

BIOPHYSICAL ASPECTS OF DIRECTIONAL HEARING IN THE TAMMAR WALLABY, *MACROPUS EUGENII*

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SUMMARY

The biophysical properties of the external ear of the Tamar wallaby, *Macropus eugenii* (Desmarest), have been investigated using probe microphones implanted in the ear canal. An acoustic axis of the pinna exists above 2 kHz which is located close to the horizontal plane for natural ear positions, whereas azimuthal location of the acoustic axis is determined by pinna orientation on the head. The maximum on-axis acoustic pressure gain of the external ear reaches 25–30 dB for frequencies near 5 kHz. This results from pressure transformation by the horn-like pinna combined with resonance of the auditory meatus. The directionality of the pinna is similar to the sound diffraction properties of a circular aperture with an average radius based on the circumference of the pinna face. These properties determine the acceptance angle of the main lobe containing the acoustic axis and the spatial location of nulls. Large binaural intensity differences, exceeding 30 dB, can be produced by the interaction of peaks and nulls between monaural directivity patterns, depending on the relative position of each pinna.

INTRODUCTION

Despite the prominence and mobility of the pinnae in many mammals, the role of the pinna in directional hearing has often been ignored by the use of closed field sound delivery (Erulkar, 1972). A notable exception has been in the study of hearing in bats, where the pinnae often exceed the dimensions of the head and have been clearly implicated in directional hearing (Grinnell, 1963; Grinnell & Grinnell, 1965; Neuweiler, 1970; Busnel & Fish, 1980; Guppy, Coles & Pettigrew, 1984; Jen & Sun, 1984). Recent neurophysiological studies on the mechanisms of sound localization in non-echolocating mammals have used real sound sources in space and have begun to re-examine the role of the pinna (Middlebrooks & Pettigrew 1981; Phillips *et al.* 1982; Semple *et al.* 1983; Aitkin, Gates & Phillips, 1984; Calford & Pettigrew, 1984; Moore, Semple, Addison & Aitkin, 1984).

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The present study examines some of the acoustical properties of the mammalian external ear which determine the directionality and pressure gain at the eardrum. This study is based on the external ear of the Tammar wallaby (*Macropus eugenii*) which has an erect and highly mobile pinna, typical of many mammals. Some preliminary data have been presented previously (Hill & Coles, 1981).

MATERIALS AND METHODS

Animals

The left and right ears of nine Tammar wallabies (*Macropus eugenii*) were used in this study. The animals were obtained from a resident colony maintained by the Research School of Biological Sciences at the Australian National University. The wallabies were adult or sub-adult females weighing 3.5–4.5 kg.

Apparatus

Biophysical measurements were made in an anechoic room (2.6 m×2.5 m×2.0 m) with a primary echo level at least 39 dB below the signal. The room contained a mobile speaker assembly comprising a vertically mounted aluminium track of 1 m radius, which could be rotated through about 330°. A trolley on the track was able to move along its length, carrying a loudspeaker. Both the movement of the track and trolley were remotely controlled for changing azimuth and elevation angles, with an accuracy for speaker position of $\pm 0.5^\circ$.

Preparation

Small, calibrated microphones ($\frac{1}{4}$ in = 6.35 mm; Brüel & Kjaer Type 4135) were implanted into the left and right ear canals through a hole in the wall of the bony meatus close to the tympanic membrane. In order to protect the delicate microphone diaphragm the protection grid was not removed. A very short piece of heat-shrink plastic was also fitted to the end of the microphone and extended about 1 mm from the top of the protection grid. Any effect of the protection grid and plastic tubing on sound pressure measurement was calibrated. With microphones in position, the head of a fresh cadaver was mounted on a small platform at the centre of rotation of the mobile speaker assembly in the anechoic room. The orientations of the head and pinnae (Figs 1, 2) were adjusted to natural positions taken from photographs and single-frame analysis of ear and head movements (Coles & Hill, 1981).

Stimuli and recordings

Continuous pure tones (0.2–40 kHz) were generated from a Hewlett-Packard function generator (Model 3300A) amplified (Pioneer BP-320) and connected to a loudspeaker (Motorola piezohorn KSN 1025A for frequency range 1.5–40 kHz or Realistic 40-1909B for frequency range 0.2–3 kHz) *via* a Hatfield attenuator (Type 2125). A calibrated microphone ($\frac{1}{4}$ in B & K Type 4135) was used to determine the free field sound pressure at the position of the wallaby head, which was maintained

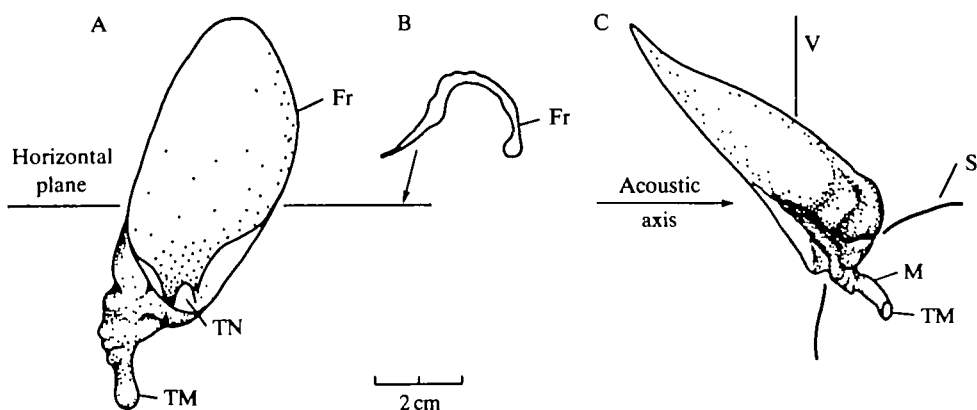


Fig. 1. The morphology of the Tammar wallaby pinna. (A) Pinna face viewed frontally (on-axis) indicating the leading edge (Fr), tragal notch (TN) and tympanic membrane (TM). (B) Horizontal cross-section midway through pinna showing asymmetry of the pinna flange. (C) Side view of pinna showing inclination to the vertical and location of acoustic axis. S, surface of skull; M, meatus; V, vertical plane. The drawings are based on photographs and endocasts of the external ear made with silicon moulding rubber. Pinna removal occurred close to the surface of the skull, at the point of rapid flare between the meatus and the pinna (see Table 1).

between 68–70 dB SPL re $20 \mu\text{Pa}$. Free field measurements were taken with the microphone facing the speaker, without the head present, but at a position on the midline, in line with the open faces of the pinnae. The output voltage from the microphones implanted into each ear canal was determined either on a measuring amplifier (B & K Type 2510) in conjunction with a third octave filter set (B & K Type 1618), or a portable sound level meter (B & K Type 2203) using an octave filter set (B & K Type 1613).

Definitions

The *longitudinal axis* was defined as the point 0° azimuth and 0° elevation (see Figs 2, 5) which projects from the centre of the head (where the free field was calibrated) to the surface of the imaginary sphere, at radius 94 cm, which is described by the speaker movements in two dimensions. The vertical plane at azimuth 0° normally contained the animal's midline. Data points representing sound pressure level were determined by speaker position and plotted on a zenithal projection of a hemisphere. This projection is based on a 0° azimuth and 0° elevation centre point and extending for 90° in all directions (see Neuweiler, 1970 and also Fig. 5) with the poles represented vertically, at the north and south. Using this projection, distortion of area, and thus of solid angle, is within 5% except for positions closer than 30° to the poles. The platform mounting the head and either pinna could be repositioned in the horizontal plane to optimize data collection on the hemispheric projection. Polar plots were also collected for the horizontal plane and some elevational planes at various azimuths.

RESULTS

Acoustic axis

For frequencies above 2 kHz there was a region in space where the sound pressure developed at the tympanic membrane and measured by the implanted microphone was a maximum (see Fig. 2A). Such an area was defined in the present experiment within ± 0.5 dB and can be represented as a single point in space accompanied by a

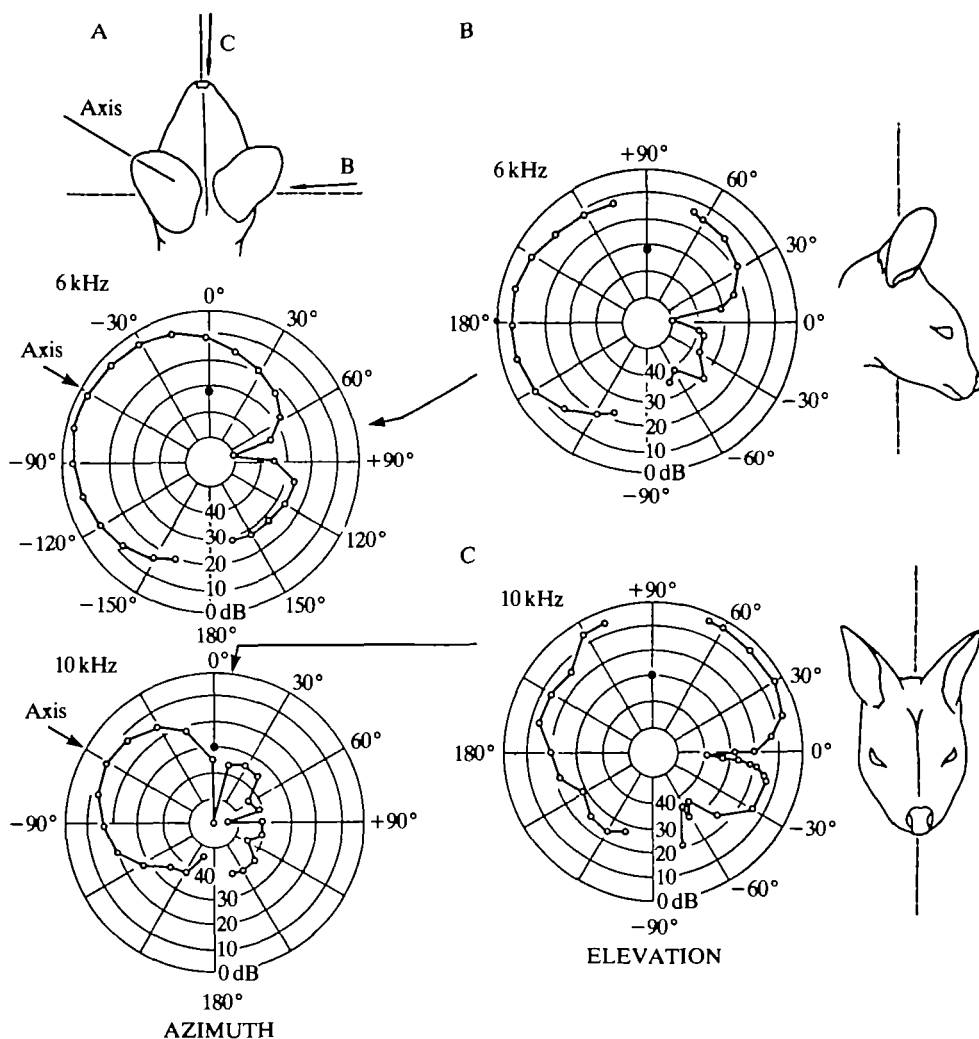


Fig. 2. Polar response patterns based on microphone response changes (dB) to stimulus direction in azimuth (A) or elevation (B) at 6 and 10 kHz. 0 dB = 100 dB re $20 \mu\text{Pa}$ with free-field sound pressure level indicated by filled circle on polar plot. Decreasing sound pressure re 0 dB is towards the centre of polar diagram. Schematic wallaby head in A indicates approximate position of the elevation planes shown in B. The position of the acoustic axis is indicated in A as the peak in the polar response pattern. In this example the wallaby pinnae are in the resting position.

1 dB confidence limit in the form of an iso-intensity contour when plotted in two dimensions (Fig. 5). This zone is defined as the *acoustic axis* and is consistent with the definition of Middlebrooks & Pettigrew (1981) and Phillips *et al.* (1982) in the cat.

Acoustic pressure gain

The pressure gain of the external ear was plotted as a function of frequency by referencing the maximum sound pressure in the ear canal (i.e. at the position of the acoustic axis) to the free field. For each test frequency the speaker was repositioned as necessary. The results are shown in Fig. 3 as a gain curve for four ears producing the maximum on-axis value at each test frequency. For the most part, the sound pressure level at the tympanic membrane has positive gain, i.e. the sound pressure is amplified relative to the free field for frequencies between 1 and 30 kHz. From Fig. 3, it can be seen that there is a rapid increase in pressure gain above about 1.5 kHz, rising to a peak of 25–30 dB between 4 and 5 kHz. Above 6 kHz the pressure gain starts to decline progressively to values below 10 dB for frequencies between 16 and 20 kHz. Additional decreases in pressure gain occur above 20 kHz resulting in attenuation of sound pressure relative to the free field between 30 and 40 kHz. Local sound diffraction inside the pinna and meatus may have contributed to the attenuation of sound at these high frequencies. In addition, it is possible that the equivalent acoustic volume of the probe microphone, although small, may become significant at high frequencies and thus affect the properties of a cavity such as the meatus. Since gain values became erratic and inconsistent above about 40 kHz detailed measurements were discontinued. There were no differences in acoustic pressure gain between left and right ears.

The effect of pinna removal on acoustic pressure gain is shown in Fig. 4A. The pinna was surgically removed until flush with the contour of the skin of the head. In the wallaby it is possible to remove almost the entire pinna flange (see Fig. 1C) but it is partially recessed in the muscles of the head and pinna itself. The most complete pinna removal that can be achieved leaves a small opening with an average diameter of about 0.8 cm (see Table 1; Fig. 1C), which is very close to the entrance of the cartilaginous meatus. Fig. 4A shows the effect of pinna removal on pressure gain, and the difference between the two curves indicates that the amplifying effect of the pinna (Fig. 4B) increases progressively from 5 to 20 dB in the frequency range 1.5–30 kHz. In the pinnaless condition (Fig. 4A), measurements at the tympanic membrane show a residual pressure gain curve which retains a distinct peak of about 15 dB in the 4–8 kHz region.

Since the length of the meatus is about 1.6 cm (Table 1; Fig. 1), the residual peak in pressure gain can be attributed to closed tube resonance where the sound wavelength is four times the length of the meatus (see Discussion). By removing the pinna as part of the external ear, it is possible to identify the contribution of the resonating meatus to the entire pressure gain although the pinna and meatus are normally acoustically coupled. In addition, the gain of the pinna as an acoustic transformer can be estimated (Fig. 4B) and compared to the expected amplification

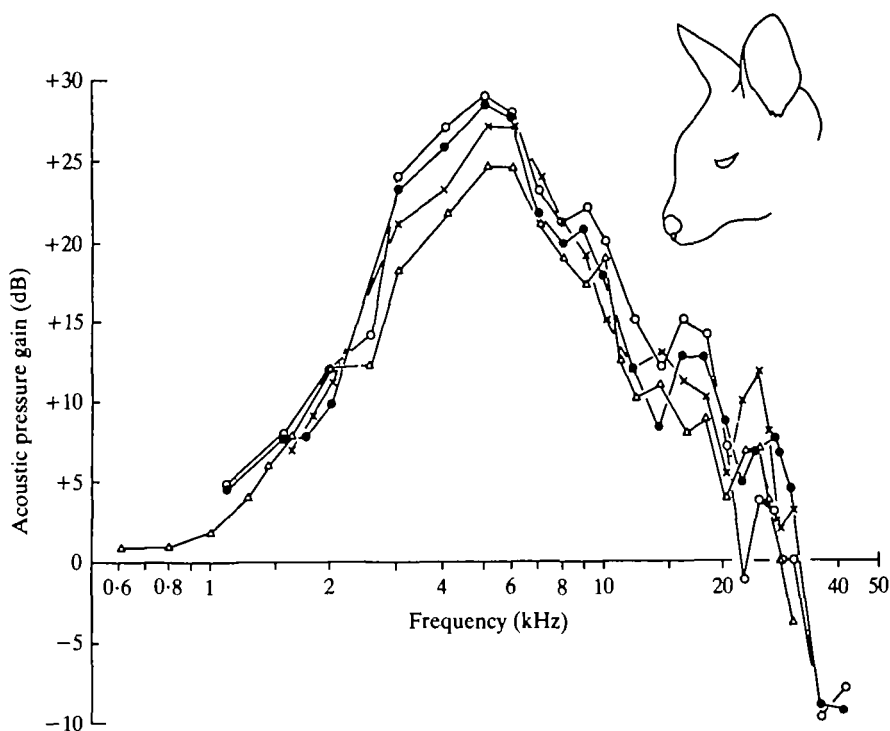


Fig. 3. Measurement of the acoustic pressure gain (in dB) for four separate ears as a function of stimulus frequency. Inset shows 'on-axis' view of the left ear.

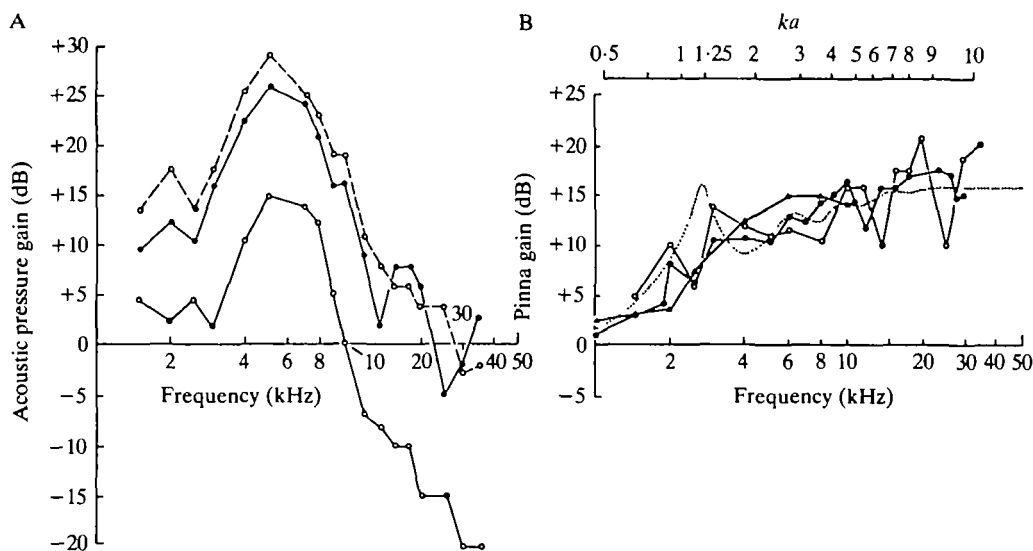


Fig. 4. Pressure gain curve of a single ear for three conditions: normal curve (solid line), enlarged pinna (dotted line) and pinna removed (open circles, solid line). (B) Pinna gain interpreted as the difference between pinna intact and pinna removed as shown in A. Dotted curve represents the expected gain curve for a conical horn based on the dimensions of the wallaby pinna as shown in Table 1. For calculation of the gain curve of a finite-length conical horn see Results and Appendix. The ka values ($= 2\pi a/\lambda$, where a is radius of opening and λ is wavelength of sound) are also indicated on the abscissa and based on the average radius of the mouth of the pinna (see Table 1, Fig. 1C and text). For $ka > 3$ the pinna becomes an efficient horn (Beranek, 1954).

values for a simple acoustic horn. In Fig. 4B the expected excess pressure at the throat of a finite-length conical horn has been plotted as a function of frequency, based on the relevant physical dimensions of the pinna (Table 1; Fig. 1).

The gain G (in decibels), for a horn, over the entire frequency range is given by:

$$G \text{ (dB)} = 20 \log_{10} \left[\frac{H_{12}}{H_{22} + R} \right], \quad (1)$$

where H_{ij} are the two-port impedance coefficients of the horn and R is the radiation impedance of the open mouth. For a conical horn, these terms are expressed in full in the Appendix and are derived from Olson (1947) using the methods of Fletcher & Thwaites (1979). The wallaby pinna must be treated as a finite-length horn since the frequency range of interest involves wavelengths which are comparable to and exceed the length of the pinna and the circumference of the mouth (see Beranek, 1954, and Discussion). However, at high frequencies, the maximum pressure gain G_{∞} , at the throat of the pinna, will tend to:

$$G_{\infty} \text{ (dB)} = 10 \log_{10} \left[\frac{S_2}{S_1} \right], \quad (2)$$

where S_2 and S_1 are the mouth and throat cross-sectional areas respectively. Therefore, for the wallaby pinna a maximum pressure gain should approach 16 dB, based on the physical dimensions (Fig. 1; Table 1). The mouth of the pinna has an average radius of 2.5 cm, which can be estimated from the circumference of the opening, which is 16 cm. The throat of the pinna is formed by a rapid change in cross-section along the external ear where the entrance to the meatus occurs (Fig. 1; Table 1). The throat has a radius of 0.4 cm, with an average path length to the mouth of about 4.5 cm. The results in Fig. 4B show that the pressure gain produced by the pinna is reasonably close to that predicted by an equivalent conical horn.

The possibility that the peak in the normal pressure gain curve seen in Fig. 4A was due to horn (pinna) resonance rather than meatus resonance was tested. This was done by making an artificial pinna from cardboard with the same shape as the normal

Table 1. *Physical dimensions of Tammar wallaby external ear (see also Fig. 1C)*

	Circumference (cm, $2\pi a$)	Average radius, a (cm)	Path length (cm)	Height (cm)	Width (cm)
Pinna mouth (face)	16	2.5	4.5*	7	3.5
Pinna throat (entrance to meatus)	2.5	0.4			
Tympanic membrane	1.6	0.25	1.6		

* Based on estimated average acoustic path length from tip of pinna to throat and base of pinna (tragus) to throat.

pinna but approximately double the linear dimensions. The enlarged pinna was then placed over the normal pinna and was seen generally to increase the pressure by about 4–5 dB (Fig. 4A) as a result of increasing the surface area of the mouth of the pinna (see Discussion). Importantly, the peak in the gain curve is maintained around 5 kHz, which does not support the idea of a horn resonance at this frequency, which would otherwise have shifted to a lower frequency as a result of the increased path length of the enlarged pinna. Thus the normal peak in the amplification of sound pressure by the external ear results mainly from meatus resonance.

Directionality

A typical frequency series of directionality plots is shown in Figs 5 and 6. The position of the acoustic axis in space can be determined from the peak sound pressure measured at the tympanic membrane and is either associated with a series of iso-intensity contours (Fig. 5) or as a maximum from a polar plot for speaker movements in the horizontal plane (Fig. 6). In the wallaby, the position of the acoustic axis depends on the orientation of the pinna on the head. Under natural conditions each pinna can be rotated without distortion, through angles of up to 100° in the horizontal plane (Coles & Hill, 1981). For example in Figs 5 and 6 acoustic axes are about 45° from the midline when the ears are set to the 'resting position' that was used for data collection in this study (see Fig. 2). A physical re-positioning of the pinna, independent of head position, was found to move the acoustic axis and the entire directionality plot accordingly, with the forward or rearward limits normally determined by the muscular control of the pinna. It is useful to note that the acoustic axis is located approximately perpendicular to the open face of the pinna in the horizontal plane (for frequency effects see below). In the vertical plane the face of the pinna (in the living animal) is normally held in an inclined position, about 40° to the horizontal plane (see Figs 1, 2).

From the two-dimensional plots shown in Fig. 5, the 1 dB contour level surrounding the acoustic axis is almost circular for low frequencies up to about 6 kHz. As stimulus frequency increases to 20 kHz, the central, high sensitivity region of the directionality plot becomes elliptical and tilted towards the midline (see Fig. 5, at 10 kHz). For frequencies above 20 kHz there was a tendency for the axial region to become somewhat flattened in the vertical plane (Fig. 5, 20 kHz). Above 30 kHz, directionality became very difficult to determine reliably. This is likely to be due to the irregularities in the shape of the pinna, and the presence of the head producing increasingly complex sound paths at very high frequencies.

It was clear that as frequency increased the ear became more directional, which is indicated both by the closeness of the iso-intensity contours near the acoustic axis (Fig. 5) and the sharpness of the main lobe (Figs 2, 6). Changes in directionality were quantified by measuring the greatest difference in sensitivity (dB_{max}) between any two positions on the directionality plot for each test frequency. The results are shown in Fig. 7 for four ears, and indicate that for frequencies below 1.5 kHz no significant directionality exists from pressure transformation by the external ear. Directionality rises steeply above 4 kHz, ranging from 30 to 60 dB for frequencies

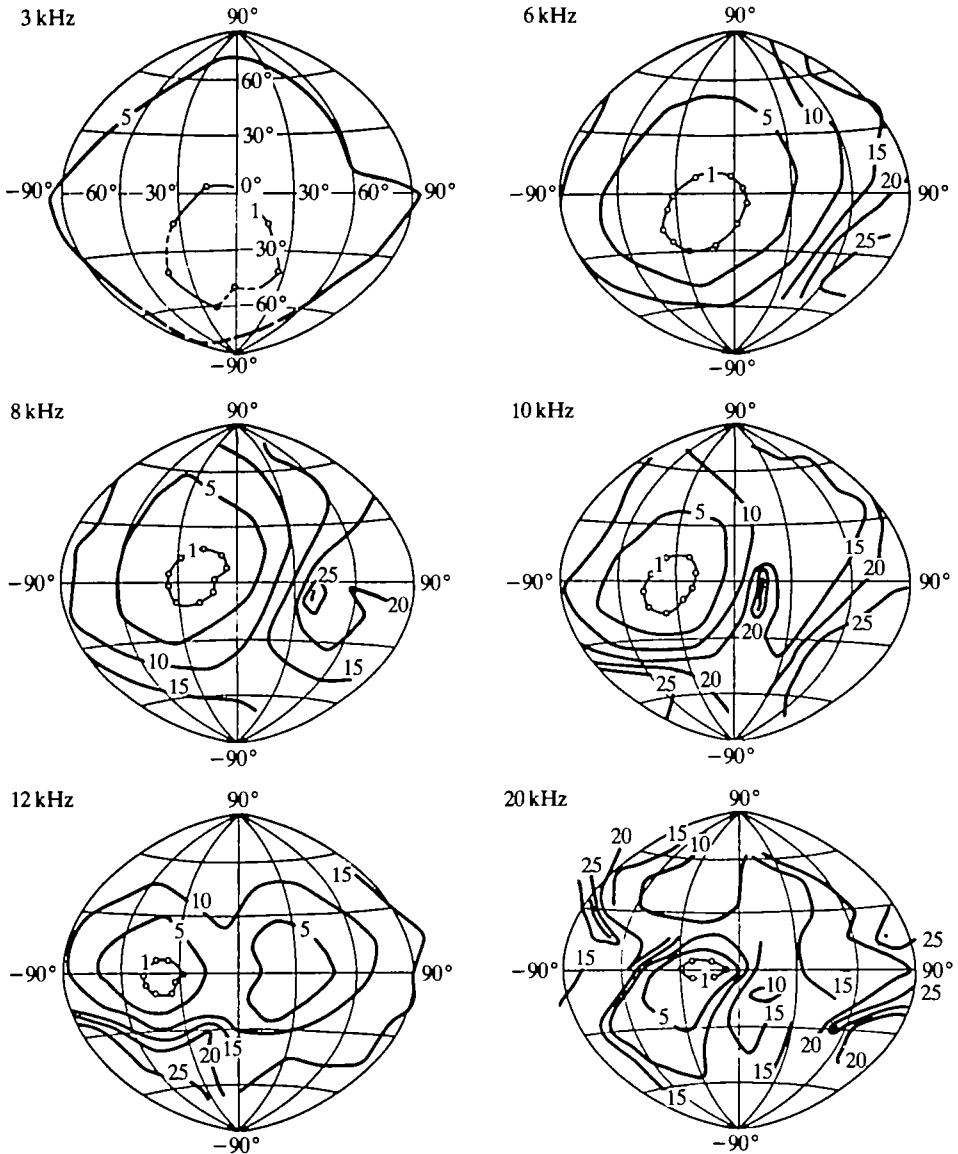


Fig. 5. A series of iso-intensity contour plots showing development of directionality for a left ear (in resting position) at six test frequencies. The acoustic axis is shown surrounded by the 1-dB contour (open circles). Continuous lines representing 5-dB decreases in sensitivity relative to peak values are also shown as contours. The closeness of the contours indicates steep angular gradients, which are usually associated with low pressure regions such as nulls (indicated as a short thick line or dot). The data plotting coordinate system is a zenithal (azimuthal) projection of a hemisphere (see Materials and Methods, and Neuweiler, 1970). A 30° interval grid is used to simplify the illustration of data points, during data collection the speaker was positioned with a $\pm 0.5^\circ$ accuracy in azimuth and elevation.

between 5 and 20 kHz. Such high directionality is largely determined by the presence of nulls in the directivity patterns (Figs 2, 5, 6, see below) and also a combination of high positive pressure gain seen in the mid-frequency range (Fig. 3).

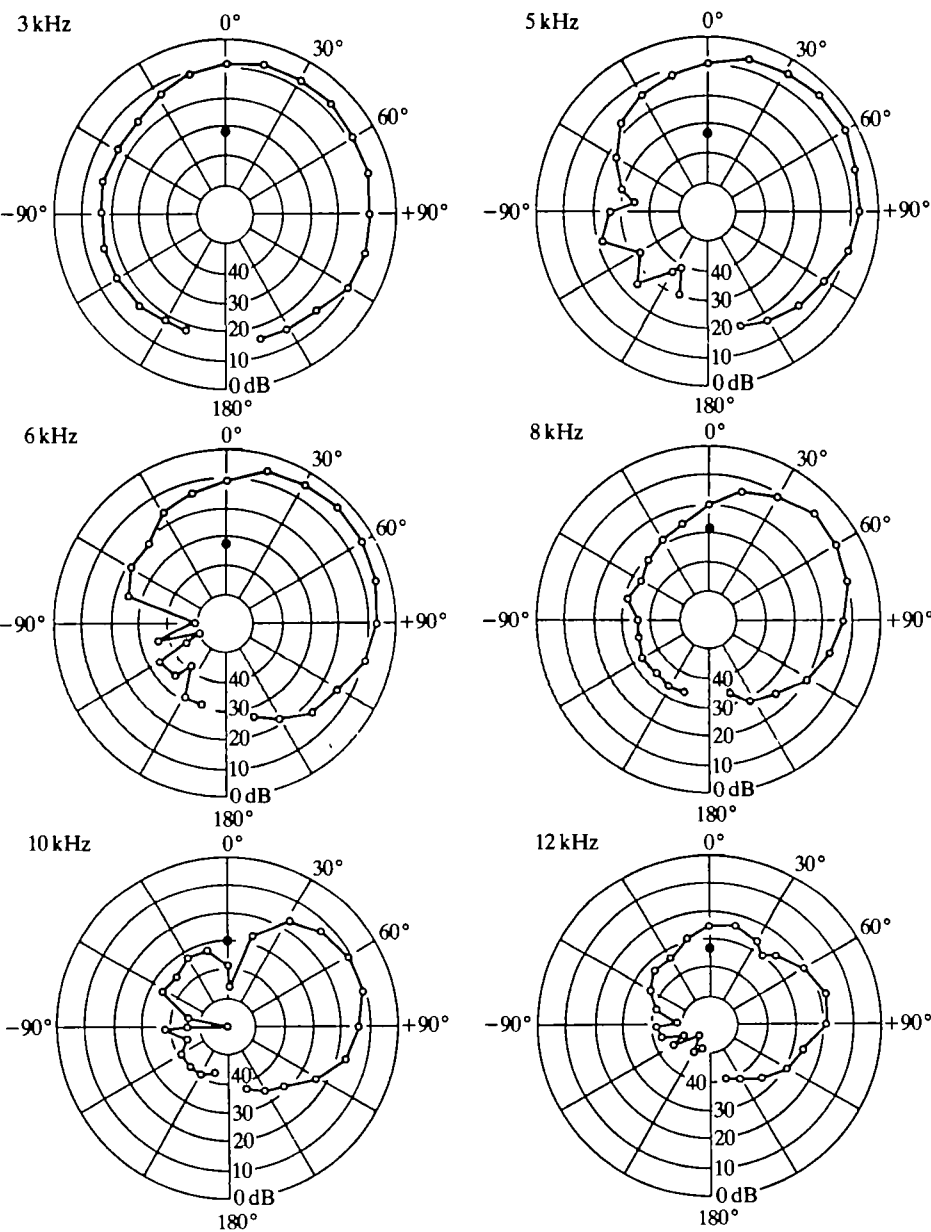


Fig. 6. Polar response curves showing directionality for a right ear, taken on the horizontal plane. Decreasing sound pressure occurs towards the centre of polar diagram as defined in Fig. 2. 0°/180° is the midline with 0° forward, +90° is ipsilateral and -90° is contralateral. The development of the acoustic axis and nulls can be compared to Fig. 5. Note that the correct alignment of the pinna in the vertical plane (see Fig. 1C) results in both the acoustic axis and the frontal diffraction null being on the horizon, for example at 10 kHz.

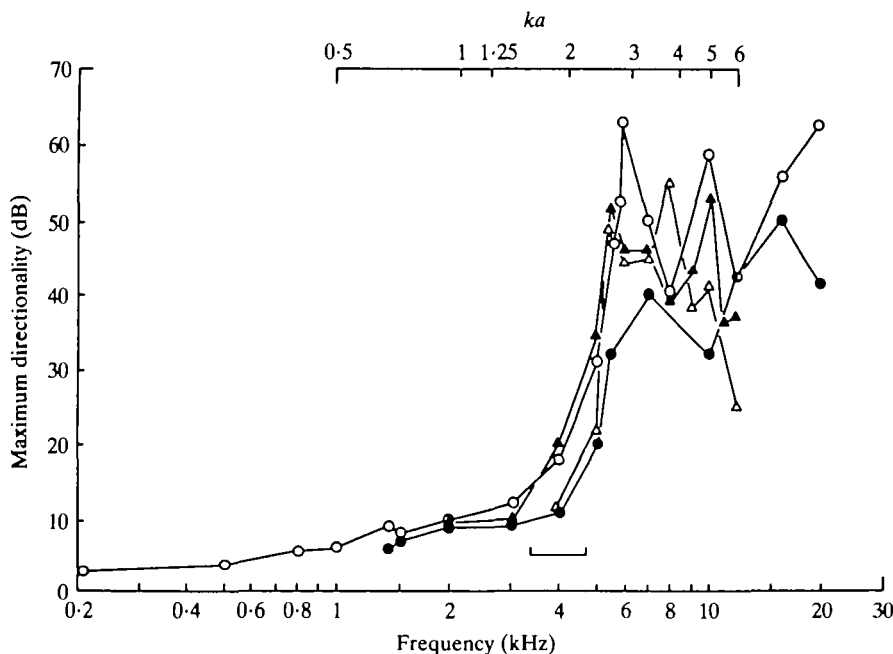


Fig. 7. The maximum directionality (defined here as the greatest difference in sensitivity in dB between any two points on a directivity pattern) as a function of stimulus frequency for four ears. Responses are nearly non-directional below about 2 kHz (acoustic axis difficult to define). The rapid rise in directionality above 4 kHz results from the development of minima or nulls in the directivity patterns (see Figs 2, 5, 6). Deep nulls combined with high amplification of sound pressure result in directionality values exceeding 40 dB above 5–6 kHz. The ka parameter ($2\pi a/\lambda$) shows that the directionality of the pinna, as for a physical system based on sound diffraction at a circular aperture, starts to increase above $ka \approx 1.25$ and becomes highly directional above $ka \approx 3$ (see Beranek, 1954; Fletcher & Thwaites, 1979). The bar at 3.4–4.7 kHz represents the range for the onset of directionality of a physical system based on a 3 to 6 dB criterion.

Another method of assessing directionality is to examine the angle covered by a given decrease in sensitivity from the acoustic axis. In physical systems, a 3 dB point (relative to the maximum response) is often used to compare directional devices (Beranek, 1954). Fig. 8 shows the estimated angular width or acceptance angle in degrees as a function of frequency, using the -3 dB point either side of the acoustic axis. Both the azimuth (Fig. 8A) and the elevation (Fig. 8B) acceptance angles have been calculated separately due to the asymmetry of the acoustic axis at high frequencies (see Fig. 5). From Fig. 8 it can be seen that the angular width of the main lobe of the directivity patterns, containing the acoustic axis, is inversely related to frequency in a systematic fashion. Non-directional directivity patterns have acceptance angles exceeding 180° , and acceptance angles ranging from 120° to 180° are seen for weakly directional patterns up to 2 kHz, where the position of the acoustic axis is difficult to define. As directionality starts to increase rapidly above 3.5 kHz (Fig. 7), the acceptance angle along the horizontal plane starts to decrease

from 120° to about 20° for frequencies near 20 kHz. A similar effect is also seen in the vertical plane (Fig. 8B).

The systematic decrease in the acceptance angle for the wallaby ear as a function of increased frequency strongly resembles the sound diffraction properties of a single aperture. The experimental data can be compared to the directionality generated by a circular aperture, for example, based on the average or effective radius of the pinna opening. The aperture of the pinna, calculated from the circumference of the face, has an average radius of 2.5 cm (see above for gain of pinna, and Table 1; Fig. 1). The expected curves are shown in Fig. 8 and are derived from the directivity function for a rigid circular piston in a plane baffle, which is equivalent to the directivity pattern for sound diffraction by a circular aperture (Morse, 1948; Beranek, 1954). By the reciprocity theorem, the directionality of the system as a sound transmitter is the same as that when it acts as a receiver. The off-axis sound pressure amplitude (p_θ) relative to the axial pressure (p) is given by

$$\frac{p_\theta}{p} = \frac{2J_1(x)}{x} \quad \text{or} \quad \frac{2J_1(ka \sin \theta)}{ka \sin \theta}, \quad (3)$$

where $J_1(x)$ is the cylindrical Bessel function of the first kind of order one, k is the wave number ($2\pi/\lambda$), a is the radius of the aperture, θ is the angle of the sound source from the acoustic axis and λ is the sound wavelength. The directivity function $[2J_1(x)]/x$ is unity for $x = 0$ but for larger values of x it has an oscillatory behaviour with amplitude decreasing asymptotically as $x^{-3/2}$. Tables are given by Morse (1948). The acceptance angle for the directional response of the wallaby ear was taken at the -3 dB level or a pressure ratio, $p_\theta/p = 0.71$. By using this criterion to determine the amplitude of the directivity function $[2J_1(x)]/x$, the value of the angle parameter $x = 1.6$. Therefore the relationship

$$ka \sin \theta \quad \text{or} \quad \frac{2\pi a \sin \theta}{\lambda} = 1.6 \quad (4)$$

can be used to plot the variation between the acceptance angle (3 dB down) and the wavelength for a circular aperture of given radius, as shown in Fig. 8. For the most part there is an excellent correspondence between the experimental data and theoretical curve for diffraction. The best fit occurs between 3 and 30 kHz; however, at low frequencies below 3 kHz the wallaby ear is somewhat more directional than would be predicted (Fig. 8A). On the other hand at higher frequencies above about 20 kHz the ear becomes less directional in azimuth than would otherwise be predicted. This effect is seen as an oval-shape of the main lobe when plotted by two-dimensional contours (Fig. 5) and may be due to the elliptical shape of the pinna face (see Discussion).

Nulls

A significant feature of the directivity patterns generated by the wallaby external ear was the presence of regions of low pressure, forming minima. The formation of these approximate nulls became obvious as stimulus frequencies exceeded 4 kHz. In

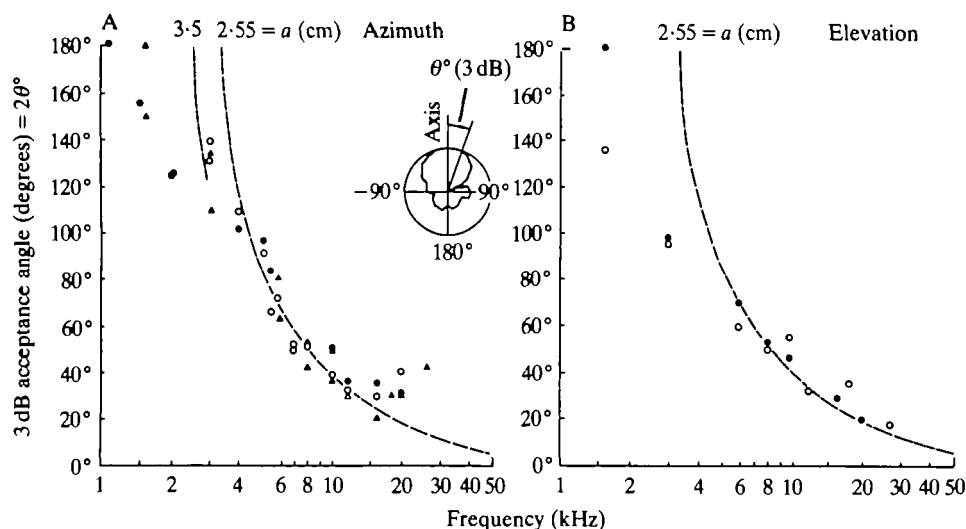


Fig. 8. Measurement of the angular width or acceptance angle (degrees) of the main lobe of the directional response of the wallaby ear for four ears. Values determined 3 dB below peak, expressed as $2\theta^\circ$ where θ° is the angle between the sound source and the acoustic axis. Due to the asymmetry of the directivity patterns (see Fig. 5) azimuth (A) and elevation (B) components are plotted separately. Expected acceptance angles are shown for sound diffraction by a circular openings of radii 2.5 and 3.5 cm (dashed curves), corresponding to the average radius and the maximum radius of the pinna opening respectively (see Table 1). For calculations of acceptance angle as a function of frequency see Results.

the lower frequency range, up to about 7.5 kHz, nulls were generated behind the pinna face up to 150° or so to the rear of the acoustic axis (Figs 2, 5).

The contour plotting method was unsuitable for examining the features of both the acoustic axis and rearward nulls due to their large angular separation and the use of a hemispherical projection. Polar plots were therefore best suited to showing the development of nulls, particularly at lower frequencies, providing the centre of the null was contained in the horizontal plane (see Figs 2, 6). As the frequency increased above 7.5 kHz a second null was seen to develop at the side of the main lobe containing the acoustic axis, i.e. within 90° . This null normally occurred only on the leading side of the plane of the pinna face, towards the front of the head as shown in Figs 2, 5 and 6, and was particularly prominent near 10 kHz. At higher frequencies, multiple nulls were seen and the directivity patterns become very complex, including double sensitivity peaks above 20 kHz (see Fig. 5).

With the pinnae in the resting position (Fig. 2) it was possible to quantify the relationship between major null regions for the ear as a function of frequency. This was done by making measurements in a plane which contained both the null and the acoustic axis (see Figs 2, 5, 6). The results are summarized in Fig. 9 for 35 nulls determined at various test frequencies in seven ears. The rearward nulls are grouped between 160° and 90° from the axis in the frequency range 4–8 kHz, whilst the sideward or leading edge nulls occur between 65° and 30° off-axis in the frequency range 8–20 kHz. The leading edge nulls tend to move progressively towards the

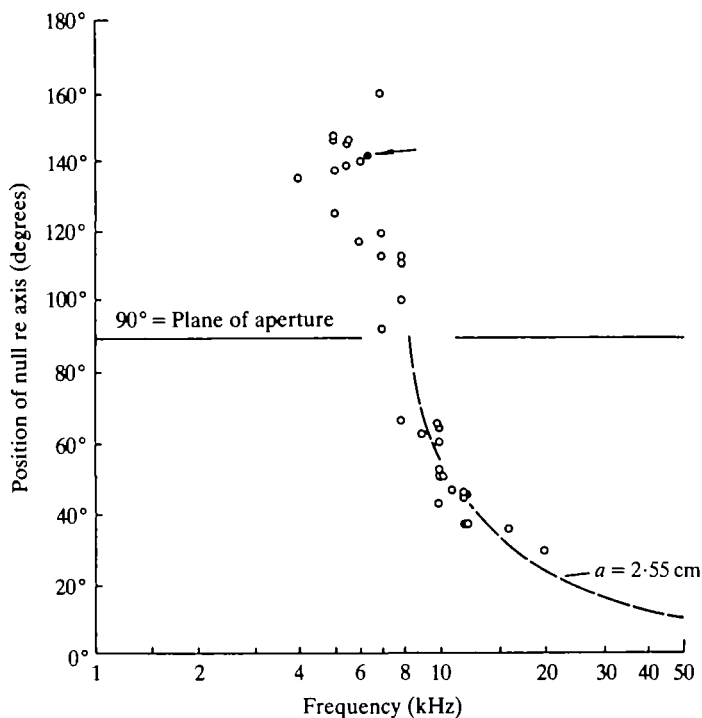


Fig. 9. Angular separation between nulls in directivity patterns and the acoustic axis, as a function of frequency. Dashed line is the expected curve for null positions generated by a circular aperture of radius $a = 2.5$ cm in an infinite baffle (which equals the average radius of the wallaby pinna face). For details of calculations see Results. This approximation can clearly apply only in front of the plane of aperture as indicated on the graph at 90° . However, if the aperture or pinna were considered to be at the end or side of a long pipe then rearward nulls are possible and a calculated null position is indicated by the arrow, taken from Beranek (1954).

acoustic axis as frequency increases, thus improving directionality in frontal space. The results shown in Fig. 9 represent a somewhat simplified view of null behaviour, since obviously several nulls can exist in a single directivity pattern and in different planes, particularly at high frequencies (see Figs 5, 6). Nevertheless, it is useful to compare the present data with the expected position of nulls based on diffraction by a circular aperture, in a similar fashion to that shown for the acceptance angle of the main lobe (Fig. 8).

For the circular aperture, positions of zero pressure or nulls will occur in the directivity pattern whenever the directivity function $[2J_1(x)]/x$ goes to zero (Morse, 1948). This will occur for $x = 3.83, 7.02, 10.17, 13.32$ etc. Thus for the first zero

$$ka \sin \theta = 3.83 \quad \text{or} \quad \sin \theta = \frac{1.22\lambda}{2a}, \quad (5)$$

which will define the semi-angle of the major lobe of the directivity pattern. The relationship in equation 5 is plotted in Fig. 9 for a circular aperture of radius (a) 2.5 cm taken from measurements of the circumference of the pinna face (see Table 1). For simplicity, the calculated curve in Fig. 9 is based on a circular aperture

in an infinite baffle and consequently the first diffraction minimum is generated at 90° , in the direction of the plane of the opening. For the wallaby external ear, this will occur at a frequency given by $1.22\lambda/2a = 1$, i.e. $\lambda = 4.2$ cm (8.2 kHz). The results in Fig. 9 show that the positions of nulls relative to the acoustic axis for the frequency range 7–20 kHz bear a close relationship to the expected values from sound diffraction. It was also possible to plot null positions behind the plane of the pinna opening, reflecting progressively weaker directionality at lower frequencies. Under these conditions, it is more appropriate to consider the location of nulls behind the plane of opening of the pinna in terms of an aperture at the end of or in the side of a long tube (see Beranek, 1954). However, this situation is much more complex than an aperture in an infinite baffle, since sound can be received from all directions and will also be diffracted around the edge of the tube to get to the front of the opening. A single value for a predicted null position from the directivity pattern of a circular aperture in the end of a long pipe has been indicated in Fig. 9 where $ka = 3$ or $\lambda = 5.3$ cm (6.4 kHz). This is taken from Beranek (1954) and compares favourably with experimental values.

Pinna removal

Pinna removal, as described previously (see Fig. 4), in addition to causing decreases in pressure gain, resulted in a marked loss of directionality. For a directivity pattern at 6 kHz, removal of the pinna results in a considerable expansion of the iso-intensity contours emphasizing the decrease in directionality (Fig. 10A). In addition, the polar plot in Fig. 10B shows the loss in directionality and elimination of the null region. The presence of the pinna is therefore essential for the normal directivity patterns measured in the ear canal; however, the head will have an increased effect on sound diffraction at very high frequencies.

Frequency shift of acoustic axis

There was a tendency for the position of the acoustic axis to vary with frequency both in azimuth and elevation. For azimuth angles above 1.6 kHz (where an acoustic axis is first definable) the acoustic axis moves away from the midline from about 40° to a maximum of about 60° for frequencies above 10 kHz (Fig. 11A). However, the effect is not completely regular and variation occurs between individual ears tested. In elevation (Fig. 11B) the acoustic axis moves gradually towards the horizontal plane. At low frequencies (below 3 kHz) the acoustic axis is at about 20° below the horizontal plane and for frequencies above 7 kHz the acoustic axis is maintained close to the horizontal plane. The results for azimuth position of the acoustic axis are dependent on the physical orientation of the pinna on the head, which for Fig. 11A relate to the resting position (see Fig. 2). In the vertical plane, the pinna face has a natural angle of inclination (see Fig. 1C) which results in the elevation position for the acoustic axis being close to the horizontal plane for most frequencies. Overall, there was only a very weak relationship between the spatial location of the acoustic axis and stimulus frequency for the wallaby external ear.

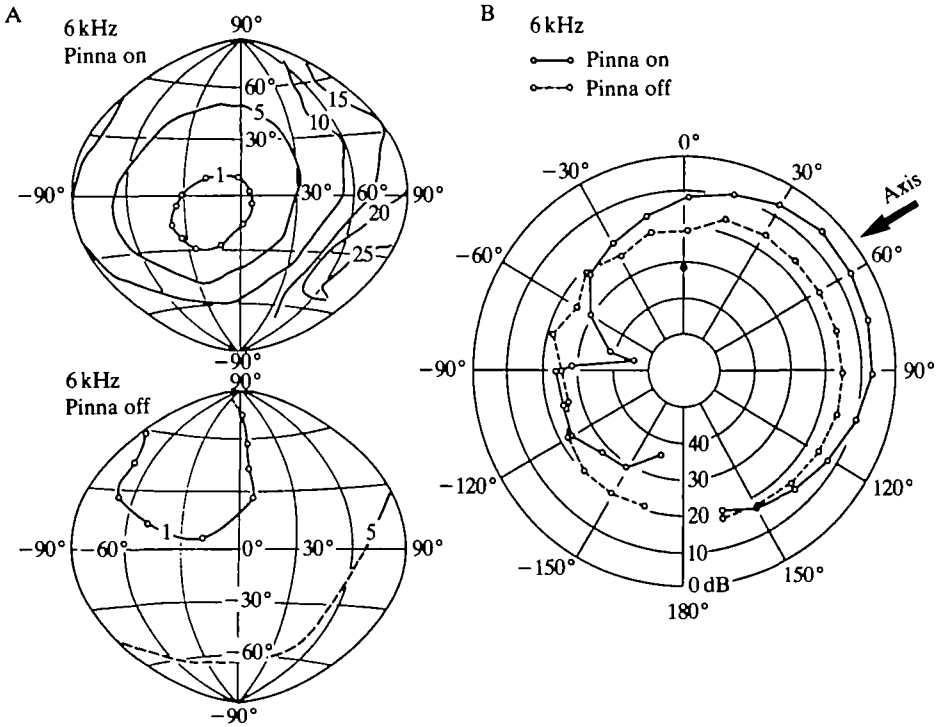


Fig. 10. Effect of pinna removal on directionality. In (A) at 6 kHz, the acoustic axis and associated iso-intensity contour pattern is severely disrupted following pinna removal, with an upward shift in the new peak of sensitivity and the 5-dB contour almost fills the hemisphere. In (B) polar plot shows loss of gain (near axis) and loss of rearward null following pinna removal. Free field sound pressure (69 dB re 20 μ Pa) is indicated by the filled circle. 0 dB level = 100 dB re 20 μ Pa, with decreasing sensitivity towards centre of polar diagram as for Figs 2, 6.

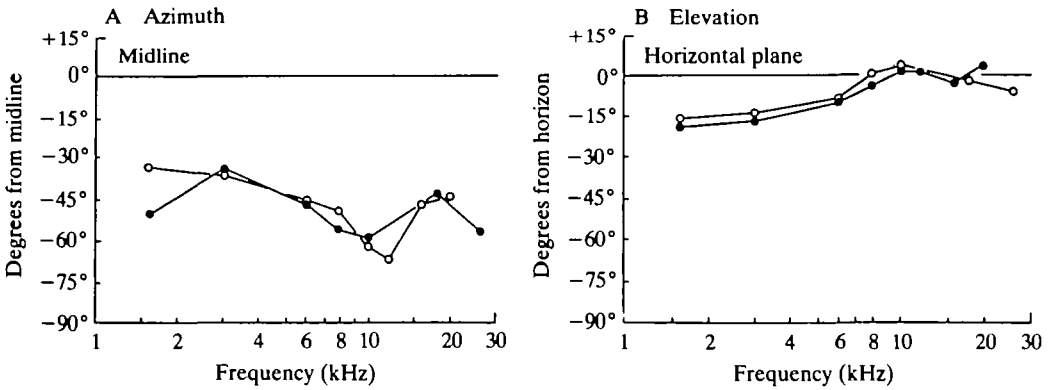


Fig. 11. The effect of frequency on the spatial location of the acoustic axis in both azimuth and elevation. Data from two ears, both maintained in the natural resting position (see Figs 1C, 2).

DISCUSSION

The present study has demonstrated that the external ear of the wallaby provides frequency-dependent amplification and directionality for sound pressure reaching the eardrum. Moreover, an acoustic axis for the ear can be identified as a property of the pinna alone, which is consistent with observations in bats (Grinnell & Grinnell, 1965; Neuweiler, 1970) and the cat (Middlebrooks & Pettigrew, 1981; Phillips *et al.* 1982; Calford & Pettigrew, 1984). The wallaby is therefore typical of many mammals which rely on the pinna and its relative position on the head for directionality and pressure gain. This is clearly distinct from primates, which have immobile pinnae combined with an increased influence of head shadow (Harrison & Downey, 1970; Shaw, 1974).

Acoustic pressure gain

On-axis measurements show that sound pressure reaching the eardrum is amplified across the frequency range 1–30 kHz to varying degrees. The physical basis for the pressure gain of the external ear (Fig. 3) can be explained by two major components.

First, the removal of the pinna causes an overall decrease in gain or amplification eventually resulting in attenuation of high frequency sound above 10 kHz. The pressure gain curve for the pinna (Fig. 4B) shows a gradual increase producing maximum values of 15–20 dB above 10 kHz. If the pinna is considered to act as an acoustic transformer or horn, it is possible to calculate an expected amplification of sound pressure at the throat based on equations 1, 6 and 7 (see Appendix). A calculation based on comparing the area of the face of the pinna to the aperture at the junction of the pinna and meatus (the point at which the pinna was removed) results in an expected amplification of 16 dB (Table 1; equation 2) which, for an efficient horn, is the maximum pressure gain. Such an expected value is close to the experimentally observed values (Fig. 4B). However, the efficiency of an acoustic horn will depend on the size of the mouth and the length of the horn, relative to the wavelengths involved (Beranek, 1954). For a finite-length horn, such as the wallaby pinna, it can be considered an efficient sound collector when the wavelength is less than about $2\pi x_1$, where x_1 is the distance from the apex to the throat (Morse, 1948), which will occur for frequencies above about 3.5 kHz. The pressure gain curve of the wallaby pinna is reasonably close to the predicted curve for a conical horn and it is a useful first approximation considering the asymmetrical shape of the pinna. The gain curve for an equivalent exponential horn would rise too steeply compared to the experimental data. It should be noted that the expected gain curves shown in Fig. 4B are exact solutions for a finite-length conical horn and involve resonance. In principle, resonance is only eliminated from the calculations when a horn is long and the open end (mouth) is wide relative to the wavelength. In the case of the wallaby pinna, horn resonance should disappear when the ratio of the circumference of the mouth compared to the wavelength (ka) exceeds about 3, i.e. the diameter of the mouth starts to exceed the wavelength. In Fig. 4B, ka values for the wallaby pinna

have been indicated and horn resonance may be expected below about 10 kHz ($ka = 3$). No significant resonance peaks can be seen at frequencies which would be multiples of the wavelength corresponding to twice the length of the pinna. The lack of such resonance is probably due to the oblique conical shape of the wallaby pinna, which may reduce the reflection coefficient at the open end. Furthermore, experimental enlargement of the pinna did not alter the peak in the normal gain curve for the external ear. A lower peak may have been expected if the pinna was resonating due to a slight increase in the length of the horn.

A second contributing factor to the acoustic gain seen in the external ear of the wallaby is revealed by the removal of the pinna. From Fig. 4A the remaining meatus section of the external ear retains a distinct peak in gain of 15 dB near 5–6 kHz. Referring to the anatomy of the wallaby ear (Fig. 1C), the pinna is removed at a point which is very close to where the meatus becomes tube-like. The residual peak in the gain curve after pinna removal strongly suggests that the flare of the external ear is sufficiently rapid to cause reflection at the junction of the pinna and meatus in the intact system (see Fig. 1C). The meatus has a length of about 1.6 cm from the base of the pinna to the tympanic membrane with relatively little change in cross-sectional area (Table 1).

If sound is reflected back into the meatus from the open end it is possible to expect tube resonance at a frequency where the wavelength is four times the length of the meatus, since the tympanic membrane represents a relatively rigid termination or closed end (Møller, 1983). Therefore the fundamental frequency for meatus resonance should occur at 5.4 kHz, i.e. $\lambda = 1.6 \times 4$ cm, followed by possible additional resonance at 4/3 times the length of the meatus at 16.2 kHz, i.e. $\lambda = 1.6 \times 1.3$ cm (odd harmonic series). The measured peaks in pressure gain for the normal and abbreviated (pinnaless) external ear both occur near 5–6 kHz, strongly suggesting meatus resonance (Fig. 4A). A second peak near 16–18 kHz may also be attributed to tube resonance, but is considerably smaller than the fundamental, because of reduced reflections from the open end, and perhaps also damping by the soft tissue of the ear canal, irregularities in shape, or even the small hairs lining the cavity. These factors would also contribute to the increasing attenuation of sound pressure in the external ear seen at high frequencies.

The present results compare favourably with the measurements of sound transformation in the cat by Wiener, Pfeiffer & Backus (1966), who found a maximum gain of 14 dB between the entrance to the meatus and the eardrum. The peak in gain, which occurred at 4–6 kHz was also predicted by modelling the meatus as a small rigid tube. Wiener *et al.* (1966) were able to establish a maximum pressure gain from (on-axis) free field measurements of 21 dB in the same frequency region, indicating a 7 dB increase in pressure gain due to the pinna. A more recent study of the cat external ear (Phillips *et al.* 1982) has claimed up to 28 dB amplification due to the pinna determined from cochlear microphonic measurements. In view of the similarity between the cat and wallaby pinna, it would seem that this value has been overestimated. The wallaby pinna produces up to 18 dB amplification based on direct acoustical pressure measurements in the intact and pinnaless condition.

The discrepancy between the two studies probably results from the extent to which the pinna and part of the meatus were removed in order to assess the contribution to pressure gain or amplification. In the study of Phillips *et al.* (1982), less than 5–8 mm of the meatus was left intact after pinna removal, compared to the normal meatus length of about 2.0 cm (Wiener *et al.* 1966). Consequently, the amplifying effect of meatus resonance on the sound pressure developed near the tympanic membrane would not be retained in the cochlear microphonic sensitivity functions studied by Phillips *et al.* (1982). By removing the pinna and most of the meatus, their results (Phillips *et al.* 1982, Fig. 6) are much closer to the sound pressure transformation by the intact external ear (free-field to eardrum) previously described in the cat by Wiener *et al.* (1966). Thus the apparent large ‘amplification by the pinna’ of about 25–30 dB around 3.5 kHz reported by Phillips *et al.* (1982) is more likely to result from meatus resonance of about 14 dB (Wiener *et al.* 1966) rather than pinna (horn) resonance as suggested by Calford and Pettigrew (1984). Similarly the present study of the wallaby external ear has also identified the contribution of meatus resonance to the pressure gain, and in addition the pressure gain resulting from the horn-like properties of the pinna.

Since there is amplification of sound pressure by the external ear in the wallaby, it may be expected to influence the hearing threshold curve. No data on absolute thresholds or frequency sensitivity exist for the wallaby. In other marsupials such as *Trichosurus vulpecula* (Gates & Aitkin, 1982) and *Didelphis virginianus* (Ravizza, Heffner & Masterton, 1969), neural and behavioural thresholds are most sensitive between 2 and 32 kHz. If similar auditory sensitivity exists for the wallaby, then the amplified sound pressure in the external ear is likely to have a significant effect on the frequency response. In the cat, there is evidence that pinnaless auditory thresholds can be up to 20 dB poorer than normal, particularly for frequencies above about 1 kHz (Flynn & Elliott, 1965). Such a result supports the present findings that the pinna acts as an acoustic transformer and would play a significant role in improving absolute sensitivity to sound.

Directionality

There is now clear evidence that the pinna when placed on the top of the head can control the directional response of the external ear for many mammals. The directional responses of the two pinnae are in an essentially mirror-image relationship, and the direction of the acoustic axis of each response pattern simply shifts, to a first approximation, as the pinna is moved. In addition, normal directivity is abolished subsequent to pinna removal. These findings in the wallaby are supported by similar observations in the cat (Middlebrooks & Pettigrew, 1981; Phillips *et al.* 1982; Calford & Pettigrew, 1984).

The physical basis for the directionality of the pinna can be explained by the diffraction properties of its horn-like opening (Fig. 1), which was useful in describing its action as an acoustic transformer (see above). From the present study, directionality increases with frequency, as is to be expected from standard wave theory. However, the wallaby pinna is not an ideal receiver due to its lack of complete

symmetry and attachment to the head at one end. Nevertheless the pinna can be considered, to a first approximation, in terms of the diffraction properties of a circular aperture (Beranek, 1954). The pinna opening has a circumference of 16 cm (Fig. 1; Table 1) and when treated as a circular aperture leads to an expected change in the acceptance angle of the main lobe as a function of frequency as shown in Fig. 8. Comparison between the directionality of the pinna and that expected for an equivalent circular aperture in an infinite baffle (-3 dB down) has a very close correspondence for most of the frequency range tested. At very low frequencies, below 3 kHz, the pinna directionality behaves like a larger aperture, corresponding more closely with the long axis of the pinna face (taken as a diameter). Likewise at high frequencies, above 20 kHz, the pinna has directionality closer to that predicted from the short axis or width of the pinna.

At high frequencies, the wallaby pinna may be better represented by an elliptical opening since it has an elongated shape (Fig. 1; Table 1). This would help to explain the flattened appearance of the major lobe for directivity patterns at high frequencies (Fig. 5), since the diffraction patterns will become increasingly less directional in the plane orthogonal to the major axis of the opening (Beranek, 1954). Nevertheless, assuming diffraction by a circular aperture is a useful first approximation for understanding the directional properties of the wallaby pinna. Similar results have been obtained for the cat's pinna by measuring the solid angle taken from the directional sensitivity of the cochlear microphonic (Phillips *et al.* 1982; Calford & Pettigrew, 1984).

The occurrence of nulls in the directivity patterns of the wallaby external ear compares favourably with the expected minima between the main lobe and the first diffraction ring (secondary lobe) of a circular opening of equivalent radius. Such nulls result from destructive interference by the sound waves entering the pinna face. In the case of a baffled opening with the same effective radius as the pinna face, the formation of diffraction nulls would be limited to frequencies above about 8.2 kHz. This is the limit for nulls occurring along the plane of the opening (90° off-axis) when $2a = 1.22\lambda$ (see Results). The nulls in the wallaby ear directivity patterns which are less than 90° from the acoustic axis do not completely encircle the main lobe as would be expected in the ideal case (see Fig. 9). This may be due to the asymmetry of the pinna, particularly in the vertical plane, since the opening is formed from an oblique truncation of the pinna's cone-like structure. The situation is also complicated by the presence of single rearward nulls below about 8 kHz which cannot occur for an opening in an infinite baffle. These nulls, which occur behind the plane of opening of the pinna, are probably comparable to the diffraction patterns which would result from an aperture at the end of a long pipe (Beranek, 1954) or possibly an oblique termination, considering the morphology of the pinna (see Fig. 1).

The directivity patterns for the wallaby ear are nearly non-directional below about 2 kHz, and similarly for the cat (Wiener *et al.* 1966; Middlebrooks & Pettigrew, 1981; Phillips *et al.* 1982; Calford & Pettigrew, 1984). A criterion for the onset of directionality is arbitrary, but the present data show a very sharp increase in

directionality near 4.5 kHz (Fig. 7). This is close to the sound wavelengths which would produce significant directionality for a circular aperture using a 3 or 6 dB criterion (see Fig. 7). Thus for the wallaby pinna and a circular aperture the relationship between the radius (or diameter) of the opening and the sound wavelength is important for determining directionality. This is often conveniently expressed as the ratio of the circumference to the wavelength or ka value (Morse, 1948; Beranek, 1954). As shown in Fig. 7, an ideal receiver would be considered non-directional for $ka < 0.5$ and highly directional for $ka > 3$ (Beranek, 1954). On this basis, the wallaby external ear can be considered to be highly directional above 6.4 kHz. The onset of directionality will occur at about $ka > 1.25$, i.e. the radius of the opening starts to exceed $\lambda/5$, which is about 2.7 kHz for the wallaby ear (Fletcher & Thwaites, 1979). Generally speaking, the average radius of a pinna opening can be used to determine the onset of directionality ($ka = 1.25$), and not the long axis or height of the pinna, as suggested by Phillips *et al.* (1982). For an elliptical type of opening, sound wavelengths equal to the long axis of the pinna face would be at the threshold of producing a high directionality response ($ka = \pi$ or 3.14).

The wallaby external ear amplifies the sound pressure reaching the eardrum at frequencies where significant directionality starts to occur. A high degree of amplification is produced by the pinna acting as an acoustic transformer and by meatus resonance. A pressure gain is maintained for frequencies above the resonance peak of the meatus by the increasing efficiency of the horn-like pinna. Above 4.5 kHz, highly directional responses for the external ear are produced by a combination of sound pressure being amplified on-axis and severe attenuation from null points both behind and in front of the plane of opening of the pinna. From these findings, the design of the external ear, in particular the pinna, can be seen to have a strategic value in the detection and localization of sound. Each pinna can rotate independently through angles of up to 100° in the wallaby, and under normal circumstances the face is held at 40° to the horizontal plane (Coles & Hill, 1981). This results in the acoustic axis always being on the horizon for frequencies producing high gain and directionality (Fig. 11). In azimuth, there is some dependence on frequency for the acoustic axis position, probably due to the slight asymmetry of cross-section (see Fig. 1B), but for the most part the azimuthal orientation of the acoustic axis depends on the position of the pinna on the head. In the cat it has been suggested that the spatial location of the acoustic axis may be frequency dependent (Phillips *et al.* 1982; Calford & Pettigrew, 1984). Unfortunately, these results could be an artifact produced by distortion of the pinna following surgical procedures and unnatural positioning of the pinnae. The location of the acoustic axis of the pinna in the ghost bat (Guppy *et al.* 1984) and moustache bat (Fuzessery & Pollak, 1984) is frequency dependent in both azimuth and elevation. In addition, the barn owl's facial ruff produces an acoustic axis which moves towards the midline sagittal plane with increasing frequency (Coles & Guppy, 1984).

In view of the directional properties of the external ear, in particular the acoustic axis, it would be a useful strategy for a wallaby to maximize its sensitivity to a sound by fixating a pinna on the source. The ability to locate a sound source containing

frequencies above about 2.7 kHz would rely on the angular resolution or spatial gradient provided by the pinna's directivity. Although angular resolution is low near the acoustic axis of the pinna (sensitivity is high) it is very high close to a null (sensitivity is low). Furthermore, the naturally inclined position of the pinna in the vertical plane ensures that the acoustic axis and diffraction nulls are located on the animal's horizon. Monaurally, pinna movement could permit location of a sound source by providing a rising or falling angular gradient. Alternatively, a binaural comparison of sound pressure could retain absolute sensitivity (summation of outputs) and produce unambiguous directional cues (differential output) as has been suggested for mammals (for a review see Erulkar, 1972). From the present study, angular resolution can range up to 10 dB/degree near nulls (see Figs 2, 5, 6) and, when contrasted neurally with a region of high sensitivity such as the acoustic axis, would yield binaural differences up to 60 dB. Such interaural intensity differences would depend on the relative position of each pinna on the head and the bandwidth of the signal. In this sense, the prominent nulls located on the leading side of each pinna in the wallaby would be important in producing frontal spatial regions with high binaural contrast.

The present study, and those concerning mammals with mobile pinnae, raise the question of the neural coding of auditory space. There are several recent reports on the presence of a topographical representation of auditory space in the mammalian midbrain (Palmer & King, 1982; King & Palmer, 1983; Middlebrooks & Knudsen, 1984) or its absence (Wise, Irvine, Pettigrew & Calford, 1982; Wise & Irvine, 1983; Shimozawa, Sun & Jen, 1984). In future experiments, it will be important to establish for mammals with mobile ears, whether such maps are monaural or binaural and also the extent to which they are dependent on ear position. The mobility of the cat's pinna has been overlooked by Harris, Blakemore & Donaghey (1981) when considering the neural coincidence between auditory and visual space. However, it is possible that an efferent copy of ear position as well as eye position may be incorporated into an auditory space map (Jay & Sparks, 1984).

APPENDIX

The impedance coefficients H_{ij} given in equation 1 for a conical horn as derived from Olson (1947) using the formulae in Fletcher & Thwaites (1979) are:

$$H_{22} = \frac{-j\rho c}{S_2} \cdot \frac{\sin k(l + \theta_1)\sin k\theta_2}{\sin k(l + \theta_1 - \theta_2)} \quad (6)$$

and

$$H_{12} = H_{21} = \frac{j\rho c}{(S_1 \cdot S_2)^{1/2}} \cdot \frac{\sin k\theta_1\sin k\theta_2}{\sin k(l + \theta_1 - \theta_2)}, \quad (7)$$

where ρ is the density and c is the speed of sound in air, k is the wave number ($2\pi/\lambda$), l is the length of the horn, $j = \sqrt{-1}$, S_1 and S_2 are the cross-sectional areas of the throat and mouth respectively. The quantities θ_1 and θ_2 are given by $k\theta_1 = \tan^{-1}kx_1$

and $k\theta_2 = \tan^{-1}kx_2$, where x_1 is the distance from the apex to the throat and x_2 the distance from the apex to the mouth.

The radiation impedance of the mouth R in equation 1 for a conical horn is a complicated expression involving Bessel functions. For convenience, values of R can be taken from the graphs found in Olson (1947).

The pressure gain G (dB) at the throat of a conical horn was calculated from equations 1, 6 and 7 by a computer program for the appropriate range of test frequencies. The results are plotted in Fig. 4B and can be compared to the gain curve for the pinna obtained by experimental methods.

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