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ACOUSTIC TRANSMISSION THROUGH THE HEAD OF THE COMMON MOLE, *TALPA EUROPAEA*

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Cues for directional hearing in mammals are traditionally based on inter-aural intensity differences (IIDs) established as a result of the diffraction of a progressive sound wave by the head and pinna, or on inter-aural time differences (ITDs) established because of the separation of the two ears in space. This 'dual hypothesis' has been extended to other animal groups despite the fact that the majority of sub-mammalian animals have head dimensions that are small relative to the wavelengths of the sounds used in communication. Under these conditions, little if any diffraction can occur and time differences become very small. As an alternative to the pressure-receiver principle of the mammalian ear, crickets (Michelsen, 1979) and the quail (Coles *et al.* 1980) use the pressure-difference principle for directional hearing. In a pressure-difference receiver, sound has access to both surfaces of the tympanic membrane (TM) because of an air-filled cavity between the ears which allows sound transmission through the head or body. When the sound pressure level (SPL) acting on the inner surface of the TM is equivalent to that acting on the external surface, the response of the TM (and, therefore, the cochlea) will be determined by the phase difference between the external and internal components. At any one frequency this phase difference will, in turn, vary with the angle of incidence of the sound.

Moles (Talpidae) have no pinna and are regarded as low-frequency hearers. Unfortunately, no audiogram has been reported for the European mole, but positive behavioural reactions have been reported to frequencies between 250 Hz and 3·5 kHz (Kriszat, 1940). They also possess an unusual middle ear structure for mammals showing extensive trabeculation of the caudal ventral skull between the ears. However, the significance of this cavity for directional hearing has not been considered previously. We report the results of experiments to determine the extent to which sound is transmitted across this cavity from one ear to the other.

The plane of the tympana is almost horizontal, the manubrial tips being separated by about 8 mm. The distance between the closest edge of each membrane is 4 mm. A Bruel and Kjaer $\frac{1}{8}$ in microphone was sealed into position so that its membrane

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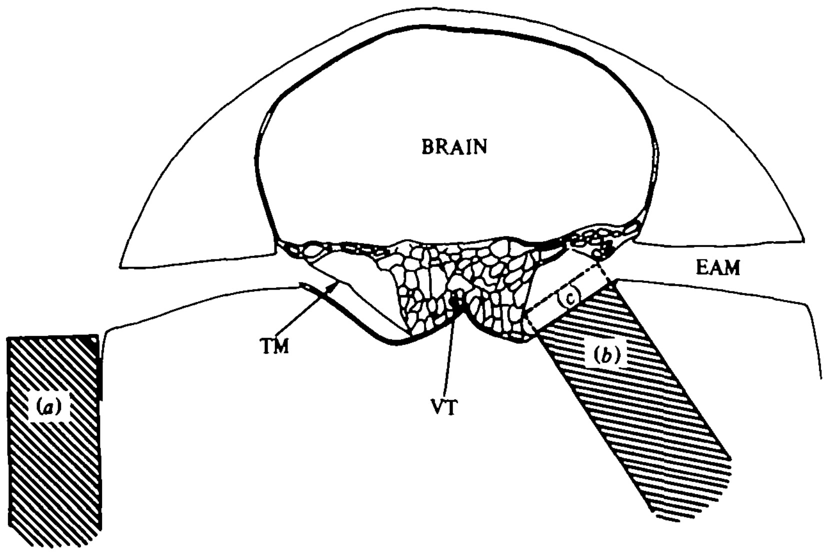

Fig. 1. Diagrammatic transverse section through a mole head to show microphone positions (a), (b) and (c). EAM, external auditory meatus; TM, tympanic membrane; VT, ventral trabeculation.

occupied the position of the removed TM (Fig. 1, position (c)). A second microphone was placed external to the opposite ear (Fig. 1, position (a)). Sound transmission through the interaural cavity was measured in seven preparations in the free field in an anechoic chamber. A representative example of the results is given in Fig. 2A, where the output of microphone (c) is plotted relative to the output of microphone (a) for a number of different frequencies when the loudspeaker was ipsilateral to microphone (a). From 500 Hz to 6 kHz, the internal SPL values are within 6 dB of the SPL values measured externally. Above 6 kHz there is increasing attenuation of the internal sound level with frequency. These experiments were repeated with the meatus proximal to microphone (a) blocked with tissue glue and petroleum jelly. This resulted in severe attenuation of the internal sound at all frequencies. Acoustic transmission across the head was then comparable to that found in similar experiments in the rat (Fig. 2B).

The effects of changing the angle of azimuth of the sound source were also determined for a number of frequencies. Fig. 3A shows that the internal SPL at 1600 Hz (Fig. 1, position (c)) was within 6 dB of the external SPL (Fig. 1 position (a)) for all angles through 360°. Phase measurements were taken internal (Fig. 1 position (c)) and external (Fig. 1 position (b)) to the TM as the sound source was rotated through 360°. When the speaker is contralateral to the recorded ear (Fig. 3B), the phases on each side of the membrane are the same; with the speaker ipsilateral, a phase difference of 180° was recorded.

These results indicate that there is good acoustic transmission through the head of the European mole for a range of low frequencies. Acoustic interaction is therefore to be expected at each tympanic membrane. The fact that the phases are matched

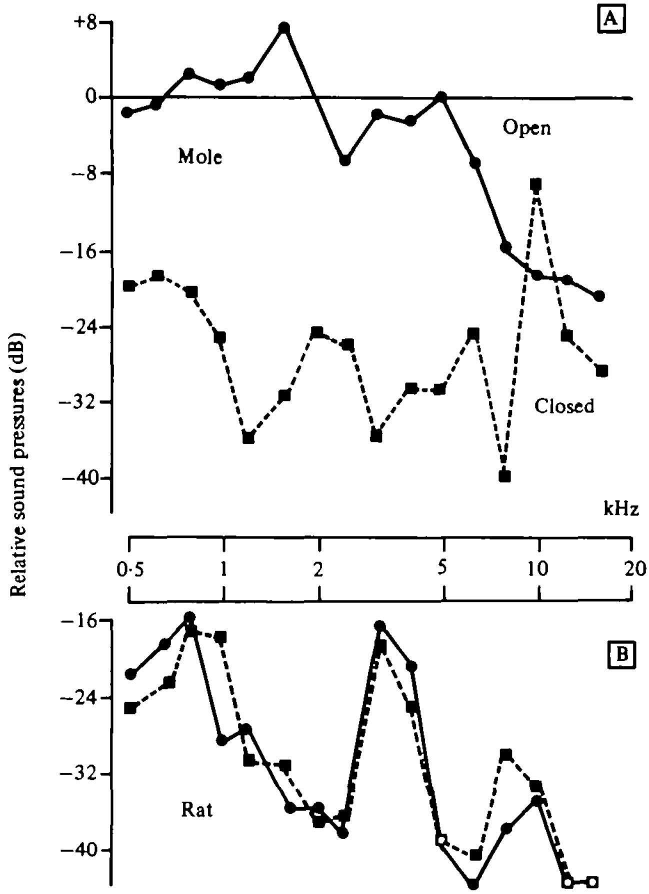

Fig. 2. Measurements of the inter-aural acoustic transmission in the mole (A) and the rat (B). Sound pressure levels were measured at the position of the tympanic membrane [(c), Fig. 1] and are given relative to the sound pressure levels measured at the opening of the meatus, [(a), Fig. 1], ●——●, with contra-meatus open; ■——■, with contra-meatus blocked.

when the speaker is contralateral to the recorded ear also suggests that the response of the TM will be 'nulled' when the sound source occupies this position. At the same time, for the ipsilateral ear the response may be enhanced by up to 6 dB because of the 180° phase difference. Very large IIDs may therefore be created by this means, even at low frequencies.

These biophysical data suggest that the ears of European moles may act as balanced, pressure-difference receivers. This is the first time that such a system has been suggested for a mammal, although many reptiles and amphibia (Henson, 1974), as well as birds and crickets, have been shown to have a direct air pathway between the tympana. Thus, pressure-difference receivers may be common to all animals, regardless of their evolutionary position, that lack pinnae and are preferentially sensitive to low frequencies of sound.

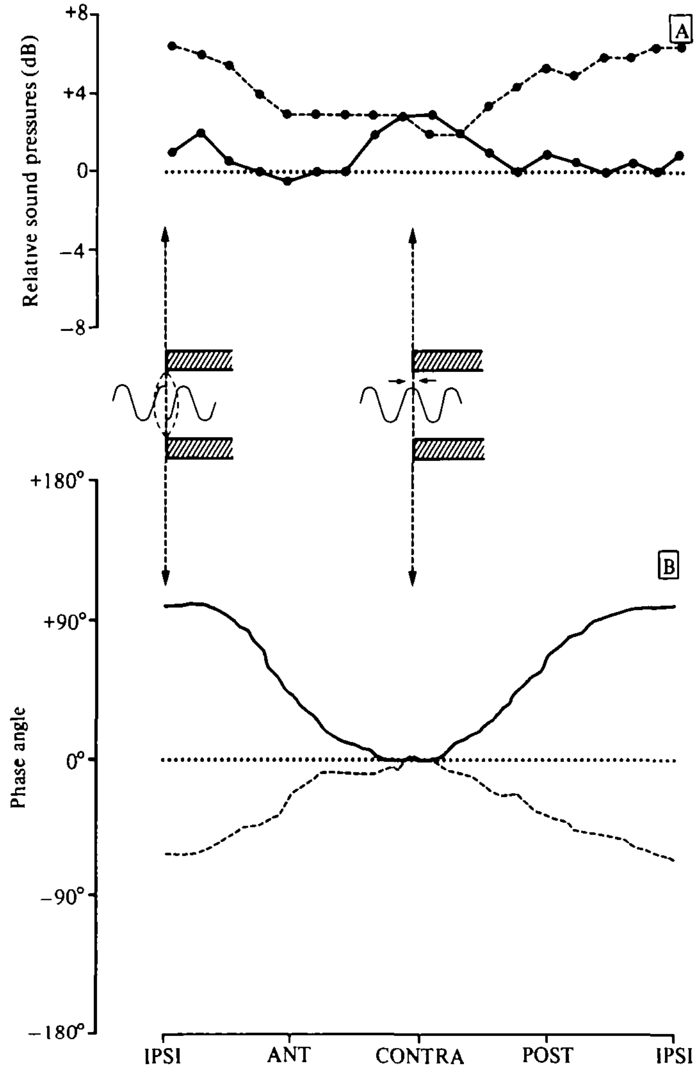

Fig. 3. Relative sound pressure levels (A), and phases (B), recorded internal (——) and external (– – –) to the tympanic membrane at a frequency of 1·6 kHz as the sound source was rotated through 360° azimuth. The sound pressures are plotted relative to the free field and are within 5 dB of each other at all angles; the phase differences change predictably from 180°, when the sound is presented ipsilaterally to the recorded ear, to 0° when the sound is contralateral. These conditions fulfil the requirements for a pressure-difference receiver.

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