

## Animals and ICE: meaning, origin, and diversity

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**Abstract** ICE stands for internally coupled ears. More than half of the terrestrial vertebrates, such as frogs, lizards, and birds, as well as many insects, are equipped with ICE that utilize an air-filled cavity connecting the two eardrums. Its effect is pronounced and twofold. On the basis of a solid experimental and mathematical foundation, it is known that there is a low-frequency regime where the internal time difference (iTD) as perceived by the animal may well be 2–5 times higher than the external ITD, the interaural time difference, and that there is a frequency plateau over which the fraction iTD/ITD is constant. There is also a high-frequency regime where the internal level (amplitude) difference iLD as perceived by the animal is much higher than the interaural level difference ILD measured externally between the

two ears. The fundamental tympanic frequency segregates the two regimes. The present special issue devoted to “internally coupled ears” provides an overview of many aspects of ICE, be they acoustic, anatomical, auditory, mathematical, or neurobiological. A focus is on the hotly debated topic of what aspects of ICE animals actually exploit neuronally to localize a sound source.

### 1 Introduction

Ears are good for at least two functions: sound localization and communication. Throughout the animal kingdom, azimuthal sound localization depends on the arrival time difference between the left and right ears, considering the sound source is in a horizontal plane with its direction measured by an angle  $\theta$  with respect to a rostral–caudal axis through the horizontal animal. To a first approximation, the time arrival difference equals  $\pm(L/c) \sin \theta$  where  $L$  is the interaural distance between the left and right tympana and  $c = 343$  m/s is the speed of sound in air, 1484 m/s in water (4.3 times as fast as in air), all at 20 °C, or several km/s in rocks and minerals. Accordingly,  $L$  is a key to azimuthal sound localization.

Most land-living animals have either *independent* ears where the left and right ears are only coupled to the outside world’s atmospheric pressure through Eustachian tubes or *internally coupled* ears as shown in Fig. 1. In general, mammals have independent ears, whereas frogs, lizards, birds, and crocodylians have internally coupled ears (ICE). The latter group, constituting the majority of the terrestrial vertebrates, was the theme for a workshop bringing together for the first time many of the experts in this area: the International Workshop on *Internally Coupled Ears: Evolutionary Origins, Mechanisms, and Neuronal Processing from a Biomimetic Perspective* (TUM Institute for Advanced Study, Garch-

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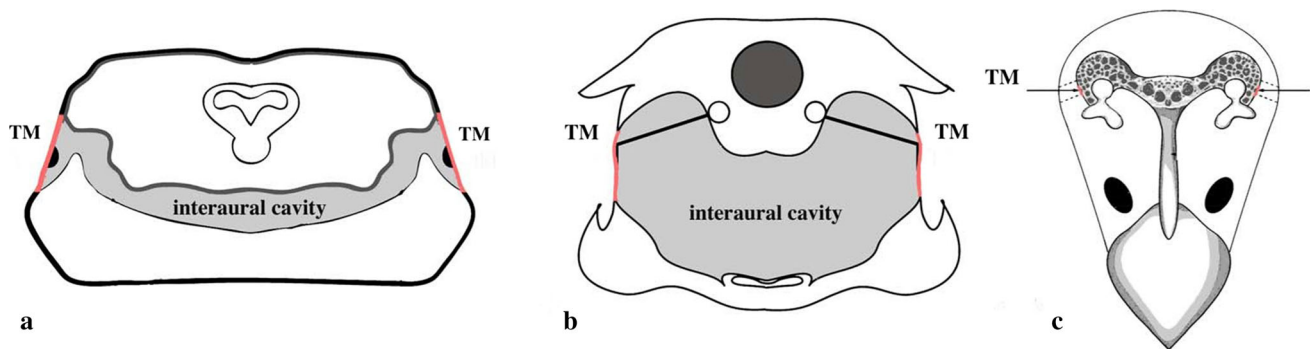
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**Fig. 1** Different realizations of internally coupled ears (ICE) in terrestrial vertebrates: **a** frogs, **b** lizards, **c** birds. The frog and lizard are illustrated with coronal slices; the bird is shown in a transverse slice as a dorsal view from above. The (colored) tympana are surfaces bounding the air-filled interaural cavity, which physically couples the left and right

eardrums. Only in the lizard case are the columellae illustrated, which transfer the eardrum vibrations from the tympanic membrane (TM) to the left and right inner ears (*open circles*), near the brain, here indicated as a *large filled circle*; figure from Christensen-Dalsgaard (2005), redrawn (color figure online)

ing/Munich, June 18–20, 2014). The present special issue of *Biological Cybernetics* is a compilation of timely essays on ICE from the main participants in this “cool” project.

The outline of this Editorial is as follows. We first analyze the appropriate terminology for internally coupled ears. Good terminology is essential to any scientific endeavor, especially for new students in the field. Then, we turn to the evolutionary origin and the underlying anatomy of ICE. On our way, we will meet pointers to the different contributions in this special issue.

## 2 Origin of icy terminology or what is ICE about?

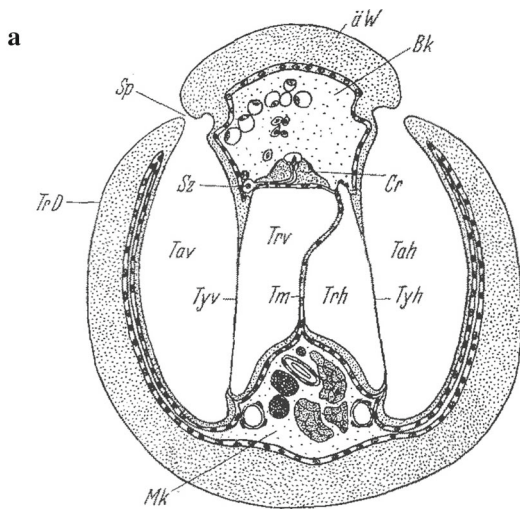
What is the correct terminology for what we now call “internally coupled ears”? As we will soon see, this question is not as harmless as it looks. Here we use the term “internally coupled ears,” or “ICE,” for all forms of mostly, though not uniquely, vertebrate audition in which the two eardrums are connected through an air-filled cavity; cf. Fig. 1. Most terrestrial vertebrates have internally coupled ears, so it is surprising that until recently the theoretical interest in ICE was scant.

Terminology is important because the proper name appeals to our imagination. The earliest name associated with the notion of ICE is pressure-gradient receiver. As we will soon see, this is a misnomer of ICE. The term of pressure-gradient receiver dates back to two papers by Autrum (1940, 1942) Insects such as the wart-biter (*Decticus verrucivorus*), a bush-cricket, were the object of his study and, particularly, the way in which the tympanic organ in a single leg could localize a sound source. Figure 2a depicts a slice through the wart-biter auditory organ that Autrum studied; Fig. 2a is his. He made an apt comparison between this insect ear and a particular capacitive directional microphone of his day, the pressure-gradient microphone (von Braunmühl and Weber 1935); cf. Fig 2b. Hence he called what he found in Fig. 2a, a pressure-gradient receiver, a terminology still used today in electrical engineering and acoustics.

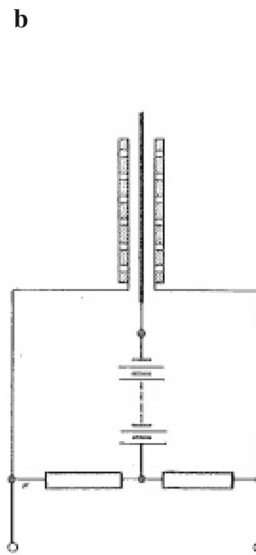
In the pressure-gradient capsule of Fig. 2b, which is Fig. 7 in the original publication of Braunmühl and Weber (1935), the distance between the two plates is small, at best a few millimeters, so that in the case of instrument- and voice-driven sound with wavelengths less than 3 cm (i.e., lower frequencies <10 kHz, quite typical of the music that was recorded) we obtain to close approximation a discretized gradient with a clear cardioid directional pattern. In Fig. 2a (Autrum 1942, Fig. 8), *Tm* is the separating tracheal membrane at the center, while *Tyv* and *Tyh* are a pair of anterior and posterior tympana (positioned in the leg) so that the resemblance of Fig. 2a, b is quite striking.

The resemblance of the bush-cricket tracheal system as shown in Fig. 2a and analyzed by Autrum (1940; 1942) to ICE, however, is minimal. There is indeed a pressure-gradient microphone in each leg and the distance between the two tympana in each leg is very small ( $\sim 0.1$  mm), justifying the notion of (discretized) gradient, but Autrum does not indicate any relation between the two “ears” located in the left and right leg, respectively, which are cm apart. It is now known (Römer and Schmidt 2016) that ears of crickets and bush-crickets receive indirect input from the spiracle in the contralateral leg, quite similar to the key element of ICE as it occurs in vertebrates. As Autrum correctly pointed out, there is just a single directional microphone in the leg, so to speak of the U47 type. In plain English, ICE may well use pressure-gradient receivers, as in bush-crickets, but it is not one itself. Biophysically, ICE is quite different, with a relatively large ( $\sim$ cm) distance between the two (left and right) tympana. In bush-crickets as in vertebrates, the ICE system generates directionality and is, by its very construction, not a receiver but a composition of two different receivers at two different positions.

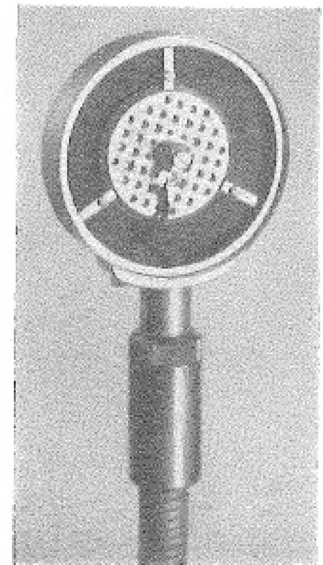
Autrum (1942, Fig. 12) had already put forward the distinction between pressure-gradient and pressure-difference receiver; see Fig. 3. It therefore seems time for turning to the latter. There is no doubt that pressure differences between



**Fig. 8.** Querschnitt durch die Tympanalregion der Vorderschiene des Warzenbeißers, etwa in Höhe der Buchstaben „Cr“ der Fig. 7. äW äußere Beinwand; Bk Blutkanal, in ihm Fettzellen (die größeren) und Blutzellen (die kleineren); an seiner der vorderen Trachee (Trv) anliegenden Wand die Sinneszellen Sz der Crista acustica (Cr); Mk Muskelkanal mit Tracheen, Muskeln, Nerven und einer Sehne; Sp Tympanalspalt (s. Fig. 6); TrD Trommelfelldeckel; Trv vordere, Trh hintere Trachee. Übrige Bezeichnungen wie in Fig. 7. 61:1. Nach SCHWABE 1906.



**Abb. 7.** Symmetrisch ausgeführte Druckgradientenkapsel in Gegentaktschaltung.



**Abb. 8.** Ansicht der einseitig geöffneten Mikrofonkapsel mit einem Außenring aus Gaze.

**Fig. 2** Correspondence or analogy between **a** the tympanic region of the wart-biter, a bush-cricket, as depicted by Autrum (1942, Fig. 8) and **b** a schematic of the pressure-gradient receiver as shown by Braunnühl and Weber (1935, Figs. 7 and 8), which is a capacitive directional microphone, and an outstanding example of microphone development. A truly renowned example was the Neumann U47, which was introduced and produced in Berlin (West) from 1949 onwards and was used in countless famous recordings, even nowadays. It is still highly valued. In Fig. 7 on the right, there are two perforated backplate electrodes (cf. Fig. 8 next

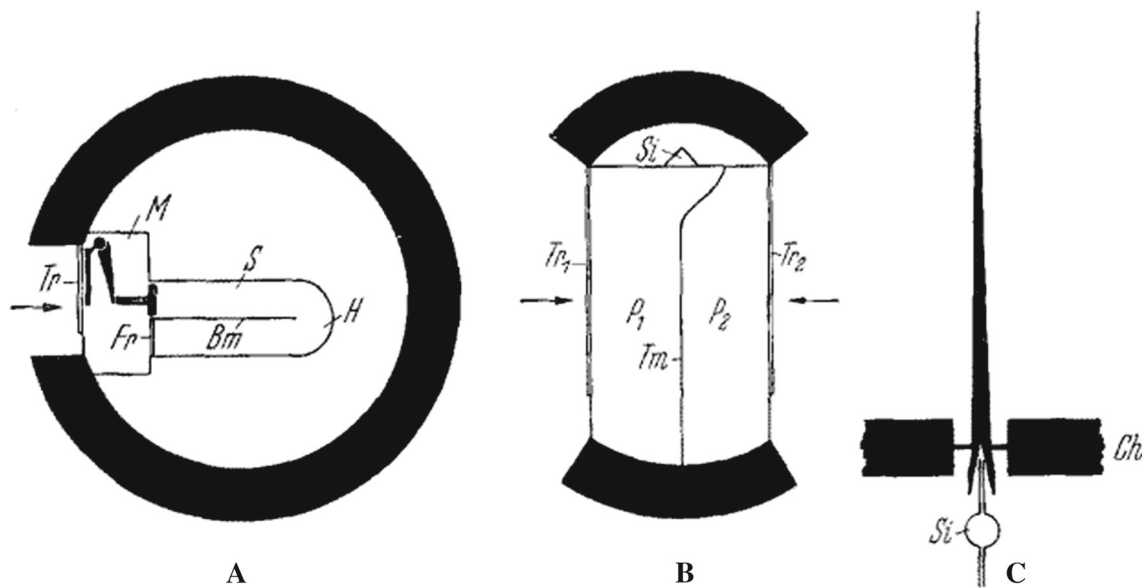
to it) at the top, segregated by a conducting diaphragm in the middle, the vertical black bar. The pressure difference  $\approx$  gradient between the two perforated electrodes, which are separated by 5–50  $\mu\text{m}$ , induces motion of the conducting diaphragm in the middle. In this way, one obtains a condenser with time-varying capacity C(t), which together with two high-ohmic R (horizontal) generates an RC circuit and, hence, a signal. The diaphragm’s analogy to Autrum’s *Crista acustica* (Cr) connected to the tracheal membrane (TM) in Fig. 2a is not accidental

left and right eardrums govern the auditory system’s response and in this way are the basis of binaural hearing. Does this, then, single out ICE? Biologically, it is generally agreed that azimuthal sound localization in vertebrates depends on detecting the time of arrival difference between left and right eardrums. To do so, there are globally two types of audition: internally coupled ears and independent ears. They both use exactly the same pressure-difference technique so that this can never be a distinguishing element of ICE alone.

One could object that what is meant is the pressure difference between the inside and outside a single eardrum but even that does not unambiguously distinguish ICE since all vertebrates with independent ears (except for snakes, which use a totally different system, Wever 1978; Friedel et al. 2008) also exploit the pressure difference between time-varying outside pressure, which is the sound, and the stationary inside pressure, which is kept fixed and equal to the atmospheric pressure through the Eustachian tubes. It has to be constantly borne in mind that tympanic amplitudes are below the  $\mu\text{m}$  range.

Figure 1 underlines that the nomenclature “Internally Coupled Ears” (ICE) uniquely characterizes the biological physics underlying audition in frogs, lizards, and birds. That is, more than half of the terrestrial vertebrates possess a coupling mediated by the air in an internal cavity between the two eardrums. The *Crocodylia* also belong to this class but have a more involved coupling between the two eardrums than the extended cylinder of Fig. 1.

Hardly any statement in biology is without exception since, so to speak, evolution has nearly always found some exceptions “proving” the rule. To the best of the authors’ knowledge, there is a only single example of strongly directional, “internally coupled,” ears known to science that is not of the ICE type as treated in this special issue of *Biological Cybernetics*. In some parasitoid flies, among others *Ormia ochracea* (Miles et al. 1995, Fig. 8; Robert et al. 1996), an internal coupling exists through a stiff cuticular structure, the so-called intertympanal bridge. Despite the small scale of at most 0.5 mm, the spatial resolution resulting from the fly’s two coupled ears and the ensuing neuronal processing



**Fig. 3** Figure 12 of Autrum’s 1942 paper with schematics explaining the difference between **a** a pressure (difference) receiver, **b** a pressure-gradient receiver, and **c** a motion receiver. All three function as *local* detectors. Autrum (1942) assigned **a** to mammals [*Tr* tympanum, *M* middle ear, *S* cochlea with basilar membrane (*Bm*), *Fr* round window] and **b** to the wart-biter ear (Fig. 2) he studied, stressing that an approximate gradient is generated by the small pressure difference  $\Delta p = p_1 - p_2$  between the tympana at a small distance ( $Tr_1$  and  $Tr_2$ ;

*Tr* abbreviates “Trommelfell,” the German for eardrum); *Si* is a sensory organ. **c** is a fast velocity receiver such as the tapered, cylindrical, hairs in the chitin (*Ch*) of crickets. All three cases refer to local receptors, hence called receivers, and so do their present equivalents. **a**, **b**’s time-varying pressures have been indicated by an arrow normal to the tympana. In **a**, there is never signal perception without a difference in pressure between inside and outside, so that Autrum (1942) had already dropped the superfluous notion of difference

is with 1–2 degrees (Mason et al. 2001; Narins 2001) quite amazing and comparable to that of humans. Since it is of a completely different character, with stiff cuticle replacing an air-filled cavity, and occurring only in some parasitoid flies, confusion is easily avoided. Its biomimetic consequences have meanwhile also started to get sounded (Miles 2009), a proper perspective for ICE as well.

*More terminology* What an outside observer can measure are the interaural time and level (intensity) differences, the ITD and ILD. This is not, though, what the animal hears since the internal coupling can, and often will, modify the ITD and ILD strongly. It is the *superposition* of external stimuli with their ITD and ILD, respectively, and the internal coupling that sculps an animal perceives. This is then what we call *internal* time and level difference, *i*TD and *i*LD, respectively, where the lower case *i* delineates the internal quantities.

The internal coupling may lead to pronounced effects. The fraction *i*TD/ITD can become as high as 3–4 in the low-frequency range and, for higher frequencies, the *i*LD can be as high as 20 dB, even though for example most lizards exhibit ILDs  $\approx 0$ . After protracted discussions, there is at the moment some agreement to introduce a special name for the fraction *i*TD/ITD, viz., *time dilation factor* (TDF).

In conclusion, sound-source localization is based on binaural hearing or, in other words, on sound perception by

two ears. This is what the notion of Internally Coupled Ears (ICE) expresses. Pressure-gradient and pressure (difference) receivers describe the action of a single, locally operating, auditory organ, as depicted by Figs. 2 and 3, and by their very nature neither refers to binaural audition, nor to binaural sound localization. That is what makes ICE a unique qualifier.

### 3 Intermezzo

Stepping back for an intermezzo and before proceeding to the evolutionary origin of ICE, a key issue comes to mind: Is there a mathematical theory underlying the many facets of ICE and based on the mere geometry of the interaural cavity and the elastic properties of the eardrums connecting the outside auditory world to the inside cavity and the auditory system that is to perform the neuronal information processing? Surprisingly, there was only an impedance theory (Fletcher 1992). As in any linear system with a periodic input, one can introduce impedances, complex numbers, as fit parameters but that is not an a-priori theory based on geometry and tympanic elasticity only. Based on the 2- and 3-dimensional wave equation that describe waves in the 3-dimensional air-filled cavity and with damping, which is important, in the 2-dimensional eardrums, Vossen et al. (2010) and Vedurmudi

et al. (2016a) were the first to present a complete mathematical theory, the former focusing on lizards and the latter encompassing the characteristics of all terrestrial vertebrates with ICE. It turns out that the 3-dimensional geometry plays a remarkable, unforeseen, role; for details including the key role played by the tympanic fundamental frequency, we refer to Vedurmudi et al. (2016b).

The existence of a full-blown mathematical theory of biological—and in particular neurobiological—phenomena is a necessary condition to be fulfilled for realizing biomimetic applications. Norbert Wiener in his book *Cybernetics* (1948) was the first to develop a vision of neural prosthetics getting implemented through mathematical algorithms. Since in his days the corresponding key notions were not yet available (van Hemmen 2014), the dream was soon over. Now they are at hand and Shaikh et al. (2016) show how ICE can lead to more efficient and robust sound localization in robotics.

#### 4 Anatomy and biophysical mechanisms underlying ICE

Internally coupled ears, or for short ICE, are found in a variety of animals. In many of these species the ability of the auditory receivers to communicate acoustically generates a strong and useful directionality, and the function of these ears is therefore interesting from a biological as well as from a physical and technological point of view.

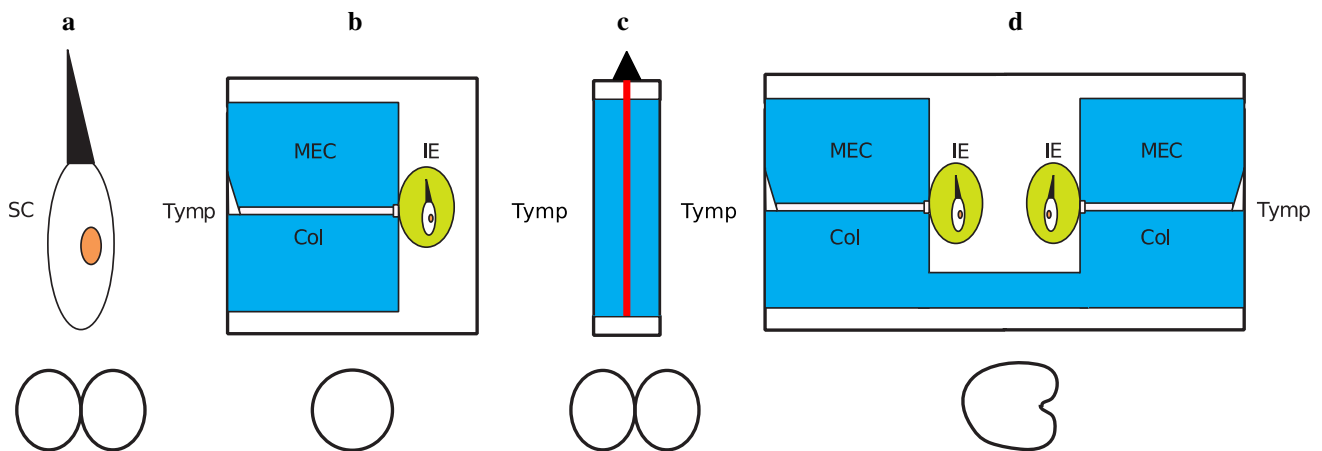
In this Special Issue on *Internally Coupled Ears*, we will focus on animals with tympanic ears, where the tym-

pana are coupled by air spaces, but inner ears can also be coupled by perilymphatic spaces, as has been reported for the non-tympanic ears of salamanders (Wever 1985). The properties of these ears and the consequences for directional hearing have not been studied, however, and the tympanic ears we will feature here are the ears of two groups of insects, the tettigoniids (crickets and bush-crickets) and acridid grasshoppers, and of the tetrapods (the land vertebrates).

#### 4.1 Basic mechanism of coupled ears

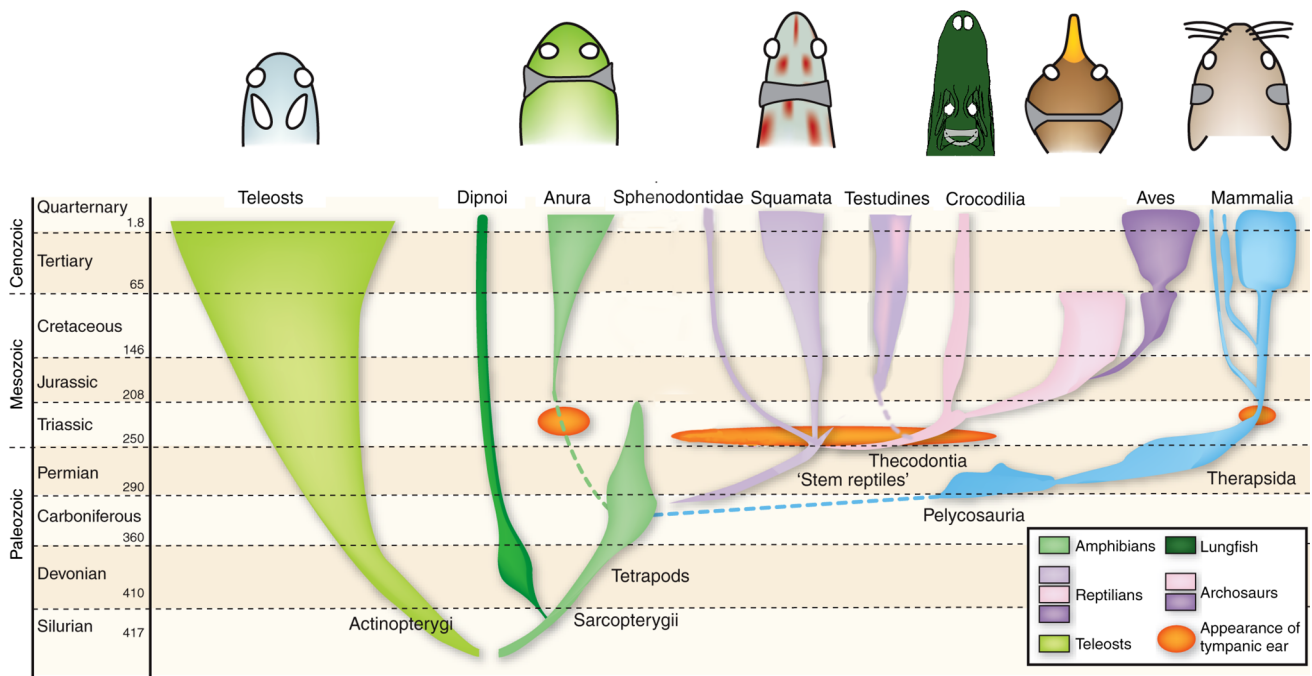
Animal sound receivers come in three main varieties (Fig. 4). The simplest is the hair cell, sensory hair or sensillum (Fig. 4a), that can follow the particle motion of the sound wave and usually has a intrinsic figure-of-eight directivity. Since the particle motion is directional in free-field sound, such sound receivers are directional, albeit with 180° ambiguity since particle motion is directed parallel and antiparallel to the propagation direction. Also, these receivers are limited by the relatively small particle motion amplitudes in the sound wave and generally only respond to close-range sound. However, if the sensillum is connected to a membrane (Fig. 4b), either directly as in insects, or via a middle ear bone as in the tetrapods, it can respond to sound pressure by collecting sound energy over the area of the membrane.

If the eardrum is backed by a closed cavity, as in Fig. 4a, such an ear would be a pressure receiver, generally being more sensitive than the naked sensillum, but non-directional since pressure is a scalar (Michelsen and Larsen 2008).



**Fig. 4** Different types of sound receivers, in a more modern representation than that of Fig. 3: **a** sensory hair, **b** pressure-gradient receiver with two membranes at a small distance and a sensory template with a sensory organ (*top*; cf. *Si* triangle of Fig. 3b) in the middle. **d** internally coupled ears (ICE). Air spaces are shown in blue. SC sensory cell, Tymp tympanum, MEC middle ear cavity, Col columella, IE inner ear. The ears shown are simplified vertebrate or

insect (**c**) ears. *Bottom row* directional diagrams. We note that the figure eight (8) in **c** was already known to Braunnmühl and Weber (1935; Fig. 2). The directionality of **d** shows the response of the left tympanum and is in general strongly frequency dependent. The diagram shows the most directional response; see also Vedurmudi et al. (2016b, Fig. 15). The above plot is based on a figure in Beranek (1954); see also Michelsen and Larsen (2008). A careful comparison with Fig. 3 is worthwhile



**Fig. 5** Evolution of tympanic ears in vertebrates. Tympanic ears evolved independently in the major tetrapod groups, at least five times (in anurans, lepidosaurs, archosaurs, turtles and mammals) during tetrapod evolution and in most cases around the Triassic. Approximate

origins of tympanic ears are shown by orange blotch. The figures above the phylogenetic trees show schematic configurations of the middle ears. Note the coupled ears in four of the groups. After Willis et al. (2013); extended

Accordingly, the CNS needs to compute the direction of sound by other means, usually through binaural comparison.

Formally, however, the pressure gradient is directly related to particle acceleration and that is not what the ear responds to. For a gradient as a differential quotient or a discrete approximation thereof, we need the difference of two function, here pressure, values at two specific positions, say,  $x$  and  $x + h$ , in an, implicitly understood, specific direction:  $[f(x + h) - f(x)]/h$  in the limit  $h \rightarrow 0$ . Rather, the ear responds to pressure differences across the membrane, as all receivers in Figs. 2, 3a, b, and 4b, c do. For the pressure-gradient receivers of Figs. 2, 3b, and 4c, this means  $[p(x + h) - p(x)]$  where  $h$  is the distance between the two nearby membranes;  $h < 1$  mm, much less than any wavelength  $\lambda$  in the ear. The simplest configuration could just be the two membranes of Fig. 4c. The template in the middle would be driven by the instantaneous pressure difference between sound components on its two sides; the left and right faces of the membranes will translate into template motion, resulting in a figure-eight directional pattern with low membrane amplitudes from frontal and caudal directions; see Michelsen and Larsen (2008) for a more formal treatment.

No tympanic ear has a freely standing membrane. Rather, in ICE the tympana as local receivers are backed by a cavity like the pressure-sensitive ears, but directional

responses are generated by enabling sound to reach the internal side of the tympanum, either via interaural connections of the middle ear cavities in tetrapods or via spiracular connections in insects (Fig. 4d). In this configuration, directionality is generated by inputs at *both* sides of the two ears. The directionality of this type of ear, the internally coupled ear, is highly dependent on the attenuation of the indirect sound component relative to the attenuation of the direct sound component, i.e., by the frequency-dependent interaural transmission gain (Michelsen and Rohrseitz 1995, formal treatment in Feng and Christensen-Dalsgaard 2007). The transmission gain (TG) as defined in Christensen-Dalsgaard and Manley (2008) is the *ratio* of the transfer function of the eardrum to contra- and ipsilateral local sound stimulation, i.e.,  $TG = H_{CL}(\omega)/H_{IL}(\omega)$ .

The transfer functions can be understood in the following way. For a given, quasi-stationary, input frequency  $\omega$ , let the ipsilateral eardrum vibration amplitude be  $u_{IL}$ . For an external ipsilateral pressure  $p_{IL}$  and contralateral pressure  $p_{CL}$ , it is given by the linear combination  $u_{IL}(\omega) = H_{IL}(\omega)p_{IL} + H_{CL}(\omega)p_{CL}$  with coefficients  $H_{IL}(\omega)$  and  $H_{CL}(\omega)$  depending on the angular frequency  $\omega$ . These coefficients are called transfer functions. Their mathematical derivation can be found in Vedurmudi et al. (2016b, Section 3) where, for the sake of mathematical convenience,  $u_{IL}$  is rather expressed in

the form  $u_{IL}(\omega) = 1/2[H_{IL}(\omega) + H_{CL}(\omega)] (p_{IL} + p_{CL}) + 1/2[H_{IL}(\omega) - H_{CL}(\omega)] (p_{IL} - p_{CL})$ .

Briefly, the greatest directional difference occurs with unity transmission gain. Here, the eardrum response can range from 0 at contralateral angles to  $2A$  (i.e., twice the amplitude  $A$  in response to the direct sound component alone) at ipsilateral angles and the directional pattern approaches a cardioid. If the indirect sound is attenuated by 6 dB, however, the eardrum response will range from 0.5 to 1.5  $A$ , with a maximal directionality of approximately 10 dB. If the indirect sound is attenuated by more than 15–20 dB (i.e., with a transmission gain below  $-15$  dB), the ear is effectively a pressure-receiver ear as in Fig. 4b.

The tympanic ear of tetrapods is an evolutionary novelty that evolved independently at least five times in the different lineages of tetrapods (Christensen-Dalsgaard and Carr 2008) (Fig. 5). The changes leading to the formation of a functional middle ear in all groups entailed converting the initially immobile hyomandibular bone into a movable stapes. The middle ear of early tetrapods has been hypothesized to have evolved as part of the spiracular breathing system (Brazeau and Ahlberg 2006). The similarities between cranial morphology of fossil sarcopterygian fish and early tetrapods suggest that the ventilatory function of the spiracle was conserved during the origin of tetrapods.

Originally, the hyomandibular bone may have functioned as a cranial brace, but it probably later functioned as an anchor for a spiracular valve. The spiracles, used for ventilation of the gills in aquatic organisms, were probably covered in the terrestrial forms, and in amphibians, lizards, and archosaurs, the tympanic ear was formed from the spiracle (Kitazawa et al. 2015). Since the spiracles opened into the mouth cavity, these tympanic ears were primitively coupled through the mouth cavity. The situation in mammals was different. Here, the incipient tympanic ear formed from lower jaw elements and incorporated two additional small ossicles, and apparently had no direct contact to the pharynx. Thus, internal coupling is probably not the primitive condition of the mammalian middle ear (Christensen-Dalsgaard and Manley 2014).

The tympanic ears of tettigonids may also have originated at least twice (separately in crickets and bush-crickets) (Strauss and Lakes-Harlan 2009). In both groups, the tympana are formed in connection with the tracheal system in the foreleg tibia, and the sensory cells are probably modified chordotonal organs present in the leg before the evolution of tympana. The two tympana are coupled through the tracheal system (Römer and Schmidt 2016). In the acridid grasshoppers, tympanic ears form from thoracic air sacs that communicate across the midline, also producing a coupled ear system.

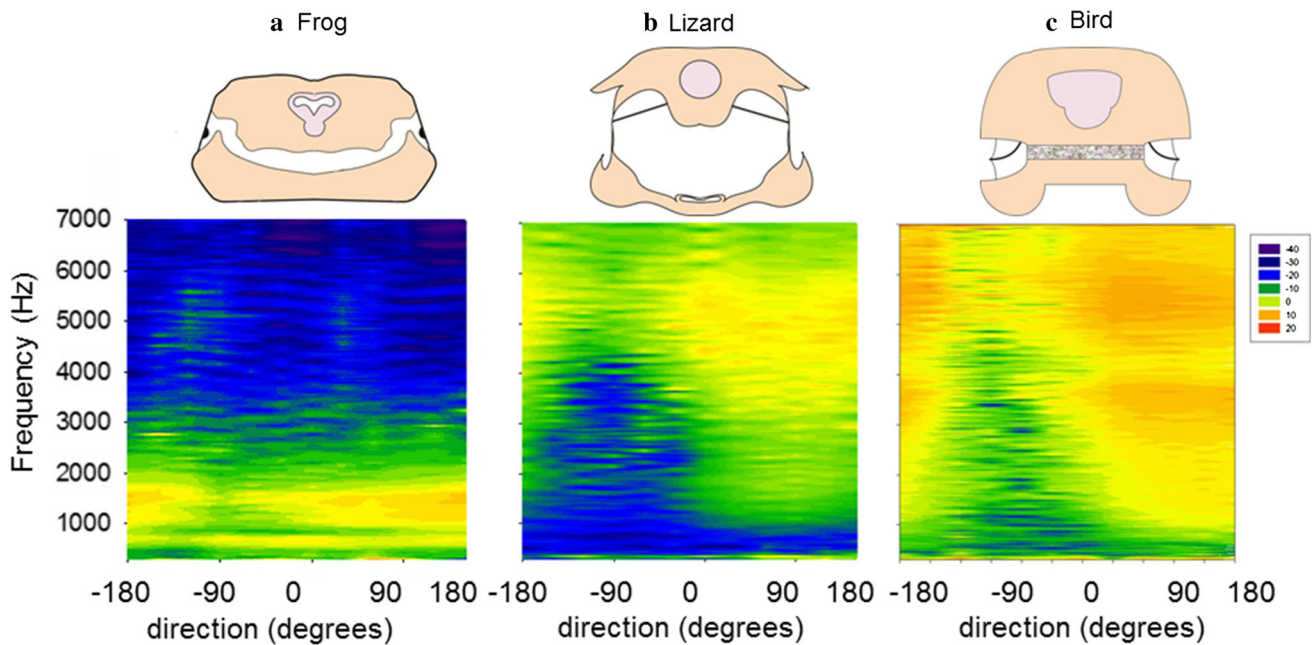
## 4.2 The small animal problem

Since the first description of internally coupled ears—or pressure-gradient receivers—by Autrum (1940), such ears have been seen as an adaptive mechanism for directional hearing. Specifically, ICE have been used to explain the “small animal problem” in hearing: Small animals are challenged, since the usual binaural cues to sound direction, diffraction, and arrival time differences, are small; both decrease with the size of the animal. Thus, selection pressure for effective sound localization can push their signals and hearing toward higher (ultrasonic) frequencies, where the sound diffraction cues generated by their bodies create useful binaural cues.

Alternatively, selection toward efficient interaural coupling can generate directionality also at low frequencies—for example at 5 kHz in a cricket, whose size is a fraction of the wavelength. In insects, this could explain the origin of their coupled ears; in tetrapods, however, this mechanistic explanation fails to address why we find the strongest ICE directionality as a general feature in lizards (see Carr et al. 2016), where the selection pressure for acute directional hearing is obscure—or why all archosaurs, irrespective of size and behavior, have ears that are strongly coupled by large interaural canals. However, as stated above, it has been suggested that at least in three major groups of tetrapods—*anurans*, *lizards*, and *archosaurs* (crocodilians and birds) the ICE represent the primitive organization of the middle ears (Christensen-Dalsgaard 2005; Christensen-Dalsgaard and Manley 2014). Therefore, the presence of interaural coupling does not necessarily represent an adaptation for directional hearing.

An example in point is the barn owl (Kettler et al. 2016): Here, the presence of a large interaural canal provides the owl with directionality around 2 kHz, which are not the frequencies (4–8 kHz) where the behaviorally important sounds are found. Most likely, their large interaural canal is an ancestral trait. Another example could be the moles that probably have developed interaural connections from pneumatizations of the skull (Mason 2016): The emergence of interaural coupling may be an epiphenomenon that is not caused by selection for directional hearing. Conversely, the existence of interaural coupling in itself does not generate strong directionality.

All tetrapod ears are coupled to some extent, at least by intermittently open Eustachian tubes as in mammals, but as outlined above, if the interaural attenuation is large or the eardrums insensitive, the ensuing directionality will be small; see also Christensen-Dalsgaard and Manley (2008) for an example. A factor that may constrain interaural coupling is the emergence of structures such as enclosed middle ear



**Fig. 6** The directionality of coupled ears. The *top row* shows simplified anatomical cross-sectional diagrams of frog, lizard, and bird skulls. The *bottom row* shows cylinder surface plots of eardrum vibration transfer functions, measured by laser vibrometry. Horizontal axis is direction (in angles; positive numbers are ipsilateral directions, 0 is frontal). Vertical axis is frequency in Hz. Eardrum vibration amplitude is shown

by a color scale in dB re 1 mm/s/Pa. **a** Grass frog (*Rana temporaria*, Christensen-Dalsgaard and Manley 2005), **b** house gecko (*Hemidactylus frenatus*, Christensen-Dalsgaard and Manley 2008), **c** zebra finch (*Taenopygia guttata*, Jensen et al. 2010). From Christensen-Dalsgaard and Manley (2014)

cavities that protect the middle ear apparatus. Also, middle ear cavities that are at least partly isolated from the pharynx can shield the ear from respiratory noise. Interestingly, humans afflicted with the condition of patulous, or permanently open, Eustachian tubes complain of autophony, strong auditory response to their own respiration and voice (Hori 2006).

Comparisons of the directionality of the coupled ear in frog (grass frog *Rana temporaria*; see Bee and Christensen-Dalsgaard 2016; Narins 2016), lizard (house gecko *Hemidactylus frenatus*, see also Carr et al. 2016; Young 2016), and bird (zebra finch, *Taenopygia guttata*; see also Larsen et al. 2016) are shown in Fig. 6. All three species show a robust directionality in a frequency band with maximal directional differences of around 10 dB in the frog and bird, but up to 20 dB in the lizard. Evidently, not only the directionality, but also the directional bandwidth is very different in the three groups. In the grass frog, the eardrum is only directional in a 1 kHz band, whereas the directional bandwidth is several kHz in the other two animals. This variation is due to different tuning of several parameters in the middle ear, including eardrum properties and interaural coupling, as discussed in the papers referenced above.

In conclusion, strongly internally coupled ears are found in a variety of animals and, in many cases, generate a useful directionality. Since many coupled ears are not pressure-gradient receivers and not very strongly directional, we therefore propose once more, and on the basis of totally different arguments, that the older terminology of pressure-gradient or pressure-difference receivers should be replaced by the term ICE.

## 5 Outlook and overview

A true puzzle and as yet unanswered is the surprisingly specific question whether and, if so, how the auditory system exploits both the time dilation factor (TDF) with plateau appreciably bigger than 1 in the low-frequency regime and the iLD well reaching 20 dB in the high-frequency domain. The papers of the present issue of *Biological Cybernetics* open a vista of fascinating possibilities. A roadmap for further study can be found in the *editorial* references below.





Participants in the International Workshop on *Internally Coupled Ears* (ICE; TUM Institute for Advanced Study, Garching bei München, June 18–20, 2014) whose essays can be found in the present special issue of *Biological Cybernetics*. Here they gather together in front of a main entrance to the “New Palace” at Oberschleissheim, north of Munich. It was the first international workshop with so many scientists working on ICE getting together and discussing the key notions and questions, trying to define what ICE is about and how it functions in different animals. Left to right, front row: Bruce A. Young, Heinrich Römer, Christine Köppl, unknown guide, Catherine Carr, Geoffrey A. Manley, Natasha Mhatre, J. Leo van Hemmen, and Axel Michelsen; back row: Ole Larsen, Hermann Wagner, Philip Joris, Daniel Tollin, Jakob Christensen-Dalsgaard, Olivia Narins, and Matthew J. Mason. Peter Narins took the photograph.

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