowl at 8, 16, 20, 25, and 32 Hz, before and after removal of all crest feathers and immobilizing any remnant filoplumes with the stick hair gel (Schwarzkopf Got2b Ultra Glued).

Tympanic membrane perforation

Tympanic membrane perforation significantly reduces sensitivity to low frequencies in both mammals and birds (Voss et al. 2001; Hill et al. 2014) and can indicate the degree to which low-frequency sensitivity in peafowl relies on the auditory system. After the crests and filoplumes had fully regrown (approximately 5 months), the same two peafowl were anesthetized with isoflurane and, with the aid of a dissecting microscope, multiple perforations with a 20-gauge hypodermic needle were made in the tympanic membranes of both ears. The columellae remained intact. The birds were

then tested daily at 8, 20, and 32 Hz for 8 days to assess hearing loss and subsequent recovery.

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The peafowl adapted relatively easily to the test cage and learned to peck the response key to receive rewards. Training the animals to listen for sounds and then to be reliable observers of low-intensity sounds required approximately 75 daily sessions, after which they produced reliable thresholds. Complete audiometric testing required another 90 days, followed by additional threshold testing after removal of the crest feathers and filoplumes, and finally, after eardrum puncture.

Audiogram

As shown in Fig. 1, there was good agreement between individual peafowl with the greatest difference between individuals being 7 dB at 5.6 kHz. The peafowls' good sensitivity (20 dB or lower) ranged from about 75 good sensitivity to right ear 8.1999 dB sensitivity in 5.6125 (m99999618(kHz.)) The pair r)-18.89g ta

Role of the crest feathers

The peafowl's crest and associated filoplumes have been reported to resonate at a narrow range of frequencies between 19.2 and 32.4 Hz (Kane et al. [2018](#)). As shown in [Fig. 2](#)

no indication that the intact crest and filoplumes reduced the impact of tympanic membrane perforation on the detection of 20 Hz since the hearing loss and recovery at 20 Hz was very similar to the loss at the slightly higher and lower frequencies at which the crest feathers did not resonate. This raises the possibility that the somatosensory component contributed by the crest/filoplume apparatus might act through the auditory pathway—such convergence of the auditory and somatosensory pathways is not unknown (e.g., Wild 1995). (Any potential contribution to sensitivity from particle velocity stimulation of the crest feathers is not known.)

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Low-frequency hearing in birds

From an anthropocentric view, it is of interest to determine which species hear frequencies lower than humans (i.e., detect frequencies below about 32 Hz at lower levels than humans), because such species may be using sound in ways we do not expect. By this definition, there are now three species of birds that hear “infrasound”: Pigeons (Kreithen and Quine 1979; He erner et al. 2013), domestic chickens (Hill et al. 2014), and now Indian peafowl. Whether such infrasonic hearing involves different anatomical or physiological mechanisms is already under investigation (for a review, see Zeyl et al. 2020). The possibility in chickens of a second mechanism has been suggested because they required additional training, especially at 32 Hz, before their final thresholds could be obtained, implying that they may perceive lower frequencies differently from higher frequencies (for details, see Hill et al. 2014). Although no such training effect was seen in the peafowl, the possibility of different mechanisms underlying the perception of low frequencies remains intriguing. Peafowl do rely on the auditory system to detect low frequencies as shown by the severe loss of sensitivity following puncture of the tympanic membrane, but there is also evidence of some contribution of the crest apparatus within the frequency range of approximately 16–25 Hz.

An estimate of resonance of the apical end of the basilar membrane in Galliformes, based on stereovilli bundle morphology, may also hint at a separate mechanism underlying low-frequency hearing (Corfield et al. 2013). The apical resonance frequencies estimated for seven Galliformes all suggested very similar lower hearing limits of about 200 Hz. We now know that three of those species—domestic chickens (Hill et al. 2014), Japanese quail (Strawn and Hill 2020), and now Indian peafowl—all hear well below the estimated 200 Hz resonance limit of the basilar papilla. Such an extension of sensitivity below the resonance of the apical end of the basilar papilla suggests that additional factors are likely to contribute to low-frequency sensitivity—perhaps

electrical tuning of hair cells as noted by Corfield and colleagues (2013), and/or a firing rate/volley mechanism in the auditory nerve similar to that in mammals that hear low frequencies (He erner et al. 2001).

The variation of low-frequency hearing in birds is important for the study of the selective pressures affecting avian hearing as well as for the mechanisms employed. Figure 4 shows the range of low-frequency hearing in birds as measured by the lowest frequency detectable at an intensity of 60 dB SPL. The 60-dB level has been useful in comparing both high- and low-frequency hearing in mammals (e.g.,

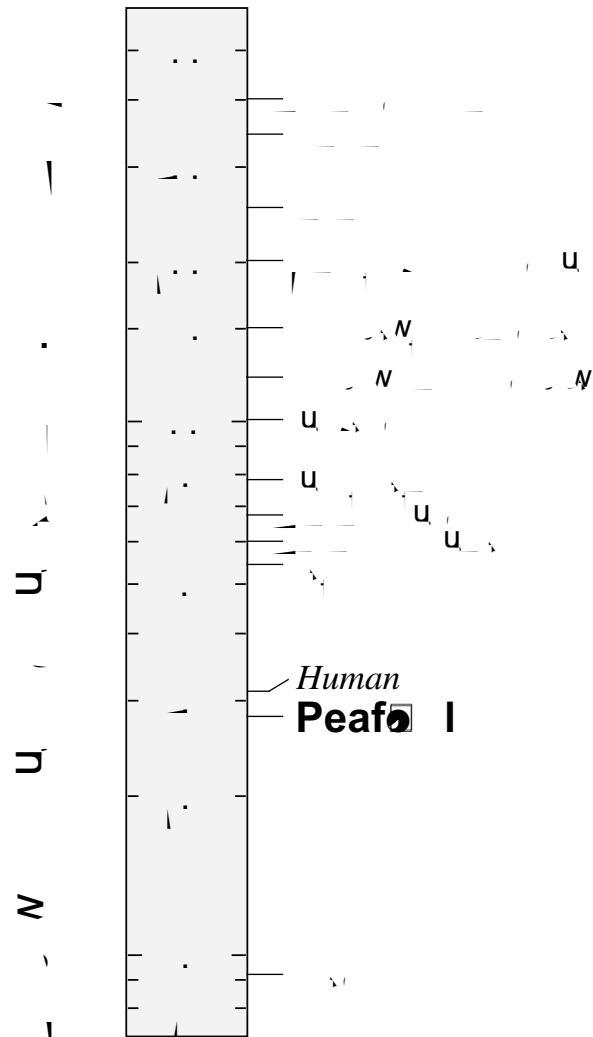


Fig. 4 Low-frequency hearing limits at 60 dB SPL, note log scale (Bullfinch-Schwartzkopf 1949; Red-winged blackbird and Brown-headed cowbird—Heinz et al. 1977; Pigeon—Kreithen and Quine 1979, He erner et al. 2013; Canary—Okanoya and Dooling 1987; Human—Jackson et al. 1999; Orange-fronted conure, extrapolated from 52 dB threshold at 250 Hz—Wright et al. 2003; Budgerigar—He erner et al. 2016; Domestic chicken—Hill et al. 2014; Kea parrot—Schwing et al. 2016; Great cormorant, extrapolated from 53 dB threshold at 500 Hz—Maxwell et al. 2017; Mallard duck—Hill 2017; Japanese quail—Strawn and Hill 2020)

He ner et al. 2001). Although other levels may eventually prove useful for making other comparisons, the use of a less stringent level such as a 30-dB or 40-dB definition of low-frequency hearing reveals much less variation among birds, hence is less desirable as a measure for exploring their variation in low-frequency capabilities. As Fig. 4 shows the low-frequency hearing limits of few birds have been determined; indeed, few species have been tested below 250 Hz. Altogether, the 13 low-frequency limits available appear to form a continuum ranging from 9 Hz (Domestic chicken, Hill et al. 2014) to approximately 400 Hz (Great cormorant, Maxwell et al. 2017). To understand how low frequencies are used, or not used, by birds of different lineages and lifestyles, we will need to know the low-frequency hearing abilities of a much larger and more representative sample of species. Such data are needed to help us interpret the underlying anatomical and physiological mechanisms, and perhaps provide insight regarding the functions served by hearing very low frequencies (cf. Zeyl et al. 2020).

Navigation

It was initially proposed that sensitivity to very low frequencies in pigeons might be an adaptation for navigation during migration (Kreithen and Quine 1979; Hagstrum 2019). However, that rationale for infrasound sensitivity cannot apply to chickens and peafowl, both of which are poor flyers and do not navigate long distances. On the other hand, mallard ducks migrate over long distances and do not hear infrasound (Hill 2017). Hence, although infrasound might be used for long-distance navigation, it is not essential. The hearing of so few other bird species has been tested at low frequencies that we are left with few theories as to why some birds hear infrasound and others do not. Moreover, we cannot assume that very low frequencies play only a single role in the lives of animals.

Courtship

The vocal calls of peafowl include frequencies ranging from about 150 Hz to as high as 8 kHz (Takahashi and Hasegawa 2008; Yorzinski and Anoop 2013). These frequencies encompass much of their hearing range, including the frequencies to which they are most sensitive. But much attention has been given to their visual courtship displays, which also produce very-low-frequency sound. Males pulse/shiver their highly visible train and rotate their wings, producing frequencies below 20 Hz, to which nearby females respond (Freeman and Hare 2015). These displays seem to be necessary for successful mating and we now know that the associated low-frequency sounds are audible across the short distances at which they are used. These low frequencies also stimulate the crest feathers (Kane et al. 2018) and our results

show that such vibrotactile input improves detectability of frequencies of 16–25 Hz, but only by about 6–7.5 dB.

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