What Is an Insect Ear?

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Ann. Entomol. Soc. Am. 86(6): 677–682 (1993)

ABSTRACT Although a sense of hearing, or the possession of ears, has been ascribed to many insects in the past, some of these published examples may not represent adaptively evolved sensory capabilities or structures. Certain purported cases of neural or behavioral responses to sound, for example, may be attributed to the resonation of nonspecialized cuticle which results from the high sound intensities used in the experiments. In addition, cuticular structures have been identified as tympanal organs without having been shown to function as hearing organs. We recommend that three criteria related to morphology, physiology, and natural behavior be satisfied before concluding that a sense of hearing exists. In this article, we survey the literature for examples of studies that lack one or more of these criteria and suggest that these studies can serve as incentives for further investigations by sensory physiologists, behaviorists, and neuroethologists.

KEY WORDS hearing, sensory, behavior

THERE ARE NUMEROUS published examples of the behavior and receptor organs associated with a sense of hearing in insects. Although many of these examples are reasonably well founded, numerous other reports of hearing or ears in the literature remain questionable. For example, the idea that moths of the family Axiidae possess tympanal organs on the seventh abdominal segment has been reported several times (Sick 1935, Forbes 1936, Bourgogne 1951, Haskell 1961, Michelsen & Larsen 1985, Spangler 1988a). So far, however, there is no conclusive evidence that these moths possess ears at all (Minet 1983). The fault does not necessarily lie with the authors of these reports but rather with the lack of any clear definition of what *is* an insect ear. An insect might be said to possess an ear because the insect appears to respond behaviorally to sound, or because it possesses a structure that resembles an ear, or if neural activity is evoked in response to sound. Yet, if an insect shows any one or a combination of these characteristics, "hearing" is not necessarily part of its natural sensory repertoire. Labeling a structure an ear, or a particular neural or behavioral response as hearing, could restrict what subsequent researchers might expect of such phenomena. We suggest that a receptor system can be misidentified as an ear, or that a supposed behavioral response be misleadingly attributed to a sense of hearing in an insect.

The purpose of this article is, first, to recommend a set of criteria that should be met before concluding that an insect has an ear; and, second, to provide some examples selected from the literature of proposed hearing or ears in insects that, based on these criteria, are incomplete and therefore potentially interesting projects to pursue. Although for brevity we have limited our discussion of insect ears to those of the tympanal type (detectors of far-field vibrations transmitted through water or air), many of the arguments presented here apply to detectors of near-field sounds (e.g., caterpillar sensory hairs [Tautz & Markl 1978]), or receptors of solid-borne vibrations (e.g., cockroach subgenual organs [Schnorbus 1971]), which may or may not be considered ears depending on the definition being used (see Michelsen & Larsen [1985] for further discussion of the latter receptor types).

We suggest that before an insect may be said to possess an ear, three criteria should be met: first, a morphologically differentiated receptor system should be identified; second, this sound receptor should respond neuronally to sounds of biologically relevant frequencies and intensities; and third, the putative ear should mediate an adaptive behavioral response to sounds, adaptive behavior being defined as actions that increase the organism's survival or fitness (Brown 1975). This qualified definition is used to distinguish adaptive behavior from simple motor responses that may arise from the stimulation of mechanoreceptors (other than ears) with sounds.

Examples of insect ears that satisfy these conditions are represented in Fig. 1. The best-

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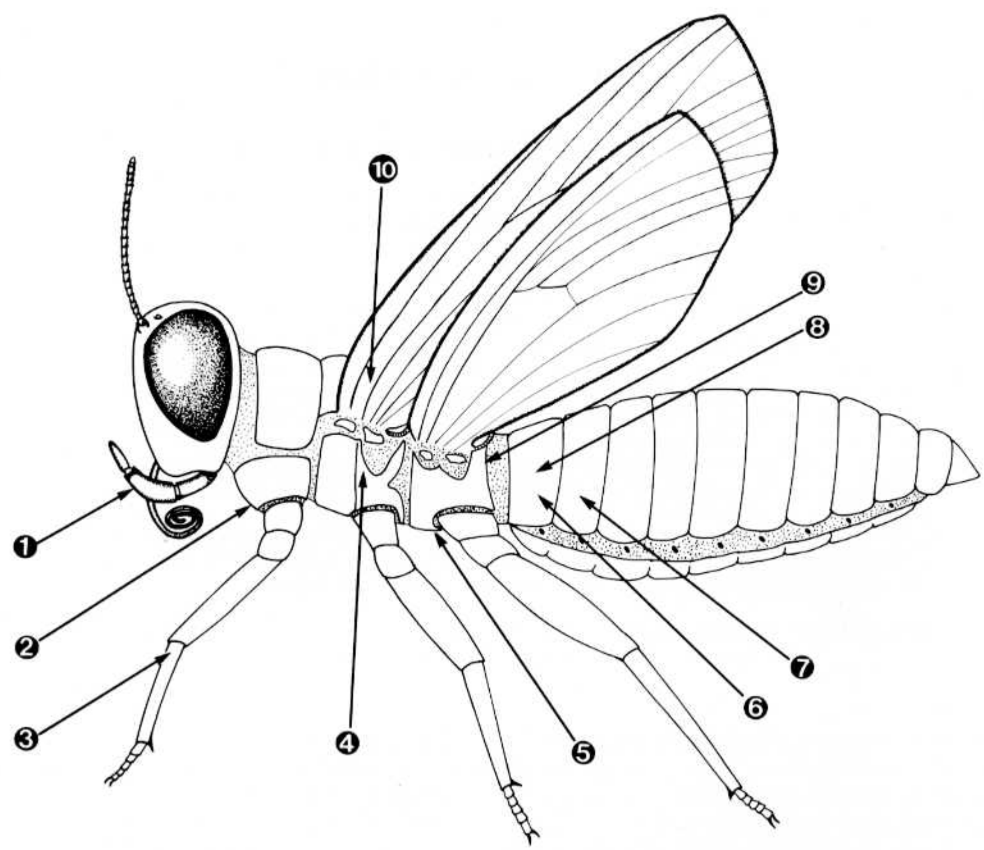

Fig. 1. Schematic diagram of a generalized insect showing the 10 body locations where functional ears (specifically those detecting far-field sounds) have been identified in insects. Each number is followed by the taxonomic group from within which these ears have been reported. However, ears may not necessarily occur in all the species within this taxa. Selected references are provided. 1. Lepidoptera: Sphingoidea, Choerocampinae (Roeder et al. 1968, 1970). 2. Diptera: Tachinidae, Ormiini (Cade 1975, Lakes-Harlan & Heller 1992, Robert et al. 1992). 3. Orthoptera: Ensifera (Huber et al. 1989, Bailey & Rentz 1990). 4. Hemiptera: Corixidae (Schaller 1951, Prager 1976). 5. Mantodea: Mantidae (Yager & Hoy 1987, Yager et al. 1990). 6. Lepidoptera: Geometroidea, Pyraloidea (von Kennel & Eggers 1933, Roeder 1974, Minet 1983, Spangler 1988a). 7. Hemiptera: Cicadidae (Young & Hill 1977, Huber 1983). 8. Orthoptera: Acrididae (Michelsen & Larsen 1985, Riede et al. 1990). 9. Lepidoptera: Noctuoidea (Roeder 1967, Spangler 1988a, Fullard 1988). 10. Neuroptera: Chrysopidae (Miller 1983).

studied examples of these include the tibial tympanal organ of crickets and katydids (longhorned grasshoppers), the metathoracic ear of the noctuoid moth, and the abdominal ear of the cicada. In these three, the necessary criteria of morphology, physiology, and behavior have been well demonstrated. For example, the mesothoracic tympanal organ sensilla of the noctuoid moth (Eggers 1919, Ghiradella 1971) are sensitive to sounds of frequencies and intensities that match those of the echolocation cries of insectivorous bats (Fullard 1988) and are responsible for mediating an adaptive behavior—the avoidance of predatory bats (Roeder 1967).

Although the ears described in Fig. 1 have been reasonably well documented, other purported examples of hearing are not so clear. Table 1 is a partial survey of published reports of what we consider to be examples of hearing or ears in insects where at least one of the three suggested criteria is missing. We suggest that because these examples do not satisfy the above three criteria, they represent interesting cases that require further examination before an adaptively evolved sense of hearing should be concluded, and that, in some cases, this sense may have been misidentified.

In some insects, tympanal organs have been identified based on structural characteristics, but no neural or behavioral evidence for hearing has been shown. A few examples from Table 1 include the "tympanal organs" of certain butterflies (Vogel 1912, Minet 1988, Cook & Scoble 1992), moths (Forbes 1936, Clench 1957), and termites (Howse 1963, 1968). It is misleading to identify a structure as a tympanum or tympanal

Table 1. Partial survey of proposed insect hearing organs, or responses to sound, which require further study before a sense of hearing can be confirmed in these insects

Taxon	Method[a]	Proposed structure, location[b]	Sound frequency, intensity[c]	Reference
Blattodea				
Blattidae				
Periplaneta americana L.	N	Lateral fold, abdomen	Click, 79–90 dB	Florentine (1967)
Isoptera				
Hodotermitidae				
Zootermopsis angusticollis Emerson	A	TO, 1st abd. segment	—	Howse (1963, 1968)
Orthoptera				
Acrididae				
Locusta migratoria L.	N	CO, hind wing	2–5 kHz, —	Pearson et al. (1989)
Gryllidae				
Gryllus campestris L.	B	—, TO, cerci, antennae were ablated	5 kHz, 80 dB	Jones & Dambach (1973)
Coleoptera				
Cerambycidae				
larvae, 6 species	A	CO & pleural disk, abdomen	—	Hess (1917)
Cicindelidae				
Cicindela lemniscata LeConte & *C. marutha* Dow	A,B	TO, 1st abd. tergum	3 kHz, 90 dB & 40–80 kHz, 73–97 dB	Spangler (1988b)
Five other species	A	TO, 1st abd. tergum	—	Spangler (1988b)
Dytiscidae				
Dytiscus marginalis L.	N	CO, abdomen	Tuned to 100 Hz, —	Hughes (1952)
Diptera				
Sarcophagidae				
Colcondamyia auditrix Shewell	B	—	Mating song of cicada	Soper et al. (1976)
Lepidoptera				
Arctiidae				
Ctenucha virginica Esper	B	—, (TOs destroyed)	150 Hz–15 kHz, 95–100 dB	Frings & Frings (1957)
Axiidae				
Axia sp.	A	TO, 7th abd. segment	—	Sick (1935), Forbes (1936)
Cossidae				
Dudgeonea sp.	A	Tympanum, 1st abd. segment	—	Clench (1957)
Hedylidae	A	TO, base of forewing	—	Cook & Scoble (1992)
Nymphalidae				
Helioconus erato L.	A,B	Sclerotized plate, hindwing base	1,200 Hz, 75–100 dB	Swihart (1967)
Saturniidae				
Four species	B	—	100 Hz–10 kHz, —	Turner (1914)
Satyridae				
Four species	A	CO, base of forewing	—	Vogel (1912)
Cercyonis pegala F.	B	—	800 Hz–10 kHz, 106–122 dB	Frings & Frings (1956)
Thyrididae				
Siculodinae	A	TO, base of forewing	—	Minet (1988)
Hymenoptera				
Formicidae				
Small black ant	B	—	Violin or whistle from 15 ft.	Metcalf (1900)
Two species	B	—	Whistles, tuning fork	Weld (1899)
Myrmicidae				
Two species	B	—	Whistles, tuning fork	Weld (1899)

[a] Methods refer to the type of experimental data presented: A, anatomical; B, behavioral (ranging from simple motor movements to complex behaviors); N, neurophysiological.
[b] TO, tympanal organ; CO, chordotonal organ; —, information not provided.
[c] —, Information not provided.

organ (which suggests a sense of hearing) based solely on anatomical characters. Although most of the ears shown in Fig. 1 are easily recognized externally as "typical" tympanal organs (paired structures characterized by a thin cuticular membrane (Haskell 1961]), other ears, such as the palp-pilifer organ of the sphingid moth (Roeder et al. 1968, 1970), the cyclopean ear of the praying mantis (Yager & Hoy 1987), and the recently described tachinid fly ear (Lakes-Harlan & Heller 1992, Robert et al. 1992), are not so conspicuous visually. Perhaps this is one of the reasons why these ears were overlooked until recently.

Other examples shown in Table 1 demonstrate neural activity or a simple motor movement in response to sound, but neither has a sensory structure been identified nor an adaptive behavior been exhibited. Common to several of these studies has been the use of intense sounds (see Table 1) to generate the reported neural or behavioral responses. We propose an alternative explanation for these results; one that does not assume the existence of an ear or a sense of hearing. Insects are covered with a cuticular exoskeleton which consists of a series of sclerotized plates joined by flexible, unsclerotized membranes. Internally, numerous chordotonal organs occur throughout the peripheral regions of the body, frequently suspended between movable joints where they function as proprioceptors (Howse 1968, Mill 1976). Sounds of high intensities will induce cuticular vibrations, imparting forces onto membranes that may approximate those normally encountered during slight movements of body parts. There are many examples of chordotonal organs not specialized as hearing organs that will respond to airborne sounds if the latter are of sufficient intensity: those whose principal function appears to be proprioceptive (Hughes 1952, Barber & Pringle 1966, Kehler et al. 1970, Burrows 1987, Yack & Fullard 1990), those that detect solid-borne vibrations (Autrum & Schneider 1948, Wever & Vernon 1959; Kalmring 1985), and those associated with undeveloped or vestigial tympana (Ball & Hill 1978, Lakes-Harlan et al. 1991). Sound frequencies to which many of these nontympanal chordotonal organs respond are between 1.5 and 4 kHz, which may simply reflect the frequency at which nonspecialized cuticle resonates (cf. Larsen & Michelsen 1978). We suggest that neural or behavioral responses (or both) to intense acoustic stimuli, particularly at lower frequencies (1–5 kHz), *might* not represent an auditory response to sound (i.e., hearing). Such acoustic stimuli may simply vibrate nonspecialized regions of cuticle and subsequently activate sensilla that normally function as proprioceptors. Because chordotonal organs are widely distributed throughout the insect's integument, it is not surprising that certain parts of the body are found to "flinch" when presented with high-intensity sounds of low frequencies (e.g., Frings & Frings 1956, 1957; Swihart 1967), considering the mass stimulation that is probably being experienced. An insect that responds to sounds of such high intensity may not necessarily be hearing those sounds through a specialized ear and cannot be said to possess an ear.

What, then, is a biologically relevant sound intensity or frequency? One should not arbitrarily determine what sound characteristics are relevant to the animal. When determining relevant sound frequencies, it is necessary to examine the frequencies of sounds that are of potential interest to the insect in its natural environment (e.g., those produced by conspecifics, predators). If, for example, an insect nerve exhibits responses to a 2-kHz sound stimulus but the conspecific sexual signal is of a different frequency, and there is no known predator that produces 2 kHz, it might be suspected that the neural response is an artifact caused by cuticular resonance (e.g., Mason 1991). When determining what are biologically relevant intensities, one should measure the intensities of these potentially interesting sounds at some adaptive distance. For an insect to exploit the information contained in a sound, it should be notified of this sound at some adaptive distance. To assume that a behavioral response to sound intensities of 80–100 dB is adaptive is to ignore the possibility that the insect would not normally listen to sounds that intense in its natural environment. The katydid *Mygalopsis marki* (Bailey) uses sounds for social purposes, and its auditory receptors have thresholds between 22 and 60 dB (Römer 1987), approximating those intensities encountered by the animal when listening to conspecifics in its natural environment (Römer & Bailey 1986). For antipredator purposes, moths that must detect insectivorous bats have ears with receptor thresholds of 35–50 dB; this allows the moth to detect a typical bat at an adaptive distance of ≈30–40 meters (Roeder 1967). As a working value, we suggest that receptors with thresholds in excess of 70 dB might not function as adaptive auditory sensilla—their role in hearing should be scrutinized.

Finally, identifying a hearing organ in an insect that has demonstrated an ability to hear is important for obvious reasons. One example of an insect exhibiting an adaptive response to sound where a specific sound receptor has not been identified, is that of the parasitic sarcophagid fly, *Colcondamyia auditrix* Shewell, which locates male cicadas by their mating songs (Soper et al. 1976). To date, the ears of these flies have not yet been identified. The need to identify the organ of sound reception may also be necessary in tympanate insects, because there are reported cases of tympanate insects, with their ears ablated, that show behavioral (Frings & Frings 1957, Jones & Dambach 1973) or neural (J.H.F., unpublished data) responses to sound. Two sets of tympanal organs on the same insect have already been reported in some mantids (Yager 1992).

In the past few years, two previously undescribed insect ears have been reported: that of the praying mantis (Yager & Hoy 1986) and of certain female parasitoid tachinid flies, *Therobia leonidei* Mesnil, and *Ormia ochracea* (Bigot) (Lakes-Harlan & Heller 1992, Robert et al. 1992). This makes a total of 10 ears identified in insects to date. Three of the ten have evolved independently within the Lepidoptera, two within the Orthoptera, and two within the Hemiptera, which means that ears have been identified in ≈5% of insect orders. Considering that tympanal organs are believed to be derived from preexisting chordotonal organ proprioceptors (Yack & Fullard 1990, Meier & Reichert 1990, Lakes-Harlan & Heller 1992, Yack & Roots 1992, Boyan 1993, Yack & Fullard 1993), and the transition from atympanate to tympanate appears to require rather few simple peripheral modifications, we propose that many insect ears await discovery. We hope that the points discussed in this article will provide some guidelines for future investigations.

Acknowledgments

We thank D. T. Gwynne (University of Toronto) for helpful comments on the manuscript. This work was supported by Natural Sciences and Engineering Research Council of Canada (NSERC) operating grants to J. H. Fullard (University of Toronto) and G.G.E. Scudder (University of British Columbia), and by an NSERC postgraduate scholarship to J.E.Y.

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Received for publication 22 March 1993; accepted 11 June 1993.