Postnatal development of sound pressure transformations by the head and pinnae of the cat: Binaural characteristics

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There are three acoustical cues to sound location: Interaural time differences (ITDs), interaural level differences (ILDs), and monaural spectral shape cues. During development, the increasing interaural distance and pinnae size associated with a growing head and pinnae result in localization cues that change continuously until maturation is complete. Here the authors report measurements of both the physical dimensions of the head and pinnae, as well as acoustical measurements of the binaural localization cues of cats aged 1.3 weeks to adulthood. For a given source location, ILD magnitude tended to increase with both frequency and age. Moreover, the range of significant ILD production (~ 10 dB) shifted with age from higher to lower frequencies. ITD magnitude increased with age. Partial correlation analyses revealed that increasing pinnae size accounted for $\sim 31\%$ of the variance in the development of ILDs while increasing head size accounted for virtually none. On the other hand, increases in both the head and pinnae sizes contributed to the development of the ITD cues accounting for $\sim 71\%$ and $\sim 25\%$ of the variance, respectively. ILD and ITD cues in cats reach maturity by ~ 16 and ~ 22 weeks, respectively, which match the time period over which the pinnae and head dimensions reach maturity.

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I. INTRODUCTION

The head and the pinnae are fundamental in shaping the spatial-location dependence of the spectral and temporal aspects of sounds that ultimately arrive at the tympanic membrane (Tollin and Koka, 2009; Kuhn, 1987). An important consequence of the acoustic directionality of the head and pinnae is their role in establishing the cues to sound source location. The three primary cues for location are generated by the spatial- and frequency-dependent reflections and diffractions of the propagating sound waves by the head and pinnae (Tollin, 2008). Interaural time differences (ITDs) arise because the distance of the path of sound to the two ears differs. Interaural level differences (ILDs) result jointly from the amplification effects of the pinnae ipsilateral to the sound source and the acoustic shadowing effect of the head and contralateral pinna that occurs primarily for high-frequency sounds. Finally, monaural spectral shape cues arise from differential reflection and diffraction of pressure waveforms from sounds originating from different directions by the head, torso, and pinnae.

The spatial- and frequency-dependence of the monaural and binaural cues to location are well documented in the adult cat (Wiener *et al.*, 1966; Middlebrooks and Pettigrew, 1981; Calford and Pettigrew, 1984; Irvine, 1987; Martin and Webster, 1989; Musicant *et al.*, 1990; Rice *et al.*, 1992; Young *et al.*, 1996; Xu and Middlebrooks, 2000; Phillips *et al.*, 1982; Tollin and Koka, 2009). Moreover, regardless of the species, the magnitudes of the cues to location and the manner in which they change with location are dependent on

the physical size and dimensions of the head and pinnae (Shaw, 1974; Middlebrooks, 1999; Xu and Middlebrooks, 2000; Schnupp *et al.*, 2003; Maki and Furukawa, 2005; Tollin and Koka, 2009). Inter-individual differences in head and pinnae size and morphology are the basis for individual differences in the cues to location. These facts also create a challenge during development where the growing sizes of the head and pinnae in mammals increase dramatically from birth, changing not only the magnitude of the acoustical transformations but also the relationship between the cues and sound location.

Cats have been a common model for anatomical, physiological, and behavioral studies of auditory system development [see reviews by Kitzes (1990) and Walsh and McGee (1986)]. Their auditory system is relatively immature at birth and their physical size relative to other species (e.g., rat, mouse, and gerbil) permits good access to the neural structures of interest. A wealth of knowledge exists on the anatomy, physiology, and behavior of the adult cat binaural auditory system to which developmental data can be compared (Irvine, 1986). However, aside from some spatially and spectrally sparse measurements of the development of the ILD cues in kittens by Moore and Irvine (1979) there has been no systematic study of the development of the complete complement of acoustical cues and their relationship to the development of the linear dimensions of the head and pinnae. In this paper we investigate the development of the physical dimensions of the head and pinnae in the cat from the onset of hearing through adulthood and the concomitant changes in the binaural acoustical transformations of sound pressure at the ear. The development of the monaural transformations based on these experiments has been published (Tollin and Koka, 2009).

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FIG. 1. Developmental growth of the head and pinnae of the cat. The two measured dimensions relevant to the development of the binaural acoustical cues to location are shown in the insets of (A) and (B). (A) Head diameter AB. (B) Outside pinna height 1-2. The measured data are from 16 animals. Data points with error bars indicate the across-animal mean $\pm$ SD of the measured dimension at that age. Data points without error bars indicate single animal measurements at that age. In each panel, the solid and dashed horizontal lines indicate the mean and 99% confidence interval, respectively, of the measured dimension taken from 12 adult animals. The parameters of the best fitting growth curve for each measured dimension is displayed in each panel along with the correlation coefficient (r) for the fit. Figures are replotted from Tollin and Koka (2009) with permission.

II. METHODOLOGY

A. Animal preparation and experimental setup

Twenty-nine domestic short-hair cats (Liberty Research, Waverly, NY) were used in this study. Most animals were female (5/29 were male). All animals had clean external ears and ear canals. The weight and linear measurements of head diameter and pinnae height and width of each animal were taken immediately before each experiment and were reported in our companion study [parts of Fig. 1 in this paper are replotted from Tollin and Koka, 2009; see insets, Figs. 1(A) and 1(B)]. Methods for these growth measurements and the acoustic measurement procedures are detailed in Tollin and Koka, 2009. All acoustic measurements reported here were computed from those measured in both the left and right ears from 289 to 625 different spatial locations. All surgical and experimental procedures complied with the guidelines of the University of Colorado Health Sciences Center Animal Care and Use Committees and the National Institutes of Health.

B. Data processing and data analysis

For data collected here, the free-field-to-eardrum impulse responses for each ear and each location were calcu-

lated as described in Tollin and Koka, 2009. These impulse responses were then truncated to 512 points (5.12-ms duration) by a 512-point Hanning window where the center of the window was set to coincide with the point of maximum amplitude in the impulse response. This windowing procedure removes the small-amplitude reflections that may be contained in the impulse response. Moreover, these raw impulse responses contain not only the desired spectral and temporal modifications of the sounds due to the head and pinnae, but also the loudspeaker, microphone, and measurement-system frequency responses. These equipment-related frequency responses were removed from each in-ear measurement by dividing the Fourier transforms of each of the impulse responses by that of appropriate calibration measurements made for each loudspeaker by placing the microphone tips at the location corresponding to where the center of the head would be. These resulting functions are referred to as the head-related transfer functions (HRTFs), as they capture for each ear and loudspeaker location the acoustical gains and delays 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. To reduce the confounding effects of the probe tube placement in the ear canal, for each ear the directional transfer functions (DTFs) were then 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.

The amplitude spectra of the DTFs were calculated after the spectra were passed through a bank of 350 bandpass filters, the center frequencies of which were spaced at intervals of 0.0143 octave spanning from 1 to 32 kHz. The 3 dB bandwidth of filters was held constant across all frequencies at 0.12 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 bandpass filters that have been used elsewhere to filter DTFs (Middlebrooks, 1999; Xu and Middlebrooks, 2000; Schnupp *et al.*, 2003). Only data up to 32 kHz were used here as the signal-to-noise ratio was poor for higher frequencies in some animals, particularly for sources contralateral to the ear being measured. This latter aspect was especially critical when computing the ILD cues as described below.

Two binaural cues to sound location were studied here. The ILD spectrum was derived by computing the differences (in decibels) in the DTFs, frequency by frequency between right and left ears at all elevations and for all azimuth angles. A positive ILD indicates that the decibel level at the right ear was higher than the decibel level at the left ear. The ILDs for particular frequencies and locations were extracted from the ILD spectra. The low-frequency ongoing ITDs in the fine structure of the sounds in this paper were measured by com-

puting for each spatial location the cross-correlation of the raw head-related impulse responses of the left and right ears (i.e., before conversion to DTFs) and by finding the delay corresponding to the maximum point in the cross-correlation function. These impulse responses were first low-pass filtered at 3.5 kHz before cross-correlation. This process was repeated for each location.

For spatial plotting purposes, the data were displayed as Mollweide projections (Bugayevskiy and Snyder, 1995). In each of these projections the nose of the animal is considered to be projecting out of the page at 0° azimuth and 0° elevation, as if the animal were looking at the reader. The Mollweide projections were plotted for elevations from -30° to +90° and all azimuths from -180° to +180°. Unweighted linear regressions were performed using the curve fitting package in SIGMAPLOT (V10, Systat Software, Inc., Richmond, CA).

III. RESULTS

Results are based on data from 29 animals (5/29 were male). Acoustical measurements were obtained in 20 of these animals, 9 of which were adults and 11 that were different ages ranging from 1.3 to 22.1 weeks (for convenience, the age in days was converted to weeks by dividing by 7 and the quotient rounded to the nearest 1/10 of 1 week; for example, 9 days divided by 7 is equivalent to 1.3 weeks). The latter 11 animals came from 5 different litters. Nine additional adults were used only for measurements of head and pinnae dimensions. Adult acoustic measurements were obtained in conjunction with physiological experiments that utilized the acoustical measurements for virtual space stimulus presentation. In this paper we show detailed data from four animals from different age groups spanning development: 1.3 weeks (K009), 5 weeks (K008), 10 weeks (K012), and adult (adult). Summary data, when shown, were computed from all animals.

A. Growth of the head and pinnae

Figure 1 replots from Tollin and Koka (2009) the linear measurements of head diameter AB and outside pinnae height 1-2 as a function of age in weeks for 16 cats starting at 1.3 weeks. The horizontal lines represent the mean and 99% confidence interval for these values in 12 adults (>52 weeks). To quantify the growth rate a three-parameter exponential rise to maximum function was fitted to the data of the form $y = y_o + a(1 - e^{-bx})$, where x is age in weeks, y_o is the extrapolated dimension at birth (0 week), a is the amount by which that dimension increases during development, ($y_o + a$) is the asymptotic value at full development, and b is the rate of growth. This equation accurately characterized the growth of each dimension (based on F -test $p < 0.0001$ for all fitted equations; correlation coefficients r are reported in the figure). The fitted parameters of the equations are shown in each panel in Fig. 1.

Based on the fitted growth curve, head diameter more than doubled increasing from 28.6 at birth to 62 mm, reaching 90% of adult value by 23 weeks. In contrast, the growth of the pinnae was much more rapid. Outside pinnae

FIG. 2. (Color online) Spatial distributions of ILD for seven frequencies (upper right, right column) in three animals aged 1.3 weeks, 5 weeks, and adult. Maximum ILD for each animal and each frequency is indicated at the upper left-hand side of each plot. Color bar (bottom) indicates the ILD in decibels.

height 1-2 increased from 14.6 to 48.4 mm, reaching 90% at 16 weeks. Bodyweight (not shown) increased from 0.2 ± 0.06 kg at ~ 1.5 weeks and asymptotes at 2.6 ± 1.1 kg by ~ 18 weeks.

During development, the dimensions of the head and pinnae were highly and significantly correlated with the weight and age of the animal (mean $r^2 = 0.91 \pm 0.05$, $n = 15$ pairwise comparisons), as expected because both structures were increasing in size. Tollin and Koka (2009) also reported that even in a group of 18 adults significant correlations were found: Outside pinna height 1-2 was significantly correlated with weight ($p < 0.01$), but the head diameter AB was not. We did not track gender differences in development because the five males in the study were utilized for the acoustical measurements at very young ages.

B. Development of the ILD cues

1. Spatial distributions of ILDs

The difference between right and left ear DTF gains results in the ILD spectra. ILD cues varied with frequency and source location and with the age of the animals. Positive and negative ILDs indicate higher DTF gain for right and left ears, respectively. Figure 2 shows the spatial distributions of ILD cues computed from 1 to 20 kHz (upper right of right-hand column) in animals at three different ages: 1.3 and 5 weeks and adult. Frequencies higher than ~ 20 kHz produced complicated plots of ILD. The plots have been appropriately normalized so that they all use a common scale to indicate the value of the ILD (Fig. 2, bottom, color bar). The maximum ILD for each animal and each frequency is indicated at the upper left-hand side of each plot. Two major developmental trends are apparent regarding ILD for any source location. First, for a given age, the maximum ILDs tended to increase with increasing frequency. Second, for a given frequency, maximum ILDs increased with animal age.

FIG. 3. (Color online) Spatial and frequency distributions of ILDs along the horizontal plane (0° elevation) for animals aged 1.3 weeks (C), 10 weeks (B), and adult (A). [(D)–(F)] ILD spectra (ILD vs frequency) for a source at 90° azimuth for the same animals in (A)–(C). Predicted ILD based on a spherical head model with an adult head diameter as input (dashed line). Solid line indicates a constant 10 dB ILD, which was the maximum ILD observed for the youngest animal in panel (F). (G) ILD spectrum at 90° azimuth for animals aged 1.3 weeks through adult.

2. Spatial and frequency distributions of ILDs along the horizontal plane

Spatial plots such as those shown in Fig. 2 are difficult to interpret over fine spatial position and frequency increments. Because the ILD is likely to be most useful as a cue to sound location for sources varying in azimuth, Fig. 3 plots the ILD as a joint function of frequency and source azimuth for sources along the horizontal plane (i.e., 0° elevation). These functions are shown for animals of three different ages: 1.3 (C) and 10 (B) weeks and adult (A). Regardless of age, ILDs are a complex function of azimuth and frequency. At low frequencies, ILDs vary little with azimuth while at high frequencies ILDs can vary by as much as ± 35 – 40 dB in adults. Two general trends were observed in Figs. 3(A)–3(C). As the animals aged, for a given frequency, the ILDs increased in magnitude [note the change in the scale of the z -axis in panels (A)–(C)]. Moreover, the ILD vs azimuth functions as a whole shifted toward lower frequencies.

To show these two points more clearly, Figs. 3(D)–3(F) show the ILD spectra (i.e., ILD vs frequency) for one location ($+90^\circ$) for the three different aged animals. Figure 3(F) shows data for the 1.3 week animal. Over the range of frequencies plotted, the maximum ILD at 1.3 weeks for this source location was only ~ 10 dB, which occurred first at a frequency of ~ 10 kHz. In each plot of the ILD spectrum for the animals of different ages [(D)–(F)] this value of ILD (10 dB) is indicated by a horizontal line. A 10 dB ILD is also approximately the ILD at which the ILD-vs-frequency functions show an inflection and begin to rise substantially above the relatively flat ILD-vs-frequency relation for low frequencies [see adult data in Fig. 3(D)]. Also plotted in these figures [(D)–(F)] is the ILD spectrum at an azimuth of 80° computed from a spherical head model (Duda and Martens, 1998) with an adult-sized head radius taken from Fig. 1(A) (32 mm). An azimuth of 80° instead of 90° was chosen for this comparison because 80° in the spherical head model yielded large

ILDs vs azimuth and frequencies compared to 90° (at 90° the maximum ILD in the head model over the frequency ranges plotted in Fig. 3 was ~6 dB). Moreover, the developmental trends apparent in the empirical ILD spectra differed little between azimuths of 80° and the 90° plotting in Fig. 3 (see discussion for rationale behind choosing 90° for this analysis). The absolute maximum ILD for any frequency and azimuth in the spherical head model was also produced for an azimuth of 80°, which was 22 dB at 22.8 kHz. Figure 3(E) shows the ILD spectrum for a 10 week old. Here the ILD magnitudes for most frequencies have increased substantially relative to the 1.3 week old. Additionally, the lowest frequency at which the ILD surpasses the 10 dB mark as shown in Fig. 3(F) was shifted toward a lower frequency, 4 kHz, than that in the younger (and smaller) animal. Finally, in an adult animal [Fig. 3(D)], the ILDs increased more and were shifted to even lower frequencies (2.5 kHz). Note that for the adult animal, over the frequency range up to 20 kHz, the head by itself (according to the spherical head model) does not produce much ILD ($< \sim 15$ dB). Rather, the increase in the magnitude of the ILDs and the frequency ranges over which substantial ILDs occur (> 10 dB) appear to result entirely from the development of the size of the pinnae. Finally, Fig. 2(G) summarizes the development of the ILD cue as a function of age and frequency for a source at 90° azimuth showing the general increase in ILD magnitude for a given frequency and the systematic shift of the ILD spectra toward lower frequencies. By the time the animals reached 16–22 weeks of age, the patterns of ILD vs frequency and azimuth were adult-like.

3. Development of the rate of change in ILD cues with changes in source azimuth

In addition to the development of the magnitude and frequency ranges of the ILD cue, another important attribute is the frequency-dependent rate of change in the ILD cues with changes in source azimuth, or the ILD-azimuth slope (in units of dB/deg). The rate of change in binaural cues such as ILD is an important determinant of spatial acuity, as typically assessed by behavioral measurement of the minimum audible angle (MAA) (Mills, 1958; Martin and Webster, 1987; Casseday and Neff, 1973; Huang and May, 1996). Here, the slopes of the ILD functions were computed as a function of frequency between $\pm 10^\circ$ about the midline (0° azimuth) for animals from 1.3 weeks through adult. This azimuth was chosen because ILDs vary most about this point and most psychophysical studies of sound location acuity are performed about 0° azimuth. Figure 4 shows the ILD slopes over a frequency range 3.5–16 kHz, which was the range where the slope was largest and varied most dramatically across ages. Also, the behavioral MAA in adult cats varies most substantially (e.g., both high and low MAAs) over this range (Martin and Webster, 1987; Casseday and Neff, 1973).

For comparison, the ILD slopes were averaged across 11 adult cats and the mean and associated 95% confidence intervals shown in Fig. 4. In the two youngest animals tested, 1.3 and 2.9 weeks, the ILD slopes were virtually flat over the frequency range plotted at ~ 0.2 dB/deg. As a comparison, the ILD slope computed from a spherical head model (Duda

FIG. 4. (Color online) Development of the ILD-azimuth slope (dB/deg) for sources $\pm 10^\circ$ about the midline. The mean and associated 95% confidence interval for 11 adults are indicated by the filled circles and error bars, respectively. Data corresponding to animals of different ages (in weeks), respectively, are indicated by the parameter. The dashed line indicates the slope of the ILD based on a spherical head model with an adult head diameter as input.

and Martens, 1998) with an adult head radius (32 mm) is shown (dashed line). As the animals aged, the ILD slopes showed a region of dramatic increase between 6 and 16 kHz. The frequency at which the local maximum of the ILD slope occurred decreased systematically with age, being ~ 16 kHz at 2.9 weeks and ~ 10 kHz by adulthood. As with the magnitude of the ILD in Fig. 3, the ILD slope reached adult values by 16–22 weeks, as indicated by slope values falling consistently within the 95% confidence intervals of the adult slopes.

4. Growth of the pinnae contributes to the increase in magnitude and frequency range of ILDs

In both Figs. 3(D)–3(F) and 4 estimates of ILDs and their slopes are plotted, respectively, from a spherical head model (Duda and Martens, 1998). It is clear in both data sets that the ILDs produced by a simple spherical head of an adult size cannot account for the large developmental changes in the magnitude of the ILDs and frequency ranges over which these ILDs are produced, at least over the frequency range examined here (up to 32 kHz). Aside from the head, the pinnae are the only other structures on the head that can account for these results.

We propose here that the pinnae, and not the head, are the most important factor in determining the ILD cues for location in small-headed mammals such as the cat because the head, by itself, cannot physically generate the large ILDs over the range of frequencies examined here. A direct test of this hypothesis would involve carefully removing the pinnae from both ears and repeating the measurements of ILD in a “head-only” condition. This was done in only one animal (see Fig. 7 in Tollin and Koka, 2009), so the results cannot be related to the developmental increase in size of the head and pinnae. As an alternative test, we assessed which aspect of developmental growth, head diameter [AB in Fig. 1(A)] or pinnae height [1–2 in Fig. 1(B)], could account for the most variance in the ILD data. Figure 5(A) plots the frequency at which the ILD first exceeded 10 dB at a location of 90° azimuth (0° elevation), as plotted in Figs. 3(D)–3(G), as a

FIG. 5. (A) Frequency where the ILD cue first reached 10 dB for a source at 90° azimuth [as in Figs. 3(D)–3(G)] as a function of head radius (circles) and outside pinnae height (triangles). Solid lines indicate the linear regression through the respective data points. The correlation coefficients are also indicated for the regression. (B) Partial correlation of the ILD metric and pinnae height with the contribution of head radius held constant. (C) Partial correlation of ILD metric and head radius with the contribution of pinnae height held constant. In (B) and (C) the solid line indicates the linear regression and the associated correlation coefficient is shown.

function of both head diameter and outside pinnae height. This ILD factor was significantly correlated with both head $r = -0.859$, $p < 0.0001$, and $n = 14$) and pinnae ($r = -0.9046$, $p < 0.0001$, and $n = 14$) dimensions. In both cases, as the head and pinnae increased in size, the frequency at which the ILD reached 10 dB decreased systematically.

As pointed out by Tollin and Koka (2009), the developmental increase in the head and pinnae dimensions was highly and positively correlated. For the animals shown in Fig. 5, the correlation between pinnae and head dimensions (not shown) was highly significant ($r = 0.9311$, $p < 0.0001$, and $n = 14$). To control for this confounding correlation, we computed the partial correlations (Hays, 1988) to examine

which of these two factors, head or pinnae growth, explained the most variance in the development of ILD. Figure 5(C) shows that when the contribution of the pinnae size was held constant, the partial correlation between the ILD factor (i.e., the lowest frequency at which the ILD just reached 10 dB) and head radius, both of which were corrected for their respective correlations with pinnae size, no longer reached significance ($r = -0.11$ and $p = 0.73$). The partial correlation of the ILD factor and head diameter adjusted for pinnae height is simply the correlation between the residuals from regressing ILD on pinnae height and the residuals from regressing head diameter on pinnae height [Fig. 5(C)]. Thus, when the correlation with the pinnae size was factored out, the increase in head diameter alone accounted for $\sim 1\%$ ($r^2 = 0.012$) of the variance in the ILD factor. On the other hand, when the contribution of head size was held constant, the partial correlation between the ILD factor and outer pinnae height (both corrected for their correlations with head radius) was significant and negative ($r = -0.56$ and $p = 0.046$). The partial correlation of ILD and pinnae height adjusted for head diameter is the correlation between the residuals from regressing ILD on head diameter and the residuals from regressing pinnae height on head diameter. In other words, as the pinnae height increased during development, the frequency at which the ILD reached 10 dB (at 90° azimuth) decreased systematically. The pinnae size, by itself, accounted for $\sim 31\%$ of the variance in this particular aspect of ILD during development, while the increasing head size accounted for virtually none. Thus, the hypothesis that the increasing pinnae size, and not the increasing head size, was responsible for the increasing magnitudes of ILDs and the frequency range of substantial ILDs (> 10 dB) during development over the frequency range examined here (up to 32 kHz) was supported.

C. Development of the ITD cue

1. Spatial distributions of ITDs

Figure 6(A) shows the spatial distributions of the low-frequency (< 3.5 kHz) ongoing ITDs in animals aged 1.3 and 5 weeks and adult. As expected, the ITDs increased with changes in source azimuth away from the midline, but were relatively constant with changes in elevation for a given azimuth. For any one azimuth, the magnitudes of the ITDs also increased with animal age. To show this more plainly, Fig. 6(B) shows the ITD as a joint function of both azimuth along the horizontal plane (0° elevation) and animal age, for animals aged 1.3 weeks through adult. For source locations at the poles ($\pm 90^\circ$ azimuth), the magnitude of the ITDs increases systematically with animal age. Although it is known that ongoing ITDs vary as a function of frequency in cats (Roth *et al.*, 1980), as predicted by the spherical head model of Kuhn (1977), this particular aspect was not investigated in this paper.

It was expected that as the head radius increased during development, the magnitudes of the ITDs would systematically increase. As one way of testing this hypothesis, Fig. 6(C) plots the maximum ITD as a function of the head radius. Maximum ITDs increased systematically from ~ 170 to

FIG. 6. (Color online) (A) Spatial distributions of the ITD for animals aged 1.3 weeks, 5 weeks, and adult. (B) ITD as a function of source azimuth along the horizontal plane (0° elevation) for animals aged 1.3 week through adult (age given by the parameter). (C) Maximum ITD as a function of head radius ($n=20$). Shaded region indicates ranges of ITD and head radius in adults. Solid line indicates the linear regression of maximum ITD on head radius; the associated correlation coefficient is also shown.

nearly $400 \mu\text{s}$, a factor of 2.35, as the head radius increased from 16 to 38 mm, a factor of 2.38. The linear regression of maximum ITD on head diameter was significant ($r=0.965$, $p<0.0001$, $y=9.76+34.4x$, and $n=20$). As expected, head size was directly correlated with the magnitude of the ITD cue to source location. This is tested more directly in Sec. III C 3.

2. Development of the rate of change in ITD with changes in source azimuth

As with ILD above, one important characteristic of the ITD cue as it pertains to psychophysical sound location acuity is the rate of change in the ITD cue with changes in source azimuth, the ITD-azimuth slope (in units of $\mu\text{s}/\text{deg}$). Figure 7(A) plots the ITD vs azimuth slope computed from $\pm 30^\circ$ around 0° azimuth for 11 infants and juveniles (ages 1.3–22 weeks) and 9 adults. The mean ITD slope and asso-

FIG. 7. (A) Development of the ITD-azimuth slope ($\mu\text{s}/\text{deg}$) as a function of age in weeks. Solid and dashed horizontal lines indicate the mean and 95% confidence interval of the ITD-azimuth slope based on measurements in nine adults. Curved line corresponds to the fitted function of the form given in the upper left. (B) Development of the ITD-azimuth slope as a function of head radius. Horizontal lines as in (A). Solid line indicates the linear regression of the ITD-azimuth slope on head radius; the corresponding correlation coefficient is indicated.

ciated 95% confidence interval for the 11 adults are shown as the solid and dashed lines, respectively, in Fig. 7(A). ITD slope increased from 2.4 to $4.7 \mu\text{s}/\text{deg}$ from 1.3 weeks of age through adult. The ITD slope about the midline increased by a factor of ~ 2 , which is comparable to the factor by which head diameter (or radius) increased during development. A three-parameter exponential rise to maximum function of the form shown in the inset of Fig. 1(A) was fitted to the ITD slope vs age data with the exponent of the function fixed to the same value as that for the function describing the growth of the head in Fig. 1(A) (-0.1). The fit of this function was significant ($r=0.93$, $p<0.0001$, F -test) with the parameters shown at the top-left of Fig. 7(A). The youngest age at which the fitted function first surpasses the 95% confidence interval for the adult data (lower dashed line) was 23 weeks.

The magnitude of the ITD for a given azimuth increased with head radius as shown in Fig. 6(C), so the slopes of the ITD-azimuth functions were also expected to increase with radius. To show this, Fig. 7(B) replots the development of the ITD slope as a function of the associated head radius. The linear regression of ITD slope on radius was significant ($r=0.94$, $p<0.0001$, $y=0.45+0.125x$, and $n=20$). The smallest head radius at which the ITD slope first surpassed the lower

95% confidence interval for the adult data was ~ 31 mm (or a 62-mm diameter), which falls squarely in the range of adult head growth shown in Fig. 1(A). By ~ 23 weeks, the ITD-azimuth slope is adult-like.

3. Growth of the head and pinnae contributes to the developmental increase in the magnitude of ITDs

It is typically assumed that the magnitude of the ITD cue is determined directly by the interaural distance. Thus, the larger the separation between the two ears, as occurs during developmental growth of the head, the larger the ITD is presumed to be. However, in mammals such as cat, the length and physical size of the pinnae are also quite substantial. The height of the pinnae in adult cats is nearly the same as the head diameter [Figs. 1(A) and 1(B)]. Like the head, then, the pinnae also present as a substantial obstacle for the sound waves to propagate around, thus potentially increasing the effective diameter of the head. As such, the pinnae themselves may contribute to the magnitude of the ITD, as has been demonstrated recently by Koka *et al.* (2008) in the rat.

Figure 8(A) shows the maximum ITD as a function of head radius and outside pinnae height in 20 animals. In the analysis of the data in Fig. 8(A), we noticed that a single data point from one animal exerted a disproportionate influence on the regression results for both maximum ITD vs head radius and pinnae height. This data point (one for ITD vs head radius and one for ITD vs pinnae height) is shaded in Fig. 8(A). This single data point also disproportionately influenced the resulting partial correlation analyses below. For this animal, the measured maximum ITD was smaller than expected and both the head radius and pinnae height were larger than expected. We suspect that the head and pinnae sizes for this animal were overestimated. In the regression analyses, this data point produced standardized residual values (raw residual divided by the population standard error, Hays, 1988) that exceeded an absolute value of 2.5 indicative of an outlier. No other data point in any of the results in this paper produced such large standardized residuals. Because of the undue influence of this single data point, we removed this data point from subsequent analysis below. This data point did not overly influence any of the preceding analyses and was not omitted in those cases (i.e., omission would not have changed the overall results). After removal of the outlying data point, the linear regressions of maximum ITD on pinnae height ($r=0.943$, $p<0.0001$, and $n=19$) and head radius ($r=0.978$, $p<0.0001$, and $n=19$) were still significant.

To test the hypothesis that the head diameter was the primary determinant of the increasing ITDs during development, and not the pinnae height, a partial correlation analysis (Hays, 1988) was conducted with maximum ITD, head diameter, and pinnae height. Partial correlation analysis is necessary here because there was a significant positive correlation between head diameter and pinnae height (not shown) in the 19 animals measured for this test ($r=0.923$ and $p<0.0001$). When the contribution of the pinnae height was held constant, the partial correlation between the maximum ITD and head radius (both corrected for their respective correlations with pinna height) was positive and significant (r

FIG. 8. (A) Maximum ITD as a function of head radius (circles) and outside pinnae height (triangles). Shaded data points were outliers that were removed from subsequent analyses. Solid lines indicate the linear regression through the remaining respective data. The associated correlation coefficients are indicated next to the fitted function. Spherical head model for low-frequency ITDs of Kuhn (1977) based on head radius (dashed). (B) Partial correlation of maximum ITD and pinnae height with the contribution of head radius held constant. (C) Partial correlation of maximum ITD and head radius with the contribution of pinnae height held constant. In (B) and (C) the solid line indicates the linear regression and the associated correlation coefficient is shown.

$=0.84$ and $p<0.0001$). The partial correlation of the maximum ITD and head radius adjusted for pinna height is simply the correlation between the residuals from regressing maximum ITD on pinna height and the residuals from regressing head radius on pinnae height [Fig. 8(C)]. Increases in head radius accounted for only $\sim 71\%$ of the variance in the increase in maximum ITD during development. Interestingly, when the contribution of the head radius was held constant, the partial correlation between the maximum ITD

and the pinnae height (both corrected for their respective correlations with head diameter) also reached significance ($r=0.501$ and $p=0.034$). The partial correlation of the maximum ITD and pinna height adjusted for head radius is simply the correlation between the residuals from regressing maximum ITD on head radius and the residuals from regressing pinnae height on head radius [Fig. 8(B)]. Thus, pinnae height by itself accounted for $\sim 25\%$ of the variance in the increase in maximum ITD during development. Thus, when the two factors that were most likely to contribute to the increasing magnitude of the ITD cue during development were examined, both head diameter (or radius) and pinnae height emerged as determinants. Although maximum ITD was also highly correlated with animal weight ($r=0.916$, $p<0.0001$, and $n=19$) and weight was highly correlated with head radius ($r=0.944$, $p<0.0001$, and $n=19$) and pinnae height ($r=0.913$, $p<0.0001$, and $n=19$), the respective partial correlation analyses revealed no significant contribution to maximum ITD due to increases in animal weight ($r<0.4$ and $p>0.1$). In this latter case, the contributions of the head radius and pinnae height to the maximum ITD remained significant and comparable to that found above.

IV. DISCUSSION

A. Development of the linear dimensions of the head and pinnae

We studied the development of head and pinnae dimensions in cats beginning at 1.3 weeks after birth. Details are found in [Tollin and Koka, 2009](#). These results are discussed here in the context of the development of the binaural cues to location. The head and the pinnae increased in size during development. Based on the growth curves, head diameter [Fig. 1(A)] increased by a factor of 2.17, from 28.6 mm at birth to 62 mm in adults and reached 90% of adult value by 23 weeks. These compare favorably with values of 29 and 63.02 mm measured in 35 newborn ([Latimer, 1931](#)) and 54 adult female cats ([Latimer, 1936](#)), respectively. Head diameter in adult males averages 5.5% larger ([Latimer, 1936](#)). The growth of the pinnae dimensions was more rapid. Outside pinnae height 1-2 [Fig. 1(B)] increased by a factor of 3.31 from 14.6 to 48.4 mm, reaching 90% at 16.4 weeks. Body-weight (not shown) increased from 0.2 ± 0.06 kg at ~ 1.5 weeks and asymptoted at 2.6 ± 1.1 kg by ~ 18 weeks. Newborn weights in kittens average 0.15 ± 0.03 kg ($n=35$, [Latimer, 1967](#)).

Because the behavioral onset of hearing in cats is ~ 1.5 weeks ([Ehret and Romond, 1981](#); [Villablanca and Olmstead, 1979](#)), the acoustical and behavioral consequences of the increasing size of the head and pinnae are functionally relevant only for ~ 1.5 weeks and older. Beginning at 1.5 weeks instead of birth the average head diameter increased by a factor of 2 and the outer pinnae dimension 1-2 increased by a factor of 2.3.

The rate of growth of the pinnae (given by parameter b in the equations in Fig. 1) was 30%–70% greater than that of the head. As such, the pinnae reach adult dimensions sooner than the head diameter. The major dimension of the pinnae, the outside height, reached 90% of adult size by 16 weeks

while head diameter took 23 weeks to reach adult size. One implication of the rapid development of the pinnae is that the monaural acoustic transformations that are heavily determined by the pinnae, such as the spectral notches, the acoustic gain, and the acoustic axis, become adult-like before the acoustical transformations that depend on head diameter, such as the binaural cues to sound location discussed in this paper. The development of the monaural cues to sound source location in the cat were shown by [Tollin and Koka \(2009\)](#) to be mature by 16 weeks, consistent with the developmental growth of the pinnae.

B. Development of the pinnae dimensions contributes to the development of the ILD cues to location

To explore the hypothesis that the development of the pinnae dimensions determined the development of the ILD cue to location, Fig. 5 plotted one of the ILD metrics, the frequency at which the ILD reached 10 dB for a source at 90° azimuth (see Fig. 4). Although this metric is somewhat arbitrary, our purpose for this was to quantitatively capture the shift in the frequency range of ILD production during development. Although not shown here, comparable shifts were observed at locations between the midline and 90° . Analysis of the shift of the ILD functions along the frequency axis is similar to the frequency axis scaling studies of [Middlebrooks \(1999\)](#), [Schnupp et al. \(2003\)](#), and [Maki and Furukawa \(2005\)](#). [Moore and Irvine \(1979\)](#) demonstrated the shift in the frequency ranges of the ILDs cues from high to low during development of the cat for all azimuths tested, but the shifts were largest at 90° . Our results confirm their observation and this was one of our rationales for using 90° to make these measurements. The partial correlation analyses indicated that the growth of the pinnae accounted for $\sim 31\%$ of the variance in the development of this particular ILD metric, while the increasing head size accounted for virtually none. The results of this analysis along with the empirical observations that the various ILD metrics reached adult-like status by ~ 16 weeks fit with the empirical measurements of pinnae growth showing adult-like size and morphology by 16 weeks. 16 weeks also matches that necessary for the monaural acoustical cues, spectral notches, acoustical gain, acoustic axis, and ear canal resonance gain and frequency, to reach maturity ([Tollin and Koka, 2009](#)).

A spherical head model ([Duda and Martens, 1998](#)) was used here to isolate the frequency ranges and magnitudes of the ILD cue as the head diameter increased during development from the component of ILD cue development due to pinnae growth. Over the frequency range of interest in this paper (<32 kHz), a sphere of adult dimensions (32 mm radius) cannot generate the large ILDs of the magnitude measured here, particularly in the frequency ranges around ~ 10 kHz [see Fig. 3(D)] where the very largest ILDs were observed. We propose that the pinnae produced these large ILDs jointly through increases in acoustic gain by the pinnae ipsilateral to the source (re the gain due to just the sphere) and additional decreases (re simple spherical head shadow) due to the deep spectral notches produced by the pinnae contralateral to the source. [Tollin and Koka \(2009\)](#) showed that

the monaural acoustical gain increased systematically with the age of the cats, as well as pinnae size, and also moved from higher frequencies (~ 15 kHz for a 10 dB gain at 1.3 weeks age) toward lower frequencies (~ 5 kHz for a 10 dB gain in adults) similar to that observed here for ILD in Fig. 3. That this increased gain was due to the pinnae was shown by Tollin and Koka (2009) in one animal by comparing the monaural gains both before and after removal of the pinnae. The pinnae themselves produced an increase in gain of ~ 10 dB. The additional ipsilateral increase and contralateral decrease in gain contribute to the much larger ILDs than would otherwise be generated by a spherical head at these frequencies. One implication of large pinnae on small-headed mammals, then, may be to effectively shift the frequency range of substantial ILDs (>10 dB, see Fig. 3) toward much lower frequencies than would otherwise be the case without pinnae.

C. Development of the head and pinnae dimensions contributes to the development of the ITD cues to location

The maximum ITDs increased systematically from ~ 170 to nearly $400 \mu\text{s}$, a factor of 2.35, as the head radius increased from 16 to 38 mm, a factor of 2.38. As might be expected, head size was directly correlated with the magnitude of the ITD cue to source location [Fig. 6(C)]. In general, the development of the ITD cue took longer than the development of the ILD cue. For example, the ITD-azimuth functions shown in Fig. 6(B) indicate that ITDs were not in the adult range until sometime around 22 weeks. Also, a grouping of the maximum ITDs and associated head radii in adults [shaded area, Fig. 6(C)] indicates that the head radius of ~ 29 – 30 mm is required to reach adult-sized maximum ITDs of $310 \mu\text{s}$ or greater. Head radii of 29 – 30 mm are only achieved by ~ 22 – 23 weeks of age, on average [Fig. 1(A)]. Finally, the ITD-azimuth slope first falls within the adult range [dashed line, Fig. 7(A)] at 23 weeks and with a head radius of ~ 32 mm. The development of the ITD cue appeared to be influenced most by the development of the head diameter (or radius) and the ITD cue was mature by ~ 22 weeks.

While the hypothesis that head diameter dictates ITDs is clear, the hypothesis that the pinnae might determine a portion of the ITD has not received much attention. The role of the pinnae in ITD production has been investigated by Roth *et al.* (1980) in the cat and Koka *et al.* (2008) in the rat. The pinnae in many mammals, such as cats, rabbits, rats, and bats to name just a few, are quite large, with dimensions on the same scale as that of the diameter of the head. In support of this hypothesis, recent reports from our laboratory have demonstrated that the pinnae in the rat contribute substantially to the overall magnitude of the ITDs—removal of the pinnae reduced the ITDs in rats by $\sim 32\%$ – 36% (Koka *et al.*, 2008). Moreover, in the rabbit, systematic movements of the pinnae can produce quite substantial changes in the ITD cue (Bishop *et al.*, 2009).

Development of the maximum ITD was highly and significantly correlated with both head radius and pinnae height. Moreover, the growths of the head and the pinnae were

highly correlated during development, as expected. This latter correlation was controlled for in the examination of the growth factor that determined the maximum ITD by performing partial correlations analysis with maximum ITD, head radius, and pinnae height. Increasing head diameter by itself was found to explain $\sim 71\%$ of the variance in the developmental increase in maximum ITD. Moreover, increasing pinnae height by itself was found to explain $\sim 25\%$ of the variance in the developmental increase in maximum ITD. Thus, when the two factors that were most likely to contribute to the increasing magnitude of the ITD cue during development were examined, the increase in head diameter emerged as the primary determinant, but there was also a sizable contribution from the pinnae height. One explanation for the role of the pinnae in ITD production as suggested by Koka *et al.* (2008) is that a considerable portion of the pinnae and the distal parts of the auditory meatus in mammals such as the cat and rat that have ear canals formed from cartilage remains in the path of the sound. Thus, the pinnae may function to make the acoustically effective diameter of the head larger, thus increasing the magnitude of the ITD. Consistent with this hypothesis, the predicted maximum ITD based on the empirically measured head radii and the spherical head model of Kuhn (1977) for low-frequency ongoing ITDs was $\sim 23\%$ less than the empirically measured ITDs [see Fig. 8(A)]. This discrepancy may result from the increased ITD due to the pinnae.

D. Implications for physiological and behavioral development

These data have implications for the concomitant development of the acoustical cues to sound source location, the neural encoding of these cues, and their ultimate use by the animal for the perception of source location. Behaviorally, adult cats localize sounds quickly and accurately with performance nearing that of humans (Moore *et al.*, 2008; Tollin *et al.*, 2004; May and Huang, 1996; Populin and Yin, 1998). And even kittens can approach sounds by around 24 days of age, although with much less precision (Clements and Kelly, 1978; Olmstead and Villablanca, 1980; Villablanca and Olmstead, 1979). The ability of kittens to make overt orienting responses to sounds suggests that the basic organization of the binaural auditory system may be established early in development. But physiological (Pujol and Hilding, 1973) and simple behavioral (Ehret and Romond, 1981) responses to sound are seen much earlier, a few days after birth. The rough circuitry of the mammalian binaural system appears to be in place and largely functional even while the peripheral system is still developing. The apparent delay in behavioral directional responding might be related to a slower rate of development of the binaural hearing mechanism, the specific cues for location, or simply motor control.

An attractive hypothesis for the prolonged development of spatial hearing is that auditory experience early in life calibrates the neural circuits that process sound location to the exact acoustical properties of the head and ears of each individual (Moore and King, 2004). In the most compelling example of this, Knudsen *et al.* (1984a, 1984b) revealed a sensitive period early in development of the barn owl where

normal acoustical input to the two ears, and thus normal cues to source location, must be present for normal sound localization behavior to develop. The duration of this sensitive period was shown to be correlated with the time course over which the head and facial ruff (like pinnae) dimensions reach maturity, ~8 weeks (Knudsen *et al.*, 1984a). These studies revealed that owls reared with altered acoustical cues (e.g., ear plug) prior to 8 weeks were able to adapt and regain normal behavioral sound localization abilities despite the altered cues; however, when the cues were altered in owls after ~8 weeks no adaptation was found. Thus, for a period of ~8 weeks, the internal mapping of the ensemble of acoustical cues to location and spatial location itself remains plastic. For the most part, the underlying anatomical and neural mechanisms of binaural hearing in the barn owl exhibited a similar time course of plasticity (Knudsen, 1983, 1985).

To the extent to which a sensitive period for the development of sound localization in cats exists, our present data detail the developmental constraints on when the peripheral acoustical transformations reach maturity. Here, the binaural spectral (ILDs) and temporal (ITDs) transformations were found to reach maturity by 16 and 22 weeks, respectively. The developmental growth of the pinnae was found to determine the development of the ILD cues, which agrees with the developmental time course of the monaural cues (spectral notches, acoustical gain, acoustic axis, etc.) demonstrated by Tollin and Koka (2009). And the developmental growth of not only the head diameter, but also the pinnae height, was found to determine the development of the ITD cues. The corresponding time periods for binaural ILD and ITD cue maturities of 16 and 22 weeks are in line with the development of the dimensions of the pinnae [Fig. 1(B)] and head [Fig. 1(A)], respectively. We hypothesize that a sensitive period for the consolidation of sound localization in the cat for the monaural cues and the ILD cues to location will occur within 16 weeks. Because the head dimensions and the associated ITD cues to location do not reach maturity until ~22 weeks, the sensitive period may be somewhat prolonged for ITD sensitivity.

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