REVIEW

Directional hearing in insects: biophysical, physiological and ecological challenges

Heiner Römer*

ABSTRACT

Sound localisation is a fundamental attribute of the way that animals perceive their external world. It enables them to locate mates or prey, determine the direction from which a predator is approaching and initiate adaptive behaviours. Evidence from different biological disciplines that has accumulated over the last two decades indicates how small insects with body sizes much smaller than the wavelength of the sound of interest achieve a localisation performance that is similar to that of mammals. This Review starts by describing the distinction between tympanal ears (as in grasshoppers, crickets, cicadas, moths or mantids) and flagellar ears (specifically antennae in mosquitoes and fruit flies). The challenges faced by insects when receiving directional cues differ depending on whether they have tympanal or flagellar years, because the latter respond to the particle velocity component (a vector quantity) of the sound field, whereas the former respond to the pressure component (a scalar quantity). Insects have evolved sophisticated biophysical solutions to meet these challenges, which provide binaural cues for directional hearing. The physiological challenge is to reliably encode these cues in the neuronal activity of the afferent auditory system, a non-trivial problem in particular for those insect systems composed of only few nerve cells which exhibit a considerable amount of intrinsic and extrinsic response variability. To provide an integrative view of directional hearing, I complement the description of these biophysical and physiological solutions by presenting findings on localisation in real-world situations, including evidence for localisation in the vertical plane.

KEY WORDS: Biophysics, Environment, Insect, Sound localisation

Introduction

Sound localisation is a fundamental attribute of the way that humans and other hearing animals perceive their external world. It enables them to locate their mates or prey, to determine the direction from which a predator is approaching and to initiate other adaptive behaviours. Ears that allow the detection of airborne sound have evolved repeatedly and independently in vertebrates (Christensen-Daalsgaard and Carr, 2008) and probably more than 20 times in insects (Yack and Dawson, 2008; Greenfield, 2016). Most hearing animals have bilateral pairs of ears. One exception is the cyclopean, unpaired ear in praying mantises (Yager and Hoy, 1986). The great advantage of having more than one ear is that binaural hearing greatly improves the ability to determine the direction of a sound source. Although most animals with paired ears are able to localise a sound source in space with varying degrees of precision, the binaural cues for sound localisation are often very tiny in the range of a few decibels and some tens of microseconds for many

Institute of Biology, University of Graz, Universitätsplatz 2, 8010 Graz, Austria.

*Author for correspondence (heinrich.roemer@uni-graz.at)

mammals (Grothe et al., 2010), and even more so for small insects. Sounds emanating from a source will generally arrive at the two ears with different intensities and different time delays, depending on the relative orientation of the head in relation to the source. Interaural intensity differences (IIDs; see Glossary) arise from diffractive effects caused by the tissue separating both ears. However, objects smaller than a tenth of the wavelength of the relevant sound have negligible diffractive effects (Morse and Ingard, 1968). This is true, for example, for a small grasshopper with a body width of 3 mm and a wavelength of 7 cm for the relevant 5 kHz sound.

The time of arrival of a sound wave at both ears can also indicate the direction of the sound source. However, the use of such interaural time differences (ITDs; see Glossary) for directional hearing is greatly limited when the distance between the ears is extremely short. For instance, this time difference would amount to only 3 μ s in a small grasshopper with both tympana separated by 1 mm. It is obvious that such short delays impose severe constraints on the sensory system to allow the reliable encoding and processing of sound. Nevertheless, results from different biological disciplines have accumulated over the last decade indicating how small insects, with a body size to wavelength ratio much less than 0.1, achieve a localisation performance similar to that of mammals. Here, I provide an integrative review of directional hearing, starting with the sophisticated biophysical solutions which can provide binaural differences despite the small body size of insects, and how these are reliably coded in few nerve cells. This will be complemented with findings about sound localisation in real world situations, including the evidence for localisation in the less-studied vertical plane. For readers interested in insect acoustic communication and hearing in general, I recommend Hoy and Robert (1996), Gerhardt and Huber (2002), Greenfield (2002), Bradbury and Vehrencamp (2011), Hedwig (2014) and Pollack et al. (2016). Albert and Göpfert (2015) and Albert and Kozlov (2016) provide more detailed reviews on antennal hearing, and Pollack (2000), Robert and Göpfert (2002), and Robert (2005) are highly recommended for various aspects of directional hearing.

Directional hearing with antennae: mosquitoes and fruit flies

Mosquitoes and fruit flies hear with their antennae. In the fruit fly *Drosophila melanogaster*, the antenna is composed of three segments (Fig. 1A): the scapus (a1), the pedicel (a2) and the distal funiculus (a3). The funiculus is tightly coupled to an appendage called the arista. Mosquito antennae consist of a basal pedicel and a long flagellum, with a dense brush of thin hairs rigidly coupled to the flagellum (Fig. 1B). Males of most mosquito species mate in swarms, a behaviour that is mediated by sound, whereby males detect and follow the faint flight tone of females with their antennae (Roth, 1948). The particle velocity component of the sound (Box 1) produced by the female wing beat declines rapidly with distance (Jackson and Robert, 2006). However, owing to active, nonlinear processes in the sensory cells (Göpfert et al., 1999;



Glossary

Background noise: any concurrent sound from abiotic sources (wind, rain, rustling leaves) and biotic sources (sound produced by other animals) that obscures the perception of a signal.

Interaural intensity difference (IID): for wavelengths roughly equal to, or shorter than, the diameter of the part of the body between both ears, a shadowing effect due to diffraction is produced at the ear further from the source, creating an IID.

Interaural time difference (ITD): sound not arising directly from in front (or behind) arrive earlier at one ear than at the other, creating an ITD.

Interneuron: neuron enabling communication between sensory or motor neurons and the central nervous system.

Laser doppler vibrometry: non-contact vibration measurements of a surface. A laser beam is directed at the surface of interest, and the vibration amplitude and frequency are extracted from the Doppler shift of the reflected laser beam frequency due to the motion of the surface.

Masking: a reduction of the signal-to-noise ratio when a signal co-occurs with background noise. Masking increases the threshold for detection by the receiver.

Neuropil: area in the nervous system of insects composed of axon endings, dendrites and glial cell processes that forms a synaptically dense region, containing no cell bodies.

Phonotaxis: orientation behavior towards or away from a sound source. **Response latency:** time difference between the onset of a stimulus and the neuronal response.

Signal: a stimulus produced by a sender and perceived by a receiver, to the average net benefit of both.

Signal-to-noise ratio: amplitude difference of signal and noise, expressed in decibels.

Transmission channel: includes all biotic and abiotic properties of the medium for sound propagation.

Göpfert and Robert, 2000, 2001; Jackson and Robert, 2006), mosquito antennae are extremely sensitive to small deflections in the nanometre range, thus enhancing the capacity of the male to detect and follow a female as she passes by. Furthermore, the viscous forces of the flow of air particles, which become dominant in a layer around an object (for a review, see Casas and Dangles, 2010), can act more efficiently on the dense brush of thin hairs present on the flagellum. This makes the antenna mechanically extremely sensitive to the particle velocity component of sound waves.

The Johnston's organ (JO) in the second antennal segment (pedicel) of the antenna is a sensory organ that detects the mechanical deflections of the flagellum. Its structure and connection to the flagellum would indicate that a relatively simple mechanism is used for the detection of sound direction. The JO consists of an enlarged pedicel filled with radially oriented chordotonal scolopidia. The flagellum is attached to a basal plate, which is recessed deeply into the pedicel. The basal plate consists of a radially pleated cuticle, invaginated into the pedicel as septa and tubular prongs (Belton, 1974). Most of the scolopidia are attached to these prongs. The JOs of male mosquitoes can host up to ~ 7500 scolopidia (corresponding to ~15,000 sensory neurons, as about 97% of mosquito scolopidia possess two sensory neurons; Boo and Richards, 1975). This is by far the largest number that has been measured when compared with the number measured on the same organ in other insect taxa.

Mechanically, the flagellum acts as an inverted pendulum; it can swing in all directions within the plane of suspension. Thus, when the flagellum is moved by the displacement of air molecules in line with the sound source, it will rock the basal plate, stimulating the sensilla that are in line with the displacement of the flagellum maximally and those at right angles to the flagellum, minimally (Belton, 1974). According to the rotation-symmetrical arrangement of the JO, if a sound source comes from a different direction, it will stimulate a different subpopulation of sensilla. This differential stimulation could be used for a directional flight response towards a female.

Acoustic communication also plays a crucial role in the mating behaviour of drosophilid flies. Male *D. melanogaster* produce courtship songs with carrier frequencies of 100–300 Hz by vibrating one of their wings (Greenspan and Ferveur, 2000). The antennal ears of mosquitoes and *Drosophila* are both particlevelocity receivers, and the sound is detected by the JO, but there are several differences with respect to their directionality, which I discuss in more detail below.

Similarly to the mosquito pedicel, the pedicel in the antenna of Drosophila also houses the JO, which has about 500 sensory neurons. Funiculus and arista together act as the sound receiver proper. Upon sound stimulation, the funiculus rotates symmetrically about its centre line (Fig. 1A; Göpfert and Robert, 2002). The rotational movement is a result of the radial insertion of the arista onto the funiculus. Thus, a major difference between the antennal receiver in *D. melanogaster* and the mosquito is the restriction of movement in the former. It rotates about a single central axis, whereas the structure of the mosquito antenna and its articulation allows deflections in all directions. Subpopulations of sensory neurons in the JO of D. melanogaster have different funicular connection sites; when the antenna is deflected in different directions, it depolarizes sensory neurons that are connected to one site on the funiculus and hyperpolarizes those that are connected to another (Pézier and Blagburn, 2013).

The directionality of the Drosophila antenna arises from two factors, which can produce surprisingly large particle velocity differences of around 25 dB between both antennae in combination (Morley et al., 2012). The movement of the funiculus-arista structure is highly sensitive to air particle movements that are perpendicular to the plane of the arista. Because the left and right aristae are oriented at different azimuthal angles, the amplitude of vibrations in the left antenna is highest for directions of 45 deg right and 135 deg left relative to the longitudinal body axis, and vice versa in the right antenna (Morley et al., 2012). In addition, boundary layer effects (for a review, see Casas and Dangles, 2010) distort the flow of air particles around the head, creating high air particle velocities at the arista contralateral to the sound source, and lower particle velocities at the ipsilateral arista (Fig. 1C). These boundary layer effects increase the left-right asymmetry in antennal vibration amplitudes when a sound source is lateralised. Thus, females performing acoustic orientation may follow a simple rule by steering away from the antenna with the larger vibration amplitude. Behavioural experiments conducted with female flies as they walk on a miniaturised trackball demonstrate that they can easily track a sound source following this rule (Batchelor and Wilson, 2019).

Sound localisation with tympanal ears: crickets, katydids, grasshoppers and parasitoid flies Crickets

Human ears are pure pressure receivers, since sound pressure can only act on the external side of the tympanal membranes and the two ears are also acoustically independent. In crickets and grasshoppers, however, both ears are acoustically coupled by an internal interaural sound channel, so that sound pressure can act on both the external and internal side of the tympanal membranes. Such ears are called pressure difference receivers. They are directional, since the phase and amplitudes of the sound pressures acting on the external and



Fig. 1. Directionality of antennal hearing. (A) The *Drosophila* antenna is composed of three segments. An appendage called the arista is mechanically coupled to the funiculus. In response to sound, the arista and funiculus rotate relative to the pedicel, as indicated. (B) Antenna of a male mosquito, composed of the pedicel and a long flagellum with numerous hair-like fibrillae (photo credit: Gernot Kunz). (C) Particle image velocimetry and laser Doppler vibrometry are employed to visualise the flow of air particles around the fly head. Color-coded oscillatory flow amplitudes (dark red=highest amplitudes) around the head of a female *D. melanogaster* at a stimulus angle of 359 deg and 315 deg, as indicated by the red arrow in the orientation diagrams above (after Morley et al., 2012).

internal surfaces of the tympana depend on the direction of the sound incidence (for reviews, see Michelsen, 1992; Michelsen and Larsen, 2008; Robert, 2005). Crickets' ears are located in the tibia of the forelegs, and female field crickets *Gryllus bimaculatus* perform phonotaxis (see Glossary) towards a singing male. Under open-loop laboratory conditions (Box 2), females demonstrate hyperacute directionality, steering towards a calling song presented only 1–2 deg off their longitudinal axis (Schöneich and Hedwig, 2010). The anatomical key for this directionality is a tracheal system that provides a sound input via different channels to the tympanum (Fig. 2A). Sound can reach the external surface of the tympanum and, in addition, the internal surface via a spiracular opening on the lateral surface of the ipsilateral prothorax. Furthermore, a transverse

trachea serves as a sound guide to the contralateral ear. The constructive and destructive interference of sound waves at the tympanum, as well as their amplitude and phase relationships, may enhance the contrast between the two ears.

The phase difference across the tympanic membrane is due to the longer pathway that the contralateral sound wave must travel along via the transverse trachea and the fact that the speed of sound in such small tubes is reduced (Larsen, 1981; Jonsson et al., 2016). In addition, the transverse trachea contains an acoustic vesicle with a thin, double-walled septum along the midline that functions as an effective phase shifter (Fig. 2A; arrowhead). Sound transmission through the septum causes a phase delay only within a narrow range of frequencies, resulting in a tuned directionality (Hill and Boyan,

Box 1. Two types of insect ears

Sound is a mechanical vibration that travels as alternating waves of high and low pressure within a medium. The variation in pressure is accompanied by movements of the particles in the medium. Close to a sound source, the energy released by the particle displacements may be much greater than the sound pressure, but the amplitude of the particle displacement resulting from a dipole sound source decreases by $1/r^3$ (where *r*=distance from the source). This differs from the propagated pressure variation, which decreases by only 1/r.

One type of insect ears – the so-called flagellar type – responds to the particle velocity component of sound waves. In mosquitoes and fruit flies, the antennae, as well as long filiform hairs found on the body wall and terminal appendages/cerci (Gnatzy and Tautz, 1980), belong to this type of sound receiver. Owing to space limitations, this Review covers only the directionality of antennal ears. Such receivers are inherently directional, because the particle velocity is a vectorial component of the sound field. As will be shown for the antennal receiver of the fruit fly, the anatomy and arrangement of components of the antenna further contribute to its directionality.

Tympanal ears are another type of insect ear that responds to the pressure component of sound waves. Despite the anatomical diversity and different locations of these ears on the insect body (on mouthparts, wings, legs, various segments of thorax or abdomen; Yack and Fullard, 1993), they all have a common basic Bauplan (Yager, 1999). A thin tympanal membrane is anchored in a cuticular frame, which is backed by an air-filled tracheal cavity to match the acoustic impedance of the surrounding air (e.g. the ear of a grasshopper in Fig. 2). The vibration of the tympanic membrane that results from pressure changes is transduced to neuronal activity by receptors of the tympanal organ, which are directly or indirectly coupled to the tympanum. These comprise scolopidial sensilla (Field and Matheson, 1998), the common receptors in all insect ears, which are thought to have evolved from mechanoreceptive precursors that are also made up of scolopidia (Boyan, 1993). The number of auditory receptors in each ear varies widely in acoustic insects: the Johnston's organ (JO) of mosquitoes has 16,000, housing as many receptors as hair cells in the cochlea of humans. The tympanal organs of cicadas and a primitive African grasshopper have been reported to have 2000 receptors, contrasting greatly with the single one reported for the ears of notodontid moths and hawkmoths (Yager, 1999; Yack, 2004; Strauß and Stumpner, 2015).

1976, 1977; Boyd and Lewis, 1983; Michelsen and Löhe, 1995; Römer and Schmidt, 2015). After the destruction of the septum, IIDs could either be completely abolished (Michelsen and Löhe, 1995) or reduced by about 5–7 dB (Löhe and Kleindienst, 1994; Hirtenlehner et al., 2014). This destruction induced an error angle of 30 deg in the phonotactic behaviour on a trackball system (Wendler and Löhe, 1993), but did not alter the phonotactic ability of females to find a sound source outdoors (Hirtenlehner and Römer, 2014).

A comparative approach with a large number of cricket species sheds some light on the evolution of the cricket's pressure difference receiver (Schmidt and Römer, 2013). A surprisingly high variety of acoustic tracheal designs were identified; almost all investigated species using acoustic communication are characterised by an acoustic vesicle associated with a medial septum. Species with a more unfavourable ratio of body size to sound wavelength tend to exhibit larger acoustic vesicles. In most species that originally communicated acoustically but lost this ability over evolutionary time, both an acoustic vesicle and a septum is absent. Moreover, some rainforest cricket species even exhibit a double acoustic vesicle and display IIDs of up to 25 dB (Schmidt and Römer, 2013, 2016). This high diversity of acoustic tracheal morphology observed among 40 cricket species from three different superfamilies might reflect the different ways the pressure difference receiver has

Box 2. Paradigms to study insect phonotaxis

In an open-loop behavioural paradigm, an insect is fixed by its pronotum on top of an optical trackball system. In this position, it can change neither the heading angle nor the distance with respect to the sound source, but researchers can measure the forward/backward movement and the lateral steering in response to sound with high temporal resolution (Hedwig and Poulet, 2005). In closed-loop compensated walking paradigms, the insect can change its heading angle to face the sound source, but the distance to the source remains the same throughout the phonotactic trial (e.g. Kramer treadmill or walking belts; Weber et al., 1981; Ofner et al., 2007). Phonotaxis in arena trials (e.g. Murphey and Zaretsky, 1972) or in the field (e.g. Hirtenlehner and Römer, 2014) occurs under closed-loop conditions. Under the latter conditions, any locomotor behaviour of the insect, such as turns to either side or approaches towards the sound source, has direct consequences on the resulting subsequent stimuli (such as a change in the stimulus angle or an increase in loudness). By making video-recordings of phonotaxis in arena trials, the researcher can conduct an off-line analysis of stimulusrelated turn angles.

Methods used to independently stimulate the ear can facilitate the study of cooperation between both ears, such as with earphones in humans. Dichotic (independent) stimulation of both ears is a tricky methodological challenge when applied to small insects, because such stimulation paradigms require the presence of a sufficiently high crosstalk barrier between the two ears, so that one ear can be stimulated without affecting the opposite ear over a wide range of sound pressure levels. In freely behaving grasshoppers (von Helversen and Rheinlaender, 1988) and katydids (Rheinlaender et al., 2006), such methods have been applied to quantify the limits for processing small ITDs (0.5-1.0 ms) and IIDs (1 dB) for sound localisation. Dichotic stimulation in physiological preparations can be more easily achieved in crickets by using a closed sound field ('earphones'; Kleindienst et al., 1981) or in locusts by replacing the acoustic stimulus using piecomechanical stimulation of the tympanum (Rheinlaender and Mörchen, 1979) or by electrical stimulation of the auditory nerve (Römer and Rheinlaender, 1983).

evolved from a precursor structure that was already present in ancestral, non-hearing species.

Katydids

Katydids, as close relatives of crickets, have ears that are also located in the fore tibia and possess paired eardrums (an anterior and posterior tympanal membrane) in each ear. The acoustic trachea extends from the acoustic spiracle in the prothorax through the leg trachea and divides in the tibia into anterior and posterior branches (Bangert et al., 1998; Lewis, 1974a). Thus, sound can act on the external surfaces of both tympanal membranes and on their internal surfaces through the acoustic trachea. However, a tracheal connection between both sides is not present; therefore, there are only two sound inputs for each ear (Fig. 2A). Considerable anatomical variation in the form of the tracheal ducts has also been observed. In most katydid species, the acoustic spiracle is a large opening in the prothorax; this spiracle is shaped like an exponential horn and followed by a tracheal expansion (auditory bulla). In species of the subfamily Phaneropterinae, the bullae can be so large that they occupy a considerable volume of the prothorax and are in complete contact with each other (Bailey, 1990). The functional significance of this contact for the acoustic cross-talk between both tracheae, and a potential sound transmission line from the contralateral spiracle to the ipsilateral internal surface of the tympanum, is unclear.

Amplitude gains ranging from 5 to 30 dB have been measured for the acoustic trachea of different katydid species (Lewis, 1974b;



Fig. 2. Anatomical basis for pressure difference receivers in crickets, katydids and grasshoppers. (A) In crickets, sound can act on the outer surface of the tympanum (black arrow) and via the ipsilateral acoustic spiracle and leg trachea on its internal surface (red arrow and red dotted line). In addition, sound from the contralateral spiracle, passing through a transverse trachea, can act on the internal surface of the tympanum (green arrow and green dotted line). The amplitude and phase relationships of all three sound components determine the directionality of the ear. In katydids, sound can equally act on the outer surface of the tympanum (black arrow) and via the ipsilateral acoustic spiracle and leg trachea on its internal surface (red arrow and red dotted line), but there is no transverse connecting trachea as in crickets. In most katydid species, the acoustic spiracle is a large opening in the prothorax, followed by a trachea formed like an exponential horn, providing a large gain for the internal sound component to the tympanum. (B) In grasshoppers, the ears are located in the sidewalls of the first abdominal segment (left and right photographs showing the outer and inner view of the tympanum, with the sensory organ attached). A horizontal section through this area demonstrates air-filled tracheal sacs, allowing low-frequency sound to act on the outer surface of the tympanum (black arrow) and to pass through to the internal surface via the opposite tympanum (red arrow). All pressure difference receivers provide high directionality despite unfavourable ratios of body size to the wavelength of the relevant sound. Scale bars: 1 mm.

Michelsen et al., 1994; Heinrich et al., 1993; Shen, 1993; Römer and Bailey, 1998). The amplitude of the gain of the acoustic trachea is strongly frequency-dependent: at low frequencies, the gain is close to 1 (=0 dB), and at higher frequencies it is 25–30 dB. Thus, the ear of these katydids is also a pressure difference receiver as in crickets, but one with a much higher internal sound pressure. The large amplitude gains of these acoustic tracheae indicate that the directionality of the ear is determined by the diffraction of sound around the thorax. The directionality in various species confirms right–left differences of around 10–30 dB (for one species of katydid, see black line in Fig. 3).

The situation is different in species with small thoracic spiracles, with a gain close to one. Katydids of the subfamily *Pseudophyllinae* have very small spiracle openings relative to their body size and small dimensions of the acoustic trachea. To address the question of how directional hearing is achieved with such a pressure receiver, researchers have focused on the variation in the external morphology of the ear. In some species, the ear exhibits cuticular folds surrounding the tympanum, some of which form cavities with small slit openings, whereas both tympanic membranes are fully exposed in other katydids. Whether and how the slit openings could influence the directionality of the ear (Autrum, 1963; Bailey and Stephen, 1978) needs further experimental investigation.

Grasshoppers

The ears of grasshoppers and locusts are located in the side walls of the first abdominal segment (Fig. 2B). The sensory organ (Müller's organ) is attached to the internal side of the tympanum. It has about 60-80 sensory cells. The distance between the tympana in the small grasshopper *Chorthippus biguttulus* is only 1–2 mm, and the space in between is occupied by air-filled tracheal sacs, providing the anatomical basis for a pressure difference receiver at lower frequencies, since sound can reach the back of the tympanum via this internal sound pathway (Fig. 2B). As in the cricket ear, a proper phase relationship must be maintained between the external and internal sound components to ensure the directionality of the grasshopper ear (Michelsen and Rohrseitz, 1995). With a phase delay of about 60 deg for sound through the internal pathway, a model for the directionality of the ear (Schul et al., 1999) could explain the excellent lateralisation of *Ch. biguttulus* (compare with Fig. 3).

Parasitoid flies

For all hearing vertebrates and insects, the anatomical separation of both ears – although sometimes minute – is essential for establishing directional cues. But the ears of parasitoid flies, located at the ventral anterior prothorax, are closely coupled and even share a common air sac (Robert et al., 1996). The body size to wavelength (λ) ratio is less than 0.03, and diffractive effects for establishing IIDs are on the order of the measured irregularities of the sound field (Robert et al., 1996). At the same time, ITDs are also minute and amount to a maximum of 1.45 µs. Thus, of all insects equipped with tympanal ears, those of the parasitoid flies represent the greatest biophysical challenge regarding directional cues. Still,



Fig. 3. Comparison of the directionality of insect ears. Binaural differences for different azimuthal angles of sound incidence for a field cricket (data from Michelsen, 1998), a katydid (data from Rheinlaender and Römer, 1980), a grasshopper (data from von Helversen and Rheinlaender, 1988) and the parasitoid fly *Ormia ochracea* (data from Robert et al., 1996). For the fly, data represent the difference in vibrational response amplitudes between both mechanically coupled tympana at the site of receptor attachment. Note that the directional profiles have in common a similar degree of directionality, and that the steepest changes in directionality occur with changes of azimuthal angles in the frontal zone, despite vastly different ears in these insect taxa.

females of these flies must solve the same task as a female cricket, because the female fly must find their male cricket hosts to deposit their eggs or larvae (Cade, 1975). In trackball experiments, the flies demonstrated hyperacute directional hearing in the azimuth (Mason et al., 2001) similar to that of crickets on a trackball, and their flight trajectories in three-dimensional space indicate their ability to precisely localize a target broadcasting the hosts' calling song in the vertical plane (Müller and Robert, 2001). How can such high accuracy in localisation behaviour be explained when the interaural differences in the sound field at the position of the tympana are negligible?

When the motion of both tympana was measured in detail using laser vibrometry, their mechanical responses showed significant differences (Robert et al., 1996). The two tympana are coupled through an inter-tympanal bridge. When forces act on the external side of each tympanum, they generate asymmetrical deflections of the inter-tympanal bridge, which functions as a flexible lever (Miles et al., 1995). The resulting IIDs and ITDs in the mechanical response of the ears are much larger than those in the acoustic field. Amplitude differences of about 12 dB (Fig. 3) and time differences on the order of 50 μ s were measured for sound presented 90 deg off the longitudinal body axis. Thus, ear mechanics increase the minimal physical directional acoustic cues, translating them into substantial binaural differences that can be processed by the sensory system. For more information on the challenge of physiological processing, see below.

Physiological challenges of processing small interaural differences

The notion that the central nervous system (CNS) processes IIDs and ITDs is not quite correct: after mechano-sensory transduction occurs in the auditory receptors, information about the direction of a sound source is only represented in the form of bilateral differences

in the discharge rate of auditory afferents, their latency or probably their different recruitment in both ears (Hennig et al., 2004; Hedwig and Stumpner, 2016). Processing such information can be a challenge for insects, owing to the relatively small number of auditory afferents and interneurons (see Glossary), and the variability in action potential activity, which causes inaccurate coding in sound features (Zimmerman, 1978; de Ruyter van Steveninck, 1997; Ronacher et al., 2004). Variability of action potential activity results from three sources: (1) stochastic processes during sensory transduction, generation of action potentials and synaptic transmission; (2) any motor act, such as singing, walking or flying, which generates non-auditory background activity in auditory sensory neurons and interneurons (e.g. Schildberger et al., 1988; Hedwig et al., 1988); and (3) substantial variability resulting from temporal distortion of the sound signal (see Glossary) through wind and thermal gradients during sound transmission (see below), further decreasing the reliable coding of directional information. In a comparison of intrinsic (1) and extrinsic components (2 and 3) of action potential variability, Neuhofer et al. (2011) showed that for most neurons in the locust auditory pathway, intrinsic variability was the dominant component and even increased at consecutive levels of processing.

There is tremendous variation in the number of auditory receptors in acoustic insects, ranging from about 15,000 observed in the JO of mosquitoes to the single one in the ears of notodontid moths and hawkmoths (Yager, 1999; Yack, 2004; Strauß and Stumpner, 2015). In the latter case, therefore, any behavioural decision or directional response of the insect must be based on discharge differences from a single pair of receptors or interneurons (Nolen and Hoy, 1984; Ratcliffe et al., 2009). Moreover, these receptors synapse onto interneurons in mechanosensory neuropils (see Glossary), which transfer the information about acoustic events to higher brain centres responsible for decision-making. In crickets, for example, such information can hit a bottleneck, because two pairs of interneurons forward the information about the calling song and ultrasonic predatory cues (AN1 and AN2, respectively) to the brain (Wohlers and Huber, 1982; Hennig, 1988). Thus, if the rightleft difference in AN1 activity is the only information available to guide auditory steering, it needs to be highly accurate and have little variability, given the hyperacute directionality shown in behaviour (Schöneich and Hedwig, 2010).

However, in a recent test conducted with female crickets, bilateral latency differences between the right and left AN1 responses were shown to be small and unreliable for auditory steering. Significant bilateral discharge differences were only observed for angles larger than ± 18 deg (Lv et al., 2020). The authors suggested the possibility that auditory steering may be achieved via a more direct thoracic pathway, which is probably activated by the activity of a descending prothoracic auditory interneuron with a high directionality, as described by Boyan (1978).

Compared with crickets, the auditory pathway in grasshoppers is formed by a substantially higher number of neurons. Approximately 60–80 receptors synapse onto 10–15 local neurons in the metathoracic ganglion, which then converge onto 15–20 interneurons that ascend to the brain (Vogel and Ronacher, 2007). Grasshoppers discriminate small IIDs of ~1 dB (see below). Ronacher and Krahe (2000) determined the neuronal correlates of such small IIDs at the receptor level. Since the female response song lasts about 1000 ms, the variability in the receptors resulting from the response to a single syllable could be averaged out by integrating over several syllables, and the male could potentially use temporal integration to arrive at the acuity observed in behaviour. However, males showed reliable directional responses after listening to only 250 ms of the song. Based on data on the variability of individual receptor responses, Ronacher and Krahe (2000) concluded that the grasshopper needs to integrate information from up to 13 receptors to display the observed behavioural precision.

Physical versus physiological time differences

As noted above, the distances between the ears of insects are very small, and the resulting ITDs fall within the range of a few microseconds. These small ITDs are unlikely to be processed by the insects' nervous system. However, the intensity of a stimulus also affects the latency of the response, resulting in an inverse relationship between the spike count and response latency (see Glossary) of an auditory receptor (Mörchen et al., 1978; Mörchen, 1980; Fig. 4). Thus, for two mirror-image receptors in both ears, a difference in the magnitude of excitation, but also in the time of arrival of action potentials in the central nervous system will be created with a lateralized sound source (Fig. 4). In this way, the auditory system can process physiological time differences of a few microseconds.

Researchers have investigated which of these two binaural cues is the more reliable one for directional hearing in crickets and grasshoppers, but obtained contradicting results for both taxonomic groups. The results for crickets in different behavioural paradigms (Givois and Pollack, 2000; Pollack, 2003; Hedwig and Poulet, 2005) indicate that bilateral differences in response strength appear to be the dominant directional cue. This is clearly different in grasshoppers, where a dichotic stimulation experiment revealed that time differences of 0.5–1 ms provided sufficient information for subsequent reliable turns to the side that received the acoustic signal first (von Helversen and Rheinlaender, 1988). Since differences in response strength in these experiments could not play a role, this is convincing evidence that binaural latency differences alone are sufficient to drive directional responses in behaviour. This



conclusion is supported by the finding that long rise ramps in a sound signal produce significantly larger latency differences in auditory receptors of grasshoppers (Krahe and Ronacher, 1993; schematically shown in Fig. 4B). The localisation performance of these grasshoppers is also better when long rise time stimuli are presented (Ronacher and Krahe, 1997).

Reichert and Ronacher (2019) applied an interesting experimental approach to examine the importance of time or intensity differences for localisation. They presented song playbacks to male *Ch. biguttulus*, varying the number and temporal positions of song syllables that provided directional cues by altering the time or amplitude differences between two speakers. Syllables with timing differences at the beginning of the song were weighted most heavily, whereas syllables with intensity differences were weighted most heavily when they were in the middle of the song. When timing and intensity cues conflicted (a situation which may often happen under natural conditions, see below), the magnitude and temporal position of each cue determined their relative influence on lateralisation, and males sometimes quickly corrected their directional responses.

Enhancement of bilateral differences through lateral inhibition

Relatively small directional differences in the response strength and latency between pairs of auditory interneurons can be strongly enhanced by contralateral inhibition, which is an important feature of the auditory pathway of insects (Hennig et al., 2004; Hedwig and Pollack, 2008). The magnitude and duration of the inhibition and, in particular, its timing relative to the ipsilateral excitation, produces different directional response profiles (Römer et al., 1981; Römer and Dronse, 1982). A special and very powerful case of directional contrast enhancement is the reciprocal inhibition between a pair of first-order, local interneurons in crickets and katydids, the omega neurons (Selverston et al., 1985). These neurons receive input from most receptors on the soma ipsilateral side and inhibit several ascending interneurons as well as their opposite counterpart. Thus, any small difference in the excitatory input is translated into a large

Fig. 4. The establishment of binaural physiological time differences in auditory receptors. (A) The intensity-

response function of an auditory receptor shows an inverse relationship between response strength and response latency. At a given SPL of 65 dB for the ipsilateral receptor, the response latency is short (about 9 ms; blue arrows; red stippled line, right y-axis), whereas the same stimulus activates the mirror-image contralateral receptor at 50 dB SPL (blue arrows), owing to an assumed directionality of the system with an interaural intensity difference (IID) of 15 dB. with a response latency of about 15 ms. Such physiological binaural time differences are orders of magnitude larger than the physical interaural time differences (ITDs) in insect ears, and can be used for directional hearing when physical ITDs are too small. (B) The magnitude of binaural latency differences also depends on the temporal structure of the stimulus; longer rise times of the stimulus amplitude (right) result in larger differences (blue shaded area). Black and red dotted lines represent thresholds for the ipsilateral and contralateral receptors, respectively. AP, action potential.

response difference between both cells. In a dichotic stimulation experiment (Box 2) in which both omega cells were simultaneously recorded in a katydid, Stradner and Römer (2008) demonstrated that IIDs as small as 1 dB produced large and significant discharge differences in this pair of interneurons. The same reciprocal inhibition also causes a strong directionality of response to the calling song along the longitudinal body axis (Römer and Krusch, 2000).

Call rate and call duration as physiological challenges for directional hearing

Acoustic signals differ widely between insect species; they vary from highly redundant signals with sound pulses or groups of pulses (chirps) repeated at a high rate over many minutes or hours to single, short pulses produced at extremely low rates. In neotropical forests, calls of katydids are usually short (<40 ms) and infrequent (<10 s of sound per individual per night; Symes et al., 2016). In the case of redundant signalling, the unreliable directional responses of afferent neurons could be averaged over time, an option that is not available for species signalling with low redundancy.

The short duration of some signals can represent a further challenge for directional hearing. For example, the response of the female katydid Leptophyes punctatissima to the male call is only 0.5 ms in duration. Such a short click elicits only one action potential in a sensory neuron at all suprathreshold values, eliminating their usual graded intensity response function (Hardt, 1988; compare with Fig. 4). Therefore, the only available directional piece of information provided by the population of 28 receptors is the different number of activated receptors in both ears, which varies with the angle of sound incidence. The same suggestion of differential receptor recruitment has been made for directional hearing in the parasitoid fly Ormia ochracea by Oshinsky and Hoy (2002). The thresholds of O. ochracea auditory receptors vary over a wide dynamic range of \sim 45 dB. The authors calculated that, for a given ipsilateral stimulus intensity of 85 dB SPL, about 90% of all receptors would be activated above threshold as compared with less than 40% in the contralateral ear. Thus, in both L. punctatissima and O. ochracea, bilateral differences in the recruitment of afferents serve as a powerful mechanism in a system that lacks the graded receptor responses with regard to intensity or direction. The reason for the phasic afferent response, however, is quite different: in L. punctatissima, it is due to the extremely short female signal, whereas in O. ochracea it is an intrinsic property of most receptors.

Ormia ochracea, with its remarkable hyperacute directional hearing (see above), has a population of 50–100 receptors per ear with unusual physiological properties. The majority of the receptors fire only one action potential in response to a stimulus, irrespective of its duration, and exhibit a strongly reduced spontaneous activity. The latency of action potentials increases as stimulus amplitudes decrease, and this latency also increases with contralateral stimulation due to the mechanical directionality of about 12 dB provided by the lever mechanism (see above); the total ipsilateralcontralateral latency difference is about 600 µs (Mason et al., 2001; Oshinsky and Hoy, 2002). However, since the fly can discriminate stimulus angles 2 deg off the body midline, the afferents must be able to reliably encode differences of about 10 µs. The obvious physiological challenge faced during such time coding is that an extremely low variation in spike timing must occur. In the phasically responding receptors, the jitter in action potential timing was remarkably low, averaging ~70 µs (Mason et al., 2001; Oshinsky and Hoy, 2002). This is still about ten times larger than the 10 µs required to code for the small stimulus angles in the frontal zone.

However, even the non-specialised, tonically responding auditory receptors in grasshoppers show a remarkable low jitter of about 150 μ s. This allows grasshoppers to increase the rate of information transmission when responding to rapid amplitude modulations in a signal (Rokem et al., 2006).

The vertical coordinate of sound localisation

Except for ground-dwelling insects like field crickets, most insects live and communicate in complex three-dimensional environments. Their microhabitats include trees and bushes, where the vertical position of signallers and receivers can differ by many metres. For these animals, the determination of the vertical plane of a sound source may be as significant as the ability to determine the azimuthal angle. A few studies on crickets, flies and katydids have revealed their remarkably precise abilities to approach acoustic targets in space.

One study was conducted with the field cricket *Teleogryllus oceanicus* in the context of bat predation (Wyttenbach and Hoy, 1997). The authors demonstrated that flying crickets were able to discriminate between ultrasound sources located at different elevations. The acuity was rather poor, however, ranging from 45 deg at the front and rear of the animal to 90 deg below the animal. Such a poor acuity is unlikely to be a problem for the prey, since the behavioural escape response (negative phonotaxis) just needs to be directed away from the predator, but not precisely in a certain direction.

By contrast, precise localisation is essential for the parasitoid fly *O. ochracea*, and three-dimensional localisation is required for the female flying at some height (1-2 m) above the cricket on the ground. Müller and Robert (2001) revealed the remarkable accuracy of the flies' phonotactic behaviour: after a flight distance of about 4 m, they approached and landed on a loudspeaker within close proximity. Thus, this insect not only demonstrates hyperacute directionality in the azimuth under open-loop conditions, but also an ability to track their target in three-dimensional space under quasinatural conditions. It is currently completely unknown how the ear provides directional cues in the vertical plane, allowing them to discriminate source elevation angles with such precision.

The katydid L. punctatissima (Fig. 5A) must orient itself in space to find a mate, as the vertical distribution of males and females can vary considerably. In an artificial grid system, all males tested reached the three speaker positions (elevated or depressed by 45 deg or at 0 deg) with only little deviation from the shortest possible path (Rheinlaender et al., 2007). Spatial orientation was further explored on a walking compensator, an experimental paradigm where any movement of the insect away from a certain location can be compensated (Ofner et al., 2007). As the loudspeaker elevation was increased, the males meandered more often, and the ratio of the ideal path length to the actual path length decreased (Fig. 5B). Males also made more turns towards the wrong side as the loudspeaker elevation increased. As expected, at speaker elevations of 90 deg (directly above the animal), no directional cues were available for the orienting insect, and all males circled repeatedly under the sound source and deviated much more frequently from the axis of the loudspeaker orientation when compared with their behaviour at smaller elevation angles.

An interesting behaviour was observed under conditions of missing directional cues. When the signal was presented from above, some males tilted their head and thorax in a forward direction, often associated with a shift in the longitudinal body axis by up to 30 deg to each side and bending of the dorso-ventral axis from the left to the right and back again (Fig. 5C). The authors



Fig. 5. Sound localisation in the third dimension. (A) Male *Leptophyes punctatissima* with large auditory spiracle (arrow) at the prothorax. (B) Reconstructed phonotactic path of a male on the walking belt at speaker elevations of 0 deg, 30 deg, 60 deg and 75 deg. Each dot refers to the position of the male when he produced his call and received the female reply. Note that this male was almost completely disoriented at a speaker elevation of 75 deg. (C) Reconstruction of the body posture of male *L. punctatissima* while they exhibit the tilting behaviour in situations of reduced or missing directional cues (e.g. at speaker elevations of 90 deg). The numbered arrows indicate: (1) tilting of head and thorax in a forward direction, (2) turning on the spot with a certain yaw angle and (3) a movement along the body axis to either side (reproduced with permission, from Ofner et al., 2007).

interpreted this behaviour as a kind of directional scanning, similar to that displayed by vertebrates that move their heads or pinnae to localize a sound source, since self-induced changes in binaural directional cues can occur if they alter the orientation of their bodies along all three axes. By comparing the previous cues with the actual binaural cues (a sequential rather than a binaural comparison), the insect could obtain an estimate of whether the source is above, below, to the left or to the right.

Ecological challenges: sound localisation in the field

For very good reasons, the experiments described so far have been conducted under laboratory conditions, since often much effort was necessary to reduce or eliminate any structure in the experimental apparatus that could potentially scatter sound waves, so that the ears of the animal receive sound only from the direction given by the sound source. However, sound localisation did evolve under the complex acoustic conditions in the field, where directional cues can be heavily distorted or even missing. In an attempt to determine the degradation of directional cues for a grasshopper in the field, Michelsen and Rohrseitz (1997) used a microphone approach and compared the sound input to both tympana. A major finding was that directional phase cues degraded less strongly with distance

compared with amplitude cues. Since pressure difference receivers respond to phase differences of sound arriving at the front and back of a tympanum (see above), the authors suggested that this type of receiver is particularly suited to overcome the stronger degradation of directional amplitude cues in natural habitats. Other researchers, inspired by the ingenious work of Kenneth Roeder and colleagues (Roeder, 1967), used the activity of auditory receptors or directionally sensitive interneurons recorded in the field to determine the magnitude of directional cues as represented in the auditory system under natural conditions (Rheinlaender and Römer, 1986; Gilbert and Elsner, 2000; Kostarakos and Römer, 2010). For both crickets and katydids, they found positions in the habitat where the animal could detect the signal, but the directional information in the discharge of the interneurons was completely lost (Fig. 6B). Even at the same location, the magnitude of directional cues could vary widely over time, probably as a result of fluctuations in local temperature or wind gradients (Kostarakos and Römer, 2010).



Fig. 6. Degradation of directional cues outdoors. (A) The song of the katydid Requena verticalis is composed of a 16 kHz and a 28 kHz component. When only the 16 kHz component is present in the signal due to frequencydependent excess attenuation of ultrasonic frequencies (right), reduced directional cues result in phonotactic approaches with large deviations from the direct path, in contrast to a signal that includes only the 28 kHz component (left; reproduced with permission from Bailey and Yeoh, 1988). (B) Response differences of the pair of AN1 neurons in Gryllus bimaculatus recorded in the field at different distances from the sound source. Stimuli were presented at 30 deg off the longitudinal body axis; positive values (±s.d.) indicate stronger responses of the ipsilateral AN1, and thus correct directional information. Note the absence of directional information (zero response difference, red dashed line) at a distance of 5 m (arrow) and the large variation in response difference. Under these conditions of missing or unreliable directional information, acoustic orientation could be based on a sequential comparison of the acoustic input (reproduced with permission from Kostarakos and Römer, 2010).

Two reasons may account for this loss: firstly, at these positions, the sound field might have been more or less diffuse owing to scattering effects within the vegetation. Secondly, for katydids, directional hearing is strongly frequency dependent, resulting from diffractive effects at the acoustic spiracle, and provides IIDs of only ~6 dB at 10 kHz, but 20 dB at 20 kHz (Rheinlaender and Römer, 1980; Shen, 1993; Schul, 1997). Dense vegetation acts as a frequency-dependent filter, strongly reducing the amplitudes of high sonic or ultrasonic components (Römer and Lewald, 1992). Thus, when the high frequencies that provide high directionality in the system are filtered out at the position of the receiver, the directionality is even further reduced. The potential effect of such frequency filtering for sound localisation is shown for a katydid species in Fig. 6A.

Gilbert and Elsner (2000) studied the degradation of directional cues for the grasshopper *Ch. biguttulus* in various types of habitat, using recordings of directional profiles of auditory receptors on gravel and in sparse and dense vegetation, which were compared with a profile in a free sound field. The maximal IID of 24.5 dB in the free sound field was reduced to 16.5 and 6.8 dB in sparse and dense vegetation, respectively. Note that such degradation of directional cues could be established over a distance of only 1 m, the likely distance over which these grasshoppers can communicate with their low-amplitude signals.

Masking by background noise (see Glossary) is a problem faced by many species in different taxonomic groups, and several behavioural and neuronal adaptations have been described to cope with this problem (reviewed in Brumm, 2014; for insects, see Balakrishnan, 2016; Römer, 2014; Schmidt and Römer, 2011; Schmidt and Balakrishnan, 2015). Whether and how masking noise also affects sound localisation abilities was studied by Reichert (2015) for male grasshoppers. Not surprisingly, when males were presented with female songs at different masking levels, noise sharply reduced the responsiveness of males to female songs. However, once the males had lateralised the female song (i.e. they had detected the signal within noise), they responded highly accurately, even at the highest noise levels. These results suggest that noise only weakly impairs directional hearing, but strongly affects signal detection. Still, for insects with low redundant signalling in noisy environments, the rate with which directional information can be used by the receiver will be reduced even further by masking. It is currently completely unknown how phonotaxis is possible under conditions where directional information is available at such low rates.

Altogether, the few outdoor studies that have been conducted on directional hearing in grasshoppers, crickets and katydids have vielded results that demonstrate that directional sensitivity is not only an inherent property of the insect's auditory system, as laboratory experiments would suggest, but strongly depends on properties of the sound transmission channel (see Glossary) from sender to receiver. How can insects cope with these conditions and perform phonotaxis? Only two studies have quantified phonotactic tracks of crickets outdoors (Mhatre and Balakrishnan, 2007; Hirtenlehner and Römer, 2014). Despite the distorted directional cues, all females arrived at the target, but larger deviations were observed in their phonotactic paths when compared with laboratory trials. In two-choice trials or more complex stimulus settings, the difference in loudness necessary for a preference was 5 or 6 dB, which was significantly higher than that necessary in arena trials (3 dB) or on trackball systems (1-2 dB).

Given the hyperacute directional sensitivity of field crickets and parasitoid flies documented under ideal acoustic lab conditions, it is tempting to speculate that such hyperacuity is necessary to succeed under the distorted directional cues outdoors. At least for field crickets, I doubt this is the case: owing to the physical nature of the habitat, females will be forced by dense patches of grass or larger obstacles on the ground to deviate from the perceived source direction and sometimes even turn in the wrong direction. In any case, their own (forced) movement will create large stimulus angles for the subsequent stimulus, which can then be discriminated even when the directional cues are distorted. The same argument holds for a female katydid that uses branches or leaves to approach a singing male, thereby also constantly deviating from the target direction as a result of her own forced turns. Moreover, under conditions where binaural hearing is impaired or where directional cues are poor or missing, acoustic orientation could be based on the sequential comparison of the acoustic input, as has been suggested for the moth Achroia grisella (Greenfield et al., 2002; Reid et al., 2016). Note that the tilting behaviour displayed by the katydid L. punctatissima also indicates that it makes a sequential comparison of such acoustic input when directional cues are missing (see above).

Conclusions

Undoubtedly, the small size of insects imposes severe biophysical challenges for directional hearing. However, new techniques have successfully been used to quantify the flow of air particles around the heads of insects with flagellar ears, or to measure the amplitude differences of vibrations of ipsilateral and contralateral eardrums in tympanate insects. These measurements have documented surprisingly large IIDs, as well as a sensitivity of 1–2 dB for IIDs, which is strikingly similar to that of mammals. In insects, ITDs are minute because of the tiny distance between their ears, but insects may be able to make use of ITDs for directional hearing after mechanical processing (parasitoid fly) or of physiological time differences that are orders of magnitude larger than the physical ITDs.

The small number of nerve cells processing IIDs and ITDs is a further challenge to directional hearing by insects, but also offers researchers the chance to study directional hearing while monitoring the activity of relevant identified neurons. Researchers have even begun to investigate the physiology of directional hearing in the wild, where directional cues are strongly distorted. The challenges of infrequent signalling or signalling with short song elements subject to masking have received little attention in the past, as has the need of many species to identify the location of a sound source in space. Although this Review has focused on binaural processing for directional hearing, some studies conducted under conditions with missing binaural cues indicate that other modes of operation (e.g. sequential, rather than binaural comparison) may allow insects to find a sound source in three-dimensional space. This poses new questions regarding the short-term memory requirements that allow insects to accomplish this task. Altogether, focusing on such questions and using an integrative approach will provide us with further fascinating insights into this system.

Acknowledgements

I thank Stefan Galander and three anonymous reviewers for very helpful comments on the manuscript.

Competing interests

The author declares no competing or financial interests.

Funding

The Austrian Science Fund (FWF), the German Research Foundation (DFG), the Austria Research Foundation (OEFG) and the Austrian Neuroscience Association (ANA) have funded my research.

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