Simple ears – flexible behavior: Information processing in the moth auditory pathway

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Abstract   Lepidoptera evolved tympanic ears in response to echolocating bats. Comparative studies have shown that moth ears evolved many times independently from chordotonal organs. With only 1 to 4 receptor cells, they are one of the simplest hearing organs. The small number of receptors does not imply simplicity, neither in behavior nor in the neural circuit. Behaviorally, the response to ultrasound is far from being a simple reflex. Moths' escape behavior is modulated by a variety of cues, especially pheromones, which can alter the auditory response. Neurally the receptor cell(s) diverges onto many interneurons, enabling parallel processing and feature extraction. Ascending interneurons and sound-sensitive brain neurons innervate a neuropil in the ventrolateral protocerebrum. Further, recent electrophysiological data provides the first glimpses into how the acoustic response is modulated as well as how ultrasound influences the other senses. So far, the auditory pathway has been studied in noctuids. The findings agree well with common computational principles found in other insects. However, moth ears also show unique mechanical and neural adaptation. Here, we first describe the variety of moths' auditory behavior, especially the co-option of ultrasonic signals for intraspecific communication. Second, we describe the current knowledge of the neural pathway gained from noctuid moths. Finally, we argue that Galleriinae which show negative and positive phonotaxis, are an interesting model species for future electrophysiological studies of the auditory pathway and multimodal sensory integration, and so are ideally suited for the study of the evolution of behavioral mechanisms given a few receptors [*Current Zoology* 61 (2): 292–302, 2015].

Keywords   Lepidoptera, Ultrasound perception, Multimodal communication

1   Auditory Behavior

The evolution of hearing in moths is a textbook example for an arms race between prey and predator, noted already by naturalists over 150 years ago (Bonsdorf 1835, in Renni, 2013). With bats entering the ecosystem of nocturnal moths and other insects - flying at night to avoid day-active predation by birds - becomes a risky business. Bats use echolocation for navigating in the dark and also for catching insects (Griffin, 1944; Griffin et al., 1960). To avoid being eaten, moths independently evolved tympanic ears many times (Yager, 1999). Earless lepidoptera are either diurnal, non-flyers (Fullard and Napoleone, 2001) or are able to briefly outfly bats (Hasenfuss, 2000). The arms race is ongoing, with e.g. countertactics by bats to avoid being detected (Görlitz et al., 2010). Here, though, we will rather illustrate that what may have started as a simple bat defense mechanism evolved into a sophisticated auditory behavior exploited for inter- and intraspecific communica-

tion. This is achieved with very few receptor cells but as we will review, is often sufficient when complemented with elegant non-neural and higher order neural mechanisms. When it comes to unraveling the neural basis of the auditory behavior mainly noctuid moth species have been used. But the multimodal mating behavior of wax moths (Galleriinae, Pyralidae) makes them a prime model species to study sensory integration and decision making at the physiological level and hence also infer the evolution of the positive phonotaxis behavior in moths.

1.1   Stereotyped and modulated defense behavior

Treat, Roeder, and colleagues (Roeder, 1962; Roeder and Treat, 1970; Payne et al., 1966) systematically studied the moths' behavior in response to ultrasonic bat cries. Using artificial stimuli as well as natural bat calls, they observed that a flying moth shows either negative phonotaxis or a startle response to a distant ultrasonic stimulus. Calls signaling a nearby bat elicited erratic flight behaviors including active dives to the ground or

looping (Roeder, 1962, 1964; Treat, 1955). These two alternative strategies are appropriate, since the bat may abort the hunt (Surlykke and Moss, 2000). In non-flying moths, perception of ultrasound leads to freezing-like behavior (Werner, 1981; Greenfield and Baker, 2003).

Many studies have reported that nocturnal moths adjust their acoustic escape response according to input from other sensory modalities. The decision to fly away, for example, is postponed if the moth is flying in a pheromone plume (Skals et al., 2005). Also, visual information is demonstrated to modulate the escape behavior. Svensson et al. (2003) found that *Cataclysta lemnata* (Pyralidae) responds to bat cries by landing and freezing during the night but with erratic flight maneuvers during the day. The latter is a valid strategy against diurnal bird predation but less successful against the threat of bats.

In addition to these various evasive responses, some moth species evolved active defense behavior by producing ultrasound pulses during their flight[①]. Non-toxic moths are reported to emit ultrasound which subsequently startles naïve bats or jams the bat sonar, whereas poisonous moths are assumed to emit sound signals to warn about their toxicity (Corcoran et al., 2010, Bates and Fenton, 1988; Barber and Kawahara, 2013). The non-toxic palatable tiger moth *Bertholdia trigona* (Arctiinae), for example, produces ultrasound during flight to disturb the hunting bat's sonar (Corcoran et al., 2009). The toxic dogbane tiger moth *Cycnia tenera* (Arctiinae) produces ultrasonic clicks which startle naïve bats and also serve as a warning signal for experienced bats (Dunning and Roeder, 1965; Corcoran et al., 2010). Interestingly, the non-toxic moths, *Euchaetes egle* (Arctiinae) and *Eubaphe unicolor* (Geometridae), are assumed to use ultrasound to pretend that they are poisonous, i.e. a kind of Batesian mimicry (Barber and Conner, 2007; Corcoran and Hristov, 2014). Corcoran et al. (2010) examined many sound-producing species and found that acoustic aposematism is signaled with only a few clicks, whereas sonar jamming consists of many clicks. Also, hawk moths (Sphingidae) produce sound during flight (Barber and Kawahara, 2013), but it is not yet known whether the intention is to jam the echolocating signal, to produce a startle response in the bat, or to warn.

1.2 Ultrasound co-opted for intraspecific communication

In moths, three distinct categories of intraspecific ul-

trasonic signals have been identified: (i) calling songs for mate attraction (Heller and Krahe, 1994; Surlykke and Gogala, 1986; Gwynne and Edwards, 1986; Spangler et al., 1984, Heller and Achmann, 1993b; Jang and Greenfield, 1996), (ii) courtship songs for mate recognition/acceptance (Nakano et al., 2008; Spangler, 1988; Simmons and Conner, 1996; Trematerra and Pavan, 1995; Kindl et al., 2011; Nakano et al., 2013, Sanderford and Conner, 1995, Sanderford et al., 1998), and (iii) territorial calls (Bailey, 1978; Alcock and Bailey, 1995). In addition, it should be mentioned that many other moth species produce ultrasound, though the function is often still unknown (Heller and Achmann, 1993a; Skals and Surlykke, 1999; Kay, 1969).

The three former communication categories, which deal with sexual behavior, are associated with sound production organs, e.g. tymbal organs (Corcoran et al., 2010), that have developed mainly in male moths. In some species, females are unable to distinguish between the male courtship song and bat calls and therefore react to both sound signals with immobilization. Such conspecific male calls are deceptive courtship songs (Nakano et al., 2006; 2010). In other moth species, females discriminate conspecific male versus bat calls. In this case the male song is a true sexual signal, stimulating female arousal. Both deceptive and true sexual songs are reported to enhance male copulation success (Greenfield and Weber 2000; Conner, 1997, 1999; Conner and Corcoran, 2012). It is not yet known whether true signals evolved from deceptive songs or whether they developed independently. The latter alternative may have arisen from slightly different precursory sounds incidentally emitted in a sexual context, as suggested by Nakano et al. (2013). Finally, a combination of true and deceptive signaling is reported as well. The yellow peach moth *Conogethes punctiferalis* (Pyralidae), for example, uses two types of calls: one long, 304 ms, and one short, 28 ms. The short call which mimics the echolocating signal of the sympatric horseshoe bat is assumed to be used for discouraging other males to approach the scene whereas the long call increases mate acceptance by the female as indicated by wing raising (Nakano et al., 2014).

2 The Tympanic Ear of Moths

Systematic studies of lepidopteran ears began around 100 years ago (reviewed in Eggers, 1928; von Kennel

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① Some species do produce ultrasound with their wings as a side-effect during flying (Lapshin and Vorontsov, 2000).

and Eggers, 1933; Minet and Surlykke, 2003; Hasenfuss, 1997, 2000). Moth ears have been found at various body locations (Fig. 1). Still, all lepidopteran tympanal organs consist of a tympanum[①], a tracheal air sac, and a scoloparium (Eggers, 1928; Minet and Surlykke, 2003, Fig. 2). A further common feature of all moth ears is that, given the few receptor cells present, moths cannot discriminate frequencies. Nevertheless, the ears might be tuned to a "best frequency" (Hofstede et al., 2013). However, other anatomical details, i.e. non-neural mechanisms, differ, enabling ecological adaptations despite phylogenetic constraints. We will illustrate this on sensitivity and directional hearing; both of which are crucial parameters for adaptive responses to ultrasound.
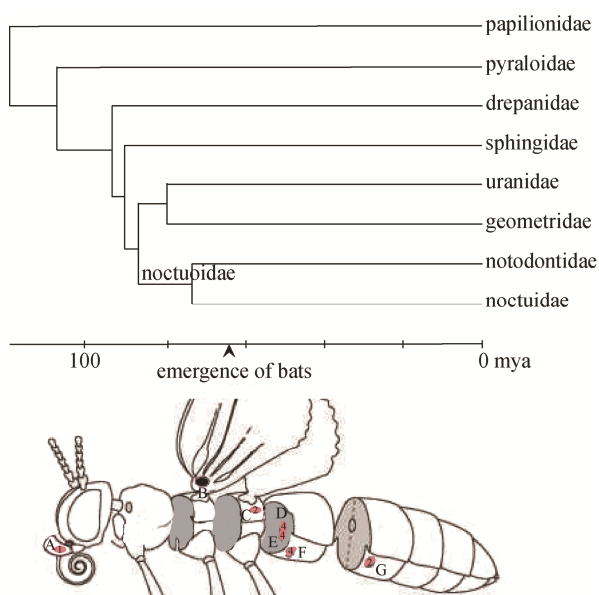

Fig. 1   Independent evolution of moth ears
Top: Phylogeny of the lepidopteran superfamilies based on Wahlberg et al. (2013). Red squared superfamilies where some species have co-opted hearing for communication. Bottom: schematic drawing of a generalized insect showing seven body locations where tympanal ears have been identified in Lepidoptera. Note that not all species within a taxonomic division do necessarily possess ears A: Sphingidae (Choerocampini, Acherontini, e.g. hawk moths); location: palp-pilifer region. B: Papilionoidea, Hedyloidea; Neuroptera: Chrysopidae; location: base of ventral forewing. C: Noctuoidea; location: within a cavity on the posterior metathorax. D: Pyraloidea; location: within a cavity on ventral surface of first abdominal segment. E: Geometridae; location: within a cavity on anterior side of first abdominal segment. F: Drepanidae; location: internalized tympanal membrane located between two air-filled chambers on first abdominal segment. G: Uraniidae; location: within cavity at the anterior (females) or posterior (males) end of the second abdominal segment. Number within location indicates number of scolopidia, for (B) = many. Modified from http://what-when-how.com/insects/hearing-insects/

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① At least one tympanum, there can also be a countertympanum

2.1   Evolution and development of the tympanic ear

In insect taxa, tympanic ears evolved from vibration-sensitive or from stretch-sensitive organs (Strauß and Stumpner, 2015). These are scolopidial chordotonal organs and were the precursor organs for all moth tympanic ears (Eggers, 1928; Boyan, 1993; Lewis and Fullard, 1996; Hasenfuss, 1997; Yack and Fullard, 1993; Yack, 1992, 2004). Through specialization, i.e. development of a tympanum, the sensitivity of the organ is increased to airborne stimuli (Meier and Reichert, 2000, von Kennel and Eggers, 1933).

Note that the independent evolution of moth ears at various body parts might be the result of homology at the genetic level (Yager, 1999), but since tympanal organs are made up of scolopidia, i.e. ears do not consist of a new receptor type, finding a unique "ear-gene" is unlikely.

Depending on the moth family, the tympanic ear contains 1 to 4 scolopidia, of which all those responding physiologically to ultrasound are named A cells (Fig. 2A). In hooktip moths (Drepanidae) Surlykke et al. (2003) found that only two of the scolopidia were responsive to acoustic stimuli. Presumably the two remaining sensory cells still function as proprioceptors, i.e. detecting low frequency mechanical displacements (Surlykke et al., 2003). On the other hand, in noctuoidae the number of sensory cells is reduced during metamorphosis (Lewis and Fullard, 1996). Noctuids reduce it by one to two phonoreceptors, the A1 and A2 cell, whereas notodontids reduced the number of phonoreceptors to a single A cell. This reduction might be explained by a partial loss of hearing during evolution due to development of a diurnal lifestyle (Hasenfuss, 2000). Behaviorally, Fullard and Napoleone (2001) did not find a relation between the number of A cells and diel flight preference, but rather that sensitivity mattered for a primarily diurnal or nocturnal lifestyle.

2.2   Sensitivity

The larger the moth, the more conspicuous it is to the bat. To enable the moth enough time to escape, larger moths can detect bat calls at intensities of around 30 dB SPL (Hofstede et al., 2013), whereas small moths detect ultrasound at intensities of around 40 dB SPL (Roeder, 1964). Thus, the threshold for ultrasound detection depends on the size of the insect, providing a similar safety margin (Surlykke et al., 1999). In addition to tuning the tympanum, moths, but not butterflies, have wing scales that absorb parts of the bat call acoustic energy
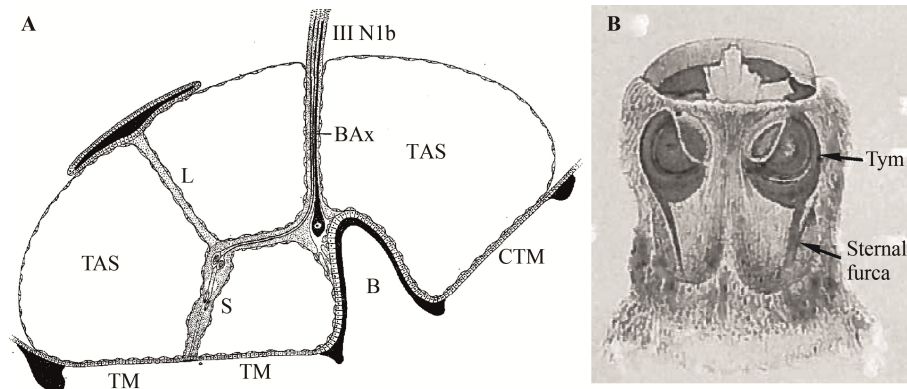
Fig. 2 The tympanic ear

A. Schematic drawing of noctuid ear, frontal section of left tympanic air sac, modified from Treat and Roeder (1959). **B.** Female *Aphomia sociella* (Galeriinae) ventral view of the first two abdominal segments showing the ears. Modified from von Kennel and Eggers (1933). B: Bügel; BAx: Axon B cell; CTM: Countertympanic membrane; L: ligament loosely connecting the scoloparium with the scutal phragma; S: scoloparium containing the scolopes and acoustic sensory cells; TAS: tympanic air sac; TM: tympanic membrane; III Nlb: tympanic nerve.

(Zeng et al., 2011). This increases the detection distance by 5%–6% for the moths. Finally, moths' ears have been shown to amplify the signal by using otoacoustic emissions (Kössl et al., 2007), another non-neural mechanism to enhance sensitivity.

2.3   Directional hearing

Both negative and positive phonotaxis require knowledge of which direction the sound comes from. Moths achieve directional hearing in various ways, also depending on body size and often through anatomical and mechanical mechanisms, rather than neural mechanisms. Large moths diffract sound enough to create binaural intensitiy differences (Payne et al., 1966; Surlykke, 1984). Medium-sized moths often have ears that function as pressure difference receivers (Hasenfuss, 1997), practically translating the angle of the sound wave into tympanic vibrations with large amplitude differences, a mechanism also found in crickets (Michelsen, 1979, 1994; Michelsen and Larsen, 1995, 2008). The third mechanism, found in tiny moths, consists of sequential integration of intensity differences (Greenfield et al., 2002). Such temporal processing to gauge decreasing or increasing intensity differences may also explain why moths infected with the mite *Myrmonyssus phaaenodectes* in one ear (the mites never infest both ears), are still capable of localizing the sound source (Treat, 1957). It remains to be tested whether all moths are capable of this sequential processing or whether this is restricted to just a few moth species. If it is a shared mechanism, then even hawk moths, with their ears closely positioned at the palps, could show directional hearing. In addition to the above mentioned arrangements, sound localization is often enhanced by a cup-shaped structure of the outer ear, similar to the pinnae of mammals (Fullard, 1984).

3   Information Processing: Morphology and Physiology of the Auditory Pathway

As the previous paragraphs have shown, moths exploit a range of anatomical mechanisms to enhance auditory processing. Next, we will present the anatomy of identified sound-sensitive cells discovered in noctuid moths (Fig. 3). Thereafter, we present bat call characteristics to illustrate the requirements for neural mechanisms detecting dangerous ultrasound signals and distinguishing those from courtship songs, respectively. Finally, we explore to what extent those common principles could guide future auditory and multimodal sensory research in Galleriinae and the evolution of positive phonotaxis in other moth families, respectively.

3.1   Anatomical organisation of the primary afferents

The projection pattern of the auditory sensory neurons has been mapped in various species of noctuid moths. In addition to the two phonoreceptors, the A1 and A2 cells, there is one B cell, which is assumed to serve as a proprioceptor. The three sensory cells project into the IIIN1b nerve, which is a sub-branch of the IIIN1 nerve connected to the metathoracic ganglion (Fig. 3A–B). The axon of the noctuid A1 cell has ramifications in the meta-, meso-, and prothoracic ganglia but remains strictly ipsilateral (Agee and Orona, 1986; Surlykke and Miller, 1982; Zhemchuzhnikov et al., 2014). The A1 cell was recently shown to terminate in the prothorax without entering the subesophageal or brain gan-

glion (Zhemchuzhnikov et al., 2014). Furthermore, no direct link between the A1 cell and motor neurons has been found (Boyan and Fullard, 1986; Boyan et al., 1990; Madsen and Miller, 1987; own observations). The A2 cell, which projects more medially than the A1 cell, remains mainly ipsilateral and has ramifications restricted to the meso- and metathoracic ganglion (Surlykke and Miller, 1982; Zhemchuzhnikov et al., 2014). A few branches of the A2 cell are reported to project contralaterally. The B cell, which has the largest axonal diameter of the three sensory cells (Ghiradella, 1971; Surlykke and Miller, 1982; Zhemchuzhnikov et al., 2014), projects closely alongside the A1 cell. Thus, it

also remains strictly ipsilateral but terminates in the subesophageal ganglion (Zhemchuchnikov et al., 2014). The A1 and A2 cell do synapse onto many interneurons. These interneurons have their somata contralateral to the site of their ascending axon collateral (Boyan and Fullard, 1986; Boyan et al., 1990; Pfuhl et al., 2014). A subset of these interneurons has rich ramifications in the meso- and metathorax and terminates in the ventrolateral protocerebrum of the brain (Pfuhl et al., 2014, Fig. 3C, D). Notably, Roeder (1966) obtained auditory responses during extracellular recordings from the same brain region.
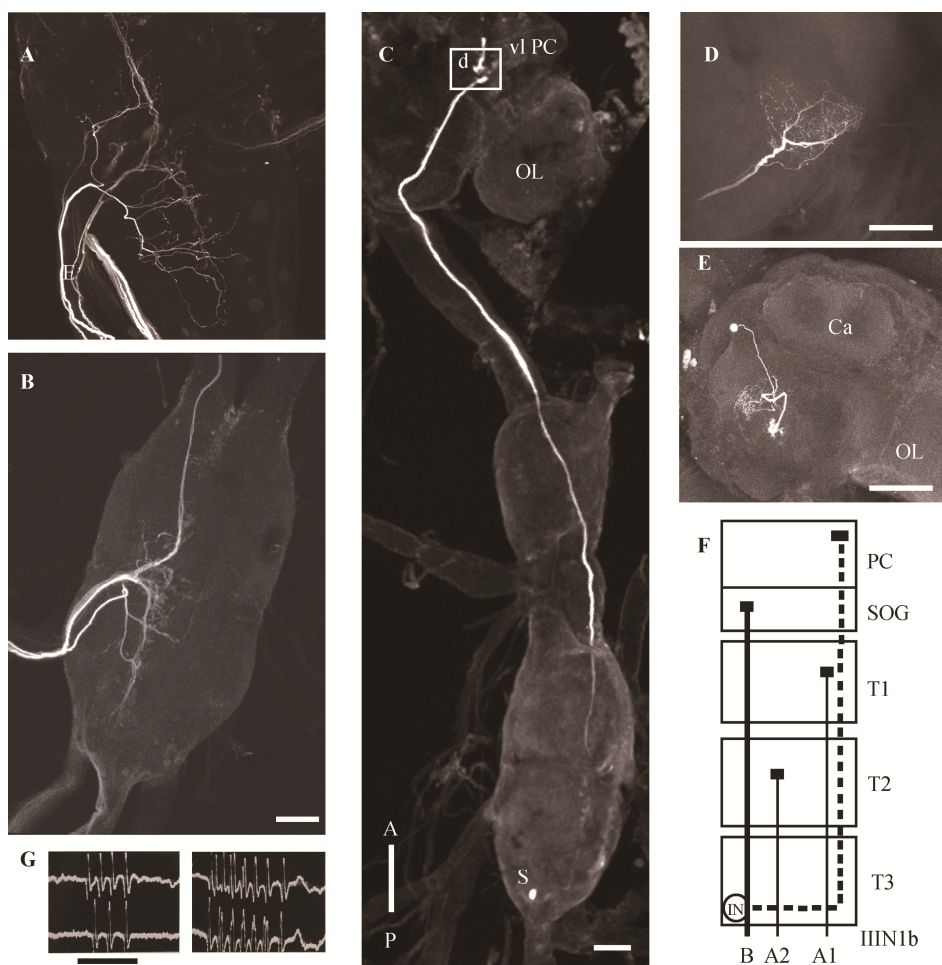
This projection pattern of the sensory afferents,

Fig. 3 The noctuid auditory pathway

A. Confocal image of tympanic IIIN1b entering the pterothorax, major ramifications of A1, A2 and B cell, species: *H. virescens*. **B.** Confocal image, different preparation, showing ascending A1 and B cell (own data, see also Zhemchuzhnikov et al. 2014). **C.** Confocal image of ascending interneuron having its soma in the metathorax and terminating in the ventrolateral protocerebrum. **D.** detail of the ramifications in the brain. **E.** Confocal image of a brain interneuron, innervating the same area as the ascending ventral cord interneurons (modified from Pfuhl et al., 2014). Scale bars in B, D, E: 100μm in C: 200μm. **F.** Scheme of the noctuid auditory pathway. The sensory afferents enter the ventral cord via the IIIN1 nerve. The A1 cell ascends to the prothorax and has many ramifications in the meso- and metathorax. The A2 cell has many ramifications in the meso- and metathoracic ganglion. The B cell has the thickest axon and terminates in the SOG. **G.** Response of the A cells to bat cries, upper trace ipsilateral, lower trace contralateral. Left shows faint bat cry, right shows intense bat cry. Species: *Feltia sp.* (modified from Roeder, 1964). Scale bar: 10 ms. A: anterior; Ca: calyx; IN: interneuron; OL: optic lobe; P: posterior; PC: protocerebrum; S: soma; SOG: subosephageal ganglion; T1: prothorax; T2: mesothorax; T3: metathorax; vl PC: ventrolateral protocerebrum: scale bars: C = 200 μm, B, D–F = 100 μm.

which implies interneurons carrying the sound information to the brain, is similar to the auditory pathways of many other insect species (Stumpner and von Helversen, 2001, Fig. 3F). The ventrolateral protocerebrum is probably a higher auditory neuropil, as sound-sensitive brain interneurons project into this area as well (Pfuhl et al., 2014, Fig. 3E). Also, a descending sound-sensitive neuron is reported to have rich ramifications in this area (Olberg and Willis, 1990).

3.2 Encoding characteristics of the A1 sensory cell

The calls of various bat species vary in their best frequency and temporal patterns. Accordingly, the sensor should have a broad frequency spectrum, but still filter out non-bat frequencies such as bird calls, cricket courtship songs, and rustling leaves. Indeed, the moth's phonoreceptors, or A cells, have a broad tuning curve but still filtering out non-ultrasound frequencies. A bat call is made up of a certain number of ultrasonic pulses of certain frequency and intensity. Commonly, the pulse repetition rate is low during the search stage and much higher during the attack stage (Fig. 4A). Further, search calls are high in intensity, whereas attack calls are low in intensity. This indicates a trade-off concerning energy spent on seeking and attacking, respectively (Jones, 1999). Since the intensity attenuates with the distance, the most informative characteristic of the call is the change in duration and pulse repetition rate. Consequently, any unused temporal pattern by the sympatric bat species can be used for the evolution of a true

courtship song (Nakano et al., 2013).

It was found that the A1 cell fires a set of spikes with about 2 ms intervals per pulse (data from noctuids, Roeder, 1964). Higher intensity of the calling signal causes an increased number of spikes per pulse, decreased latency to the first pulse, and shorter interspike intervals (Fig. 4B). Sustained long pulses, over 1 sec in duration, and short single pulses, below 2 ms or shorter, have no effect on moth behavior. The former is due to adaptation and the latter to insufficient excitation of the A1 cell. At high intensities the A1 cell saturates. To increase the intensity range, the second phonoreceptor has a detection threshold 15–20 dB above the A1 cell (Roeder, 1966, 1974; Surlykke and Miller, 1982). Such an intensity range fractionation was also found in species having more than two phonoreceptors (Surlykke and Filskov, 1997; Skals and Surlykke 2000).

3.3 Physiological properties of auditory ventral cord interneurons

Roeder (1966) classified interneurons based solely on electrophysiological responses into three types: repeater neurons, pulse marker neurons, and train marker neurons (see also Paul, 1974). Repeater interneurons respond similarly to ultrasound as does the A1 cell (Fig. 4C). Thus, they can inform the nervous system about the duration of the pulse, i.e. they are suggested to function as duration detectors (Clemens and Henning, 2013). This category of interneurons has been characterized by staining techniques (Boyan and Fullard, 1986; Boyan et
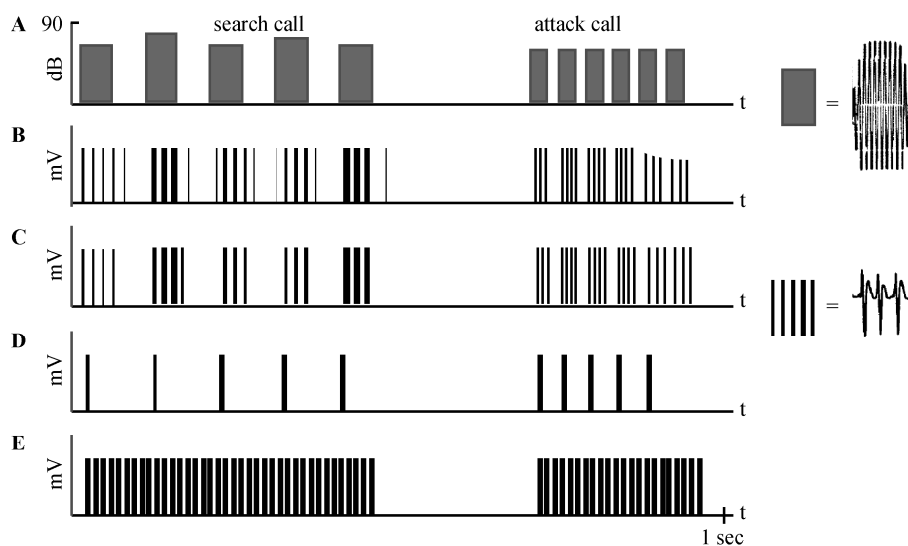

Fig. 4   Schematised physiology of the acoustic cells
A. Stimulus, 50 kHz, pulse duration of 50 ms and pulse repetition rate of 10 Hz. Two intensity illustrated. **B.** Response of the A1 cell, note the afterdischarge, spontaneous activity is not drawn. **C.** Response of a repeater interneuron, faithfully replicating the A1 cell spikes. **D.** Response of a pulse marker neuron, responding at the onset of a pulse. **E.** Response of a train marker neuron, responding during pauses too. Thickness of line symbolizes number of spikes within a burst. Not drawn to scale.

al., 1990; Pfuhl et al., 2014). Morphologically these repeater interneurons are most likely identical with the ventral-cord interneurons mentioned above, which project to the ventrolateral protocerebrum of the brain (Pfuhl et al., 2014). Pulse-marker interneurons, on the other hand, spike once for each pulse, which indicates that those neurons encode changes in the interpulse interval and pulse repetition rate, respectively (Fig. 4D). This neuron category does not fire in the pauses between pulses. The pulse marker neurons may constitute an efficient arrangement for categorizing ultrasound stimuli into dangerous and not dangerous signals. Behaviorally, there is some evidence that moths use the pulse repetition rate of the bat call to assess predation risk (Acharya and McNeil, 1998), but note that they used articifial sounds. For natural bat calls the duration and repetition rate changes simultaneously (Surlykke and Moss, 2003). When the bat is far away, the pulse marker neurons will fire at a relatively low frequency corresponding to the low repetition rate of the search call. Higher repetition rate of the bat's pulses are reported to cause increased spike frequency in the pulse marker neurons, but only up to a limit. If the repetition rate exceeds this limit, the pulse marker neurons seem to be unable of representing this appropriately. This is presumably due to the decreased firing rate of the A1 cell to the terminal call of a bat (Fullard et al., 2013). By using recorded bat calls, Fullard et al. found that the A1 cell changes its firing from bursts with short interspike intervals, below 2 ms, to non-bursting continuous firing with large interspike intervals, i.e. above 5 ms. This "failure" to respond to the final buzz of a bat might be due to the absence of a selection pressure (Fullard et al., 2003) or a mechanism to encode the highest predation risk which we do not yet fully understand.

Based on their physiological characteristics, pulse marker neurons are suggested to serve a role in interpreting the behavioral significance of the ultrasound signal. If such a neuron has a best frequency, it is referred to as a resonance neuron (Hutcheon and Yasom, 2000). Boyan et al. (1990) recorded from one putative resonance neuron in *H. virescens*. So far, there are no reports about the morphology of this interneuron category.

The third neuron type, the train-marker neuron, fires tonically during the whole call, including the pauses (Roeder, 1966). Like the pulse marker neurons mentioned above, this category of interneuron is anatomically not yet described. Pulse-marker neurons might be sufficient to signal a change in repetition rate, and hence trigger behavioral switches in the moth. On the other

hand, train marker neurons could play a role in distinguishing conspecific male calls from bat calls.

3.4   Sound-sensitive brain interneurons

Knowledge about auditory neurons in the moth brain is still scarce. However, a few ultrasound-responding brain interneurons have recently been reported in heliothine moths. Particularly interesting is the report of one multimodal, centrifugal antennal-lobe neuron responding to sound and odor (Zhao et al., 2013). This ipsilateral neuron type, which was morphologically and physiologically identified in two geographically isolated species of heliothine moths, innervates all antennal-lobe glomeruli and extends numerous fine processes in the dorso-medial protocerebrum. Also of interest, Anton et al. (2011) found, in *Spodoptera littoralis*, that antennal-lobe projection neurons were sensitized one day after the moths had been exposed to bat sounds. Projection neurons of moths being exposed to control sounds, however, showed no sensitization. Whether the antennal-lobe centrifugal neuron plays a role in modulating odor information is an open question.

In addition to the centrifugal neuron, another type of sound-sensitive brain interneuron has been reported in the heliothine moth (Pfuhl et al., 2014). This neuron, which was characterized via intracellular recording/ staining as well, responded phasically to ultrasound stimuli. Notably, it innervated the ventrolateral protocerebrum, i.e. the same region as targeted by sound-responding ventral-cord interneurons, as mentioned above (Fig. 3E). Also, as reported by Pfuhl et al. (2014), one recording from the lateral protocerebrum of the heliothine moth, demonstrated a multimodal neuron responding to ultrasound and odor. The morphology of the neuron was not described, however. So far, there exists only one recording from a descending sound-sensitive neuron; Olberg and Willis (1990) found such a neuron showing phasic on- and off-responses to pheromones, visual cues, and ultrasound.

4   The Role of Sound in the Unusual Mating System of Galleriinae

The moth subfamily Galleriinae (Pyralidae) represents a special group characterized by a unique mating system, where males call to lure females - not *vice versa* which is typical for the vast majority of Lepidoptera. Males of these species form leks and attract females collectively (Alem et al., 2011; Greenfield and Coffelt, 1983). In *Achroia grisella*, males attract females by ultrasound alone and emit pheromones acting as an aphrodisiac signal in close range communication. Cordes et al.

(2014) studied calling behavior in *A. grisella* males when exposed to bat calls. They found that some males take greater risks than others. More precisely, they resume calling quickly after the bat call ceases. This makes them more conspicuous for not only bats, but also for females, and their behavior might hence serve as an honest signal for choosy females.

In contrast to *A. grisella,* using sound for inviting females and pheromones for close range communication, males of *Galleria mellonella* and *Aphomia sociella* have exchanged the use of the two sensory stimuli - attracting mates by means of sex pheromones (Kalinová et al., 2009; Lebedeva et al., 2002), while producing ultrasound for close-range courtship (Finn and Payne, 1977; Spangler, 1984; Spangler et al., 1988). Female arrival initiates male courtship characterized by running around the female, wing beating, and a specific type of ultrasound production. The male behavior affects females´ receptivity and sexual arousal (associated with wing fanning. Also, males of *G. mellonella* and *A. sociella* are reported to produce ultrasound rival songs as a result of homotypic interactions within the lek (Jia et al., 2001; Kindl et al., 2011). In all three species mentioned above, the series of behavioral steps in the mating process is controlled by multimodal input including chemical, acoustical, and mechanical stimuli. Though mating systems in *G. mellonella* and *A. sociella* share many similarities, there are evident differences as well. One distinction is that females of *A. sociella* produce sex pheromones, whereas *G. mellonella* females do not (Kindl et al., 2012).

As described above, the mating system of Galleriinae moths is highly multimodal. Still, with respect to the auditory system, the moths may use a rather simple decision criterion to distinguish between bat calls and male calls. Rodriguez and Greenfield (2004) found, in *A. grisella* females, that an ultrasound signal, characterized by a pulse repetition rate of 30 Hz, elicited an evasive escape response when moths were flying and attraction when they were walking. If the pulse repetition rate was lowered below 30 Hz, however, females would not walk towards the ultrasound source, i.e. show no positive phonotaxis. The female's selectivity to a particular parameter of the signal, as described here, could be achieved by means of a type of resonance neuron having its resonance frequency near the repetition rate of the bat call, i.e. ca. 84 Hz (Rodriguez and Greenfield, 2004; Bush and Schul, 2006). When it comes to choosing between males, *A. grisella* use very fine differences in the pulse lengths of male mating calls. Behaviorally,

a resolution of 80 microsec was found (Jang and Greenfield, 1996), nearly twice as long as the temporal acuity of the tympanum (Rodriguez et al., 2005). Besides discriminating fine temporal cues like pulse lengths, *A. grisella* also integrate over larger time scales, i.e. seconds; that is to orientate towards the male, females use changes in sound intensity over time. This sequential processing is most likely achieved at the interneuron level and not due to A cells differing in their integration time. All this shows that the auditory system of Galleriinae constitute an excellent model system for studying the neural underpinnings of negative and positive phonotaxis as well as how auditory information is integrated with odor signals and mechanical signals.

5 Conclusion

Each moth species lives in its unique ecosystem, full of predators, with bats being a major threat. The bat species, respective its echolocation parameters, will influence the frequency tuning and sensitivity of the predated moth species' ear (Hofstede et al., 2013). Mechanical and non-neural mechanisms of the moth ear contribute to filtering and amplification of the signal. The broadly tuned receptor diverges the signal onto many interneurons providing feature extraction as found in other insects (Hildebrandt et al., 2015). Since the informative signal is a change in the temporal pattern of the bat call, one A cell diverging on ascending interneurons can decode a search from an attack bat call. However, it is not clear yet, whether pulse duration, pulse repetition rate, or both, is the crucial parameter for a change in behavior. Species with true courtship songs suggest pulse duration as the most informative parameter. That is, if the song differs in duration from bat calls, moths respond with a positive phonotaxis instead of a negative phonotaxis. This suggests that only minor adjustments at the neural level are required for the evolution of a positive phonotaxis. It remains to be seen whether special "song" neurons will be found in moth species showing true courtship songs.

Furthermore, even in moth species, where the only function of moth ears is bat detection, the response of moths to those calls is conditional on other stimuli and everything but a simple reflex. Faint bat cries do not automatically elicit an escape response as this comes at the cost of lost opportunity for mating. Accordingly, Skals et al. (2005) showed that the escape response is delayed when simultaneously perceiving pheromones. Recently, a possible mechanism through which auditory stimuli can modulate the olfactory perception was sug-

gested (Anton et al., 2011; Zhao et al., 2013).

In summary, the independent evolution of the moth ears and the even later evolution of sound-producing organs in moths provide an excellent model system to identify evolutionary and physiological constraints on how aversive signals can become attractive signals.

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