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Innovative Biomechanics for Directional Hearing in Small Flies

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▶ Abstract

In humans and animals alike, the localization of sound constitutes a fundamental processing task of the auditory system. Directional hearing relies on acoustic cues such as the interaural amplitude and time differences and also, sometimes, the signal spectral composition. In small animals, such as insects, the auditory receptors are forcibly set close together, a design constraint imposing very short interaural distances. Due to the physics of sound propagation, the close proximity of the sound receivers results in vanishingly small amplitude and time cues. Yet, because of their directionality, small auditory systems embed original and innovative solutions that can be of inspirational value to some acute problems of technological miniaturization. Such ears are found in a parasitoid fly that acoustically locates its singing cricket host. Anatomically rather unconventional, the fly's auditory system is endowed with a directional sensitivity that is based on the mechanical coupling between its two hemilateral tympanal membranes. The functional principle permitting this directionality may be of particular relevance for technological applications necessitating sensors that are low cost, low weight, and low energy. Based on silicon-etching technology, early prototypes of sub-millimeter acoustic sensors provide evidence for directional mechanical responses. Further developments hold the promise of applications in hearing aid technology, vibration sensors, and miniature video-acoustic surveillance systems.

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▶ Introduction

In the sense of evolution, sensory systems constitute "adaptive packages" of biological

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engineering that have been proven sufficiently refined and efficient by the combined processes of natural and sexual selections. From this evolutionary vantage point, the considerable diversity of insect auditory systems (Hoy and Robert, 1996) can be regarded as an array of original and adapted solutions to the particular problems of acoustic detection using small sensors. Because they evolved under the particular constraints imposed by small body size, insects are likely to be of significant inspirational value for general problems of miniaturization. Our investigations are focused on questioning whether insects at the small end of the biometric range (millimeter and less) can be endowed with auditory organs, whether they can be directionally sensitive, and if so, what mechanisms are responsible for such directionality?

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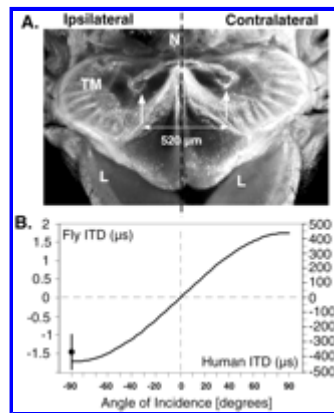
► Design Constraints for a Miniature Auditory System

One such small insect is a parasitoid fly that acoustically locates and attacks singing field crickets (Cade, 1975). As part of their reproductive cycle, female parasitoid flies *Ormia ochracea* must find their cricket hosts as a source of food for their larval offspring. Remarkably, successful song localization can take place in complete darkness, that is, in the presence of acoustic information alone, but in the absence of visual and olfactory cues (Ramsauer and Robert, 1999, 2000). Hence, because of its crucial role in reproduction, audition is of great importance in the evolutionary history of these flies: promoting an increased reproductive success, efficient audition is likely to be under acute selective pressure.

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Both detection and localization of the singing host are mediated by a pair of auditory sensory organs situated on the anterior thorax just above the first pair of legs, which are directly below the fly's neck (Robert *et al.*, 1992) (Fig. 1A). The ears of the fly are endowed with two thin tympanal membranes, the eardrums, that are set very close together across the midline of the animal. In fact, while the tympanal membranes together span about 1.2 mm in width, the mechanoreceptive sensory organs are separated from each other by only 520 μm (Robert *et al.*, 1994) (Fig. 1A). As expected from the fly's small size and the resulting minute interaural distance, the largest interaural time difference (ITD) generated by a passing sound wave does not exceed 2 μs (Robert *et al.*, 1996). In the best possible case, for an azimuthal angle of incidence of 90° off the longitudinal axis of the animal, the ITD was measured with probe microphones to be 1.45 μs (SD: 0.49 μs , $n = 10$) (Fig. 1B). Such time difference is clearly much too small to be encoded by the nervous system of the fly. For humans, in comparison, ITDs at such an angle of incidence are much larger (Fig. 1B), varying from 500 μs to 700 μs , depending on head size, the sound path considered, and the frequency considered. It thus becomes apparent that microsecond-range ITDs, and possibly smaller ones, ought to constitute a major difficulty for the auditory system of the fly, both at the mechanical and neural coding levels. Another difficulty arises when the second directional cue, the interaural intensity difference (IID), is considered. The behaviorally relevant frequency range is that of the cricket's calling song, which spans from 4.6 to 5.2 kHz. Since at such frequencies the ratio of wavelength (66 mm at 5.2 kHz) to interaural distance (520 μm) is larger than 100, diffraction is very unlikely to occur around the fly's body, or at her ears (Morse and Ingard, 1968). Measurements made with custom probe microphones (100- μm acceptance diameter) and with 1/8-in microphones (Brüel & Kjaer type 4138, Naerum, Denmark) failed to indicate diffraction-elicited sound pressure differences around the fly that could constitute IID cues.

Figure 1. Auditory anatomy and temporal acoustic cues. (A) The auditory organs of the parasitoid fly *Ormia ochracea* are located on the anterior thorax, between the first pair of legs (L) and the neck (N). The tympanal membranes (TM) are adjacent to each other and set close together by the midline of the animal (vertical dashed line). Providing a connection between the two TMs across the midline, the intertympanal bridge is made of thicker cuticle than TMs and has the shape of a coat hanger. Two depressions at both ends of the intertympanal bridge indicate the insertion point of the sensory organs (arrows). Arrows also point to the



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interaural distance. (B) Interaural time difference (ITD) as a function of the angle of incidence of the sound stimulus. Right ordinate: ITDs calculated for humans (ear separation of 170 mm). Left ordinate: ITDs at the fly's ears calculated for an interaural distance of 0.6 mm. Data point (with standard deviation) shows ITD measurement made at -90° azimuth and 5 kHz tone, with two probe microphones located at the TMs.

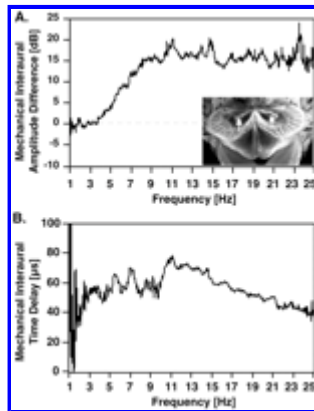
Admittedly, the minuscule ITD ($1.7 \mu\text{s}$) and IID ($<1 \text{ dB}$) generated from an incident sound wave constitute less than reliable acoustic cues for directional hearing. This finding, however, stands in sharp contrast to the behavioral capacity of this fly to localize the song of her host, as demonstrated in the field and laboratory ([Robert et al., 1992](#); [Walker, 1993](#); [Ramsauer and Robert, 2000](#)).

▶ Innovative Tympanal Mechanics

Taking place at the peripheral level of the tympanal membranes, the first step in the process of hearing pertains to the conversion of acoustic energy into mechanical energy. Thus, tympanal mechanics was examined in response to incident sound waves, either with pure tones mimicking cricket songs, or with band-limited white noise. Using microscanning laser vibrometry ([Robert and Lewin, 1998](#)), displacement velocities were assessed over several hundred measurement locations on both tympanal membranes and on the associated cuticular elements. In response to random noise as well as pure tone stimuli, the amplitude and phase responses of both tympanal membranes differ strongly from those expected for two independent pressure receivers set 0.5 mm apart ([Fig. 2](#)). Firstly, independent receivers would indicate immeasurably small differences in amplitude, whereas the fly's tympana undergo large differences in their vibrations above about 4.5 kHz ([Fig. 2A](#)). Secondly, independent receivers such as microphones indicate interaural time delays on the order of $2 \mu\text{s}$ ([Fig. 1B](#)), an ITD significantly smaller than the delays (also measured as the phase lag at maximal deflection) observed in the mechanical response of the tympanal membranes (on average: $55 \mu\text{s}$; SD: $12 \mu\text{s}$, $n = 769$ frequency points) ([Fig. 2B](#)). In effect, these measurements indicate that the mechanical response of the tympanal membranes has a pronounced directionality. Interaural time and intensity differences in the mechanical response of the tympana are significantly larger than those available in the acoustic field. The analysis of tympanal deflection shapes (see [Fig. 3A](#)) provides evidence that such differences between the ipsilateral and contralateral responses are due to the particular mechanical properties of this small tympanal system. Reflecting the asymmetrical responses reported earlier ([Fig. 2](#)), deflection shapes at frequencies around 5 kHz indicate that while the ipsilateral tympanum undergoes an outward deflection, the contralateral tympanum experiences an inward deflection, but of much lesser amplitude ([Fig. 3B](#)). Such asymmetry in the response is due to the fact that the two hemilateral tympanal membranes are not vibrating independently. The tympana are in fact connected, across the midline, by a specialized cuticular structure ([Robert et al., 1994, 1996](#)).

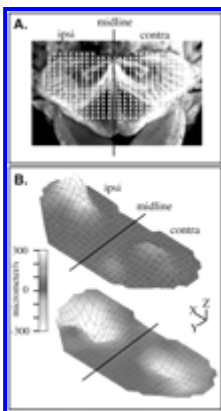
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Figure 2. Mechanical response of the tympanal membranes in amplitude and time. (A) Difference amplitude spectrum of the mechanical response at the anatomical



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locations indicated in the inset (arrows). The contralateral mechanical response is subtracted from the ipsilateral one. (B) Time delay between the ipsilateral and contralateral mechanical responses, calculated from the difference phase spectrum. Sound stimulus at 45° incidence in azimuth, band-limited white noise (1–30 kHz).



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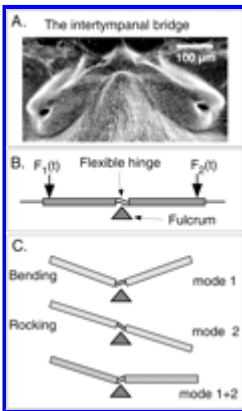
Figure 3. Tympanal deflection shapes. (A) Tympanal vibration velocity was monitored at 364 locations over tympanal and non-tympanal areas. Coherence values exceeded 0.95, indicating little contamination by uncorrelated noise. Stimulus: band-limited random noise (1 to 30 kHz; 94 dB SPL [sound pressure level]) at 90° azimuth to the longitudinal axis of the fly. Ipsilateral and contralateral conventions as indicated. (B) Upper panel shows maximum outward deflection of the ipsilateral tympanal membrane at 5 kHz excitation frequency. Lower panel depicts the maximum inward deflection reached half a period later, e.g., 100 µs later. X axis: lateral; Y: ventral; Z: axis of measured tympanal deflections. For animation of deflection, please visit: www.unizh.ch/~ormia/research_flies.html

► The Process of Intertympanal Coupling

In an effort to unite structure and function in a functional explanation, the reconstitution of actual tympanal deflections provides key information on the anatomical basis for the observed mechanical behavior. The particularity—and perhaps uniqueness—of these ears is that they are physically connected by an unpaired cuticular structure, the intertympanal bridge (Figs. 1A, 4A). This bridge is thicker (2–10 µm), and therefore stiffer, than the surrounding tympanal membranes (0.2–1 µm) to which it attaches. Thus, the tympana are mechanically linked by a relatively rigid cuticular bridge, a fact that can also be easily assessed by gently deflecting one tympanic membrane downwards with a human hair, and observing the other deflect upwards as a result.

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Figure 4. The anatomy of mechanical coupling, and vibrational modes of the flexible intertympanal bridge. (A) Close-up of the intertympanal bridge connecting the tympanal



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membranes. (B) Simple mechanical model of the bridge as a seesaw endowed with two rigid bars connected by a flexible central hinge (\approx). (C) On the basis of the laser vibrometric micromechanical analysis, it is suggested that two basic modes can characterize the observed mechanical response. Bending occurred at low frequencies (mode 1; <4 kHz), whereas rocking was measured at intermediate frequencies (mode 2; 5–7 kHz). At higher frequencies (15 kHz and above), bending and rocking modes combine to elicit motion in one tympanum only (mode 1 + 2).

Deflection shapes obtained by microscanning laser Doppler vibrometry for different stimulus frequencies (*e.g.*, 2, 5 or 15 kHz) reveal that this micromechanical system can produce several different patterns of deflection that are reminiscent of the movements of a flexible seesaw (Fig. 4B). The simple mechanical model shown in Figure 4B has been proposed as a reasonable functional, and intuitively accessible, approximation of this unconventional peripheral auditory system (Miles *et al.*, 1995; Robert *et al.*, 1996). The physical action of the intertympanal bridge is to convert small acoustic ITDs into larger time *and* amplitude differences at the mechanical level. The functional principle for this effect resides in the somewhat complex linear interaction between two coupled oscillators—the tympanal membranes. Very briefly, for low frequencies of stimulation (2 kHz), the deflections of the ipsilateral and contralateral membranes show little difference in amplitude and phase. In this case, the forces applied to the bridge (Fig. 4B) have a phase difference of only 1° and result in sympathetic deflections, owing to the bending of the bridge (Fig. 4C, mode 1). At this frequency of excitation, the first mode of deflection dominates the response. Excitation of this first mode results in little directionality—or asymmetry—in the mechanical response, as shown for frequencies lower than about 3 kHz (Fig. 2A). As stimulus frequency increases, a transition to the second mode of deflection is expressed by the rocking motion of the bridge (Fig. 4, mode 2). Noteworthy is the fact that for intermediate frequencies (*i.e.*, 5 kHz) and a given effective interaural distance, the phase difference in the driving forces increases. At 5 kHz, this phase is very small— 2.6° —yet, it is sufficient to drive this system to its rocking mode (Fig. 3B). A combination of these two modes (rocking and bending) will take place at even higher frequencies (*e.g.*, 15 kHz) and result in the deflection of the ipsilateral tympanum, but in the silencing of the contralateral one (Fig. 4C, mode 1 + 2). Hence, the relative flexibility of the bridge, be it localized at the fulcrum point or distributed along the lateral arms, constitutes the key to the directionality of the observed mechanical response.

In addition, experiments of mechanical actuation in the absence of sound have demonstrated that mechanical coupling is mediated and can be explained by the action of the intertympanal bridge alone (Robert *et al.*, 1998). The mechanical actuation of one tympanum at amplitudes of about 10 nanometers—mimicking the displacement amplitudes observed during acoustic stimulation—elicits a correlated mechanical displacement of the other tympanum. The finite flexibility of the intertympanal bridge accounts for the IIDs and ITDs in the mechanical deflections, for which two modes dominate at different frequencies (Robert *et al.*, 1996). Hence, in summary, the mechanical structure of the hearing organs increases the minimal acoustic interaural time and amplitude difference cues into more substantial mechanical cues that can be processed by the nervous system (Robert *et al.*, 1996).

► Intertympanal Coupling as an Evolutionary Novelty

As such, the process of mechanical coupling between tympanal membranes, and its

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amplification effect on interaural auditory cues, seems to be unique to flies. In essence, intertympanal coupling constitutes a novel mechanism for directional hearing, representing a third kind of directional receiver for terrestrial animals. One other kind of directional system is found in most vertebrates, and is based on two acoustically isolated pressure receivers set apart on the head of the animal. In other small animals, such as frogs (Narins *et al.*, 1988) and some birds (Calford and Piddington, 1988), the auditory receivers are acoustically coupled (pressure-difference receivers), a system that has been shown to result in the amplification of the perceivable ITDs and IIDs available in the sound field.

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▶ **Conclusions**

One of the outcomes of the research presented here has been to explore the possibility of transferring the mechanism of intertympanal coupling to microsensor technology. Abstracting the functional principle unraveled in the parasitoid fly may indeed contribute to the development of subminiature microphones. Besides the inherent directionality of the receiver's mechanics despite its small size, two other, definite and foreseeable, advantages of fly-inspired acoustic receivers would be their low cost and low energy consumption. Indeed, one of the possible attractive aspects of such a system is the fact that the first stage of acoustic processing is made on a mechanical basis, without the intervention of energy-consuming electronics. Using micro-electromechanical systems technology (MEMS), our early prototypes etched on silicon wafers provide evidence that coupled pressure receivers no larger than 500 μm are directionally sensitive at about 5 kHz. Further optimization promises the development of subminiature microphones endowed with directionality in the range of human speech. Finally, possible applications can be envisaged that could contribute to the development of hearing aids or miniature personal communication devices endowed with improved receiver acoustics, or small surveillance systems capable of pinpointing a source of noise.

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▶ **Footnotes**

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