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A MECHANICAL ANALYSIS OF THE NOVEL EAR OF THE
PARASITOID FLY *Ormia ochracea*

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Abstract

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. A mathematical model of the mechanical response of the ear to a sound stimulus is presented. It is shown that the directional sensitivity of the system is achieved by processing the sum and the difference of the acoustic pressures acting on the tympana. In order to illustrate the mechanics of the system, an electronic circuit is developed which processes the output signals from two closely spaced omnidirectional microphones (which represent the eardrums) to construct two output signals (which represent the inputs to the sensory cells). Experimental results are shown which demonstrate that this electronic analogue possesses similar directional sensitivity to that of the fly's ears.

1 Introduction

We have shown recently that the mechanical structure of the ear of the parasitoid fly *Ormia ochracea* (Order: Diptera; Family: Tachinidae)^{1,2} endows the fly with a remarkable ability to sense the direction of an incident sound wave³. Measurements of the mechanical response of the ears of this fly indicate that when sound arrives from one side, the ear that is closer to the sound source responds with significantly greater amplitude than the ear which is further from the source. This significant difference in tympanal response is surprising considering that the ears are so close together that the incident sound arrives at the two ears with a difference in arrival time of only 1 to 2 μsec . The close proximity of the ears causes any differences in the incident

pressure due to diffraction to be unmeasurable. The interaural difference in mechanical response is due to the coupling of the ears' motion by a cuticular structure which joins the two tympana, known as the intertympanal bridge.

A simple mechanical model of the ears of *Ormia ochracea* has been shown to accurately represent the response due to sound from any incident direction³. An examination of this model shows that the system can be represented in terms of two, uncoupled resonant modes of vibration. One mode consists of the two tympana vibrating out of phase, or rocking about the fulcrum of the intertympanal bridge. The other mode, which has a higher natural frequency than the rocking mode, consists of the two tympana moving in-phase. With the right set of system parameters, these modes combine to give a response over a fairly broad range of frequencies in which one tympanum moves with substantially greater response than the other when sound arrives from one side. Other insects such as some cicadas^{4,5} have coupled ears which respond in a similar way but *Ormia* appears to be the only animal to rely on a direct mechanical link between the ears to accomplish this. A goal of the present investigation is to mimic this system to construct a simple directionally sensitive receiver. This will help to illustrate the principles used in this animal for achieving directional hearing. It is found that the ears of *Ormia ochracea* employ a mechanical realization of a concept devised by Blumlein⁶ in 1931 to electronically process signals from two closely spaced microphones in order to record a stereophonic signal.

In the following, we will briefly describe the analytical model of the fly's coupled ears. The governing equations will then be manipulated to motivate the design of a simple analog electronic circuit which accomplishes nearly the same task as the mechanical structure in the ears of *Ormia ochracea*. The inputs to the circuit are signals from two closely spaced omnidirectional microphones. The two outputs are shown to have Cardioid directivities which are oriented in opposite directions. With the proper orientation of the pair of microphones relative to a sound source, one output from the circuit will give the sound traveling away from the source and the other output will give the sound traveling in the opposite direction, toward the source. The circuit provides a means of constructing a small stereo microphone with excellent channel separation.

2 Analytical Model of the Response of the Ears of *Ormia ochracea*

Figure 1 shows the ears along with a mechanical system which is used to illustrate the mechanism employed to achieve directional sensitivity. The anatomy of the ears is discussed in detail by Robert, Read, Hoy² and Miles, Robert, and

Hoy³. The tympanal membranes consist of the pair of corrugated regions. The model system consists of two rigid bars joined by a spring k_3 and dash-pot c_3 . The remaining springs and dash-pots connect to the extreme ends of the bars. The responses $x_1(t)$ and $x_2(t)$ of the two ends of the bars represent the responses of the inputs to the acoustic sensory organs³. $x_1(t)$ and $x_2(t)$ may be determined by solving

$$\begin{bmatrix} k_1 + k_2 & k_3 \\ k_3 & k_2 + k_3 \end{bmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} + \begin{bmatrix} c_1 + c_2 & c_3 \\ c_3 & c_2 + c_3 \end{bmatrix} \begin{pmatrix} \dot{x}_1(t) \\ \dot{x}_2(t) \end{pmatrix} + \begin{bmatrix} m & 0 \\ 0 & m \end{bmatrix} \begin{pmatrix} \ddot{x}_1(t) \\ \ddot{x}_2(t) \end{pmatrix} = \begin{pmatrix} f_1(t) \\ f_2(t) \end{pmatrix} \quad (1)$$

where m is the effective mass at each end and $f_1(t)$ and $f_2(t)$ represent the forces applied at the two tympanal membranes. These two forces will have essentially identical amplitudes and very small phase differences due to the small amount of time it takes for sound to travel across the ears.

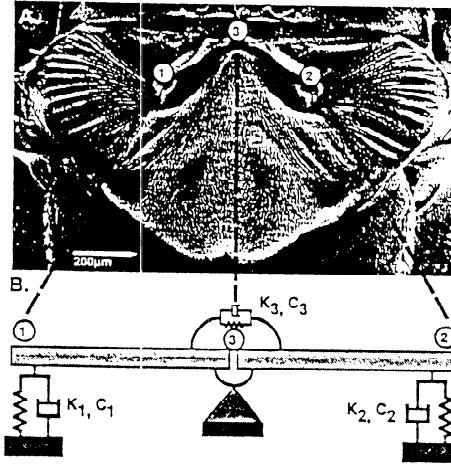


Figure 1. Ear of *Ormia ochracea* and mechanical model.

If the system is symmetric about the fulcrum then we can let $k_1 = k_2 = k$. The eigenvalues of the unforced, undamped system are found to be $\omega_1^2 = k/m$ and $\omega_2^2 = (k + 2k_3)/m$. The natural motion, or mode shape corresponding to the first eigenvalue, ω_1^2 is found to be $X_1 = -X_2$, so that the two coordinates move in opposite directions with equal magnitudes. The second mode shape, corresponding to ω_2^2 is $X_1 = X_2$ so that both tympana translate in the same manner. The directional sensitivity of the ears results from the combined

responses of these two resonant modes. The parameters of the system are such that when sound arrives from one side, the responses of these two modes add on the ear closest to the source and they cancel on the ear furthest from the source. This will be shown in the following by manipulating equation (1).

If we consider the special case of excitation resulting from a plane, harmonic sound wave, the pressure at the pivot point may be written as $Pc^{i\omega t}$, where $\hat{i} = \sqrt{-1}$. If $x_1(t)$ is the response of the ear closest to the sound source then

$$\begin{aligned} f_1(t) &= F_1 e^{i\omega t} = P s e^{i\omega(t + \frac{\tau}{2})} \\ f_2(t) &= F_2 e^{i\omega t} = P s e^{i\omega(t - \frac{\tau}{2})} \end{aligned} \quad (2)$$

where s is the surface area of each tympanal membrane and τ is the transit time for the wave to travel between the two points of application of the force on the tympanal membranes. 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 of the force and c is the sound speed which is roughly 344 m/s. F_1 and F_2 are the complex amplitudes of the effective forces, $F_1 = P s e^{i\omega \frac{\tau}{2}}$ and $F_2 = P s e^{-i\omega \frac{\tau}{2}}$.

By manipulating equation (1), the response of each end of the tympanal bridge may be expressed as

$$\begin{aligned} x_1(t) &= \frac{e^{i\omega t}}{2m} \left(\frac{F_1 + F_2}{\omega_2^2 - \omega^2 + 2\omega_2 \xi_2 i\omega} - \frac{F_2 - F_1}{\omega_1^2 - \omega^2 + 2\omega_1 \xi_1 i\omega} \right) \\ x_2(t) &= \frac{e^{i\omega t}}{2m} \left(\frac{F_1 + F_2}{\omega_2^2 - \omega^2 + 2\omega_2 \xi_2 i\omega} + \frac{F_2 - F_1}{\omega_1^2 - \omega^2 + 2\omega_1 \xi_1 i\omega} \right), \end{aligned} \quad (3)$$

where ξ_1 and ξ_2 are the damping ratios of the two modes. Examination of the numerator of each term in equation (3) shows that the responses $x_1(t)$ and $x_2(t)$ depend on combinations of the sum and difference of the forces on each side of the ear. The first mode (rocking mode) depends on the difference in the two forces while the second mode (translating mode) depends on the sum of the forces. The denominators in equation (3) determine the relative contribution of each mode and depend on the driving frequency ω . These terms represent the frequency response functions of the two modes. The mechanical system essentially combines the sums and differences of the pressures on the two ears in order to achieve a cancellation of the response on one side and an addition on the other. In the following, we will show that with the right set of parameters, a system having a response described by equation (3) will have a

bi-cardioid directional response. An extensive comparison of measured results and predictions based on equation (3) has been presented by Miles, Robert and Hoy³. It has been shown that the model gives excellent agreement with measurements.

In order to examine the sensitivity of the response to sound arriving from different directions we will replace F_1 and F_2 in equation (3) by the expressions in the discussion preceding equation (3). We will also assume that the system is operated in the frequency range near the rocking mode $\omega \approx \omega_1 \ll \omega_2$. Since $\omega \ll \omega_2$ the denominators of the first terms in equation (3) become approximately ω_2^2 . Equation (3) may then be approximated by

$$\begin{aligned} x_1(t) &\approx \frac{sPe^{i\omega t}}{2m} \left(\frac{2 \cos(\omega\tau/2)}{\omega_2^2} + \frac{i \sin(\omega\tau/2)}{\omega_1 \xi_1 i \omega} \right) \approx \frac{sPe^{i\omega t}}{m} \left(\frac{1}{\omega_2^2} + \frac{\tau}{4\omega_1 \xi_1} \right) \\ x_2(t) &\approx \frac{sPe^{i\omega t}}{2m} \left(\frac{2 \cos(\omega\tau/2)}{\omega_2^2} - \frac{i \sin(\omega\tau/2)}{\omega_1 \xi_1 i \omega} \right) \approx \frac{sPe^{i\omega t}}{m} \left(\frac{1}{\omega_2^2} - \frac{\tau}{4\omega_1 \xi_1} \right) \end{aligned} \quad (4)$$

where we have assumed that $\omega\tau/2 \ll 1$. From equation (4) we can see that if $\omega_2^2 \approx \frac{4\omega_1 \xi_1}{d/c}$ then the responses of the two tympana as a function of the angle of incidence of the sound are

$$\begin{aligned} x_1(t) &\approx sP \frac{e^{i\omega t}}{m\omega_2^2} (1 + \sin(\phi)) \\ x_2(t) &\approx sP \frac{e^{i\omega t}}{m\omega_2^2} (1 - \sin(\phi)) \end{aligned} \quad (5)$$

where we have again used the fact that $\tau = d \sin(\phi)/c$. Equations (5) show that the responses of the tympana $x_1(t)$ and $x_2(t)$ will have Cardioid directivity patterns which are oriented in opposite directions.

3 Biomimicry of the Ormiine Ear

Our analysis presented above shows that the mechanical system depicted in figure 1B performs signal processing of the sum and difference of the pressures acting on the two tympana. In order to illustrate how the system works, it is instructive to examine an "equivalent" electronic circuit which is shown in figure 2 below. The basic idea behind this "Equivalent Circuit Ormiaphone" is identical to that proposed by Blumlein^{6,7} for recording stereo acoustic images using a pair of closely spaced microphones. In effect, the circuit converts very small phase differences at the two sensors, $f_1(t)$ and $f_2(t)$ into amplitude

differences at the outputs, $y_1(t)$ and $y_2(t)$. This is a primary goal of most small directionally sensitive receivers.

The circuit first computes the sum and difference of the inputs, as in the numerators in equation (3). The difference signal is low-pass filtered and amplified so that the final outputs become analogous to the right side of equations (4) and (5). Note that the low-pass filter has the same effect as the frequency response of the rocking mode in equation (4) which is $\approx 1/(\omega_1 \xi_1 i\omega)$.

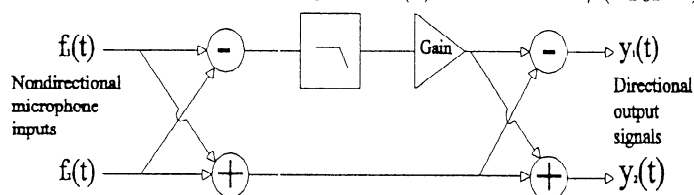


Figure 2. Block Diagram of Equivalent Circuit

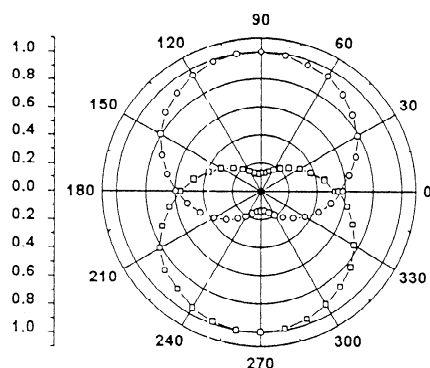


Figure 3. Equivalent Circuit Ormiaphone Directivity at 5kHz

The circuit shown in figure 2 has been built using operational amplifiers. Figure 3 shows measured directivities at 5kHz using this circuit. The omnidirectional microphones used to provide the input signals were Brüel & Kjær model 4138 1/8 inch microphones placed .275 inch apart. The directivities are found to be Cardioid patterns which are oriented in opposite directions as predicted in equations (5).

4 Conclusions

A simple analytical model of the response of the ears of the parasitoid fly *Ormia ochracea* has been used to design an analog circuit which mimics the

mechanism used by the fly to achieve directional sensitivity in a very small sensor. Measured results obtained using the circuit along with a pair of non-directional microphones are presented which show that the system achieves the desired bi-Cardioid directivity pattern.

5 Acknowledgments

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1. Robert, D., Amoroso, J., and Hoy, R. R. 1992 *Science* **258**, 1135-1137. The evolutionary convergence of hearing in a parasitoid fly and its cricket host.
2. Robert, D., Read, M. P., and Hoy, R. R. 1994 *Cell & Tissue Research* **275**, 63-78. The tympanal hearing organ of the parasitoid fly *Ormia ochracea* (Diptera, Tachinidae, Ormiini)
3. Miles, R. N., Robert, R., and Hoy, R. R. 1995 *Journal of the Acoustical Society of America* **98** (6), 3059-3070. Mechanically coupled ears for directional hearing in the parasitoid fly *Ormia ochracea*.
4. Fletcher, N. H. and Hill, K. G. 1978 *Journal of Experimental Biology* **72**, 43-55. Acoustics of sound production and of hearing in the bladder cicada *Cystosoma saundersii* (Westwood).
5. Fletcher, N. H. 1992 *Acoustic Systems in Biology*. New York: Oxford University Press.
6. Blumlein, A. D., 1931 British patent 394,325. *Directional Effect in Sound Systems*.
7. Gerzon, M. A. 1994 *Journal of the Audio Engineering Society* **42**, 435-453. Applications of Blumlein shuffling to stereo microphone techniques.