

Mechanically coupled ears for directional hearing in the parasitoid fly *Ormia ochracea*

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An analysis is presented of the mechanical response to a sound field of the ears of the parasitoid fly *Ormia ochracea*. This animal shows a remarkable ability to detect the direction of an incident sound stimulus even though its acoustic sensory organs are in very close proximity to each other. This close proximity causes the arrival times of the sound pressures at the two ears to be less than 1 to 2 μs depending on the direction of propagation of the sound wave. The small differences in these two pressures must be processed by the animal in order to determine the incident direction of the sound. In this fly, the ears are so close together that they are actually joined by a cuticular structure which couples their motion mechanically and subsequently magnifies interaural differences. The use of a cuticular structure as a means to couple the ears to achieve directional sensitivity is novel and has not been reported in previous studies of directional hearing. An analytical model of the mechanical response of the ear to a sound stimulus is proposed which supports the claim that mechanical interaural coupling is the key to this animal's ability to localize sound sources. Predicted results for sound fields having a range of incident directions are presented and are found to agree very well with measurements. © 1995 Acoustical Society of America.

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INTRODUCTION

When an animal processes sensory information, especially as a prelude to orientation or locomotion, few tasks are more important than determining the incident direction of a stimulus. For an animal to localize an auditory stimulus it is typically necessary that both ears be excited by the pressure field. The only cues available for localization are minute differences in the intensity and time of arrival of the sound between the ear nearest and the ear farthest from the sound source. An animal's ability to localize sound depends on its ability to detect these minute differences. In relatively large animals where the distance between the ears is substantial relative to the wavelength of sound, interaural time, and intensity differences are large enough to be detectable by the central nervous system. In smaller animals where the distance between the ears is small relative to the acoustic wavelength, the interaural differences in intensity and arrival time can be extremely small. Many animals in this category have developed mechanisms for effectively increasing these differences before the sound stimulus reaches the auditory receptor cells [Michelsen (1992)].

There are several ways that the auditory system of an animal can be organized to process interaural difference cues. It is common for animals to have two ears that are as widely separated as possible. Acoustic pressure incident on each eardrum, or tympanum, results in the deflection of an auditory sensory organ which transduces this mechanical input into neural response. In many animals, particularly large mammals, the ears are totally isolated from each other, resulting in each ear acting as a simple pressure receiver, in

that the eardrum of each ear is excited only by sound from the outside.

However, in many small animals that need to localize sound sources, the dimensions of the animal are such that the two ears cannot be placed far enough apart to experience significant interaural differences. In these animals it is found that each ear is driven by a combination of the pressures that arrive at each side of the body. The acoustical interaction between these pressures can cause the net pressure and subsequent response of the ear that is furthest from the sound source (contralateral) to be lower than that of the ear closest to the sound source (ipsilateral) [Fletcher and Thwaites (1979), Michelsen *et al.* (1994a), Palmer and Pinder (1984), Aertsen *et al.* (1986)]. The interaction can also increase the effective interaural distance, resulting in an expanded interaural time difference.

In previous studies of directional hearing, the interaction between the ipsilateral and contralateral pressures has always been found to be due to sound traveling through some air-filled passage such as a trachea which connects to two sides of the body. In this paper we investigate an animal in which the ears are so close together that a reasonable way to achieve this effect is to employ interaural mechanical coupling through the use of the cuticle between the ears. This differs from the mechanism used by other small animals in that here the cuticle provides a direct mechanical link between the eardrums rather than relying on air to provide an acoustical link.

The novel ear considered here is that of the parasitoid fly, *Ormia ochracea* (order: Diptera; family: Tachinidae)

(Robert *et al.*, 1992, 1994). Unlike most ears, the fly's left and right acoustico-sensory organs are not physically separated but are contained within a common air-filled chamber, a mere 450 to 520 μm apart from each other. The small size and anatomy of the ears studied here precludes them from functioning as a pair of uncoupled pressure receivers. The size of the ear is such that an acoustic wave travels from one distal border of a tympanum to the other in less than four microseconds. This small time delay in the incident pressure is insufficient for reliable neural encoding of directional information (Mörchen *et al.*, 1978). Yet, the behavior of this animal indicates a remarkable ability to localize sound sources.

In order to reproduce, the gravid female fly must find and deposit her parasitic larvae on a live field cricket, which is the specific host for the parasite (Cade, 1975). The larvae ultimately consume the cricket. The female parasitoid locates her host at night, apparently relying only on auditory cues from the cricket's mating call (Walker, 1986). The cricket's calling song is relatively pure in frequency (peak frequency of 4.8 kHz and a corresponding wavelength of about 7 cm). The parasitoid tachinid fly is small, about the size of a housefly, and its entire hearing organ spans about 1.5 mm. This substantial dimensional mismatch between wavelength and interaural distance results in extremely small interaural differences in intensity and arrival time from an incident acoustic wave. The scattering of sound by the fly can be crudely modeled by representing the fly's body as a rigid sphere. For a sound wave having a frequency in the vicinity of 5 kHz, a rigid sphere of similar dimension will produce negligible sound scattering [Morse and Ingard (1968)].

In the following, it is shown that this hearing organ utilizes a relatively rigid mechanical connection between the tympana in order to achieve interaural differences in tympanal response. The mechanical coupling consists of a flexible mechanical lever which connects the two sensory organs and pivots about a fulcrum. In this animal, the use of a structural or mechanical coupling between the tympana acts to increase the time delay for the effect of sound to travel from the location of the ipsilateral sensory cells to that of the contralateral sensory cells by a factor of about 20. In addition to a substantial expansion in the interaural time delay, the mechanical system also produces significant interaural level differences which will also greatly facilitate the neural processing of directional information. This mechanical interaural coupling comprises a new mechanism for directional hearing and provides a highly effective alternative to acoustically coupled ears.

In the following, we briefly describe the functional anatomy of the hearing organ and outline the experimental apparatus used to examine its response to sound. Results from measurements of the mechanical response of the ear to a sound stimulus are presented to describe the essential mechanisms for directional hearing in this animal. These data strongly suggest that mechanical interaural coupling plays a crucial role in enabling the animal to localize sound sources. This is the first report of the use of mechanical coupling to achieve directional hearing.

Finally, a simplified mechanical model is proposed

which accounts for the mechanical coupling between the ears. It is shown that by a reasonable choice of the parameters of this model, predictions agree very well with measured mechanical response data for various incident directions of the sound stimulus. The excellent agreement between the predicted and measured results supports the claim that mechanical interaural coupling is responsible for directional sensitivity in this system.

I. ANATOMY OF THE ORMIINE EAR

Externally, the ear is located on the front face of the thorax, directly behind the head [Fig. 1(a)]. A detailed description of the anatomy is presented by Robert *et al.* (1994). A conspicuous pair of thin cuticular membranes on the prosternum (prosternal tympanal membranes—PTM) serves as tympanal membranes for hearing [Fig. 1(b)]. Attached to the tympanal membranes, within an enlarged common prosternal chamber, are a pair of auditory sensory organs, the bulbae acusticae. The bulbae acusticae are attached to the membranes through a stiff cuticular rod, or apodeme, which connects to the tympanum at the tympanal pit (TP). The rigid structure of the apodeme is such that it is reasonable to expect deflections at the tympanal pit to be transferred directly to deformation of the bulba acustica. The pair of tympanal pits is connected to each other and to the pivot point shown in Fig. 1(a) through a cuticular structure we will refer to as the intertympanal bridge. In the following, the intertympanal bridge will be shown to play an important role in the mechanics of the system and will be described in more detail in Sec. IV and Fig. 8. Each bulba acustica contains about 70–75 auditory receptor cells. It is innervated by the auditory nerve, which is a branch of the frontal nerve of the fused thoracic ganglia. The primary auditory afferents project to highly restricted regions within the fused thoracic ganglia.

Measurements of the auditory tuning curves for this ear show that it is most sensitive in the frequency range near 5 kHz (Robert *et al.*, 1992).

II. EXPERIMENTAL METHODS

To investigate the mechanics of the ears, the vibrations of the tympanal membranes, tympanal pits, and intertympanal bridge were measured as they responded to a sound field. The primary elements of the measurement system were a laser vibrometer, a holder for the fly, a loudspeaker, and a microphone. Measurements of the membrane vibrations were performed using the laser vibrometer while the ear was subjected to sound waves incident from various angles. Because the laser vibrometer permits a noncontacting, noninvasive vibration measurement and because the laser light can be focused onto an area of approximately 5 μm in diameter, it was possible to measure the membrane vibration at a large number of locations. Laser vibrometers have been used to measure tympanal vibrations in a number of different animals [Dragsten (1974), Schiolten *et al.* (1981), Klump and Larsen (1992), Lakes-Harlan and Heller (1992), Michelsen *et al.* (1994b)].

The measurements were performed on adult female *Ormia ochracea* (Tachinidae, Ormiini) from the laboratory

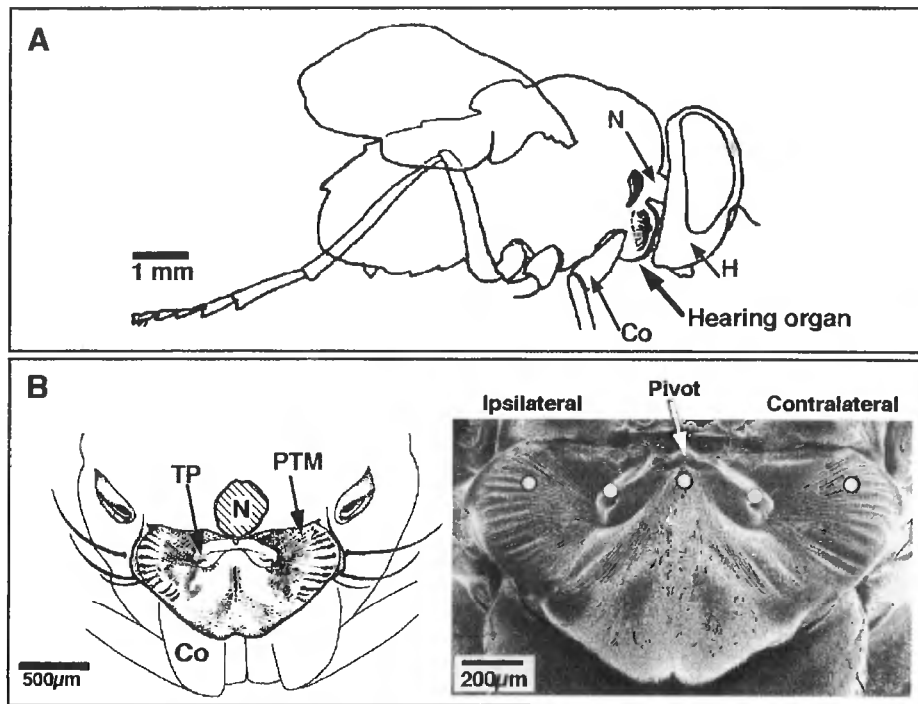


FIG. 1. Location and external anatomy of the ears of *Ormia ochracea*. (a) Line drawing of the fly illustrating the location of the hearing organ. The ears are located in front and between the coxae of the prothoracic legs (Co), below the neck (N), and directly behind the head (H). (b) Frontal views of the ears with the head removed. Left panel is a line drawing; right panel is a scanning electron micrograph. The prosternal tympanal membranes (PTM) show radial corrugations. These corrugations converge upon the tympanal pit (TP) to which, internally, the sensory organ is attached. The white dots are measurement locations.

colony (see Robert *et al.*, 1994). Flies were subjected to cold anesthesia and waxed to the positioning device. Surgical removal of the head was necessary to expose the tympanal membranes to the laser beam.

The experimental setup is shown in Fig. 2. The sound induced vibrations of the ear were measured using a Polytec laser vibrometer. This unit consists of a Polytec OFV-300 optical head and Polytec OFV-2100 control electronics. The laser vibrometer measures velocities with amplitudes as low as $0.5 \mu\text{m/s}$ over a frequency range of 0.1 Hz to 500 kHz. The laser head was mounted on an Oriel motorized micrometer driven stage which allowed precise positioning. The velocity of a surface was measured by detecting the Doppler shift in the frequency of the emitted and reflected laser light. The output of the laser vibrometer is a voltage which is proportional to velocity.

The fly was supported on a stage which was mounted along with the optical head of the laser vibrometer on a Newport Research Series optical vibration isolation table (dimensions 4 ft \times 8 ft \times 1 ft). The stage for the fly was designed to allow accurate positioning of the animal in the sound field and to permit adjustments to optimize the quality of the vibration signal from the laser. The fly was placed approximately 30 cm from the laser. The quality of the output of the laser depends on its ability to sense reflected light from the ear. Care was taken to place the fly in a position where the optical signal was optimum and where the sound field was not disturbed by adjacent instruments and structures. The optical sensitivity of the system was found to be sufficient so that it was not necessary to enhance the reflectivity of the measured surface by adding reflective particles such as glass

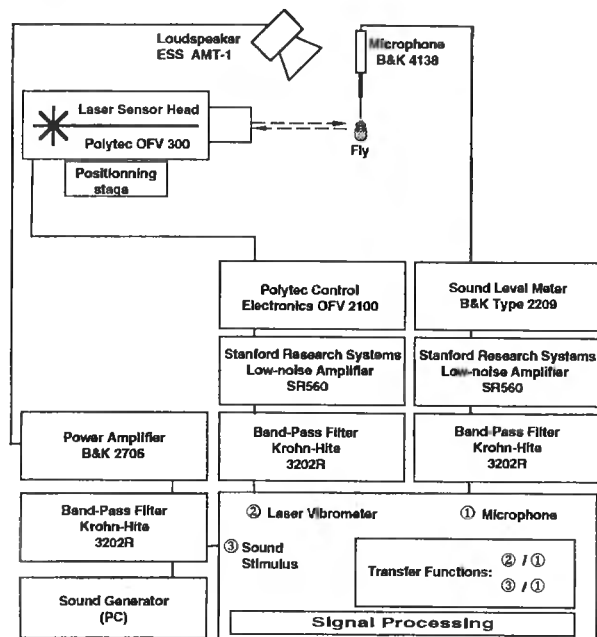


FIG. 2. Schematic of experimental setup. A Polytec laser vibrometer consisting of a OFV 300 Sensor Head and OFV 2100 Control Electronics was used to measure the vibration of the ear due to random, bandlimited white noise produced by a high-frequency loudspeaker (ESS AMT-1 tweeter). The overall sound pressure level was 104 dB *re*: $20 \mu\text{Pa}$; the bandwidth was 1–25 kHz. The sound field in the vicinity of the fly was measured using a Brüel & Kjær model 4138 $\frac{1}{8}$ -in.-diam microphone. The microphone was placed as close as possible to the hearing organ. The random signals from the laser vibrometer and the microphone were bandpass filtered and then processed to compute the transfer function between the dynamic displacement of the ear and the incident sound pressure. The transfer function was computed as the ratio of the cross power spectrum of the two signals to the autopower spectrum of the microphone signal.

beads as has been the practice in other studies [Klump and Larsen (1992)].

The sound field was created using a high performance tweeter (ESS model AMT-1 part 675-1147) which is capable of sound production over a frequency range of 1 kHz to beyond 30 kHz with a minimum of distortion. The tweeter was placed approximately 15 cm from the fly. The sound pressure was measured at a position as close to the fly's ear as possible. A Brüel & Kjær model 4138 microphone having a diameter of $\frac{1}{8}$ in. (3.2 mm) was placed in a holder directly above the fly. Since it was important that the microphone measure the pressure applied to the membrane, care was taken to ensure that the microphone was very close to the ear without adversely modifying the sound field. The fact that the microphone did not disturb the sound field was verified by noting that the tympanal response measured by the laser vibrometer was the same with or without the microphone placed next to the ear. The sound field in the vicinity of the ear was measured and found to vary by less than ± 1 dB.

The acoustic stimulus consisted of a burst of bandlimited white noise lasting 0.01 s and having a frequency range of 1 to 30 kHz. The signals from the laser and the microphone were digitized using a Microstar 2400/6 A/D board (12 bit analog-to-digital conversion). A simple transient window was applied to the time domain data prior to processing the data using a fast Fourier transform algorithm (FFT) in a digital signal processor. The time durations of the stimulus and of the analysis window were shorter than the time required for sound to reflect from surfaces in the room and return. This eliminated any effect of room reflections. The spectral analysis allowed the estimation of the cross power spectra, autospectra, and transfer functions of the membrane displacement (or velocity) relative to the acoustic pressure as a function of frequency. The transfer functions were computed using averages of ten sample records. The frequency resolution of the spectral analysis (Δf) was 31.25 Hz. Since the system is not lightly damped and the response does not exhibit sharp resonant peaks when viewed in the frequency domain, this frequency resolution was found to be more than adequate for characterizing the spectral response.

The coherence between the signals from the laser vibrometer and the microphone was computed in order to indicate the quality of the measurement. We typically obtained coherence above 0.95 over the frequency range from 1 to 25 kHz. Data were rejected when the coherence fell below 0.8. This indicates that a minimum of extraneous noise influences our measurement.

III. MECHANICAL RESPONSE MEASUREMENTS

Figure 3 shows the magnitudes of the transfer functions in decibels with a reference level of 1 mm/Pa between the displacement of the ears measured by the laser vibrometer and the incident acoustic pressure measured by the microphone. The fly was positioned relative to the loudspeaker such that the incident sound wave was oriented at a 45° angle relative to the fly's longitudinal axis. The average spectra and standard deviations are shown in Fig. 4.

Figure 3 shows that in the frequency range above about 5 kHz, the tympanal pit (TP) which is closest to the sound

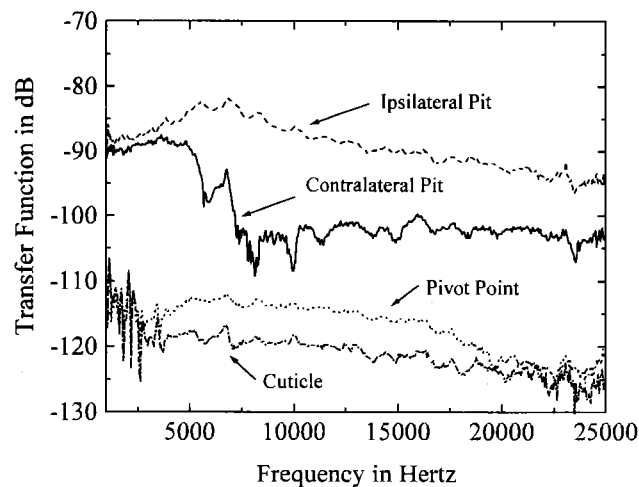


FIG. 3. The magnitudes of the measured transfer functions in decibels with a reference level of 1 mm/Pa between the displacement of the ormiine ears and the incident acoustic pressure measured by the microphone. The direction of the measured displacement is perpendicular to the surface of the tympanum. The measurement locations are indicated in Fig. 1.

source (ipsilateral) responds with as much as 20 dB greater amplitude than the tympanal pit which is farthest from the sound source (contralateral). This level difference is remarkable when one considers that the distance between these two measurement points is roughly 1/200th the wavelength of sound at 5 kHz. The incident pressure field may be considered to be very nearly uniform over a distance of this magnitude. Measurements of the acoustic pressure in the vicinity of the specimen show that these differences in mechanical response are not due to inhomogeneities in the incident sound field. The small size of the structure relative to the wavelength of sound, particularly in the frequency range below 10 kHz, precludes significant acoustic gradients. Inter-aural differences in the mechanical response are due to the dynamical properties of the system, itself.

It should be noted that the responses of the ears are found to be symmetric in that when the sound source is rotated such that the ipsilateral and contralateral sides are reversed, the side of the ear closest to the source always responds in the manner shown as the ipsilateral pit in Fig. 3. The figure also shows the response of a point halfway between the two tympanal pits [labeled pivot in Fig. 1(b)] along with a measurement point on the prosternal cuticle. These two locations are found to respond with much lower amplitude than any point on the tympanum.

In order to better visualize the sound-induced vibrations, the deflection shapes of the ears are shown in Figs. 5–7 at three different frequencies. These data were obtained by measuring the transfer functions between the displacement and the acoustic pressure at a number of locations across the width of the ear. As in the data of the previous figures, the incident sound field was oriented at 45° relative to the axis of the animal. Knowing the complex transfer function, one can compute the time domain response at any given frequency.

The responses at 15 locations across the ears are shown as a function of time which covers one period of the motion, T . The period is $T = 1/f$, where f is the frequency in hertz. The deflection shape measured at 2 kHz indicates that the

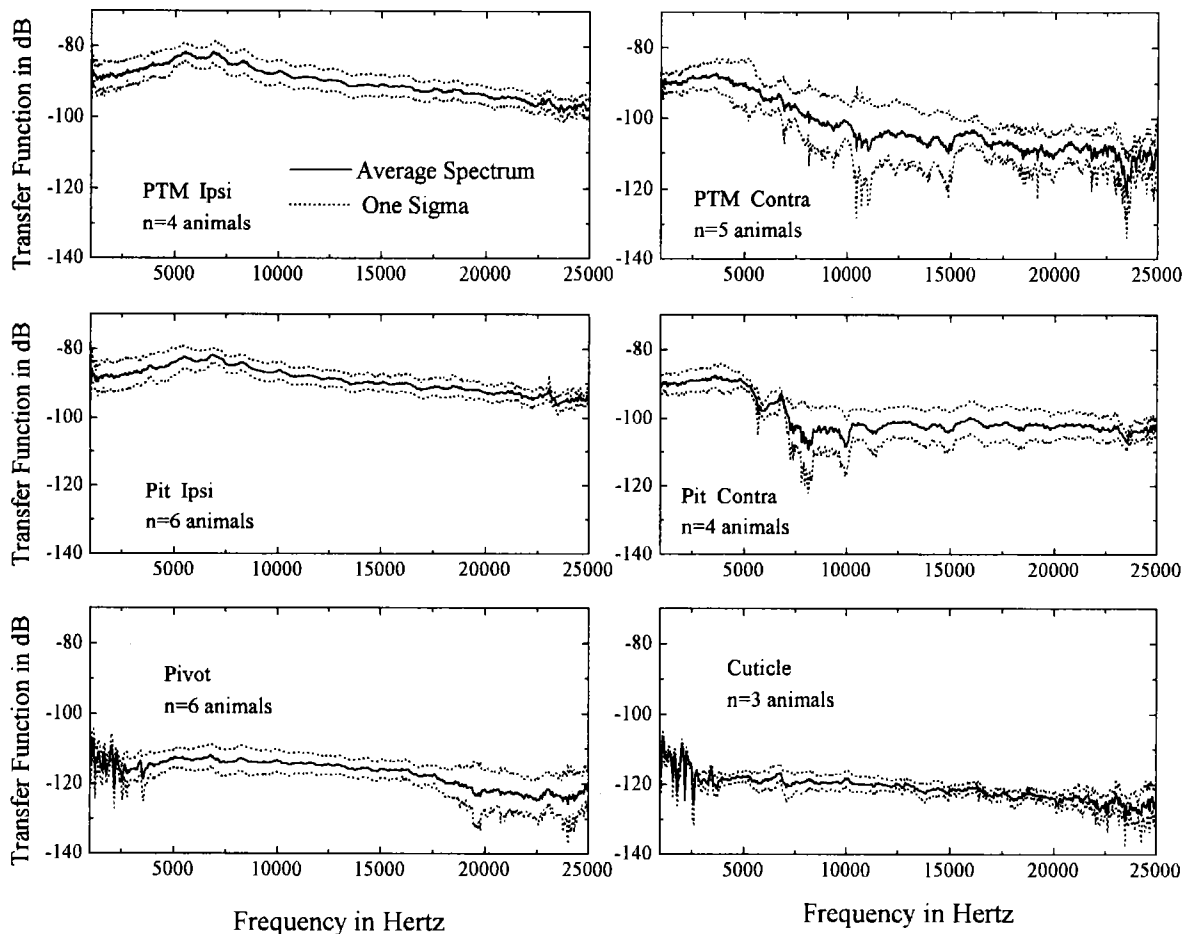


FIG. 4. Average transfer functions, number of samples, and standard deviations for the data in Fig. 3. The measurement locations are indicated in Fig. 1.

two ears move with similar magnitude and phase (Fig. 5). The data shown at 6 kHz indicate the two ears move in nearly opposite phase (Fig. 6). The ipsilateral and contralateral tympanal structures essentially rock about the central pivot point (position 0.0). At the higher frequency of 15 kHz (Fig. 7), the ipsilateral side responds with significantly greater amplitude than the contralateral side as expected from the data shown in Fig. 3.

It should be noted that the data shown in Figs. 5–7 are taken from an experiment on one animal and the data of Figs. 3 and 4 represent an average of the responses of several animals. Differences in the response amplitudes and time delays or phase are observed in different animals but the general character of the deflection shapes is represented well in Figs. 5–7.

The response measured in the frequency range near 5–6 kHz is the result of strong mechanical coupling between the ipsi- and contralateral ears. If the two sides were mechanically isolated, the vibration would show negligible interaural differences as are found in the incident sound field. The existence of mechanical coupling is apparent in the anatomy of the intertympanal bridge which joins the two tympanal pits. By manually pressing against one tympanal membrane one observes a marked deflection of the other tympanal membrane but in the opposite direction of the one being pushed.

As mentioned in the Introduction, the usual way for small animals to employ interaural coupling for achieving

directional hearing is through the use of an acoustical, or air-filled, pathway. In *O. ochracea*, the anatomy suggests that an acoustical interaction is possible between the ears along with the mechanical coupling. This is due to the fact that the tympanal membranes are backed by a common air-filled chamber. One could imagine that the air in the chamber might act as a coupling spring given the appropriate geometrical and material properties. Acoustically coupled ears such as this have been observed in cicadas although they are considerably larger than that studied here [Fletcher and Hill (1978), Fletcher (1992), Young and Hill (1977)]. To examine the possibility of an air spring between the ears we opened the chamber behind the ears by removing a prothoracic leg. This essentially eliminates the stiffness of the air in the chamber. The mechanical response of the ears to either sound or direct mechanical stimulation was found to not be significantly altered. This suggests then that the primary source of the coupling between the ears is the cuticle forming the intertympanal bridge.

IV. MECHANICAL MODEL

The strong interaural coupling as indicated in Figs. 5–7, particularly at 6 kHz, suggests that the intertympanal bridge joins the two ears in the manner of a flexible lever. This is quite apparent when one manually applies a force to one membrane; the bridge clearly rocks about the point halfway

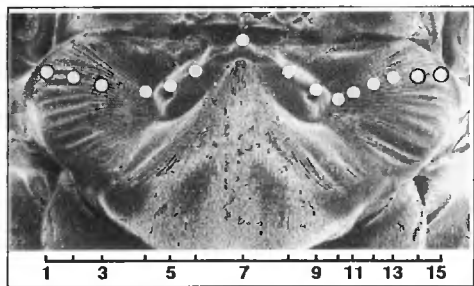
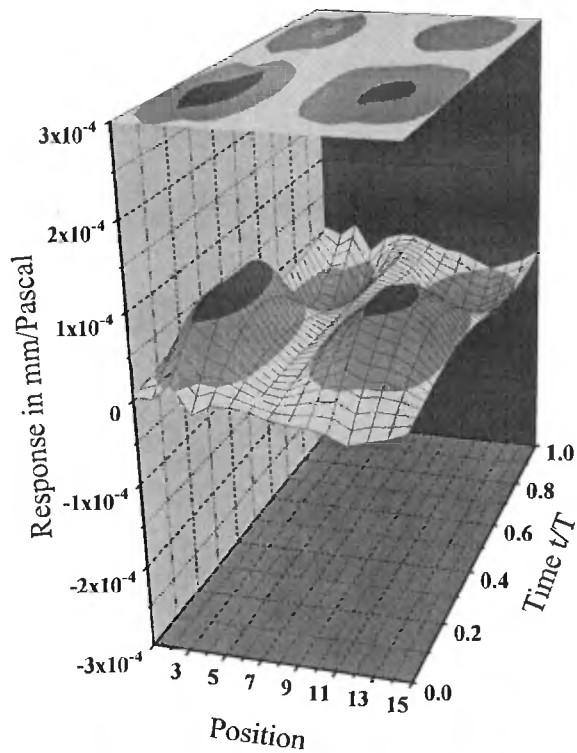


FIG. 5. The deflection shapes of the ears at 2 kHz. These data were obtained by measuring the transfer functions between the displacement and the acoustic pressure at a number of locations across the width of the ears. The deflection is shown as a function of time where the time axis indicates the time relative to one period of the oscillation T . An outward deflection of the membrane is shown as a positive response in the vertical axis. As in the data of the previous figures, the incident sound field is oriented at 45° relative to the longitudinal axis of the animal. The sound was incident from the left so that the ipsilateral ear corresponds to lower values of position.

between the tympanal pits, causing the two membranes to deflect in opposite directions. These observations lead one to a simple model of the intertympanal bridge as shown in Fig. 8.

One can view the system of Fig. 8 as an extreme example of a pressure difference receiver in which the interaction of the two ears must occur very quickly due to the small differences in arrival times of the external pressures. When sound first arrives at the ipsilateral eardrum, its motion produces forces on the contralateral ear via the intertympanal bridge, which tend to cancel the effects of the external pressure received there. Rather than employing an acoustical interaction, as in conventional pressure difference receivers, the cuticular structure of the intertympanal bridge appears to provide the coupling.

The simplified model of Fig. 8 neglects many effects such as wave resonances associated with the tympanal mem-

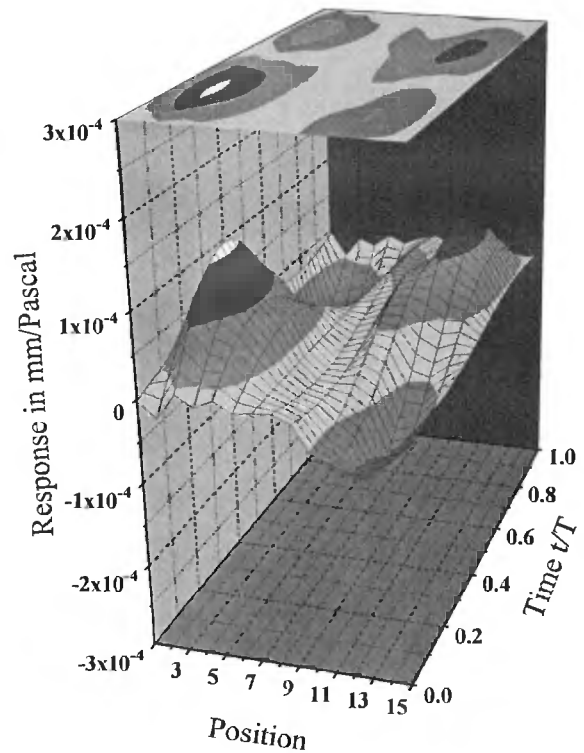


FIG. 6. The deflection shapes of the ears at 6 kHz. These data were obtained as in Fig. 5.

branes. Our present aim is to propose a description which includes only the essential characteristics and not to develop a comprehensive dynamical model. The model shown here is based on considering those elements which are expected to

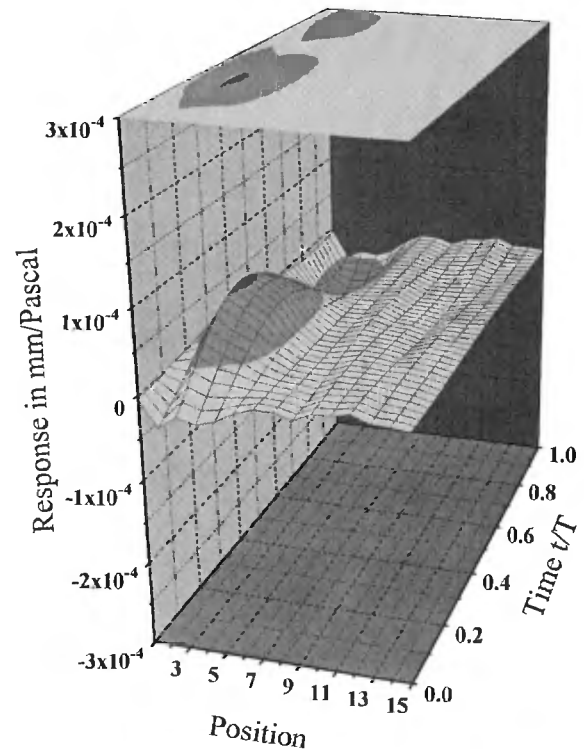


FIG. 7. The deflection shapes of the ears at 15 kHz. These data were obtained as in Fig. 5.

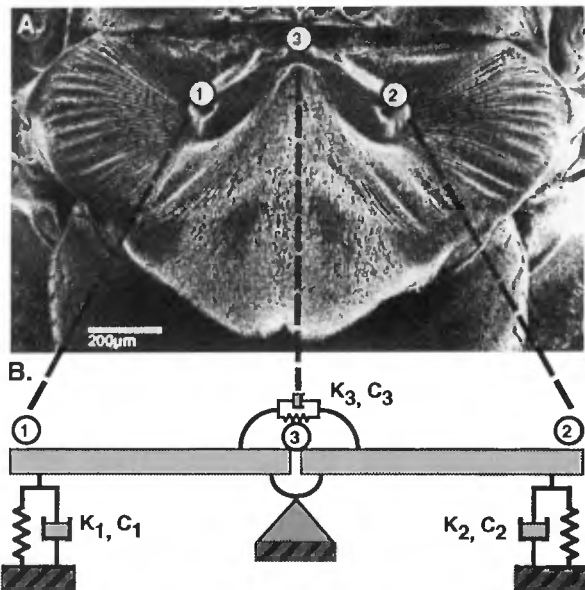


FIG. 8. Mechanical model. In this idealization, the intertympanal bridge is assumed to consist of two rigid bars connected at the pivot through a coupling spring k_3 and dash-pot c_3 . Springs and dash-pots located at the extreme ends of the bridge (1 and 2) approximately represent the dynamical properties of the tympanal membranes, bulbae acusticae, and surrounding structures.

contain the most kinetic and potential energy during vibration. The primary elements of the system are the tympanal membranes, intertympanal bridge, apodemes connecting the tympanal pits to the sensory organs, and the sensory organs. Because of the stiffness of the intertympanal bridge and the apodemes, it is reasonable to assume that the sensory organs move in unison with the tympanal pits. Our previous anatomical study [Robert *et al.* (1994)] reveals that the masses of the sensory organs are several times greater than any other moving part of the system. It is reasonable to assume then that the kinetic energy is concentrated in the sensory organs. The mass moment of inertia of the rigid bars in our proposed model in Fig. 8 may be calculated knowing the location of the sensory organs relative to the pivot point 3 along with its mass.

An incident acoustic pressure acting on the tympanal membranes results in a continuous distributed force field which may be approximately represented as two point forces, each applied at a specific location on each membrane with an amplitude given by the product of the acoustic pressure and membrane surface area. When the pressure wave is incident at some angle relative to the fly's longitudinal axis, these two point forces, $f_1(t)$ and $f_2(t)$, will differ only slightly in phase, and will have essentially equal amplitudes owing to the relatively short distance between their points of application and the speed of sound propagation. If the direction of propagation of the incident wave is at an angle ϕ relative to the fly's longitudinal axis, then the time delay between the ipsilateral and contralateral forces is $\tau = d \sin(\phi)/c$, where d is the distance between the effective points of application and c is the sound speed which is roughly 344 m/s. If we consider the point of application of the force to be at the location of greatest response on the tympanal membrane (approximately the center of the larger ridges, close to the PTM

measurement locations shown in Fig. 1), then the distance between the force locations is $d \approx 1.2$ mm. An incident sound wave which is inclined at a 45° angle relative to the fly's longitudinal axis results in a time delay between the two forces of $\tau \approx 2.5 \mu\text{s}$.

In effect, the mechanical system expands interaural amplitude and time differences. This results from its sensitivity to the difference between the forces on the two sides of the ear, $f_1(t)$ and $f_2(t)$. Because the intertympanal bridge pivots about its center, the system is very sensitive to the difference in these forces. This can be seen by using the idealized system shown in Fig. 8 to model the transfer functions of the responses of each end of the intertympanal bridge, $x_1(t)$ and $x_2(t)$, relative to the incident pressure at the pivot point, which is the location of the microphone in the data of the previous figures. In the following, we will examine the response of the model system of Fig. 8 to illustrate how the system works. It will first be shown that even if one does not know the values of the parameters in the model, the governing equations provide at least a qualitative prediction of the response that agrees with the measurements. After having demonstrated that the governing equations are consistent with the measured results, values of the parameters in the model will be selected to permit a numerical evaluation of the equations and a quantitative comparison with the experimental results. It will be shown that the model system in Fig. 8 very closely represents the actual response of the ears.

The responses $x_1(t)$ and $x_2(t)$ of the two ends of the intertympanal bridge shown in the idealization in Fig. 8 may be obtained by solving

$$\begin{bmatrix} k_1 + k_3 & k_3 \\ k_3 & k_2 + k_3 \end{bmatrix} \mathbf{x} + \begin{bmatrix} c_1 + c_3 & c_3 \\ c_3 & c_2 + c_3 \end{bmatrix} \dot{\mathbf{x}} + \begin{bmatrix} m & 0 \\ 0 & m \end{bmatrix} \ddot{\mathbf{x}} = \mathbf{f}, \quad (1)$$

where the unknown response vector is $\mathbf{x} = \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix}$, the applied force is $\mathbf{f} = \begin{pmatrix} f_1(t) \\ f_2(t) \end{pmatrix}$, and $(\dot{})$ denotes differentiation with respect to time t . The constant m accounts for the effective mass of all moving elements of the system and is assumed to be concentrated at each end of the intertympanal bridge.

Equation (1) may be used to determine the transfer functions between each response coordinate, $x_1(t)$ and $x_2(t)$, and the incident pressure at the pivot point, $p(t)$. In the following, these transfer functions will be expressed in two forms in order to facilitate an understanding of how the system works. We will first use a "direct" approach which follows from solving the coupled Eq. (1) directly in the transform domain and then we will use a "modal" approach in which the response is expressed as a linear combination of two uncoupled types of motion.

To simplify the notation, let $H_{f_1 p}(\omega)$ and $H_{f_2 p}(\omega)$ denote the transfer functions as a function of the frequency, ω , in radians/s of the ipsilateral and contralateral forces, $f_1(t)$, and $f_2(t)$, relative to the acoustic pressure at the microphone location, $p(t)$. These transfer functions are given by $H_{f_1 p}(\omega) = s e^{i\omega\tau/2}$ and $H_{f_2 p}(\omega) = s e^{-i\omega\tau/2}$, where τ is the time for the incident sound to travel between the points where the forces act as given above and s is the surface area

of each tympanic membrane. By directly solving Eq. (1), the transfer functions between the responses and the pressure at the pivot may be shown to be

$$H_{x_1p}(\omega) = \frac{s(k_3 + \hat{i}\omega c_3) \times (e^{i\omega\tau/2} - e^{-i\omega\tau/2}) + s(k + \hat{i}\omega c - m\omega^2)e^{i\omega\tau/2}}{(k + \hat{i}\omega c + k_3 + \hat{i}\omega c_3 - m\omega^2)^2 - (k_3 + \hat{i}\omega c_3)^2},$$

$$H_{x_2p}(\omega) = \frac{s(k_3 + \hat{i}\omega c_3) \times (e^{-i\omega\tau/2} - e^{i\omega\tau/2}) + s(k + \hat{i}\omega c - m\omega^2)e^{-i\omega\tau/2}}{(k + \hat{i}\omega c + k_3 + \hat{i}\omega c_3 - m\omega^2)^2 - (k_3 + \hat{i}\omega c_3)^2}, \quad (2)$$

where $H_{x_1p}(\omega)$ and $H_{x_2p}(\omega)$ are the transfer functions between the responses of the two ends of the intertympanic bridge, $x_1(t)$ and $x_2(t)$, relative to the pressure at the pivot point, $p(t)$. To simplify the notation we have assumed that the ears are identical so that $k_1 = k_2 = k$ and $c_1 = c_2 = c$.

To see how the mechanical structure enhances interaural differences, note that as the values of the coupling terms k_3 and c_3 become large, the expressions become strongly dependent on the difference between $H_{f_1p}(\omega)$ and $H_{f_2p}(\omega)$ which means that $x_1(t)$ and $x_2(t)$ become dependent on the difference between $f_1(t)$ and $f_2(t)$. This can be seen physically by first imagining that the coupling terms k_3 and c_3 take on infinite values. In this case the intertympanic bridge acts as a single rigid bar. Equal forces (or acoustic pressures) applied to each end will produce no motion. The bar will respond only to the difference in the forces. As the system moves in response to unequal forces on each end, the two sides will be constrained to move in opposite directions with equal amplitude, such that $x_1(t) = -x_2(t)$. This would result in an interaural phase difference of 180° at all frequencies and no interaural level difference. The contralateral side of the ear will then move with the same amplitude as the ipsilateral side but will be delayed by a time interval equal to one-half the period of the oscillation. At 5 kHz this corresponds to a time delay of 100 μ s. Recall that the ipsi- and contralateral acoustic stimuli are delayed by only about 2.5 μ s. A rigid intertympanic bridge would thus provide a mechanical pressure difference receiver which enhances the interaural time delay by a factor of 40 at 5 kHz. The rigidly coupled pivot system would, however, provide no interaural level difference.

Now suppose that the mechanical coupling due to k_3 and c_3 in our model system is finite instead of completely rigid. This allows the two eardrums to respond with different amplitudes and, with the appropriate choice of k_3 and c_3 , only slightly reduces the enhancement in interaural time delay. The system thus provides a very simple means of greatly expanding both interaural time delays and interaural level differences. The relatively large (but finite) stiffness of the connection at the pivot point is an important feature of the dynamical model.

Equations (2) were obtained by solving Eq. (1) by a direct approach. One can also gain further insight into how the system works by expressing the transfer functions using a modal approach. In this method, the motion is decomposed into two "natural" modes of vibration. There are only two modes of motion in this system because the model contains two response coordinates, $x_1(t)$ and $x_2(t)$, and hence has

two degrees of freedom. The modal solutions for the transfer functions given in Eqs. (2) may be obtained by well-known methods [see, for example, Rao (1990)] and are given by

$$H_{x_1p}(\omega) = \frac{(H_{f_1p}(\omega) - H_{f_2p}(\omega))/(2m)}{\omega_r^2 - \omega^2 + 2\omega_r\xi_r\hat{i}\omega} + \frac{(H_{f_1p}(\omega) + H_{f_2p}(\omega))/(2m)}{\omega_i^2 - \omega^2 + 2\omega_i\xi_i\hat{i}\omega}, \quad (3)$$

$$H_{x_2p}(\omega) = \frac{(H_{f_1p}(\omega) + H_{f_2p}(\omega))/(2m)}{\omega_r^2 - \omega^2 + 2\omega_r\xi_r\hat{i}\omega} - \frac{(H_{f_1p}(\omega) - H_{f_2p}(\omega))/(2m)}{\omega_i^2 - \omega^2 + 2\omega_i\xi_i\hat{i}\omega},$$

where

$$\omega_r = \sqrt{k/m}, \quad \omega_i = \sqrt{(k + 2k_3)/m}, \quad (4)$$

$$\xi_r = c/(\omega_r m), \quad \xi_i = (c + 2c_3)/(\omega_i m).$$

In Eqs. (3) and (4) ω_r and ω_i are natural frequencies and ξ_r and ξ_i are the damping ratios of the two resonant modes of the system. From Eqs. (4) it is evident that if the coupling spring k_3 is much stiffer than k , then $\omega_i \gg \omega_r$. The first mode, corresponding to ω_r , consists of both ends moving out of phase, or pure rocking. The second mode consists of both ends moving in the same direction with equal amplitude. The total response is a combination of these natural motions of the system. The rocking mode responds only to the difference in the forces applied to the ears while the translation mode responds only to the sum of the forces.

Note that each term on the right side of Eq. (3) will become larger as ω approaches the corresponding natural frequency, $\omega \approx \omega_r$ or $\omega \approx \omega_i$. Equations (2) and (3) may be shown to give equivalent results for the transfer functions $H_{x_1p}(\omega)$ and $H_{x_2p}(\omega)$.

To examine the behavior of the transfer functions in Eq. (3) we will substitute our previous result for the transfer functions between the applied forces and the pressure at the microphone location, $H_{f_1p}(\omega) = se^{i\omega\tau/2}$ and $H_{f_2p}(\omega) = se^{-i\omega\tau/2}$, where, again, τ is the time delay in the arrival times of the sound wave at the two points where the force is applied. Substituting these expressions into Eq. (3) and expressing the complex exponential functions in terms of sines and cosines give

$$H_{x_1p}(\omega) = \frac{s \hat{i} \sin(\omega\tau/2)/m}{\omega_r^2 - \omega^2 + 2\omega_r \xi_r \hat{i} \omega} + \frac{s \cos(\omega\tau/2)/m}{\omega_r^2 - \omega^2 + 2\omega_r \xi_t \hat{i} \omega}, \quad (5)$$

$$H_{x_2p}(\omega) = \frac{s \cos(\omega\tau/2)/m}{\omega_r^2 - \omega^2 + 2\omega_r \xi_r \hat{i} \omega} - \frac{s \hat{i} \sin(\omega\tau/2)/m}{\omega_r^2 - \omega^2 + 2\omega_r \xi_t \hat{i} \omega}.$$

In the following it will be shown that Eq. (5) can predict the type of motion shown in the measured data of Figs. 5–7. At very low frequencies, near $\omega \approx 0$, $\sin(\omega\tau/2) \approx 0$ and $\cos(\omega\tau/2) \approx 1$. Equations (5) then become

$$H_{x_1p}(\omega) \approx H_{x_2p}(\omega) \approx \frac{s/m}{\omega_r^2}. \quad (6)$$

We thus expect the ipsilateral and contralateral sides to move together at very low frequencies. This is essentially what is observed in the data of Fig. 5 at 2 kHz.

At somewhat higher frequencies, where $\omega \approx \omega_r$, the terms that are proportional to $\sin(\omega\tau/2)$ become more significant contributors to the total response. Depending on the values of the parameters in Eq. (4), we can expect there will be a frequency range where

$$H_{x_1p}(\omega) \approx -H_{x_2p}(\omega) \approx \frac{s \hat{i} \sin(\omega\tau/2)/m}{\omega_r^2 - \omega^2 + 2\omega_r \xi_r \hat{i} \omega}. \quad (7)$$

In this case, the two ears move in nearly opposite phase. This is close to what is seen in the data of Fig. 6 at 6 kHz.

At still higher frequencies, where $\omega_r < \omega < \omega_t$, all terms in Eq. (5) will be significant. However, those terms for the ipsilateral ear, $H_{x_1p}(\omega)$ add together while those for the contralateral ear, $H_{x_2p}(\omega)$, subtract. We can then expect the two ears to respond with significantly differing amplitudes in this frequency range. This effect is apparent in the data at 15 kHz in Fig. 7.

Equations (2)–(7) show that the steady-state response of the system to harmonic excitation at a given frequency or the response to a weakly stationary random load is characterized quite well (at least qualitatively) by the model of Fig. 8. It is also useful to look at the response in the time domain due to a steady-state harmonic excitation.

A harmonic plane acoustic wave will produce a pressure at the location of the pivot point which may be expressed as $p(t) = P \sin(\omega t)$, where P is the amplitude of the acoustic pressure and ω is the frequency in radians/s. The pressure applied at the ipsilateral membrane will be $p_1(t) = P \sin(\omega t + \omega\tau/2)$ and that at the contralateral membrane will be $p_2(t) = P \sin(\omega t - \omega\tau/2)$. The natural mode which consists of pure rocking motion will be driven only by the difference in these pressures, $p_1(t) - p_2(t) = P(\sin(\omega t + \pi/2) - \sin(\omega t - \pi/2)) = 2P \cos(\omega t) \sin(\omega\tau/2)$. The mode consisting of in-phase motion of the tympanal pits is driven by the sum of the two pressures, $p_1(t) + p_2(t) = 2P \sin(\omega t) \cos(\omega\tau/2)$. Because the time dependence of the force applied to the rocking or out-of-phase mode is proportional to $\cos(\omega t)$ and that applied to the in-phase mode is proportional to $\sin(\omega t)$, these modes are driven by effective forces which differ in phase by 90° . The responses in the steady state (after initial transients have died out) of the ip-

silateral and contralateral tympanal pits may be expressed as a linear combination of the responses to these forces:

$$x_1(t) = A_r \sin(\omega t + \phi_r) + A_t \cos(\omega t + \phi_r), \quad (8)$$

$$x_2(t) = A_r \sin(\omega t + \phi_r) - A_t \cos(\omega t + \phi_r),$$

where A_r is the amplitude of the response of the rocking mode and A_t is the amplitude of the response of the translating mode. These amplitudes may be expressed in terms of the excitation frequency ω and the system parameters as

$$A_r = \frac{Ps}{m} \left(\frac{\sin(\omega\tau/2)}{\sqrt{(\omega_r^2 - \omega^2)^2 + (2\omega_r \xi_r \omega)^2}} \right), \quad (9)$$

$$A_t = \frac{Ps}{m} \left(\frac{\cos(\omega\tau/2)}{\sqrt{(\omega_r^2 - \omega^2)^2 + (2\omega_r \xi_t \omega)^2}} \right).$$

The phase constants in Eq. (8) are

$$\phi_r = -\arctan\left(\frac{2\omega_r \xi_r \omega}{\omega_r^2 - \omega^2}\right), \quad (10)$$

$$\phi_t = -\arctan\left(\frac{2\omega_r \xi_t \omega}{\omega_r^2 - \omega^2}\right).$$

The expressions for $x_1(t)$ and $x_2(t)$ in Eq. (8) consist of the sum of two terms, each corresponding to one of the natural modes of the system. It is evident that these two terms add for $x_1(t)$, the ipsilateral ear, while they subtract for the contralateral ear $x_2(t)$. The resulting differences in amplitude and phase in the responses of the ears depend in a rather complicated way on the parameters of the system. It is evident from Eq. (8), however, that significant interaural differences in response are possible in this system even though the time delay in the effective forces on the two ears, τ , is quite small.

The expressions for the transfer functions given in Eqs. (2) or (3) may be evaluated to compare with the measured data. In order to evaluate Eq. (2) one must first determine the values of the spring and dash-pot constants and the mass m . The effective mass may be computed assuming that the sensory organ is significantly more massive than the other elements of the system. If we assume that the apodeme which joins the bulba acustica to the tympanal pit is a lightweight, rigid structure, the mass m may be thought to be concentrated at the tympanal pit. The actual distance between the bulba and the pivot point is slightly greater than that between the tympanal pit and the pivot point. This can affect the effective mass but it can easily be accounted for. m may then be estimated from the measured volume of the sensory organ, assuming its density to be that of water. This gives a mass of $m = 2.88 \times 10^{-10}$ kg.

The remaining parameters used in the model in Eq. (2) are $k_1 = k_2 = 0.576$ N/m, $k_3 = 5.18$ N/m, $c_1 = c_2 = 1.15 \times 10^{-5}$ N s/m, $c_3 = 2.88 \times 10^{-5}$ N s/m, and $s = 0.288 \times 10^{-6}$ m². The value of s has been taken from Robert *et al.* (1994). The natural frequencies and modal loss factors are found from Eq. (4) to be $\omega_r = 44,700$ rad/s (7120 Hz), $\omega_t = 195,000$ rad/s (31,000 Hz), $\xi_r = 0.89$, and $\xi_t = 1.23$. It is interesting to note that the identified system parameters lead to values of ξ which are near unity indicating that the system is nearly criti-

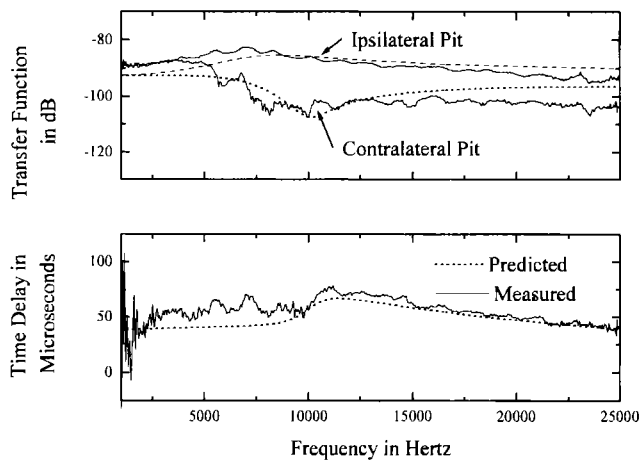


FIG. 9. Comparison of measured and predicted response of the tympanal pits of the fly's ears. The amplitude of the motion at each pit as well as the time delay between the responses are predicted very well. These data show that the interaural level differences and interaural time delays apparent in the measured mechanical response can be accounted for by interaural mechanical coupling. The time delay was computed from the phase of the transfer function.

cally damped. This is a very reasonable result for a hearing organ since critical damping will lead to accurate response to transient inputs.

The spring and dash-pot constants have been estimated by minimizing the error between the results from the approximate model of Eq. (2) and the measured data for the tympanal pits shown in Fig. 5. The transfer function data shown in Fig. 5 was measured using a sound field having an incident angle of 45° relative to the longitudinal axis of the fly. It will be shown in the following that although the model parameters were identified to give good agreement at 45° , very good predictions are obtained for a wide range of incident sound angles. In addition to providing good estimates of the transfer functions in the frequency domain, results will be shown that indicate equally accurate predictions of the transient, time domain response of the system.

Figure 9 shows a comparison of measured and predicted response of the tympanal pits for the ears of the fly. The amplitude of the motion at each pit as well as the time delay between the responses are predicted very well. The relatively pure tone at 5 kHz in the cricket song means that the relevant time delay in this system is the phase delay which is easily computed from the phase of the transfer function. The data of Fig. 9 show that the interaural level differences and interaural time delays apparent in the measured mechanical response can be accounted for by interaural mechanical coupling. The measured data show a time delay on the order of $50 \mu\text{s}$ for frequencies below 10 kHz. The small time delay ($2.5 \mu\text{s}$) in the incident sound wave has been expanded by a factor of 20, due to the strong interaural mechanical coupling caused by the intertympanal bridge. The predicted curve agrees fairly well with the measured data.

V. EFFECT OF SOUND ANGLE OF INCIDENCE

In the previous section we have shown that the analytical model depicted in Fig. 8 produces good agreement with

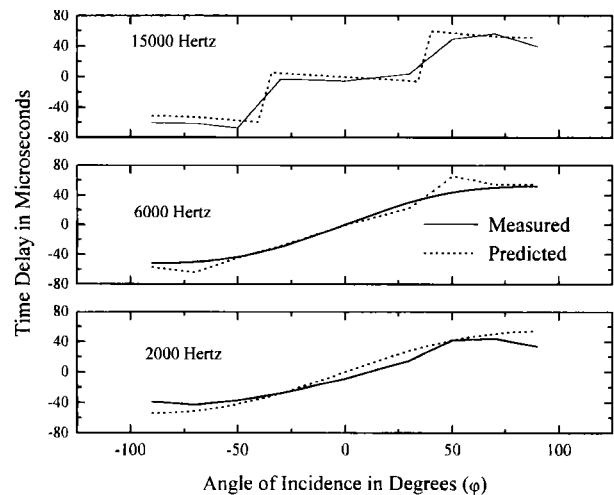


FIG. 10. The measured and predicted interaural time delays between the mechanical responses of the two tympanal pits. The predictions are based on the analytical model given above which depends on the angle of incidence relative to the forward direction, ϕ . The model does a very reasonable job of accounting for the incident direction of the sound field.

measurements of the transfer functions between the response of the eardrums and the incident pressure when the sound field is incident at a 45° angle relative to the longitudinal axis of the fly. In this section, we will examine the system's response due to sound arriving from other incident directions. In the next section we will examine the response of the ear due to transient inputs.

It is reasonable to expect that the interaural differences in mechanical response experienced by the fly's eardrums will depend on the angle of incidence of the sound. Figures 10 and 11 show the measured and predicted interaural time delays and interaural level differences between the mechanical responses of the two tympanal pits. The predictions are based on the analytical model given above which depends on the angle of incidence ϕ . Note that the parameters of the model were determined using data obtained with an angle of

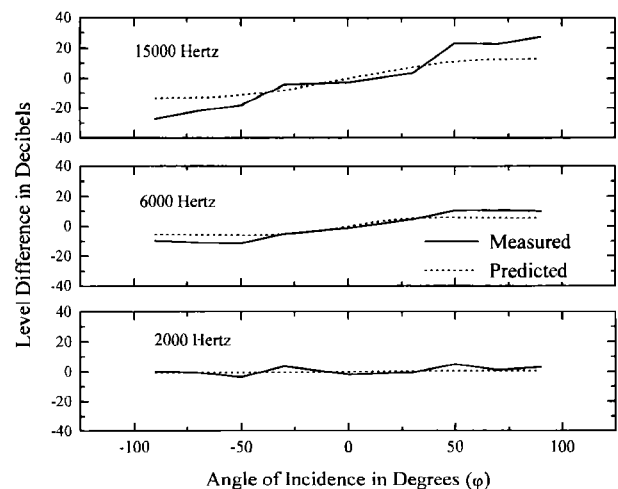


FIG. 11. The measured and predicted interaural level differences between the mechanical responses of the two tympanal pits. The predictions are based on the analytical model given above which depends on the angle of incidence ϕ . The measured and predicted results show very good agreement.

incidence of 45° . The excellent agreement between the predictions and measurements in Figs. 10 and 11 shows that the model does a very reasonable job of accounting for the incident direction of the sound field.

Figures 10 and 11 show the interaural differences at frequencies of 2, 6, and 15 kHz for incident angles varying from -90° to 90° . These data were computed from the measured and predicted transfer functions between the response of the tympanal pits and the pressure at the pivot point. Knowing the two transfer functions corresponding to each tympanal pit, one can determine the transfer function and corresponding level or time differences between the tympanal pits. The figures show excellent agreement between predictions and measurements at all frequencies and angles.

Figure 10 shows that as the angle of incidence varies from zero to either $\pm 90^\circ$, the magnitude of the time delay approaches a maximum of about $60 \mu\text{s}$. The level differences at 2 kHz shown in Fig. 11 indicate minimal influence of the incident angle. At the higher frequencies, however, greater level differences are observed and they depend more strongly on incident angle.

VI. TRANSIENT RESPONSE

In the previous sections we developed an analytical model for the transfer functions between the response of the tympanal pits and the incident pressure along with equations to predict the response in the time domain due to a harmonic input. Although the transfer functions and harmonic response can give considerable insight into how the system works, it is also important to examine the response to behaviorally relevant signals. Since the purpose of the directional hearing mechanism in *Ormia ochracea* is to localize sounds produced by crickets, we should consider the ears' response to cricketlike sounds. As mentioned previously, the sound produced by the cricket preyed on by the fly consists of a relatively pure tone at a frequency of roughly 5 kHz. In this section we show results of measurements and predictions of the responses of the ipsilateral and contralateral tympanal pits to a transient 5-kHz acoustic tone incident at a 45° angle. The measurements were performed using a similar experimental setup to that of the previous sections. The predicted results were computed by numerically solving the governing Eq. (1) using the central difference method. The measured incident pressure at the pivot point was used to simulate the pressure applied on each tympanal membrane [to compute $f_1(t)$ and $f_2(t)$ in Eq. (1)].

Figure 12 shows a comparison of the predicted and measured response of the tympanal pits as a function of time. Both a time delay and a level difference are apparent between the responses of the two tympanal pits. The magnitudes of these differences are consistent with those shown in the transfer function data at 5 kHz in the previous section. The predicted and measured results are quite similar.

Figure 12 shows that while the ipsilateral and contralateral incident pressures shown in the top panel are nearly identical due to the small time delay between them, the differences in mechanical responses of the ears are quite apparent. It is also important to note that the interaural differences

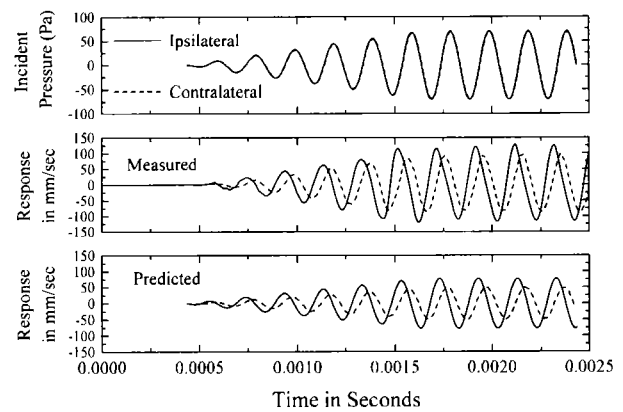


FIG. 12. Measured and predicted responses of the ipsilateral and contralateral tympanal pits of *Ormia ochracea* due to a simulated cricket song. Similar measured results have been obtained on numerous specimens for a range of incident pressure levels.

in mechanical response appear as soon as the eardrum begins to move.

VII. CONCLUSIONS

The auditory system of the parasitoid fly *Ormia ochracea* has been shown to exhibit a remarkable sensitivity to the direction of an incident sound stimulus. This is accomplished by an unusual anatomical structure in the ear which results in mechanical coupling between the two eardrums or tympana. The coupling causes the mechanical response to be sensitive to the difference in the sound field acting on the two eardrums.

A simple analytical model of the response of the ear is presented which provides good agreement with mechanical response measurements. The predicted results support the claim that interaural mechanical coupling is responsible for the directional sensitivity of this system. No pressure sensing ears have been previously described which employ a similar mechanism for sensing directional information.

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