JASA ARTICLE

The acoustical effect of the neck frill of the frill-necked lizard (*Chlamydosaurus kingii*)

John Peacock,[1,a)] Monica A. Benson,[1] Nathaniel T. Greene,[2] Daniel J. Tollin,[1] and Bruce A. Young[3]
[1]*Department of Physiology and Biophysics, University of Colorado School of Medicine, Aurora, Colorado 80045, USA*
[2]*Department of Otolaryngology, University of Colorado School of Medicine, Aurora, Colorado 80045, USA*
[3]*Kirksville College of Osteopathic Medicine, A. T. Still University, Kirksville, Missouri 63501, USA*

ABSTRACT:
Animals localise sound by making use of acoustical cues resulting from space and frequency dependent filtering of sound by the head and body. Sound arrives at each ear at different times, with different intensities, and with varying spectral content, all of which are affected by the animal's head and the relative sound source position. Location cues in mammals benefit from structures (pinnae) that modify these cues and provide information that helps resolve the cone of confusion and provide cues to sound source elevation. Animals without pinnae must rely on other mechanisms to solve localisation problems. Most non-mammals lack pinna-like structures, but some possess other anatomical features that could influence hearing. One such animal is the frill-necked lizard (*Chlamydosaurus kingii*). The species' elaborate neck frill has been speculated to act as an aid to hearing, but no acoustical measurements have been reported. In this study, we characterise the frill's influence on the acoustical information available to the animal. Results suggest that the change in binaural cues is not sufficiently large to impact localisation behavior within the species' likely audiometric range; however, the frill does increase gain for sounds directly in front of the animal similar to a directional microphone. *© 2022 Acoustical Society of America.*

https://doi.org/10.1121/10.0012221

(Received 13 December 2021; revised 14 June 2022; accepted 15 June 2022; published online 15 July 2022)

[Editor: Jonas Braasch] Pages: 437–444

I. INTRODUCTION

Animals are able to localise sound by having two ears in different locations separated by the head. As a consequence, incoming sound will not be the same at both ears; it will arrive at each ear at a different time, resulting in an interaural time difference (ITD); with differing intensity resulting in an interaural level difference (ILD); and with different spectral content due to interactions with the head, body, and pinnae. These three acoustical cues provide information that aids the identification of sound source location [see, e.g., Blauert (1997) and Grothe *et al.* (2010)].

Various animals have evolved special structures to help enhance these acoustical cues, the most notable of these being the pinnae of mammals and the facial ruff of the barn owl (Keller *et al.*, 1998; Knudsen and Konishi, 1979). Most other species lack any prominent external features (although some make use of internal structures; see Sec. IV); however, any structure located around the opening to the ear will inevitably change the nature of incoming sound and produce information that could be helpful to sound localisation. Studies in guinea pigs showed that, in addition to pinnae, this species prominent zygomatic arch effectively turns the side of the animal's head into an acoustic receiver (Greene *et al.*, 2014). Knowing this to be the case, we can speculate that various features on other species might similarly act as an aid to hearing.

Lizards exhibit a wide variety of ear morphologies (Miller, 1966; Wever, 1978). In the external ear, differences can be seen in the width, depth, and overall shape of the ear canal, and many taxa contain other unique anatomical features in the ear [some of which are under active control and thus may be "tunable" by the animal (Young, 2016)]. While much of this variation will be related to protection of the tympanic membrane or other non-auditory functions, it has been noted that many of these variations appear more directly related to hearing (Baird, 1970; Versluys, 1898). Some taxa with the most elaborate variations, such as *Gekko*, are known to have superior hearing compared with other squamates (Wever *et al.*, 1963, 1964).

The frill-necked lizard (*Chlamydosaurus kingii*) is one species with a particularly large structure surrounding its ear. It possesses an elaborate neck frill, one of the largest such structures seen in any extant reptile. The frill consists of a fold of skin that normally sits flat against the neck and is connected to the jaw by means of cartilaginous spines. The animal can thus open the jaw and allow the frill to stand erect [see Montandon *et al.* (2019) for further details on the frill]. The ears of the frill-necked lizard are positioned anterior to this frill as illustrated in Fig. 1, and it has been suggested that the animal uses its erect frill to help it localise sound. In a study of the muscles of the frill-necked lizard,

---

[a)] Electronic mail: john.2.peacock@cuanschutz.edu

FIG. 1. (Color online) Drawings of the frill-necked lizard with the frill in the erect and relaxed position to illustrate the position of the ear relative to the frill. The tympanic membrane is coloured in blue and outlined with a dashed line.

Charles W. De Vis recalls an incident he witnessed in Queensland, Australia:

> "On one of the two occasions on which I have seen the lizard adopt its biped mode of locomotion… I was much interested to see it halt abruptly, erect its frill, and at the same moment turn its head enquiringly from side to side—then trot on again for twenty yards or so, and repeat its attitude of attention—thus it did, till it reached the tree it was making for, then darting a few feet up its bole it clung there immovable for more hours than my leisure could afford for observation" (De Vis, 1883).

De Vis then suggests that the frill might serve an acoustic purpose, conducting sound to the tympanic membrane "perhaps aided by the channels formed by its converging folds." However, De Vis concludes that his study of the animal's muscles do not "of themselves indicate very clearly that the appendage is in a strict sense an auditory conch," although he points out that his observations do not strictly rule out an auditory function.

To the best of our knowledge, no other observation of the animal making the actions described by De Vis have been reported, and subsequent more thorough and systematic studies of frill-necked lizard behavior have dismissed the idea of an auditory function for the frill. The observational study by Shine (1990) concluded that the frill's primary function was likely "anti-predation and intraspecific display," with the frill most commonly used "in displays by males and in interactions between adult lizards."

However, as described above, the position of the frill means that it will change the sound arriving at the ear when it is erect as compared to when it is relaxed. Whether these altered sounds are of use to the animal remains unknown. The magnitude and frequency range of these changes are uncertain, and any substantial alterations may only happen outside the animal's limited range of hearing (see Sec. IV).

To begin to determine whether the presence of the frill could provide some useful information, we characterised the acoustical properties of the frill in subadult lizards by playing sounds from locations around the animal, and with microphones placed at each ear. Our results show that holding the frill erect does produce a measurable acoustical effect. In this article, we describe the acoustical significance of the frill and whether or not it could be useful to the animal.

II. METHODS

A. Animal preparation

Two cadaveric subadult frill-necked lizards were acquired from a commercial supplier. The total length of the lizards was 320 and 340 mm, the snout-vent length was 100 and 110 mm, and the frill diameters were 78 and 82 mm. This compares to a snout-vent length of ∼260 mm and frill diameters of 140–180 mm in the largest specimens measured by Shine (1990). The animals were fully thawed, and the heads, frill, and tympanic membrane were visually inspected for signs of damage prior to beginning measurements.

Two probe tube microphones (type 4181, Bruel and Kjær, Nærum, Denmark) were used to measure the sound at each ear. The microphones were fitted with flexible tubing that was fixed to the lizard's head with the top positioned at the tympanic membrane. Each specimen was secured on a platform in the center of the speaker array (described below), and measurements were made with the frill in the relaxed position. The frill was then opened and held erect with glue and an acoustically transparent flexible wire mesh. Photographs of the wild animal holding the frill erect were referenced in attempts to ensure the frill was held as a natural a position as possible; however, there are likely to have been some differences in the tension and curvature of the frill as opposed to the situation in the living animal.

B. Experimental setup

The sound presentation setup and procedures were identical to those described in previous studies (Greene *et al.*, 2014; Koka *et al.*, 2008, 2011; Tollin and Koka, 2009a,b). The methods are described below, but more detailed descriptions can be found in Greene *et al.* (2014).

The signals were generated by an RP2.1 [Tucker-Davis Technologies (TDT), Alachua, FL], attenuated with a TDT PA5, amplified with a TDT HB7, and delivered to 25 identical speakers with two TDT PM2Relay modules. The loudspeakers were selected from a larger set (∼100) on the basis of best-matching frequency responses. The loudspeakers were attached to a 1 m radius semicircular boom with a spacing of 7.5° between speakers (covering azimuth angles of +90° to −90°). This was attached to a motor that allowed the speakers to be rotated around the lizard, the axis of rotation being aligned with the animal's interaural axis (with the alignment being confirmed with lasers). We first made measurements with the boom positioned at an elevation of −45° (in front of and below the animal) and then subsequently rotated it up and around in 7.5° steps until it reached −180° (directly behind the animal). A distance of 1 m from the speakers means the measurements are in the far field for all tested frequencies.

Measurement stimuli consisted of 11th order maximum length sequences (MLSs) (Rife and Vanderkooy, 1989) repeated continuously 128 times from each loudspeaker. The MLS stimuli were presented at full 24-bit resolution at a rate of 97 656.25 Hz. Additional measurements were made playing tones at different frequencies to more accurately calculate ITDs. Tones were only played for an elevation of 0°.

C. Data processing and analysis

The impulse responses for each ear and at each location were calculated by circular cross correlation of the stimulus and the microphone recording (Rife and Vanderkooy, 1989). The impulse responses were then truncated to 512 (5.24 ms) points by a Hanning window beginning at 700 samples (7.17 ms) after the start of the stimulus presentation, thereby approximately centering the maximum deflection of the impulse response.

Head related transfer functions (HRTFs) were derived by dividing the frequency response of each speaker recording by that of the same loudspeaker without the specimen in place, thereby removing the loudspeaker and microphone frequency response from each measurement. The resulting function, the HRTF, represents the acoustical gain and delay introduced by the head. To reduce the effects of probe tube placement, directional transfer functions (DTFs) for each ear were calculated from the HRTFs by dividing the HRTF made at each spatial location by the geometrical mean of all the measured HRTFs across all measurement locations for that ear. The spectral features resulting from the exact placement of the probe tube microphone are expected to be similar for all measurement locations, so this "common" spectral feature is removed from the HRTFs, resulting in the DTFs (Middlebrooks *et al.*, 1989). DTFs are essentially the sound source direction-dependent components of HRTFs. Over the frequency range we measured, the average HRTFs (common component) differ by less than 1 dB between frill up vs down conditions.

Finally, the amplitude spectra of the DTFs were calculated using a 512-point fast Fourier transform (FFT) after the spectra were passed through a bank of bandpass filters that simulate the effects of auditory peripheral filtering. The filter bank consisted of 500 Butterworth filters with center frequencies spaced at intervals of 0.0143 octaves spanning from 0.25 to 32 kHz. The 3 dB bandwidth of filters was held constant across all frequencies at 0.0571 octaves, and the upper and lower slopes of the filters fell off at ∼105 dB/octave. These filters have properties similar to the bank of triangular bandpass filters described in the literature (Schnupp *et al.*, 2003; Xu and Middlebrooks, 2000).

III. RESULTS

A. DTF gain

Figure 2 shows surface plots of DTF gain in the left ear as a function of frequency for sounds coming from the front of one of the two lizards. The plot shows data at five frequencies from 1 to 8 kHz. This frequency range was chosen as it likely spans the majority of the species' hearing range (see Sec. IV). In these plots, the data are displayed as Aitov projections (Bugayevskiy and Snyder, 1995). The data are displayed as if the animal were looking out of the page toward the reader, with the nose positioned at 0° azimuth and 0° elevation.

Unsurprisingly, given the simple ovoid shape of the animal's head, high gain areas appear immediately to the left and right of the head in all conditions and at all frequencies, suggesting that the animal's ears show a baseline dipole acoustic directivity. At 1 kHz (and below), gain appears reasonably low and uniform, and the gain appears to be comparable in the frill up and frill down conditions.

At 2 kHz, a small (approximately 2 dB) increase in gain is observed directly in front of the animal, which appears somewhat more prominent in the frill up than frill down condition. More dramatic and noticeable differences emerge at higher frequencies (>2 kHz), where a prominent hotspot in the gain is visible nearly directly in front of the animal and where the difference between the frill up and frill down conditions rises to as much as 8–10 dB. More complicated and more prominent peaks and troughs are seen in the frill up data, and we begin to see larger differences develop between the two conditions. Overall, it appears that an erect frill acts to provide additional gain and directionality for sounds coming from the front hemifield.

Figure 3 shows the same gain data as in Fig. 2, but for sound coming from positions behind the animal. In this projection, the animal is facing in the opposite direction to Fig. 2 and is facing directly into the page. A similar pattern is seen as for the front hemifield, with limited changes at 1 and 2 kHz and more complicated features emerging at higher frequencies.

Figure 4 shows the maximum gain measured in the front hemisphere against frequency. The blue lines show data for the frill up condition, and the red lines show data from the frill down condition, and different lizards are distinguishable by symbols (open or closed). Above 1500 Hz, we begin to see the data from the two conditions diverge, with the frill up condition showing a systematic increasingly larger gain with increasing frequency. With the frill erect, the maximum gain is approximately double what is seen with the frill relaxed.

In Fig. 5, we see the location of the maximum gain in both in azimuth (top) and elevation (bottom). As in previous figures, the red lines indicate the frill down condition and the blue lines indicate the frill up, and different lizards are distinguishable by symbols (open or closed). We can see that the maximum gain for both frill up and down conditions occurs at the same azimuth angle for frequencies below 2500 Hz. Above this frequency, we see differences begin to emerge with the position of the gain moving further off to the side of the animal, and this occurs much earlier for the frill down condition than for the frill up. However, once we reach around 5500 Hz, this situation appears reversed.

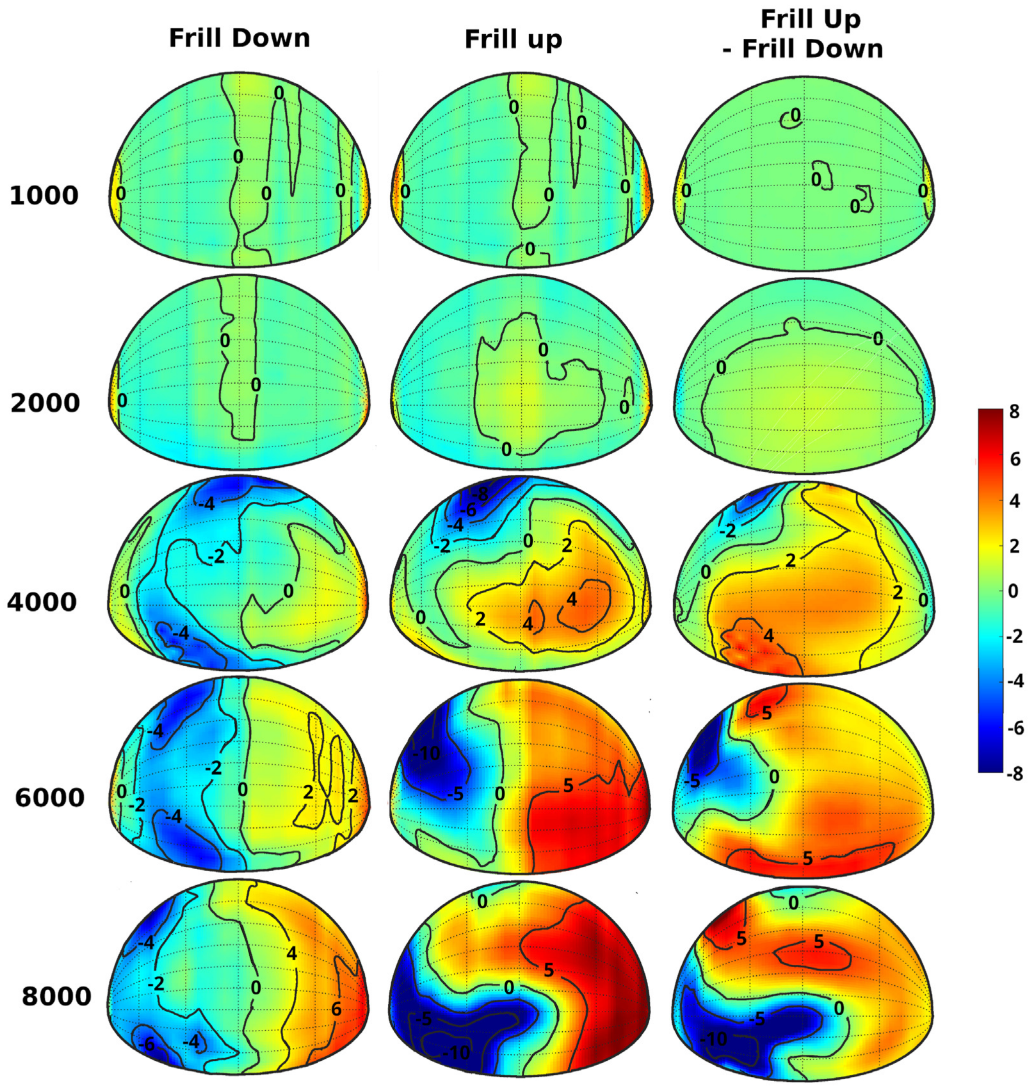

FIG. 2. (Color online) DTF gain in the left ear as a function of frequency (from 1 to 8 kHz) for sounds coming from the front of the animal. The magnitude of the gain is indicated by colour.

A much more dramatic result is seen when examining the change in the elevation angle of the maximum gain (Fig. 5, bottom panel). There is a very clear shift from the back of the animal to the front when the frill is held erect. With the frill down, the maximum gain is between 90° and 180° (directly above to directly behind the head), while in the frill up condition, the maximum gain averages around −15° to −45° (in front and below the head).

B. Binaural sound localisation cues

Most terrestrial vertebrates use differences in the acoustical properties of sounds arriving at their two ears to determine sound source location. Figure 6 shows the magnitude of the ILDs, calculated as the difference in gain between the left and right ears, across frequencies, at different elevation and azimuth angles, and for both the frill up and frill down conditions in one of the two lizards. The top two panels show data at an elevation of 0° and at different azimuth angles, while the bottom two panels show data at 0° azimuth and changing elevation. Different angles of elevation and azimuth are indicated by colour.

For fixed elevation and changing azimuth, we see that below 1–2 kHz ILDs are very small, but at higher frequencies we see ILDs increase consistent with the expected relationship between the small head size of these animals. ILDs are comparable across frill conditions for low frequencies but begin to diverge at higher frequencies, rising to as high as 9 dB at 8 kHz for the frill down condition and to a peak of near 16 dB at 6–7 kHz for the frill up condition. The magnitude of the ILD shows a progression across space, generally increasing with increasing azimuth angle (as expected for the lateral placement of the ears). For fixed azimuth and changing elevation, a more complex story is seen. At some positions directly behind that animal, we do see a reduction in the ILD when the frill is held erect but see more increases in the ILDs at other elevations.

To better characterise how ILD depends upon frequency, Fig. 7 shows the mean ILD slope from −30 to +30

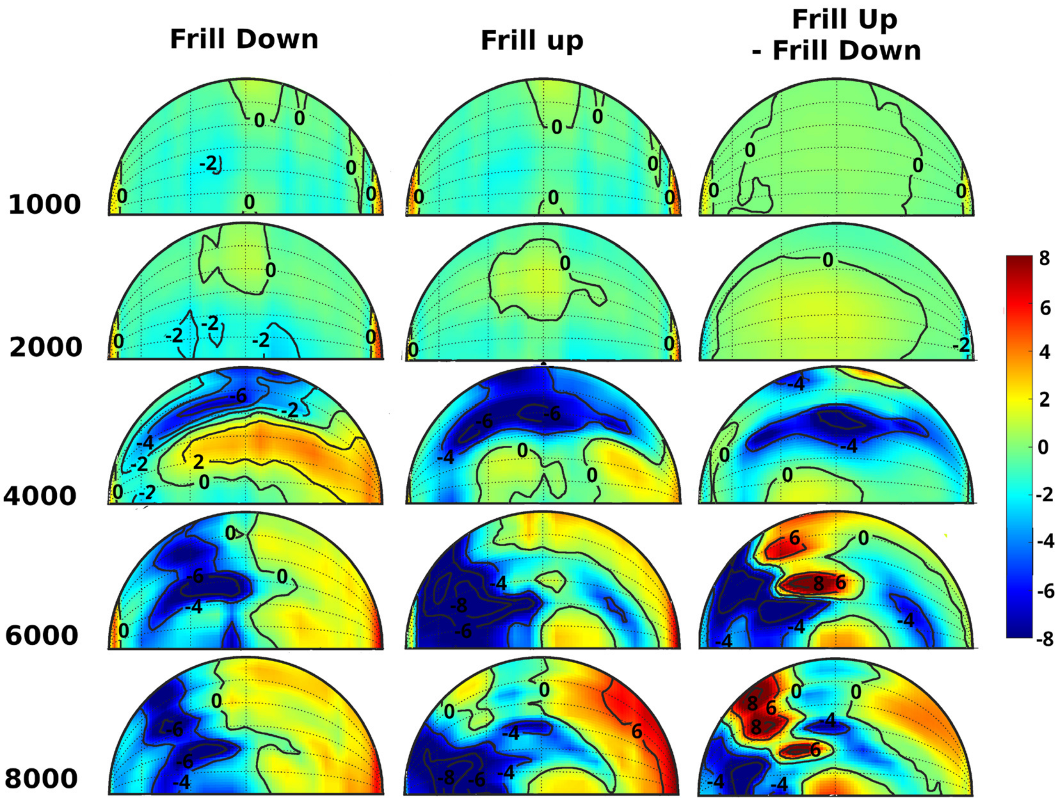

FIG. 3. (Color online) DTF gain in the left ear as a function of frequency (from 1 to 8 kHz) for sounds coming from behind the animal. The magnitude of the gain is indicated by colour.

azimuth for both lizards and all conditions. Results from both lizards are distinguishable by symbols (square and circle), and the frill up and frill down measurements are distinguishable by colour (red and blue). Responses are highly consistent across both lizards and across all conditions for

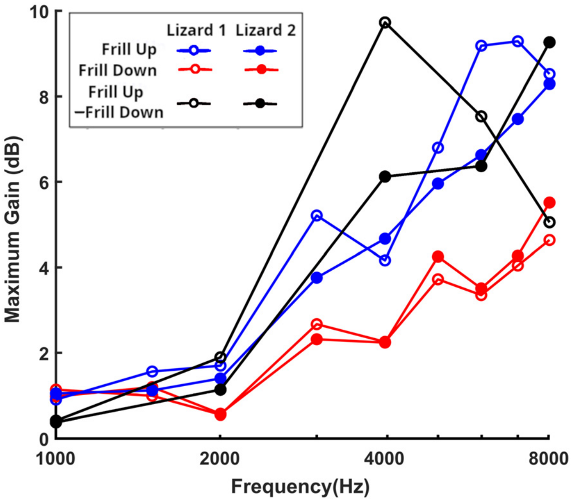

FIG. 4. (Color online) The maximum gain measured in the front hemisphere vs frequency. The blue lines show data for the frill up condition, the red lines show data from the frill down condition, and the black lines show the ratio of frill up to frill down. Different lizards are distinguishable by symbols (open or closed).

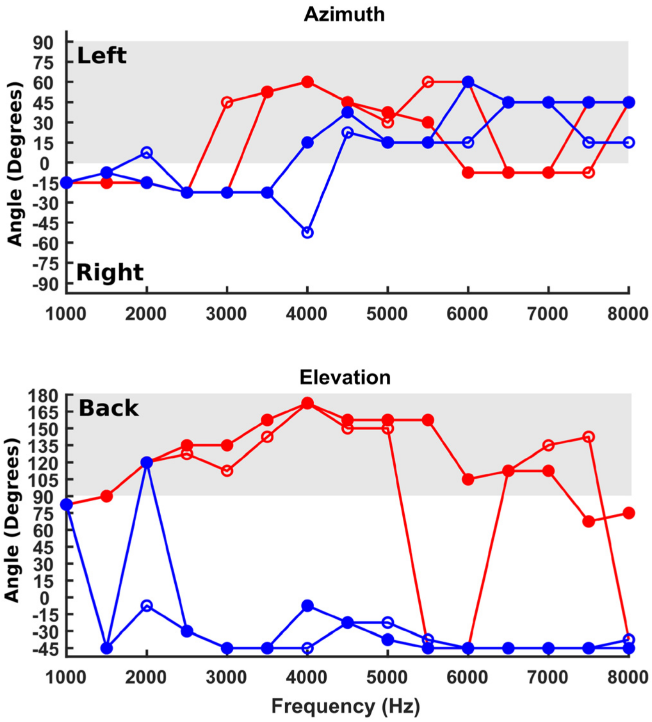

FIG. 5. (Color online) The location of the maximum gain in both in azimuth (top) and elevation (bottom). The blue lines show data for the frill up condition, and the red lines show data from the frill down condition, and different lizards are distinguishable by symbols (open or closed).

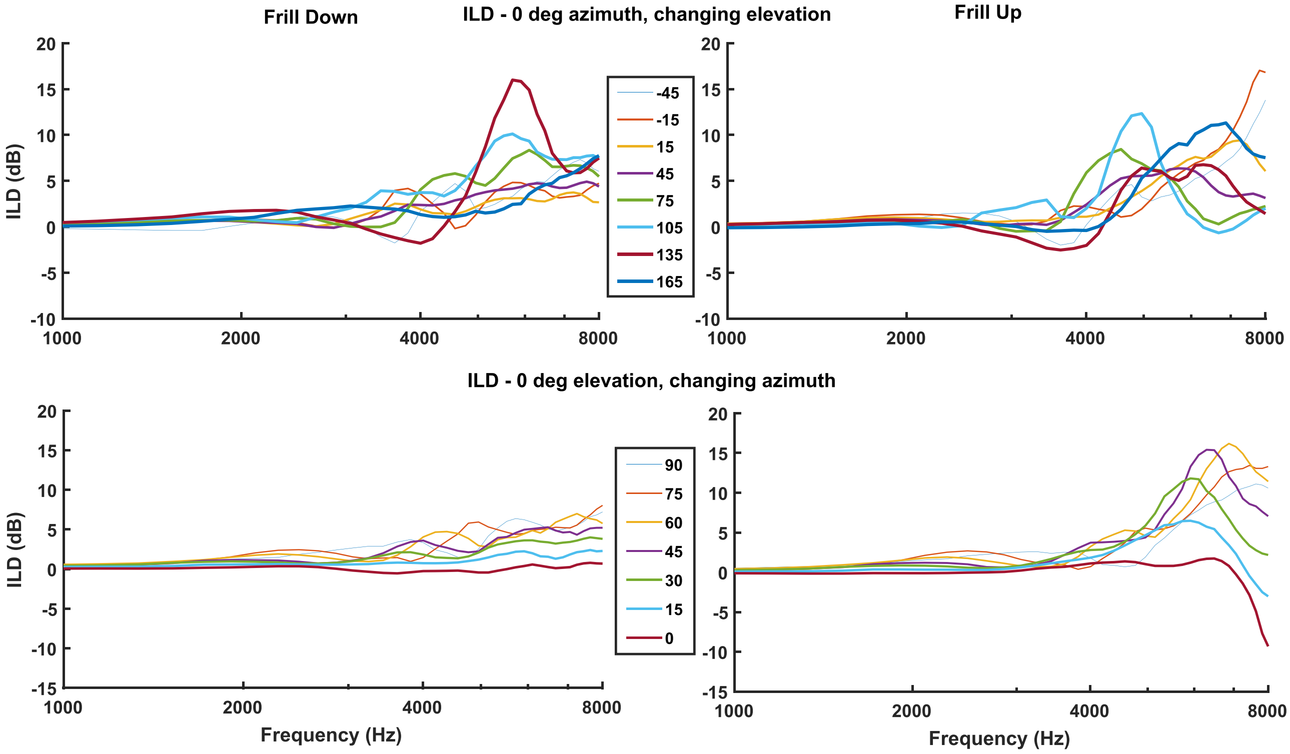

FIG. 6. (Color online) The magnitude of the ILDs, calculated as the difference in gain between the left and right ears, across frequencies, at different elevation and azimuth angles, and for both the frill up and frill down condition. The top two panels show data at an elevation of 0° and at different azimuth angles, while the bottom two panels show data at 0° azimuth and changing elevation. Different angles of elevation and azimuth are distinguishable by colour as indicated in the legend.

low frequencies. Results from the two measurement conditions begin to diverge for higher frequencies, beginning just below 2 kHz. ILD is suppressed, even becoming negative (pointing in the wrong direction) for frequencies between 2 and 4 kHz in the frill up condition. This trend rapidly reverses at yet higher frequencies where the frill up condition displays substantially higher ILDs.

In Fig. 8, we show the ITDs calculated for a 1000 Hz tone at an elevation of 0°. As in Figs. 4 and 5, results from both lizards are distinguishable by symbols (square and circle), and the frill up and frill down measurements are distinguishable by colour (red and blue). The maximum ITD at this frequency was $\pm 150\ \mu s$. Measurements in mammals have demonstrated that pinnae can increase the size of ITDs (Tollin and Koka, 2009b), but our data here show no significant difference in ITD as a result of the position of the frill. ITDs were also calculated at other frequencies between 250 and 4000 Hz, but the pattern remained the same at all frequencies with no differences between the frill up and frill down conditions. It appears that the frill does not alter ITDs in any way that could enhance sound localisation.

IV. DISCUSSION

A. The hearing ability of the frill-necked lizard

The audiogram of the frill-necked lizard has not yet been reported, but the hearing ability of other lizard species has been measured via the auditory brainstem response (ABR). Brittan-Powell *et al.* (2010) measured ABRs in the green anole (*Anolis carolinensis*) and found good hearing from 1 to 7 kHz. This is the species most closely related to the frill-necked lizard for which we were able to find data;

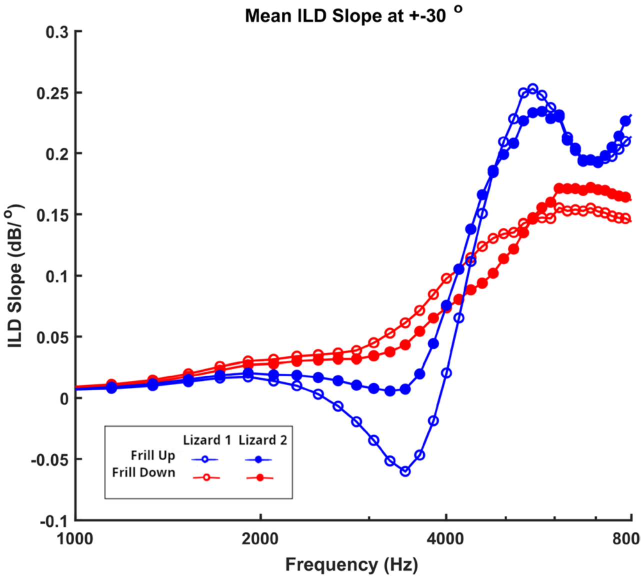

FIG. 7. (Color online) The mean ILD slope at ±30 azimuth for both lizards and all conditions. This is calculated by subtracting the ILDs at ±30 and dividing by 60. The blue lines show data for the frill up condition, and the red lines show data from the frill down condition, and different lizards are distinguishable by symbols (open or closed).

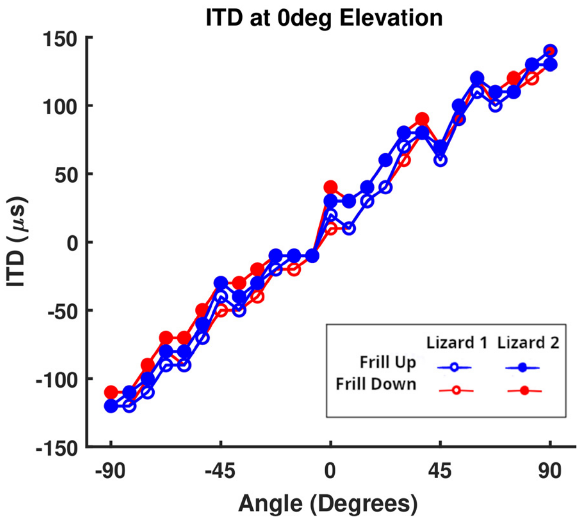

FIG. 8. (Color online) The ITDs calculated for a 1000 Hz tone at an elevation of 0°. The blue lines show data for the frill up condition, and the red lines show data from the frill down condition, and different lizards are distinguishable by symbols (open or closed). As with Fig. 5, the positive angles are to the left of the animal, while the negative angles are to the right.

however, it is a much smaller species, and we would expect the upper limit of hearing to be lower in larger species. One such larger species that has been well studied is the Tokay gecko (*Gekko gekko*), in which hearing ability has been measured in numerous ways (e.g., Brittan-Powell *et al.*, 2010; Manley *et al.*, 1999; Werner and Wever, 1972). The upper limit of hearing in these studies is generally found to be closer to 5 kHz. We predict that the hearing range of the frill-necked lizard will not be greater than for the anole and will probably be closer to the gekko due to its more similar size. Such an upper limit of hearing is normal across most lizards.

The frill does start to generate some noticeable acoustical changes starting at around 2 kHz, and these get larger as we move to higher frequencies. Thus, if we assume an upper limit of hearing at 5 kHz, similar to most other lizards, it is likely that some of the acoustical changes caused by the frill are audible to the species. The neck frill does begin to generate still more significant acoustical cues at frequencies higher than the frill-necked lizard can likely hear. Our results show how simple "pinna-like" structures can generate acoustical information but that higher frequency hearing is required to make use of it. This is likely why only mammals, which do hear higher frequencies, possess these structures.

B. Acoustical localisation cues produced by the neck frill

The results in Figs. 2 and 3 show how the neck frill is acoustically transparent at frequencies below 2 kHz, but at higher frequencies (shorter wavelengths) it produces directionally dependent variation in the gain, with the magnitude of this gain increasing with increasing frequency. A similar result is also seen when examining ILDs. Here, again we see changes in the magnitude of the ILDs with an erect frill and changes that vary with sound source location.

That being said, the usefulness of the differences we find is limited by their relatively small magnitude as compared to the pinna cues that mammals use to localise sound. The DTF gain never rises much above 8 dB (at the frequencies we report), but for mammals, the gain can reach as high as 20–30 dB at the frequencies they use [see, e.g., measurements from our laboratory in guinea pigs (Greene *et al.*, 2014), rats (Koka *et al.*, 2008), and chinchillas (Jones *et al.*, 2011)], which is due almost entirely to the pinnae.

It must be noted that the acoustical cues produced by the neck frill will not be the only information available to the animal to aid in sound localisation. Non-mammals (as well as monotremes and some therian mammals) do possess internal passages between the ears (Mason, 2016), which allow their ears to function as pressure difference receiver microphones (Hemmen *et al.*, 2016; Vedurmudi *et al.*, 2020). These interaural canals allow sound to travel through the head: the tympanic membrane therefore acts as a pressure difference receiver and will greatly alter the effective ILD and ITD and thus enhance the cues available to the animal. To the best of our knowledge, there are no published descriptions of the morphology of the Eustachian tubes and/or interaural passages in the frill-necked lizard. However, micro-CT analysis performed on the specimens used in this study clearly showed an interaural passage between the contralateral middle ear cavities. The size and structure of this interaural passage is quite similar to what was previously described in monitor lizard *Varanus* (Vedurmudi *et al.*, 2020).

In some species, these interconnected ears can lead to an almost 40 dB difference in eardrum vibration between the ears (Christensen-Dalsgaard and Manley, 2008; Vossen *et al.*, 2010). Thus, a study of the acoustical influence of the neck frill does not fully characterise the directional cues available to the animal. Studying the effects of the canals is beyond the scope of this study; however, this could be explored in future studies by making simultaneous measurements of tympanic membrane vibration alongside the acoustical signal.

These considerations aside, it is the case that to achieve accurate sound localisation, some anatomical structure must be in place to resolve the cone of confusion by producing directionality in the vertical and front/back dimensions. In the absence of such a structure, e.g., pinnae or frill, a source in front of an animal will have roughly the same binaural cues as a source at the complementary angle behind the animal (e.g., 45° in front vs 135° behind).

C. The frill as a directional microphone

As previously described, De Vis (1883) observed a lizard holding its frill erect and then actively moving its head around as if in search of sound. The description suggests that the lizard used its erect frill to work as a directional microphone. This possibility is supported by our measurements that demonstrate the frill's role in increasing the directivity of the ears. This is not to suggest that the frill's sole function, or even its primary function, is as an aid to hearing, but that the structure's acoustical influence means that a hearing function for it is not impossible. As mentioned in the Introduction, the available information suggests the frill's likely primary function is in intraspecific communication, and an additional acoustic function would not interfere with this.

It should be remembered that our lizards were subadults and had not reached their maximum size. The relationship between frill size and body length has been described (Shine, 1990), and so we know that larger animals will have proportionally larger frills. It is well known that the directivity index of a microphone or speaker depends upon both frequency and the diameter of the membrane (Blackstock, 2000). A larger frill should result in a larger effective membrane diameter. This would further increase the effective radius of the ears, resulting in further increases in directivity. Published studies have shown the acoustics of pinna scaling (Middlebrooks, 1999; Schnupp *et al.*, 2003; Tollin and Koka, 2009a), and from these we would expect the acoustical information we see in our lizards to be shifted to lower frequencies in a full-sized adult, and thus the information is more likely to fall within the animal's range of hearing. Combined, this would mean the frill's potential usefulness as an aid to hearing is greater in an adult than in a juvenile animal.

V. CONCLUSIONS

We made measurements of the acoustical influence of the neck frill in subadult frill-necked lizards. We observed changes in directional gain when the frill is held erect. Our results shows that an erect frill increases the gain and directivity of the ear and thus could function as a directional microphone and help resolve front–back confusions.

Baird, I. L. (**1970**). "The anatomy of the reptilian ear," in *Biology of the Reptilia*, edited by C. Gans and T. S. Parsons (Academic Press, London), Vol. 2, pp. 193–275.

Blackstock, D. T. (**2000**). *Fundamentals of Physical Acoustics* (Wiley, New York).

Blauert, J. (**1997**). *Spatial Hearing: The Psychophysics of Human Sound Localization* (MIT, Cambridge, MA).

Brittan-Powell, E. F., Christensen-Dalsgaard, J., Tang, Y., Carr, C., and Dooling, R. J. (**2010**). "The auditory brainstem response in two lizard species," J. Acoust. Soc. Am. **128**, 787–794.

Bugayevskiy, L., and Snyder, J. (**1995**). *Map Projections: A Reference Manual* (Taylor and Francis, London).

Christensen-Dalsgaard, J., and Manley, G. A. (**2008**). "Acoustical coupling of lizard eardrums," J. Assoc. Res. Otolaryngol. **9**, 407–416.

De Vis, C. W. (**1883**). "Myology of *Chlamydosaurus kingii*," Proc. Linn. Soc. New South Wales **8**, 300–320.

Greene, N. T., Anbuhl, K. L., Williams, W., and Tollin, D. J. (**2014**). "The acoustical cues to sound location in the guinea pig (*Cavia porcellus*)," Hear. Res. **316**, 1–15.

Grothe, B., Pecka, M., and McAlpine, D. (**2010**). "Mechanisms of sound localization in mammals," Physiol. Rev. **90**, 983–1012.

Hemmen, J. L. V., Christensen-Dalsgaard, J., Carr, C. E., and Narins, P. M. (**2016**). "Animals and ICE: Meaning, origin, and diversity," Biol. Cybern. **110**, 237–246.

Jones, H. G., Koka, K., Thornton, J. L., and Tollin, D. J. (**2011**). "Concurrent development of the head and pinnae and the acoustical cues to sound location in a precocious species, the chinchilla (*Chinchilla lanigera*)," J. Assoc. Res. Otolaryngol. **12**, 127–140.

Keller, C. H., Hartung, K., and Takahashi, T. T. (**1998**). "Head-related transfer functions of the barn owl: Measurement and neural responses," Hear. Res. **118**, 13–34.

Knudsen, E. I., and Konishi, M. (**1979**). "Mechanisms of sound localization in the barn owl (*Tyto alba*)," J. Comp. Physiol. **133**, 13–21.

Koka, K., Jones, H. G., Thornton, J. L., Lupo, J. E., and Tollin, D. J. (**2011**). "Sound pressure transformations by the head and pinnae of the adult Chinchilla (*Chinchilla lanigera*)," Hear. Res. **272**, 135–147.

Koka, K., Read, H. L., and Tollin, D. J. (**2008**). "The acoustical cues to sound location in the rat: Measurements of directional transfer functions," J. Acoust. Soc. Am. **123**, 4297–4309.

Manley, G. A., Köppl, C., and Sneary, M. (**1999**). "Reversed tonotopic map of the basilar papilla in *Gekko gecko*," Hear. Res. **131**, 107–116.

Mason, M. J. (**2016**). "Internally coupled ears in living mammals," Biol. Cybern. **110**, 345–358.

Middlebrooks, J. C. (**1999**). "Individual differences in external-ear transfer functions reduced by scaling in frequency," J. Acoust. Soc. Am. **106**, 1480–1492.

Middlebrooks, J. C., Makous, J. C., and Green, D. M. (**1989**). "Directional sensitivity of sound-pressure levels in the human ear canal," J. Acoust. Soc. Am. **86**, 89–108.

Miller, R. (**1966**). "The cochlear duct of lizards and snakes," Am. Zool. **6**, 421–429.

Montandon, S. A., Fofonjka, A., and Milinkovitch, M. C. (**2019**). "Elastic instability during branchial ectoderm development causes folding of the *Chlamydosaurus* erectile frill," Elife **8**, 1–23.

Rife, D., and Vanderkooy, J. (**1989**). "Transfer-function measurement with maximum-length sequences," J. Audio Eng. Soc. **37**, 419–444.

Schnupp, J. W. H., Booth, J., and King, A. J. (**2003**). "Modeling individual differences in ferret external ear transfer functions," J. Acoust. Soc. Am. **113**, 2021–2030.

Shine, R. (**1990**). "Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae)," Biol. J. Linn. Soc. **40**, 11–20.

Tollin, D. J., and Koka, K. (**2009a**). "Postnatal development of sound pressure transformations by the head and pinnae of the cat: Binaural characteristics," J. Acoust. Soc. Am. **126**, 3125–3136.

Tollin, D. J., and Koka, K. (**2009b**). "Postnatal development of sound pressure transformations by the head and pinnae of the cat: Monaural characteristics," J. Acoust. Soc. Am. **125**, 980–994.

Vedurmudi, A. P., Young, B. A., and van Hemmen, J. L. (**2020**). "Active tympanic tuning facilitates sound localization in animals with internally coupled ears," Hear. Res. **387**, 107861.

Versluys, J. (**1898**). "Die mittlere and äussere Ohrsphäre der Lacertilia and Rhynchocephalia" ("The middle and outer spheres of the ear of the Lacertilia and Rhynchocephalia"), Zool. Jahrbücher Abteilung Anat. Ontog. Tiere **12**, 161–406.

Vossen, C., Christensen-Dalsgaard, J., and Leo van Hemmen, J. (**2010**). "Analytical model of internally coupled ears," J. Acoust. Soc. Am. **128**, 909–918.

Werner, Y. L., and Wever, E. G. (**1972**). "The function of the middle ear in lizards: *Gekko gecko* and *Eublepharis macularis* (Gekkonoidea)," J. Exp. Zool. **179**, 1–16.

Wever, E. G. (**1978**). *The Reptile Ear* (Princeton University, Princeton, NJ).

Wever, E. G., Peterson, E. A., Crowley, D. E., and Vernon, J. A. (**1964**). "Further studies of hearing in the gekkonid lizards," Proc. Natl. Acad. Sci. U.S.A. **51**, 561–567.

Wever, E. G., Vernon, J., Peterson, E., and Crowley, D. (**1963**). "Auditory responses in the Tokay gecko," Proc. Natl. Acad. Sci. U.S.A. **50**, 806–811.

Xu, L., and Middlebrooks, J. C. (**2000**). "Individual differences in external-ear transfer functions of cats," J. Acoust. Soc. Am. **107**, 1451–1459.

Young, B. A. (**2016**). "Anatomical influences on internally coupled ears in reptiles," Biol. Cybern. **110**, 255–261.