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How Internally Coupled Ears Generate Temporal and Amplitude Cues for Sound Localization

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In internally coupled ears, displacement of one eardrum creates pressure waves that propagate through air-filled passages in the skull and cause displacement of the opposing eardrum, and conversely. By modeling the membrane, passages, and propagating pressure waves, we show that internally coupled ears generate unique amplitude and temporal cues for sound localization. The magnitudes of both these cues are directionally dependent. The tympanic fundamental frequency segregates a low-frequency regime with constant time-difference magnification from a high-frequency domain with considerable amplitude magnification.

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Internally coupled ears (ICE), in which the two tympanic membranes (eardrums) are functionally coupled by an air-filled passage through the skull, occur in most frogs, lizards, alligators, and birds, conservatively, more than 15,000 species. In this auditory system the eardrums are driven by a combination of external sound pressure and internal cavity pressure resulting from the vibration of the opposite eardrum [1–3]. If the interaural distance \( L \) between the eardrums is small, the time difference between excitation of the opposing membranes due to an external pressure is too small for effective neuronal processing, precluding sound localization using temporal cues. Furthermore, for most vertebrates, the interaural level (or intensity) difference is negligible, whatever the source direction. With ICE, however, an animal can amplify the time differences as well as generate considerable (e.g., \( \leq 20 \text{ dB} \)) direction-dependent amplitude differences between the eardrum vibrations. Thus ICE enables even animals with a small interaural distance to localize sound sources.

An earlier analytical paper [2] was formulated to explain data gathered from a few species of Gekkonid lizards [1]. In contrast, we present here a general model of ICE, which has been formulated with four goals. First, to be applicable to the full range of anatomical variation, relative to both head and tympanum size, observed in animals with ICE. Second, one of the main anatomical variations among the species with ICE is the diameter of the coupling passageway; the model incorporates this (Fig. 1). Third, while not neglecting the pressure-wave’s dependence upon the specific geometry, our emphasis is on the sensory cues arising from the dynamical patterns of tympanic displacements. In so doing we account for a uniform plateau, whatever the direction \( \theta \), in the fraction of internal and interaural time differences, the so-called time expansion factor, for lower frequencies (typically, \( < 0.7 \text{ kHz} \)) as well as the amplitude amplification at much higher frequencies (say, around 1.3 kHz). Fourth, the proffered model relates both the temporal and intensity domains through the fundamental frequency \( f_0 \) of the tympanic membrane, which acts as the transformer between the external auditory stimuli and the internal sound processing.

Previous studies [4,5] found that lizards have two discrete populations of cochlear hair cells, one that responds to amplitude cues and the other to temporal cues. These two hair-cell populations both project (ultimately) bilaterally, giving the organism a neuronal template to contrast the amplitude and temporal patterns arising from the tympana. We are following Jørgensen et al. [6] in postulating an algorithm for determining amplitude (level) differences, more specifically, a neuronal subtraction of logarithmic vibration amplitudes of the two membranes. The biological physics is that of hair-cell response being governed by the (Weber-Fechner) logarithm of the amplitude whereas the “subtraction” is that of excitation minus inhibition \((E/I)\) and is a nonlinear criterion. We refer to this subtraction as the internal level difference (ILD) and contrast it with the interaural level difference (ILD), i.e., the logarithmic amplitude difference between the external sound inputs to both ears. It is also known that certain neurons are sensitive to time differences between eardrum vibrations [7–9]. We refer to this metric as the internal time difference (ITD), in contrast to the interaural time difference (ITD). Herein we demonstrate how ITDs and ILDs emerge solely due to the internal acoustic coupling between the eardrums.

The model presented herein is universal in the sense that, with an appropriate change in parameters, it is applicable.
to all species with ICE. We model the internal cavity as an air-filled cylinder of length $L$ based on typical head sizes observed in Nature. We fix the cavity volume $V_{\text{cav}}$ and calculate the cylinder radius using $a_{\text{cav}} = \sqrt{V_{\text{cav}}/\pi L}$. The three-dimensional model for the cavity is illustrated in Fig. 1. The smaller circles at either end of the cylinder correspond to the eardrums.

The inputs are modeled as plane waves of a certain wavelength of a pure tone incident on both ears. Since typical wavelengths are much larger than the membrane diameter, we can safely assume the incident pressure to be of uniform amplitude $p_{\text{ex}}$,

$$ p_0 = p_{\text{ex}} e^{i\omega t} e^{ik\Delta/2}, \quad p_L = p_{\text{ex}} e^{i\omega t} e^{-ik\Delta/2}. $$

$\Delta = L \sin \theta$ is the differential distance between the sound source and the two ears with $\theta$ as the source direction with respect to the head’s median axis; unless stated otherwise, $\theta = \pm 90^\circ$. Furthermore, for the (external) interaural time difference, ITD $= \Delta/c$ with $c$ as velocity of sound in air, while $\omega = 2\pi f$ is the angular frequency of an incident sound wave. Finally, the wave number is given by $k = \omega/c$.

At our frequencies of interest ($< 4$ kHz), viscous acoustic damping can be neglected so we follow common acoustic models [10–12] and describe the air inside the cavity using linear acoustics with cylindrical coordinates. In this approach, the air moves due to a local pressure $p(x, r, \phi; t)$ obeying the three-dimensional wave equation

$$ \frac{1}{c^2} \frac{\partial^2 p(x, r, \phi; t)}{\partial t^2} = \Delta_{(2)} p(x, r, \phi; t) + \frac{\partial^2 p(x, r, \phi; t)}{\partial x^2}. $$

$$ \Delta_{(2)} = -\frac{1}{r} \frac{\partial}{\partial r} + \frac{1}{r^2} \frac{\partial^2}{\partial \phi^2}. $$

$\Delta_{(2)}$ is the two-dimensional Laplacian in polar coordinates.

On the eardrum, the air velocity is related to $p$ by [11]

$$ -\rho \frac{\partial v}{\partial t} = \nabla p. $$

We require both that $p$ be continuous and smooth in $\phi$, and that the normal velocity vanishes at the borders [10]:

$$ v_r|_{r=a_{\text{cav}}} = 0. $$

Separating variables, we obtain a specific solution for frequency $f = \omega/2\pi$ and with spatial part

$$ p_{qs}(x, r, \phi) = (A_{qs} e^{i\omega x} + B_{qs} e^{-i\omega x}) f_{qs}(r, \phi), $$

$$ f_{qs}(r, \phi) = J_q(\nu_{qs} r/a_{\text{cav}})(C_{qs} \cos q\phi + D_{qs} \sin q\phi). $$

$J_q$ is the order-$q$ ($q = 0, 1, 2, \ldots$) Bessel function of the first kind and $\nu_{qs}$ the $s$th positive zero of $J_q$, $\nu_{qs}$. The wave number in the $x$ direction is given by $\zeta_{qs} = (k^2 - \nu_{qs}^2/a_{\text{cav}}^2)^{1/2}$. The $f_{qs}$ are an orthogonal set of functions when integrated over a disk of radius $a_{\text{cav}}$. The general solution is given by a linear combination of $p_{qs}(x, r, \phi)|_{\theta = \pm \beta}$.

In order to determine $A_{qs}$ and $B_{qs}$ we need an expression for the membrane vibrations. In vertebrates, the membrane’s inner surface is bound to a cartilage or bony element of the middle ear (commonly, the extracolumella); this attachment is typically asymmetrical and places a significant mechanical load on the membrane [13].

We therefore consider the eardrum as a sectorial membrane rigidly clamped between angles $\phi = \pm \beta$, meaning that its vibrating part is limited to a circular sector between $\beta < \phi < 2\pi - \beta$ with vanishing amplitude between $\phi = \pm \beta$; cf. Fig. 1. The extracolumella is effectively of infinite mass and motionless, a reasonable approximation since the extracolumella and attached proximal elements are typically (300×) heavier than the rest of the membrane.

Finally, the radius $a_{\text{tym}}$ of the equivalent circular membrane is calculated from the area of a realistic eardrum of surface $A$ through $a_{\text{tym}} = \sqrt{A/\pi}$.

The eardrum is modeled as a damped linear-elastic membrane obeying

$$ \frac{\partial^2 u}{\partial t^2} - 2\alpha \frac{\partial u}{\partial t} + c_m^2 \Delta_{(2)} u = \frac{1}{\rho_m d} \Psi(r, \phi; t) $$

with displacement $u(r, \phi; t)$, damping coefficient $\alpha$, density $\rho_m$, thickness $d$, and wave-propagation velocity $c_m = \sqrt{T_0/\rho_m}$ where $T_0$ is the membrane tension.

Furthermore, $\Psi(r, \phi; t)$ is the total pressure driving the membrane, which is fixed at its radial boundary, $r = a_{\text{tym}}$, and due to the extracolumella, at $\phi = \pm \beta$.

The membrane eigenmodes are found by first solving (5) in the free, undamped case, i.e., for $\Psi = 0$ and $\alpha = 0$. We substitute

$$ u_{mn}^+(r, \phi; t) = g_{mn}(r, \phi) e^{\pm i\omega_{mn} t}, $$

$$ g_{mn}(r, \phi) = \sin \kappa | \phi - \beta | J_{s} \left( \mu_{mn} r \right), $$

where $\kappa |m| = m\pi/(2(\pi - \beta))$ ($m \geq 1$) and $J_{s}$ is the order-$\kappa$ Bessel function of the first kind; $\mu_{mn} a_{\text{tym}}$, is its $n$th zero.
and \( \omega_{mn} = c_M \mu_{mn} \) is the corresponding eigenfrequency. The \( g_{mn} \) are an orthogonal set of functions when integrated over the membrane disk \( \{ r \leq a_{\text{tym}}; \beta \leq \phi \leq 2\pi - \beta \} \).

We consider the case where the membrane is driven by a uniform pressure, i.e., \( \Psi(r, \phi, t) = p_\text{ex} e^{i\omega t} \). In the quasistationary state, the forced membrane vibrates with a frequency equal to that of the input. The solution is found by substituting a linear combination of \( g_{mn}(r, \phi) e^{i\omega t} \) into

\[
\sum_{m=1,n=1}^{\infty} \Omega_{mn} C_{mn} g_{mn}(r, \phi) e^{i\omega t} = p_\text{ex} e^{i\omega t},
\]

where \( \Omega_{mn} = \rho \mu d[(\omega^2 - \omega_{mn}^2) - 2\omega \alpha] \). The \( C_{mn} \) can be calculated through the membrane mode orthogonality.

In ICE, the coupled membranes are driven by both the external pressure (1) and the internal pressure (2). Substitution of linear combinations of \( g_{mn} \) and the internal pressure \( p(x, r, \phi) e^{i\omega t} \) as a linear combination of the pressure modes (4) into (5) gives

\[
\sum_{m,n}^{\infty} \Omega_{mn} C_{mn} g_{mn}(r, \phi) e^{i\omega t} = p_0/L - p(0/L, r, \phi),
\]

where \((x = 0)\) and \((x = L)\) denote the ends of the cylinder. We have also canceled the time-dependent terms in (9).

Because of the no-penetration condition, we equate the air velocity (3) to that of the surface composed of the eardrum and the remaining cylinder base \( a_{\text{tym}} < r < a_{\text{cav}} \). This velocity is nonzero on the vibrating membrane and zero on the extracolumella and remaining cylinder base; cf. Fig. 1, indicating the context of the above boundary condition. In our convention, velocities along the \( x \) axis out of the cylinder are taken to be positive.

We now face the problem that the membrane and cavity modes are not mutually orthogonal. In other words, each membrane mode couples with every cavity mode. We circumvent this problem by approximating [14] the boundary conditions for (2) and (3) in that we effectively replace each membrane by a circular piston operating on the internal pressure \( p \) and moving with the membrane’s average velocity \( \bar{u}_{0L}^\text{ave} \) so that

\[
\bar{u}_{0L}^\text{ave} = \frac{1}{\pi a_{\text{cav}}^2} \int \text{d}S u_0/L, \quad \bar{u}_{0L}^\text{ave} = i\omega \mu_{0L}^\text{ave},
\]

\[
v_x(0, r, \phi) := -\bar{u}_{0L}^\text{ave}, \quad v_x(L, r, \phi) := \bar{u}_{0L}^\text{ave}.
\]

The second relation in (11) directly follows from (10). By doing so, we implicitly exploit the fact that typical vibration amplitudes for tympanic membranes are of the order of nanometers. We can therefore still use the same cavity eigenmodes as before. Furthermore, the higher cavity modes have eigenfrequencies that are in general well beyond (> 10 kHz) the typical lizard’s hearing range and will not play a significant role. The modal expansion of the air velocity is computed by substituting (4) in (3). This is the piston approximation as depicted in Fig. 2. A direct consequence of the piston approximation is that the higher pressure modes vanish and internal pressure is only composed of the 00 modes, corresponding to a standing wave along the \( x \) axis,

\[
p(x, r, \phi; t) = \rho a^2 L \sin kL \left[ u_{0L}^\text{ave} \cos k(L-x) + u_L^\text{ave} \cos kx \right] e^{i\omega t}.
\]

Finally, by substituting this result into the membrane equation (5), we can calculate \( u_{0L}^\text{ave} \) as a function of the input direction and frequency,

\[
\frac{2\rho c^2}{L} u_{0L}^\text{ave} = \frac{P_L + P_0}{1/\Lambda + \Gamma_+} + \frac{P_L - P_0}{1/\Lambda + \Gamma_-},
\]

where

\[
\Lambda = \frac{\rho c^2}{V_{\text{cav}}} \sum_{m,n}^{\infty} \left( \int g_{mn} \right)^2, \
\Gamma_+ = -kL \cot kL/2, \quad \Gamma_- = kL \tan kL/2,
\]

so that \( |\Lambda| \leq (\rho c^2 S/V_0) \sum_{m,n}^{\infty} 1/|\Omega_{m,n}| < \infty \) by Cauchy-Schwarz, with \( S \) as the tympanic area. \( \Lambda \) quantifies the frequency response of an uncoupled membrane whereas the \( \Gamma_\pm \) result from the internal pressure. In order to calculate \( \Lambda \) we chose a cutoff of \( N = 30 \) modes. Higher modes are suppressed by the high damping at their corresponding eigenfrequencies.

In order to compare our model with experimental results, we define the average vibration velocity in dB re mms^{-1} Pa^{-1}, meaning the decibel velocity in mm/s for an input pressure amplitude of 1 Pa as \( v_{\text{db}} = 20 \log_{10} |\bar{u}_{0L}^\text{ave}| \).

Using parameters based on standard anatomical data (see Table I) and an extracolumellar angle \( \beta = \pi/30 \), we get membrane-vibration velocity \( c_M = 5.4 \text{ m/s} \) for the Tokay gecko (Gecko) and \( c_M = 2.9 \text{ m/s} \) for the water monitor (Varanus)—a rather different perspective.
Before proceeding we turn to a few experimental checks of the general ICE theory. The price we pay for generality is that we do not delve into possible microstructures of the tympana. Figures 3(a) and 3(b) show the respective frequency dependence of the membrane vibrations for ipsilateral $\theta = 90^\circ$ and contralateral $\theta = -90^\circ$ stimuli for both Gecko and Varanus.

In the case of Gecko, the contralateral response has a minimum near $f_0$, whereas the spectral response of Varanus shows multiple peaks corresponding to higher membrane eigenfrequencies. The occurrence of multiple peaks instead of a single one in the biophysically relevant range is due to the fact that the Varanus eardrum is heavily underdamped [much smaller $\alpha$; cf. Eq. (5)], resulting in higher modes being less suppressed. Nevertheless, our ICE model explains the frequency behavior in both cases.

In the following, we focus on three universal aspects of ICE: (1) The internal time difference (iTD), which for frequencies $< f_0$ greatly exceeds the interaural time difference (ITD); (2) the internal level difference (iLD), which exhibits a pronounced maximum once the iTD has strongly increased; and (3) the segregation of the iTD and iLD domains by the fundamental frequency $f_0$ of the tympanum. Both iTD and iLD depend on the sound-source direction.

The internal time difference (iTD) corresponds to the actual time difference between left and right membrane vibrations as experienced by the animal,

$$iTD = \text{Arg}(\tilde{u}_0^\text{ave}/\tilde{u}_L^\text{ave})/\omega.$$  \hspace{1cm} (15)

For Gecko, the interaural time difference (ITD) equals $\text{Arg}(p_0^L/p_0^L)/\omega = L \sin \theta/c$, the time taken by sound to travel across the head. It is independent of frequency and for our parameters it is $\approx 64 \mu s$ for $\theta = \pm 90^\circ$. Figures 4(a) and 4(b) show the frequency and direction dependence of the iTDs for Gecko and Varanus, respectively. In the case of Gecko, the iTDs have a low-pass response; i.e., they are more or less constant up to a certain frequency and drop sharply thereafter, with $iTD/ITD = 1$ at $f \approx f_0$. From a neuronal-processing point of view, this is convenient as it mirrors the behavior of the ITDs but is strongly increased by a factor of about 3 [15]. The number 3 is not unique, rather the value depends on the specific geometry of the internal cavity. Figure 4(b) illustrates its variation.

Although the membrane vibration amplitudes are directional by themselves, the difference between left and right tympanum is more sensitive to $\theta$. For the input (1), the internal level difference (iLD) is defined as the logarithmic difference between left and right ($0/L$) membrane amplitudes of (8).

![FIG. 3. Experimental and calculated $v_{dB}$ for ipsi- ($\theta = 90^\circ$) and contralateral ($\theta = -90^\circ$) stimuli for Gecko (top) and Varanus (bottom). The flaccid membrane of Varanus (with low $\alpha$) gives peaks at $f_0$ as well as at higher membrane resonances. As elsewhere, all membrane eigenfrequencies are indicated by vertical dashed lines; cf. Fig. 5(b). The first resonant peak (or trough) allows a straightforward determination of tympanic eigenfrequency $f_0$ in the alive animal. All experimental data presented were gathered by using laser Doppler vibrometry.](image1)

![FIG. 4. Frequency and direction dependence of the iTDs for Gecko (top) and Varanus (bottom). (a) For Gecko, the iTDs exhibit a plateau of $iTD \approx 3 ITD$ up to about $f = f_0$ and sharply fall thereafter. As indicated, the plateau exists irrespectively of the direction $\theta$; cf. left column. The iTDs can thus be effective low-frequency cues. (b) For Varanus, the iTDs slowly increase up to $f_0$ and then decrease; the discontinuity is an artifact of $2\pi$. The young animal can therefore only exploit a restricted low-frequency range of iTDs up to, say, 200 Hz, nevertheless illustrating that the time expansion factor iTD/ITD can differ from 3 appreciably.](image2)
is direction dependent through corresponding peaks also at higher membrane eigenmodes. where iLDs peak close to iLDs for Gecko (top) and Varanus (bottom). (a) For Gecko, the iLDs peak close to $f = f_0$ and decrease slowly thereafter. They can therefore serve both as effective high-frequency hearing cues and as an efficient means of determining $f_0$ in alive animals. Clearly, the higher tympanic eigenmodes play no role. (b) For juvenile Varanus with small $\alpha$ and $f_0 \approx 400$ Hz, we see corresponding peaks also at higher membrane eigenmodes.

$$\text{iLD} = 20 \log_{10} \left| u_L^{\text{ave}} / u_0^{\text{ave}} \right| = 20 \log_{10} \left| u_L^{\text{ave}} / u_0^{\text{ave}} \right|,$$

$$u_L^{\text{ave}} / u_0^{\text{ave}} = (1 + B) / (1 - B)$$

(16)

where

$$B = i \left( (1 + \Delta \Gamma) / (1 + \Delta \Gamma) \right) \tan(k\Delta/2)$$

(17)

is direction dependent through $\Delta = L \sin \theta$. The $\Gamma_{\pm}$ in (17) stem from (14). Once left and right inputs effectively have the same amplitude, we can put the interaural level difference (ILD) equal to zero. For Gecko, the iLD has a bandpass-like behavior. It is zero for both very low and high frequencies and peaks close to the membrane eigenfrequency $f_0$, cf. Fig. 5(a). The iLDs steeply increase across $\theta = 0^\circ$ and are at a maximum or minimum at $\theta = \pm 90^\circ$. For Varanus, Fig. 5(b) shows an iLD spectrum with multiple peaks near membrane resonances, corresponding to a much lower damping (smaller $\alpha$). Moreover, at the fundamental membrane eigenfrequency $f_0$, the directional response peaks at $\theta = \pm 30^\circ$. A possible explanation of this deviating behavior is that the experiments were performed on juvenile monitor lizards, suggesting that increased membrane damping and cavity volume in adults should give similar results to those shown for the adult Gecko.

With ICE we have come across a hearing system that relies on iTDs at low frequencies and iLDs at higher frequencies, with the transition between the two regimes being governed by the fundamental eigenfrequency $f_0$ of the tympanic membrane; see Fig. 6. In this way the fundamental frequency of the eardrum creates a partition of the sensory landscape.

FIG. 5. Calculated frequency and direction dependence of the iLDs for Gecko (top) and Varanus (bottom). (a) For Gecko, the iLDs peak close to $f = f_0$ and decrease slowly thereafter. They can therefore serve both as effective high-frequency hearing cues and as an efficient means of determining $f_0$ in alive animals. Clearly, the higher tympanic eigenmodes play no role. (b) For juvenile Varanus with small $\alpha$ and $f_0 \approx 400$ Hz, we see corresponding peaks also at higher membrane eigenmodes.

FIG. 6. Transition between the iTD and iLD frequency regime for directions $\theta \neq 0^\circ$. At lower frequencies iTDs work better as directional cues, e.g., with iTD/iTD $\approx 3$ (blue plateau) for adult geckos, while at higher frequencies the iLD becomes pronounced, even though for most lizards the external ILD $\approx 0$. The transition between the two kinds of cues is governed by the eardrum’s fundamental frequency $f_0$.

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