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The acoustical cues to sound location in the Guinea pig (*cavia porcellus*)

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Abstract

There are three main acoustical cues to sound location, each attributable to space-and frequency-dependent filtering of the propagating sound waves by the outer ears, head, and torso: Interaural differences in time (ITD) and level (ILD) as well as monaural spectral shape cues. While the guinea pig has been a common model for studying the anatomy, physiology, and behavior of binaural and spatial hearing, extensive measurements of their available acoustical cues are lacking. Here, these cues were determined from directional transfer functions (DTFs), the directional components of the head-related transfer functions, for eleven adult guinea pigs. In the frontal hemisphere, monaural spectral notches were present for frequencies from ~10 to 20 kHz; in general, the notch frequency increased with increasing sound source elevation and in azimuth toward the contralateral ear. The maximum ITDs calculated from low-pass filtered (2 kHz cutoff frequency) DTFs were ~250 μ s, whereas the maximum ITD measured with low frequency tone pips was over 320 μ s. A spherical head model underestimates ITD magnitude under normal conditions, but closely approximates values when the pinnae were removed. Interaural level differences (ILDs) strongly depended on location and frequency; maximum ILDs were < 10 dB for frequencies < 4 kHz and were as large as 40 dB for frequencies > 10 kHz. Removal of the pinna reduced the depth and sharpness of spectral notches, altered the acoustical axis, and reduced the acoustical gain, ITDs, and ILDs; however, spectral shape features and acoustical gain were not completely eliminated, suggesting a substantial contribution of the head and torso in altering the sounds present at the tympanic membrane.

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Keywords

sound localization; interaural time difference; interaural level difference; head related transfer function; directional transfer function

1. Introduction

The dimensions and morphology of the head and pinnae are fundamental in shaping the spatial-location dependence of the spectral and temporal aspects of sounds that ultimately arrive at the tympanic membrane (Jones et al. 2011; Shaw 1974; Tollin and Koka 2009a; b). An important consequence of the acoustic directionality of the head and pinnae is their role in establishing the cues to sound source location. Three primary cues for location are generated by the spatial- and frequency-dependent reflection and diffraction of the propagating sound waves by the head and pinnae. Interaural time differences (ITDs) arise from path-length differences from lateral sound sources between the two opposing ears on either side of the head. Interaural level differences (ILDs) result jointly from this arrangement, and primarily occur with high frequency sounds. ILDs largely arise due to the amplification effects of the pinna ipsilateral to the source, and the reflection and refraction about the head resulting in attenuation at the contralateral ear. Finally, monaural spectral shape cues arise from differential reflection and diffraction of pressure waveforms of sounds by the head, torso and pinnae, as well as the constructive and destructive interference of sound waves at the tympanum that result in broadband spectral patterns that change with source location particularly in elevation.

Behavioral, anatomical, and physiological studies of sound localization mechanisms have suggested that there can be considerable differences (Harper and McAlpine 2004; Heffner 1997; Irving and Harrison 1967; Kelly 1980; Lesica et al. 2010) but also similarities (Brand et al. 2002; Harper and McAlpine 2004; Heffner 1997; Irving and Harrison 1967; Kelly 1980; Lesica et al. 2010; McAlpine and Grothe 2003; Tollin et al. 2013) among different species, making cross species generalizations difficult and potentially misleading; for example, the anatomical and physiological mechanisms for localization based on ITDs is believed to differ between mammals and avian and reptilian species (Bierman et al. 2014; Carr et al. 2009; Lesica et al. 2010; McAlpine et al. 2001). Some of these differences might be reconciled by taking into consideration the magnitudes and frequency ranges of the sound localization cues that are physically available for each particular species, the so-called “physiological range” of the cues. In other words, proper interpretation of the data from sound localization studies requires detailed knowledge of the properties of acoustical information available to the species under study.

To date there have been considerable investigation into the cues available to a variety of different species, including human (Middlebrooks and Green 1990; Middlebrooks et al. 1989; Wightman and Kistler 1989), cat (Irvine 1987; Moore and Irvine 1979; Musicant et al. 1990; Phillips et al. 1982; Rice et al. 1992; Roth et al. 1980; Tollin and Koka 2009a; b), monkey (Slee and Young 2010; Spezio et al. 2000), ferret (Carlile 1990a; b; Schnupp et al. 2003), tammar wallaby (Coles and Guppy 1986), various species of bat (Aytekin et al. 2004; Firzlaiff and Schuller 2003; Fuzessery 1996; Jen and Chen 1988; Obrist et al. 1993), gerbil

(Maki and Furukawa 2005), chinchilla (Jones et al. 2011; Koka et al. 2011), mouse (Chen et al. 1995; Lauer et al. 2011), rat (Harrison and Downey 1970; Koka et al. 2008), rabbit (Kim et al. 2010) and barn owl (Keller et al. 1998; Moiseff 1989).

Here we extend these studies to include the guinea pig. Guinea pigs have long been a model system for the anatomy and physiology of sound localization, including mechanisms of ITD coding (McAlpine et al. 1996; 2001; Palmer et al. 1990; Shackleton et al. 2003; Skottun et al. 2001), spatial sensitivity in the superior and inferior colliculi (Behrend et al. 2004; Palmer and King 1982; Sterbing et al. 2002), binaural masking level difference (Caird et al. 1991; Jiang et al. 1997), and binaural sluggishness (Shackleton and Palmer 2010). While there have been some studies of the cues available to guinea pigs, these studies were either of limited scope (Carlile and Pettigrew 1987; King and Palmer 1983; Sterbing et al. 2003) or cues were indirectly measured via cochlear microphonics (Palmer and King 1985). Therefore, there lacks a comprehensive, detailed assessment of the ensemble of localization cues available to the guinea pig over the full range of sound locations. Here, we took extensive measurements of the directional transfer functions (DTFs; Middlebrooks and Green 1990), the directional components of the head-related transfer functions (HRTFs), on 11 adult guinea pig cadavers. From the DTFs, the primary acoustical cues to location were computed and the role of the pinna in generating these cues was examined by repeating the acoustical measurements following pinnae removal.

2. Methods

2.1 Animal preparation

All surgical and experimental procedures complied with the guidelines of the University of Colorado Anschutz Medical Campus Animal Care and Use Committees and the National Institutes of Health. At the start of each experiment, adult pigmented guinea pigs obtained from an approved vendor (Elm Hill Labs, Chelmsford, MA) were initially anesthetized with an intraperitoneal (IP) injection of ketamine (22.5 mg/kg) and xylazine (2.5 mg/kg), and euthanized with an overdose of sodium pentobarbital (100 mg/kg, IP). The weight, head diameter, and the length and width of the pinnae of each animal were measured immediately prior to acoustic measurements (see Figure 1A,B).

After anatomical inspection, a small hole was made from the posterior wall of the cartilaginous portion of the ear canal to the nape of the neck with a 14-gauge needle, through which a 50-mm-long flexible silicone probe tube (Brüel and Kjær, part # AF-0555, 1.65 mm outer diameter) was inserted. The tip of the tubes were positioned at the opening of the bony section of each ear canal, which was approximately 2 mm from the tympanic membrane (assessed via otoscopic visualization; also depicted in Figure 1C), and fixed in place with cyanoacrylate. The distal ends of the tubes were connected to two microphones (Brüel and Kjær, 1/4" probe tube microphone Type-4182). The animal was then placed on a small acrylic platform in the center of the foam-lined, sound-attenuating chamber (see below) with its interaural axis aligned in the center of an arc of loudspeakers using three lasers mounted at both poles and at the midpoint of the arc. Care was taken to ensure the platform did not obscure any speaker locations and that the animal's head was propped in a natural alert position. The role of the pinnae was assessed by repeating the acoustical measurements after

the pinnae were removed. Pinnae positions were not altered or standardized across animals, thus some variability in ear positioning was observed across the population. Surgical removal of the pinna did not alter the position of the probe tube microphone in the ear canal and animals remained properly centered in the loudspeaker arc.

2.2 Experimental setup

The experimental setup and procedures used were similar to those described in Koka et al. (2011; 2008), and Tollin and Koka (2009a; b). All experiments were performed in a $\sim 3 \times 3 \times 3$ m (interior dimensions) double-walled, sound-attenuating chamber (IAC, Bronx, NY). Stimuli were presented from 25 identical loudspeakers (Morel MDT-20) attached to a custom-built [polar coordinate system (Leong and Carlile 1998; Middlebrooks and Pettigrew 1981)] semicircular boom with radius of 1 m. The 25 loudspeakers were spaced in azimuth along the boom at 7.5° apart, from $+90^\circ$ (left) to -90° (right). The axis of rotation of the boom was aligned with the interaural axis of the animal (i.e., through the ears). DTFs were recorded from a total of 775 different locations, covering azimuth ($+90^\circ$ to -90°) and elevation (-45° in the frontal hemisphere to $+180^\circ$, exactly behind the animal).

The acoustic measurement stimuli consisted of 11th order maximum length sequences (MLS; Rife and Vanderkooy 1989) repeated without interruption 128 times from each loudspeaker. The MLS stimuli were presented at full 24-bit resolution at a rate of 97,656.25 Hz (Tucker-Davis Technologies, RP2.1, TDT, Alachua, FL). A single sequence of the 11th order MLS is comprised of 2047 samples ($2^{11}-1$) and is thus 20.96 ms in duration. The resulting acoustic waveforms were simultaneously recorded in the left and right ear canals using two probe tube microphones (see Fig. 1C for probe-tube placement), amplified, collected using two analog to digital converter channels, and stored on a PC hard disk for off-line analysis. An acoustic calibration measurement was also made in the absence of the animal to capture the spectral characteristics of the loudspeakers and microphones.

2.3 Data processing and analysis

The impulse responses for each ear at each location were calculated by circular cross-correlation of the original 11th order MLS stimulus and the in-ear recording from the probe tube microphone (Rife and Vanderkooy 1989). The impulse responses were then truncated to 512 (5.24 ms) points by a Hanning window beginning 700 samples (7.17 ms) after the start of the stimulus presentation, thereby approximately centering maximum deflection of the impulse response. This windowing procedure removes the small-amplitude reflections from the wall opposing the active speaker (~ 2 m distance) that may be contained in the impulse responses, which is approximately 7 ms after the maximum amplitude.

HRTFs were derived by dividing the frequency response of the in-ear recording by that of the appropriate loudspeaker calibration measurement, thereby removing the loudspeaker and microphone frequency response from each in-ear measurement. The resulting function is referred to as the HRTF, as it represents the acoustical gain and delay introduced by the head and the pinnae. However, the resulting HRTF can be highly dependent on the exact placement of the tip of the probe tube microphone in the ear canal relative to the tympanic membrane (Middlebrooks et al. 1989). To reduce the confounding effects of the probe tube

placement in the ear canal, DTFs for each ear were calculated from the HRTFs by dividing the HRTF made at each spatial location by the geometrical mean of all the measured HRTFs across all measurement locations for that ear. The spectral features resulting from the exact placement of the probe tube microphone in the ear canal are expected to be similar for all measurement locations (i.e., they are not dependent on spatial location), so this “common” spectral feature is removed from the HRTFs, resulting in the DTFs (Middlebrooks and Green 1990). In essence, the DTFs are the sound source direction-dependent components of HRTFs.

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

For spatial plotting purposes, the data were displayed as Aitov projections (Bugayevskiy and Snyder 1995). In this projection, the animal's nose is oriented out of the page at 0° azimuth and 0° elevation, as if the animal were looking at the reader. Unless stated otherwise, spatial plots are shown for frontal data (i.e. elevation from -45° to +90° and azimuth from +90° to -90°).

2.4 Influence of animal preparation on HRTF recordings

Here we made measurements on recently euthanized animals. Similar techniques have been used previously to measure the acoustical cues in anesthetized (Koka et al. 2011; Tollin and Koka 2009a; b), frozen (Koka et al. 2008; Obrist et al. 1993; Wotton et al. 1995), formalin-fixed (Aytekin et al. 2004; Firzlaff and Schuller 2003; Fuzessery 1996), alcohol-fixed (Obrist et al. 1993), and cadaver animals (Chen et al. 1995; Coles and Guppy 1986; Harrison and Downey 1970; Maki and Furukawa 2005; Martin and Webster 1987; Middlebrooks and Pettigrew 1981; Moore and Irvine 1979). These previous studies have found negligible effects of animal condition; nevertheless, two control experiments were conducted to ensure that recordings were stable and comparable to those in live animals. First, we compared recordings made at +90° from the beginning and end of the experiment. The average difference in frequencies between 0.5 and 22 kHz, across ten of the male animals was 0.8 ± 1.1 dB in the left, and 0.4 ± 0.7 dB in the right ear. Second, we made measurements in one additional (female) animal while anesthetized, then repeated measurements following euthanasia. We compared the common component of the HRTF measurements across conditions, and the observed difference was 0.16 ± 2.18 dB in the left and 0.63 ± 1.48 dB in the right ear. In both analyses, the observed changes resulting from animal preparation are quite small and do not appear to substantially affect our analyses or results. Additionally, virtually all of our results in cadaveric specimens are wholly consistent with prior measurements of acoustic cues by King and Palmer (1983), Carlile and Pettigrew (1987), Sterbing et al. (2003) and Behrend et al. 2004).

2.5 Influence of room reflections upon ILD and ITD measurements

In order to rule out the possibility that standing acoustic waves generated in our recording chamber may provide a source of ITDs and ILDs occurring at low frequencies, a control experiment was performed with two probe tube microphone tips held 20.0 mm apart and positioned at the center of the loudspeaker arc. Acoustic recordings were made for sounds of different frequencies and different spatial locations in azimuth. The temporal waveform delay between the two microphones did not show any dependence on stimulus frequency for all stimulus frequencies ≥ 250 Hz. The empirical temporal maximal delays were constant across all frequencies (≥ 250 Hz) at 51 μ s, which is consistent with the predicted delay (within the 10.24 μ s resolution of our measurement system). Moreover, the sound pressure levels (SPLs) measured at the two microphones did not differ for frequencies >250 Hz, thus ensuring that our ILD measurements were not perturbed by standing waves. These control measurements confirm that neither the experimental sound chamber nor standing waves themselves are a confounding parameter to our measurements over the frequencies of interest (≥ 250 Hz).

3. Results

The results are based on DTF measurements from ten adult male and one adult female pigmented guinea pigs. Unless otherwise specified, measurements and analyses refer to the ten male animals. Head and pinnae dimensions were measured in each animal as shown in Fig. 1A-B. Effective head diameter was taken at the widest part of the skull (between points A and B in Fig. 1A), occurring a few mm rostral to the meatus at the points of the zygomatic process (the bizygomatic breadth) of the temporal bone (Gilbert 1981); this is the maximum transverse diameter of the head. Interaural diameter was also measured between the entrances of each ear canal (between A' and B' in Fig. 1A). The mean weight, head diameter, and the length and width of the pinnae for the male guinea pig population (from the last 5 of the 10 male animals) were 1095 ± 101 g, 49.4 ± 3.8 mm (AB), 21.6 ± 3.4 mm (EF) and 32 ± 6.7 mm (CD), respectively (head and pinnae dimensions are shown in Fig. 1A,B). For the female, measurements were 900 g, 48.05 mm (AB), 24.01 mm (EF) and 28.95 mm (CD) (the last two measurements left and right ears were averaged). For each animal, the linear dimensions of the left and right pinnae were essentially the same. The interaural diameter (e.g., between A' and B' in Fig. 1A) across the male animals was $30.04 \pm 0.02\%$ smaller than the head diameter measured at the widest part of the skull (the percentage difference in the female animal was comparable). The implications for these different estimates of effective head diameter are discussed in Section 3.2.3.

3.1 Monaural aspects of the acoustic directional transfer functions

3.1.1 Frequency range and spatial location dependence of broadband spectral notches—Systematic changes were observed in the frequency of the first (lowest frequency) spectral notch with changes in source location (e.g., Rice et al. 1992). Notch depth ranged from 15-25 dB. Figure 2A shows DTFs for the left ear of one animal (GP4) for elevations ranging from -45° to $+90^\circ$ in 7.5° steps for 0° azimuth and Fig. 2B show the DTFs for azimuths ranging from -90° (contralateral ear) to $+0^\circ$ in 7.5° steps at 0° elevation. Spectral notches were observed for frequencies above ~ 9 kHz in all animals. The frequency

of both the minimum and the low-frequency edge of the first spectral notch generally increased with increasing source elevation at a given sound source azimuth. Similarly, the first notch often varied with source azimuth at a given elevation, and is evident, to a small extent, in the example shown in Fig. 2B. The first notch frequency was easily detectable in all animals and systematically moved with both azimuth and elevation for sources in the frontal hemisphere; however, the notch was difficult to detect or shifted frequency erratically with source locations above and behind the animals. Across the nine guinea pigs, the notches tended to increase from ~10 to 20 kHz as the source increased in elevation (at 0° azimuth) from -45° to 90° and between 9.5 and 18 kHz as the source azimuth varied between $\pm 90^\circ$ (at 0° elevation). For sources in the front hemisphere, the dependence of first notch frequency on both azimuth and elevation results in diagonal notch-frequency contours where the first notch frequency systematically increases as sounds are moved from low elevations in the ipsilateral hemifield to upper elevations in the contralateral hemifield as demonstrated for one animal in the contour map shown in Fig. 2E; first-notch frequency contour maps were similar in the other animals studied. Notch frequency varied much more quickly and irregularly in the contralateral hemifield, but interestingly, only at azimuths lateral to $\sim -45^\circ$.

3.1.2 The role of the pinnae in generating broadband spectral notches—In order to test the hypothesis that selective filtering by the pinnae generate spectral notches, the pinnae were surgically removed and the acoustic measurements repeated in eight of the nine animals. Fig. 2C and D show the effect of pinnae removal on the broadband spectral notches in one animal (same animal as in Fig. 2A,B). The data demonstrate that pinnae removal substantially affected the broadband spectral notch feature from the DTFs for source changes in both elevation (Fig. 2C) and azimuth (Fig. 2D). In all cases, removal of the pinnae resulted in broader and shallower (e.g., notch depths of only ~5 dB or less after pinnae removal rather than 15-25 dB with pinnae intact) spectral notches, an upwards shift in frequency, as well as an overall reduction in the acoustical gain (next section) observed in the surrounding frequencies. The amount of gain reduction observed in these cues varied somewhat across subjects, likely resulting from variability in the pinnae removal procedure. These data support the hypothesis that the broadband spectral notches occurring from ~9-20 kHz in guinea pigs are largely produced by the pinna.

3.1.3 Spatial distribution of DTF amplitude gain—The acoustical gain provided by the head and pinnae at a given frequency varied with source direction. Fig. 3 shows the distribution of DTF gain at seven frequencies for sources in the frontal (left column: pinnae intact) hemisphere (i.e., +90° is ipsilateral) in the same animal as shown Fig. 2 (GP4). Fig. 4 shows DTF gain, in both front and rear hemifields, at a subset of frequencies for an additional animal (GP10). DTF gain is shown for the left ear only, as the right ear is nearly mirror symmetric in most animals. DTF gain in the pinna intact condition (left columns) varied considerably with location for frequencies above ~2 kHz. In the front, a distinct, roughly circular high gain area develops below ~8 kHz and shifts from a low to a high elevation, as well as from ipsilateral to central source locations with increasing frequency sounds. A second area of high gain is visible at ipsilateral locations for frequencies over ~12 kHz, resulting in the formation of a diagonal spectral notch. Both high gain areas and the

resulting spectral notch shift towards higher, more contralateral locations with frequencies increasing up to approximately 16 kHz, where the first high gain area dissipates. The remaining high gain area continues its upward, contralateral shift up to approximately 26 kHz, above which the amplitude gain becomes complex and non-systematic. Maximum acoustical gain (~15 dB) increased with frequency up to 14-16 kHz, above which the gain plateaued. In the rear hemifield, gain is roughly symmetric with the front for low frequencies (< ~4 kHz). At higher frequencies, the response is dominated by a large low-gain region directly behind the animal's head/body that is generally stable with frequency, except at frequencies with prominent spectral notches (e.g. 12 kHz).

The non-directional gain associated with the resonance frequency of the ear canal and concha was estimated from the common components of the HRTFs (see Methods). The common components of the HRTFs (not shown) averaged across animals revealed a constant peak in the gain of 10.9 ± 3.0 dB ($n = 9$ animals). The peak consistently occurred at ~5.5 kHz across animals, which is directly comparable to the combined gain of the concha and ear canal of guinea pigs as reported by Sinyor and Laszlo (1973). Note that the gains shown in Figures 3 and 4, and discussed in this section, do not contain the ear canal/concha gain as this gain was removed during the DTF computation procedure.

3.1.4 The acoustical axis and directivity of DTF amplitude gain—The spatial distribution of the DTF gain is quantified with two parameters. First, we calculated the acoustical axis, defined as the direction of maximal acoustical gain in the DTF gain at a particular frequency as has been performed in several other species (Middlebrooks and Pettigrew 1981; Phillips et al. 1982). Second, we assessed directionality by estimating the area in the DTF gain within 3 dB of the maximum gain, in the front hemifield (-45° to 90° elevation). Figure 5 shows the equivalent solid angle, that is, the area of a circle seen by an observer at the origin ($0^\circ, 0^\circ$) as a function of frequency. This area is reported in units of $\pi \times$ steradians (sr), where the solid angle of a half-hemisphere (half the largest possible) is equal to 2π sr. Frequencies below 3 kHz were not considered, as the 3dB contour is large (containing virtually all of the half-hemisphere), and can be irregular at low frequencies. The 3 dB area generally decreased at higher frequencies in each animal; however, the 3 dB area abruptly decreases towards 0 sr between 13-16 kHz, where the spectral notch dominates the DTF gain. The data calculated in this manner can be compared directly to the directionality generated by a circular aperture, and thus can be used to estimate the effective size of the pinna opening. We fit (robust non-linear least squares) a circular aperture model to each animal's measured gain areas (Calford and Pettigrew 1984; Coles and Guppy 1986), with aperture radius as the only free parameter. Note that although data is only shown at 1 kHz intervals, all data points within the frequency range were included in the analysis. Several example predictions are shown in Fig. 5 (dashed lines) to aid visualization. The model was poorly fit to four of the ten data sets (GP 1, 2, 8, & 10) which were excluded from further analysis. The remaining curve fits generally showed only moderate correspondence with the experimental data (average $R^2 = 0.48$), likely due in part to the bimodal (and the corresponding decrease in) gain areas observed between 13-16 kHz, and predict a mean aperture diameter of 88 mm (± 15 mm standard deviation). These data suggest that a circular aperture model is a poor fit for guinea pig ears, and that the acoustically estimated pinnae

apertures are larger than the empirically measured pinnae dimensions; however, the ensemble data across animals in Fig. 5 shows some frequency dependence. In particular, frequencies above ~6 kHz generally fall within a range of predicted pinnae apertures from ~30-50 mm, which is in closer agreement to the empirically measured pinnae dimensions, and is consistent with a prior report in guinea pig (Carlile and Pettigrew 1987).

The acoustic axis, or the direction producing the highest gain, for each animal varied systematically as a function of frequency for mid to high frequency sounds (i.e. > 3 kHz, and <30 kHz). The gain above and below this range tend to show broad and/or disorganized gain maps. Within this range, however, the acoustic axis tends to show a continuous shift from around 90° towards the midline and up. As mentioned above, the axis tends to show a sudden jump back to near 90° around 12-14 kHz, at which point the central, upward trend continues. This trend is clearly illustrated in Fig. 6, which shows the average movement of the acoustic axis across animals. The acoustic axis varies in azimuth (Fig. 6A) between 90 and 30°, and in elevation (Fig. 6B), between -30 and 15°.

3.1.5 Contributions of the pinna to acoustical gain and the acoustical axis—

The role of the pinnae in shaping the directional properties of the DTF gain, that is, the directionality and acoustic axis, was investigated in 9 animals by comparing the DTF gain maps in the intact animal to those with their pinna and concha surgically removed. Figure 3 (center column) shows representative data in one animal (GP4). Compared to the intact animal, the DTF gain maps for high frequencies in the Head Only condition show fewer peaks and troughs, more broad high gain areas, and a more consistent acoustic axis (~50° azimuth, 0-30° elevation) with increasing frequency. The pinna provide low gain (< ~2 dB) at frequencies below ~8 kHz. At high frequencies, however, the pinna can provide gain of ~15 dB depending upon the location and frequency of the sound source. Notably, this gain is strongly direction-dependent resulting in high gain areas that shift upwards and towards the midline, as well as a diagonal low gain area. It is clear, therefore, that acoustic directionality of the guinea pig at high frequencies is dependent upon intact pinna.

As suggested above, the frequency-dependent shift in the acoustic axis is likewise affected by the pinna. In the intact animal, the acoustic axis shifts in azimuth from ipsilateral to medial locations and from low to high elevations with increasing frequencies. Following removal of the pinna, the acoustic axis shows a similar but much more gradual shift in azimuth from lateral to medial locations, and a much more consistent elevation just above horizontal across frequency. Additionally, the jump back from medial to lateral positions between 10-15 kHz due to the spectral notches bisecting the regions of high gain (see Fig. 3 “Head + Pinna” vs “Head Only” plots at 12 and 14 kHz, and Fig. 6) is mostly eliminated, though a small deviation remains likely due to incomplete pinna removal in some animals. The acoustic axis is similar between intact and pinna-removed conditions for low (below 5 kHz), and high (above 20 kHz) frequencies in azimuth, and for high (above 25 kHz) frequencies in elevation.

3.2 Binaural aspects of the acoustic directional transfer functions

3.2.1 Interaural Level Differences - Variation with Frequency—ILD spectra were calculated as the difference in DTF gain between the left and right ears in each animal, wherein each element of the ILD spectra corresponds directly with the ILD at that corresponding frequency. Figures 7A and B shows ILD as a function of frequency at several elevations (0° azimuth), and azimuths (0° elevation) respectively. Figures 7C and D show the ILD functions for the same locations following pinna removal, which will be compared below in Section 3.2.2. ILD varied dramatically with azimuth, consistent with comparable measurements in similarly sized mammalian species (Rabbit: Kim et al. 2010; Chinchilla: Koka et al. 2011; Rat: Koka et al. 2008). ILD was small (a few dB) at low frequencies, and increased at higher frequencies (peaking around 18 kHz). Between 10 and 18 kHz, the spectral notch in the contralateral ear helped generate ILDs that were larger than those expected based simply on physical head diameter.

To further assess ILD dependence on frequency, we calculated the frequency-dependent rate of change of the ILD cue with changes in source azimuth, that is, the slope of the ILD function between $\pm 30^\circ$ as a function each frequency (dB/degree); results obtained with a smaller spatial separation (e.g. $\pm 15^\circ$) were not materially different. The rate of change of the binaural cues across azimuth has been previously shown to be useful in predicting an animal's spatial acuity, as measured by behavioral assessment of the minimum audible angle (e.g., Heffner et al. 1994), which we will address in greater detail in the Discussion. Average ILD slope functions are shown from three representative animals (GP4, GP8 & GP9) in Figure 7E, and the average ILD slope across all 10 animals is shown in Fig. 7F (mean $\pm$ 95% confidence interval; black line and gray area, respectively). In order to highlight the variability observed in the population, the total range observed across animals is also shown (bounded by gray lines), as well as the peak ILD observed in each animal (colored symbols, same as in Fig. 5). The across-animal average ILD slope increased with frequency from approximately $0.05\text{dB}/^\circ$ at 1 kHz to just over $0.25\text{dB}/^\circ$ at ~ 18 kHz, before dropping back below $0.15\text{dB}/^\circ$ above 30 kHz. However, variability in ILD slopes across animals is largest above 10 kHz, and thus the peak of the average shown is somewhat smaller than the average across-animal maximum ILD slope of $0.30 \pm 0.09\text{dB}/^\circ$, suggesting that spectral notch frequency varies substantially across animals. Such variability is demonstrated by the large differences observed between 10 and 17 kHz in the examples shown in Fig. 7E.

In order to assess the degree to which ILD slope depends upon head diameter we made two comparisons. First, we measured responses in one additional female guinea pig, which had slightly smaller head width (AB: 48.05 mm, $\sim 3\%$ narrower), pinna length (CD: 28.95, $\sim 10\%$ shorter), and body weight (900g, $\sim 18\%$ lighter). Correspondingly, this animal generally showed smaller ILD values (peak ILD slope of $0.23\text{dB}/^\circ$). Second, we plotted the ILD slope predicted by a spherical head model (Duda and Martens 1998) with a diameter equal to the average measured head width (49.4 mm; ears were assumed to be 90° from straight ahead), which is shown as a red line on Fig. 7F. As expected, at frequencies above ~ 10 kHz the empirically measured ILD slope deviates from the model prediction in both shape and magnitude due the presence of spectral filtering by the pinnae; however, the model also underestimates the ILD slope magnitude at low frequencies. In order to investigate this

disparity, we fit (nonlinear least squares) the ILD slope measured for each animal to predictions made by the spherical head model, in which the only free parameter was sphere radius. Interestingly, the model fit predicted a head diameter of 114 ± 19 mm, more than double the empirically measured head diameters.

3.2.2 Spatial dependence of the ILD cue and contributions of the pinna—

Similar to DTF gain, the ILD cue varied with both azimuth and elevation, in addition to frequency. Figures 8 and 9 shows spatial maps of ILD at the same frequencies, and from the same animals for which the DTF gain maps are shown in Fig. 3 and 4. ILD cue maps were calculated as the difference in DTFs between the left and right ears (i.e. $+90^\circ$ is ipsilateral). Consistent with the results shown in Figure 7, ILDs in the front hemifield were small (< 5 dB) and generally symmetrical for frequencies below ~ 8 kHz, and larger (up to 30 dB) and more complex at higher frequencies. In particular, ILDs vary in both azimuth and elevation between 10 and 18 kHz due to the effects of the pinna on spectral composition at the two ears. In the rear hemifield, ILDs at low frequencies ($< \sim 4$ kHz) were generally symmetric with the front, except directly behind the animal where ILDs were compressed across azimuth. At higher frequencies, the ILD can show a direction reversal (typically at ~ 8 kHz) that starts high and decreases in elevation with increasing frequency. Yet higher frequencies reveal spectral shaping by the pinnae that produces large ILDs in both the front and rear hemifields, and which is generally symmetric with the front.

Spectral notches generated by the pinna shift ILD contours in a location-dependent manner. This is clearly illustrated by removal of the pinna (Fig. 8, center column, Head Only), which acts to reduce both overall ILD magnitude and spatial complexity at high frequencies. The location-dependent gain produced by the pinna, i.e. the difference between the intact (Head + Pinna) and pinna removed (Head Only) conditions, is shown in the right-hand column (Pinna Only). While the effect at low frequencies is clearly small, the interplay between spectral notches in the two ears is evident in the complex arrangements of peaks and troughs at high frequencies. These results are also visible in comparing Fig. 7A/B to C/D, which shows a decrease in the large ILD peak present at approximately 10 kHz following pinnae removal. Additionally, the ILD vs azimuth slope predicted by a spherical head model (Duda and Martens 1998) with a diameter equal to our average adult guinea pig head (the red line in Fig. 7F), shows the greatest divergence from the empirical measurements in the frequency range where spectral notches and large ILDs are observed (between ~ 10 and 18 kHz).

3.2.3 Interaural Time Differences – spatial dependence—

The ongoing low-frequency ITD was calculated as the delay corresponding to the maximum in the cross-correlation function of the low-pass filtered (2 kHz) acoustic impulse responses, as described in the Methods. The ITDs observed in one animal (GP10, same as in Figs. 4 and 9), representative of the population, are shown as a function of source location in the front hemisphere in Fig. 10A, and the rear hemisphere in 10B. ITDs are shown with respect to the lead (positive, red) or lag (negative, blue) in the right ear. The ITD was symmetrical about the midline in both front and rear hemifields, and largely independent of elevation except immediately behind the animal, where ITDs vary more rapidly across azimuth near the midline.

In order to analyze responses across the population, ITDs recorded in the front hemifield were collapsed across elevation. The mean ITD ($\pm$ SEM) across the 10 male animals is shown as a function of azimuth in Fig. 10C for the Head + Pinna (solid line). Results from nine of these animals following pinna removal (Head Only, dotted line) are considered in a separate section below. Consistent with the results observed in the example animal shown in Fig. 10A, the average ITDs across the population was symmetric across the midline, thus only data from the right side is shown. Average ITD slope between $\pm 30^\circ$ was 3.32 ± 0.08 us/degree and the maximum absolute ITD was 253 ± 6.7 us. The female guinea pig showed a comparable maximum ITD of 260 us (not shown) despite having a slightly smaller head diameter.

Superimposed on the curves in Fig. 10C are the predicted ITDs from a spherical head model (Woodworm 1938), calculated using the mean male head width (49.4 mm), and a model similarly generated following human ITD measurements (Kuhn 1977). The ITDs predicted by the Kuhn model (red triangles) are similar in magnitude to the intact condition (maximum of 218 us), though not in shape, as it overestimates at moderate angles ($< \sim 60^\circ$) and underestimates at large angles ($> \sim 80^\circ$). In contrast, the spherical head model (blue squares) only slightly underestimates ITDs when compared to the pinna-removed data (maximum of 186 us). Notably, these results were produced using a head diameter measured at the widest part of the head. Comparable results generated using the interaural distance (A'-B' in Fig. 1A; measured between canal openings on either side of the head), which is 30% smaller, produce substantially lower predicted ITD magnitudes (maximum ITDs predicted by the Kuhn and Woodworm models were 132 (is and 113 μ s respectively), which underestimates the empirical maximum ITDs by $\sim 40\%$.

3.2.4 Frequency dependence of the ITDs—Previous results suggest that ITDs are larger for low- than high-frequency sounds in humans (Kuhn 1977) and animals (chinchilla: Koka et al. 2011; Lupo et al. 2011; cat: Roth et al. 1980; guinea pig: Sterbing et al. 2003). The analysis of ITD as in Section 3.2.3 obscures the possible frequency dependence of ITD. To investigate this frequency dependence, ITDs were measured in three animals for short tone-burst stimuli. The mean ITD across animals for tones with frequencies between 300 Hz and 3 kHz at four different azimuths along the horizontal plane (0° , 30° , 60° and 90°) are shown in Fig. 10D. At each of the three lateral azimuths, the ITDs increased with decreasing frequency with a transition frequency between 1.5-2.0 kHz. The maximum ITDs, observed at 90° , varied substantially with frequency, from over 300 μ s at 300 Hz to below 200 μ s at 3 kHz. Maximum mean ITD observed was 324 μ s, remarkably similar to the 330 μ s observed by Sterbing et al. (2003). As predicted by Kuhn (1977), and consistent with the data from cats (Roth et al, 1980) and chinchilla (Koka et al, 2011; Lupo et al., 2011) the low frequency ITDs in the guinea pig were $\sim 50\%$ larger than the high frequency ITDs.

3.2.5 Contributions of the pinna to ITDs—The difference between the model predictions and empirically measured ITDs suggests an additional mechanism affects sound transmission time into the guinea pig ear. As mentioned above, Fig. 10C includes the average ITD measured across nine animals following pinna removal. Recordings reveal substantially lower (196 ± 10 μ s) maximum absolute ITDs, $\sim 23\%$ lower than in the intact

($253 \pm 6.7 \mu\text{s}$) condition, and, interestingly, closely matches the ITDs predicted by the spherical head model (Woodworth 1938). Overall, the pinnae appear to increase the effective width of the head somewhat, thus increasing the ITD magnitude and slope resulting from each azimuthal angle.

4. Discussion

4.1 Monaural localization cues

The pinna contributes to all three sound localization cues by providing directionally-dependent variations in the acoustic gain at different frequencies. In particular, the filtering properties of the pinna introduce spectral notches that vary with source elevation (Tollin and Yin 2003). In the guinea pig, these spectral cues are most prominent in the frontal hemisphere with notch center frequencies generally varying between 10-20 kHz. Although some of the characteristics regarding the acoustic gain and directionality are similar to those observed in previous reports in guinea pig (Carlile and Pettigrew 1987; Palmer and King 1985; Sterbing et al. 2003), none of these prior studies systematically reported all of the cues together, including the monaural spectral notch cues. In the following section, we discuss the mechanisms that contribute to generating the monaural gain functions observed. We begin with an analysis of the pinna as a simple acoustic receiver, and continue with a discussion of the complex gain functions it generates at higher frequencies.

Spectral notch frequency varied systematically with changes in source azimuth and elevation similar to, though over a different yet overlapping frequency range (between 10-20 kHz), previous reports in human (6-12 kHz; Middlebrooks 1999), rhesus (5-15 kHz; Spezio et al. 2000), marmoset (12-24 kHz; Slee and Young 2010), cat (8-18 kHz Musicant et al. 1990; Rice et al. 1992; Tollin and Koka 2009b; Xu and Middlebrooks 2000; Young et al. 1996), chinchilla (6-18 kHz; Jones et al. 2011; Koka et al. 2011), rat (16-30 kHz; Koka et al. 2008), gerbil (25-45 kHz; Maki and Furukawa 2005), mouse (15-40 kHz; Lauer et al. 2011), and bat (30-50 kHz; Aytekin et al. 2004; Firzlaff and Schuller 2003; Fuzessery 1996; Wotton et al. 1995). Previously, it has been postulated (Jones et al. 2011; Tollin and Koka 2009b) that pinna dimensions determine the frequency band over which these spectral notches occur, where comparatively smaller pinna sizes result in a higher frequency range of notches. These studies described two species, cat and chinchilla, with similar head and body dimensions, which also exhibit first spectral notches over similar frequency ranges (8-18 kHz and 6-18 kHz, respectively). However, the pinna dimensions of the guinea pig are nearly half (~30 mm vs ~50 mm) those of the cat and chinchilla, suggesting pinna aperture diameter is not the sole feature upon which spectral notch frequency is dependent. Consistent with this observation, the marmoset has pinna dimensions (~25 mm) comparable to the guinea pig, and shows spectral notches at somewhat higher frequencies, from 12-24 kHz (Slee and Young 2010). On the other hand, juvenile chinchillas (Fig. 4E in Jones et al. 2011) and cats (Fig. 2D in Tollin and Koka 2009b) have pinnae dimensions similar to those of adult guinea pigs (~30 mm), and produce the same ~10-20 kHz range of spectral notches.

Consistent with the apparent disagreement between pinnae dimensions and first notch frequencies in guinea pig compared to most species, there was a mismatch in guinea pig pinna dimensions and the predicted acoustical directivity of the gain functions. Specifically,

the area in the DTF gain within 3 dB of the maximum was smaller than predicted by a circular aperture model of the pinna, and the goodness of fits of the circular aperture model to the measured gain areas were relatively low (mean $R^2 = 0.48$). These results are in contrast with previous reports that utilized this technique in other similarly sized animals, which yielded relatively good estimates of the pinna dimensions from the 3dB gain area (cat: Calford and Pettigrew 1984; tammar wallaby: Coles and Guppy 1986; chinchilla: Koka et al. 2011), and higher goodness of fits (e.g. chinchilla, $R^2 = 0.85$: Koka et al. 2011).

Two anatomical features of the guinea pig may explain the disparity in predicted pinna size: the lack of protruding, erect and forward-facing pinnae (as shown in Fig. 1B; and which are found in most other small mammals discussed above), and the prominent zygomatic arch that extends from the anterior portion of the skull towards the external auditory meatus. Interestingly, when the dimensions of the side of the guinea pig head that cradles the pinnae are combined with the width of the pinna, the resulting measurements approximately match the predicted 88 mm diameter circular aperture suggested by the acoustic directivity function. The prominent zygomatic arch, therefore, may form a structure similar in appearance and function to the facial disk found in some avian species (e.g. barn owl; Coles and Guppy 1986; Keller et al. 1998), extending the acoustical aperture beyond the extent of the pinna. Similarly, the complex anatomical features observed within the guinea pig pinna likely explain the low goodness of fit to the circular aperture model, similar to results observed previously in cats ($R^2 = 0.52$, Tollin and Koka 2009a), which have similarly and perhaps more complex pinna anatomy.

The acoustic axis recorded in guinea pigs shows an additional similarity with other species, where the axis shifts from lateral to medial locations for frequencies increasing to approximately 10 kHz. There is an emergence of a second high-gain area for frequencies above 10 kHz. Due to the presence of the spectral notches at these frequencies, there is an abrupt ipsilateral jump in the acoustic axis back towards the lateral pole, above which frequency the acoustic axis continues its lateral to medial trend with frequency. This discontinuity in acoustic axis location at moderately high frequencies disappears following removal of the pinna, again emphasizing the role of spectral notches in generating direction-dependent variations in acoustic gain. Our results showing the influence of the pinna on the direction of the acoustic axis is comparable to those described previously by Carlile and Pettigrew (1987), although that study only examined sound sources along the horizontal plane. The residual, albeit much weaker, frequency dependence of the acoustic axis following pinna removal is similar to observations in barn owls following removal of the facial ruff feathers (Coles and Guppy 1988), a procedure that is comparable to a partial removal of the pinna in many mammalian species, and provides further support for an acoustical aperture extending beyond the pinna in guinea pig.

4.2 Binaural localization cues

4.2.1 Interaural level difference cues—The dominant azimuthal sound localization cue for high-frequency sounds, ILD, varies directly with frequency and azimuthal sound location. ILDs were small for low (<4 kHz) frequencies, and varied systematically with azimuth up to approximately 18 kHz. The average (across all 9 animals) rate of change in

ILD across the midline (measured at $\pm 30^\circ$) shows a steady increase in ILD from 0.05 to 0.15 dB/ $^\circ$ between 1 and 12 kHz, and peaks at ~ 0.26 dB/ $^\circ$ at 19 kHz. Interestingly, the maximum ILD slope recorded for each animal averaged somewhat larger (0.30 dB/ $^\circ$) than the maximum of the average (note the overall range marked by gray lines in Fig. 7F), suggesting that the spectral notches present in this frequency band vary substantially across animals. The mean maximum ILD slope (e.g. 0.30 dB/ $^\circ$) in the guinea pig is lower in magnitude compared to species with somewhat larger head sizes, and greater than in animals with a smaller head size (e.g. rat: ~ 0.4 dB/ $^\circ$, Koka et al. 2008). The range of frequencies over which ILDs vary systematically with azimuth (below ~ 12 kHz) is nearly identical to that observed in chinchilla (Koka et al. 2011), is comparable to the range observed in cats (< 8 kHz, Tollin and Koka 2009a), and lower in frequency than in the rat (< 18.5 kHz, Koka et al. 2008). The pinnae were critical to producing ILDs that were larger than expected based on linear head dimensions, since pinna removal substantially reduced ILD magnitude.

ILD dependence on head diameter was assessed by comparing to a smaller female guinea pig, and generating ILD predictions from a spherical head model. However, although the spherical model closely predicts ILD sensitivity below ~ 10 kHz, the head diameter predicted an effective head diameter of more than double the empirically measured values. This disparity is likely a result of the placement of the guinea pig head and ears directly in front of the body, and lack of a distinct neck. This arrangement would delay and further attenuate sound transmission around the back of the head/body, thus increasing the effective distance between the two ears. This result suggests that a sphere is a poor choice with which to model the head of a guinea pig, similar to results from other species (chinchilla, Koka et al. 2011, cat, Tollin and Koka 2009), though for different reasons (body vs pinna position). Nevertheless, ILD scaled with head size such that the smaller female showed lower ILD magnitudes than the population of larger males, consistent with our predictions from measurements in other species.

4.2.2 Interaural time difference cues—As with ILDs, ITDs - the dominant azimuthal sound localization cue for low-frequency sounds - vary with frequency and sound source azimuth. The low-frequency ongoing fine-structure ITDs varied systematically across the midsagittal plane, and produced a maximum ITD of approximately 253 μ s at 90° with the pinnae intact. Maximum ITD is generally assumed to roughly scale with head width, and correspondingly guinea pigs exhibit similar maximum ITDs to animals with similar head sizes (chinchilla: $\sim 250 \mu$ s Koka et al. 2011; ferret: $\sim 200 \mu$ s Schnupp et al. 2003), larger values than species with smaller heads (bat: $\sim 75 \mu$ s, Aytekin et al. 2004; rat: $\sim 160 \mu$ s, Koka et al. 2008; gerbil: $\sim 120 \mu$ s, Maki and Furukawa 2005), and smaller values than species with larger heads such as human (800-900 μ s, Middlebrooks and Green 1990; Tollin and Koka 2009a), cat ($\sim 350 \mu$ s, Roth et al. 1980; Tollin and Koka 2009a), and rhesus ($\sim 475 \mu$ s (Spezio et al. 2000)).

The high dependence of ITD on head diameter, in contrast to the results of modeling ILD discussed above, is further supported by the results of both a spherical head model (Woodworth 1938), and the Kuhn (1977) model, and predicted values comparable in magnitude to empirically recorded ITDs. This similarity is also in contrast to the underestimates of ITD by the models reported for chinchilla (Koka et al. 2011), gerbil (Maki

and Furukawa 2005), rat (Koka et al. 2008), cat (Tollin and Koka 2009a), and marmoset (Slee and Young 2010). In the present study, effective head diameter was taken at the widest part of the skull (i.e., between A and B in Fig. 1A); however, diameter of the head measured between the openings of the two ear canals (between A' and B' in Fig. 1A) was ~30% less than when measured at the widest part. Additionally, ITDs measured in the female guinea pig were slightly larger than average despite having a slightly smaller than average head diameter, possibly resulting from the wider (though shorter) than average pinnae. Recent corrections to the Woodworth model by Aaronson and Hartmann (2014) might be useful in the future to more accurately model time delays in species with radically non-spherical head morphologies, like the guinea pig.

Consistent with reports in other species, pinna removal decreased maximum ITDs in guinea pigs by ~23% (from 196 to 253 μ s) though this decrease was somewhat smaller than reported for chinchilla (~25%, Koka et al. 2011) and rat (~36%, Koka et al. 2008). The dominance of head diameter on setting ITD magnitude may result from the placement of the ear canals lower on the head, the smaller pinna size relative to head diameter, and the flatter, less pronounced pinnae found in guinea pigs than in these previously studied species.

Finally, ITDs in the guinea pig were found to depend upon frequency, with larger ITDs at lower frequencies. Frequency dependent ITDs have been observed in human (Kuhn 1977), cat (Roth et al. 1980; Tollin and Koka 2009a), gerbil (Maki and Furukawa 2005), chinchilla (Koka et al. 2011; Lupo et al. 2011) and guinea pig (Sterbing et al. 2003). The frequency dependence of ITD observed in the present study was very similar to that reported by Sterbing et al. (2003). For example, the maximum ITDs of 324 μ s occurring for a 300 Hz tone presented at 90° is virtually identical to the 330 μ s reported by Sterbing et al. (2003) at ~400 Hz.

4.3 Implications for behavioral and physiological studies

We are unaware of any prior rigorous and comprehensive behavioral tests of guinea pig sound localization ability (however, see Clements and Kelly 1978), thus we are unable to directly compare the acoustical cues to behavioral data. However, by analyzing the range of cues available to guinea pig, and comparing these values to other similar species, we can make some conservative predictions regarding the behavioral ability of guinea pig in localizing and discriminating sounds in space. Previous studies have shown minimum ILD discrimination in humans, primates, cats and ferrets between 1–4 dB (Houben and Gourevitch 1979; Keating et al. 2013; Mills 1960; Scott et al. 2007; Wakeford and Robinson 1974) (see Tsai et al. 2010 for review). Similarly, consideration of acoustic measurements from our lab (Koka et al. 2011) along with psychophysical data (Heffner et al. 1994) suggest that chinchillas should be able to discriminate ILDs of at least 4 dB, which coincides with the 13.7° spatial acuity reported by Heffner et al. (1994) for broadband noise high-pass filtered at 8 kHz. Assuming an identical discrimination ability in guinea pigs, the average peak ILD slope of ~0.3 dB/° leads to a prediction that guinea pigs are able to discriminate high frequency sound sources that are separated by at least ~ 13.3°, virtually identical to the similarly sized chinchilla.

For low-frequencies, Heffner et al. (1994) reported chinchilla discrimination ability of 15.7° to 500 Hz low-pass filtered noise, which, when compared to the average ITD slope of $3.5 \mu\text{s}/^\circ$ (Koka et al. 2011), suggests a chinchilla ITD discrimination threshold of $55 \mu\text{s}$. This value is comparable to reports in rabbit ($50\text{--}60 \mu\text{s}$, Ebert et al. 2008), ferret ($23 \mu\text{s}$, Keating et al. 2013), and cat ($\sim 30 \mu\text{s}$, Wakeford and Robinson 1974). By assuming guinea pigs have a similar ITD discrimination threshold of $55 \mu\text{s}$, and taking into account the average ITD slope of $3 \mu\text{s}/^\circ$ reported here, we can predict a low-frequency spatial discrimination ability of 18.3° , slightly broader than reported in chinchilla. However, single units in the inferior colliculus have been reported to show a just-noticeable-difference as low as $\sim 30 \mu\text{s}$ (Shackleton et al. 2003), which predicts better discrimination ability of $\sim 10^\circ$. Overall, these results suggest that guinea pigs should have both high- and low-frequency sound localization acuity that is comparable to the chinchilla, though likely still worse than the cat (Heffner and Heffner 1988; Populin and Yin 1998). Future behavioral studies are needed to definitively characterize guinea pig minimum audible angles and general spatial hearing capabilities.

4.4 Conclusions

The guinea pig is a common animal model for auditory research, and correspondingly there have been many studies of the sensitivity of guinea pig auditory neurons to sound localization cues. In particular, the guinea pig has been a particularly popular model for studying the neurophysiology of spatial hearing using the virtual acoustic space technique (Behrend et al. 2004; Sterbing et al. 2003), as well for studies of neural sensitivity to ITD cues (Liu et al. 2006; McAlpine et al. 1996; Shackleton et al. 2003; Skottun et al. 2001; Zohar et al. 2011) and ILD cues (Palmer et al. 2007) in the inferior colliculus.

Unlike many similarly sized species (e.g. cat, chinchilla, mouse, rat, bat) that have prominent cone-shaped ears, guinea pigs have relatively small pinnae that primarily lie flat against the side of the head similar to human pinnae. Consistent with these species, the structure of the guinea pig pinna is relatively stereotyped (at least across the population contained within the current study), with folds and concatenations at consistent locations across individuals, which generate both the high-gain areas that vary with frequency and the first spectral notches that vary systematic with elevation. This feature, combined with the similar audiogram (Heffner et al. 1971), suggests that the guinea pig is a good model of human hearing. Unlike most other species, however, pinna removal reduces the variability in frequency and space, but does not completely eliminate the spatial gain modulation. Furthermore, modeling (Fig. 5) predicts that the effective size of the pinnae and supporting structures are roughly twice the diameter of the individual pinna measured empirically. Instead, it appears that the guinea pigs' prominent zygomatic arch results in the entire side of the head effectively acting as an acoustic receiver, increasing the sound collection ability of the system.

The acoustic results reported here shed additional light on the ranges of the cues to sound localization that would be expected in the average laboratory adult guinea pig. These values can then be used to aid interpretation of physiological response properties as well as place constraints on models of neural coding. In particular, our replication here of not only the

frequency dependence of ITDs in guinea pigs, first documented by Sterbing et al. (2003), but also of the magnitude (~330 μ s) of these low-frequency ITD cues is noteworthy. Predictions of guinea pig ITD and ILD sensitivity were made based on the behavioral ability of another species of similar size and frequency sensitivity (chinchilla), and from a prior report on ITD sensitivity of single cells in the central nucleus of the inferior colliculus. However, actual sound localization and source discrimination ability awaits a direct test of guinea pig behavior.

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- Head diameter predicts interaural time but not level differences with azimuth.
- Spectral shape cues, notches, vary systematically with source elevation from 10-20 kHz.
- Monaural gain is greater than predicted by a circular aperture model of the pinnae.
- Face/torso anatomy appears to substantially affect sound localization cues.

Figure 1.

Anatomical aspects of the guinea pig external and middle ear. A: The average guinea pig head diameter (AB; between the zygomatic arches) across 5 animals was measured to be 49.4 ± 3.8 mm. Measurements between the ear canals were also taken (A'B'). B: Illustration of the guinea pig head and external ear. Hair tufts have been removed to expose the pinna. The average pinna width (CD) was 32 ± 6.7 mm and the average pinna length (EF) was 21.6 ± 3.4 mm. C: Coronal section of a guinea pig skull (illustration traced from a high-resolution CT scan) depicting the placement of the probe tube microphones inside the cartilaginous ear canal (designated by the dotted grey lines), at the distal-most portion of the bony auditory canal. Scale bar: 5 mm.

Figure 2.

High frequency spectral notches vary systematically in the ipsilateral hemifield. Monaural broadband spectral shape cues for the left ear of one animal (GP04) with intact (A, B) and surgically removed (C, D) pinnae. A, C: DTF gain as a function of frequency for locations varying in elevation ranging from -45° to $+90^\circ$ in 7.5° increments (at 0° azimuth). B, D: DTF gain as a function of frequency for locations varying in azimuth, ranging from -90° to $+90^\circ$ in 7.5° increments (at 0° elevation). E: Spectral notch frequencies recorded in the intact left ear vary with both azimuth and elevation.

Figure 3.

Spatial gain is increased but not dependent upon intact pinna in the guinea pig. Spatial distribution of DTF gains for seven frequencies in the left ear (+90°, ipsilateral) of one animal (GP04). Three conditions are shown: left column, animal with intact head and pinna (“Head + Pinna”); middle column, animal following pinnae removal (“Head Only”); right column, pinna contribution to the DTF gain (“Pinna Only”) which is computed as the difference between the “Head + Pinna” and “Head Only” measurements. The color bar indicates the gain in decibels (dB).

Figure 4.

Spatial gain in the front and rear hemifields in another animal (GP10). Responses are shown at three frequencies highlighting: front-back symmetry at low frequencies (2 kHz), the large low-gain area directly behind the animal at high frequencies (8 kHz), and the effects of spectral notches (12 kHz).

Figure 5.

Pinna dimensions are insufficient to explain the observed DTF gain. Solid angle area (in units of $\pi \times$ steradians) representing the surface area on a unit sphere representing gain within 3 dB of the maximum of the DTF gain plots for 9 animals. Lines indicate the circular aperture model (see text) predicted dependence of the solid angle area on sound frequency for four different aperture diameters (i.e. effective pinnae diameters); these four aperture diameters (30, 50, 70, and 90 mm) are substantially larger than the empirically-measured pinnae sizes for the 9 animals shown (each symbol corresponds to data from a different animal).

Figure 6.

The acoustic axis as a function of frequency for locations varying in azimuth (A) and elevation (B). The black line indicates the average location of the acoustic axis across 9 animals, with the shaded area indicating the standard error of the mean (SEM).

Figure 7.

ILD spectrum for one animal (GP04) and ILD slope as a function of frequency across the population of animals. The ILD spectrum is the frequency-by-frequency difference between left and right ear DTFs at a given location. Positive ILD indicates higher gain at the left ear than the right. ILDs do not change with varying source elevation (along 0° azimuth) (A), but change substantially with source azimuth along the horizontal plane (0° elevation) (B). Panels C and D show the ILD spectrum for the same locations following pinnae removal; ILDs were not greatly affected for sources varying in elevation (C), but were dramatically reduced for sources varying in the horizontal plane (D). E, F: The slope of the ILD function for sources $\pm 15^\circ$ about the midline (dB/deg) as a function of frequency for two example animals (E), and the population (F). The black line indicates the average ILD slope across all 9 animals, along with the corresponding standard error of the mean (mean $\pm$ SEM, gray shaded area) and overall range observed (gray lines). Colored symbols indicate the maximum ILD slope (at the appropriate frequency) observed for each animal (as in Fig. 5).

Figure 8.

ILD magnitude increases with source azimuth, frequency, and intact pinna. The spatial distribution of ILDs for seven different frequencies with respect to the left ear (+90°, ipsilateral) are shown from one animal (GP04). There are three different conditions shown: left column, animal with intact head and pinna (“Head + Pinna”); middle column, animal following pinnae removal (“Head Only”); right column, pinna contribution to the ILD (“Pinna Only”) which is computed as the difference between the “Head + Pinna” and “Head Only” measurements. The color bar indicates the ILD magnitude in decibels (dB).

Figure 9.

ILD magnitude in the front and rear hemifields in one additional animal (GP10). The rear responses shown reveal: ILD compression (thus increased ILD slope) at low frequencies (2 kHz), direction reversal at higher frequencies (8 kHz), and large magnitude ILDs resulting from spectral shaping by the pinna (12 kHz).

Figure 10.

ITD magnitude varies with azimuth and not elevation. (A) Spatial distribution of low-frequency ITDs for one animal (GP10) as a function of source location, where +90° is ipsilateral to the left ear and -90° is contralateral. Positive ITDs (red) indicate that the signal leads at the left ear. (B) ITD magnitude in the rear hemifield is compressed near the midline at low elevations. (C) Mean ITD ($\pm$ SEM) across nine animals as a function of azimuth for both “Head + Pinna” (solid black line) and “Head only” (dotted black line) conditions. The predicted ITDs based on the average animal head diameter across all animals are also shown (blue squares, Woodworth (1938) spherical head model; red triangles, Kuhn (1977) low-frequency ITD model). (D) Pure tone ITDs as a function of tone frequency, are quite similar to those reported by Sterbing et al. (2003). The average ITDs recorded using short-duration pure-tone stimuli in three animals are shown for 82.5°, 60°, 30°, and 0° azimuth.