



Cues for Directional Hearing in the Fly *Ormia ochracea*

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Insects are often small relative to the wavelengths of sounds they need to localize, which presents a fundamental biophysical problem. Understanding novel solutions to this limitation can provide insights for biomimetic technologies. Such an approach has been successful using the fly *Ormia ochracea* (Diptera: Tachinidae) as a model. *O. ochracea* is a parasitoid species whose larvae develop as internal parasites within crickets (Gryllidae). In nature, female flies find singing male crickets by phonotaxis, despite severe constraints on directional hearing due to their small size. A physical coupling between the two tympanal membranes allows the flies to obtain information about sound source direction with high accuracy because it generates interaural time-differences (ITD) and interaural level differences (ILD) in tympanal vibrations that are exaggerated relative to the small arrival-time difference at the two ears, that is the only cue available in the sound stimulus. In this study, I demonstrate that pure time-differences in the neural responses to sound stimuli are sufficient for auditory directionality in *O. ochracea*.

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INTRODUCTION

The fly *Ormia ochracea* (Diptera:Tachinidae) possesses an auditory system that performs analogous functions to those of vertebrate hearing (detection, recognition, segregation, and localization or sources), albeit for a restricted range of stimuli (Gray et al., 2007). The flies are parasitoids and females must locate a cricket host in order to reproduce (Wineriter and Walker, 1990). They accomplish this by localizing the calls of singing male crickets using an auditory system dedicated to this task (Cade, 1975). Tympanal hearing is unusual for flies. All known examples are species that are parasitoids of acoustic insects (Allen, 1995; Robert et al., 1999; Lehmann, 2003), and these include two families (Tachinidae and Sarcophagidae) in which tympanal hearing has evolved independently through convergent adaptation of the same precursor organ (Edgecomb et al., 1995; Robert et al., 1996a; Lakes-Harlan et al., 1999).

Due to the small size of the flies (ears are < 0.5 mm apart) relative to the wavelength of cricket sound (~7 cm), acoustic directional cues are severely restricted (Kuhn, 1987). Sound waves impinging on the fly auditory system generate no interaural level difference (ILD) and interaural time differences (ITDs) are very small (maximum 1.5 μ s for a sound source at 90° relative to the midline axis). Nevertheless, flies can localize a cricket sound source with exceptional accuracy (<2° azimuth, Mason et al., 2001).

Abbreviations: BMAA, biomimetic antenna array; ICE, internally coupled ears; ILD/ITD, interaural level/time difference; MEMS, micro-electromechanical system; nITD/nILD, neural interaural level/time difference; tITD/tILD, tympanal interaural level/time difference.

Directional hearing in *Ormia* is derived from a specialized mechanical coupling between the two tympanal membranes (Robert et al., 1998). Mechanical coupling of the two eardrums amplifies the small direction-dependent ITDs in the sound field, and generates ILDs in the tympanal vibration responses, so that both cues are present in the tympanal (Robert et al., 1996b) and neural responses (Mason et al., 2001; Oshinsky and Hoy, 2002). Modeling of *Ormia* auditory mechanics (Miles et al., 1995) demonstrated that intertympanal coupling results in a system with two resonant modes of vibration in response to acoustic stimulation (**Figure 1**): a symmetric mode, in which the two tympani vibrate with equal amplitude and phase; and an antisymmetric mode, in which the two tympani vibrate with equal amplitude but opposite phase. Under normal acoustic conditions, a sound source located directly ahead of the fly (0° azimuth) generates vibration in the symmetric mode (each tympanum driven by identical sound pressure waves). Sound impinging from any other direction, however, will stimulate a combination of both modes of vibration with the result that the two tympani will respond with different (direction-dependent) amplitudes and phases of vibration, with maximum interaural differences of ~ 12 dB in amplitude and ~ 50 μ s delay (Robert et al., 1996b).

Analyses of the mechanical properties of *Ormia* tympanal membranes (Miles et al., 1995; Robert et al., 1996b; Akçakaya and Nehorai, 2008) have demonstrated that the mechanical coupling between the two eardrums enhances the system's sensitivity to the minute direction-dependent differences in arrival time of sound at the two ears. The nature of this effect is two-fold. (1) The arrival-time difference is amplified to result in a larger ipsilateral-leading phase difference between vibrations of the two tympani, creating a tympanal interaural time difference (tITD). (2) The amplitude of contralateral tympanal vibration is reduced relative to ipsilateral, creating a tympanal interaural level difference (tILD).

The majority of auditory receptors associated with each ear respond with tonic bursts at the onset of sound pulses (Oshinsky and Hoy, 2002) with response latencies that are dependent on tympanal vibration level, such that tILDs result in direction-dependent interaural latency differences in receptor responses. These neural interaural time differences (nITD) scale with the azimuth of the sound source location (Mason et al., 2001; **Figure 2**). Receptor thresholds vary, however, and another effect of tILDs is (direction dependent) differential recruitment of receptors in the two ears, such that directional sound sources will also generate interaural differences in the amplitude of summed neural responses – neural interaural level differences (nILD).

The directional mechanism of interaural coupling in ormiine ears was at first considered to be a unique evolutionary innovation. However, *Ormia* directional hearing is now considered to be a specialized example of a taxonomically widespread phenomenon by which acoustic directional cues (mainly ITDs) are amplified via interactions between the two ears to generate larger ITDs and ILDs in tympanal vibration which can then be used to encode directional information in neural responses. Internally coupled ears (ICE) include the majority of vertebrate auditory systems (van Hemmen

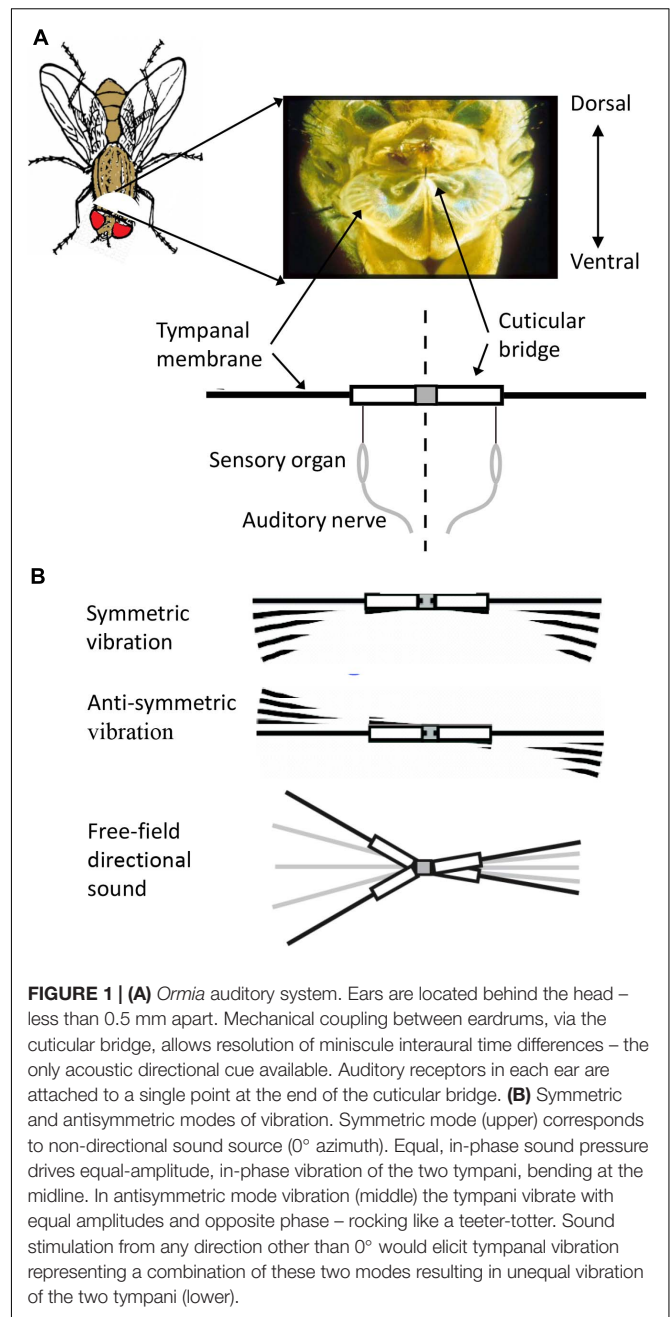
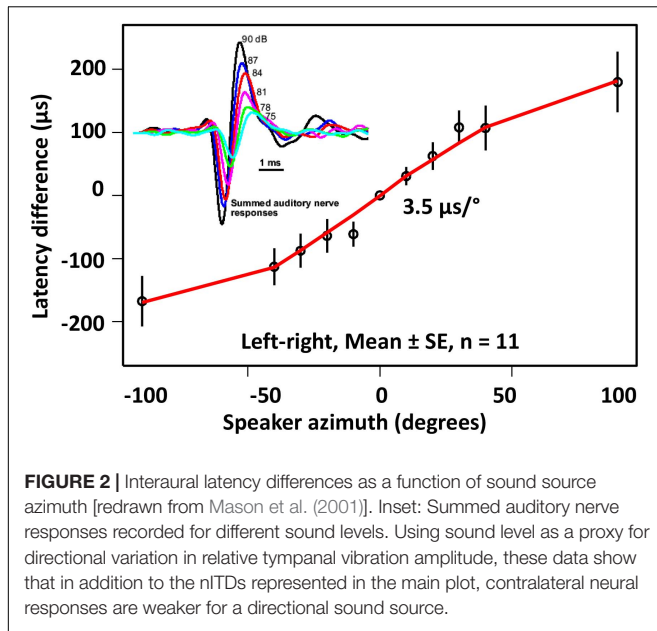


FIGURE 1 | (A) *Ormia* auditory system. Ears are located behind the head – less than 0.5 mm apart. Mechanical coupling between eardrums, via the cuticular bridge, allows resolution of miniscule interaural time differences – the only acoustic directional cue available. Auditory receptors in each ear are attached to a single point at the end of the cuticular bridge. **(B)** Symmetric and antisymmetric modes of vibration. Symmetric mode (upper) corresponds to non-directional sound source (0° azimuth). Equal, in-phase sound pressure drives equal-amplitude, in-phase vibration of the two tympani, bending at the midline. In antisymmetric mode vibration (middle) the tympani vibrate with equal amplitudes and opposite phase – rocking like a teeter-totter. Sound stimulation from any direction other than 0° would elicit tympanal vibration representing a combination of these two modes resulting in unequal vibration of the two tympani (lower).

et al., 2016), and general models of ICE have been derived (Vedurmudi et al., 2016a).

The principle of directionality via coupled hearing has been the basis of multiple auditory adaptations (Römer and Schmidt, 2016), just as insect ears in general show a striking diversity of independent evolutionary origins (Yack and Dawson, 2008). *Ormia* hearing in particular has been a subject of considerable interest as a model for evolutionary arms races between this eavesdropping parasitoid and its acoustically communicating hosts (e.g., Zuk et al., 1995; Wagner and Basolo, 2007; Sakaguchi and Gray, 2011).



Ormia auditory directionality has also emerged as an adaptable model for novel technology, and the past couple of decades have seen considerable interest in biomimetic applications of the flies' intertympanal coupling principle to engineering problems related to source localization for waveform signals, with two main areas of research. Efforts to design biomimetic directional microphones (BDMs, with application, for example, in hearing aids) have sought to mimic the mechanical properties of the fly eardrums in micro-electro-mechanical-system (MEMS) devices (Ishfaqe and Kim, 2018; Zhang et al., 2018). Efforts to design biomimetic antenna arrays (BMAAs) have applied the principle of coupled detectors to electromagnetic signal localization (Grüner et al., 2019). Much of this work has focused on quantifying the contribution of sensor coupling to directional resolution (Akçakaya and Nehorai, 2008; Grüner et al., 2019), tuning the effective bandwidth of the system (Rahaman and Kim, 2020), extending the mechanism to more than one axis (Lisiewski et al., 2011), and optimizing noise-robustness and sensitivity in the readout of ILDs and ITDs (Miles et al., 2009).

Previous work has shown that directional information is represented in the fly auditory system by amplified ITDs in the responses of auditory receptors (Mason et al., 2001). Other work (Oshinsky and Hoy, 2002) suggests interaural differences in the amplitude of neural responses based on differential receptor recruitment may also play a role in directional hearing. There is also evidence that small time-differences between competing auditory sources may play a role in source segregation in *Ormia* (Lee et al., 2009), and that noise sources may introduce a systematic bias in directional sensing that is a direct consequence of the coupling mechanism (Lee and Mason, 2017). Thus, as in vertebrate hearing, ITDs and ILDs may both contribute to directional hearing in *Ormia ochracea*, although the way these cues are combined in fly directional hearing is not fully resolved.

This study examines in more detail the relationship between ITDs and ILDs at the tympanal and neural levels, and the contribution of these cues to directional hearing using a series of experiments that measure behavioral, tympanal and neural responses to stimuli with manipulated phase and amplitude to generate ITDs in isolation. The aim is to answer a fairly simple and specific question – can the flies make use of pure time differences in auditory responses to generate directional responses to acoustic stimuli? The results show that interaural time differences do mediate directional responses in the absence of interaural level differences. I consider implications of these data for how ITD and ILD mechanisms may represent alternative solutions to differing physical and evolutionary constraints.

MATERIALS AND METHODS

Animals

Experiments were conducted on lab-reared gravid female *Ormia ochracea* derived from specimens originally collected in Gainesville FL. Flies were maintained at 25°C and 75% humidity on a 12-h:12-h light:dark regime and fed nectar solution (The Birding Company, Yarmouth, MA, United States) *ad libitum*.

Acoustic Stimuli

Single tone pulses (5 kHz, 10 ms duration, 0.1 or 0.5 ms rise/fall time) or synthetic cricket chirps (10 pulses at 50/s) were delivered from two speakers at 84 dB SPL (unless otherwise specified). Acoustic stimuli were synthesized using Tucker-Davis Technologies (TDT) hardware (System 3) and custom scripts written in C or Matlab. The stimuli were amplified (NAD S300), passed through a programmable attenuator (TDT model PA5) and broadcast from piezoelectric horn tweeters (Radio Shack Realistic, Taiwan). Stimulus amplitude and timing were controlled by computer and calibrated with a probe microphone (B&K Type 4182, Denmark). The relative phase and amplitude of simultaneous stimuli were adjusted to manipulate auditory ITDs and ILDs independently (see below).

Experimental Measurements

Behavior

Phonotactic responses were recorded with flies mounted on a spherical treadmill which transduced walking movements for recording by computer (Mason et al., 2001). This open-loop setup allowed stimulus conditions to be held constant throughout the duration of presentation. For comparisons of flies walking direction under different stimulus conditions I measured the angle of the fly's trajectory at the halfway point of each (virtual) walking path.

Tympanal Vibration

Following behavioral experiments, flies' heads were removed and tympanal vibration measured under identical acoustic conditions, using a laser Doppler vibrometer (LDV) (Polytec OFV 3001 controller, OFV 511 sensor head).

Auditory Nerve Recording

For some stimulus conditions, I recorded summed auditory nerve responses simultaneously from both ears, under stimulus conditions similar to behavioral and tympanal measurements, using tungsten wire electrodes (AM Systems, 0.25 mm). Amplified (AM Systems Model 1800) neural responses were averaged (50 sweeps) and recorded by computer (TDT AD1, 100 kHz sampling rate).

Behavioral, physiological, and mechanical measurements were all carried out in the same setup, with behavioral and mechanical measurements made on the same individuals. Physiological recordings were made on separate cohort of specimens under identical conditions.

I first repeated the measurement of eardrum responses to directional stimuli using the same setup as the other experiments and confirmed comparable results to those in the literature. I then conducted a set of experiments (1–3) aimed at manipulating nITDs and nILDs separately, to address the question of how much each of these response parameters contributes to the coding of auditory directionality.

RESULTS

Auditory Cues for Sound Localization

Figure 2 shows variation in the timing and amplitude of summed auditory nerve responses over a 15 dB range of stimulus levels comparable to the range of tILDs. Previous studies (Oshinsky and Hoy, 2002) have suggested that these nILDs could contribute to the coding of sound source direction, with some data suggesting that nILDs provide more accurate directional information than nITDs (Pollack and Mason, 2014).

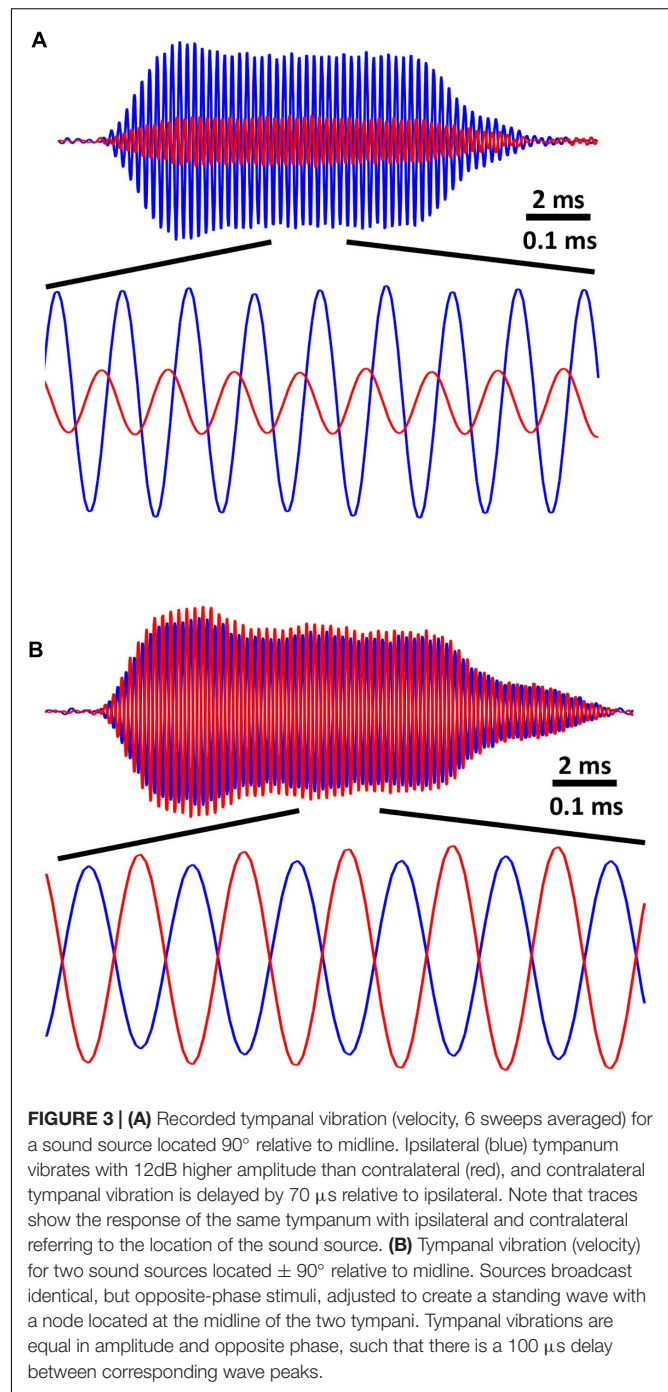
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Experiment 1 – Standing Wave

This experiment was designed to exploit the antisymmetric mode of tympanal vibration by placing a fly at the node of an acoustic standing wave.

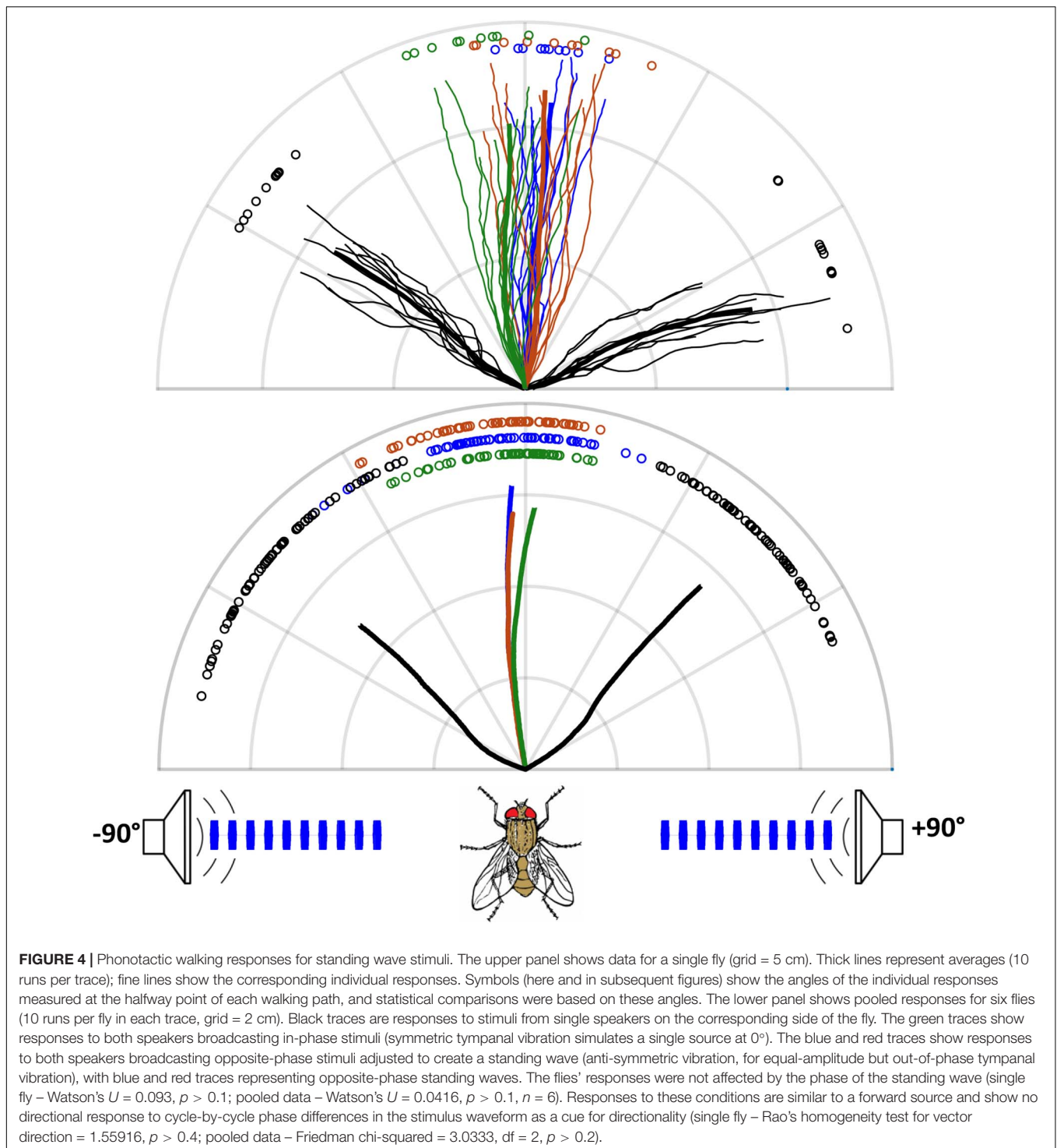
Flies were tethered in place atop the spherical treadmill (Mason et al., 2001), between two speakers positioned at $\pm 90^\circ$. Stimuli were calibrated with a probe microphone just above the midline of the tympanal membranes, and the amplitude and timing of identical, but opposite-phase, acoustic stimuli from each speaker were adjusted to create a null at the fly's midline. With a node positioned at the midline of the fly (i.e., the junction of the two tympani), sound pressure acting on the two tympana is equal-amplitude and opposite phase, and the tympanal membranes should rock in the antisymmetric mode of vibration (**Figure 1**). Reversing the phase of the standing wave would reverse the relative phases of tympanal vibration so that if this phase difference provided a directional cue, flies' directional response should also change.

By broadcasting the same stimuli in phase from both speakers, I could also generate a summed waveform at the midline of the fly.



This condition should elicit symmetric mode tympanal vibration (mimicking a phantom source at 0° azimuth, Lee et al., 2009).

Flies' behavioral responses (phonotaxis toward synthetic cricket chirps) were recorded ($n = 6$) for: (i) directional signals from each speaker individually; (ii) the standing wave condition (signals canceling at the fly's midline), recorded for both relative phases of tympanal vibration (i.e., left-leading and right-leading); and (iii) the summing signals condition. After behavioral recordings I measured tympanal vibration under



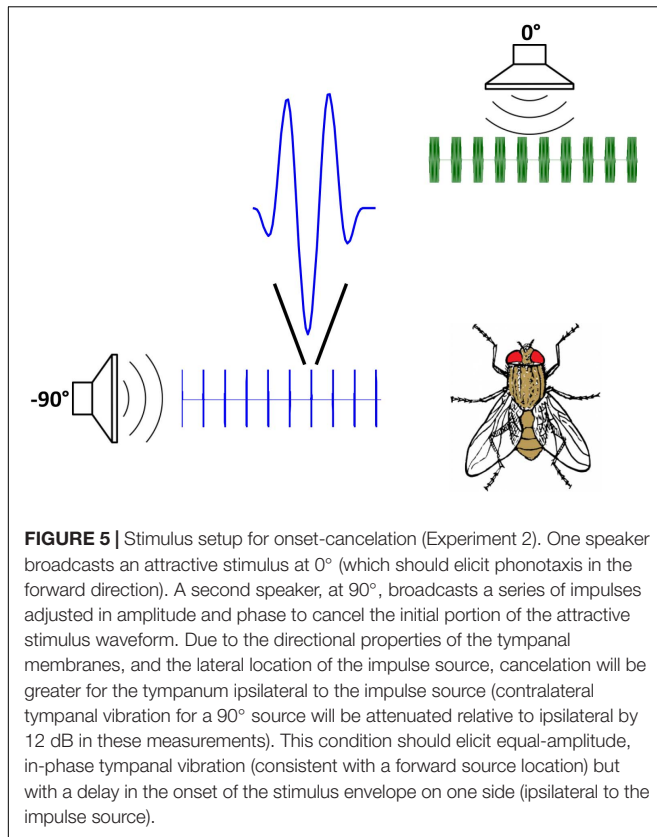
identical conditions using the LDV to validate the stimulus conditions. I show the tympanal vibration data first.

Tympanal Responses

First, I verified the behavior of the system for conventional free-field auditory stimulation. Tympanal vibration in response to a single source located at 90° was exactly as predicted by the

original analyses of the mechanics of the system (Miles et al., 1995; Robert et al., 1996b). Tympanal vibration in responses to an ipsilateral (90° azimuth) sound source was greater in amplitude by 12 dB and leading by 70 μ s relative to the source-contralateral tympanum (Figure 3A).

In the standing wave condition, ipsi- and contralateral tympanal vibrations are equal-amplitude and 180° out of



phase, equivalent to a $\pm 100 \mu\text{s}$ tITD (depending on the phase of the standing wave, **Figure 3B**). In the summed stimulus condition, the tympani showed equal-amplitude, in-phase vibration (symmetric mode) similar to a sound source directly ahead (0° azimuth, data not shown).

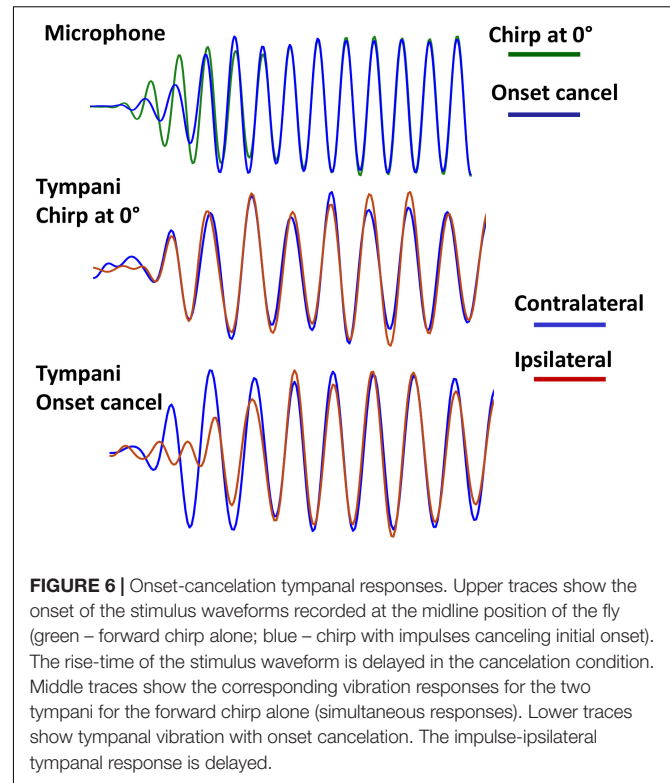
Behavioral Responses

Flies' sound localization behavior was highly consistent within each stimulus condition (**Figure 4**). In response to stimuli broadcast from either speaker alone, flies showed appropriately oriented phonotaxis. There was no difference in the orientation of phonotaxis between the standing wave and summed stimulus conditions and no effect of a phase reversal in the standing wave. In each condition flies walked directly ahead (0° azimuth). Pure asymmetric mode tympanal vibration did not generate directional cues, despite a $100 \mu\text{s}$ tITD.

Previous work has demonstrated, however, that small differences in the timing of stimulus onset can affect fly responses and mediate selective attention to one among multiple simultaneous sources, via a precedence effect (Lee et al., 2009). The next experiment examined whether time differences in the stimulus amplitude envelope can mediate auditory directionality in response to a single source.

Experiment 2 – Onset Cancellation

In this experiment, conditions were similar to experiment 1, except that one speaker was placed at 0° azimuth (directly forward of the fly), while a second speaker was placed at 90°

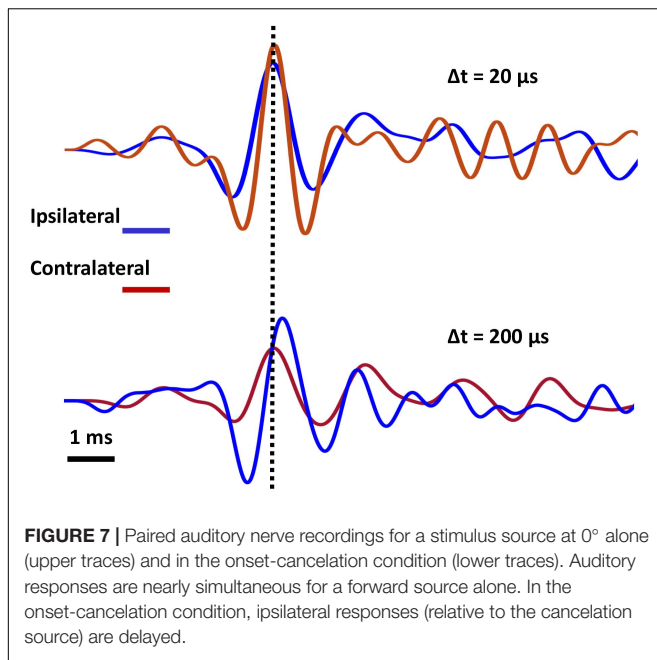


(lateral to the fly). The forward speaker broadcast a synthetic cricket chirp, which should elicit phonotaxis in the forward direction. The second speaker broadcast a train of brief impulses, approximating a half-cycle of the 5 kHz chirp waveform, timed to coincide with the initial onset of the individual pulses of the synthetic chirp, and phase-adjusted to cancel the initial cycle of each chirp pulse (**Figure 5**). Due to the directional properties of the tympanal membranes, and because the impulse source is located lateral to the fly (90° azimuth), its effect will be greater on the ipsilateral tympanum than the contralateral by 12 dB (see above, **Figure 3**).

The overall result of this stimulus arrangement is that the onset cancellation has a greater effect on the ipsilateral side (relative to the impulse source) than the contralateral, resulting in a delay in the rise-time of the amplitude envelope of the chirp pulses at the ipsilateral tympanum (**Figure 6**). This has no effect on the overall amplitude of the stimulus at either tympanum but results in a delay in onset timing that is also measurable in summed auditory nerve responses (**Figure 7**). The additional apparatus required for nerve recordings made it more difficult to calibrate the stimuli in these experiments. Interaural delays measured in auditory nerve responses were variable, with a mean \pm s.d. nITD in the cancellation condition of $48.6 \pm 125.5 \mu\text{s}$ ($n = 7$).

Behavioral Responses

Fly behavior ($n = 5$) clearly indicated that interaural differences in the timing of stimulus onset constituted a directional cue in the absence of an amplitude difference (**Figure 8**). Phonotactic

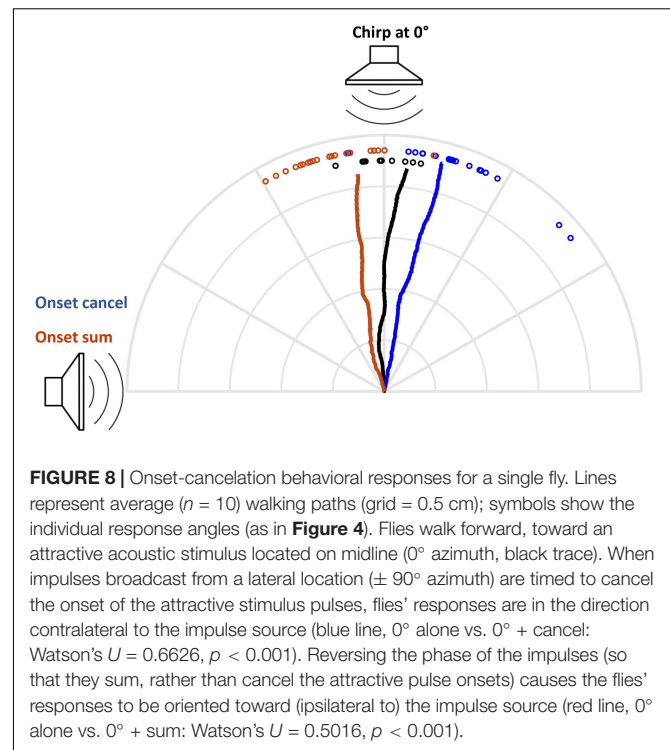


walking paths were diverted contralateral to the impulse source (toward the side with leading chirp pulse onsets). Reversing the phase of the impulse waveforms (summing rather than canceling ipsilateral pulse onsets) reversed the effect, and phonotaxis was diverted ipsilateral to the impulse source.

For comparison with free-field auditory directionality, I shifted the position of the attractive sound source to determine what source azimuth elicited responses with similar directionality to the onset-cancellation condition. The directional effect of onset cancellation was equivalent to a source azimuth of 2° (Figure 9).

DISCUSSION

Although flies are not sensitive to cycle-by-cycle phase differences in the stimulus waveform, they do show a directional response for stimuli that differ only in the timing of the amplitude envelope, as shown by experiment, and which generate only latency differences in the responses of auditory receptors. However, the magnitude of these directional responses (i.e., the perceived source direction as indicated by the direction of the flies' walking path) is somewhat smaller than would be predicted by measurements of the nITD induced by the stimuli, although still within the range of nITDs elicited by directional sound sources in free field stimulation. Measurements of nITDs in response to variation in sound source azimuth (Mason et al., 2001) showed a slope of 3.5 $\mu\text{s}/^\circ$. The mean value in these measurements was approximately 50 μs , which would correspond with an angle of incidence of ~ 15 degrees. While these results clearly demonstrated that interaural time differences alone can mediate auditory directionality, they clearly do not rule out a contribution from interaural level differences. Experiments involving dichotic stimulation in orthopteran insects (grasshoppers, katydids, and crickets) have demonstrated a separate contribution of ITD and

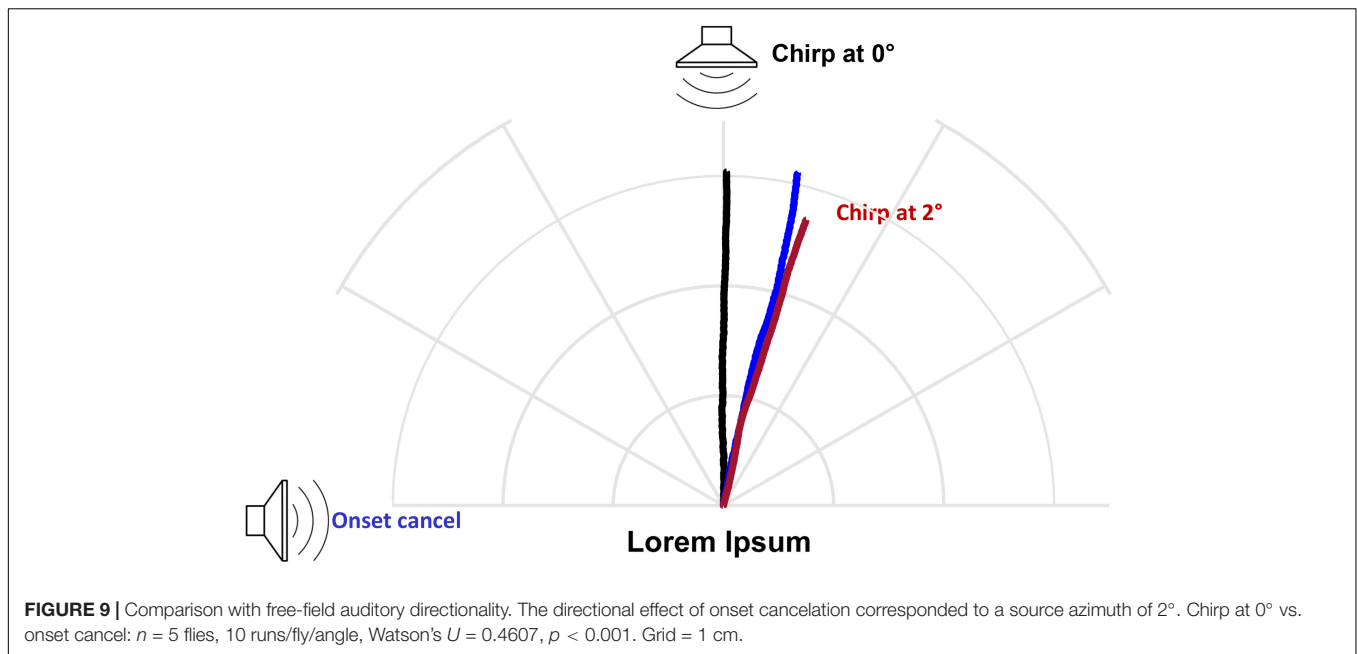


ILD cues in directional hearing (Rheinlaender and Mörchen, 1979; Kleindienst et al., 1981; von Helversen and Rheinlaender, 1988; Rheinlaender et al., 2006).

Temporal cues play an integral role in auditory processing (beyond the obvious importance in temporal pattern recognition for the pulsatile acoustic signals of their cricket hosts). Flies' auditory receptors respond almost exclusively to pulse onsets (Oshinsky and Hoy, 2002) and the strength of the response (the fly's perceived stimulus level) is determined by the amplitude increment relative to the noise-floor (effective amplitude, Lee and Mason, 2017). Small time-differences between competing sources mediate selective responses (Lee et al., 2009). While small interaural time-differences (for a single source) mediate directionality.

In a number of functional characteristics, *Ormia* hearing is convergent with more familiar (i.e., vertebrate) auditory mechanisms, and these may be seen as common principles arising from adaptation to the physics of sound. There are also clear differences, however, which could be consequences of the specific implementation of directionality in *Ormia* ears. For example, noise can disrupt directional acuity in *Ormia* and this is not alleviated by spatial separation of noise and signal (flies show no spatial release from masking, Blauert, 1997). Instead, under some circumstances, separation of signal and noise sources increases directional masking in *Ormia* (Lee and Mason, 2017).

What we know about the flies' hearing suggests that they accomplish as much as possible via peripheral filtering, with their auditory system functioning as a high-resolution, rapidly responding, symmetry detector that makes discrete measurements corresponding to the onset of each pulse in the



signal. Flies simply orient to the direction that balances auditory input in time and amplitude. The lack of spatial release from masking and biased response to noise is a consequence of this (Lee and Mason, 2017) and even the precedence effect that mediates source segregation is based on the refractoriness of peripheral receptors (Oshinsky and Hoy, 2002; Lee et al., 2009). This simplified set of information (relative to vertebrate hearing systems) allows for the major functions of hearing: segregation, recognition, and localization of sources, albeit for a specific pre-determined set of stimuli (host communication signals).

The major evolutionary innovation for *Ormia* hearing is that tympanal coupling relieves them from size limitation in auditory directionality. Comparative and phylogenetic studies (Edgecomb et al., 1995, Robert et al., 1996a) have identified the suite of morphological adaptations that constitute the tympanal ear of this group, and the homologous structures in atympanate flies. Hearing arises as a single-origin evolutionary innovation shared by members of the subfamily Ormiini. The sensory organ itself is derived from a proprioceptive chordotonal organ present, but of uncertain function, in atympanate flies. Surprisingly, tympanal hearing based on the same homologous precursor organ, but independently evolved, was also identified in one species belonging to a second family of flies (Sarcophagidea, Lakes-Harlan et al., 1999). This species shows a number of convergent characteristics with *Ormia*, including a parasitoid life cycle with an acoustic insect (cicada) as host and directional hearing via coupled eardrums (Robert et al., 1999), although the details of tympanal mechanics are distinct in this species.

Despite the fact that auditory directionality via ICE is now known to be a rather widespread phenomenon (van Hemmen et al., 2016), *Ormia* should still be considered a highly specialized example, with a number of striking adaptations that appear to optimize their directional acuity despite the relative simplicity (and small scale) of their auditory processing apparatus (both

mechanical and neural). An interesting contrast between *Ormia* and other (vertebrate) examples of ICE is that in most systems, there is a segregation in the frequency domain of the directional cues derived from the coupling mechanism, with ITDs at lower frequencies (relative to the fundamental frequency of the tympanum) and ILDs at higher frequencies (Vedurmudi et al., 2016b), whereas these cues are combined in *Ormia* (Robert et al., 1996b). On the other hand, the auditory system in *Ormia* is adapted to exploit the specific temporal and spectral structure of the host cricket acoustic signals; working in a relatively narrow frequency band and detecting the onset timing of individual sound pulses in the trill like call of the host. Expanding the usable bandwidth of systems designed to mimic *Ormia* hearing has been a major focus for biomimetic engineering efforts inspired by *Ormia* (Zhang et al., 2018). The subfamily Ormiini, though not a large group, includes nearly 70 species (Lehmann, 2003), with different species exploiting hosts with diverse acoustic signals in terms of both frequency and temporal characteristics. Comparative studies examining how auditory directional mechanisms are adapted to this diversity of signal parameters should be of great interest.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

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Conflict of Interest: The author declares that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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