

Directional hearing in insects with internally coupled ears

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Abstract Compared to all other hearing animals, insects are the smallest ones, both in absolute terms and in relation to the wavelength of most biologically relevant sounds. The ears of insects can be located at almost any possible body part, such as wings, legs, mouthparts, thorax or abdomen. The interaural distances are generally so small that cues for directional hearing such as interaural time and intensity differences (IITs and IIDs) are also incredibly small, so that the small body size should be a strong constraint for directional hearing. Yet, when tested in behavioral essays for the precision of sound source localization, some species demonstrate hyperacuity in directional hearing and can track a sound source deviating from the midline by only 1° – 2° . They can do so by using internally coupled ears, where sound pressure can act on both sides of a tympanic membrane. Here we describe their varying anatomy and mode of operation for some insect groups, with a special focus on crickets, exhibiting probably one of the most sophisticated of all internally coupled ears in the animal kingdom.

Keywords Interaural intensity difference · Acoustic trachea · Evolution · Sound localization · Crickets

1 Introduction

The average reader of the “Journal of Biological Cybernetics” performing a search for “animal ears” would focus on the head of an animal. In general, this would be a successful search tactic to gather information about most organisms that are described as model systems in all other contributions appearing in this Special Issue about Internally Coupled Ears (ICEs), which address hearing in vertebrates. However, in the case of insects, this search strategy misses approximately 90 % of all references to ears. Insect ears that include eardrums (tympana) have evolved on nearly all body parts, including the wings of butterflies, the abdomen of moths and short-horned grasshoppers (locusts), the thorax of parasitoid flies and mantids, the forelegs of crickets and katydids, and the mouthparts of hawk moths. Even within a single taxon, such as moths, ears have evolved several times independently, appearing on various locations of the body. For reviews about this tremendous diversity, see [Yack and Fullard \(1993\)](#), [Hoy and Robert \(1996\)](#), [Yack \(2004\)](#) and [Yack and Dawson \(2008\)](#). The most ancient ears are those found in insects; the fossil records date back to about 250 million years ([Gu et al. 2012](#)). One reason that ears have evolved in insects so easily is due to a basic property of their bauplan, namely their exoskeleton, which serves as the attachment site for mechanosensory cells. These anatomical features may be sufficient to allow responses to be made to even minor vibrations induced by pressure waves, even without the further development of the cuticle into a thin tympanum, as is evident in the example of an atympanate bladder grasshopper, which has no fewer than six pairs of ears that are located along the abdominal segments ([van Staaden and Römer 1998](#)). If air-filled cavities connected to the tracheal system (another characteristic of the insect bauplan) occur behind the complex of cuticle and sensory cells, all requirements for an insect

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tympal ear are fulfilled, and various body parts can be induced to vibrate in response to sound (Boyan 1993; Shaw 1994; Field and Matheson 1998).

2 The problem

The selection pressure for the evolution of such ears was different: In crickets and katydids, hearing evolved to facilitate acoustic communication, whereas in moths and mantids, predation by bats potentially drove the selection for a diversity of ears (Fullard 1990; Hoy 1992; Conner and Corcoran 2012). No matter the origin of the auditory system, the detection and identification of acoustic signals have only been two parts of the task. If the sound source lies at some distance from the receiver, the signal needs also to be correctly localized. The most obvious example of this is a prey species escaping away from the predator-induced sound, but other examples include communication systems that have evolved to enable insects to find and approach members of the opposite sex before mating.

Sound localization in mammals, including humans, is based on two kinds of binaural cues: amplitude differences (IIDs) and time of arrival differences (ITDs) of sound waves reaching the ears. Insects, however, are much smaller than mammals, and even within the same insect taxon, large variations in size exist (see Fig. 1 for an example of crickets). Their small size presents a basic problem for the establishment of binaural cues: The interaural disparity is so small that ITDs range from 1.5 μ s (in a parasitoid fly, see Robert et al. 1996) to 5–23 μ s (in crickets of different sizes). At the same time, significant diffraction that allows to generate reasonable IIDs occurs only when the ratio of the body size to the sound wavelength ($l : \lambda$) exceeds a value of 0.1 (Morse and Ingard 1969). Imagine, for example, that the three small cricket species in Fig. 1 are communicating with a calling song at a carrier frequency (CF) of 4.4, 3.8 and 7.5 kHz, which correspond to $\lambda \sim 7.8, 9$ and 4.5 cm, respectively. The $l : \lambda$ ratio would be well below 0.1. Such an unfavorable $l : \lambda$ relationship is the rule, rather than the exception among crickets, and has been documented in a survey of 25 different cricket species, where the $l : \lambda$ ratio of 23 of these species ranged from 0.01 to 0.09, and for the remaining two species, was barely above 0.1 (Schmidt and Römer 2013). The case of directional hearing in crickets and katydids (long-horned grasshoppers) is even more puzzling, since the ears are located on the forelegs, which are much smaller in diameter compared to the body, so that there is virtually no anatomical substrate for providing significant IIDs through diffraction at the relevant communication frequencies. However, despite this strong biophysical constraint, many species have evolved to provide solutions to the problem, sometimes demonstrating a remarkable precision in their abilities to localize sound (reviewed by Robert

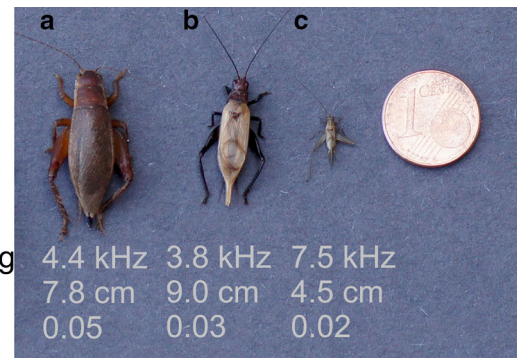


Fig. 1 Size variation of three cricket species: **a** *Amblyrhethus* sp.; **b** *Paroecanthus podagorus*; **c** *Anaxipha* sp. and their differences in carrier frequency (CF) of their calling songs with the corresponding wavelength (λ). Body size (l)-to- λ ratio well below <0.1 indicates that no significant diffraction of sound can be expected to generate useful IIDs

2005). For example, the steering accuracy of phonotaxis in female crickets walking on an open-loop trackball system was measured when the male calling song was presented at frontal angles of sound incidence. In the frontal zone, females reliably discriminated the side of acoustic stimulation, even when the sound source deviated by only 1° from the animal's longitudinal axis, and for angles of sound incidence between 1° and 6° , the females precisely walked toward the sound source (Schöneich and Hedwig 2010). How do these crickets achieve such hyperacuity?

3 The solution

The remarkable directionality displayed by many insect ears is due to the fact that they are internally coupled (for basic principle of directional receivers in insects see Robert 2005; Michelsen and Larsen 2008). As we will see, such coupling can lead to great increases in the strength of directionality, even at low frequencies where diffraction results in unreliable IIDs. Thus, as in the various vertebrate examples given for ICEs, which are discussed in other articles in this Special Issue, sound can reach the external and internal surfaces of the tympanum. The amount of eardrum vibration is determined by differences in the amplitude and phase of the sound pressures that act on both surfaces.

3.1 The anatomical basis for ear coupling

The anatomical basis for such pressure-difference receivers is rather diverse, but is indirectly related to the small body size of insects. Consider the well-studied case of the locust, where the tympanum and connected sensory organ are located in the first abdominal segment (Fig. 2). Even in this relatively large insect, virtually no sound-absorbing tissue exists between the tympana that can acoustically isolate the ears from one other; in fact, large air sacs generate acoustic transparency. This

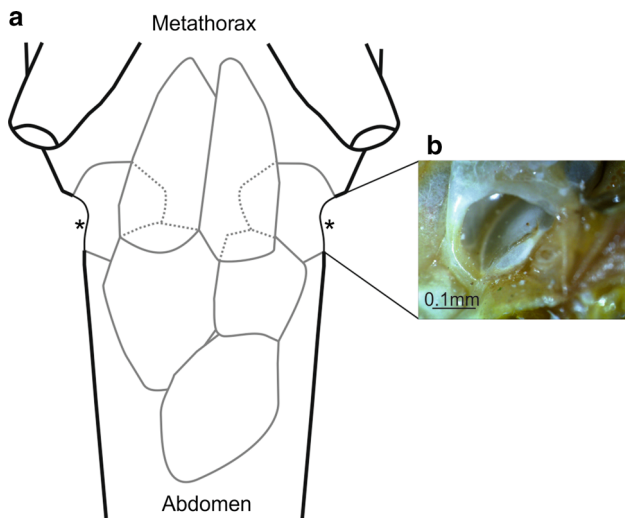


Fig. 2 **a** Horizontal section through the auditory region of *Schistocerca gregaria* (seen from below). The tympana (indicated with a star) on each side of the body are coupled through large, acoustically transparent air sacs. At low frequencies around 4–5 kHz, directionality is determined by sound transmission through air sacs. **b** View on the tympanum of the ear in *Schistocerca gregaria* located in the first abdominal segment

effect depends, however, on the sound frequency. Locusts have a hearing capacity that extends from about 1 kHz far into the ultrasonic range, and their body is large enough to cause considerable diffraction at frequencies >10 kHz, but not at low frequencies. Thus, at around 5 kHz, their directional hearing is dominated by the pressure-difference receiver (i.e., coupling of both ears). Such internal coupling affects the transmission gain for sound propagating through the internal air sacs by around –6 dB, meaning that sound arriving at the internal surface is attenuated by 6 dB compared to sound arriving at the external side. At frequencies higher than 10 kHz, little transmission of sound from contralateral occurs, so that the ear acts more like as unconnected pressure receivers (Michelsen and Rohrseitz 1995; Schul et al. 1999).

In cicadas, the two tympana are located on both sides of the abdomen and are acoustically coupled by large tracheal

air cavities (Fonseca 2014). Sex-specific differences between females and males with respect to contralateral sound inputs exist, which allow sound transmission to the inner surface of the ear. In females, the contralateral spiracle and tympanum have been identified as the most important structures for internal coupling and the pressure-difference mechanism. They facilitate low-frequency directionality with IIDs of ~15 dB within the range of the main calling song frequencies, 3–7 kHz (Fonseca and Popov 1994). In males, however, the sound-producing organ (the timbal) also serves as an important (contralateral) acoustic input that enables directional hearing due to its ability to mechanically resonate at the calling song frequency (Fonseca 1993; Fonseca and Popov 1994; Fonseca and Hennig 2004).

Figure 3a shows another type of sound receiver, which looks like a classical pressure-difference receiver. In katydids (long-horned grasshoppers), the ear is located in the tibia of the foreleg, and a specialized opening in the lateral body wall (spiracle) is connected with a tracheal tube leading to the internal side of the tympanal membrane. Thus, sound waves can impact on either side of the tympanum, but unlike in the example of the locust (Fig. 2), both pressure components originate from the same side. Sound travels at a lower speed inside the trachea and will, therefore, reach the inner tympanum a few micro-seconds later than it reaches the external tympanum, providing the basis for the observed pressure-difference mechanism in the ear (Autrum 1940; Michelsen et al. 1994a; Montealegre-Z and Robert 2015). However, a morphological characteristic of many species is a horn-shaped tracheal tube or acoustic bullae, which acts like an exponential horn to amplify sound to the internal surface of the tympana by 10–30 dB (Lewis 1974; Hill and Oldfield 1981; Heinrich et al. 1993; Hoffmann and Jatho 1995). In such a case, the ear acts more like a pressure receiver, but one where the internal component is higher in amplitude compared to the external one (Michelsen et al. 1994a; Michelsen 1998). The amplitude gain resulting from the transmission properties of such an acoustic tracheal tube mainly bene-

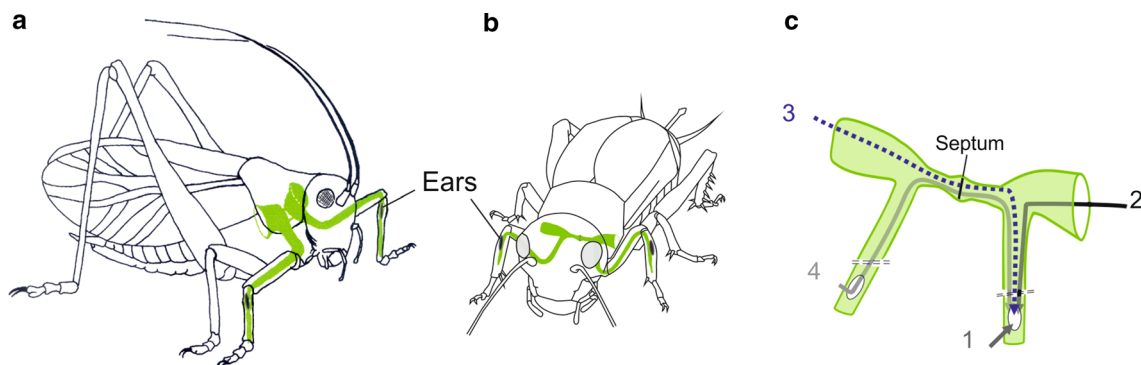


Fig. 3 Schematic drawing of the acoustic tracheal system (shown in green) in katydids (a) and crickets (b). Close-up of the tracheal arrangement in crickets (c) with the four sound pressure components driving the tympanal membrane of the ear

fits sound signal perception rather than directional hearing because it greatly improves the hearing sensitivity (Hoffmann and Jatho 1995). The high level of directionality documented for katydids does not result from diffractive effects of sound at the thin legs, but from diffraction occurring at the site of the spiracular openings in the body wall (Lewis 1983; Michelsen et al. 1994b). However, such useful directional cues based on diffraction can only be achieved for calling songs with frequencies in the higher audio and ultrasonic range.

Even in this pressure receiver dominated by the internal pressure, there is the so far unexplored potential for a pressure-difference receiver. In some species, the acoustic bullae are highly inflated and almost completely fill the thorax, with the consequence that a large amount of their surface area is in direct contact (Bailey 1990). It has not been tested yet whether such close contact of tracheal structures could result in a cross talk between both sides and, thus, represent a form of internally coupled ears in katydids.

Probably, the most elaborate of all internally coupled ears in the animal kingdom is the one that has been described in field crickets; its anatomical basis is schematically shown in Fig. 3b, c. As in katydids, crickets have their ears in the tibia of the forelegs, with two tympana and the associated sensory organ. Field crickets also possess a spiracular opening and a tracheal tube leading to the internal surface of the tympana, like katydids, but this trachea is not formed like an exponential horn. A unique and functionally important characteristic of the system is a tracheal tube that connects both auditory sides, the transverse trachea. Along the midline, the transverse trachea is clearly expanded, forming the so-called acoustic vesicle, in which a soft double membrane (septum) disrupts the trachea that connects both ears. Theoretically, the system allows four different routes that pressure waves can impact the tympanal membrane: through (1) the external sound pressure, (2) the internal sound pressure originating from the ipsilateral spiracle, (3) the internal sound pressure from the contralateral spiracle and (4) the internal sound pressure from the contralateral tympanum (Michelsen et al. 1994b; Fig. 3c). It is obvious that the forces that result in the vibration of the tympanum depend on the difference between the external and internal pressures, and the latter alters in amplitude and a phase shift due to changes in the propagation velocity inside the tracheal tubes. Detailed measurements of sound transmission, with respect to both amplitude and the phase relationship of each of the auditory inputs, have been obtained for the field cricket, *Gryllus bimaculatus*, with different directions of sound incidence (Michelsen et al. 1994b). The authors showed that both the amplitude and phase of the sound transmitted from the contralateral spiracle through the transverse trachea and the septum change dramatically depending on the sound frequencies, which ranged from 3 to 10 kHz. The changes in the phase relationship between sound from ipsilateral and contralateral result from the dif-

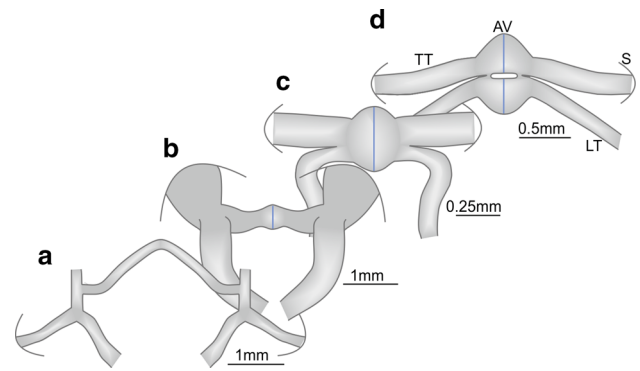


Fig. 4 Differences in acoustic tracheal design shown for a species belonging to the subfamily Gryllacridinae **a** considered primarily non-hearing and three cricket species: **b** *Gryllus bimaculatus*; **c** *Oecanthus* sp.; and **d** *Paroecanthus podagrosus*. TT Transverse trachea, AV acoustic vesicle (blue line indicates the septum), S spiracle, LT leg trachea

ferent path lengths, a reduced sound velocity inside the small tubes (estimated about 250 m/s; Larsen 1981; Michelsen et al. 1994) and the action of the medial septum. A proper phase relationship between sounds that travel through the connecting trachea and the ipsilateral inputs only exists within a narrow range of frequencies around those of the species-specific calling song frequencies (Michelsen and Löhle 1995). The result is a frequency-dependent directional pattern with maximum IIDs ranging up to 26 dB in different cricket species (IIDs measured for the differences in sound incidence at 90° and -90°) (Michelsen and Löhle 1995; Schmidt et al. 2011). The contribution of the septum for directional hearing was examined by perforating the soft membrane; it reduced the IIDs available for localization from 10 dB (measured as the difference between 30° and -30° stimulation) to about 2 dB in *G. bimaculatus* (Michelsen and Löhle 1995). Therefore, the conclusion was that the septum is the essential “phase-shifter” in this system.

However, although the destruction of the septum changed essential characteristics of the phonotactic behavior and localization became less precise, it did not prevent sound localization in a homogenous sound field under laboratory conditions (Wendler and Löhle 1993). Even under field conditions, females could reliably track a male calling song although the same partial destruction of the septum had reduced the directionality of the system by 5.2 dB (Hirtenlehner et al. 2014). Even more puzzling was the finding that in a closely related species, *Gryllus campestris*, the same septum perforation caused a dramatic decline in IIDs over all frequencies tested. This illustrates two things: The medial septum is clearly not the only source for the important phase shift that occurs between the internal and external sound pressures, and subtle differences in the size and shape of the tracheal components of different species (see below) may cause strong differences in directionality.

4 The evolution of ICE in crickets

Apparently, for a proper directionality of these internally coupled ears of crickets, the anatomical details of the tracheal tubes, such as their length and diameter, are important. However, such complex arrangement of tracheal elements in the pressure-difference receiver could not evolve from scratch, so we should ask what its most primitive condition might have been as the starting point in evolution? A comparative anatomical examination of acoustic tracheal structures in a number of species revealed a surprising variety of tracheal types (Schmidt and Römer 2013). Figure 4 illustrates a few tracheal designs that encompass the major differences observed among these species. The simplest type of ICE appears to be an unspecialized transverse trachea with no acoustic vesicle and septum (Fig. 4a). Such a design exists in species that are considered as primarily non-hearing. Considerable differences between species exist in terms of their absolute and relative acoustic vesicle size. The two rain-forest species *Oecanthus* sp. and *Paroecanthus podagrosus* (Fig. 4c, d), for example, exhibit an acoustic vesicle that is 8 and 3 times larger, respectively, than that of *G. bimaculatus*. The most striking elaboration in tracheal design is a double acoustic vesicle (e.g., *P. podagrosus*). Such a morphological feature will have functional relevance in terms of the sound transmission in tracheal tubes, because sound from contralateral can take two parallel routes and can pass through two vesicle membranes on its way to the ipsilateral ear. This has been confirmed physiologically in *P. podagrosus* by destroying one of the two acoustic vesicles, which led to a significant decrease in IIDs (Schmidt and Römer unpublished). Differences also exist with regard to the tracheal tubes located near the spiracle, which can be considerably expanded (*G. bimaculatus*), similar to that of katydids, or have a homogenous tracheal diameter over its complete length (Fig. 4a, c, d).

Using such diversity of acoustic tracheal structures, we may speculate about the evolution of directional hearing in crickets. It has been suggested that acoustic communication in crickets may have evolved originally from a close range interaction of sender and receiver (Alexander 1962). Thus, originally there was no need for sound localization at all. With the advent of an increased active range of the signal and long-range communication, females at greater distances were faced with the task of sound localization that might have been not yet—or only poorly—implemented. Therefore, specific improvements to employ and refine a pressure-difference receiver for sound localization became necessary (the concept of task-punctuated evolution; Nilsson 2009). Consistent with this view is that relatives of crickets that possess no ears and do not use sound for intraspecific communication lack morphological features such as acoustic vesicles or bullae (Jeram et al. 1995; Schmidt and Römer 2013). In the case of Rhaphidophoridae, even a clearly developed transverse

trachea connecting both ears is absent; this might represent the tracheal configuration of a close range communication. Based on neuroanatomical studies, this taxon may even represent a more primitive group than the Gryllacrididae (Stritih and Stumpner 2009; Strauß et al. 2014). However, it is still under debate if the non-hearing state of these lineages is the ancestral or derived condition (Song et al. 2015; Strauß and Stumpner 2015). The close link between acoustic communication and tracheal design is also documented by the fact that in the true crickets (family Gryllidae), the secondary loss of acoustic signaling and/or hearing was accompanied by a reduction in the acoustic tracheal system (Schmidt and Römer 2013).

5 Many open questions left

Unfortunately, we are still far from understanding the physics of sound transmission in the narrow acoustic tracheal tubes, which vary widely in size and anatomy (see Fig. 4). The variety of tracheal configurations among cricket species suggests that a number of different, biophysically relevant parameters can be combined to produce the amplitude and phase shifts during tracheal tube transmission, which finally result in reliable interaural cues for sound localization. Probably, the dominant role of the acoustic vesicle and septum for providing high IIDs (Michelsen and Løhe 1995) has to be revisited. For example, in cricket species, such as *Aphonormorphus* sp. and *Stenaphonus macilentus* (both belonging to the subfamily Podoscirtinae), that secondarily lost acoustic signaling over evolutionary time but still have ears, we found IIDs up to 16 dB. This is surprising because they have a reduced acoustic tracheal system (i.e., thin transverse trachea, no acoustic vesicle; Schmidt and Römer unpublished). What is the biophysical basis for such relatively high directionality? We would argue that the selection pressure for the evolution of an acoustic vesicle and a distinct septum in crickets was not only to maximize IIDs. Although reliable sound localization under natural conditions with high fluctuating directional gradients will require higher binaural cues compared to the 1–2 dB sufficient in the laboratory (Schöneich and Hedwig 2010; Kostarakos and Römer 2010; Hirtenlehner and Römer 2014), females with a manipulated septum resulting in reduced IIDs by 5 dB were nevertheless successful in their phonotactic approach to the speaker (Hirtenlehner et al. 2014).

A reasonable explanation for the presence of highly enlarged (double) acoustic vesicles can probably be found in the evolutionary scenario outlined above, where we assumed that hearing in crickets evolved from a close range communication system, in which the ability for sound localization was not necessary. In this situation, the ear had only to be tuned to the carrier frequency of the male calling song. When the active range of the signal due to resonant signaling expanded,

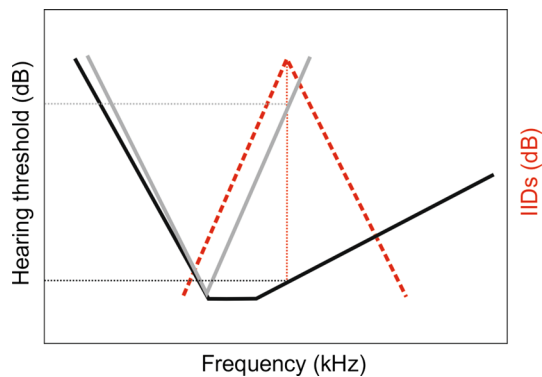


Fig. 5 Schematic illustration of the effect of increased frequency selectivity (*black and gray line*) and the match with the directional tuning (*red dashed line*): In a scenario of low acoustic competition for the communication channel, the sensitivity tuning (shown in *black*) can be rather broad and thus fairly well matched with the directional tuning over a rather large range of frequencies. However, when acoustic competition is high and sharp frequency tuning has been observed (*gray line*), the result is a mismatch of both filters. In such a case, a receiver gains optimal directional cues (high IIDs), but only poor information about the “what” in an acoustic signal (indicated by the high hearing threshold; dotted gray line). The modification of acoustic tracheal design might play a role in the evolution of matching both filters (Schmidt et al. 2011)

females were faced with the localization problem, which was solved by internally coupling both ears with a transverse trachea and a septum in between (Michelsen 1998). Due to the biophysical constraints of internally coupled ears, the system for localization was tuned to a specific frequency. And here is the problem: There are two frequency-selective filters in the receiver, one for sensitivity and one for directionality, and ideally, they both should be matched to the male calling song frequency to provide information about the “what” and “where” of a signal. Apparently, this is not an easy task for evolution, since a survey of both filters in the same individuals had shown that a mismatch between the sensitivity and directionality tuning is not uncommon in crickets, and independent variation of both is possible (Kostarakos et al. 2009). If the tuning of directionality and sensitivity is mismatched, a sender would sacrifice either the sensitivity or the amount of directional cues in the receiver, when calling at a given frequency. It is thus reasonable to assume that specifically in environments with high background noise such a match will be important. When the competition for the air-borne sound channel resulted in a sharp tuning of the sensitivity filter to guarantee an optimal performance of sound detection at a high signal-to-noise ratio, the directionality should also be matched to the very same frequency (Schmidt et al. 2011; see Fig. 5). The species where such a match has been found is *P. podagrosus*, with a double acoustic vesicle arrangement as shown in Fig. 4c. It is tempting to speculate that the perfect match between sensitivity and directionality may be a result of this evolutionary innovation. However, the same double vesicle occurs in other cricket taxa as well (e.g., species of

the subfamilies Nemobiinae and Gryllinae and Phalangopsinae and Podoscirtinae subfamily group), and for all of these, we have neither data on the sensitivity nor the directionality of the ear, so far.

Apart from variations in the acoustic tracheal system, another trait that varies strongly is the size and magnitude of sound-induced vibrations of the two tympana in each ear. In contrast to field crickets, the anterior and posterior tympana in tree crickets (Oecanthinae) and members of swordtail crickets (Trigonidiinae) are of similar very small size (see Fig. 1). Both membranes have similar frequency responses and move out of phase with each other, producing compressions and rarefactions of the tracheal volume backing the tympanum (Mhatre et al. 2009). As the authors argue, the mechanism suggested for producing directional cues in field crickets with only a single principal tympanal acoustic input (i.e., the posterior tympanal membrane) on each leg would be insufficient in the tree cricket system where two functional tympanal membranes (the anterior and the posterior tympana) are involved, leaving open the question of whether and how directionality is produced in the ears of these insects.

6 Conclusions and outlook

Pressure-difference receivers of insects come about in numerous morphological variations, which provide acoustic inputs to the internal side of tympana, in addition to the external input. Crickets have evolved the most elaborate form of internal coupling of both ears with tremendous diversity of acoustic tracheal morphologies. We are just beginning to understand what factors may have facilitated the evolution of some of the acoustic tracheal structures. Given the diversity of tracheal shapes described here, modeling approaches are one way to go, and Michelsen and Larsen provide an in-depth discussion about the parameters to be considered. However, in order to apprehend the evolution of directional hearing in crickets, future studies will need to also integrate anatomical, neurophysiological, as well as biophysical approaches.

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