

Biomimetic investigation of the impact of the ear canal on the acoustic field sensitivity of aye-ayes

Hamidreza Nemati, Ehsan Dehghan-Niri *

Intelligent Structures and Nondestructive Evaluation (ISNDE), Civil Engineering Department, New Mexico State University, Las Cruces, NM 88003, USA

ARTICLE INFO

Article history:

Received 23 August 2022

Received in revised form 15 November 2022

Accepted 11 December 2022

Available online 27 December 2022

Keywords:

Aye-aye

Tap-scanning

Acoustic sound field

Pinna

Ear canal

ABSTRACT

The aye-ayes (*Daubentonia madagascariensis*) are an extremely rare lemur species and the world's largest nocturnal primate. Tapping on tree bark with its unique elongated middle finger, the aye-aye listens closely for signs of cavities or insect larvae inside; this is a unique acoustic-based foraging behavior called "percussive foraging" or "tap-scanning." Tap-scanning requires the animal auditory system to exhibit exceptional acoustic receptive field sensitivity. This study provides an insight into how the ear canal of aye-ayes might have an impact on their acoustic field sensitivity; this was achieved using a biomimetic approach to simulate the tapping mechanism. To this end, the aye-aye's pinna and ear canal were 3D printed. The pinna in the cupped position was preserved, and the acoustic field was evaluated in the time and frequency domains. The results suggest that the pinna with the ear canal can substantially enhance the receptive field sensitivity of the aye-aye's auditory system by shaping a focal area at the tapping location. Furthermore, changes in the sound field receiving beam pattern for higher frequencies resulted in an increase in the receiver dominant frequency, indicating the evolution of the aye-ayes' external ear to create a physical filter for excluding unnecessary low frequencies in the focal area.

© 2022 Elsevier Ltd. All rights reserved.

1. Introduction

Sound is an essential source of information for many animals and is one of the primary tools for survival. It is vital for communicating, foraging, navigating across animal territories, and conveying the presence of predators. Several animals, including bats, cetaceans, dolphins, woodpeckers, and aye-ayes, use self-generated acoustic cues for sound discrimination [1,2]. Certain animals with exceptional auditory capabilities have developed and optimized the most efficient acoustic sensing systems. Among the above-mentioned animals, woodpeckers and aye-ayes are the best examples of animal adaptation; their auditory sensing systems have evolved over the past million years to allow them to detect cavities in the outer 1–4 cm of a tree bark [3,4]. Both animals possess intricate anatomy in their auditory system that receive and localize sounds from the near-by point source. Therefore, it is argued that their ear must be specialized for near-field sound reception. The near-field is the region of space relatively close to the emitting source (e.g., approximately two wavelengths), where the sound pressure and acoustic particle velocity are not in phase. Conversely, the far-field starts approximately two wave-

lengths away from the sound source [5]. Owing to the propagation mechanism, acoustic waves around a sound source (i.e., tapping) in the near-field area have unconventional qualities in the temporal, spatial, and spectral domains. Although several researchers have studied numerous behavioral and physiological aspects of the auditory capabilities of woodpeckers [6–10], little is known about the near-field acoustic-based sensing and detection capabilities of the aye-ayes. This study attempts to experimentally investigate a few features that might have an impact on the exceptional acoustic sensing of aye-ayes.

The aye-ayes (*Daubentonia madagascariensis*) are unique to primates, both behaviorally and morphologically. They are a species of lemurs endemic to the rainforests of Madagascar and are the most enigmatic of all living species [11]. They are perhaps best known for the acoustic extractive foraging behavior called "percussive foraging" or "tap-scanning" [12]. They have evolved a suite of specialized morphological adaptations, including large mobile pinnae, ever-growing rodent-like incisors, excellent vision in the near-ultraviolet range, elongated sensitive third digit, and a large brain [13–16]. However, the most striking features of aye-ayes are their extremely narrow and flexible middle digits and enormous ears. They tap rhythmically along the surface of a decaying tree to facilitate the detection of tree cavities that potentially contain grubs (see Fig. 1). Such scanning techniques enable the investigation of

* Corresponding author.

E-mail addresses: niri@nmsu.edu, nde@asu.edu (E. Dehghan-Niri).

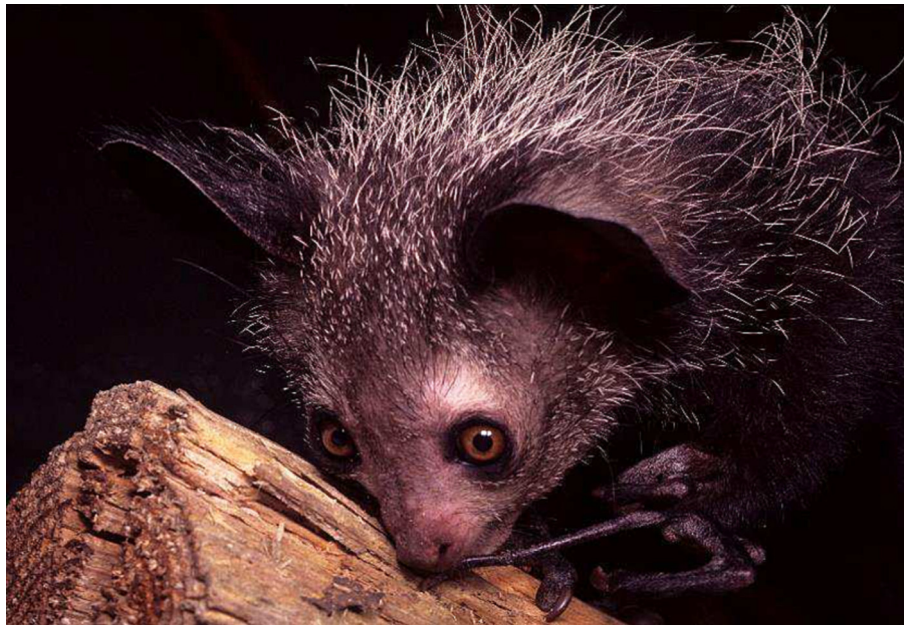


Fig. 1. An aye-aye during tap-scanning. Aye-ayes use their large pinna and elongated slender middle finger to accurately identify grubs and larvae hidden beneath the tree bark (Photograph: David Haring, Duke Lemur Center).

internal structural property variation of wooden parts. Furthermore, compared to other lemuroid prosimians, the pinnae of aye-ayes are proportionately larger [16]. Their large and membranous mobile bat-like pinnae rotate forward during tap-scanning. The aye-ayes detect the prey hidden beneath the tree bark by listening attentively to this drumming sound. When aye-ayes locate a cavity, they gnaw into the wood using their powerful jaw muscles and sharpened incisors to expose larvae. Further, they hook the larvae with their claws and lift them out [16]. These morphological adaptations play a significant role in the extractive foraging behavior of aye-ayes, which allows them to locate and exploit the resources unavailable to other animals in the wild. In addition, aye-ayes have the largest and most convoluted brains among all prosimians [17]. Their large brains show remarkable systematic capabilities that are uncommon in other animals. One might suspect that their large brains and peculiar foraging behaviors are linked [18]. Several studies have been conducted to show the correlation between the large brain size and complex sensorimotor intelligence in aye-ayes [12,17,19]. Along with these fascinating features, aye-ayes have an exceptionally active acoustic actuator and versatile acoustic sensing capability, making their biological system an appealing model for engineering sensory and robotic systems. For instance, one possible technological application of the animal's percussive foraging behavior may be in instrumented tap testers. Tap testing, also known as coin testing, is one of the oldest nondestructive testing (NDT) methods. It is regularly used for evaluating the condition of wood in service and inspection of laminated structures as well as honeycomb constructions [20]. The conventional tap testing method and most of the current tap-based technologies have the issue of subjectivity, lack of high-resolution results, and a low signal-to-noise ratio (SNR) [20–22]. The bio-inspired approach presented in this paper can help NDT practitioners to overcome the mentioned shortcomings.

A few studies have shown that the external ear, ear canal, and other morphological features such as local grooves or ridges, and the head, have dominant effects on mammalian far-field auditory systems [23–27]. Much of the knowledge about biological auditory systems comes from lateral and localization studies that considered interaural time differences (ITDs), interaural level differences

(ILDs), and spectral information [28,29]. The ITDs and ILDs are produced by the propagation and diffraction of sounds by the body, head, and pinnae. Similar to humans, other animals also use these cues, some of which may be absent in the human auditory system, such as the effects of ear movements. In the early 1900s, the duplex theory proposed by Lord Rayleigh explained how a combination of ITD and ILD cues could help humans localize a sound source [28]. They vary systematically according to the location of the sound source. For instance, sound at the eye level at any elevation can produce identical ITDs and ILDs, as long as the lateral direction is constant. Because a majority of animals have two ears, several effects of the human auditory system can also be found in other species [30]. Therefore, ITDs and ILDs have a significant impact on the hearing of many animals. However, the impact of these effects on the localization depends heavily on the head size, ear position, ear distance, and ear orientation [31]. This theory has been the basis of numerous studies on the localization process in the human and animal auditory systems. The acoustical transformation occurring between a point source and a receiving ear, known as the head-related transfer function (HRTF), is typically used to convey the above-mentioned cues for an auditory system to localize a sound source in space [32–35]. Some researchers have used a 3D printed dummy head to generate the human HRTF data [36,37]. The evaluation of the auditory systems and the HRTF of several animals including bats [27,38,26,39,40,41], cats [42–44], juvenile ferrets [45], chinchillas [46], gerbils [24], monkeys [47], rabbits [23], and other animals [48], have been the focus of several studies. However, these studies primarily focused on evaluating far-field localization (i.e., more than 1 m) and lateralization of the auditory system with one primary assumption that the target location (sound source) is not previously known to the animal under study. Furthermore, several studies have been conducted on the frequency aspect of aye-ayes' acoustic sensing during long-distance communication [49,50]; however, a sensing system that has become overspecialized for acoustic field measurement has not been completely studied yet. Biological auditory systems possess a frequency sensitivity effect on acoustic sensing. In addition, the shape and morphology adaptation of the acoustic sensing, particularly the external ear geometry, have adapted to create a

specialized plane wave field directionality (e.g., developing a focal point around the tapping area). Although aye-ayes can maximize sensitivity to a wide range of distances, the acoustic sensing specialization due to tap-scanning adaptation might entail trade-offs.

Why is an aye-aye's auditory system believed to be the primary sensing system enabling the tap-scanning process? Several studies have indicated that aye-ayes have exceptional auditory sensitivity to the sounds emitted from the insect larvae movements and the various tones emitted in response to tapping. Sonnerat suggested that aye-ayes use their acute auditory system to detect prey movements within the wood [51]. During foraging, large flexible ears are cupped forward and downward towards a point directly in front of the nose to listen to reverberations from the tree. In some circumstances, tapping behavior can trigger auditory activity in subterranean prey. If this assumption is correct, it is proof that the aye-ayes' super-strong and exceptionally-sensitive near-field auditory system can identify low-amplitude acoustic waves generated by the worm movements a few centimeters beneath the tree bark. Sandwith reported that an aye-aye taps many objects that attract its attention. Sandwith believes that an exceptionally cutaneous sense of the middle digit enables the aye-aye to discriminate between surface vibrations. Furthermore, tapping can stimulate insect larvae to make audible movements [52]. In a study conducted by Erickson, long and straight subsurface artificial channels were constructed in 15 woodblocks to mimic the mines created by insect larvae. The channels were 20, 30, and 40 cm long, 1 cm wide, and 5 mm deep. The wooden samples were exposed to captive adult male and female aye-ayes. Surprisingly, the aye-ayes opened the channels at regular intervals, with the centers of the excavations spaced approximately 7.5 cm apart. These observations suggest that, in addition to the aye-ayes' sensitive auditory system, the cutaneous sense of the third digit may be sensitive to differential surface vibrations [53]. Erickson believes that olfactory, tactile, and visual clues alone are not sufficient to locate cavities and prey accurately. Erickson inferred these results from individuals gnawing in areas with cavities but no surface holes, indicating that aye-ayes can consistently discriminate true cavities from false indicators, even when the visual or olfactory cues are absent. These observations suggest that animals use echolocation to capture prey. These arguments are consistent with the findings of Kaufman et al. on the brain sections of the aye-aye, which show a relatively large frontal cortex size with a decrease in visual structures, but a comparatively large inferior colliculus, a midbrain section responsible for sound [17]. Erickson studied several captive aye-ayes to demonstrate that, while prey sounds may increase the frequency of a cavity excavation, the aye-ayes opened cavities in wooden samples regardless of whether they were empty or filled with dead or live mealworms [16]. Consequently, the acoustic features associated with the cavity sound provide indirect cues for prey detection. To examine whether the acoustic cues reveal the cavity location, Erickson designed five studies to identify the different features of the cavities that provide these cues. Erickson conducted a series of behavioral experiments to demonstrate how the density of cavity content affects the foraging process. In this regard, the cavities were backfilled with low-density materials (air, acoustic foam, or gelatin) and high-density materials (sand, hardwood, or metal). The excavation was successful with nearly equal frequency, which implies that the sound reverberation in air-filled cavities is not essential for detection. Moreover, there was no difference in the excavation frequency when changing the density of the cavity content [1]. In another study, aye-ayes opened cavities containing active mealworms slightly more often than those with no prey, suggesting that the animal may be able to identify cavities that contain live insects. In other words, aye-ayes locate prey by hearing audible movements below the surface [16]. All behavioral studies emphasized that aye-ayes rely on the auditory interpretation of

tapping signals, and these auditory cues are vital in prey localization.

As discussed above, the aye-ayes' exceptional near-field hearing enables the animal to uniquely distinguish (classify) the different tones emitted from the wood during tapping to localize cavities; this is attributed to the large pinnae of the aye-aye, which shape and move freely. In other words, the importance of tap scanning and the functional demands of integrating two sensory modalities—haptic touch and audition—are linked with the evolution of large and elaborate ear structures [54–56]. The pinna was measured to be 75 mm wide and 46 mm high on average [54]. Ramsier et al. leveraged the auditory brainstem response (ABR) method and confirmed that aye-ayes have relatively enhanced auditory sensitivity between 2.8 and 22.6 kHz, which is equivalent to wavelengths larger than 15 mm and less than 122 mm [49,12]. This broad auditory range might be a good sign of the high sensitivity of the aye-ayes' tap-scanning in small cavities. In a recent research by the present authors, it was shown that the shape and morphology of the aye-ayes' pinnae changed the acoustic field to improve noise reduction and reception of the generated sound from tapping. The authors partially validated that the shape of the pinna can also affect the sensing frequency, which affects the acoustic sensing and detection capabilities of aye-ayes [57]. The results suggest that the cupped shape conformation of the pinna can substantially enhance the acoustic sensitivity of the aye-aye's auditory system by increasing the SNR and sensitivity to higher frequencies [57]. However, several unanswered questions remain regarding the effects of different parts of the ear, including the ear canal.

It has already been demonstrated [57] that the pinnae deformation in the aye-aye and the internal morphology might increase the acoustic beam resolution by creating a small focal point concentrated at the tip of the middle finger during tapping. While aye-ayes tap-foraging behavior has been the primary focus of most researchers to date, their auditory sensitivities are relatively unstudied. Several biological aspects may contribute to the exceptional auditory system of aye-aye. This paper investigates the effects of the pinna and ear canal on aye-ayes' auditory system in a monaural sensing fashion to precisely detect sounds generated in the near-by point source. The importance of monaural cues in human auditory localization was recognized as early as the turn of the last century [58]. Monaural localization (ML) is a single microphone localization technique based on an understanding of the pinna function and the role of the outer ear structures in producing monaural cues for sound localization. This paper is organized as follows. The material selection and 3D printing procedures are discussed in the Methods section. It is followed by the Experimental Setup section. The effects of the aye-ayes' pinna and ear canal on the acoustic field are evaluated using time and frequency domain analyses in the Results section. It is followed by the Conclusion section.

2. Methods

The study was conducted using a biomimetic approach to simulate the tapping process of the aye-ayes. In this approach, the aye-ayes' external auditory systems were 3D printed to investigate the effects of each component on the ear's receptive field and acoustic sensing. The micro-CT scan of a frozen carcass in the Duke Lemur Center (DLC) yielded detailed information on different parts of the aye-ayes' head. Fig. 2 shows the rendering representations of the frozen body of Merlin (the aye-aye under study) obtained from the micro-CT scan in two different views. The visualization and rendering were performed using the functions provided by the Autodesk Meshmixer software. The software is a design-to-fabricate tool for working with 3D meshes and offers several

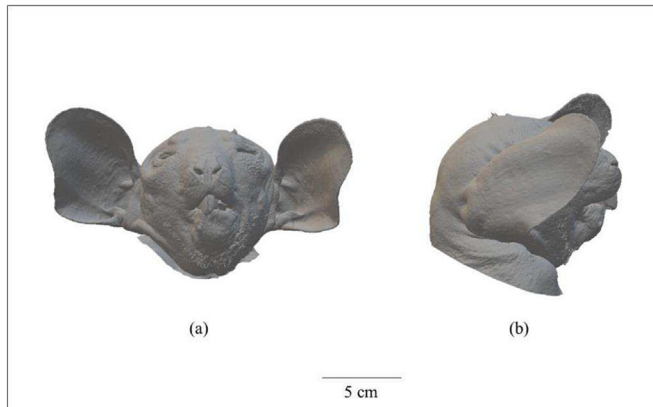


Fig. 2. The CT scan of the aye-aye; the pinnae are in a cupped position: (a) front view (b) side view.

fascinating functionalities to help the user in the modeling and 3D printing processes. Autodesk Meshmixer is available for free download at <http://www.meshmixer.com>.

2.1. Wood material selection

In the biomimetic approach for simulating the aye-aye's tapping process, one critical question was: what type of wood should be considered? The structural properties of deadwood could also influence the extractive foraging behavior of aye-ayes. As reported by Thompson et al., no statistically significant differences in height and diameter were observed between the foraged and non-foraged deadwood trees. However, aye-ayes preferred trees with smaller diameters for foraging; this may be due to the ability of aye-ayes to grip trees effectively during percussive foraging [3]. Further, the internal structures of foraged and non-foraged deadwood resources were compared. They tentatively hypothesized that the area behind the larval mines towards the tree core might play a crucial role in the percussive foraging process of aye-ayes. [53]. A fascinating facet of the aye-aye's tap-scanning process is that it allows the animal to diagnose small discontinuities in several complex materials, such as wood. Insect larvae can be extracted from various locations, including bamboo branches and trunks of dead trees, fallen dead wood, dead branches of living trees, and rarely living trees [59]. In other words, aye-ayes consume invertebrates from both dead and live trees. However, they frequently forage on the trunks and branches of dead trees [59,60]; the deadwood's ability to conduct sound may be an essential factor in the foraging behavior of aye-ayes. Generally speaking, wood is classified as two groups: hardwoods and softwoods. The internal and external properties of each group may explain the animal foraging preference. The modulus of elasticity, modulus of rigidity, and density are the primary material properties that describe the behavior of each wood. In addition, the speed of sound waves passing through the medium is one of the most significant characteristics of each material. Velocity is a function of wood density and the modulus of elasticity [61]. For instance, the more decayed and fragmented the wood inside a tree, the slower the sound travels between two points. Therefore, different types of wood can exhibit different vibrational properties. The aye-aye is more likely to forage trees with greater internal density [3]. The interior regions usually function as sounding boards during the tap-scanning process to help the animal accurately detect potential grub [3]. It is also possible that aye-aye selects deadwood that is better able to transmit sound and therefore helps them more accurately locate cavities and

abnormalities beneath the tree bark to reduce the likelihood of false positives during larval mine detection. Based on the above discussion and to simplify tap testing, a commercial lumber named *Pseudotsuga menziesii* (commonly called Douglas fir) was used as the softwood to perform tapping in this study. *Pseudotsuga menziesii* is one of the most important timber trees in the world [62]. The wood has a density of 460 to 500 kg/m³ and its modulus of elasticity has been estimated between 10.3 and 13.4 GPa [63]. The material property of the wood is in a descent consistency compared to the ones reported in literature [1,3,64] that aye-ayes forage upon. A more detailed information on the wood characteristics and the associated material properties could be found in Green et al. [63].

2.2. 3D printing preparation

The effects of (a) the pinna and (b) the ear canal on the sound field were considered to understand the biological auditory sensing system of aye-ayes utilized during tap-scanning. To this end, these parts were 3D printed, as shown in Fig. 3. The 3D printing was performed using a continuous fiber fabrication machine named Markforged Mark Two (Gen 2). For the 3D printing process, the fill density of the device and the layer height were set to 37 % and 0.1 mm, respectively. A nylon filament called "Onyx" developed by Markforged was used as the 3D printing material. Onyx is a high-strength thermoplastic material with an outstanding surface finish and high resistance to chemical agents. It is made from commercial nylon combined with short carbon fibers [65]. Several studies have shown that the pinnae and head soft tissue can be replaced by synthetic materials used in artificial heads [66], and the effect of the pinna and head material is negligible if the pinna, ear canal, and head geometry are accurately captured. For example, results from artificial animal and human heads, such as those from the KEMAR mannequin, have shown good correspondence with acoustically measured HRTFs [38,67,68]. This supports the assumption that replacing the ear canal and pinnae with artificial 3D printed ones can provide acceptable levels of error when the effect of soft tissue material is neglected.

2.3. Experimental setup

As previously stated, aye-ayes have evolved a suite of well-known apomorphies. During tapping, the acoustic actuation part or sound source for the aye-aye is the tip of the middle finger hitting the surface of the object of interest. Specialized metacarpophalangeal joints in the third digits give the finger an extraordinary range of movement in tapping and probing for prey. Once the aye-aye tap-scans, the resulting differential soundings from a tree's interior structure travel through the air and bounce off the animal's large, alert, high-frequency attuned pinna and the exterior part of the ear and further enter the ear canal. The sound is later processed by a relatively enlarged inferior colliculus in the brain [12]. In other words, the brain utilizes subtle differences in intensity, timing, and spectral cues to allow the animal to discriminate sound sources and localize cavities. The tapping rate in aye-ayes was estimated to be 97.7 ± 19.9 ms, with the dominant energy of each tap ranging between 2 and 27 kHz [12]. This result was obtained from the recorded sounds of tapping on the softwood.

To mimic the percussive foraging of aye-ayes in a semi-automated manner, a miniature piezoelectric hammer (PCB model 086E80) (Fig. 4(e)) was mounted on a Universal Robotics manipulator (UR5) (Fig. 4(a)). This light miniature instrumented impulse hammer (4.8 g), had a sensitivity of 22.5 mV/N with a 222 N peak measurement range. The UR5 was programmed to scan the area of

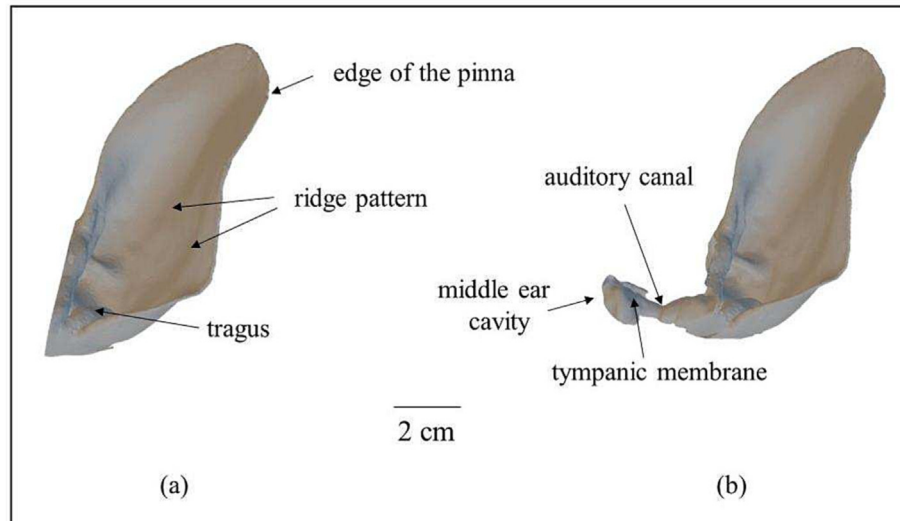


Fig. 3. The CT scan of an aye-aye's ear anatomy: (a) pinna; (b) pinna and ear canal.

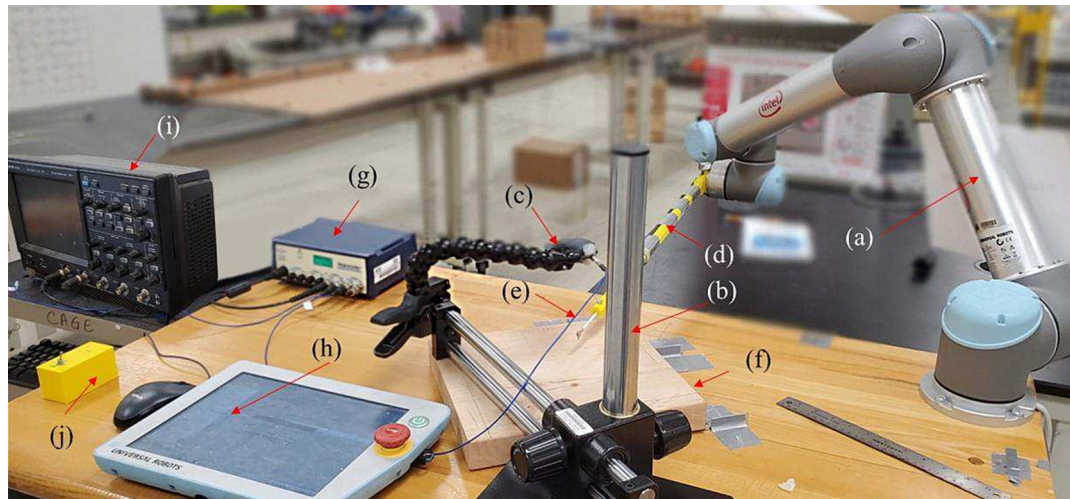


Fig. 4. Experimental setup: (a) UR5 robotic arm manipulator; (b) pinnae holder and 3D coordinate adjustable frame; (c) 3D printed pinna with 1/4" free-field, prepolarized 377C01 microphone; (d) extension and the hammer holder; (e) miniature instrumented impulse hammer; (f) woodblock; (g) four-channel power supply unit (signal conditioner); (h) UR5 12" touchscreen; (i) oscilloscope; (j) control switch.

interest in the lumbar region under study. To avoid any potential interference of the UR5 arm in the acoustic field, a 30 cm extension and a holder were designed (Fig. 4(d)). The hammer simplified the complexity of the biological features of the aye-aye's third digit; however, it is consistent in terms of the dimensions of the finger. A prepolarized calibrated measurement microphone (PCB Piezotronics, Inc., model 377C01 and 426B03 preamplifiers) (Fig. 4(c)) with a nominal diameter of 6.3 mm and a frequency range of 4 Hz to 80 kHz was placed 10 cm away from the woodblock to capture the acoustic wave emissions coming from the tapping position. The sound pressure was measured on the azimuth plane or horizontal angle. In other words, the plane of the microphone diaphragm was almost perpendicular to the horizontal surface of the woodblock. Commercially available lumber with dimensions of 30 cm × 30 cm × 5 cm was used as the deadwood (Fig. 4(f)). The woodblock was fixed on the table using some foams in between as support to diminish the effects of the contact acoustic propagation on the tap-induced sound pressures. The block was divided

into 25 × 25 gridded points in the x and y directions at an interval of 6 mm as the area of interest on the sample (144 × 144 mm area in total) to perform tapping. To filter out uncertainties related to the sound source, material, and random noise, tapping was performed three times at each point. The reason behind this is that it was observed that the acoustic fields converge to a certain contour plot after averaging three accumulated tapping signals. The averaged value was used as the output signal in the post-process analysis. A control switch was designed to repeat tapping at an arbitrary point (see Fig. 4(j)). At each point, the output signals were pre-amplified and later digitized with a 5 MHz sampling rate and 16-bit resolution using an oscilloscope (WaveJet 334 touch, Teledyne LeCroy) (Fig. 4(i)). After setting all tapping parameters, the receptive field of the microphone alone and the cupped pinna with and without the ear canal were measured from the area of interest. As previously mentioned, the tests were performed using a single receiver (ML). Fig. 4 shows the experimental setup and associated components used for the sound field measurements.

3. Results

The effects of the 3D printed pinna with and without an ear canal on the aye-ayes' acoustic sensing were investigated. First, the receptive field of the microphone alone was evaluated to eliminate the effects of microphone directionality on the measured sound field. Next, the effects of the pinna and ear canal on the aye-ayes' auditory system were considered in a cupped position. Cupping has a significant impact on the sound reception and directionality of ears receiving the approximate plane wave sound [69]. The effects of the pinna's shape on the auditory perception and detection capabilities of aye-ayes have already been examined in the previous study [57]. The objective of that study was to measure the acoustic properties of the external ear in the upright and cupped positions. The cupped shape conformation of the pinna could significantly improve the near-field auditory sensitivity through three mechanisms: (1) an increased SNR, (2) creating potential focal points to increase the spatial resolution, and (3) an increase in the receiver peak frequency by changing the sound pressure beam pattern for higher frequencies, which can enhance the sensitivity owing to a smaller wavelength [57]. Consequently, in this study, each 3D printed part was maintained relative to the plane and position of the wooden block in a cupped position on the holder, as shown in Fig. 4(c). The angle at which the aye-aye pinna was mounted on the holder was selected based on qualitative observations reported by previous researchers [70,4,16].

To remove any uncertainties associated with the intensity of the simulated tapping (sound source), each signal recorded after the impact of the miniature hammer was normalized to the maximum value of the impact signal in all three cases, which is referred to as the normalized response throughout this paper. Fig. 5 shows the responses from the tapping simulation at an arbitrary point in the focal area, which is identified later. As shown in Fig. 5(a), a typical impact response with a duration of 30 ms was used for the temporal analysis of the acoustic field. For illustrative purposes, Fig. 5(b) shows the normalized received signals in the three mentioned cases (the microphone alone, the microphone and cupped pinna, the microphone and cupped pinna with the ear canal). Fig. 5(c) shows the corresponding responses in the frequency domain. From the signals, it is evident that the magnifying effect of the ear canal for the cupped pinna is approximately three times greater than that of the microphone alone. Furthermore, the peak frequency shifted to a higher frequency when the pinna was in the cupped position. The increase in the dominant frequency amplitude is even greater in the case of cupped pinna with an ear canal; a 40 % growth was observed and the normalized amplitude almost doubled compared to the cupped pinna without an ear canal. A higher SNR (magnification of the received signal) and a larger dominant frequency resulted in greater auditory sensitivity,

which consequently improved the detection capability of the aye-aye in the search for tiny cavities. To better assess the impact of the ear canal on the acoustic field, the received signals were analyzed in both the time and frequency domains.

3.1. Time domain

The receptive field versatile auditory system of the aye-aye was measured in the time domain for the cupped pinna with and without the ear canal. The cupping was done such that the position of the pinna relative to the woodblock was precisely the same in the two measurements. To this end, the average of the maximum values of the normalized received signal envelopes for the three simulated tapping source points was calculated at each gridded point. First, the acoustic receptive field of the microphone alone for non-normalized and normalized signals was determined (see Fig. 6(a), and (b)). This independent acoustic measurement evaluation was essential to remove the effect of the microphone acoustic field by isolating the effect of some parts of the ear on the acoustic field provided in the next steps. The microphone was placed at a fixed distance with respect to the height, i.e., z axis, (approximately 100 mm) from the center of the area of interest, as schematically demonstrated in the figures. The miniature hammer tapped the woodblock sequentially using a robotic arm. The starting point was located at the top left corner of the sample (azimuth axes are at the origin of the Cartesian coordinates).

As previously mentioned, when forming the pinna in a cupped shape, the aye-aye can create a strong focal area to increase the SNR and spatial resolution [57]. In the first step, the effect of the pinna alone on the sound field was considered. To generate the acoustic field, the average of the maximum values of the normalized received waveforms (normalized to the maximum impulse) from three simulated tapings at each point was used. To eliminate the effect of the microphone on the acoustic field, a magnification factor was introduced [57]. This factor was derived by dividing the normalized acoustic receptive field of the cupped pinna by the normalized response of the microphone (shown in Fig. 6(b)). This response function could isolate the impact of the pinna and remove the effect of the microphone on the acoustic receptive field. Fig. 7 illustrates the magnification factor resulting from the cupped pinna of the aye-aye. The pinna at a cupped position resulted in the creation of a focal area (dashed circles on the top and bottom left represented as high gain areas). The maximum magnification value in this area was approximately 4 (five times higher than the field generated by the microphone alone), which corresponded to an increase of 12 dB in the SNR. This value was smaller than that reported in the first study of the present authors [57] because of the uncertainties associated with the experimental setup in their biomimetic approach. The observed direction-dependent reso-

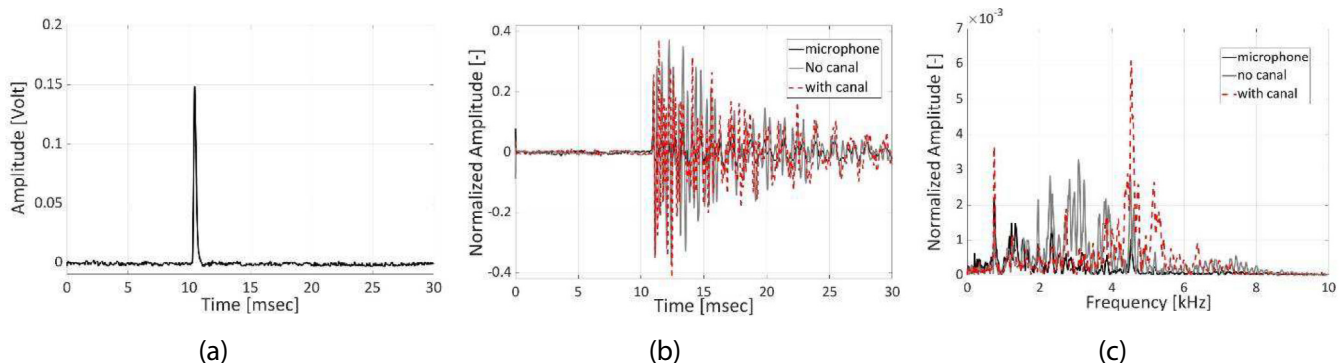


Fig. 5. Example of received signals: (a) piezoelectric hammer impulse; (b) normalized microphone response; (c) frequency response of normalized microphone response.

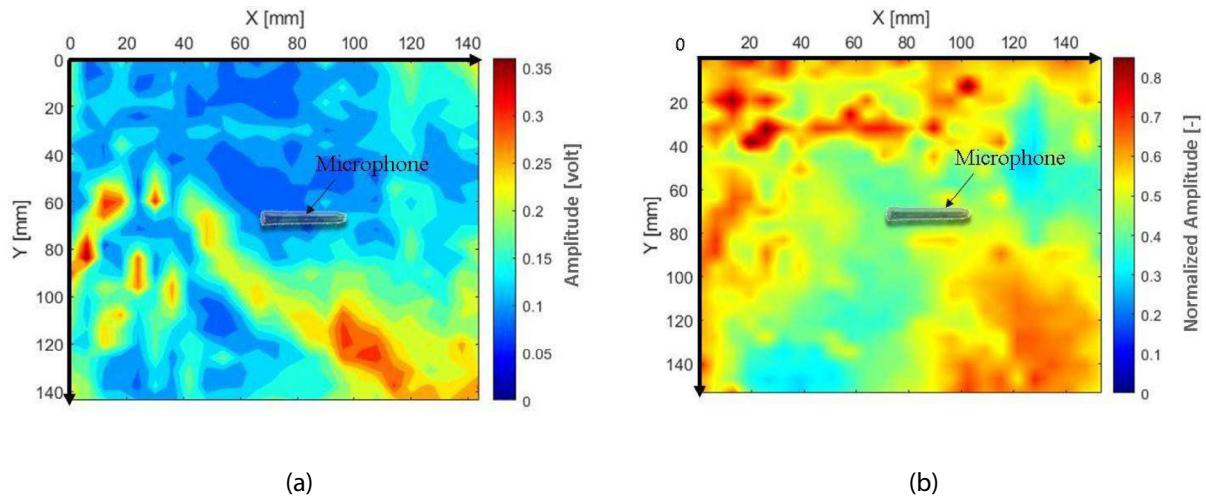


Fig. 6. Acoustic field of microphone response: (a) the non-normalized response; (b) the normalized acoustic field.

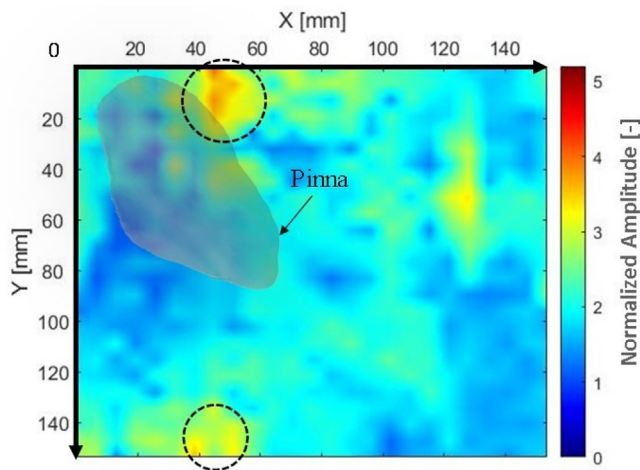


Fig. 7. Acoustic field of the microphone and pinna response.

nances could be influenced by the aye-aye's ear canal morphological features, including the ear canal entry shape, which could be used as an additional localization cue. Therefore, the effects of these features were also considered.

Fig. 8 shows the normalized acoustic fields of the pinna with the canal. The most fascinating observation is the generation of strong focal areas in the presence of the ear canal (two dashed circles). Fig. 8 shows that the magnification factor in the focal area, in this case, increases up to 5 (25 % increase), which is equivalent to a 14 dB increase in SNR (this value corresponds to a 2 dB increase in the SNR because of the ear canal). In other words, this result is superior to those provided in Figs. 6 and 7. In all these cases, the generated focal area was around the sound source location (tapping point). In addition, the acoustic receptive field plot resulting from the pinna and ear canal showed a directional pattern. Consequently, the shape and morphological features of the aye-ayes' ears could significantly enhance cavity localization and abnormality detection. According to these findings, the unique shapes of the

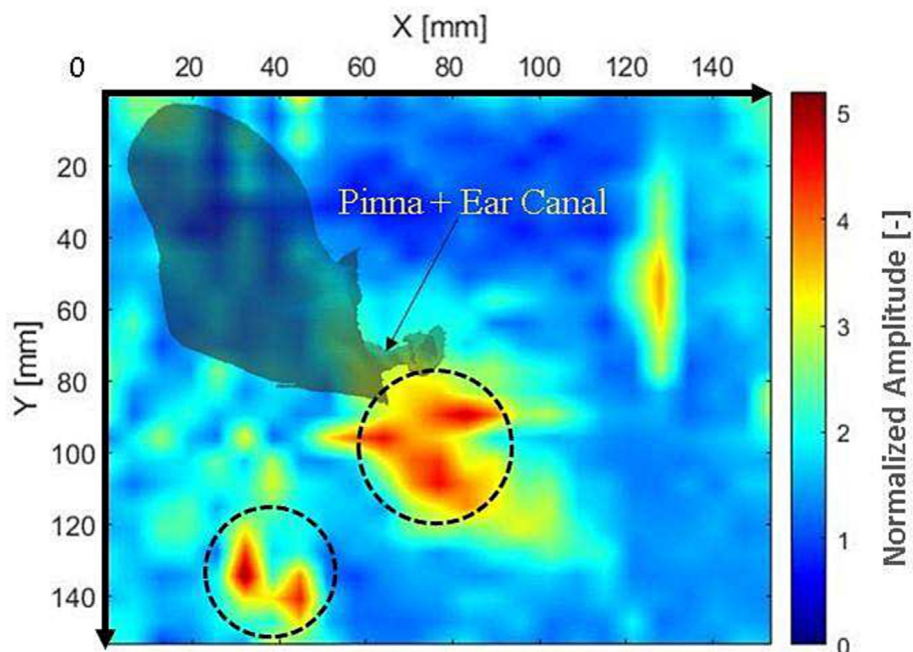


Fig. 8. Acoustic field of the microphone and pinna with the canal.

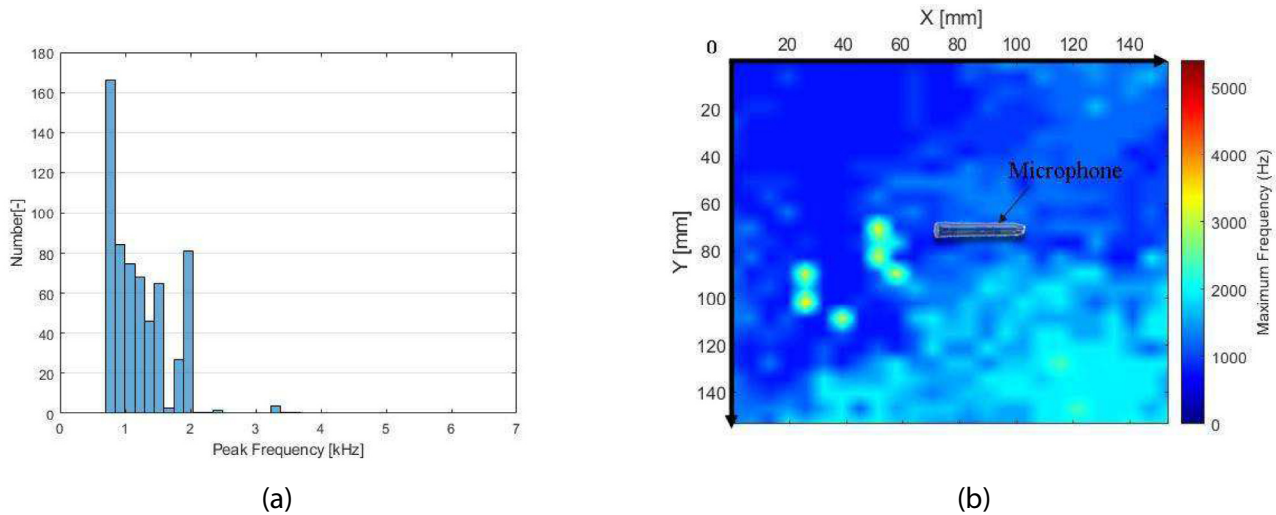


Fig. 9. Frequency domain analysis of the microphone response. (a) Histogram of peak frequencies for all simulated impacts. (b) The interpolated contour plot of each peak frequency.

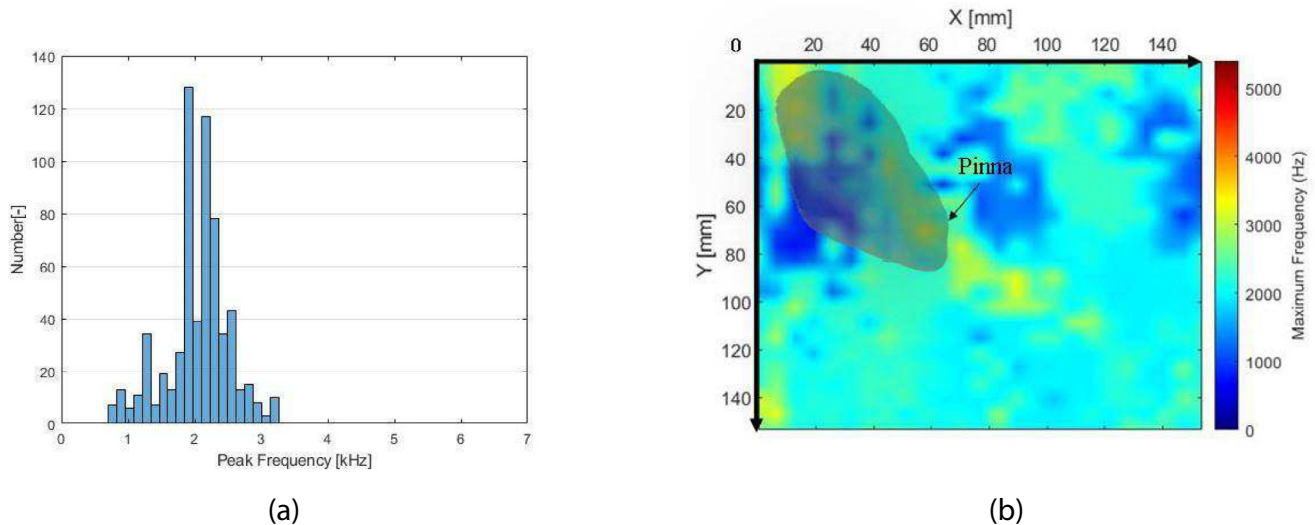


Fig. 10. Frequency domain analysis of the microphone and pinna response. (a) Histogram of peak frequencies for all simulated impacts. (b) The interpolated contour plot of each peak frequency.

outer ear and ear canal modified the propagated sound properties in terms of magnitude and SNR.

3.2. Frequency domain

Previously, the sound field was measured in the time domain, and the results were discussed quantitatively in terms of temporal magnification. Based on time-domain analysis of the acoustic field, the aye-aye's pinna and ear canal can substantially magnify the acoustic field response by creating a focal area or potentially focal point. Here, a frequency analysis was performed on the received acoustic wave-forms. In this regard, the peak frequency (dominant frequency) of each received signal is determined. The associated histogram for the peak frequency in each case is shown in Figs. 9-11(a). According to the histograms and dominant frequencies represented in these figures, the dominant frequencies for the pinna with ear canal are substantially increased in the focal

area with the maximum value of 5.4 kHz. It is evident from these figures that the received signals showed higher sensitivity at larger frequencies in the presence of the pinna and ear canal. This can be attributed to the fact that a smaller wavelength (or larger frequency) results in higher sensitivity to smaller cavity detection. Interestingly, the maximum values were observed near the focal areas determined in the temporal analysis. The results also suggest that the added features, more specifically the ear canal, substantially improve the SNR for a particular peak frequency and result in conspicuous qualitative changes in beam patterns. In other words, the ear canal and its morphological features create a physical filter to filter out unnecessary frequencies more efficiently and act as amplifiers for higher frequencies. The rise in the magnification of a specific frequency while removing unnecessary sound components around the focal point can be one of the key elements allowing the aye-aye to show extraordinary near-field detection capability during their tap-foraging process.

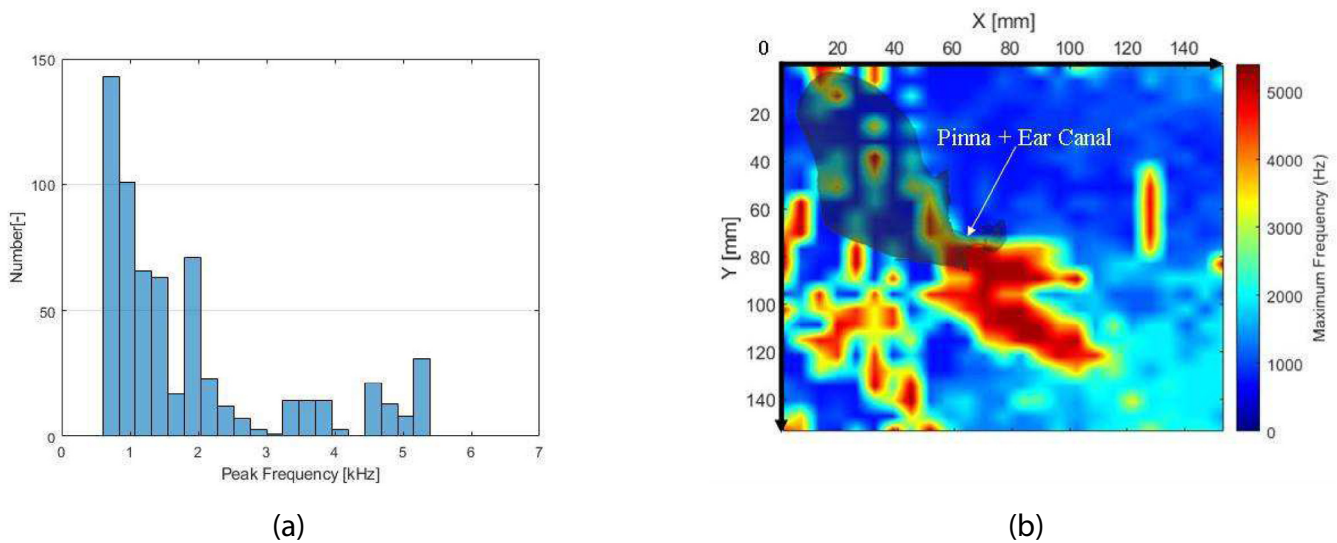


Fig. 11. Frequency domain analysis of the microphone and ear canal response. (a) Histogram of peak frequencies for all simulated impacts. (b) The interpolated contour plot of each peak frequency.

4. Conclusions

Aye-ayes have several derived morphological traits in their sensing and locomotion systems that facilitate percussive foraging or tap-scanning processes. The morphology of the aye-aye's pinna and ear canal and their intricate anatomy results in a complex acoustic field. This study investigated the effects of the ear canal on the exceptional acoustic sensing and detection capabilities of the aye-aye. To this end, the sound fields of two different scenarios were compared through a cupped conformation: (1) the pinna alone and (2) the pinna and the ear canal. The results obtained from the biomimetic setup indicated that the pinna-related features, and more specifically, the ear canal components, substantially enhanced the acoustic receptive field sensitivity by creating a conspicuous focal area or potentially small focal point to increase the acoustic beam resolution and SNR. Furthermore, changing the sound field beam pattern increased the receiver peak frequency or dominant frequency, which can drastically enhance the sensitivity of the auditory system to minor defects. In summary, the findings of this study revealed that the ear canal has a significant impact on developing a sensitive biological acoustic field measurement system by increasing the magnification of a specific frequency while removing unnecessary sound components around the focal point, which can be one of the key elements allowing the aye-aye to demonstrate extraordinary near-field detection capability during their tap-foraging process. The external ear of the aye-aye evolved to create a physical filter to exclude unnecessary frequencies and potentially enhance neurological filtering during the data processing stage. While the current study evaluated the effects of the entire outer ear and ear canal, the effects of the animal's complex head were not considered. The impact of the other features on the near-field acoustic sensing of the aye-aye is currently being studied using numerical and biomimetic approaches.

CRediT authorship contribution statement

Hamidreza Nemati: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Ehsan Dehghan-Niri:** Conceptualization, Methodology, Software, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Data availability

Data will be made available on request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

This research was supported by the US National Science Foundation CAREER AWARD under Grant No. 2047033. This work was performed in part at the Duke University Shared Materials Instrumentation Facility (SMIF), a member of the North Carolina Research Triangle Nanotechnology Network (RTNN), which was supported by the US National Science Foundation (Grant ECCS-1542015) as part of the National Nanotechnology Coordinated Infrastructure (NNCI). The CT scan of non-living body of an aye-aye provided by the Shared Materials Instrumentation Facility at Duke University allowed the authors to perform this study in the Intelligent Structures and Nondestructive Evaluation (ISNDE) laboratory. In addition, the authors gratefully acknowledge the immense help of Dr. Erin Ehmke from DLC. The authors would also like to thank David Haring from DLC for providing a photo of the aye-aye during tap-scanning.

References

- [1] Erickson CJ, Nowicki S, Dollar L, Goehring N. Percussive foraging: stimuli for prey location by aye-ayes (*Daubentonia madagascariensis*). *Int J Primatol* 1998;19:111–22.
- [2] Chesmore ED. Application of time domain signal coding and artificial neural networks to passive acoustical identification of animals. *Appl Acoust* 2001;62:1359–74.
- [3] Thompson KE, Bankoff RJ, Louis EE, Perry GH. Deadwood structural properties may influence aye-aye (*Daubentonia madagascariensis*) extractive foraging behavior. *Int J Primatol* 2016;37:281–95.
- [4] Bankoff RJ, Jerjos M, Hohman B, Lauterbur ME, Kistler L, Perry GH. Testing convergent evolution in auditory processing genes between echolocating mammals and the aye-aye, a percussive-foraging primate. *Genome Biol Evol* 2017;9:1978–89.
- [5] Kinsler LE, Frey AR, Coppens AB, Sanders JV. *Fundamentals of acoustics*. John Wiley & Sons; 2000.

- [6] Lohr B, Brittan-Powell EF, Dooling RJ. Auditory brainstem responses and auditory thresholds in woodpeckers. *J Acoust Soc Am* 2013;133:337–42.
- [7] Lucas J, Freeberg T, Krishnan A, Long G. A comparative study of avian auditory brainstem responses: correlations with phylogeny and vocal complexity, and seasonal effects. *J Comparative Physiol A* 2002;188:981–92.
- [8] Sullivan KA. Information exploitation by downy woodpeckers in mixed-species flocks. *Behaviour* 1984;91:294–311.
- [9] Collins MD. The role of acoustics in the conservation of the ivory-billed woodpecker (*campephilus principalis*). *J Theor Comput Acoust* 2021;29:2150020.
- [10] Vidana-Vila E, Navarro J, Alsina-Pages RM, Ramírez A. A two-stage approach to automatically detect and classify woodpecker (fam. picidae) sounds. *Appl Acoust* 2020;166:107312.
- [11] Soligo C. Anatomy of the hand and arm in *daubentonia madagascariensis*: a functional and phylo- genetic outlook. *Folia Primatol* 2005;76:262–300.
- [12] Ramsier MA, Dominy NJ. Receiver bias and the acoustic ecology of aye-ayes (*daubentonia madagascariensis*). *Commun Integr Biol* 2012;5:637–40.
- [13] Melin AD, Moritz GL, Fosbury RA, Kawamura S, Dominy NJ. Why aye-ayes see blue. *Am J Primatol* 2012;74:185–92.
- [14] Moritz GL, Dominy NJ. Thermal imaging of aye-ayes (*daubentonia madagascariensis*) reveals a dynamic vascular supply during haptic sensation. *Int J Primatol* 2012;33:588–97.
- [15] Milliken GW, Ward JP, Erickson CJ. Independent digit control in foraging by the aye-aye (*daubentonia madagascariensis*). *Folia Primatol* 1991;56:219–24.
- [16] Erickson CJ. Percussive foraging in the aye-aye, *daubentonia madagascariensis*. *Anim Behav* 1991;41:793–801.
- [17] Kaufman JA, Ahrens ET, Laidlaw DH, Zhang S, Allman JM. Anatomical analysis of an aye-aye brain (*daubentonia madagascariensis*, primates: Prosimii) combining histology, structural magnetic resonance imaging, and diffusion-tensor imaging. *Anatomical Rec Part A: Discoveries Mol Cell Evolut Biol* 2005;287:1026–37.
- [18] Erickson CJ. Perspectives on percussive foraging in the aye-aye (*daubentonia madagascariensis*), in: *Creatures of the Dark*, Springer, 1995, pp. 251–259.
- [19] Gibson K. Cognition, brain size and extraction of embedded food. *Primate Ontogeny Soc Behav* 1986;93:105.
- [20] Bossi R, Giurugiutu V. Nondestructive testing of damage in aerospace composites, in: *Polymer composites in the aerospace industry*, Elsevier, 2015, pp. 413–448.
- [21] Jover N, Shafiq B, Vaidya U. Ballistic impact analysis of balsa core sandwich composites. *Compos Part B Eng* 2014;67:160–9.
- [22] Halabe U. Non-destructive evaluation (nde) of composites: techniques for civil structures, in: *Non-Destructive Evaluation (NDE) of Polymer Matrix Composites*, Elsevier, 2013, pp. 483–517e.
- [23] Kim DO, Bishop B, Kuwada S. Acoustic cues for sound source distance and azimuth in rabbits, a racquetball and a rigid spherical model. *J Assoc Res Otolaryngol* 2010;11:541–57.
- [24] Maki K, Furukawa S. Acoustical cues for sound localization by the mongolian gerbil, *meriones unguiculatus*. *J Acoust Soc Am* 2005;118:872–86.
- [25] Miksis-Olds JL, Nystuen JL, Parks SE. Detecting marine mammals with an adaptive sub- sampling recorder in the bering sea. *Appl Acoust* 2010;71:1087–92.
- [26] Wotton JM, Haresign T, Ferragamo MJ, Simmons JA. Sound source elevation and external ear cues influence the discrimination of spectral notches by the big brown bat, *ptesicus fuscus*. *J Acoust Soc Am* 1996;100:1764–76.
- [27] Muller R. A numerical study of the role of the tragus in the big brown bat. *J Acoust Soc Am* 2004;116:3701–12.
- [28] Macpherson EA, Middlebrooks JC. Listener weighting of cues for lateral angle: the duplex theory of sound localization revisited. *J Acoust Soc Am* 2002;111:2219–36.
- [29] Blauert J. *Spatial hearing: the psychophysics of human sound localization*. MIT Press 1997.
- [30] Blauert J. *The technology of binaural listening*. Springer; 2013.
- [31] Wallach H. The role of head movements and vestibular and visual cues in sound localization. *J Exp Psychol* 1940;27:339.
- [32] Algazi VR, Avendano C, Duda RO. Elevation localization and head-related transfer function analysis at low frequencies. *J Acoust Soc Am* 2001;109:1110–22.
- [33] Ziegelwanger H, Majdak P. Modeling the direction-continuous time-of-arrival in head-related transfer functions. *J Acoust Soc Am* 2014;135:1278–93.
- [34] Bronkhorst AW. Localization of real and virtual sound sources. *J Acoust Soc Am* 1995;98:2542–53.
- [35] Middlebrooks JC. Individual differences in external ear transfer functions reduced by scaling in frequency. *J Acoust Soc Am* 1999;106:1480–92.
- [36] Harder S, Paulsen RR, Larsen M, Laugesen S, Mihocic M, Majdak P. A framework for geometry acquisition, 3-d printing, simulation, and measurement of head-related transfer functions with a focus on hearing-assistive devices. *Comput Aided Des* 2016;75:39–46.
- [37] O'Connor D, Kennedy J. An evaluation of 3d printing for the manufacture of a binaural recording device. *Appl Acoust* 2021;171:107610.
- [38] De Mey F, Reijnders J, Peremans H, Otani M, Firzlaft U. Simulated head related transfer function of the phyllostomid bat *phyllostomus discolor*. *J Acoust Soc Am* 2008;124:2123–32.
- [39] Wotton JM, Haresign T, Simmons JA. Spatially dependent acoustic cues generated by the external ear of the big brown bat, *ptesicus fuscus*. *J Acoust Soc Am* 1995;98:1423–45.
- [40] Meymand SZ, Pannala M, Müller R. Characterization of the time-variant behavior of a biomimetic beamforming baffle. *J Acoust Soc Am* 2013;133:1141–50.
- [41] Muller R, Lu H, Buck JR. Sound-diffracting flap in the ear of a bat generates spatial information. *Phys Rev Lett* 2008;100:108701.
- [42] Tollin DJ, Koka K. Postnatal development of sound pressure transformations by the head and pinnae of the cat: monaural characteristics. *J Acoust Soc Am* 2009;125:980–94.
- [43] Xu L, Middlebrooks JC. Individual differences in external-ear transfer functions of cats. *J Acoust Soc Am* 2000;107:1451–9.
- [44] Young ED, Rice JJ, Tong SC. Effects of pinna position on head-related transfer functions in the cat. *J Acoust Soc Am* 1996;99:3064–76.
- [45] Schnupp JW, Booth J, King AJ. Modeling individual differences in ferret external ear transfer functions. *J Acoust Soc Am* 2003;113:2021–30.
- [46] Jones HG, Koka K, Thornton JL, Tollin DJ. 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* 2011;12:127–40.
- [47] Spezio ML, Keller CH, Marrocco RT, Takahashi TT. Head-related transfer functions of the rhesus monkey. *Hear Res* 2000;144:73–88.
- [48] Rebillat M, Benichoux V, Otani M, Keriven R, Brette R. Estimation of the low-frequency components of the head-related transfer functions of animals from photographs. *J Acoust Soc Am* 2014;135:2534–44.
- [49] Ramsier MA, Cunningham AJ, Finneran JJ, Dominy NJ. Social drive and the evolution of primate hearing. *Philos Trans R Soc B* 2012;367:1860–8.
- [50] Price EC, Feistner AT. Responses of captive aye-ayes (*daubentonia madagascariensis*) to the scent of conspecifics: a preliminary investigation. *Folia Primatol* 1994;62:170–4.
- [51] Straus, WL, Jr. *Primates (comparative anatomy and taxonomy). i. strepsirhini*. by wc osman hill, pp. xxiv+ 798. 5 pounds 5 shillings. university press, edinburgh. 1953; ii. *haplorhini: Tarsioidae*. by wc osman hill, pp. xx+ 347. 63 shillings. university press, edinburgh. 1955. 1956.
- [52] Sandwith H. On the habits of the “aye-aye” (*cheiromys madagascariensis*, l. cuv.). *Zool J Linn Soc* 1859;4:28–30.
- [53] Erickson CJ. Tap-scanning and extractive foraging in aye-ayes, *daubentonia madagascariensis*. *Folia Primatol* 1994;62:125–35.
- [54] Coleman MN, Ross CF. Primate auditory diversity and its influence on hearing performance. *Anatomical Rec Part A: Discoveries Mol Cell Evolut Biol* 2004;281:1123–37.
- [55] Kirk EC, Gosselin-Ildari AD. Cochlear labyrinth volume and hearing abilities in primates. *Anatomical Rec: Adv Integr Anatomy Evolut Biol: Adv Integr Anatomy Evolut Biol* 2009;292:765–76.
- [56] Lebrun R, De Léon MP, Tafforeau P, Zollikofer C. Deep evolutionary roots of strepsirrhine primate labyrinthine morphology. *J Anat* 2010;216:368–80.
- [57] Nemati H, Dehghan-Niri E. The acoustic near-field measurement of aye-ayes' biological auditory system utilizing a biomimetic robotic tap-scanning. *Bioinsp Biomim* 2020;15:056003.
- [58] Carlile S, King AJ. Monaural and binaural spectrum level cues in the ferret: acoustics and the neural representation of auditory space. *J Neurophysiol* 1994;71:785–801.
- [59] Sterling EJ. Aye-ayes: specialists on structurally defended resources. *Folia Primatol* 1994;62:142–54.
- [60] Sterling E. Feeding behavior of the aye-aye (*daubentonia madagascariensis*) on nosy mangabe, madagascar, in: *XIVth Congress of the International Primatological Society*, Strasbourg, 1992.
- [61] Ross RJ, et al., *Wood handbook: wood as an engineering material*, USDA Forest Service, Forest Products Laboratory, General Technical Report FPL-GTR-190, 2010: 509 p. 1 v. 190 (2010).
- [62] Lavender DP, Hermann RK. Douglas-fir: the genus *pseudotsuga* (2014).
- [63] Green DW, Winandy JE, Kretschmann DE. Mechanical properties of wood, *Wood handbook: wood as an engineering material*. Madison, WI: USDA Forest Service, Forest Products Laboratory, 1999. General technical report FPL; GTR-113: Pages 4.1–4.45 113 (1999).
- [64] Sefczek TM, Randimbaharinirina D, Raharivololona BM, Rabekianja JD, Louis EE. Comparing the use of live trees and deadwood for larval foraging by aye-ayes (*daubentonia madagascariensis*) at kianjavato and torotorofotsy, madagascar. *Primates* 2017;58:535–46.
- [65] Papa I, Silvestri AT, Ricciardi MR, Lopresto V, Squillace A. Effect of fibre orientation on novel continuous 3d-printed fibre-reinforced composites. *Polymers* 2021;13:2524.
- [66] Greff R, Katz BF. Round robin comparison of hrtf simulation systems: Preliminary results, in: *Audio Engineering Society Convention 123*, Audio Engineering Society, 2007.
- [67] Algazi VR, Duda RO, Duraiswami R, Gumerov NA, Tang Z. Approximating the head-related transfer function using simple geometric models of the head and torso. *J Acoust Soc Am* 2002;112:2053–64.
- [68] Gumerov NA, O'Donovan AE, Duraiswami R, Zotkin DN. Computation of the head-related transfer function via the fast multipole accelerated boundary element method and its spherical harmonic representation. *J Acoust Soc Am* 2010;127:370–86.
- [69] Wiener FM, Ross DA. The pressure distribution in the auditory canal in a progressive sound field. *J Acoust Soc Am* 1946;18:401–8.
- [70] Sterling EJ, McCreless EE. Adaptations in the aye-aye: a review. *Lemurs* 2006:159–84.