

SOUND PRESSURE TRANSFORMATION AT THE PINNA OF *MUS DOMESTICUS*

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Accepted 15 May 1995

Summary

Sound pressure transformation properties at the pinna of laboratory mice *Mus domesticus* were studied by measuring the sound pressure level of a continuous tone at a series of frequencies at the tympanic membrane as a function of the position of a sound source under free-field stimulation conditions. The spectral transformation, the interaural spectral difference, the isopressure contours and the interaural pressure difference contours were plotted. Sound pressure transformation functions showed some prominent spectral notches throughout the frequency range tested (10–80 kHz). However, the notch frequency did not appear to be systematically related to sound direction. The study of interaural pressure difference demonstrated that, when delivered from some angles within the ipsilateral frontal hemisphere, the sound pressure at the tympanic membrane of certain frequencies may be lower than that determined at the corresponding contralateral angles. For each sound frequency tested, there was an angle (the acoustic axis) within the ipsilateral frontal hemisphere from which the delivered sound reached a maximal pressure level at the tympanic membrane. However, the acoustic axis often changed to a

new angle after removal of the ipsilateral pinna. In addition, sound delivered from the acoustic axis did not always generate a maximal pressure transformation. The isopressure contours determined within 2–5 dB of the maximal pressure were circumscribed, and their contained angular areas were found to decrease with increasing sound frequency. The 2 dB maximal pressure area may appear at more than one angular area for some test frequencies. Removal of the ipsilateral pinna or modification of pinna posture expanded isopressure contours irregularly and split the 2 dB maximal pressure area into several parts. The sound pressure difference determined between the angles of maximal and minimal sound pressure (the maximal directionality) increased with sound frequency regardless of pinna posture. Acoustic gain of the pinna at the acoustic axis reached 6–12 dB, depending upon sound frequency. However, the pinna gain was not always maximal at the acoustic axis for a given frequency.

Key words: audition, directionality, mouse, *Mus musculus*, pinna, sound pressure transformation.

Introduction

In acoustically guided behavior, most mammals move their pinnae conjunctively or disjunctively during sound localization. While the head of an animal is a major source of reflections and diffractions in the sound field, the two pinnae are the most distinctive parts of that three-dimensional geometry (Roth *et al.* 1980). The deflections and reflections of sound by the pinna surface have been shown to affect both interaural time and pressure differences, which are the two main cues for sound localization along the horizontal plane, and to produce interaural spectral differences to localize sound in the elevational plane (van Bergeijk, 1962; Neti *et al.* 1992). Because of this, the directionality of sound pressure transformation at the pinna of an animal contributes importantly to the directional sensitivity of auditory neurons, which provide the neural basis for sound localization.

Previous studies have demonstrated that pinna posture affects the directional sensitivity of auditory neurons in bats (Grinnell and Grinnell, 1965; Jen and Sun, 1984; Sun and Jen, 1987), cats (Middlebrooks and Pettigrew, 1981; Aitkin *et al.* 1984; Middlebrooks and Knudsen, 1987) and possums (Aitkin *et al.* 1984). In addition, by measuring the sound pressure level with a probe microphone placed adjacent to the tympanic membrane or by measuring the amplitude of the cochlear microphonic as a function of sound direction, many studies have demonstrated that the pinna serves to amplify and transform the sound pressure level according to the location of the sound source. Furthermore, it has been shown that the pinna contributes to frequency-dependent sharpening of directionality when the wavelengths of sound are comparable to, or smaller than, the dimensions of an animal's head, pinna

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and ear canal (Flynn and Elliott, 1965; Wiener *et al.* 1966; Batteau, 1967; Fisher and Freedman, 1968; Harrison and Downey, 1970; Djupesland and Zwislocki, 1972; Gardner and Gardner, 1973; Shaw, 1974, 1982; Mehrgardt and Mellert, 1977; Moore and Irvine, 1979; Fuzessery and Pollak, 1985; Musicant *et al.* 1990; Phillips *et al.* 1982; Semple *et al.* 1983; Calford and Pettigrew, 1984; Moore *et al.* 1984; Palmer and King, 1985; Coles and Guppy, 1986; Carlile and Pettigrew, 1987; Jen and Chen, 1988; Guppy and Coles, 1988; Coles *et al.* 1989; Carlile, 1990a,b; Obrist *et al.* 1993; Rice *et al.* 1992; Samson *et al.* 1993).

In auditory research, the laboratory mouse has several advantages as an experimental model for human audition. For example, in addition to relatively modest initial and maintenance costs, this animal offers healthy populations with genetic uniformity, exhibits low between-subject variability and provides a subject of known age and environmental history at the time of research (Willott and Urban, 1978). In the past 25 years, over 700 published articles have described various aspects of the auditory system of the mouse (Henry and McGinn, 1992). Among them, numerous behavioral and electrophysiological studies have demonstrated that the mouse has a hearing range extending from 0.5 to 100 kHz with a maximal sensitivity at 15–16 kHz (Ehret, 1974, 1977; Markl and Ehret, 1973; Ehret and Moffat, 1985; Harnischfeger, 1978; Heffner and Masterton, 1980; Stiebler and Ehret, 1985). In addition, the postnatal hearing development of the mouse has been described (Brown, 1973; Ehret and Romand, 1992; Romand and Ehret, 1990; Sales and Smith, 1978; Willott and Shnerson, 1978). In contrast, only a behavioral (Ehret and Dreyer, 1984) and a recent electrophysiological study (McFadden and Willott, 1994) have been devoted to examining the sound localization ability of the mouse and the directional sensitivity of its auditory neurons.

The purpose of this study was to examine the contribution of the directionality of the pinna to the directional sensitivity of auditory neurons in the mouse. We used a small probe microphone to determine the sound pressure transformation functions at the pinna of the laboratory mouse *Mus domesticus* by measuring the pressure level of a series of sound frequencies at its tympanic membrane. We also examined the effect of pinna removal and variation of pinna posture on the sound pressure transformation functions.

Materials and methods

Ten adult mice *Mus domesticus* (body mass 29–37 g) were used for this study. The measurement procedures were the same as in a previous study (Jen and Chen, 1988). The body of each dead mouse (killed by asphyxiation with CO₂) was positioned on the edge of a 71 cm high steel table inside a custom-built sound-attenuated room. The inter-tragus distance, the inter-pinna-tip distance and the dimensions of the pinnae were measured to the nearest mm with calipers. The ceiling and inside walls of the room were covered with 0.076 m (3") convoluted polyurethane foam to reduce echoes. The head of

the mouse was extended from the edge of the table and was supported ventrally by cardboard such that the dorsal head, including the pinnae, was free from any obstruction. The head of each mouse was oriented such that the intersection of the interaural axis and medial plane was aligned towards 0° in azimuth and 0° in elevation of the loudspeaker position. The snout of each mouse was inclined about 5° downwards. All supporting structures were placed 25–35 cm behind the mouse and were covered with absorbent cotton and cheesecloth to reduce echo reflection.

Under these conditions, when a 1/4" microphone (Brüel & Kjaer 4135) was placed beside a loudspeaker which delivered a 50 kHz, 112 dB SPL sound towards the wall, echoes, if any, were indistinguishable from the background noise. The distance between the loudspeaker and the wall was 73 cm. The same sound was also delivered along the horizontal plane from the loudspeaker placed at the front, and 30°, 60° and 90° contralateral and ipsilateral, to the mouse ear. When the microphone was placed at the mouse ear and was pointed towards the supporting structures, echoes were less than 1–2 dB. However, considering the fact that this reflection came from behind the mouse and given the forward position of the mouse pinnae, the effect of such reflection on the observed responses was minimal and negligible.

Continuous pure tones were generated from a function generator (Krohn-Hite model 1200 A) and fed into a decade attenuator (Hewlett Packard 350D) before being led to a power amplifier and broadcast from a small condenser loudspeaker (AKG model CK 50). To monitor the sound pressure at the tympanic membrane of a mouse, a 1/4" microphone (Brüel & Kjaer 4135) with a custom-built plastic probe adaptor containing an extended tube (see Jen and Chen, 1988) was inserted through a small hole (approximately 1 mm diameter) made on the ventroposterior wall of the bony meatus near the tympanic membrane of each mouse. Insertion of the probe microphone was practised on several mice in order to identify the appropriate point for insertion along the bony meatus. The tympanic membrane was visible under the microscope through the hole made at this point. When the probe microphone was inserted through this hole and advanced for 1.5 mm, the tip of the extended tube was at the tympanic membrane. The sound pressure recorded by the microphone was determined using a measuring amplifier (Brüel & Kjaer type 2607).

After insertion of the probe microphone through the small hole, the elastic bony meatus sealed around the probe to provide a snug fit. In addition, the hole was sealed with Vaseline petroleum jelly to prevent any possible leakage of sound energy around the outside of the probe. In order to ensure that each time the tip of the probe adaptor was positioned at the tympanic membrane and that the probe position remained unchanged during manipulation of the pinnae, the microphone was secured by means of Permoplast, a firm but malleable putty-like material. Post-experiment dissection on each mouse head confirmed that the probe tip was located at the tympanic membrane.

The sound pressure transformation function was studied by

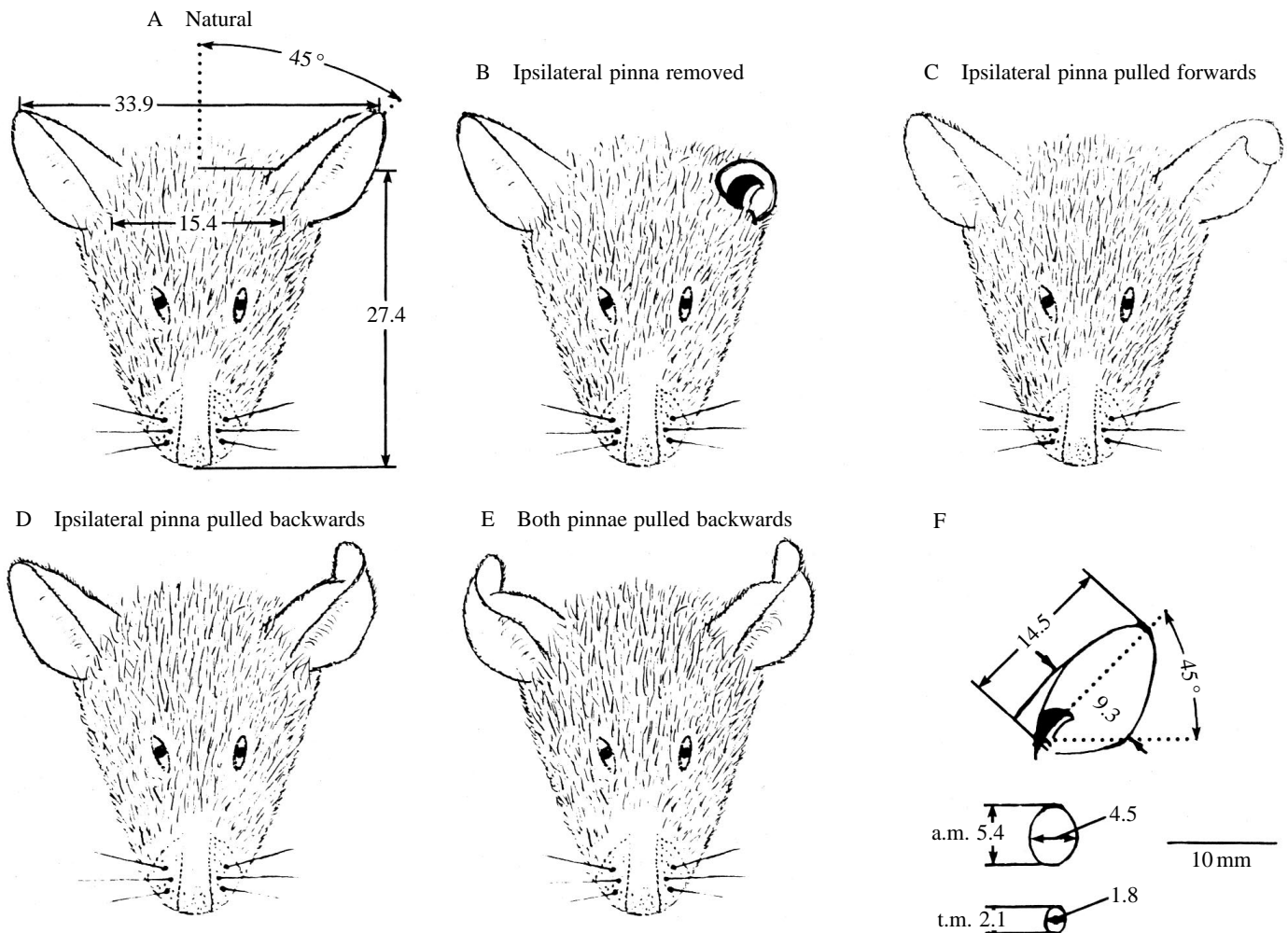


Fig. 1. Sketches of the head of *Mus domestica* showing frontal (A–E) and lateral (F) views of the scoop-shaped pinna flange and the different pinna postures and conditions used for determining the directionality of sound pressure transformation in this study. The mean dimensions of the pinna, external auditory meatus (a.m.) and tympanic membrane (t.m.) are also shown (in mm). The ipsilateral pinna is the pinna ipsilateral to the inserted probe microphone (see text for details).

measuring the sound pressure of continuous pure tones of six test frequencies (10, 20, 40, 60, 70, 80 kHz) delivered from the loudspeaker, which was attached to a 24 cm long aluminum arm and was positioned at 10° increments within $\pm 60^\circ$ in elevation and $\pm 90^\circ$ in azimuth of the frontal hemisphere by means of two servomotors. In addition, the sound pressure of a continuous tone was determined at frequency intervals of 0.5 or 1.0 kHz between 10 and 80 kHz when the loudspeaker was placed at 11 selected positions ($0^\circ, 0^\circ$; 30° and 50° lateral; $0^\circ, 30^\circ$ up and down; 50° lateral, 30° up and down). These laborious manual measurements provided information about the sound pressure transformation of the mouse pinna with a good frequency resolution at these 11 angles. The position of the loudspeaker was monitored using a calibrated oscilloscope outside the sound-attenuated room.

For the six selected sound frequencies, sound pressure transformation functions were studied when both pinnae were in a natural posture (Fig. 1A), with the ipsilateral pinna (relative to the inserted microphone) removed (Fig. 1B), with

the ipsilateral pinna pulled slightly forwards (by means of a small loop of thin thread stitched to the tip of the pinna; Fig. 1C), with the ipsilateral pinna pulled backwards (Fig. 1D) and with both pinnae pulled backwards (Fig. 1E). On the basis of these studies, isopressure contours were drawn for each sound frequency by determining the boundary where the sound pressure was attenuated by 2, 5, 10, 15, 20 and 30 dB from the maximal sound pressure measured. For convenience, these boundaries are referred to as 2, 5, 10, 15, 20 and 30 dB isopressure contours. The angular areas enclosed by these isopressure contours are referred to as 2, 5, 10, 20 and 30 sensitive areas (SAs).

Results

The shape and dimension of the pinna

The frontal and lateral views of the scoop-shaped pinna flange relative to the head of the mouse are shown schematically in Fig. 1. At the two sides of the head, the two

symmetrical pinnae angulated 45–47° posterolaterally, with the pinna mouth oriented outwards. The mean interaural distance was 15.4 ± 0.91 mm (mean \pm s.d., $N=4$) and the mean inter-pinna-tip distance was 33.9 ± 1.05 mm. The mean distance between the edge of the snout and the top of the head was 27.4 ± 0.16 mm (Fig. 1A). From the lateral view, the mean length and the widest width of the pinna were 14.5 ± 0.33 and 9.3 ± 0.08 mm (Fig. 1F). The mean size of the oval-shaped external mouth of the auditory meatus (a.m.) was 5.4 ± 0.37 mm \times 4.5 ± 0.2 mm and the mean size of the a.m. at the tympanic membrane (t.m.), where the tip of the probe microphone was located, was $2.1 \pm 0.02 \times 1.8 \pm 0.04$ mm.

Sound transformation spectra at the right and left pinnae

We first measured the sound pressure at the tympanic membrane of a series of test frequencies at 0.5 kHz intervals between 10 and 80 kHz. Sound pressures for the same series of frequencies were then remeasured after careful removal of the mouse, keeping the probe microphone at the same position. The difference between the two sets of measurements was taken as the sound transformation spectrum at the pinna.

Fig. 2 shows the sound spectra of a frontal sound (delivered from 0°, 0°) determined at the free field (Fig. 2Ai,ii) and at the tympanic membrane of the left and right ears (Fig. 2Bi,ii) of a mouse. In spite of few minor differences, the overall sound spectra monitored at the free field and at the tympanic membrane of both ears are very similar. We believe that the few minor differences between the two sound spectra curves are probably due to the extreme difficulty in placing the probe microphone in the exact mirror image positions at the tympanic membranes of both ears. This is evident from the fact that curves Fig. 2Aii,Bii are slightly higher than curves Fig. 2Ai,Bi. Conversely, the similarity of the two curves is probably due to the symmetry of both pinnae. This pinna symmetry also contributed to the similarity of the sound transformation spectra of both pinnae (Fig. 2Ci,ii; obtained by calculating the difference between Fig. 2Ai and Bi; Fig. 2Aii and Bii). Fig. 2Di,ii shows another example of the similarity of sound transformation spectra at the two ears, in this case when the sound was delivered from 0° and 30° contralateral to each microphone-inserted ear. Fig. 3 shows the sound transformation spectra at the right pinna of two mice determined with a sound delivered from different azimuthal (Fig. 3A,B) or elevational (Fig. 3C,D) angles.

From Figs 2 and 3, three main conclusions can be drawn. First, the sound spectra and the sound transformation spectra determined for the right and left pinnae are very similar. Second, there are several spectral notches in the sound transformation spectra. However, the number of spectral notches and the notch frequency do not appear to be closely correlated with the sound direction. Instead, the first few spectral notches appear always to occur at similar frequencies, in contrast to a previous study in cats (Musicant *et al.* 1990). Third, whereas a positive pressure relative to free-field measurements was obtained for most test frequencies when the

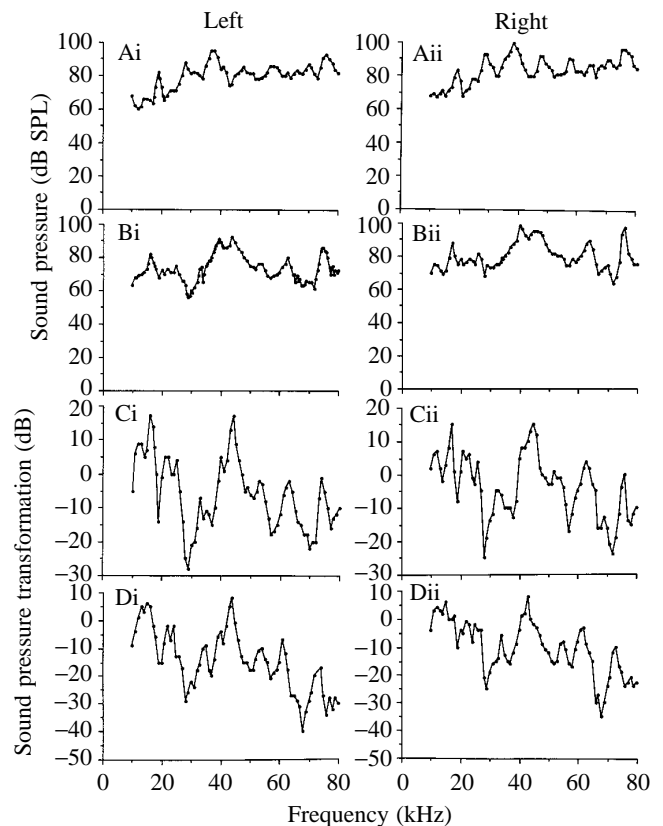


Fig. 2. The sound pressure of continuous tones of different frequencies monitored at the free field (Fig. 2Ai,ii) and at the left (left panel) and right (right panel) tympanic membranes of a mouse (Fig. 2Bi,ii). The sound was delivered from the front (0°, 0°) and its frequency was incremented by 0.5 kHz between 10 and 80 kHz. (Ci,ii) The sound transformation spectra at each pinna obtained by subtracting Ai,ii from Bi,ii, respectively. (Di,ii) The sound transformation spectra at each pinna when the sound was delivered from 0° and 30° contralateral to the microphone-inserted ear (the sound spectra monitored at the free field and at the tympanic membrane for this loudspeaker position are not shown).

loudspeaker was placed at ipsilateral angles, a negative value was obtained for certain frequencies (Fig. 3D).

Interaural spectral difference

As a sound was delivered from different angles around the head of a mouse, the sound pressure at the tympanic membrane changed accordingly because of the shadowing effect of the head and pinna. This shadowing effect can be examined by calculating the interaural spectral difference and interaural pressure difference (IPD).

Because of the symmetry of the two pinnae and the similarity of the sound transformation spectra at the two ears, together with the extreme difficulty in placing the probe microphone at the same position in each ear, we studied the interaural spectral difference by simply calculating the difference in sound pressure determined at the mirror image angles of the ipsilateral and contralateral frontal hemispheres. That is, the pressure measured for a sound delivered from a

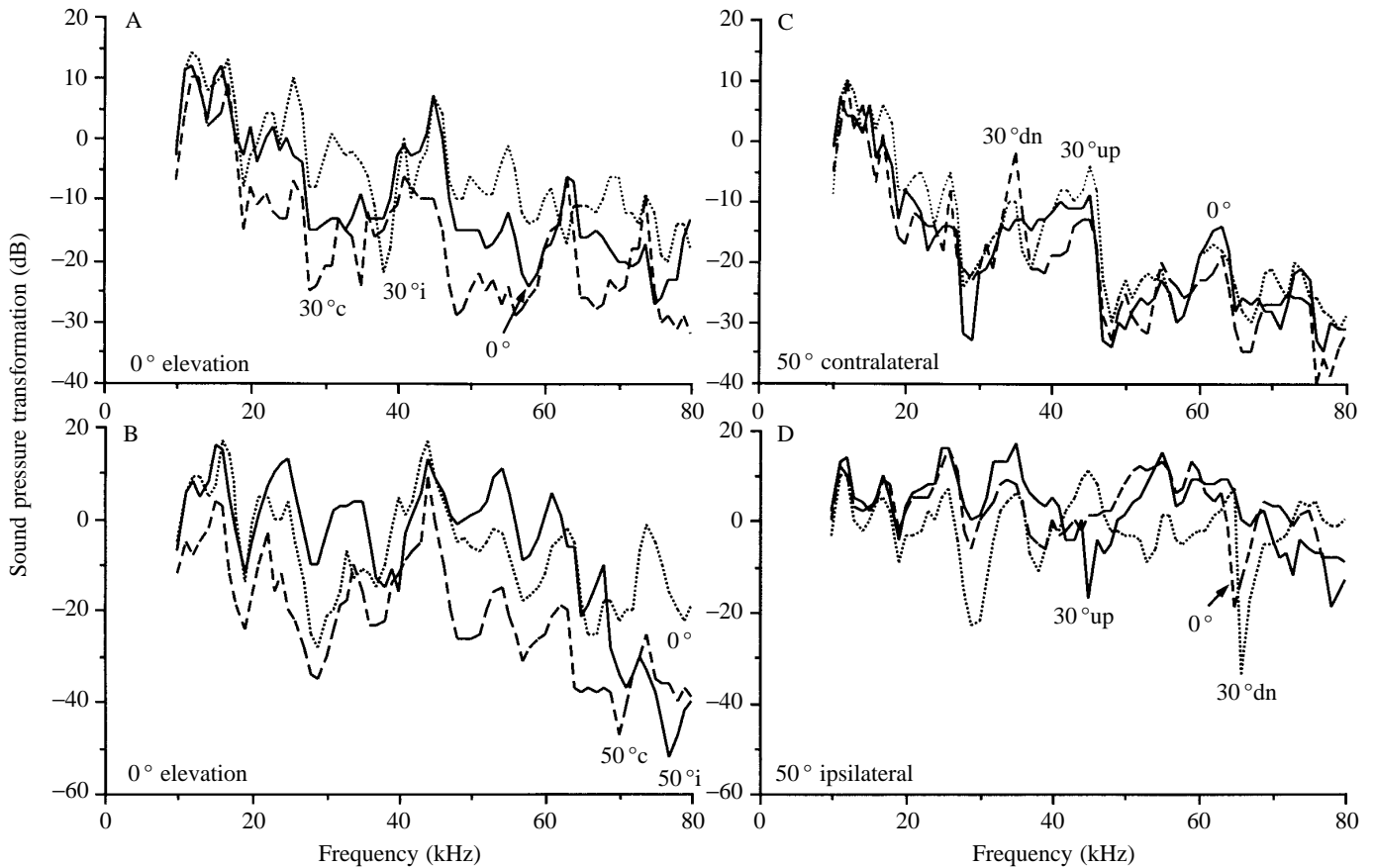


Fig. 3. Sound pressure transformation spectra at the right pinna of two mice determined using a sound delivered from same elevation (shown at the lower left corner of each spectrum) but at different azimuthal angles (indicated at each curve of A and B) or from the same azimuth (shown at the lower left corner of each spectrum) but at different elevational angles (indicated at each curve of C and D). All abbreviations (i, ipsi; c, contralateral; dn, down) refer to the direction of the sound, which was delivered at an angle that was at ipsilateral, contralateral, upper and lower portions of the frontal hemisphere relative to the microphone-inserted ear (see text for details).

contralateral angle is subtracted from that measured for the same sound delivered from the corresponding ipsilateral angle.

As shown in Fig. 4, the prominent spectral notches contained in the sound transformation spectra (e.g. Figs 2Ci,ii,Di,ii, 3) were also found in the interaural spectral difference. Although the interaural spectral difference varies with sound frequency, the size of this difference does not increase systematically with increasing frequency. In addition, the pressure of some sound frequencies measured for the ipsilateral ear can be lower than that measured for the contralateral ear, thus generating a negative interaural sound pressure difference for these sound frequencies. Furthermore, the sound frequencies at which such negative interaural pressure differences occur varied with sound direction. These observations are consistent with a previous study on cats (Musicant *et al.* 1990).

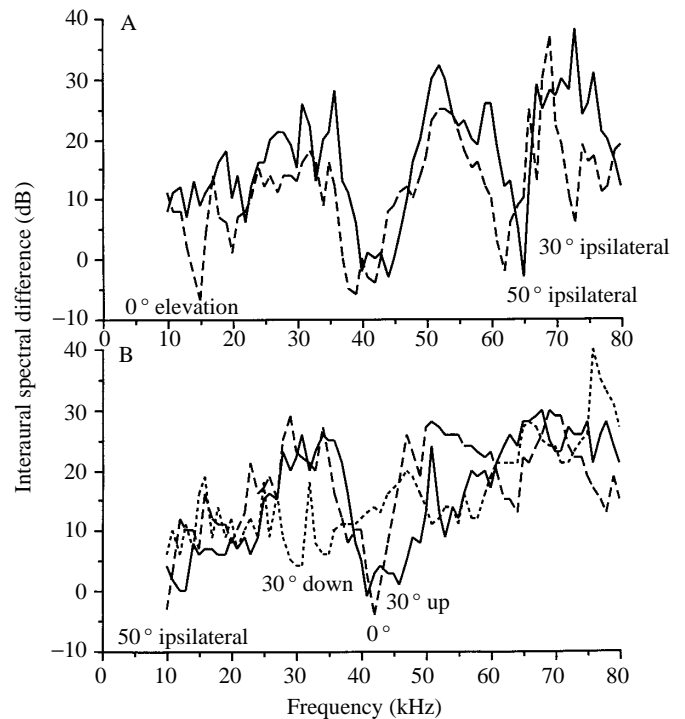


Fig. 4. The interaural spectral difference of two mice determined using a sound delivered from the same elevation (0°) but at two different azimuths (indicated below each curve in A) or from the same azimuth (50° ipsilateral) but at three different elevations (indicated below each curve in B) (see text for details).

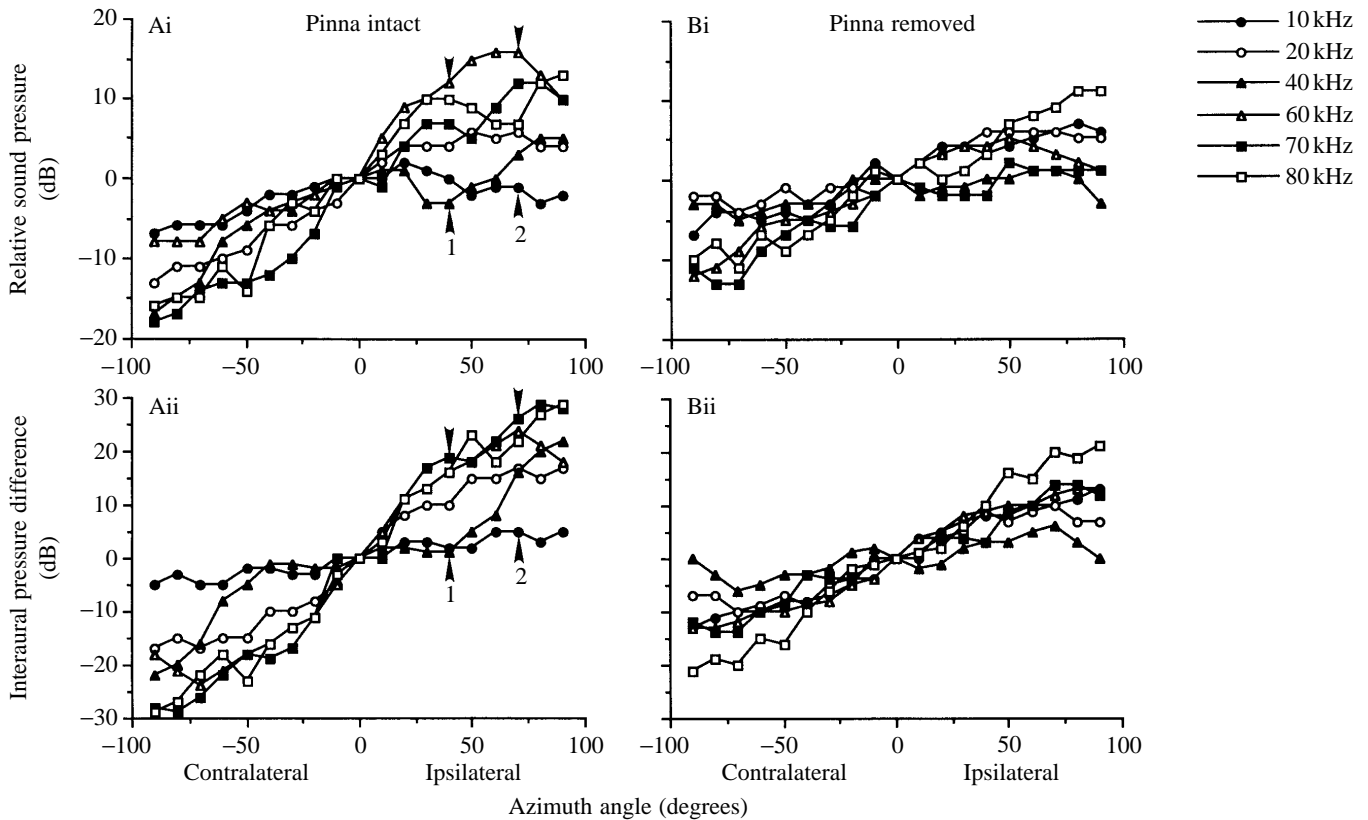


Fig. 5. Average sound pressure transformation curves of 10, 20, 40, 60, 70 and 80 kHz sounds showing the shadowing effect of the head and pinna of *Mus domesticus*. These curves were determined when both pinnae were in the natural posture (Ai,ii) and when the pinna ipsilateral to the microphone-inserted ear was removed (Bi,ii). In Ai and Bi, the ordinates represent the sound pressure monitored at each azimuthal angle (shown in the abscissa) relative to that monitored at the front (0° azimuth, 0° elevation). The interaural pressure differences (IPDs) as a function of azimuthal angles for the same six frequencies determined under these two pinna conditions are shown in Aii (pinna intact) and Bii (pinna removed). The ordinates and abscissae represent IPDs in dB and azimuth in degrees. All curves determined with different frequencies are shown using different symbols (shown at the far right). Contralateral or ipsilateral, azimuthal angles contralateral or ipsilateral to the microphone-inserted ear (see text for details).

Interaural pressure difference in the horizontal plane

We also studied the effect of head shadowing by determining the IPDs for a single sound frequency along the horizontal plane. We first measured the sound pressure at the tympanic membrane of one ear when the sound was delivered from different azimuthal angles. We then calculated the difference in sound pressure at each angle relative to that measured at the front ($0^\circ, 0^\circ$) for each sound frequency, and its sound pressure transformation curve was drawn. This study was conducted on two mice when their pinnae were in a natural posture (Fig. 5Ai) and when the pinna ipsilateral to the microphone-inserted ear was surgically removed along the rim of the entrance of the external auditory meatus (Fig. 5Bi).

As expected, the sound pressure for each test frequency was higher for a sound delivered from ipsilateral angles than from contralateral ones. It was also higher when both pinnae were intact than when the ipsilateral pinna had been removed (compare Fig. 5Ai and Fig. 5Bi). IPD curves were obtained by inverting the curves in Fig. 5Ai,Bi along the ordinate and calculating the difference between the original and the

inverted curves. The IPD curves for all six frequencies were drawn by connecting the IPD at each azimuthal angle (Fig. 5Aii,Bii).

As reported in a previous study (Musicant *et al.* 1990), the IPDs generated by high-frequency sounds were not always higher than those generated by low-frequency sounds at any given azimuthal angle. For example, when the six sound frequencies were sequentially delivered from 40° and 70° ipsilateral, the relative sound pressure measured (arrowheads 1 and 2 in Fig. 5Ai) and the IPD calculated for the 80 kHz sound (arrowheads 1 and 2 in Fig. 5Aii) were not always the highest values.

The change in the relative sound pressure and in IPDs for all six sound frequencies generally varied linearly between $\pm 40^\circ$ to 50° (Fig. 5). We examined the change in the sound pressure and in IPD by calculating the slope (dB degree^{-1}) of the linear portion of each transformation curve and IPD curve. Although the absolute change in sound pressure varied with sound frequency, a linear regression analysis of the plot of the slope in relation to sound frequency revealed that the slope increased with sound frequency when the pinnae were intact

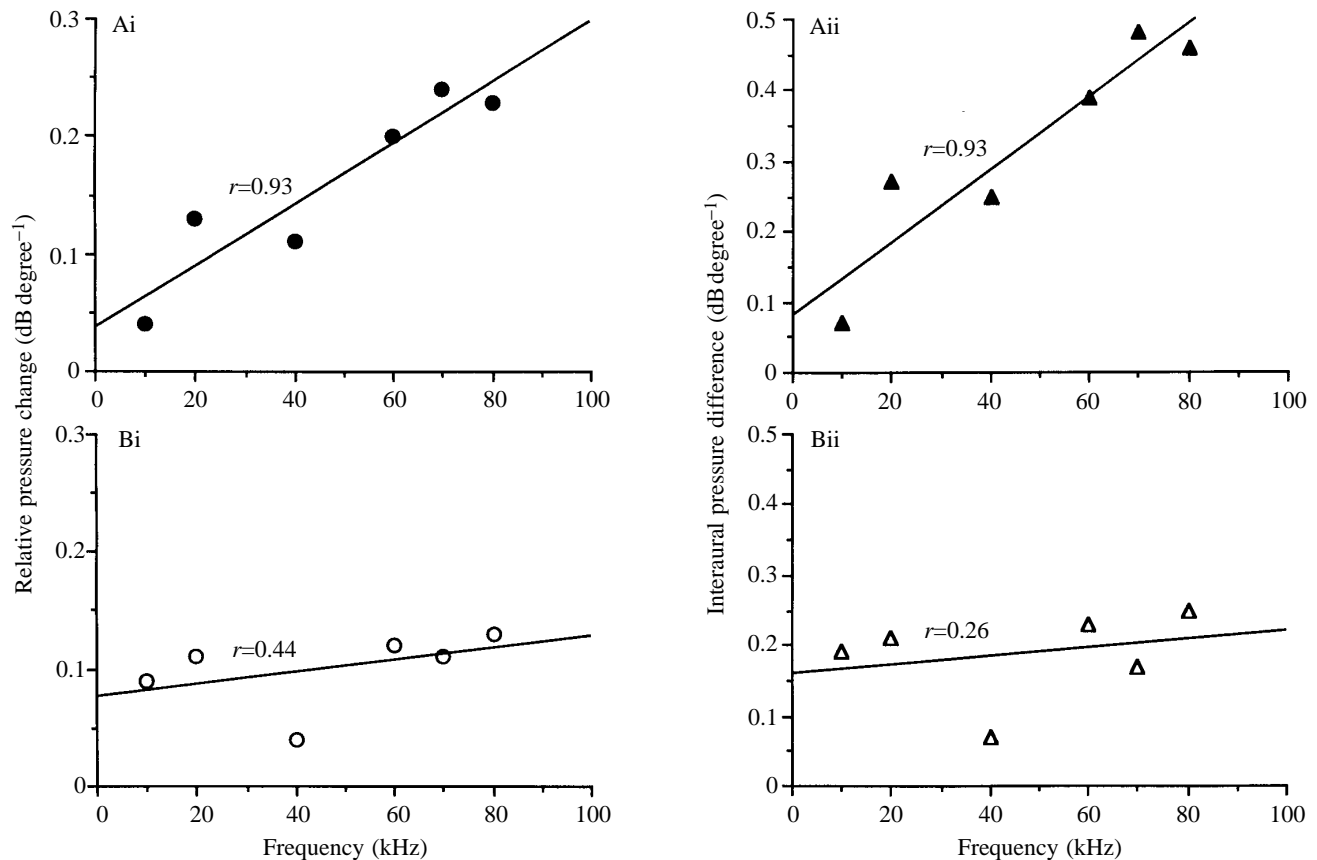


Fig. 6. Average relative pressure change (dB degree⁻¹) as a function of sound frequency determined when both pinnae were in a natural posture (Ai) and when the ipsilateral pinna was removed (Bi). The respective average changes of interaural pressure difference (dB degree⁻¹) as a function of sound frequency are shown in Aii and Bii. The linear regression line and correlation coefficient for each plot are shown (see text for further details). The *P* values are 0.0036 for Ai and Aii; 0.913 for Bi and 0.3094 for Bii.

(Fig. 6Ai). However, this correlation was greatly reduced after removal of the ipsilateral pinna (Fig. 6Bi). This was because pinna removal reduced the slope to a greater extent for the high-frequency sounds than for the low-frequency ones. Consistent with this observation, the slopes of the relationships between IPD and azimuth angle increased significantly with sound frequency (Fig. 6Aii) but removal of the ipsilateral pinna greatly reduced this correlation (Fig. 6Bii).

Directionality pattern of sound pressure transformation at the pinna

Directionality of sound pressure transformation at the pinna of the mouse determined using six frequencies was studied by plotting the average isopressure contours for two mice with both pinnae in the natural posture [Fig. 7, sensitive area (SA) contour maps]. The dark area in each SA contour map represents the 2 dB SA. Within each 2 dB SA, there was always a specific angle at which a delivered sound reached a maximal pressure at the tympanic membrane. This angle was always located in the upper portion of the ipsilateral hemisphere but not in the center of each 2 dB SA. This angle was called the acoustic axis in previous studies (Middlebrooks and Pettigrew, 1981; Phillips *et al.* 1982; Coles and Guppy, 1986).

The 2 dB SAs are not only different in size and shape but can also be found in more than one angular area in the contour patterns of certain frequencies (e.g. 10, 20 and 60 kHz). They tended to shift ipsilaterally and slightly upwards with increasing frequency. The remaining irregular SAs contained by the isopressure contours are either circumscribed or open. Each SA contains a greater angular area for the low-frequency than for the high-frequency sounds. In other words, the dynamic range of the measured pressures is smaller for lower frequencies than it is for higher frequencies; thus, there are more SAs for the high- than for the low-frequency sounds (compare Fig. 7A,B,C with Fig. 7D,E,F). This inverse frequency-dependent area of isopressure contours is supported by a linear regression analysis of all 2 and 5 dB SAs (obtained from these two mice and a third one) in relation to sound frequency. The SAs decrease significantly with sound frequency (Fig. 8).

We also studied the IPDs at all angular positions tested by drawing a pressure difference area (DA) based upon the difference in sound pressure measured at the corresponding angles in the ipsilateral and contralateral hemispheres. In each DA contour map (Fig. 7, DA contour maps), the dark area represents the angular area which has the greatest interaural

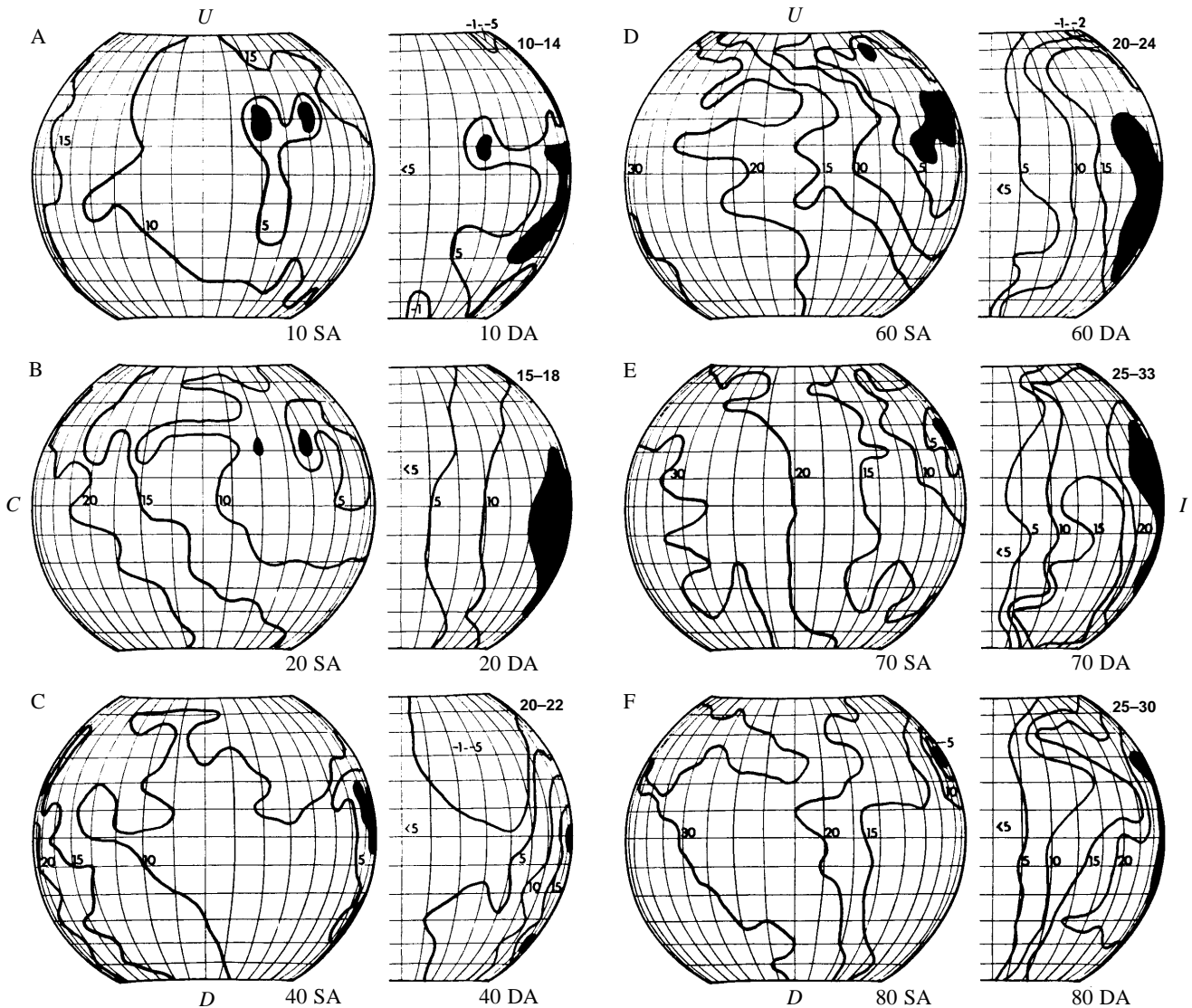


Fig. 7. Average isopressure contour patterns of directionality of sound pressure transformation at the head and pinna of *Mus domestica* as determined using six sound frequencies and shown by the sensitive area (SA) and interaural pressure difference area (DA). Each sound frequency (kHz) is shown at the lower right of each contour map. The dark area in each SA contour map represents the angular area within 2 dB of the maximal sound pressure measured. The remaining circumscribed or open solid lines represent isopressure contours (i.e. SA boundary) within 5, 10, 15, 20 or 30 dB of the maximal sound pressure measured. In contrast, the dark area in each DA contour map represents the angular area that shows the greatest interaural pressure difference (range is shown in the upper right-hand corner). The contour lines indicate the boundary of DA that has an interaural pressure difference greater than 20, 15, 10 or 5 dB. Areas with negative values indicate where the sound pressures measured at ipsilateral angles were lower than those measured at the corresponding contralateral angles. *C* or *I*, azimuthal angles which are contralateral or ipsilateral to the microphone-inserted ear. *U* or *D*, elevational angles which are above or below the horizontal plane.

pressure difference (the range of which is shown at the upper right-hand corner). The remaining circumscribed or open solid lines represent the boundary of each DA with an interaural pressure difference greater than 5, 10, 15 and 20 dB. The angular area with an interaural pressure difference less than 5 dB, including negative values, is also shown (see 10, 40 and 60 DA contour patterns).

Effect of ipsilateral pinna removal on the directionality pattern of sound pressure transformation

The contribution of the pinna to the directionality pattern

of sound pressure transformation was determined by plotting the isopressure contours, SAs and DAs for all six frequencies after surgical removal of the ipsilateral pinna (Fig. 9).

Removal of the ipsilateral pinna reduced the dynamic range of the measured pressures for all six test frequencies. This was evident from the reduced number of SAs, which was more obvious for the low than for the high frequencies. In addition, pinna removal either split (compare Fig. 7B,C,D,E with Fig. 9B,C,D,E) or expanded (compare Fig. 7F with Fig. 9F) the 2 dB SA contour line, causing it to spread over a wider

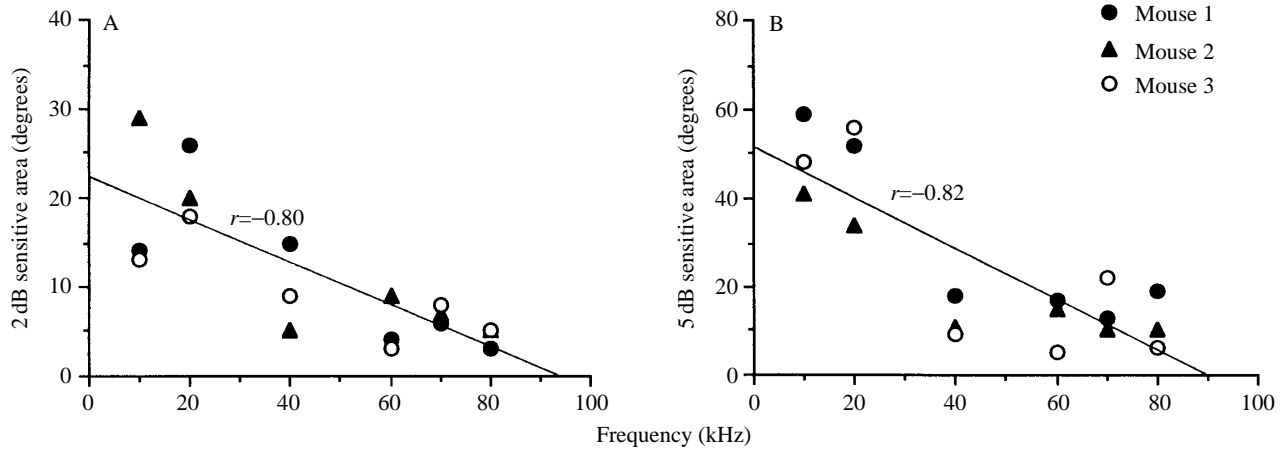


Fig. 8. Plots showing the inverse relationship between the 2 dB (A) and 5 dB (B) sensitive angular areas and sound frequency. Data collected from each of three mice are shown using different symbols. All measurements were made with both pinnae in a natural posture. The linear regression line and the correlation coefficient for each plot are shown. Note: in both plots, sensitive angular areas decrease significantly with sound frequency. In both plots, $P < 0.0001$.

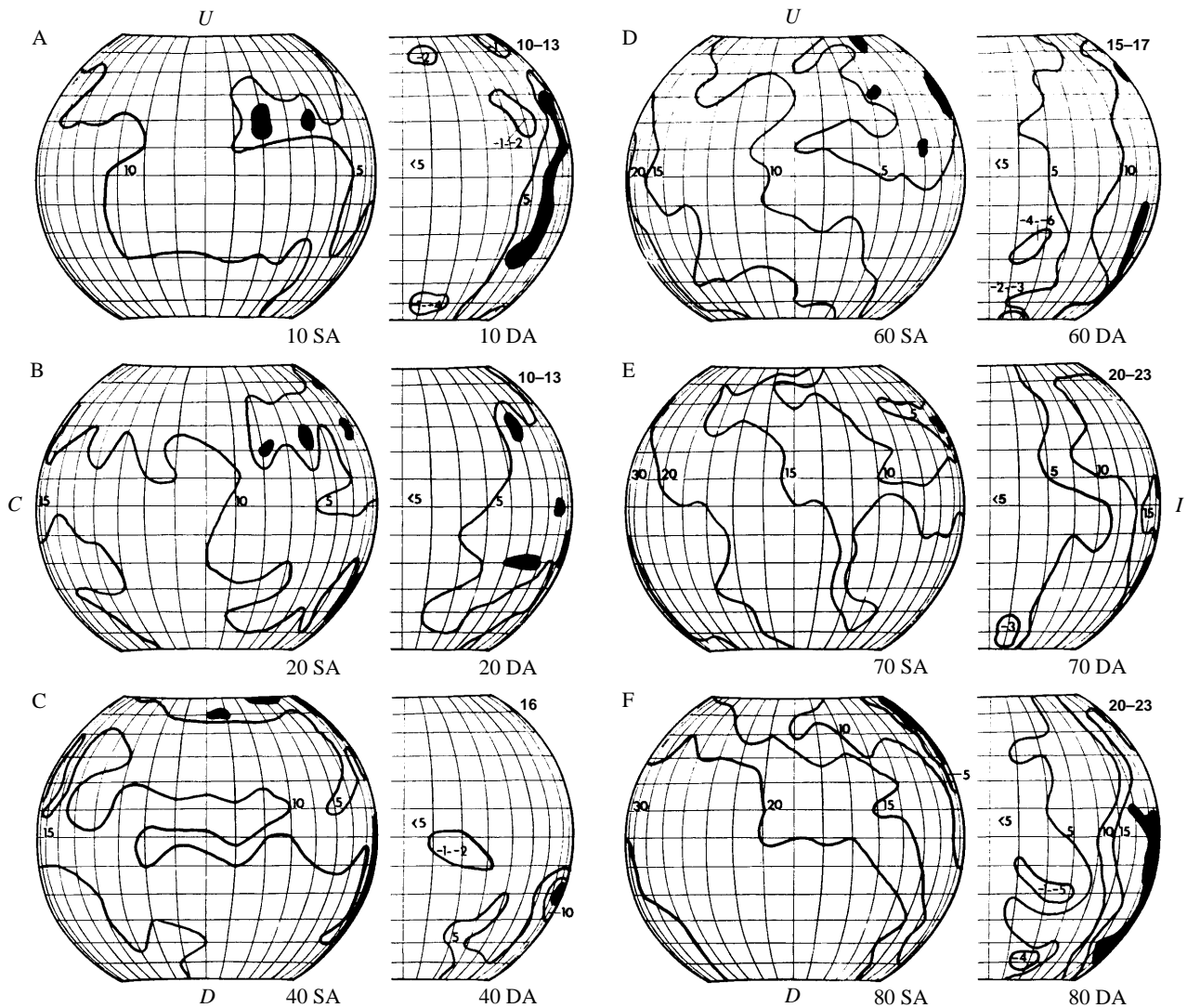


Fig. 9. The effect of ipsilateral pinna removal upon the average isopressure contour of directionality of sound pressure transformation at the pinna of *Mus domesticus* as determined using six sound frequencies and shown by the sensitive area (SA) and interaural pressure difference area (DA) (other details as in Fig. 7).

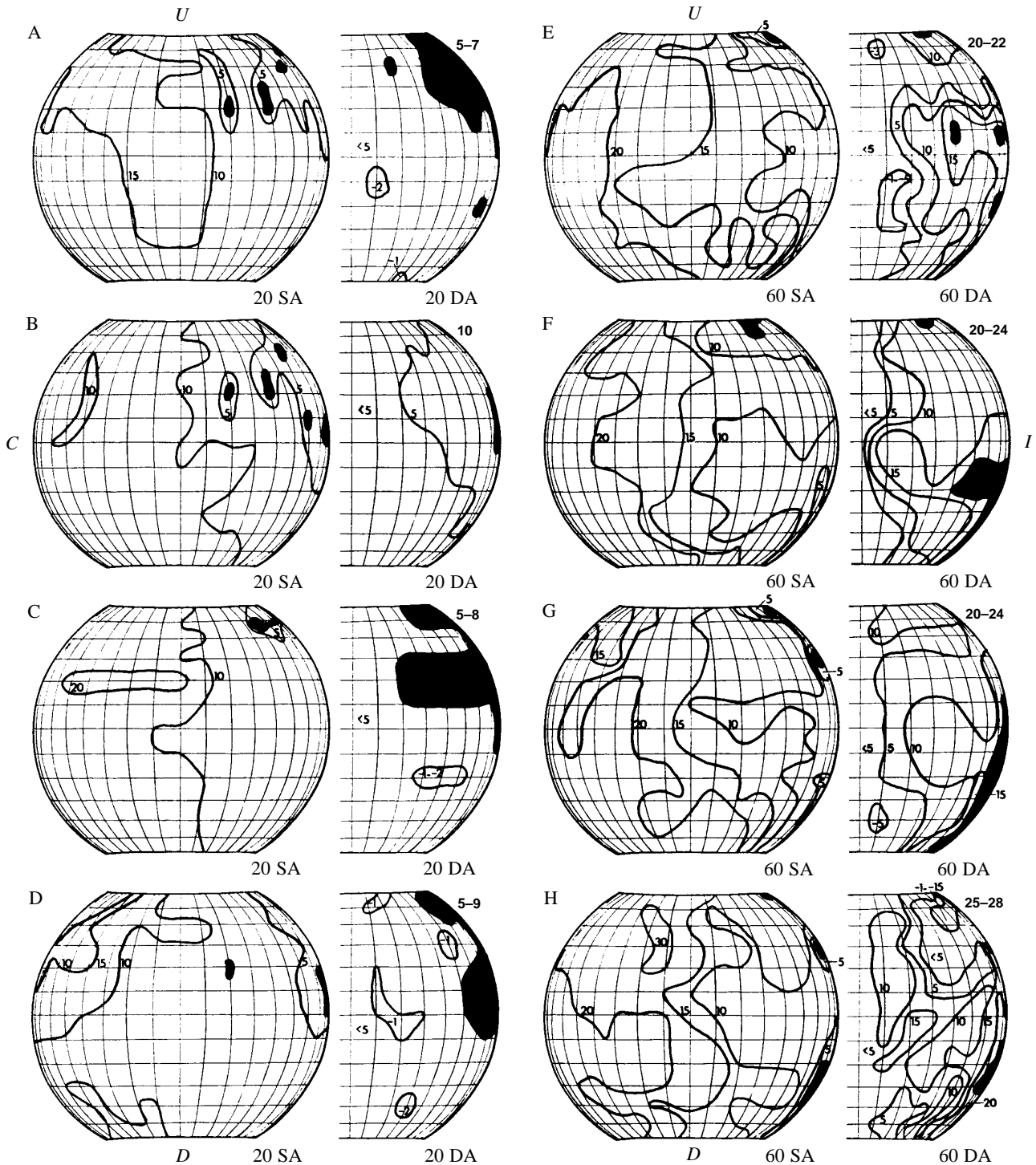


Fig. 10. The effect of different pinna postures upon the isopressure contour patterns of directionality of sound pressure transformation at the pinna of one *Mus domestica* determined using two sound frequencies (20 and 60kHz) and shown by the sensitive area (SA) and interaural pressure difference area (DA). (A,E) Both pinnae in the natural posture (Fig. 1A); (B,F) ipsilateral pinna pulled slightly forwards (Fig. 1C); (C,G) ipsilateral pinna pulled slightly backwards (Fig. 1D); (D,H) both pinnae pulled slightly backwards (Fig. 1E) (other details as in Fig. 7).

angular area. Pinna removal also, as expected, reduced the maximal sound pressure difference between the corresponding angles of two half-hemispheres, thus reducing the number of DA contour lines. Each DA retracted towards the lateral portion of the ipsilateral hemisphere (compare all DA contour

maps of Fig. 9 with those of Fig. 7). In addition, all but one (20 kHz) DA contained one or two angular areas with negative interaural pressure difference. The area of greatest interaural pressure difference was also split into several parts (e.g. Fig. 9, 20, 60 and 70 kHz).

Effect of pinna posture on the directionality pattern of sound pressure transformation

The effect of pinna posture on the directionality contour pattern of the sound pressure transformation of one mouse was examined by plotting all SAs and DAs after the ipsilateral pinna or both pinnae had been displaced into different postures (see Fig. 1C–E). Only 20 and 60 kHz sounds were used for this study (Fig. 10).

Fig. 10A,E shows the directionality contour patterns of the sound pressure transformation at the naturally postured pinnae. As expected, the dynamic range of the measured pressures and the maximal interaural pressure difference were larger for the 60 kHz sounds than for the 20 kHz sounds, and there were a greater number of SAs and DAs for the former than for the latter (compare Fig. 10A with Fig. 10E). In addition, both DAs contain angular area(s) with a negative interaural pressure difference.

Pulling the upper portion of the ipsilateral pinna slightly forwards appeared to increase the dynamic range of the measured pressures, as shown by the medial expansion of all SAs and DAs. This pinna posture also split (Fig. 10B) or increased (Fig. 10F) the 2 dB SA contour and eliminated the area of negative interaural pressure difference in the two DA contours. Conversely, pulling the upper portion of the ipsilateral pinna slightly backwards consolidated and shifted the 2 dB SA contour towards the upper lateral portion of the ipsilateral hemisphere for the 20 kHz sounds (Fig. 10C), but it split the 2 dB SA contour into two separate areas for the 60 kHz sounds

(Fig. 10G). This pinna posture appeared to reduce the dynamic range of the measured pressures and the maximal interaural pressure difference. It retracted all DAs laterally and produced an area of negative interaural pressure difference for both DAs.

Pulling the upper portion of both pinnae backwards split the 2 dB SA contour into different angular areas for both 20 and 60 kHz sounds (Fig. 10D,H). In the 20 kHz sound contour patterns, the 10 dB SA contour occupied almost three-quarters of the entire frontal hemisphere. The area of negative interaural pressure difference also split into four (Fig. 10D). For the 60 kHz contour patterns, such pinna posture not only irregularly expanded each SA even further but also produced complex DA contour patterns. The area of negative interaural pressure difference also shifted to the upper portion (Fig. 10H).

Maximal directionality and sound frequency

In addition to examining the directionality pattern of isopressure contours for each sound frequency, we studied the correlation between the maximal directionality and the spatial location of the acoustic axis in relation to sound frequency. We defined the maximal directionality as the difference (in dB) between the maximal and minimal sound pressures derived at each test frequency. In other words, the pressure obtained at the angle of minimal sound pressure was subtracted from the pressure measured at the acoustic axis (Coles and Guppy, 1986).

As revealed by the linear regression analyses of data obtained from three mice used in this aspect of study, maximal directionality increased significantly with sound frequency

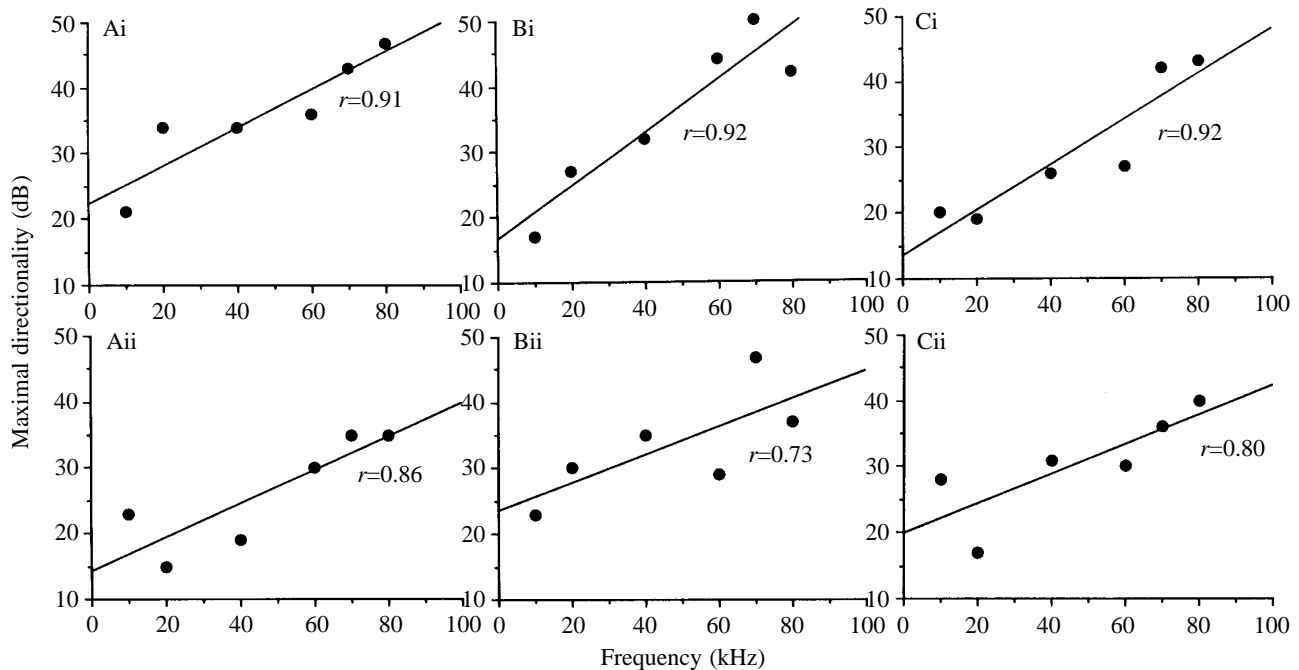


Fig. 11. The relationship between maximal directionality (dB) and sound frequency (kHz) for three *Mus domesticus*. For each frequency, the maximal directionality was expressed as the difference between the maximal and minimal sound pressures measured at two specific angles (i.e. sound pressure at the acoustic axis minus sound pressure at the angle of minimal pressure). Respectively, data in Ai, Bi and Ci were obtained when both pinnae were in a natural posture and for Aii and Bii when the ipsilateral pinna had been removed. The data in Cii were obtained when the ipsilateral pinna was pulled forwards. The linear regression line and correlation coefficient for each plot are shown. The *P* values are 0.0059 for Ai, 0.0140 for Aii, 0.0047 for Bi, 0.0498 for Bii, 0.0047 for Ci and 0.0280 for Cii.

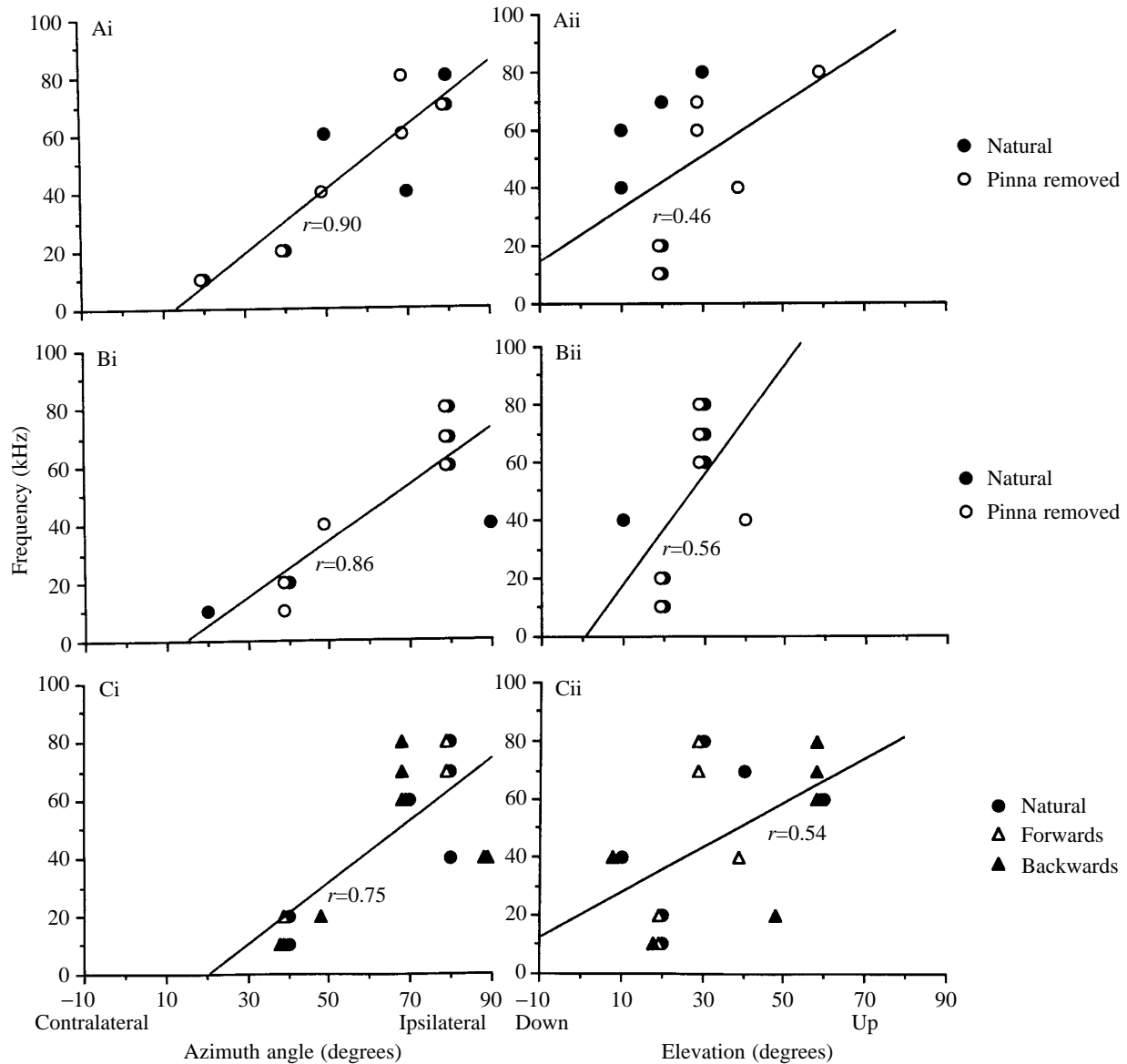


Fig. 12. Variation of the angle of maximal sound pressure of the pinna (i.e. acoustic axis) in azimuth (Ai,Bi,Ci) and elevation (Aii,Bii,Cii) as a function of sound frequency. In Ai, Aii and Bi, Bii, values obtained before and after removal of the ipsilateral pinna are shown using filled and open circles, respectively. In Ci,Cii, values were obtained at different pinna postures. Filled circles, both pinnae kept at a natural posture; open triangles, ipsilateral pinna pulled forwards; filled triangles, ipsilateral pinna pulled backwards. The P values are <0.0001 for Ai, 0.0662 for Aii, 0.0002 for Bi, 0.0291 for Bii, 0.0002 for Ci and 0.0104 for Cii.

when both pinnae were in a natural posture (Fig. 11Ai,Bi,Ci). This correlation was maintained after removal of the pinnae (Fig. 11Aii,Bii) or pulling the ipsilateral pinna forwards (Fig. 11Cii), although the correlation coefficient became smaller.

Variations in the spatial location of the acoustic axis of each mouse with sound frequency under different pinna postures (see Fig. 1) were examined by plotting the azimuthal and elevational angles of the acoustic axis for all six sound frequencies. In spite of individual variation, each acoustic axis tended to shift towards the lateral portion of the ipsilateral hemisphere with increasing frequency, regardless of pinna postures. A linear regression analysis revealed a strong

correlation between the azimuthal angle of the acoustic axis and sound frequency (Fig. 12Ai,Bi,Ci). There is a slight tendency for the acoustic axis to move upwards with increasing sound frequency, but the correlation between the elevational angle of the acoustic axis and sound frequency was low (Fig. 12Aii,Bii,Cii).

Spatial maximum and spectral maximum

As described earlier, when a pure tone was delivered from the acoustic axis, its sound pressure reached a maximum at the tympanic membrane of the mouse. Musicant *et al.* (1990) used the term 'spatial maximum' to describe the acoustic axis in order to differentiate it from the 'spectral maximum'. The latter

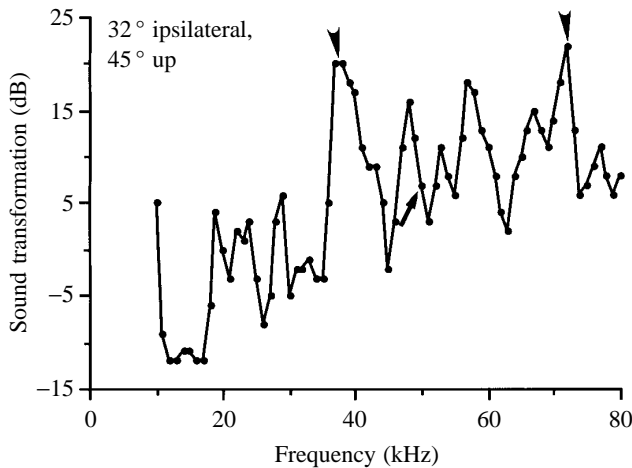


Fig. 13. Sound transformation spectrum at the right ear of a mouse determined using a 50 kHz sound delivered from the acoustic axis (32° ipsilateral and 45° up). Although the sound pressure reached a maximum at the tympanic membrane of the mouse, sounds of 37–38 and 72 kHz (indicated by arrowheads) rather than of 50 kHz (indicated by an arrow) were most amplified relative to the free-field measurements.

represents the frequency component which is most amplified relative to the free field for a given sound direction. They reported that, when a sound was delivered from the acoustic axis, the sound frequency of a spatial maximum may not be the same as that of the spectral maximum.

We have found a similar pattern in the mouse. For example, when a 50 kHz sound was delivered from the acoustic axis (32° ipsilateral and 45° up) of a mouse, the sound pressure reached a maximum at the tympanic membrane (7 dB above the free-field measurement). However, when the sound transformation spectrum was studied at this angle (Fig. 13), the sound pressure generated by the 50 kHz sound (indicated by an arrow) was not the maximum. Instead, the maximal sound pressure transformation was generated by sounds of 37–38 and 72 kHz (arrowheads).

Acoustic pressure gain by the head and pinna at the acoustic axis

The average acoustic pressure gain by the head and pinna at the acoustic axis for a given sound frequency was obtained by calculating the difference between the sound pressure measured at the tympanic membrane and at the free field. The sound pressure at the free field was measured by maintaining the adaptor-attached microphone at the same place after careful removal of each mouse. This average pressure gain was calculated at the acoustic axis before (Fig. 14A, curve a) and after (Fig. 14A, curve b) removal of the ipsilateral pinna.

As shown by Fig. 14A, curve a, the sound pressure gain due to head and pinna ranged between 6 and 11 dB. However, all these were values drastically reduced to below 5 dB or even to a negative value after pinna removal, suggesting that the pressure gain at the acoustic axis due to the head alone is quite limited (Fig. 14A, curve b).

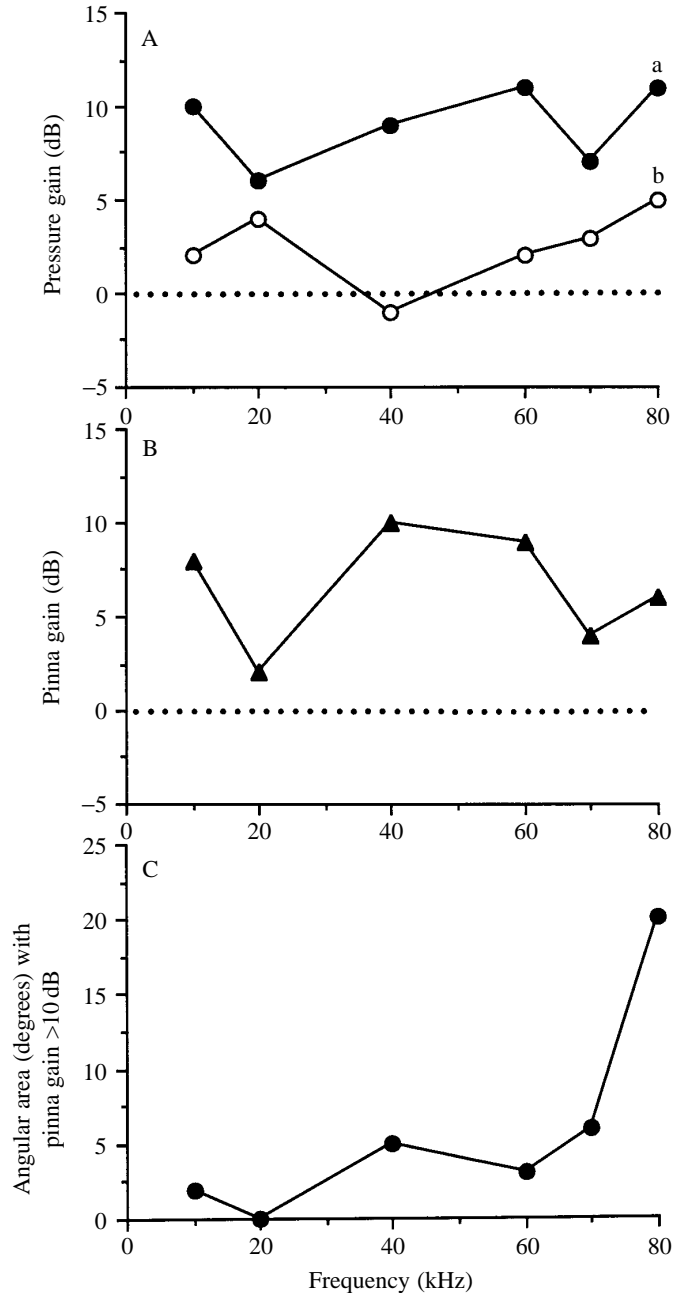


Fig. 14. (A) Average sound pressure gain of the pinna of *Mus domesticus* determined at the acoustic axes for different sound frequencies. Each point represents the difference in sound pressure relative to free-field measurements at the acoustic axis before and after removal of the mouse. Curves a and b, respectively, were obtained before and after removal of the ipsilateral pinna. (B) Average pinna gain of *Mus domesticus* obtained by calculating the difference between curves a and b in A. The dotted lines in A and B represent zero sound pressure gain. (C) Relationship between the angular area with a pinna gain greater than 10 dB and sound frequency (see text for further details).

An estimate of the sound pressure gain provided by the ipsilateral pinna alone was obtained by calculating the difference between curves a and b in Fig. 14A. This calculation

shows that the pinna gain ranged between 2 and 10 dB, with a maximal gain of 10 dB at 40 kHz (Fig. 14B).

We also studied the pinna gain at all angles in the frontal auditory space of the mouse. This was achieved by calculating the difference in sound pressure at each angle before and after pinna removal (i.e. the difference between the SAs of Figs 7 and 9). The size of the angular area with a pinna gain larger than 10 dB in relation to sound frequency was then compared across the six test frequencies. The 80 kHz sound produced the largest angular area (Fig. 14C), although 40–60 kHz sounds produced the largest pinna gain at the acoustic axis (Fig. 14B). This result indicates that the pinna gain at the acoustic axis for a given sound frequency is not always larger than those at other angles. For example, when sounds of 70–80 kHz were delivered from the acoustic axis, they generated a pinna gain of 4–6 dB (Fig. 14B). When they were delivered from other angles, they generated a pinna gain of more than 10 dB (Fig. 14C).

Discussion

Sound pressure transformation at the pinna

When a sound is delivered away from the midline, the sound pressure and the arrival time at the two ears of an animal are different because of the shadowing effect of the head and pinna. The animal utilizes these two cues to localize the sound source (van Bergeijk, 1962). By studying the directionality of sound pressure transformation at the pinna of the mouse using sound frequencies spanning its hearing range (Ehret, 1974, 1977; Markl and Ehret, 1973; Ehret and Moffat, 1985; Harnischfeger, 1978; Heffner and Masterton, 1980; Stiebler and Ehret, 1985; Willott and Urban, 1978), we have demonstrated that the amount of shadowing by the head and pinna varies with sound direction and frequency. We found that the dynamic range of the measured pressures tends to increase with increasing frequency. This is demonstrated by a greater number of SAs for the high- than for the low-frequency sounds (compare Fig. 7A,B,C with Fig. 7D,E,F) and the inverse frequency-dependent expansion of isopressure contours (Fig. 8). In addition, the maximal IPDs and number of DAs increase with sound frequency, regardless of pinna posture (Figs 7, 9, 10).

Our study of sound pressure transformation shows that prominent spectral notches appear across the test frequencies of 10–80 kHz (Figs 2, 3). These spectral notches are generally maintained in the interaural pressure difference spectra (Fig. 4). Because these notch frequencies generated negative pressure transformation (Figs 2, 3), they contributed to the negative interaural pressure difference at certain frequencies (Figs 4, 7, 9, 10). The present study also shows that the high-frequency sounds do not always generate larger pressure transformation values (Figs 2, 3, 5Ai) or interaural spectral difference (Figs 4, 5Aii) for a given sound direction. All these findings are similar to those for a previous study in cats (Musicant *et al.* 1990).

The presence of spectral notches was first reported in a study

of human subjects (Shaw, 1974, 1982) and later in cats (Chan *et al.* 1986; Musicant *et al.* 1986, 1990) and ferrets (Carlile and King, 1994). Musicant *et al.* (1990) suggested that the spectral notches may provide necessary spectral cues which may be utilized by the nervous system for sound localization.

The present studies of the isopressure contour patterns (i.e. the SA area) and interaural pressure difference contour patterns (i.e. DA areas) are characterized by several features. (1) The shape and size of each SA and DA are affected by sound frequency. (2) The maximal isopressure contour (i.e. 2 dB SA) and the maximal DA can be represented in more than one angular area for certain frequencies. (3) Areas with negative interaural pressure difference are contained in the DAs for certain frequencies. (4) All these characteristics are affected by pinna posture and pinna removal (Figs 7, 9, 10).

Similar to these findings, Musicant *et al.* (1990) have reported that the number and shape of 5 dB isopressure contours in cats also varied with sound frequency. For example, the 5 dB isopressure contours split into two separate areas, spread over a large area, and split again before recombining to form one single area as sound frequency increased from 13.6 to 15.9 kHz (Fig. 19 of Musicant *et al.* 1990).

Pinna and auditory directionality

The neural basis for sound localization in an animal lies in the directionality of its auditory neurons. One important influence on this directionality is the sound pressure transformation at the pinna. The observation that the SA and DA contour patterns (Figs 7, 9, 10) and the acoustic axis (Fig. 12) not only change with sound frequency but also with pinna posture or pinna removal demonstrates the importance of the pinna in the directionality of the sound pressure transformation. This is also substantiated by the observation that removal of the pinna greatly reduced the rate of sound pressure change (Fig. 6Bi), the rate of IPD change (Fig. 6Bii) and the number of DAs (compare Fig. 7 with Fig. 9).

All these observations suggest that the pinna of an animal should contribute importantly to the directionality of its auditory neurons. This is supported by previous neurophysiological studies in bats (Grinnell, 1963; Grinnell and Grinnell, 1965; Jen and Sun, 1984; Sun and Jen, 1987), cats (Middlebrooks and Pettigrew, 1981; Aitkin *et al.* 1984; Middlebrooks and Knudsen, 1987) and possums (Aitkin *et al.* 1984), in which the angle of maximal directionality of auditory neurons changes with pinna posture.

Directionality of sound pressure transformation, acoustic axis and sound frequency

In agreement with previous findings (Moore and Irvine, 1979; Phillips *et al.* 1982; Semple *et al.* 1983; Calford and Pettigrew, 1984; Moore *et al.* 1984; Coles and Guppy, 1986; Carlile and Pettigrew, 1987; Jen and Chen, 1988; Guppy and Coles, 1988; Coles *et al.* 1989; Carlile, 1990*a,b*; Obrist *et al.* 1993; Rice *et al.* 1992), the directionality of sound pressure transformation at the pinna of the mouse becomes sharper with

increasing sound frequency. This is demonstrated by the increasing rate of sound pressure change and IPD change with sound frequency (Fig. 6Ai,ii), the inverse relationship between the 2 and 5 dB SAs with sound frequency (Fig. 8) and the significant correlation between maximal directionality and sound frequency (Fig. 11).

This frequency-dependent characteristic of the sound pressure transformation at the pinna of the mouse is also demonstrated by the observation that the maximal sensitive area (i.e. 2 dB SA) shifted with sound frequency (Figs 7, 9, 10). This is manifested by the shift of the acoustic axis with sound frequency (Fig. 12), an observation that has been made in bats (Jen and Chen, 1988; Guppy and Coles 1988; Coles *et al.* 1989; Obrist *et al.* 1993), cats (Moore and Irvine, 1979, Musicant *et al.* 1990; Phillips *et al.* 1982; Rice *et al.* 1992; Semple *et al.* 1983; Calford and Pettigrew, 1984; Moore *et al.* 1984), tammar wallabies (Coles and Guppy, 1986), ferrets (Carlile, 1990a,b) and guinea pigs (Carlile and Pettigrew, 1987).

In the mouse, the acoustic axis tends to shift towards the lateral extremity of the ipsilateral hemisphere with increasing frequency, regardless of pinna posture (Fig. 12Ai,Bi,Ci). This observation is comparable to findings for cats (Phillips *et al.* 1982; Calford and Pettigrew, 1984) and wallabies (Coles and Guppy, 1986), but different from reports for bats (Jen and Chen, 1988; Guppy and Coles, 1988; Coles *et al.* 1989). In the vertical plane, there is a weak tendency for the acoustic axis to shift upwards with increasing sound frequency (Fig. 12Aii,Bii,Cii), which is similar to the situation in cats (Calford and Pettigrew, 1984; Phillips *et al.* 1982), wallabies (Coles and Guppy, 1986) and some species of bats including *Eptesicus fuscus* (Jen and Chen, 1988), *Nyctophilus gouldi* and *Macroderma gigas* (Guppy and Coles, 1988) and *Plecotus auritus* (Coles *et al.* 1989). Using a fine frequency resolution to study sound pressure transformation properties, Musicant *et al.* (1990) reported that the acoustic axis of the cat pinna systematically shifts from the frontal to the lateral and from the lower to the higher portion of the ipsilateral hemisphere with increasing frequency. However, there were abrupt shifts in the azimuthal and elevational locations of the acoustic axis during this transition.

Previous studies have suggested that this trend for the acoustic axis to shift with changing sound frequency is primarily related to the orientation of the pinna of an animal (Calford and Pettigrew, 1984; Jen and Chen, 1988). These studies suggest that a pinna orienting forwards and upwards, such as that of *Eptesicus fuscus*, would shift the acoustic axis medially and dorsally with increasing frequency. In contrast, a pinna which orients outwards and slightly upwards, like that of cats (Phillips *et al.* 1982; Calford and Pettigrew, 1984), wallabies (Coles and Guppy, 1986) and mice (Fig. 1A), would shift the acoustic axis laterally and dorsally with increasing frequency (Fig. 12).

When both pinnae were in the natural posture, the acoustic axis and the 2 dB SA were always located in the upper portion of the ipsilateral hemisphere, regardless of sound frequency

(Fig. 7). This is probably due to the outward and upward orientation of the pinnae. As the mouse is a ground-dweller, the lower half of its frontal auditory hemisphere is obstructed by the ground during its search for food. Thus, the maximal sensitivity to sound coming from the upper frontal hemisphere appears to have adaptive value. In addition to olfactory and visual cues, such maximal auditory sensitivity also appears to be beneficial for the mouse, which is able quickly to detect the sounds generated by any potential predators approaching into its auditory field. The observations that the pinna posture can change the spatial location of the acoustic axis and the directionality of the sound pressure transformation pattern (Fig. 10) suggest that the mouse is theoretically able to maximize its auditory sensitivity during acoustically guided activity.

Our study also demonstrates that the acoustic axes for a given frequency determined before and after pinna removal are not at the same angle. This is substantiated by the observation that the 2 dB SAs either occupy different positions or become fragmented into several areas after pinna removal (compare Fig. 7 with Fig. 9).

The pinna gain at the acoustic axis

When a sound is delivered from different angles in the mouse frontal hemisphere, an interaural sound pressure differences will be generated because of the shadowing effect of the head and pinna. The amount of head and pinna shadowing increased with sound frequency (DAs of Fig. 7). Although the sound pressure gain of the ipsilateral pinna can be estimated by comparing the differences in the IPDs (compare Fig. 5Aii with Fig. 5Bii), the rate of IPD change with sound direction (compare Fig. 6Aii with Fig. 6Bii) and the isopressure contour patterns before and after removal of the ipsilateral pinna (compare Fig. 7 with Fig. 9), it can be more directly calculated from the pressure difference observed before and after pinna removal at the acoustic axis, at which head shadowing is minimal.

When a given sound is delivered from the acoustic axis, sound pressure always reaches a maximum at the tympanic membrane. However, the pinna gain at the acoustic axis is not always larger than those determined for the same sound delivered from other angles (compare Fig. 14B with Fig. 14C). This is because the reduction in sound pressure for a given frequency determined at the acoustic axis after pinna removal is smaller than that determined at other angular areas.

In conclusion, the present study of sound pressure transformation at the pinna of the mouse presents many findings that agree with, but also extend, those of previous studies. These findings include the presence of prominent spectral notches in the complex transformation functions, the negative interaural pressure differences at certain frequencies, the difference between spatial and spectral maxima, and the fragmentation or spreading of maximal isopressure area with sound frequency and pinna posture. Even though species-specific differences may exist, results from previous studies and the present one lead us to speculate that these features may

be common characteristics of the sound pressure transformation at the pinna of an animal.

This work was supported by a grant from the Human Frontier Science Program and a grant from the NIDCD (247). We thank Mr Ka-Choi Tang for helping with some of the data processing.

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