Performance analysis of the *Ormia ochracea*’s coupled ears

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The *Ormia ochracea* is able to locate a cricket’s mating call despite the small distance between its ears compared with the wavelength. This phenomenon has been explained by the mechanical coupling between the ears. In this paper, it is first shown that the coupling enhances the differences in times of arrival and frequency responses of the ears to the incoming source signals. Then, the accuracy of estimating directions of arrival (DOAs) by the *O. ochracea* is analyzed by computing the Cramér–Rao bound (CRB). The differential equations of the mechanical model are rewritten in state space and its frequency response is calculated. Using the spectral properties of the system, the CRB for multiple stochastic sources with unknown directions and spectra is asymptotically computed. Numerical examples compare the CRB for the coupled and the uncoupled cases, illustrating the effect of the coupling on reducing the errors in estimating the DOAs.

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\textit{I. INTRODUCTION}

Most available array processing methods employ the time differences of arrival between the elements of a sensor array to estimate the directions of arrival (DOAs) of the incoming waves. Since the performance of such arrays is directly proportional to the size of the array’s aperture, large aperture arrays are often required. However, this is costly and may be impractical in many tactical and mobile applications. This paper demonstrates a high-performance array with very small aperture, namely, of the parasitic fruit fly called the *Ormia ochracea*.

The *O. ochracea* is known to have a mechanical coupling between its ears to enhance its hearing. There are also other small animals having interactions between their ears for the same purpose\textsuperscript{1–5} but the mechanical coupling is unique for the *O. ochracea*. This coupling is necessary for the *O. ochracea*’s perpetuation. The female *O. ochracea* must locate and deposit her parasitic maggots on or near a male field cricket, relying on the cricket’s mating call, which is relatively pure in frequency (peak frequency 4.8 kHz). However, there is a tremendous incompatibility between the distance between the two ears (≈1.2 mm) and the wavelength (≈7 cm) of the cricket’s mating call. This disaccord leads to extremely small interaural intensity and time of arrival differences between the ear closest to (ipsilateral) and the ear farthest from (contralateral) the sound source. It is believed that the coupling mechanism magnifies these binaural differences and subsequently improves the sound source localization accuracy\textsuperscript{3,6–10}

A mechanical system that models the mechanical coupling between the ears of the *O. ochracea* is introduced in Ref. 6. Miles et al.\textsuperscript{6} showed experimentally that this model is well matched to the fly’s ear in terms of frequency and transient responses.

In this paper, it is analytically shown that the mechanical coupling between the *O. ochracea*’s ears is significant for localization accuracy. First, the system in Ref. 6 is represented in state space. Then the model is solved and its time and spectral properties are illustrated. The impulse response of the system is found, and after sampling it, by taking its discrete-time Fourier transform (DTFT), the frequency response is computed. The frequency and impulse responses for coupled and uncoupled versions of the system are compared to demonstrate the effect of coupling on the intensity and time differences between the two ears. A statistical model with multiple stochastic sources and measurement noise is then developed to analyze the effect of the coupling on localization performance. The asymptotic Cramér–Rao bound (CRB) on estimating the source DOA is computed in two-dimensional space, i.e., for simplicity the estimation of only the azimuth angle is considered. It is assumed that the DOA and the power spectra of the input signals are unknown. Finally, numerical examples that compare the CRB’s of the coupled and the uncoupled systems are presented, showing the improvement in the localization accuracy due to coupling.

\textit{II. MODELING}

In this section, a brief review of the anatomy of the female *O. ochracea*’s ears is provided. The mechanical model used in Ref. 6 is described, associating its parameters with the parts of the ear. Then, to demonstrate the effect of the coupling, the impulse and frequency responses of the coupled and the uncoupled systems for a far-field source are computed and compared with each other.

Figure 1(a) shows the female *O. ochracea* and its ear structure. We observe the following.

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the above model were empirically found for a $45^\circ$ incident angle, but they were shown to hold also for a wide range of angles.\(^6\)

The differential equations for the mechanical model in Fig. 1(b) can easily be written in matrix form following Ref. 6:

$$
\begin{bmatrix}
  k_1 + k_3 & k_3 \\
  k_3 & k_2 + k_3
\end{bmatrix}
\begin{bmatrix}
  z_1(t) \\
  z_2(t)
\end{bmatrix}
+ 
\begin{bmatrix}
  c_1 + c_3 & c_3 \\
  c_3 & c_2 + c_3
\end{bmatrix}
\begin{bmatrix}
  \dot{z}_1(t) \\
  \dot{z}_2(t)
\end{bmatrix}
+ 
\begin{bmatrix}
  m & 0 \\
  0 & m
\end{bmatrix}
\begin{bmatrix}
  \ddot{z}_1(t) \\
  \ddot{z}_2(t)
\end{bmatrix}
= f(t, \Delta),
$$

where

- $f_i(t, \Delta) = p_i(t, \Delta), i = 1, 2, $ where $p_1(t, \Delta)$ and $p_2(t, \Delta)$ both correspond to the same input sound source and are the pressure waves at the ipsilateral and contralateral ears, respectively, and $s$ is the surface area of each tympanal membrane (see Fig. 1);
- $z_1(t)$ and $z_2(t)$ are displacements at the first and second ends of the intertympanic bridge, respectively [see Fig. 1(b)];
- $m$ is the effective mass of all moving elements and it is assumed to be concentrated at each end of the intertympanic bridge; and
- $\Delta$ corresponds to the time difference of arrival between the two ears: $\Delta = d \sin \phi / v$, where $\phi \in [-90^\circ, 90^\circ]$ is the DOA, $d$ is the distance between force locations, and $v$ is the speed of sound, which is roughly 344 m/s.

In order to find the solutions for $z_1(t)$ and $z_2(t)$, Eq. (1) is rewritten as a state space model

$$
\dot{x}(t) = Ax(t) + Bf(t, \Delta),
$$

$$
y(t) = Cx(t),
$$

where $x(t) = [x_1(t), x_2(t), x_3(t), x_4(t)]^T = [z_1(t), z_2(t), \dot{z}_1(t), \dot{z}_2(t)]^T$ is the state variable vector, $A$ and $B$ are constant matrices, which are functions of the model parameters in Eq. (1), and $C$ is a constant matrix depending on the observations; see, for example, Ref. 11. $C$ is chosen such that $y(t) = [y_1(t), y_2(t)]^T = [z_1(t), z_2(t)]^T$. Using the variation of constants formula,\(^{12}\) the solution for the state space model can be computed by

$$
x(t) = \Phi(t, t_0)x(t_0) + \int_{t_0}^t \Phi(t, \tau)Bf(\tau, \Delta)d\tau,
$$

$$
y(t) = Cx(t),
$$

where $x(t_0) = \Phi(t, t_0)x(t_0)$ is the initial condition and $\Phi(t, \tau)$ is the transition matrix depending on the matrix $A$.

Figures 2–4 show the impulse, amplitude, and phase responses, respectively, for both the coupled and uncoupled systems. Figure 2 illustrates the impulse responses, $h(t, \Delta) = [h_1(t, \Delta), h_2(t, \Delta)]^T$, calculated for $\phi = 45^\circ$ using Dirac delta function in Eq. (3) as an input. The responses $h_1(t, \Delta)$ and $h_2(t, \Delta)$ correspond to the ipsilateral and contralateral ears, respectively. It is apparent that the interaural differences be-

![Fig. 1](https://example.com/fig1.png)

**FIG. 1.** (a) Anatomy of the female *Ormia ochracea*’s ear. Top: side view of the y. Bottom: front view of the ear after the head was removed. (b) Top: front view of the ear after the head was removed. Bottom: mechanical model (Ref. 6).

- The ear is located on the front face of the thorax, which is behind the head.
- Prosternal tympanic membranes serve for hearing.
- Bulbae acustica (sensory organs) are connected to the tympanic pit.
- The tympanic pits and the pivot point are connected to each other by a cuticular structure referred as intertympanic bridge. This improves the usage of interaural differences.

A simple mechanical model, composed of springs and dash-pots, is proposed in Ref. 6 to explain the mechanical coupling between the ears [Fig. 1(b)] with $k_i$’s and $c_i$’s ($i = 1, 2, 3$) as the spring and dash-pot constants, respectively. In this model, the intertympanic bridge is assumed to consist of two rigid bars connected at the pivot point through a coupling spring $k_3$ and dash-pot $c_3$. The springs and dash-pots at the extreme ends of the bridge approximately represent the dynamic properties of the tympanic membranes, bulbae acustica, and surrounding structures. The numerical values of
between the two ear outputs are enhanced for the coupled system [Figs. 2(a) and 2(b)]. These differences can be explained more clearly in the frequency domain. Therefore, the amplitude and phase responses are calculated by taking the DTFT (Ref. 13) of the sampled impulse responses. Figure 3 shows that the gap between the ipsilateral \( H_1(e^{j\omega}, \Delta) \) and contralateral \( H_2(e^{j\omega}, \Delta) \) amplitude responses is bigger for the coupled system [Figs. 3(a) and 3(b)]. This confirms the improvement of the intensity differences between the ear outputs. Similarly, Fig. 4 demonstrates how the phase difference between the responses of the two ears is amplified, so is the difference in the arrival time of the sound source to the two ears for coupled system [Figs. 4(a) and 4(b)]. This analysis may explain how the extremely small interaural differences in intensity and arrival time are increased by the coupling to a level that the \textit{O. ochracea} could use the improved binaural cues to process the information more effectively.

III. PERFORMANCE ANALYSIS

In this section, a statistical model is presented and the CRB on DOA estimation of model (3) is computed.

A. Statistical model

The model consists of \( M \) multiple stochastic inputs \( p_m(t) \) \( (m=1,2,\ldots,M) \) and additive measurement noise \( e(t) = [e_1(t), e_2(t)]^T \) with \( e_1(t) \) and \( e_2(t) \) corresponding to the measurement noise at the ipsilateral and contralateral ears, respectively (Fig. 5). That is, \( M \) different angles for \( M \) different input signals are chosen to model the environment. This model gives rise to

\[
y(t, \Delta) = \sum_{m=1}^{M} p_m(t) \times h(t, \Delta_m) + e(t), \quad t = 1,2,\ldots,N,
\]

where \( \Delta = [\Delta_1, \Delta_2, \ldots, \Delta_M]^T \) and \( \Delta_m \) is the time difference between two ears corresponding to the incidence angle \( \phi_m \) of the input signal \( p_m(t) \). The impulse response \( h(t, \Delta_m) \) depends on the angle \( \phi_m \), due to the fact that for any signal \( p_m(t) \) the equality \( p_m(t-\Delta_m) * h(t) = p_m(t) * h(t-\Delta_m) \) always holds. Thus, it can be concluded that the system has different impulse responses and respective frequency responses for different incidence angles.
mean wide-sense stationary system in Eq. (5) well as with the CRB on the variance of the error of estimating the input further assumptions are made: 

\[ \Theta = [\Delta_1, \Delta_2, \ldots, \Delta_M, S_{\phi_1}, \ldots, S_{\phi_M}, \sigma_e^2]^T \]

\[ = [\Theta_1, \ldots, \Theta_{2M+1}] \]

(iii) \[ H(e^{i\omega}, \Delta_m) = [H_1(e^{i\omega}, \Delta_m), H_2(e^{i\omega}, \Delta_m)]^T (m = 1, 2, \ldots, M) \] is the frequency response vector of the system related to the input signal \( p_m(t) \) with incidence angle \( \phi_m \) and "\( (\cdot)^H \)" denotes the Hermitian transpose.

**B. Cramér–Rao bound**

Let \( y(t, \Delta) \) be defined as in Eq. (4) and satisfy the assumptions defined in Sec. III A. Then, the elements of the Fisher information matrix corresponding to unknown parameter vector \( \Theta = [\Delta_1, \Delta_2, \ldots, \Delta_M, S_{\phi_1}, \ldots, S_{\phi_M}, \sigma_e^2]^T \) can be found (for large \( N \)) as follows:\[14,15\]

\[
[J(\Theta)]_{kl} = \frac{N}{4\pi} \int_{-\pi}^{+\pi} \text{tr} \left( \frac{\partial S_y(\omega, \Theta)}{\partial \theta_k} S_y^{-1}(\omega, \Theta) \frac{\partial S_y(\omega, \Theta)}{\partial \theta_l} \right) d\omega,
\]

\[
[J(\Theta)]_{kl} \approx \frac{1}{2} \sum_{r=1}^{N} \text{tr} \left( \frac{\partial S_y(n, \Theta)}{\partial \theta_k} S_y^{-1}(n, \Theta) \frac{\partial S_y(n, \Theta)}{\partial \theta_l} S_y^{-1}(n, \Theta) \right),
\]

(6)

where \( S_y(n, \Theta) \) is the discrete Fourier transform (DFT) of the system output with frequency index \( n \), which is obtained by sampling \( S_y(\omega, \Theta) \) in the frequency domain.\[13\]

Recall that \( \Delta_m = d \sin(\phi_m) / v \). Hence, to find the CRB of estimating the DOA, \( \phi_m \), the transformation formula\[15\] is utilized as follows:

\[
\text{Var}(\hat{\phi}_m) \equiv \left( \frac{\partial g(\Theta)}{\partial \Theta} \right)^{-1} \left( \frac{\partial g(\Theta)}{\partial \Theta} \right)^T J^{-1}(\Theta) \left( \frac{\partial g(\Theta)}{\partial \Theta} \right)^{-1} J^{-1}(\Theta) \left( \frac{\partial g(\Theta)}{\partial \Theta} \right)^T,
\]

(7)

where

(i) \( g(\Theta) = [g_1(\Theta), \ldots, g_M(\Theta)]^T \), with the \( m \)th element defined as \( g_m(\Theta) = \arcsin(v \Delta_m / d) \) and

(ii) \( J(\Theta) \) is the Fisher information matrix with \([J(\Theta)]_{kl}\) as defined in Eq. (6) \((1 \leq k, l \leq 2M+1)\).

**IV. NUMERICAL RESULTS**

The CRBs of estimating the DOAs for the coupled and uncoupled systems are compared to show the effect of the coupling. The following scenario for different signal to noise ratios (SNRs) is used.

It is assumed that in Eq. (4), \( p_i(t) \) with incidence angle \( \phi_1 \) is the incoming signal that is to be localized and similarly \( p_m(t) \) and \( \phi_m(t) \) \((m = 2, 3, \ldots, M)\) are the signal from the environment and corresponding incidence angle, respectively. For simulation purposes only, \( \phi_m \) is randomly chosen (\( \phi_m \) is uniform in \([-90^\circ, 90^\circ]\)). Accordingly, SNR is defined as
The effect of coupling on the hearing system of the *O. ochracea* was analyzed. By examining the impulse and frequency responses of the model, it was shown that the coupling increased the time and amplitude differences between the two ears. Using our statistical model, the CRB of estimating the DOA for unknown input signal spectra was asymptotically computed. Comparing the CRB of the coupled with the uncoupled system, the enhancement provided by the mechanical coupling was illustrated. The experimental results regarding the azimuthal localization capacity of the *O. ochracea* were analytically proven. Future work will analyze the system and calculate the CRB in continuous time.

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**FIG. 6.** (Color online) Square root of the CRB on the DOA estimation vs SNR.