



## Vertebrate pressure-gradient receivers

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### ABSTRACT

The eardrums of all terrestrial vertebrates (tetrapods) are connected through Eustachian tubes or interaural canals. In some of the animals, these connections create pressure-gradient directionality, an enhanced directionality by interaction of sound arriving at both sides of the eardrum and strongly dependent on interaural transmission attenuation.

Even though the tympanic middle ear has originated independently in the major tetrapod groups, in each group the ancestral condition probably was that the two middle ears were exposed in the mouth cavity with relatively high interaural transmission. Recent vertebrates form a continuum from perfect interaural transmission (0 dB in a certain frequency band) and pronounced eardrum directionality (30–40 dB) in the lizards, over somewhat attenuated transmission and limited directionality in birds and frogs, to the strongly attenuated interaural transmission and functionally isolated pressure receiver ears in the mammals.

Since some of the binaural interaction already takes place at the eardrum in animals with strongly coupled ears, producing enhanced interaural time and level differences, the subsequent neural processing may be simpler. In robotic simulations of lizards, simple binaural subtraction (EI cells, found in brainstem nuclei of both frogs and lizards) produces strongly lateralized responses that are sufficient for steering the animal robustly to sound sources.

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### 1. Introduction

The ability to determine the direction of a sound source is fundamentally important for all hearing organisms. In mammals and some birds, most notably the barn owl, a large part of the auditory pathway is dedicated to processing of binaural cues related to directional hearing, chiefly interaural time difference (ITD) and interaural level differences (ILD). The mammalian ears are two largely independent pressure receivers. At low frequencies where diffraction is negligible the amplitude response of a pressure receiver is non-directional, and sound direction must be computed by the CNS by binaural comparison, mainly of interaural time differences. At higher frequencies, however, diffraction creates larger interaural level differences; therefore, a strategy for mammals has been to increase sensitivity to higher frequencies where sound diffraction cues are more reliable (Heffner and Heffner, 1992). This is a specialized organization among vertebrates, however. The ears of many of our vertebrate relatives differ

in one important respect: their middle ears are connected through relatively large interaural passages that enable acoustical interaction between the two eardrums. Depending on the strength of acoustical coupling such interactions can lead to strongly increased directionality already at the eardrum, even at low frequencies where diffraction does not produce any reliable interaural differences.

Such interaural coupling leading to a pressure-gradient receiver characteristic was first described in insects 70 years ago (Autrum, 1940) as an adaptive solution to the ‘small animal problem’, since the acoustical interaction enables small animals to have directional cues at low frequencies (i.e. where the wavelengths are much larger than the head size), where the ‘normal’ diffraction and arrival-time cues are negligible. For example, acoustical connections through the cricket trachea generate a useful directionality at the frequency (5 kHz) of the cricket calls (Michelsen and Larsen, 2008), definitively a derived condition in crickets and their near relatives. In vertebrates, in contrast, we now assume that a coupled eardrum system is the ancestral condition of the tympanic ears (Christensen-Dalsgaard and Manley, 2005; Christensen-Dalsgaard and Carr, 2008; Köppl, 2009; Manley, 2010; Novacek, 1977) that originated independently in all the major vertebrate groups. This assumption follows from the observation that the early tympana covered spiracular openings into the mouth cavity (Clack, 1997).

*Abbreviations:* ITD, Interaural time difference; ILD, Interaural level difference; CM, Cochlear microphonics; IC, Inferior colliculus; EI, Excitatory–inhibitory; CNS, Central nervous system.

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Therefore, the early tympanic middle ears were probably exposed in the mouth cavity, and closed middle ear cavities are specialized, derived structures. It may therefore not be so surprising that coupled ears are found in diverse vertebrate groups – anurans, lizards, crocodiles and birds. Fig. 1 shows schematic drawings of the middle ear in three representative tetrapods: frogs, lizards and birds. In all cases relatively large, open air spaces connect the two middle ear cavities. In the following, I will describe the physics of such coupled ears and the anatomical and physiological evidence of increased directionality in the vertebrate groups.

## 2. Biophysics of the coupled ear

The increased directionality of the coupled eardrums is caused by interaction of sound at the external and internal surface of the eardrum (see Feng and Christensen-Dalsgaard, 2007; Michelsen and Larsen, 2008). The driving force for the eardrum vibrations is the instantaneous pressure difference across the membrane. Evidently, if sound arrives at the internal surface of the eardrum with the same amplitude as on the external surface, eardrum motion can be completely cancelled or amplified, depending on the phase difference. It is also evident that if the internal sound component is attenuated, directionality will decrease. In general, if the indirect sound component is attenuated by the ratio  $B$  the resulting difference will vary between  $1 - B$  and  $1 + B$  (see Feng and Christensen-Dalsgaard, 2007 for a more formal treatment). For example, if sound is attenuated by 6 dB by interaural transmission, the attainable eardrum vibrations will range from 0.5 to 1.5 times the amplitude of the uncoupled eardrum, i.e. the maximal directional difference will be close to 10 dB. This also means that if interaural transmission is reduced further, directionality will decrease and become largely insignificant when the interaural attenuation is larger than 15 dB. Also the interaural time differences are amplified by interaural coupling. The phase of eardrum movement is the difference between the phase of the direct and indirect component (weighed by the interaural transmission gain). The phase difference between the indirect component and direct component is caused by filtering by the interaural cavities and

creates an interaural time difference that can be more than three times larger than the arrival-time differences at the two ears (Christensen-Dalsgaard and Manley, 2008; Michelsen and Larsen, 2008).

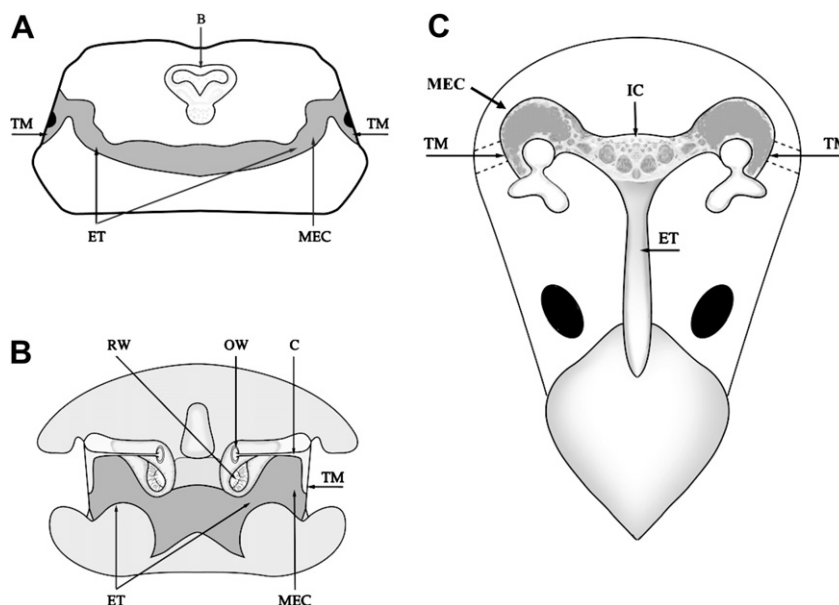
Interaural transmission can be affected by two major factors. One is the loss through the contralateral tympanum, and the other factor is attenuation through the interaural pathways. If the tympanum is insensitive the internal sound can be attenuated by 20 dB or more. An example of this is the basilisk (*Basiliscus vittatus*), where the eardrum vibrations are much smaller than in other lizards studied and the directionality consequently reduced by 20 dB (Christensen-Dalsgaard and Manley, 2008). Sound transmission can also be reduced by the interaural pathways, for example by constrictions in the Eustachian tubes or, speculatively, by the extensive trabeculations in the avian interaural canal. Therefore the presence of interaural connections is not a sufficient condition for increased directionality.

The response of coupled ears is strongly frequency dependent. At low frequency the phase differences between internal and external sound components will be minimal; therefore the driving force will be small, and the eardrum will show little sensitivity and directionality. At high frequencies, the phase difference will exceed one cycle, and the directionality will be a complicated function of frequency. Thus, the typical coupled ear only responds with useful directionality in a certain frequency band. However, the interaural transmission is also frequency dependent, since it depends on the acoustical properties of the mouth cavity or canals connecting the eardrums and on the frequency response of the eardrums. Here, it is conceivable that optimal coupling is found at frequencies outside the range of interest of the animals (most likely the case for the barn owl ear, see below).

## 3. Acoustically coupled ears in the vertebrates

### 3.1. Lizards

The most recently described examples of acoustically coupled ears are the ears of lizards. These ears, it has turned out, are almost



**Fig. 1.** Schematic diagram of interaural connection in a lizard, frog and bird. The middle ear of an anuran (A: *Rana sphenocephala*, redrawn from a section shown in Wever, 1985), a lizard (B: *Sceloporus*, redrawn from Wever, 1978), and a bird (C: zebra finch, *Poephila guttata*, from a preparation, courtesy of O.N. Larsen). Note the large and continuous air spaces in frog and lizard, and the trabeculated interaural canal connecting the bird middle ear cavities (from Christensen-Dalsgaard, 2005).

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