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The Evolutionary Convergence of Hearing in a Parasitoid Fly and Its Cricket Host

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Parasitism is a widespread and diverse life strategy that connects species throughout the animal kingdom. Female parasitoid flies of the genus *Ormia* must find a specific cricket host on which to deposit their parasitic maggots. To reproduce, female flies must perform the same task as female crickets: find a singing male cricket. These flies have evolved a unique hearing organ that allows them to detect and locate singing male crickets. Through evolutionary convergence, these flies possess a hearing organ that much more resembles a cricket's ear than a typical fly's ear, allowing these parasitoids to take advantage of the sensory ecological niche of their host.

Throughout the evening from spring through fall, male field crickets of the genus *Gryllus* sing loud and persistent songs to attract females for mating. However, female crickets are not all that calling males may attract. Acoustically active female parasitoid flies of the genus *Ormia* (order Diptera, family Tachinidae, tribe Orminii) are also attracted to singing male crickets (*1*). The gravid female fly locates the calling male cricket and deposits maggots (length $\sim$400 μm) on or near him. The larvae burrow into the host cricket, grow, feed, and kill him within 10 days; the fully grown larvae then emerge and pupate.

Female flies and female crickets must solve the same auditory problem: to detect and locate a male cricket by hearing his calling song over long distances. On the basis of physiological, anatomical, and behavioral studies, we report that ormiine flies have solved this problem by means of an ear that incorporates—in structure and function—the design principles common to all hearing organs in insects, including crickets, that must detect high-frequency sounds over great distances. This example of convergent evolution in a hearing organ demonstrates the constraints on morphological design that are imposed by behavioral function as well as by principles of physical acoustics.

Many flies produce acoustic signals. Mosquitoes use acoustic signals in courtship (*2*), and songs are prominent in the courtship of *Drosophila* (*3*). However, there is a major difference between the hearing organs in these flies and those in crickets that reflects the different acoustic demands made upon their hearing abilities (*4*). Most flies and mosquitoes emit low-frequency sounds (100 to 500 Hz) that operate over short distances (millimeters to centimeters). In contrast, crickets emit intense, higher frequency sounds (typically above 3 kHz) that attract female crickets over much longer distances (at least 15 m). The acoustic design features of the standard dipteran hearing organ—the Johnston's organ of mosquitoes and fruit flies—are based on a feathery antennal structure that senses local air movements in the near field of a sound source (*4*, *5*). In contrast, the structure and function of tympanal hearing organs in crickets (and other acoustically active insects such as katydids, grasshoppers, moths, cicadas, and mantises) permit detection in the pressure field (far-field) of sound (*4*). Key features of tympanal organs include a specialized thin, external cuticular membrane (tympanum) that is closely associated with internal tracheal air sacs, and a receptor organ consisting of a group of scolopale-type sensory cells (*4*, *6*). Tympanal organs, like the auditory organs of terrestrial vertebrates, are sensitive to minute changes in air pressure that are propagated from a distant sound source. In structure and in function the hearing organ of acoustically active parasitoid flies is tympanal, more like the ears of their hosts than like those of other flies.

The parasitoid ormiine flies that we used either were captured in the field, near Gainesville, Florida, or were first-generation stock reared from wild-caught flies (*7*). We characterized the morphology of the hearing organ of *Ormia ochracea* by embedding the whole thorax in plastic (JB-4, Polyscience Inc.) and sectioning and staining with toluidine blue and other conventional stains. To determine the auditory sensitivity of this novel dipteran ear, we recorded neural responses to acoustic stimuli by conventional extracellular recording techniques (*8*). The neural response was from higher order auditory cells, but in other species such activity reflects hearing sensitivity (*9*).

Our neurophysiological recordings confirm that the auditory system of parasitoid flies is tuned to the songs of their hosts. *Ormia ochracea* larviposits on or near the

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field cricket, *Gryllus rubens*, whose song has an energy peak in the frequency range of 4 to 5 kHz (*10*). We found that the auditory organ of female *O. ochracea* is most sensitive in the range 4 to 6 kHz, as seen in the tuning curve (Fig. 1). Thus, the best sensitivity of the female fly's ear is nearly matched to the peaks in the power spectra in cricket songs (Fig. 1) (*11*). Hearing thresholds of female flies are extraordinarily low: 20 dB SPL (SD: ±4 dB; $n = 7$ flies) at 5 kHz (*12*), and consistent with long-distance detection.

The auditory tuning curve in *O. ochracea* is sexually dimorphic, differing strongly between males and females. The male tuning curves are 40 to 50 dB less sensitive than the female's to the frequencies (4 to 6 kHz) found in cricket songs (Fig. 1). This is not unexpected because it is the females, not the males, that must hear and locate singing crickets in order to complete reproduction. This sexual dimorphism makes sense in these flies, yet sexual dimorphism in hearing is rare in the animal kingdom (*13*). We also found that both male and female flies were similarly sensitive to ultrasonic frequencies ranging from 15 to 50 kHz, with thresholds between 70 and 80 dB SPL. Both sexes of ormiine flies are active in the evening, when they would be exposed to possible predation by insectivorous bats that navigate and hunt by ultrasonic biosonar. Nocturnally flying insects from five different orders react to ultrasound with a startle or escape response, and the auditory thresholds to ultrasound of mantises and lacewings are comparable to the thresholds found in these tachinids (*9*).

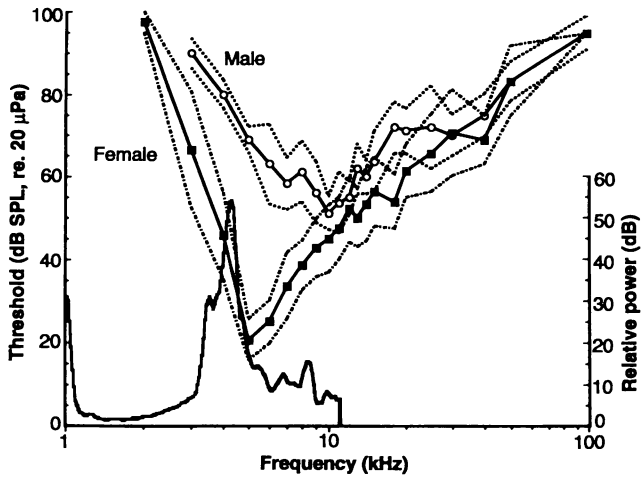

Fig. 1. Frequency tuning curves (top curves labeled male and female) for the extracellular neural audiogram recorded from the neck connective of *O. ochracea* compared with the frequency power spectrum (bottom curve) representative of the calling song of the host species, *Gryllus rubens*. The left scale applies to the neural audiogram, the right scale to the song power spectrum. Tuning curves for seven females and four males show sexual dimorphism: the females are much more sensitive than the males to 4 to 6 kHz. The low thresholds (high sensitivity) for the females, in their best frequency region, corresponds nearly to the peak of the energy emission spectrum of the calling song of the host species. Both male and female flies show convergent secondary sensitivity to ultrasonic frequencies. Dotted lines indicate the standard deviation limits of the mean tuning curves.

It is the anatomy of the ormiine ear, however, that firmly establishes its convergence upon an orthopteroid-like tympanal design (*14*). The fly's eardrums are a pair of transparent, membranous, bladder-like enlargements on the prosternum; they form the prosternal tympanal membranes (PTMs) (Fig. 2A). The forward-facing PTMs are normally hidden behind the fly's head. Internally, the PTMs form the anterior wall of a single large, air-filled chamber in the thorax. Within this prosternal chamber are a pair of auditory sensory organs, the bulba acustica (BAc). Each BAc is a bulbous, cellular enlargement of a rod-like apodeme that spans the breadth of the prosternal chamber and inserts directly upon the PTM. Presumably, sound-induced vibrations of the PTM would set in motion the BAc through direct coupling. The prosternal chamber connects to the outside through a bilateral pair of tracheae (T), each opening out through mesothoracic spiracles (MSp's) on the dorsolateral thorax (Fig. 2, A and B). Thus, although sound may impinge directly on the PTMs, it may also enter the prosternal chamber through the MSp's.

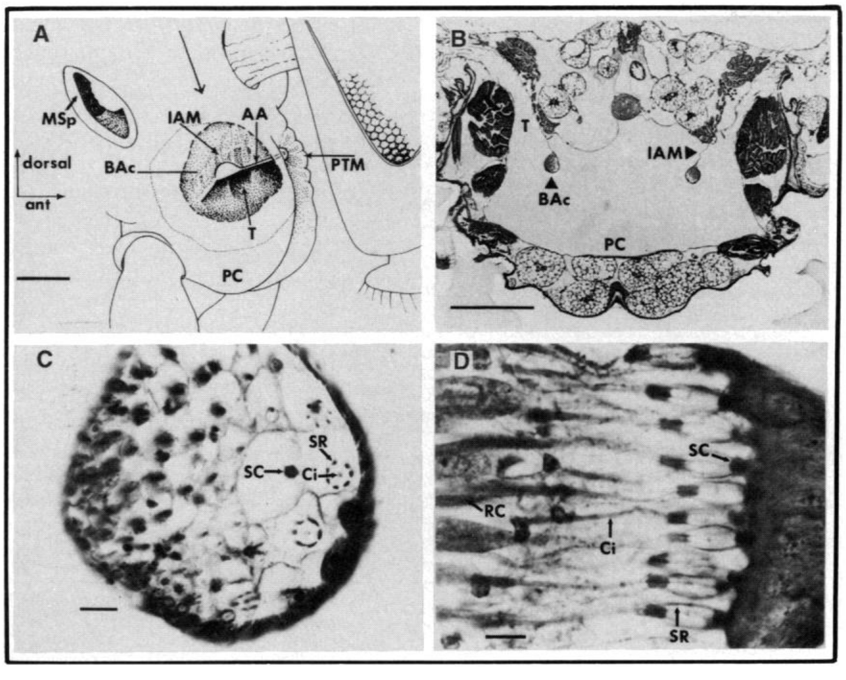

Fig. 2. (**A**) Schematic drawing of the auditory apparatus of *Ormia*. The prosternal tympanal membrane (PTM) forms the anterior face of the air-filled prosternal chamber (PC) and acts as an eardrum. The bulba acustica (BAc) is the scolopophorous sensory organ, which is attached to the PTM by a cuticular anterior apodeme, the auditory apodeme (AA). The apodeme and BAc are attached to the roof of the PC by means of a sheet-like, internal accessory membrane (IAM). The PC connects to the outside through a pair of horn-shaped tracheae (T) that open out to the mesothoracic spiracles (MSp's). The auditory nerve from sensory receptors of the BAc leads back to the thoracic ganglion. The downward-pointing arrow at the top of the figure gives the axis of the cross section shown in (B). Scale bar, 250 µm. (**B**) Cross section of the entire thorax at the level of both BAc's, showing that both auditory organs are contained in an undivided air-filled chamber and that they are attached to the roof of the chamber by IAMs. Horn-shaped tracheae (T) connect to the MSp's. Scale bar, 250 µm. (**C**) Cross section through the BAc shows scolopidia at various levels including scolopale caps (SCs), hexagons of scolopale rods (SRs), and the central cilium (Ci) of the sensory neuron. Scale bar, 6 µm. (**D**) Longitudinal section of the BAc depicting SCs, SRs, and Ci's as well as the bipolar receptor cells (RCs) and their dendrites. Scale bar, 6 µm. Histological sections of the BAc in (C) and (D) demonstrate that it is a chordotonal (scolopophorous) organ.

The cellular anatomy of the BAc is that of a typical tympanal chordotonal organ (*6, 15*). Its sensory units are multicellular scolopidia, each consisting of a bipolar sensory neuron and several accessory cells, including the diagnostic scolopale cell. A defining feature of scolopale cells is a hexagonal arrangement of scolopale rods, which contribute to the cell's fusiform shape and which fuse and terminate distally to meet a bullet-shaped scolopale cap. We found that each BAc of *O. ochracea* contains between 60 and 70 scolopidia. The scolopale cells in the ear of the tachinid fly, like those of orthopteroid insect ears, show the classical scolopale anatomy, including hexagons of scolopale rods (Fig. 2C) and unmistakable scolopale caps (Fig. 2D). The BAc is innervated by an anterior branch of thoracic nerve II (frontal nerve).

Because the PTM apparently functions as an "eardrum" in the auditory apparatus of ormiine flies, it is of interest that it is sexually dimorphic and enlarged in females relative to males. Our conclusion that the PTM is an ormiine adaptation for hearing is supported by the results of an examination of a nonormiine (presumably nonhearing) tachinid fly, *Myiopharus doryphorae*, in which the prosternum and the prosternal membranes in both sexes are much smaller than in *O. ochracea.*

Earlier workers reported that larviparous female, but not male, tachinids are attracted to singing crickets or to loudspeakers playing tape-recorded songs (*1*). Our field experiments with captive flies indicate that intact tympanal membranes are crucial for hearing cricket songs. When 17 intact and sham-operated flies were released in a flight cage (2 by 2 by 2 m), 11 were attracted to a loudspeaker broadcasting a cricket song. None of ten flies with punctured tympanal membranes and broken auditory apodemes were attracted to the loudspeaker, although they could fly. The behavior of the two groups is significantly different (Fisher's exact test, $P < 0.001$) (*16*). Moreover, we have physiological evidence for the auditory function of the prosternal membranes; puncturing both PTMs and associated auditory apodemes eliminated the neural response described above.

From evolutionary as well as mechanistic points of view, both female crickets and female parasitoid flies are under similar selective pressures on the design characteristics of their ears. Their sense of hearing must serve the same ends: completion of reproduction depends on hearing and locating a singing male cricket over great distances. In insects, long-distance, high-frequency hearing is subserved by scolopophorous tympanal organs, as in moths, praying mantises, cicadas, locusts, katydids, and crickets. To this list we now add these tachinid flies (*17*), and we propose that this dipteran tympanal organ evolved through convergent evolution due to similar selective pressures: for a fly to act like a cricket, it must hear like one.

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The Complete Skull and Skeleton of an Early Dinosaur

Paul C. Sereno* and Fernando E. Novas

The unearthing of a complete skull and skeleton of the early dinosaur *Herrerasaurus ischigualastensis* sheds light on the early evolution of dinosaurs. Discovered in the Upper Triassic Ischigualasto Formation of Argentina, the fossils show that *Herrerasaurus*, a primitive theropod, was an agile, bipedal predator with a short forelimb specialized for grasping and raking. The fossils clarify anatomical features of the common ancestor of all dinosaurs. *Herrerasaurus* and younger dinosaurs from Upper Triassic beds in Argentina suggest that the dinosaurian radiation was well under way before dinosaurs dominated terrestrial vertebrate communities in taxonomic diversity and abundance.

Fragmentary skeletons of the earliest and most primitive dinosaurs were discovered more than 30 years ago in Upper Triassic rocks in South America and include *Staurikosaurus pricei* from the Santa María Formation of southern Brazil (*1*) and *Pisanosaurus mertii* and *Herrerasaurus ischigualastensis* from the Ischigualasto Formation of northwestern Argentina (*2–5*). These formations, deposited approximately 225 million years ago, record the initial phase of dinosaur evolution before their domination of terrestrial vertebrate communities (*6*). The remains of these early dinosaurs, however, are too fragmentary to provide a coherent view of the origin and early radi-

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