The bat head-related transfer function reveals binaural cues for sound localization in azimuth and elevation

Murat Aytakin, Elena Grassi, Manjit Sahota, and Cynthia F. Moss

Department of Psychology and Institute for Systems Research, Neuroscience and Cognitive Science Program, University of Maryland, College Park, Maryland 20742

(Received 21 March 2004; revised 26 August 2004; accepted 12 September 2004)

Directional properties of the sound transformation at the ear of four intact echolocating bats, *Eptesicus fuscus*, were investigated via measurements of the head-related transfer function (HRTF). Contributions of external ear structures to directional features of the transfer functions were examined by remeasuring the HRTF in the absence of the pinna and tragus. The investigation mainly focused on the interactions between the spatial and the spectral features in the bat HRTF. The pinna provides gain and shapes these features over a large frequency band (20–90 kHz), and the tragus contributes gain and directionality at the high frequencies (60 to 90 kHz). Analysis of the spatial and spectral characteristics of the bat HRTF reveals that both interaural level differences (ILD) and monaural spectral features are subject to changes in sound source azimuth and elevation. Consequently, localization cues for horizontal and vertical components of the sound source location interact. Availability of multiple cues about sound source azimuth and elevation should enhance information to support reliable sound localization. These findings stress the importance of the acoustic information received at the two ears for sound localization of sonar target position in both azimuth and elevation. © 2004 Acoustical Society of America. [DOI: 10.1121/1.1811412]

PACS numbers: 43.66.Qp, 43.66.Pn, 43.80.Lb, 43.64.Bt, 43.64.Ev [JAS] Pages: 3594–3605

I. INTRODUCTION

Echolocating bats, as auditory specialists, present a valuable model for the study of spatial hearing. These flying mammals produce ultrasonic vocalizations and listen to the echoes reflected from objects around them. Their vital activities, such as spatial orientation, prey detection, localization, and capture can be accomplished entirely with the use of a biological sonar system. An important question is whether specialized sound localization capacity is required for successful orientation by echolocation in bats. If so, what specializations are evident that can help to deepen our understanding of spatial hearing?

Azimuthal discrimination experiments by Simmons *et al.* and horizontal tracking experiments by Masters *et al.* report about 1.5° accuracy in the echolocating big brown bat, *Eptesicus fuscus*. This species uses broadband frequency-modulated (FM) echolocation signals, which are well suited for spatial localization. Lawrence and Simmons measured the minimum audible angle (MAA) along the vertical axis and report discrimination by *E. fuscus* of about 3°. In a later study, Wotton and Simmons closely studied the bat’s MAA in the midsagittal plane at 5 different elevations (+1/−40°, +1/−20°, and 0°). They reported that the bat’s MAA falls between 2.9° and 4.1° at around 0° and +1/−20° elevation and increases to 6.7° at around −40° and 8.3° at around 40°. In the same study, when the bat’s tragus was deflected, the MAA increased significantly, 18.3°−20.1°, at around −20° elevation; however, the MAA in the upper hemisphere did not show a measurable change with the tragus manipulation. In these studies, the bats used biosonar to perform the localization tasks.

Studying bats in a passive listening localization task, Koay *et al.* used a conditioned avoidance procedure to measure left–right azimuthal sound source discrimination by *E. fuscus*. They reported that the bat’s threshold for discrimination is 14°, comparable to a number of other mammalian species they tested. Further, they reported that this bat species could not discriminate narrow-band sounds that were positioned at 30° off the midline at low frequencies (5.6 to 8 kHz). They concluded that *E. fuscus* is not able to use interaural time difference (ITD) cues at sound frequencies where interaural phase differences would be available. Koay *et al.* estimated the maximum ITD experienced by the bats during the experiment to be approximately 55 μs. Although the results of this study suggest that *E. fuscus* cannot use interaural phase differences for sound localization, the result does not eliminate the possibility of ITD localization using the envelope of wideband sounds.

To explore sound localization one step further, attention has been given to the directional properties of the external ears. Studies of the directionality of sound-pressure transformation at the pinna of several different bat species have been conducted. In these studies, sound pressure at the tympanic membrane was measured at different frequencies by moving a narrow-band sound source in space and recording signals at the base of the ear canals. Disturbance of the iso-pressure contours and a decrease in the gain of the sound pressure for all frequencies tested was reported after removing the pinna and the tragus together. Using a similar approach, Fuzessery measured acoustic pressure transformation by the intact ears of the pallid bat, *Antrazous pallidus*. He reported that monaural spectral features of the HRTF of this species show parallel patterns to what has been reported in other mammals, such as humans and cats. He also showed that binaural difference cues changed with both azimuth and elevation. Grinnell and
Grinnell\textsuperscript{12} reported a similar observation in the directional dependence of evoked potential recordings from the inferior colliculus (IC) of FM bats, Plecotus townsendii and Myotis lucifugus. They found that directional sensitivity of the neural responses changed with small changes in sound source angle in both the horizontal and vertical planes. Moreover, they reported that directional sensitivity was different at different frequencies. Based on these observations and assuming that directional responses of the left and right ICs are similar, they hypothesized that bats can use interaural level differences (ILD) obtained from several different frequencies to localize both sound source azimuth and elevation. Fuzessery and Pollak\textsuperscript{13} conducted cochlear microphonic recordings in mustached bats, Pteronotus parnellii, a species that produces signals with a combination of constant frequency and FM components. These researchers also proposed a similar role for ILD in horizontal and vertical sound localization. These important findings stand apart from the common view that interaural differences are used for azimuthal localization. Thus, the role of binaural cues for localization of sound source elevation warrants further study.

Sounds reaching the ear are transformed in a directionally dependent manner as a result of their interaction with the body, the head, and the pinnae. The direction-dependent transformations can be modeled as a linear time-invariant systems transfer function, commonly known as the head-related transfer function (HRTF). Contrary to what the name suggests, the torso, in particular neck and shoulders, also introduce strong effects on the properties of the HRTF.\textsuperscript{14}

To our knowledge, the most detailed published measurement of the HRTF in bats was reported by Wotton \textit{et al.}\textsuperscript{15} The study focused on elevation cues: in particular, spectral notches and peaks in the HRTF of the big brown bat, Eptesicus fuscus. They measured the HRTF of full and half-head preparations and reported a linear relationship between center frequency (CF) of spectral notches (30 to 50 kHz) and sound source elevations ($\pm 30^\circ$ to $0^\circ$). They also reported that the relation between notch CF and elevation was disrupted when the bat’s tragus was deflected. Based on their findings, Wotton \textit{et al.} suggested that position of the spectral notches along the frequency axis could contribute to vertical localization in bats, as is the case in other animals that have been studied, such as cats\textsuperscript{16} and humans.\textsuperscript{17}

Wotton \textit{et al.}\textsuperscript{6,18} provided behavioral evidence for the role of the position of a spectral notch in sound source localization along the vertical plane. They trained the bats to discriminate a linear FM sound with a spectral notch at a particular frequency, and they demonstrated that spectral notches in the HRTF are perceived by the bat.\textsuperscript{18} Bats showed a significant decrease in their performance in this behavioral task when the target sound source was presented at a particular elevation at which the filtering characteristics of the external ear produced a spectral notch at the same frequency. In another experiment, they showed that deflection of the bat’s tragus resulted in an increase in vertical MAA.\textsuperscript{7} Based on these and other MAA measurements\textsuperscript{2,5,6} they suggested that there are distinct sound localization cues for azimuth and elevation, consistent with the classic dichotomy of separate cues for horizontal and vertical sound localization.

In our paper, we present the HRTF of an echolocating FM bat, Eptesicus fuscus. Our first goal was to confirm earlier reports by Wotton \textit{et al.}\textsuperscript{15} and extend observations to intact preparations that preserve the head, neck, body, and wings. The measurements were taken from the entire frontal hemisphere at a high spatial and spectral resolution to capture a complete and detailed HRTF. We carried out analyses of HRTF data that enabled us to investigate the interactions between spatial and spectral features of the HRTF that were not previously reported. By comparing measured transfer functions in the absence of pinna and tragus, we examined the contribution of the external ear structures to the directional properties of the HRTF. In our analysis presented here, we emphasize the acoustic features that are believed to play a role in mammalian sound localization. This approach has led us also to consider a role for binaural cues for vertical localization by animals that hear in the ultrasonic range.

\section{II. METHODS}

We constructed an apparatus and developed the methods to permit measurements of the head related transfer function (HRTF) of the intact bat, in the frontal hemisphere. A 1-m-radius hoop was used to carry out the acoustic measurements (Fig. 1). The hoop was mounted upright and fixed to a rectangular frame, which was attached to the ceiling and floor of a large room ($7 \times 6$ m) lined with acoustic foam. This device could rotate around its vertical axis and could be locked on a reference dial at any selected azimuth angle with $1^\circ$ resolution. A custom 1.6-cm-diameter ultrasound loudspeaker (design by Lee Miller, Odense, Denmark, frequency response flat $\pm 3$ dB between 20 and 100 kHz) was attached to a sliding fixture that could be locked at any position on the hoop. The hoop was marked in $5^\circ$ steps, indicating elevation coordinates.

\subsection{A. Animal preparation}

Measurements were taken from four intact Eptesicus fuscus specimens (S1, S2, S3, S4). Each bat was perfused with 4\% paraformaldehyde, followed by a saline flush. A
microphone with a 1.5-mm-diameter metal probe (FG 3453-Knowles Electronics) was inserted into each of the bat’s ear canals after rupturing the tympanic membrane. Lithium batteries (1.5 V) were used to power the microphones. The microphones were glued in place (Loctite 411 with Zipkicker accelerator) and sealed tightly around the ear canal to avoid any leak of sound pressure. Cross-talk between the microphones was measured before each experiment, and it was no greater than $-60 \text{ dB}$. The bat was suspended horizontally with its wings spread, as in flight, and the pinnae were preserved in an upright position.

The bat’s head was positioned at the center of the hoop pointing at the $0^\circ$ azimuth and elevation. Photographs of the bat were taken to make necessary coordinate transformations to align the bat’s eye–nostril axis to $0^\circ$ azimuth and $0^\circ$ elevation. The coordinate transformations that were applied to S1, S2, S3, and S4 were $40^\circ$, $30^\circ$, $0^\circ$, and $22^\circ$ downward tilt, respectively. Two laser pointers were installed at positions $-90^\circ$ and $90^\circ$ azimuth, each aimed at the tip of the corresponding tragus. These laser beams were permanently illuminated to monitor the position of the bat and to ensure the correct position of the frame in the calibration stage. Another laser pointer was used to adjust the directionality of the speaker with respect to the bat’s head any time the elevation of the speaker was changed.

To investigate the contribution of the pinna and the tragus to the directional properties of the HRTF, a separate set of measurements for tragus-absent and pinna-absent ears was conducted. Tragus-absent measurements were taken from S3 and S4 by keeping the right ear intact (control ear) and deflecting the tragus of the left ear. Pinna-absent measurements were taken from S2, S3, and S4 by cutting away the pinna and returning the tragus of the left ear to its natural position. Measurements of the HRTF from the intact right ear allowed comparisons across different sets of measurements to control for any time-related changes that may have occurred in the condition of the bat. During data collection from S3, an unintended change in the orientation of the bat after the first set of measurements prevented a detailed comparison of the HRTF features between the intact and manipulated ears.

B. Data acquisition

The data were recorded for sounds broadcast from a loudspeaker at a distance of 84 cm from the center of the bat’s head. Microphone recordings from 685 different speaker positions on the frontal hemisphere were taken. Spatial positions were sampled from a double-polar coordinate system with $5^\circ$ resolution in both dimensions. Speaker positions were specified by their azimuth and elevation values. Azimuth values changed from $-90^\circ$ to $90^\circ$ from left to right of the midline, while elevation values changed from $-90^\circ$ to $90^\circ$ from below to above the horizon.

Computer-generated signals, consisting of 2-ms-duration downward linear frequency-modulated (FM) sweeps, were broadcast at a rate of 33 Hz. The duration and interpulse interval of the signals were selected to prevent overlap of the broadcast signals with echoes from the hoop and surrounding walls. The signals recorded with the implanted microphones were amplified and bandpass filtered (10–100 kHz) using a commercial filter unit (Stewart). The signals were sampled through a data acquisition system (IOTech Wavebook/512) connected to a Pentium III PC computer. The outputs from the microphones were monitored at all times on a two-channel oscilloscope (LeCroy).

C. Signal processing

Fifty signals per channel (left and right ears) were recorded, with a sampling rate of 500 kHz for each speaker position. To improve SNR, these signals were time aligned and averaged, making sure that the relative time delay between channels was unchanged. Then, HRTFs for the left and the right ears at each source direction were calculated as the ratio of the Fourier transform (2048-point FFT) of the averaged signals to the Fourier transform of the averaged signals obtained from free-field sound recordings. Free-field sound recordings were taken from the speaker position $0^\circ$ azimuth and $0^\circ$ elevation with both microphones placed at the center of the coordinate frame before they were implanted in the bat’s ears.

The magnitude of the HRTF was smoothed in logarithmic frequency domain using a rectangular sliding window. The width of the sliding window was chosen to obtain a quality factor of 20. In this case, the quality factor is defined as the proportion of the window’s center frequency to its width. This quality factor was chosen based on measured tuning curves of cells in the inferior colliculus of E. fuscus to achieve biologically realistic frequency resolution.

For some analyses, the HRTF was divided into direction-dependent and direction-independent linear time-invariant systems. The magnitude of the direction-independent component (here referred to as the common transfer function, CTF) was calculated as the spatial average of the magnitude function across the entire set of HRTF measured. The phase of this component was computed, based on a minimum-phase assumption. The direction-dependent component, also called direction-dependent transfer function (DTF), was calculated by dividing the HRTF by the CTF.

Spatial interpolation was applied to the measured HRTF at each frequency using spherical harmonic expansion. This process allowed us to obtain HRTF for the directions that were not sampled during the measurements. After interpolation, iso-level contours were obtained using built-in MATLAB functions.

III. RESULTS

A. Acoustic gain

Acoustic gain can be defined as the ratio of sound intensity at the ear canal to sound intensity in free field at a particular frequency. Thus, acoustic gain is the magnitude of the HRTF at that frequency. The direction of the maximum gain of HRTF (or DTF) across azimuth and elevation, at a particular frequency, is commonly known as the acoustic axis.

Figure 2(a) depicts the maximum gain (MG) provided by the HRTFs of the left (solid) and the right (dashed) ear of S1 as a function of frequency, across all the directions. Each curve shows distinct peaks and troughs, the acoustical modes

of the external ears. A plateau at the lower frequencies spans a frequency region between 10 and 30 kHz. A peak can be seen at the higher end of the spectral range. The peak point of this mode is around 57 and 67 kHz for the right and the left ears, respectively. A trough in between the plateau and the peak occurs at 43 kHz for the right ear and 50 kHz for the left. Across most of the frequency range, except the trough, the gain is positive and reaches a maximum of 25 dB for the left ear.

1. Asymmetry between the left and the right ears

Another interesting feature of the data is that the left ear’s and the right ear’s MG of HRTF and DTF are not identical, suggesting asymmetry between the ears. This asymmetry may be a result of structural and/or orientation differences between ears. Orientation differences between the two pinnae could be natural or might have been created during preparation of the animals for acoustic measurements. However, the asymmetry might also be an artifact caused by the placement of the microphones in the ear canals. Many HRTF studies have investigated effects of microphone position in the ear canal on the directional changes in HRTF. \(^{23-25}\)

These studies have reported that transformation in the ear canal is independent of sound direction. Thus, microphone placement in the ear canal likely does not contribute to directional changes in the HRTF. To evaluate unintended effects of microphone placement in both ears that may potentially produce asymmetry, we examine the common transfer function (CTF) and the MG of the direction-dependent component of the HRTF, i.e. the direction-dependent transfer function (DTF). Effects of the ear canal and its interactions with the microphones on the HRTF are accounted for in CTF [Fig. 2(b)]. Any structural differences between the ears, before the ear canal opening, would still be present in DTF (for a technical discussion, see Refs. 17 and 26). However, some asymmetry in the MG of DTF still persists between the two ears [see Fig. 2(c)]. In particular, above 35 kHz the left ear shows a higher gain than the right ear.

The local troughs in both DTFs [Fig. 2(c)] are the result of differences in center frequencies of the troughs in MG functions and CTFs, shown in Figs. 2(a) and (b), respectively. The center frequencies of the troughs for both ears shift to a lower frequency in the CTF. We hypothesize that the asymmetry between the left and the right ear DTF is a result of structural and/or orientation differences between the two ears.

2. Pinna and tragus manipulations

Figure 3 illustrates the left and right MG of HRTF, CTF and MG of DTF of S4. The left ear of S4 was manipulated after the intact ear measurement, while the right remained untouched to serve as a control. Figures 3(a) and (d) show MG of HRTFs of the left and right ears, respectively.

As expected, the right ear characteristic functions overlap across different measurement sessions, ensuring that no significant decay of the preparation occurred [Figs. 3(d), (e), and (f)]. Shaded areas represent the range of change of characteristic functions along the frequency axis across three sets of measurements. Notice also that CTFs of the left ear show only small variations across the different manipulations. In contrast, the MG of the left ear HRTF for the intact and the tragus-absent cases differ above 57 kHz, where tragus removal causes a drop in the gain [Figs. 3(a), (b), dashed line]. Notice that this effect persists in the maximum gain of the DTF of the left ear [Fig. 3(c)]. This observation suggests that the presence of the tragus affects the acoustical mode, caus-
ing an improvement in gain and directionality and a small change in the frequency of the resonant mode.

Following removal of the pinna on the left ear, the maximum gain drops up to 6 dB between 20 and 35 kHz and up to 14 dB at frequencies above 57 kHz. The maximum gain of the DTF, after the pinna was removed, shows a very shallow increase with frequency [Fig. 3(c), dotted line].

MG of HRTFs obtained from S4 [Figs. 3(a) and (d)] and S1 [Fig. 2(a)] were slightly different from each other, not only across subjects but also across ears in the same subject. These differences may be a result of natural variations in ear shape and/or differences in pinna orientation and microphone placement in the subjects’ ear canals. However, MG of DTFs show a similar pattern across subjects.

B. Monaural spectral properties

The HRTF includes direction-dependent spectral features that can be used for the computation of sound localization by the auditory system. Spectral notches are the most systematic of these features, and are believed to play an important role in vertical sound localization.15 Figure 4 shows the contour plots of the DTF magnitudes measured from the left ear of S2, as a function of frequency, on three sagittal planes, 23° ipsilateral (top), midsagittal 0° (middle), and 23° contralateral (bottom).

1. Position of spectral notches along the frequency axis changes with elevation

DTFs at different sagittal planes share a similar profile. Relatively higher intensities are observed for the planes that are more ipsilateral (negative azimuths in this case) as a result of head shadow [Fig. 4(a)]. A peak covering almost the entire frontal hemisphere below 55 kHz is interrupted by a primary spectral notch that shifts from 30 to 55 kHz with increasing elevation [Figs. 4(a), (b) and (c)] and remains

FIG. 4. Left ear DTF contour plot for sagittal planes at 23° ipsilateral (top row), 0° (middle row), and 23° contralateral (bottom row). Intact (a), (b), (c) and pinna-absent (d), (e), (f) cases for S2. Contour lines are plotted with 3-dB separation.
fixed at approximately 55 kHz at higher elevations. This notch changes roughly linearly for elevations −60° to 20° [Figs. 4(b) and (c)]. A secondary notch appears between 55 and 90 kHz over the elevation range of −60° to 0° [Fig. 4(b)] and and −60° to 20° [Fig. 4(c)], respectively. A third notch trend is observed between −50° and −20° elevations along the lower border of a second peak for frequencies above 55 kHz [Figs. 4(a) and (b)].

2. The pinna is essential for the elevation-dependent nature of the spectral notches

Figures 4(d), (e), and (f), illustrate the changes in DTF as a result of pinna removal in the same subject. As can be seen, primary and secondary notch trends are no longer present for the pinna-absent ear. Starting at 70 kHz, a linear notch trend, less visible in the intact ear measurements [Figs. 4(a), (b), (c)], shows similar elevation-dependent behavior as the primary and secondary notch trends in the lower hemisphere. Moreover, at high elevation and frequency, a different group of spectral notches surrounds a peak in this region. With the removal of the pinna, less directional dependence of spectral profile is observed.

3. Spatial notches are azimuth- and elevation dependent

The frequency where a notch reaches its lowest point is defined as the notch center frequency. In Fig. 5 the spatial changes in the frequency of the primary notch, obtained from the HRTF of S1, for both ears are represented as a function of azimuth and elevation. The contour lines in the figure represent directions that share the same primary notch center frequency in the HRTF. To distinguish the primary notch, from other notches, a clustering algorithm in the three-dimensional domain of azimuth, elevation, and frequency was applied. This algorithm groups points that are close together in this 3D space. Interpolation between the obtained points was achieved using spherical harmonic decomposition. Iso-frequency contour lines of the center frequencies for both ears extend from ipsilateral low elevations to contralateral high elevations. The center frequencies monotonically increase with elevation in the medial-frontal space in both ears.

C. Monaural spatial features

1. Spatial patterns of HRTF consist of directional lobes separated by deep spatial nulls that are co-localized with the spectral notches

In Fig. 6, intact and pinna-absent DTF magnitude contour plots at selected frequencies are compared. The figures are based on data collected from the left ear of S2. Contour maps of the intact ear differ from the ones corresponding to the pinna-absent manipulation. In the intact case, a large lobe covers almost the entire ipsilateral and part of the contralateral frontal hemisphere for frequencies below 40 kHz. Above 40 kHz, two sidelobes, in addition to the main lobe, appear. Deep spatial nulls separate the main lobes and the sidelobes.

In the pinna-absent case, the main lobe for all frequencies covers a much larger spatial area in the frontal hemisphere. At lower frequencies (32 kHz), the main lobe occupies a large portion of the contralateral side. The acoustic axis falls between 0° and −34° of azimuth, around the 0° elevation plane, for almost the entire frequency region. In general, for the pinna-absent ear not only is the spatial selectivity low (larger lobes) but also the gain across frequency. This observation is in agreement with the effect of the pinna removal on MG of HRTF and DTF in Fig. 3.

It is interesting to note the relation between the spatial nulls in the HRTF magnitude at a particular frequency, and the presence of spectral notches at that frequency. Figure 6 (left column) illustrates this relationship via overlaid spatial contour maps and spatial position of the spectral notches, white dots, at given frequencies. Note that spectral notches are co-localized with spatial nulls. This is a result of a rapid change in spatial location of the deep nulls in a small frequency range.
2. **Direction of the acoustic axis changes with frequency**

Another important observation is that, in the intact case, the acoustic axis (maximum point of the lobe) moves to higher elevations and lower azimuths as frequency increases (Fig. 7). Figures 7(a) and (b) show the elevation and the azimuth of the acoustic axis as a function of frequency obtained from the HRTF of S2. Acoustic axis elevation shows a

---

**FIG. 6.** Spatial contour map of HRTF magnitude at selected constant frequencies (32, 48, 71, 81 kHz) for intact and pinna-absent cases of S2. Contour lines are plotted with 3-dB separation. Overlaid on the left ear plots are white dots representing the existence of spectral notches in the corresponding HRTF, at that particular frequency.
linear increase from $-50^\circ$ at 10 kHz to $10^\circ$ at 42 kHz. A second linear trend between 50 and 90 kHz also shows an increase in acoustic axis elevation from $-15^\circ$ to $10^\circ$. At the frequency region (40 to 50 kHz) where the first linear trend is interrupted a second spatial lobe becomes prominent, as can be seen in Fig. 6 (48 kHz). Note that behavior of the acoustic axis is very similar in both ears.

The azimuth of the acoustic axis shifts towards $0^\circ$ azimuth (from $+/\pm 40^\circ$ to $+/\pm 10^\circ$) as frequency increases from 20 to 90 kHz. From Fig. 7 one can conclude that external ears provide more sensitivity to the sounds arriving from directly in front of the bat at frequencies above 50 kHz.

3. The pinna and the tragus contribute to the directionality of the HRTF

One can observe in Fig. 6 that the main lobes and the sidelobes become more directional with sound frequency. We quantified the frequency-dependent increase in directionality using a directivity index. The directivity index is defined as the log ratio of the acoustic power delivered by a directional receiver on the acoustic axis to that of an omnidirectional with the same sensitivity in a diffused sound field. The directionality of the spatial maps of the left ears of S1, S2, and S4, as a function of frequency, are given in Fig. 8 for manipulated (left) and control (right) ears. For all subjects spatial directionality of intact ears increases monotonically with frequency (Fig. 8, solid lines), indicating that acoustic energy is collected from a restricted directional range as the frequency increases. Thus, this finding is consistent with the observation that the HRTF becomes more spatially selective with sound frequency. Using linear regression, an increase in the directionality was computed for the intact left and right ears, respectively: 0.148 and 0.121 dB/kHz for S1, 0.13 and 0.135 dB/kHz for S2, and 0.150 and 0.139 dB/kHz for S4. Note that the slopes were slightly different between the left and the right ears of S1 and S4, consistent with the asymmetry between the left and right MGF described earlier (Fig. 2).

The effects of the manipulation of the left ear of S2 (pinna-absent) and S4 (pinna-absent and tragus-absent) on directionality of the HRTF as a function of frequency can also be seen in Fig. 8 (dashed lines for tragus-absent and dotted lines for pinna-absent cases). For both S2 and S4 [Figs. 8(b) and (c)] directionality still increases monotonically, but removal of the pinna decreases directionality. The decrease in directionality is small below 30 kHz and more apparent above 57 kHz for S4; however, for S2 it occurs over...
a much larger frequency range. Removal of the tragus also causes a decrease in the directionality over 57 kHz for S4.

D. Interaural level differences

1. Spatial characteristics of the ILD becomes complex with sound frequency

Spatial contour maps of interaural level differences (ILD) at different frequencies are displayed in Fig. 9 for S2. For frequencies below 40 kHz, ILD changes monotonically from the right to the left, as a function of azimuth (Fig. 9, 38 kHz). In contrast, at higher frequencies this monotonic change no longer holds for the frontal hemisphere. In fact, at high frequencies negative ILDs (Ref. 25) were observed: negative ILD refers to measurements for which sound pressure at the contralateral ear is larger than the ipsilateral ear.

FIG. 9. Interaural level difference (ILD) spatial contour maps for 38, 48, 58, 68, and 80 kHz of S2. Contour lines are plotted with 3-dB separation.
The contour plot for 48 kHz (Fig. 9) shows that the monotonic ILD trend along the azimuth was disrupted with a negative ILD pattern around the center (0° azimuth and elevation.). Above this frequency, negative and positive ILD patterns alternate along the vertical axis around the midsagittal plane. The occurrence of this alternating ILD pattern increases with sound frequency. Note that large ILD values also appear at directions around the mid-segmental axis.

2. ILD changes on the cones of confusion

Figure 10 shows the distribution of the angle of the spatial gradient vector of ILD with respect to the vector perpendicular to the cone of confusion surface, for each HRTF measurement location, as a function of frequency, for S4. A gradient vector’s norm and orientation indicate the amount and the relative direction of composite local changes of the ILD at a given sound source direction and frequency. Having all the local gradient vectors orienting perpendicular to the surface of the cone of confusion would indicate that ILD change is independent from sound source elevation. Distributions are obtained as normalized histograms of the angles at each frequency. Normalization was undertaken by weighting each angle by a factor. The weight for each position was obtained as the ratio of the local gradient vector norm to the spatial integral of the norm of all the gradient vectors. This way the local ILD change at a particular position contributed to the distribution in proportion to the overall change in ILD on the frontal hemisphere. The histogram should show a peak around 90° if ILD changes on the cone of confusion, and it should peak around 0° if it does not. The distributions show a peak around 0°, below 40 kHz, extending to 20° on each side, suggesting a constant ILD along the cone of confusion. Above 40 kHz, histograms show peaks around 90°, suggesting that local change of ILD is dominant on the cones of confusion.

E. Interaural time differences

Figure 11 illustrates the interaural time differences (ITD) obtained from S1. ITD was calculated based on the spectrogram correlation of the impulse responses. For this process a 100-channel, second-order Butterworth bandpass filter bank, consisting of filters with 1/3-octave bandwidth and envelope detectors, was used. The cross correlation obtained from outputs of the right-and the left ear frequency channel pairs was summed across frequency. The time lag of the maximum of this summed cross correlation was taken as the ITD for that sound source location. ITD changed approximately between −75 and 75 μs as the sound source moved from right to left for all the subjects.

IV. DISCUSSION

Accurate sound localization is essential for bats when they negotiate complex acoustic environments. Extraordinary sensitivity to echo delay, used by the bat for target range discrimination, has been reported (for a review, see Ref. 28). However, less is known about the acoustic cues used by bats to localize sound source direction. Several behavioral studies reported accurate azimuthal and elevational sound localization performance in echolocating bats.3, 23 The bats’ accuracy in sound localization depends on robust localization cues created by the directional properties of the ears and/or specializations of acoustic information processing that take place in the auditory system. Studying the HRTF is an important step in our understanding of sound localization, as localization cues available to all mammals are captured entirely by the HRTF. Investigating bat sound localization from the HRTF is limited to a situation where the pinnae are immobile during passive listening. E. fuscus has mobile pinnae, and thus, HRTF-based analysis cannot capture the role of the pinna mobility in sound localization. Yet, our results can still apply to the localization of brief sounds when the pinnae may be immobile during the sound reception. Bats have been shown to localize brief sounds with high accuracy. Thus, our results are likely to be relevant to the understanding of sound localization in echolocating bats.

Our analysis of the echolocating bat HRTF suggests that the pinna plays a role in shaping its directional features. Comparisons between the intact-and the pinna-absent ears showed that the pinna improves the directionality and the gain of the HRTF. The pinna also affects the directional properties of the spectral notches.

Spectral notches systematically changed with sound direction in the bat HRTF. There were three prominent notch trends, which were between 30 and 50 kHz, 55 and 90 kHz for sound source positions on the lower hemisphere, and 55 and 90 kHz for sound source positions on the upper hemisphere. A closer look at the spatial distribution of these notches showed that iso-frequency lines of notch center frequencies extend diagonally from contralateral at low elevations to ipsilateral at high elevations, exhibiting both elevation and azimuth dependence. Iso-frequency lines of notch
center frequencies from both ears result in a grid-like organization of these lines, as observed earlier in cats by Rice et al. Another salient feature of the HRTF is the presence of spatial nulls. These nulls were found in between the main lobe and the sidelobes of the HRTF. A comparison between the spatial positions of the spectral notches and the spatial nulls indicates that the two are overlapping (Fig. 6, left column). In addition to our observations, many earlier studies on the directional properties of the bat external ear also mention that the acoustical axis moves in the frontal hemisphere and increases in directionality with sound frequency. In relation to these characteristics of the HRTF, the spatial nulls also move with the acoustical axis. These changes in spatial nulls within a small frequency region are related to a deep and sharp notch in the HRTF. Ear manipulations in this study revealed that the pinna contributes to this phenomenon.

We observed that the ILD also shows both azimuth and elevation dependence. An azimuth-dominant change in ILD appears at low frequencies, between 10 and 40 kHz. For frequencies above 40 kHz, the ILD spatial distribution was more complex and sensitive to the elevation of the sound source. Wotton et al. reported that the absence of the tragus causes disturbances in the primary notch trend of the bat HRTF. In a related behavioral study these authors reported tragus deflection produced a dramatic increase in the bat’s vertical MAA in the frontal-lower hemisphere, where they observed the primary notch trend of the HRTF from the intact ear. They hypothesized that bats uses the primary notch trend as a cue for localization of the sound source elevation.

We found that the tragus contributes to the gain and the directionality of the HRTF at frequencies between 70 and 90 kHz. Aside from these effects, we did not observe disturbances in the vertical dependence of spectral notches in the frequency range of 30–50 kHz following tragus removal, as reported in the Wotton et al. study. ITD based on the measured HRTF changed between −75 and 75 μs. Although this range of change is relatively small, we believe that ITD could be a reliable cue for sound localization during echolocation. The range difference discrimination threshold of E. fuscus is 30–60 μs; thus, it may be possible for a bat to detect echo arrival differences from the echo delay difference between the two ears using FM sweeps.

1. A model for sound localization

Earlier theoretical and experimental studies of sound localization have asserted that mammals localize sound using binaural difference cues (ILD and ITD) for azimuth and monaural spectral cues, such as spectral notches, for elevation in the frontal (lower) hemisphere. However, neither the monaural cues that are investigated here nor the ILD in our data behaves in a way that is consistent with this localization scheme. By contrast, both the ILD and the spectral notches were dependent on sound source azimuth and elevation.

Our observations are in agreement with some earlier reports. Grinnell and Grinnell and Fuzessery and Pollak suggested a role for ILD in vertical localization in other bat species. In addition to bats, earlier studies report elevation-dependent ILD changes in humans and other mammals such as ferret. However, these reports did not lead to further studies of the role of ILD on vertical sound localization in bats and other animals.

Wotton et al. briefly mentioned a weak relation between the primary notch trend and sound source azimuth. They mentioned a possible role for the spectral notch in binaural sound localization, as was suggested in cats; however, they focused on the role of the spectral notch in vertical sound localization. They reported that elevation-dependent notch trends are limited to the lower hemisphere, and suggested that this observation can explain the vertical MAA difference between high and low elevations along the vertical plane. Moreover, disturbance of the primary notch trend and the increase in the MAA at lower elevations in bats with deflected tragus were considered to provide further support for the role of the spectral notch in vertical sound localization. Combining their behavioral and HRTF data, Wotton et al. suggested separate sound localization cues for vertical and horizontal components of the sound source position.

We observed that the pinna contributes more to the direction-dependent spectral patterns than does the tragus. In addition, we showed that spectral notches are not limited to the lower hemisphere. Spectral notches mainly surround the acoustic energy peaks in the HRTF spatial patterns, and they can appear for sound sources at high elevations. We found that there is a coupling between the spatial nulls and the spectral notches and most important, the spatial nulls give rise to complex ILD patterns. Consequently, elevation dependence of the ILD is related to the directional properties of the spectral notches. Thus, ILD and spectral notches should not be viewed as entirely separate cues that could be used exclusively for horizontal and vertical sound localization, respectively.

We propose that both the ILD and the spectral notches contribute to localization of sound source azimuth and elevation, probably in cooperation with other spectral features of the HRTF. The fact that both cues can provide horizontal and vertical information about sound source position improves the robustness of computation for sound localization. This new scheme can replace the simple dichotomy of acoustic cues for sound localization in azimuth and elevation.

Several recent psychoacoustical findings showed that human subjects’ vertical localization performance was not in accordance with the single-notch theory. The single-notch theory predicts that subjects should perceive a sound source at a vertical position that depends on the frequency of the spectral notch embedded in the sound source. This prediction is based on the relationship between the sound source elevation and the notch frequency in the HRTF. Ladengdik and Bronkhorst, using virtual acoustic techniques, observed that human subjects’ localization acuity did not change when the spectral notch cue was removed from HRTFs.

Our data suggest a model of sound localization in which the absence of the primary notch cue should not cause loss of acuity in vertical localization outside the midsagittal plane, since the ILD cue is still available. The fact that in our model...
the spectral features in the HRTF from both ears contribute to the computation of sound source localization is also in agreement with the study by Hotman et al. In this study it was shown that spectral cues from left and right ears are weighted to construct an elevation percept around the mid-sagittal plane.

We suggest that computation of sound location in the bat auditory system should be based on information received from both ears. Localization cues that were investigated here are not distinctly separate for sound source azimuth or elevation, but rather can contribute together to the estimation of sound source location.

V. SUMMARY AND CONCLUSIONS

A spatial-spectral analysis of the HRTF of *E. fuscus* is reported. HRTFs obtained from intact, pinna-absent, and tragus-absent ears are compared to understand contributions of external ear structures to the directional transformation of the sounds at the ear canals.

We made key observations that may have important consequences to our understanding of bat sound localization. We found that both ILD and spectral notches, believed to be important localization cues, are dependent on sound source azimuth and elevation.

These findings lead us to a localization model for *E. fuscus*, for which both of these cues contribute to localization of sound source direction. This model provides robustness in sound localization by employing multiple cues for sound source azimuth and elevation.

ACKNOWLEDGMENTS

This work was supported by a grant from the National Science Foundation (IBN-0111973) and by a P-30 Center Grant from the National Institute of Deafness and Other Communication Disorders (P30 DCO4664). We thank Kari Bohn, Kaushik Ghose, Timothy Horiuchi, Amy Kryjak, Aaron Schurger, Shiva Sinha, Jonathan Simon, and Rose Young for their help with data collection. We also thank Dr. Bradford May for his valuable comments on an earlier version of this manuscript.