Convergent evolution of insect hearing organs from a preadaptive structure

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Flies of the taxon *Emblemasomatini* (Sarcophagidae: Diptera) independently evolved an ear with the same anatomy and location as the *Ormiini* (Tachinidae: Diptera). Both ears represent a first case of convergent evolution of homologous insect ears, which raises the question for a preadaptation. Physiological and anatomical data indicate a preadaptive-sound-insensitive, but vibration-sensitive scolopidial chordotonal organ in non-hearing flies. As selective pressure for the evolutionary transformation from a vibration receiver into a sound receiver, fast and precise cues for the localization and detection of the sound producing hosts can be presumed.

Keywords: ear; chordotonal organ; proprioception; scolopidia; parasitoids; Diptera

1. INTRODUCTION

Many taxa of insects have independently evolved ears on different parts of their bodies (Boyan 1993; Fullard & Yack 1993; Hoy & Robert 1996). The evolution of the wealth of insect ears can only be unravelled by comparative studies. Genetic analyses face the difficulty that unlike the regulation of the development of eyes (Oliver & Gruss 1997) conserved genes have not been found for the development of ears. Furthermore, the genetic model insect *Drosophila* is lacking a tympanic organ, although it possesses an auditory sense for which mutant lines with hearing deficits recently have been isolated (Eberl *et al.* 1997). A typical tympanic organ of insects includes a thin tympanic membrane backed by an air-filled tracheal chamber and a sense organ consisting of scolopidial units. Such units are widespread among the insects and are involved in transduction of mechanosensory stimuli such as substrate vibration, airborne sound and changes in body posture (proprioception; reviewed in Field & Matheson 1998). The scolopidial units contain usually one sensory cell, a scolopidial cell and two accessory cells. Histological and genetic analysis revealed no general difference between scolopidial units of the various sense organs responding to the different stimuli. Mainly based on the segmental arrangement and embryonic development of the scolopidial organs, it has been postulated that insect ears have evolved from proprioceptive organs (Boyan 1993, 1998; Fullard & Yack 1993; Meier & Reichert 1990; Yack & Fullard 1990). Recent functional analysis revealed that unspecialized scolopidial organs may also react to airborne sound and that specialization increases the sensitivity resulting in a tympanate ear (Shaw 1994a,b; Van Staaden & Römer 1998). However, these results cannot explain how scolopidial organs insen-

sitive to airborne sound can be transformed into a tympanate ear and it does not explain why ears seem to develop at various, though specific, sites of the insect body (Fullard & Yack 1993; Hoy & Robert 1996). An especially suitable example to answer these questions are the tympanate ears of Diptera, which occur in two taxa (parasitic flies, Tachinidae, and flesh flies, Sarcophagidae) with auditory behaviour. These parasitoid fly species exploit the acoustic communication systems of host species for larviposition. The tachinid species, e.g. *Ormia ochracea* (Bigot) and *Therobia leonidei* (Mesnil) are parasitoids of different orthopterans (Barraclough & Allen 1996; Cade 1972; Lakes-Harlan & Heller 1992; Leonide 1969; Robert *et al.* 1992). The ears of these two species of tachinids have been described (Lakes-Harlan & Heller 1992; Lakes-Harlan *et al.* 1995; Robert *et al.* 1992, 1994; Stumpner & Lakes-Harlan 1996). By contrast, in the Sarcophagidae (Feener & Brown 1997; Soper *et al.* 1976) nothing is known about the ear, although the species *Emblemasoma auditrix* (Shewell, formerly *Colcondamyia auditrix*; Pape 1996) can be attracted to tape-recorded calling songs of males of the cicada *Okanagana rimosa* (Say; Lakes-Harlan *et al.* 1998; Soper *et al.* 1976). Here we present a first study of the anatomy and physiology of the ear of *Emblemasoma auditrix*. Based on the comparative studies of the tachinid ear, we follow the question why the ear evolved twice independently at the same location and we investigate the preadaptive properties of the presumed ancestral sense organ of a non-hearing fly (Lakes-Harlan *et al.* 1997).

2. MATERIAL AND METHODS

Female *Emblemasoma auditrix* (Sarcophagidae) were collected from the Lower Peninsula of Michigan, USA, by broadcasting the host's (*Okanagana rimosa*) calling song from a tape recorder. The calling song of *O. rimosa* was copied from a master tape kindly provided by Professor T. Moore, Ann Arbor. The animals were transferred to Göttingen, Germany, and the morphology,

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Figure 1. Anatomy and histology of the hearing organ of the flies *E. auditrix* ((a, b, d, e) Sarcophagidae; female), *T. leonidei* ((h, i) Tachinidae; male) and of homologous structures in *S. bullata* ((c, f, g) Sarcophagidae). (a) Lateral view of the head and the thorax of a female *E. auditrix*. The arrowhead points towards the ear, located directly behind the head. (b, c) Horizontal sections through the scolopidial organs of *E. auditrix* (b) and *S. bullata* (c). Scolopidia in both organs are longitudinally arranged (ac, accessory cells; mu, muscle; sc, scolopales; se, sensory cells). (d, f, h) Scanning electron micrographs of the prosternum of *E. auditrix* (d), *S. bullata* (f) and *T. leonidei* (h). The homologous structures are labelled: c, coxa; n, neck; ps, presternum, pbs, probasissternum; tym and psm, tympanal membrane and prosternal membrane, respectively. The attachment site of the sensory organ is indicated by an arrowhead. (e, g, i) Horizontal sections through the prothorax of *E. auditrix* (e), *S. bullata* (g) and *T. leonidei* (i). The sensory organs (so) attach to the prosternal apodeme (ap) and extend to the tympanal membrane (tym (e, i)) or the prosternal membrane, (psm (g)), respectively. In all species a single large prosternal tracheal air sac is present (ptr), although it is more widened in *E. auditrix* and *T. leonidei*. Scale bars: (b, c) 10 μ m, (a, d-i) 250 μ m.

biophysics and physiology of the hearing system of 25 specimens were analysed. Non-hearing *Sarcophaga bullata* var. *ivory* (Sarcophagidae) were taken from a laboratory colony. The hearing tachinid *Therobia leonidei* was collected in Greece (Lakes-Harlan & Heller 1992; Lehmann & Heller 1998; Stumpner & Lakes-Harlan 1996).

For scanning electron microscopy the prothoraces of flies were dehydrated in an ethanol series, critical point-dried, sputtered with gold and viewed on a Zeiss Novoscan 30 scanning electron microscope. The central projection of the scolopidial sense organ was stained by immersing the sensory organ in 5% nickel chloride in a glass capillary followed by silver

Figure 2. Central projection of the scolopidial cells of the prothoracic hearing organ of *E. auditrix* ((a, d) Sarcophagidae) and *T. leonidei* ((c, f) Tachinidae), and of the prothoracic chordotonal organ of *S. bullata* ((b, e) Sarcophagidae). In all three species the afferents arborize in the median ventral association centres (mVAC, arrows) of the three thoracic neuromeres as is obvious in the parasagittal sections (d–f) of the whole-mounts shown above. Abbreviations: a, anterior; d, dorsal; DLV, dorsal lateral tract of ventral fasciculus; ln, leg neuropile; n, neck connective; pn, prosternal nerve; VTV, ventral median tract of ventral fasciculus. Scale bars: 100 μ m.

intensification of the central nervous system (CNS; for details, see Mücke & Lakes-Harlan 1995). The histology of the sense organ within the prothorax as well as the CNS was revealed by serial sections taken from plastic-embedded preparations (Mücke & Lakes-Harlan 1995).

The vibrations of the tympanal membrane or of the attachment site of the chordotonal organ were measured laser-vibrometrically (Polytec OFV-2100). Therefore, the fly was mounted ventral side up on a small holder. The head was bent slightly dorsally to expose the areas of interest. Repeating wobbled sine-wave tones were used as stimulus (Meyer & Elsner 1995) and power spectra were calculated.

Sound stimuli were synthesized with a PC-controlled sound board and presented with a single speaker (Lang *et al.* 1993). Vibrational stimuli were delivered with a piezo transducer (Physic Instruments) fastened to the attachment site of the sensory organ or to the frontal leg. Head movements rotating around the body length axis were performed by attaching the head to a rotating device driven by a minishaker (Bruel & Kjael). Vibration and movement stimuli were generated using LabView 4.0 (National Instruments) and the neuronal responses were registered online with the same software. A sharpened tungsten electrode was placed near the sensory nerve for

recording of summed action potential activity after dorsal dissection of the animal. Similar to investigations in the hearing tachinids, the hearing threshold was determined electrophysiologically by suction electrode recordings from axons of auditory interneurons running in the neck connective (Stumpner & Lakes-Harlan 1996).

3. RESULTS AND DISCUSSION

(a) *Anatomy of the ear of Emblemasoma auditrix*

First, we identified the sensory basis for the auditory behaviour in *Emblemasoma auditrix* (Sarcophagidae). The hearing organ of *E. auditrix* is the widened prosternum (ventral part of the prothorax). The ear is hidden behind the head in a sitting fly and the tympanal membranes are facing frontally (figure 1a,d). The two bilaterally symmetrical tympanal membranes are separated by sclerotized parts, the probasisternum, and the presternum and extend to the coxal sclerites (figure 1d). A single prosternal air sac can be found underneath both tympanal membranes (figure 1e). Within the air sac, two scolopidial organs are located, each attached (i) at the junction of the presternum and one tympanal membrane, and (ii) at

Figure 3. Biophysics and physiology of the hearing organ of *E. auditrix* and of the proprioceptive-vibratory organ of *S. bullata*. (a) Velocity-spectrum of the vibrations of the tympanal membrane of *E. auditrix* measured by laser-vibrometry ($n=4$). Shown are the mean curves of four animals, each averaged over 100 tests; 0 dB refers to 5 mm s^{-1} . (b) Hearing threshold of *E. auditrix* measured at the neck connective ($n=3$) and spectrum of the calling song of the host cicada (*Okanagana rimosa*; hatched area). The registered summed potentials represent the responses of ascending interneurons to sound stimuli. A mismatch between the best hearing frequency (*ca.* 5 kHz) and spectral peak of the calling song of *O. rimosa* (*ca.* 9 kHz) can be observed. (c) Electrophysiological threshold curves of the scolopidial organs of both species (open squares: *E. auditrix*, $n=3$; filled squares: *S. bullata*, $n=5$). The attachment site of the organ has been directly stimulated with a piezo transducer. (d) Spectra of the vibration amplitude of the attachment site of the sensory organ from five *S. bullata* measured by laser-vibrometry. The front leg has been stimulated with vibrational stimuli with $0.8 \mu\text{m}$ amplitude of each frequency, respectively. The hatched area indicates the threshold curve of the amplitude of vibrational stimuli ($n=5$). The piezo transducer has been attached directly to the presternum.

the respective prosternal apodeme (figure 1*b,e*). The sense organ is orientated roughly parallel to the body length axis. The scolopidia are orientated in the same direction and are located in a dense group at the base of the organ close to the apodeme. The organ consists of approximately 30 scolopidia, each unit comprising one sensory cell and a scolopale cell, plus accessory cells. The scolopidia are of uniform size, *ca.* $10 \mu\text{m}$ in length and $4 \mu\text{m}$ in diameter.

These auditory receptor cells project with their axons caudally into the thoraco-abdominal ganglion complex. Main arborizations invade the median ventral association centre (mVAC) found in all three thoracic neuromeres (figure 2*a*). This mVAC is homologous to neuropiles in the auditory systems of other hearing insect taxa and in many chordotonal systems (figure 2*a,d*; Boyan 1993, 1998; Merritt & Murphey 1992; Pflüger *et al.* 1988).

(b) *Physiology of the ear of Emblemasoma auditrix*

The enlarged prosternum of *E. auditrix* represents a sound-sensitive ear. Vibrations of the tympanal membrane in response to airborne sound were demonstrated by means of laser vibrometry (figure 3*a*). High-velocity vibrations at the attachment site of the sense organ could be elicited from 3–30 kHz. These vibrations are trans-

duced into acoustically evoked neuronal responses. In contrast to the tympanal vibrations the threshold curve of auditory interneurons is sharply tuned at a characteristic frequency (CF) of 5 kHz (figure 3*b*). The sensitivity at the CF is relatively low with 50 dB sound pressure level (SPL). At behavioural relevant frequencies (around 9 kHz; which correspond to the main frequencies in the host's calling song, figure 3*b*) the sensitivity is even lower with 65–70 dB SPL (figure 3*b*). First measurements of the summed activity of afferents gave much more variable results compared to interneuronal activity in the neck connective. The CF of the afferents was similar to that of interneurons and at no frequency afferents were significantly more sensitive than interneurons (H. Stölting, unpublished results). However, the spectrum of the vibrations of the tympanal membrane does not match the threshold curve of the hearing. In particular, the CF is not represented as a peak in the spectra of the tympanal vibration. The mismatch can be explained either by an intrinsic tuning of sensory cells (as proposed for tympanal receptor cells of bushcrickets; Oldfield 1985) or by differential movements of the sense organ in respect to the tympanic membrane (as seen in grasshoppers; Breckow & Sippel 1985; Meyer & Elsner 1995).

Figure 4. Phylogenetic relationship within the Calyptrata (after McAlpine *et al.* 1987). An ear evolved in the groups of Emblemasomatini and Ormiini. Call., Calliphoridae; Myst., Mystacinobiidae; Rhin., Rhinophoridae; Oest., Oestridae.

(c) Convergent evolution of ears in Diptera

The sarcophagid ear described above is an apomorphic character of the sarcophagid taxon Emblemasomatini, as is the ear in the tachinid taxon Ormiini. It is used as a unique systematic character to separate these taxa from sister groups in both families (figure 4; McAlpine *et al.* 1987). Homology of both ears is strongly suggested for the following reasons. As in *E. auditrix*, the prosternum, for example of *Therobia leonidei* (Ormiini), is the site of the elaborated ears (figure 1*h,i*; Lakes-Harlan & Heller 1992). The same structural elements, such as tympanic membranes, sclerites, prosternal air sac and a sense organ, attaching to the same structures can be found in both groups. The central projections of auditory receptor cells of tachinid flies also arborize within the mVAC of the three thoracic neuromeres (figure 2*c,f*), as is the case in *E. auditrix*. Differences between Emblemasomatini and Ormiini are found in the density of central projections (figure 2), the dimensions of the ear (figure 1*d,h*), the number of sensory units and, perhaps, the biophysics (Robert *et al.* 1998). For example, *T. leonidei* has sexually dimorphic large inflations (Lakes-Harlan & Heller 1992; Stumpner & Lakes-Harlan 1996) and up to 200 sensory units. The hearing threshold curves are species specific (with respect to tuning and sensitivity) and might be adapted to the host's signal (see below). The homology of both ears, which evolved independently from each other, raises the question whether a structure exists in Diptera which might be or might have been preadaptive for the evolution of ears.

(d) Chordotonal origin of the dipteran ears

The preadaptive structure for the evolution of dipteran ears is presumably a scolopidial organ at the presternum of atympanate flies (Lakes-Harlan & Heller 1992). In a comparative study, Edgecomb *et al.* (1995) examined the peripheral elements of the sense organ as well as internal elements, like the tracheal system of non-hearing flies and hearing tachinids to a great detail confirming the idea of homologous organs. Anatomically, the organ extends

from the sternal apodeme to the presternum (figure 1*c,f,g*, for *Sarcophaga bullata*). Also, other prosternal elements of the ears like membranes, sclerotized exoskeletal elements and a large tracheal air sac can be recognized (figure 1; Edgecomb *et al.* 1995). The afferents project into all three thoracic neuromeres and send collaterals into each respective mVAC (figure 2*b,e*). In contrast to the hearing species, these afferents are not restricted to the ipsilateral side (figure 2*b*), which, however, is not unusual for chordotonal afferents (Pflüger *et al.* 1988). On the other hand, auditory receptors of insects in general are usually restricted to the ipsilateral half of the ganglion (Boyan 1993, 1998), perhaps facilitating precise localization of acoustic signals by a bilaterally separated information processing. The function of the chordotonal sense organ, however, is unknown (Hengstenberg 1991).

Is this homologous chordotonal organ physiologically preadapted? The chordotonal organ of *S. bullata* (Sarcophagidae) does not respond to airborne stimuli up to 90 dB SPL (data not shown). By contrast, direct stimulation of the attachment site with a vibrating probe reveals a sensitive response to vibration frequencies from below 100 Hz to 10 kHz (figure 3*c*). Thus, the organ is able to transduce signals in a frequency range used by signals of potential hosts. Reported threshold curves of vibration sensitive scolopidial organs of other insects usually have their CFs at much lower frequencies (<1000 Hz), subgenal receptor cells react to more than 5 kHz (Kalmring 1985). However, other chordotonal organs of insects might also react to high frequency vibration and therefore be 'preadapted' to become hearing organs. Our observations of prosternal movements of *S. bullata* suggest that the natural stimulation is likely to occur either during head movements or during vibrations transmitted via the legs. Laser-vibrometric measurements show that the presternum moves with large amplitudes (up to 20 µm) during head movements (stimulation frequencies: 2–25 Hz). However, with summed electrophysiological recordings from the nerve containing the chordotonal afferents, no head-movement-related activity was detected. Vibrating one front leg (with a constant amplitude of 0.8 µm at different frequencies) also resulted in movements of the attachment site of the chordotonal organ (figure 3*d*). Stimulus-correlated neuronal activity could be recorded electrophysiologically, however, responses from other sense organs than the presternal organ might have been recorded as well and made the interpretation equivocal. Nevertheless, stimulation frequencies above 4 kHz resulted in movement amplitudes sufficient to elicit electrophysiological responses when stimulating the presternum directly (figure 3*d*), indicating high-pass filter properties of the sensory organ.

(e) Biological function and hypothetical evolution

How could a vibrational sensitivity make a chordotonal organ preadapted for the evolution of a hearing organ? It is perceivable that ancient parasitoids used chemical cues to locate their hosts, as do many living parasitoids (Godfray 1994). During their final approach they might have detected vibrational signals emitted during sound production of the host with their presternal organ. In this respect it seems interesting that flies lack highly sensitive vibratory organs in the tibia of the leg (the subgenal

organ; Lakes & Pollack 1990). Vibrational signals spread in wooden plants over large distances and are used by many insect species (Markl 1983). Using vibratory signals provides much better directional information compared to volatile chemical signals. Detecting the acoustic cues of the host then resulted in a combination of long-range detectability and good directionality. This improved acoustic sensitivity was achieved through some modifications of the peripheral structures of the prosternum, without the evolution of a completely new sense organ and its neuronal network. Vibratory communication signals have been found in some species of singing cicadas (Gogala *et al.* 1996). It remains to be shown whether vibrational stimuli are still used and how similar the vibratory network in non-hearing species is to the auditory network in hearing species. Behavioural observations in phonotactic experiments show that *E. auditrix* often approaches a loudspeaker by walking the last 5–50 cm (Lakes-Harlan *et al.* 1998). The evolution of the tachinid ear has been discussed in the context of bat avoidance (Robert *et al.* 1992). This seems rather unlikely for the Sarcophagidae, because (i) they are active during daytime, and (ii) the chordotonal organ of related non-hearing species does not react to airborne stimuli.

Whatever the primary selective pressure was, these evolutionary modifications took place at least twice independently from each other (figure 4) and are at least nowadays correlated to the lifestyle. All known hearing fly species are parasitoids of sound-producing insects and the acoustic sense is used for host location. Hearing tachinids are parasitoids of crickets and bushcrickets, and hearing sarcophagids parasitize cicadas, in the case of *E. auditrix*, males of the periodical cicada *Okanagana rimosa*. The spectral peak of the calling song of *O. rimosa* lies between 7 and 11 kHz and females of *E. auditrix* were easily attracted in the field by playing the calling song of the host (Soper *et al.* 1976). The flies exhibited a phonotactic response behaviour in the frequency range of the calling song, but not to 5 kHz, again indicating a mismatch to the hearing threshold curve (Lakes-Harlan *et al.* 1998).

Using the well-suited example of hearing organs in Diptera, our results indicate that the ear has been evolved from a chordotonal precursor organ which is in agreement with the hypothesis proposed for other insect species (Boyan 1993; Fullard & Yack 1993; Hoy & Robert 1996; Meier & Reichert 1990; Van Staaden & Römer 1998; Yack & Fullard 1990). For the first time, to our knowledge, we present physiological data showing how a functional transformation might have taken place, whereby peripheral modifications might be sufficient to construct an ear at suitable sites of the insect body maintaining the gene cascade for the generation of scolopidial sense units.

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