

Localization and frequency resolution in antennal hearing of insects

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Insects rely on their hearing in order to communicate, identify and locate potential mates, and avoid predators. Due to their small sizes, many insect species are not able to use the interaural time and intensity differences employed by vertebrates for the localization of sound, but have instead evolved other mechanisms to perform this task. One such mechanism is the antenna, which provides directionally sensitive acoustic information. In contrast to tympanic ears, which detect scalar pressure fields, antennal ears detect the vector-valued velocity fields of sound. We argue that this detection scheme at small length scales, combined with the dipolelike radiation of sound emitted from flying insects, results in short ranges of detection. These short ranges imply that the acoustic signals transmitted between two insects flying past each other will be brief and rapidly changing with time, presenting a challenge in extracting precise frequency information. However, this frequency information has been shown to be essential for insects to identify and locate potential mates. In the current work, we propose potential mechanisms that insects may employ in order to extract precise frequency and directional information from these transient signals, thereby circumventing the apparent limitations.

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I. INTRODUCTION

Acoustic communication is ubiquitous among vertebrates and insects. Survival and fitness often depend on an organism's ability to detect sound, in order to identify predators, locate mates, and remain in contact with other members of the species. Vertebrates and many species of insects use pressure sensors in the form of tympanic membranes to detect and localize sound [1,2]. In vertebrates, directionality is typically inferred from the time and intensity differences of the acoustic waves arriving at the two ears [3]. These differences, however, are obscured in insects, whose length scale is much shorter than the wavelength of the sound [4,5]. In this regime, the acoustic wave is minimally scattered by the body of the

receiving insect, leading to approximately the same intensity at the two ears. Further, if the distance between two insect ears is much smaller than the wavelength of sound, the phase difference between the two signals is negligible [6].

Insect species that employ pressure sensors, such as crickets and moths, communicate using high frequencies, thereby avoiding these limitations [4,5,7]. Insects that communicate using low frequencies, such as mosquitoes, flies, and bees, employ an entirely different mechanism for localizing sound. They instead use directionally sensitive antennae [8–10]. The featherlike flagellum pivots in response to variations in the velocity field of the surrounding air particles. Active sensory elements known as *scolopidia* are attached to the base of the flagellum [11,12]. The scolopidia act as stretch receptors in insects, transmitting neurological signals in response to mechanical deflection of the flagellum [13,14]. The direction in which the flagellum pivots corresponds to the direction of the sound source. Each direction is therefore poised to activate a specific subset of the sensory neurons, allowing the insect to identify the direction of the sound source [15–17]. Flying insects locate sound sources in three-dimensional (3D) space. However, these antennae have, at most, two spatial

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degrees of freedom. To date, it remains unclear how 3D spatial information is encoded in the movement of two-dimensional structures [18].

Insects with antennal hearing have been shown to use each other's flight tones to acoustically detect one another [8,10,17,19,20]. These flight tones, emitted from the beating of insect wings, have been shown to be nearly sinusoidal, with higher harmonics falling outside of their hearing range. Thus, experiments have focused on the response of the flagellum and Johnston's organ to pure tones [15,21–24]. While this is a natural starting point, it treats the sound sources as stationary and hence does not capture important details of detecting insects in flight. In the natural environment, the sound sources are moving relative to the receivers. Further, the sound intensity profile of beating insect wings is nonuniform and falls off rapidly with distance from the source [25–27]. We should expect the combination of these effects to result in a perceived signal that has time-varying amplitude, frequency, and phase offset.

In the current work, we first discuss two physical limitations experienced by insects. The first is their short range of detection [27], which may arise from the insects' wingbeats acting as acoustic dipole sources [18,25]. The second limitation is the Gabor limit [28–30], which imposes upper bounds on the precision with which one can extract frequency and temporal information from a transient signal. We then propose and discuss several potential mechanisms that insects could employ in order to gain additional acoustic information. These mechanisms entail the extraction of information from signal modulations produced during a flyby event, where two insects enter and then exit each others' detection range. We discuss the expected amplitude, frequency, and phase modulations in the acoustic signal upon arrival at the receiver. Finally, we propose that one or more of these modulations may be used by insects with antennal hearing in order to reliably detect acoustic signals from conspecifics.

II. PHYSICAL LIMITATIONS OF ACOUSTIC DETECTION

We now consider the physical limitations that accompany acoustic detection at the small length scales of insects. We first review prior experimental measurements, arguing that the short hearing range of insects with antennal ears arises from a combination of three physical features. First, the featherlike flagella act as particle velocity sensors, rather than pressure sensors [16]. Second, the wingbeats of flying insects act as acoustic dipole sources, rather than monopole sources [25,26,31]. Third, detection occurs within a range much shorter than the wavelength of the emitted sound, hence in the near-field regime [4,5]. We explore the implications of these three limitations on the range of detection by insects. We then review the spectral limitations that accompany transient signals. Finally, we plot the expected flyby signal reaching the receiver and show the difficulty of extracting precise frequency information from short signals, when using the Fourier transform.

A. Range of detection

It has been previously shown that insects' wingbeats can be approximated by acoustic dipoles [18,25,26], which produce

acoustic fields that fall off rapidly with distance. Further, the featherlike antenna is believed to detect the velocity field produced by a sound source, rather than the pressure field that is sensed by tympanic ears [9]. The combination of the dipole approximation and the detection of particle velocity rather than pressure suggests that the strength of signals communicated between insects falls off as $1/r^3$, where r is the distance between the sound source and the receiver [4,5,32]. In Appendix A, we provide an analytic calculation, showing how this inverse cubic dependence arises in the near-field regime, where the distance from the sound source is much smaller than the wavelength of sound.

The inverse cubic dependence has been measured in flying female mosquitoes (*Toxorhynchites brevipalpis*) [31]. Another study showed that both male and female mosquitoes (*Aedes aegypti*) exhibit an acoustic velocity field falling off faster than $1/r^2$ but slower than $1/r^3$ [26]. By comparison, the monopole-like sources detected by larger animals produce pressure fields that fall off approximately as $1/r$. This stark difference indicates that the signal amplitude is very sensitive to changes in distance, due to the inverse cubic dependence. This sensitivity could potentially be useful for inferring the distance of a sound source, especially when that distance is changing with time. However, it also implies that insects with antennal ears would have a short range of acoustic detection, as the inverse cubic relationship yields approximately an 18 dB reduction of the signal for a factor of 2 increase in distance. This short range has been measured to be just a few cm for mosquitoes [15,27,31] and in the millimeter range for fruit flies [33] and honey bees [34].

B. Gabor limit

The short range of acoustic communication between insects with antennal hearing implies that the signals received from flyby events are transient. A finite duration of the signal, in turn, imposes a limitation on the frequency resolution of the receiver. The Gabor uncertainty principle states that an event cannot be localized with arbitrarily high resolution in both the time and frequency domains simultaneously, using Fourier transform pairs [28,29]. A signal confined to a short period of time thus requires a wide bandwidth for accurate representation in the frequency domain. Likewise, resolving details confined to a narrow frequency bandwidth requires long periods of time (Fig. 5 of Appendix B).

The Gabor limit states that the representation of any signal is bounded by

$$\Delta t \Delta f \geq \frac{1}{4\pi} \approx 0.08 \text{ cycles}, \quad (1)$$

where Δt and Δf are the standard deviations of the signal's amplitude envelope in the time and frequency domains, respectively. Δt quantifies the signal duration, while Δf quantifies its bandwidth. We note that it is as yet unknown whether or not insects use Fourier transform methods for extracting frequency information. However, the Gabor limit provides a useful benchmark for estimating the frequency resolution used for communication between insects, which one expects to be limited by the amount of time spent within detection range of each other.

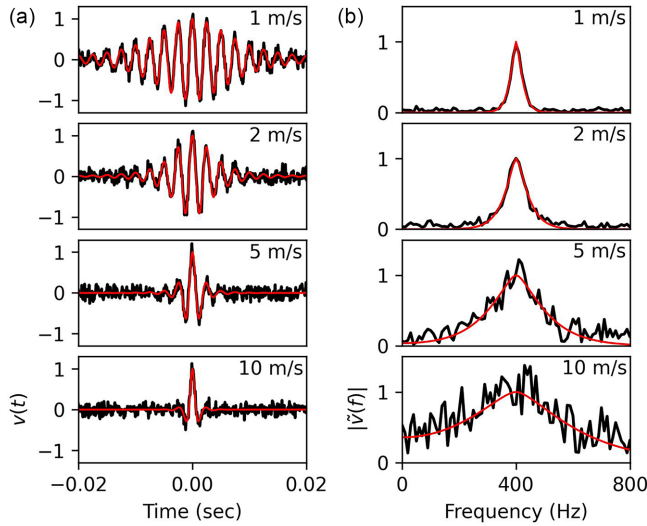


FIG. 1. Acoustic velocity field strength [panel (a)] and corresponding Fourier transforms [panel (b)] experienced during flyby events. Datasets are normalized to their peak values in both the time and frequency domains. Relative flyby speeds are shown in the corners of each panel. For all panels, the wingbeat frequency is $f = 400$ Hz, and the closest point between source and receiver is $d_0 = 1$ cm. We show the signals both in the deterministic limit (red) and with Gaussian white noise (with a standard deviation of 0.1) superposed onto each of the signals in the time domain (black).

C. Transient flyby signal

We now provide a concrete example of these physical limitations. Consider two insects flying past each other with separation distance, $r(t) = \sqrt{d_0^2 + (Vt)^2}$, where d_0 is the distance between the insects at closest pass, set to occur at time $t = 0$. V represents the relative speed at large distances, in the limit where t goes to $\pm\infty$. With the inverse cubic relationship between distance and the velocity field of sound, we should expect the receiver to measure a signal strength of the form

$$v(t) \propto \frac{\cos(2\pi ft)}{(d_0^2 + (Vt)^2)^{3/2}}, \quad (2)$$

where f is the frequency of the signal of interest. Note that we are not yet considering the Doppler shift or the directional component of the signal. In Fig. 1(a), we show this signal in the time domain, with 10% additive Gaussian white noise, for several values of V . In Fig. 1(b), we show the Fourier transforms of the signals, which exhibit peaks and become increasingly dominated by noise for increasing V . This example illustrates the difficulty in extracting precise frequency information from noisy, transient signals using linear transformation methods such as the Fourier transform.

III. POTENTIAL ALTERNATIVE MECHANISMS

As argued in a prior section, the acoustic signals transmitted between insects are short and rapidly changing, thus rendering traditional signals—with static amplitudes, frequencies, and phase offsets—inadequate for assessing acoustic detection of moving sources. With this framework, we propose alternative mechanisms that may be employed by insects

in order to extract precise frequency and directional information from rapidly changing acoustic signals. We consider the feasibility of insects using the Doppler shift, distortion products, and rapid phase shifts in order to circumvent the physical limitations imposed by their morphology.

In Figs. 2(a) and 2(e), we illustrate the velocity field produced by a dipole source at one instance in time (see Appendix A). The magnitude of this field is highly sensitive to the distance from the source, and also depends on the orientation of the receiver relative to the source's direction of travel. The magnitude of the field is strongest in front of and behind the insect, and weaker at other orientations, as supported by experimental measurements [18,25,26].

In Figs. 2(a)–2(d), we show how the time-varying amplitude and frequency of the measured signal are affected by the orientation angle of the flyby event. For these calculations, we keep the distance of closest pass constant. Likewise, in Figs. 2(e)–2(h), we show how these quantities vary for different flyby distances, while keeping the orientation angle fixed. The peak value of the signal measured by the receiver depends heavily on the point of closest pass and weakly on the orientation angle. However, the orientation more strongly influences the sharpness and skewness of the amplitude envelope. Experimental measurements have indeed shown that sounds emitted by flying mosquitoes display amplitude envelopes of this shape [31]. We therefore speculate that this variety of shapes may serve as cues for insects to identify the proximity and direction of travel of potential mates.

A. Doppler shift

We now consider the possibility of insects using Doppler shifts as cues for gaining information about sound sources. In Fig. 2, we show the frequency as a function of time, as measured at the receiver, for several flyby scenarios. The shift in frequency becomes increasingly rapid for closer flyby events [Fig. 2(h)], but is independent of the relative flyby angle [Fig. 2(d)]. The instantaneous frequency measured at the receiver can be approximated as

$$f(t) \approx f_0 - \frac{1}{\lambda_0} \frac{dr}{dt}, \quad (3)$$

provided that the speed of the source, relative to the receiver, is small compared to the speed of sound. λ_0 and r represent the wavelength of the sound and the receiver's distance from the source, respectively. f_0 is the frequency of the sound in the reference frame of the source. We consider the largest Doppler shift possible, which occurs when two insects approach each other head-on and then depart directly away from each other. The magnitude of the frequency difference between an approaching and departing sound source moving at constant speed is thus $\delta f = \frac{2}{\lambda_0} \left| \frac{dr}{dt} \right|$.

We now estimate whether this frequency shift would be large enough to be perceived, using the Gabor limit as a benchmark for the frequency resolution of insects. The time spent within detection range is $\delta t = 2r_0 / \left| \frac{dr}{dt} \right|$, where r_0 is the insects' range of detection. Inserting δt and δf into Eq. (1), we find that the frequency shift is sufficiently large when

$$\frac{r_0}{\lambda_0} \geq \frac{1}{16\pi} \approx 0.02. \quad (4)$$

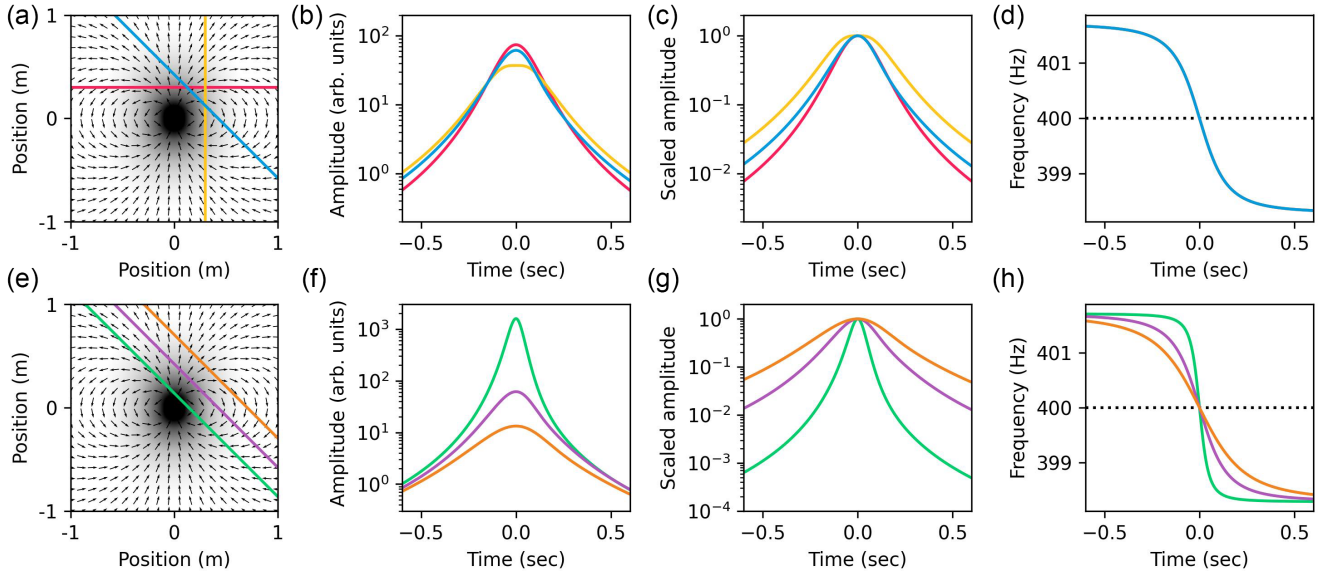


FIG. 2. (a) Velocity field of an acoustic dipole at one instance in time. The heatmap illustrates dependence of the field strength on the distance from the source. The three dashed lines correspond to three potential flight paths of the receiver, traveling left to right and top to bottom. (b) Amplitude envelopes of the velocity field, as experienced by the three receivers illustrated in panel (a). (c) Same data as panel (b) but normalized to the peak values. (d) Frequency of the sound experienced by the receivers relative to the frequency emitted by the source (black dotted line). This change in frequency defines the Doppler shift. Panels (f)–(h) show the perceived amplitudes and frequencies corresponding to the flight paths depicted in panel (e), traveling left to right. For all panels, the relative flyby speed is 2 m/s.

Interestingly, this limitation does not depend on the flight speed of the insects, $|\frac{dr}{dt}|$, as it affects the spread in the time and frequency domains in reciprocal manner. The only quantities needed are the range of detection and the wavelength of the sound of interest.

To check if the Gabor limit is satisfied for mosquitoes, we approximate the wavelength of the sound produced by their wingbeats to be $\lambda_0 \approx 1$ m [23]. For detection of the frequency shift, we would then need a detection range of at least 2 cm. This limitation should be easily satisfied, as the range of detection for mosquitoes has been estimated to be $r_0 \approx 10$ cm [27].

However, an additional, physiological limitation needs to be considered. If one listens to a pure tone for a long period of time, one's precision of the tone's frequency does not increase indefinitely with time, as it would if measured with a digital frequency analyzer. Instead, the limit of frequency precision would saturate, possibly due to the finite number of receptors, as well as other biological limitations. Approximating the flight speed of mosquitoes to be $|\frac{dr}{dt}| \approx 1$ m/s (0.5 m/s for each of the two insects) [35], we would expect a frequency shift of $\Delta f \approx 2$ Hz. To detect this frequency shift, a mosquito would need to be able to resolve fractional frequency differences of $\frac{\Delta f}{f_0} \approx \frac{2}{400}$, where we have approximated the flight tone of interest to be $f_0 \approx 400$ Hz [23]. The level of frequency resolution in insects would hence need to be comparable to that of humans, who can resolve ratios of $\frac{\Delta f}{f_0} \approx \frac{2}{1000}$ [1].

Mosquitoes fly rather slowly compared to other insects. Bees, flies, locusts, moths, butterflies, and dragonflies have all been measured to fly several times faster than the mosquito, with flight speeds ranging from 2 to 10 m/s [36–38], resulting in Doppler shifts on the order of $\frac{\Delta f}{f_0} \approx 0.01$ –0.1. Some species of flies and moths have even been found to greatly

exceed speeds of 10 m/s [35]. We note that the actual shifts in frequency will vary widely with the large span in frequencies with which insects communicate. For example, two fruit flies, each moving at 2 m/s and emitting 250 Hz flight tones, would experience a maximum Doppler shift of $\Delta f \approx 6$ Hz. In contrast, moths flying at the same relative speed and emitting a 50 kHz frequency of interest would experience a maximum Doppler shift around 1 kHz. We therefore speculate that the Doppler shift may contain essential information that insects use in order to determine the proximity and relative speeds of predators, prey, or potential mates.

B. Distortion products

We now consider a nonlinear effect that could serve to magnify the Doppler shift during a flyby event. Distortion products are responses of a nonlinear system at integer combinations of two or more tones from the input. They are ubiquitous to vertebrate ears and generally regarded as a byproduct of nonlinear signal amplification [1]. Male mosquitoes have been shown to produce nonlinear distortion products from simultaneously detecting their own flight tone along with those of a female [23,39,40]. However, unlike vertebrates, these additional tones were shown not to be a byproduct, but to be essential for the male to be able to detect the female.

To understand distortion products, let us consider a nonlinear system governed by the normal form equation for the supercritical Hopf bifurcation. This simple equation has been extensively used in studying the dynamics of vertebrate ears, as it captures several of the basic phenomena of the active, nonlinear mechanics [41–43]. Further, this framework has been used to develop numerical models of the Johnston's organ of mosquitoes [44,45]. The strength of this framework

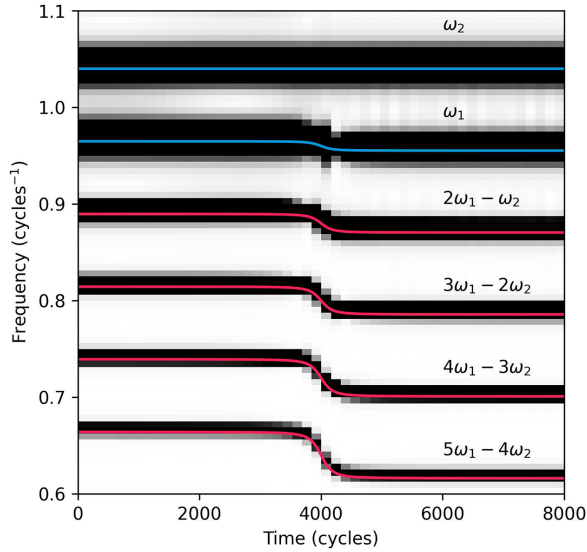


FIG. 3. Spectrogram of the response of a Hopf oscillator in the quiescent state ($\mu = -0.1$) to a two-tone stimulus during a flyby event. ω_2 is held constant, while ω_1 experiences a Doppler shift. Response strength increases from white to black. Primary tones (blue) and distortion products (red) values are identified with text.

lies in its simplicity and generalizability, as high-dimensional numerical models operating near the onset of autonomous oscillations can be mapped onto the normal form equation and described in this simplified framework. Since the dynamic state of the male mosquito flagellum transitions between quiescent and self-sustained oscillator states [19,23], the Hopf framework provides a natural choice for describing its dynamics.

The state of the detector is described by complex variable, $z(t)$. The dynamics of this variable are governed by

$$\frac{dz}{dt} = (\mu + \omega_0) - |z|^2 z + F(t), \quad (5)$$

where ω_0 is the characteristic frequency of the system and $F(t)$ is an external complex-valued forcing term. μ denotes the control parameter of the system, with negative values yielding quiescent systems and positive values resulting in systems that autonomously oscillate, in the absence of a stimulus. The interface between these two regimes ($\mu = 0$) defines the Hopf bifurcation.

When a two-tone stimulus is applied to this system [$F(t) = A_1 e^{i\omega_1 t} + A_2 e^{i\omega_2 t}$], responses can be measured not just at the two primary tones, ω_1 and ω_2 , but also at the distortion-product frequencies,

$$\omega_{pq} = p\omega_1 - q\omega_2, \quad (6)$$

where p and q are integers. In Fig. 3, we show the response of the Hopf oscillator to a two-tone stimulus during a flyby event. We see that the Doppler shift is magnified in the distortion products, with larger shifts observed for increasing distortion-product order. In Appendix C, we provide another example and additional details of how distortion products magnify frequency modulation. We speculate that these distortion products may serve to enhance acoustic cues from flyby events in mosquitoes and potentially other insects.

C. Rapid phase shift

Even if the Doppler shifts in the primary tones and distortion products should prove too small to detect, an additional effect could be of importance to flying insects. Unlike monopole sources, the acoustic radiation of dipole sources has angular dependence (see Appendix A). We should expect the signal in front of and behind the insect to be a half cycle out of phase with each other. This assumption is supported by experimental measurements from tethered mosquitoes [26]. Therefore, in addition to the previously described amplitude modulations and Doppler shifts, we should expect a rapid shift in the phase offset of the measured signal. To isolate the effects of this feature, in the following we will neglect the dynamic changes in amplitude and frequency described in the prior sections.

In Appendix D, we show that a single sensor, with any angle of orientation relative to the source's direction of travel, will experience at least one rapid half-cycle phase shift during the flyby event. This is due to the angular dependence of the vector-valued velocity field [Eq. (A9)]. To test the effects of this rapid phase shift, we apply a single-tone sinusoidal stimulus with dynamically varying phase offset to the Hopf oscillator (see Appendix D). In Fig. 4, we see that this phase shift induces a brief modulation in amplitude, with larger modulations for more rapid phase shifts. Note that this effect is distinct from the amplitude modulations discussed in the prior sections. Since the times at which these phase shifts occur depend on the relative angle between the source's and receiver's direction of travel, this phase shift could, in principle, be used to infer the direction of travel of the sound source.

IV. DISCUSSION

The localization of a sound source constitutes one of the key requirements for hearing in the natural environment, as its precision and speed may determine the survival of an animal. Vertebrate animals use pressure sensors to detect sound and have therefore evolved auditory systems that contain two ears, sufficiently separated in space to allow them to infer the direction of the incoming sound. Directional information is captured by the interaural time and intensity differences between the two ears [3]. Additional directional information can be obtained from the asymmetrical structure of the outer ear, which filters sound differently at the two sensors, dependent on the direction of the incoming sound. Insects, however, detect sounds of wavelengths that are much longer than the length scale of their bodies [4–6]. In this regime, the phase and intensity differences between the two ears are negligible, strictly limiting the utility of pressure sensors. While some insects have evolved to have directionally sensitive pressure-difference receivers [6], many utilize antennae for the detection and localization of sound [8,10]. Insects with antennal ears, therefore, face a unique set of challenges not experienced by land vertebrates. They extract information from the vector-valued velocity field of sound, rather than the scalar pressure field [16,17].

The velocity field naturally contains directional information of the sound source, which is absent in the pressure field [32]. This could allow insects to extract the directional

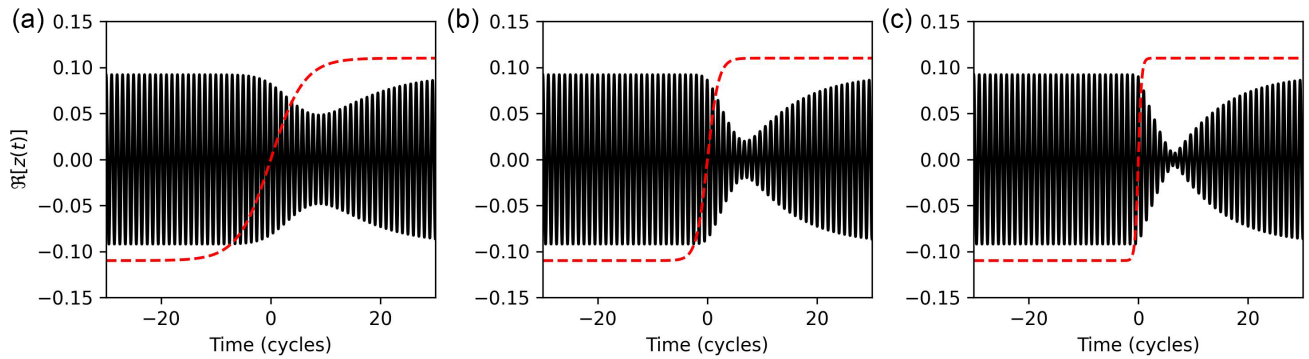


FIG. 4. Amplitude modulation in the real part of the response of a Hopf oscillator to a phase shift in the stimulus waveform. The red, dashed curves illustrate the phase offset as a function of time. The time constant associated with the phase shift was set to $\tau_{ps} = 3, 1$, and 0.3 for panels (a)–(c), respectively.

information, but with the cost of having a reduced acoustic range of detection, due to the velocity field decaying more rapidly with distance. This small acoustic range, in turn, results in shorter signals experienced by the sensory systems and therefore limits frequency resolution.

The current study proposes potential mechanisms by which sensors within the antennal ear could overcome the unique set of challenges of insect auditory detection. We note, however, that the solutions proposed in this paper entail the use of a single sensor in a single ear. Further, these solutions do not consider morphological details, such as the asymmetries in the flagellar structure, which likely shape the response based on the direction of the sound source. More comprehensive models can certainly be constructed to account for these asymmetries and to include an array of sensors to describe the full spatial arrangement of neural elements within the Johnston's organ [14,46].

In Fig. 2, we observe that the direction of the sound source, relative to the receiver's direction of travel, changes significantly and rapidly throughout each flyby event, suggesting that many, if not all, of the sensory elements will be stimulated at some point during the event. Hence, each flyby event would result in a unique trajectory of the relative angle of the velocity field. Each trajectory would therefore correspond to a unique order and duration in which the sensory elements would be stimulated. The information from the array of sensors could thus be used to infer the position and velocity of the source. While the array will therefore extract more information than an individual sensor, the analysis of an individual element constitutes an important first step toward building a comprehensive model of the full auditory organ. Hence, we focus here on exploring the capabilities of a single sensor to extract directional, frequency, and amplitude information about an incoming signal.

The analysis of this paper relies on three assumptions. First, we assume the featherlike flagella act entirely as particle velocity sensors [16]. Second, the wingbeats of flying insects act as pure acoustic dipole sources [25,26,31]. Third, that detection occurs in the near-field limit, where the distance between source and receiver is much shorter than the wavelength of sound [4,5]. We note that the relaxation of any one of these assumptions, while keeping the other two, would result in an acoustic signal that falls off as the inverse square of the distance, which is still much more rapid than the $1/r$

dependence most familiar to humans. The nonuniform radiation of the dipole source velocity field, combined with the high sensitivity of intensity with distance, results in a nonstationary acoustic signal arriving at the receiver. These signals contain many frequency components, but can be described by a sinusoid with simultaneous amplitude, frequency, and phase modulation. We have analyzed, in isolation, the effects of nonstationary amplitude, frequency, and phase offset, arguing that each component could potentially carry meaningful information for the detection of flying insects.

We have discussed the physical limitations that accompany antennal hearing, namely, the short range of detection and the low frequency resolution that arises from the Gabor limit. We then proposed several potential mechanisms that could be employed by insects with antennal hearing in order to obtain additional acoustic information. These mechanisms entail capturing information contained in the modulations of the acoustic signals. We discussed the transient amplitude-modulated signal experienced by a receiver moving past a sound-emitting insect in flight, and showed that the shape of the amplitude envelope depends heavily on the distance between insects. We then discussed the Doppler shift and its potential role in sound localization, showing that the shift in frequency is magnified in the distortion-product response. Finally, we discussed the rapid phase shifts that arise from the angular asymmetry in the velocity field of an acoustic dipole, showing how this could be used to gain additional directional information. We propose that insects may use a combination of these mechanisms in order to overcome the challenges that accompany acoustic detection at small length scales.

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DATA AVAILABILITY

The data that support the findings of this article are openly available [47].

APPENDIX A: VELOCITY FIELD OF AN ACOUSTIC DIPOLE

To determine the acoustic field produced by a monopole at the origin, we must solve the wave equation,

$$\frac{1}{c^2} \frac{\partial^2 \Phi}{\partial t^2} - \nabla^2 \Phi = -q(t)\delta(\vec{x}), \quad (\text{A1})$$

where $q(t)$ represents an arbitrary function related to the motion that generates the sound, c is the speed of sound in the material, and $\Phi(\vec{x}, t)$ is the velocity potential [32]. The velocity potential is particularly useful to work with because both the pressure and velocity fields can be calculated using

$$p = -\rho \frac{\partial \Phi}{\partial t} \quad \text{and} \quad \vec{u} = -\nabla \Phi, \quad (\text{A2})$$

respectively. ρ represents the density of the material. Equation (A1) has the solution

$$\Phi_{\text{mon}}(r, t) = \frac{q(t - \frac{r}{c})}{4\pi r}, \quad (\text{A3})$$

where r is the distance from the origin. Notice that the solution is spherically symmetric and is delayed by time, $\frac{r}{c}$, which accounts for the finite speed of sound in this compressible material.

To find the velocity potential of a dipole source, we must solve

$$\frac{1}{c^2} \frac{\partial^2 \Phi}{\partial t^2} - \nabla^2 \Phi = -\frac{\partial}{\partial z} [q(t)\delta(\vec{x})], \quad (\text{A4})$$

which has the solution

$$\Phi_{\text{dip}}(r, \theta, t) = \frac{\cos \theta q(t - \frac{r}{c})}{4\pi r^2} + \frac{\cos \theta \frac{dq}{dt}(t - \frac{r}{c})}{4\pi cr}, \quad (\text{A5})$$

where the head and direction of travel of the insect are oriented at $\theta = 0$ [26,32]. We consider sinusoidal sound waves with

$$q\left(t - \frac{r}{c}\right) = Qe^{i\omega(t - \frac{r}{c})}. \quad (\text{A6})$$

Inserting this into Eq. (A5), we find

$$\Phi_{\text{dip}}(r, \theta, t) = \frac{\cos \theta Qe^{i\omega(t - \frac{r}{c})}}{4\pi r^2} \left[1 + \frac{2\pi ir}{\lambda} \right]. \quad (\text{A7})$$

We can then calculate the velocity field using $\vec{u} = -\nabla \Phi$. We find

$$\vec{u}_{\text{dip}}(r, \theta, t) = \frac{Qe^{i\omega(t - \frac{r}{c})}}{4\pi r^3} \left[\left(2 + 2\left(\frac{2\pi ir}{\lambda} \right) - \left(\frac{2\pi r}{\lambda} \right)^2 \right) \cos \theta \hat{r} + \left(1 + \frac{2\pi ir}{\lambda} \right) \sin \theta \hat{\theta} \right]. \quad (\text{A8})$$

In the limit where $\frac{2\pi r}{\lambda} \ll 1$, we find

$$\vec{u}_{\text{dip}}(r, \theta, t) = \frac{Qe^{i\omega(t - \frac{r}{c})}}{4\pi r^3} [2 \cos \theta \hat{r} + \sin \theta \hat{\theta}]. \quad (\text{A9})$$

APPENDIX B: GABOR LIMIT

Here, we illustrate the Gabor limit by showing several signals in both the time and frequency domains (Fig. 5). In the

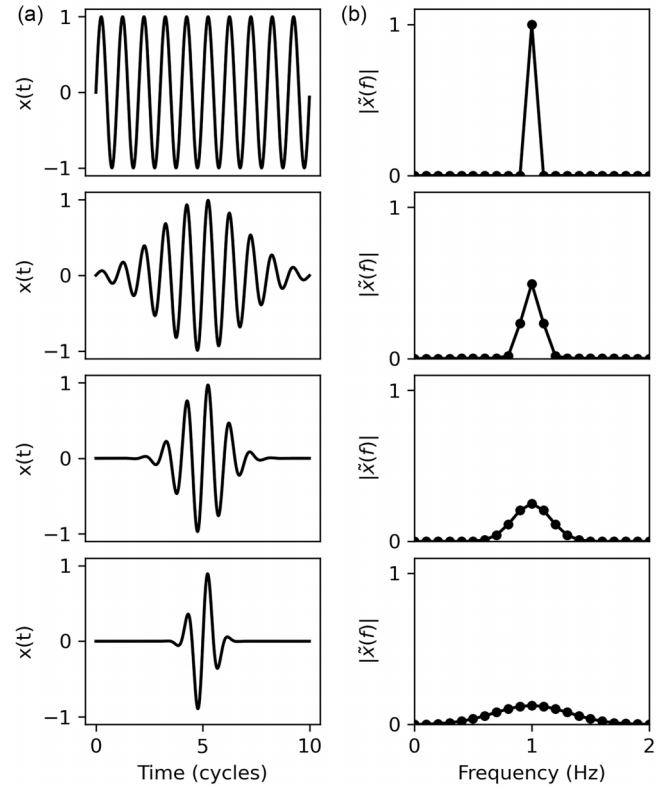


FIG. 5. (a) Sinusoidal signals with Gaussian amplitude envelopes in the time domain. The signals are each 10 periods in duration and were sampled at 100 samples/period. (b) Magnitude of the Fourier transforms of each of the signals in panel (a). Data points correspond to individual frequency bins.

frequency domain, a pure tone can be represented using just one frequency bin, where the duration of the signal determines the bin width. However, for signals confined to a time-varying amplitude envelope, more frequency bins are required for accurate representation. The number of frequency bins increases for signals confined to shorter periods of time.

APPENDIX C: DISTORTION PRODUCTS AND FREQUENCY MODULATIONS

We now provide a calculation that shows how the Gabor limit applies to frequency-modulated signals and how distortion products can be used to overcome this limitation. We use the frequency modulations of male mosquito wingbeats as an illustrative example. Mosquitoes rely on precise frequency information for the ability to locate and communicate with conspecifics [23,39,48]. They have also been observed to display rapid modulations of their wingbeat frequency when in close proximity to a potential mate [40,49,50]. It has been proposed that these rapid frequency modulations may serve as mating cues between male and female mosquitoes. However, the short acoustic range of mosquito communication imposes a constraint on the duration of the audible signal detectable by mosquitoes in motion. A consequence of the previously discussed Gabor limit is that a short signal duration limits the frequency resolution of detection.

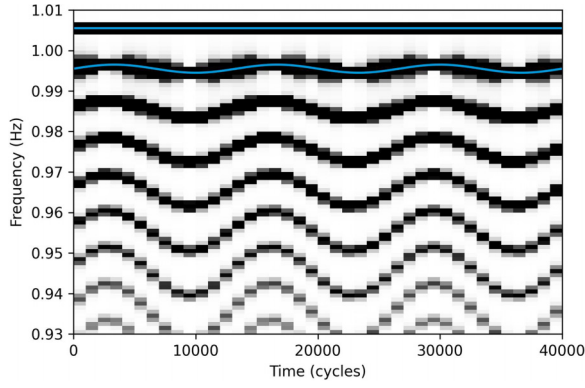


FIG. 6. Spectrogram of the response of a Hopf oscillator in the quiescent state ($\mu = -0.1$) to a two-tone stimulus. The blue curves indicate the stimulus tones. Slow modulations of the lower-frequency tone can be seen in the response at this frequency and in the distortion products.

We calculate the limitations in resolving these frequency modulations when using the short-time Fourier transform. We illustrate the limitation by showing the response of a quiescent Hopf oscillator to a two-tone stimulus, where one of the tones is frequency modulated (Fig. 6). The constant-frequency tone represents the detection of the mosquito's own wingbeats. We see that the magnitude of modulation increases with increasing distortion-product order. Every vertical slice of the spectrogram is a Fourier transform of a time window of the signal. We assume nonoverlapping time windows; however, these results remain valid for overlapping windows as well. We define the selected window of time to be T_{window} , which contains N samples. The larger the window size, the greater the frequency resolution will be in each vertical slice of the spectrogram. There are $N/2$ positive frequency bins, uniformly spaced from 0 to the Nyquist frequency (half of the sampling rate). Thus, the width of each frequency bin is

$$\Delta f = \frac{f_{\text{sample rate}}/2}{N/2} = \frac{1}{T_{\text{window}}}, \quad (\text{C1})$$

which is independent of the sampling rate. Each pixel in the spectrogram has a width of T_{window} and a height of $\Delta f = 1/T_{\text{window}}$. When the pixels are compressed in one dimension, either vertically or horizontally, they expand in the other. In fact, pixel area is conserved and unitless: $T_{\text{window}} \times \Delta f = 1$.

We consider a frequency-modulated signal of the form

$$F(t) = \sin[2\pi f(t)t],$$

$$f(t) = f_0 + \frac{\delta f}{2} \sin[2\pi f_{\text{mod}} t], \quad (\text{C2})$$

where $f(t)$ and f_0 represent the instantaneous frequency of the signal and the carrier frequency, respectively. f_{mod} is the frequency of the modulator, and $T_{\text{mod}} = 1/f_{\text{mod}}$ is the modulation period. To ensure sufficient frequency resolution for capturing the modulations of interest, we need $\delta f \geq 2\Delta f = 2/T_{\text{window}}$. However, if the window is too large, the modulations will be averaged out over time. We therefore assert at least two pixels per modulation period, the minimum needed to resolve the modulation: $T_{\text{mod}} \geq 2T_{\text{window}}$. Together, these two inequalities yield the bounds on the time window required to resolve the

modulations of interest:

$$\frac{2}{\delta f} \leq T_{\text{window}} \leq \frac{T_{\text{mod}}}{2}. \quad (\text{C3})$$

When producing a spectrogram, we have the freedom to select a time window that captures the features of interest. However, we consider the limiting case where δf is small, or T_{mod} is short. The limit occurs when equality holds among all three quantities, and we have only one choice for the time window. For a given modulation period, the smallest fluctuation in frequency that can be resolved is

$$\delta f_{\text{min}} = \frac{4}{T_{\text{mod}}} = 4f_{\text{mod}}. \quad (\text{C4})$$

If the modulations are weak (small δf), then the modulation period must be sufficiently long in order to resolve them. Conversely, if the modulations are rapid, then they must have sufficient magnitude to be resolved. This limitation does not depend on the sampling rate, the choice of the time window, or details of the carrier signal.

We now consider the results of a study that showed modulation frequencies in mosquitoes to be $f_{\text{mod}} \approx 12.5$ Hz [49]. According to Eq. (C4), the minimum change in frequency that could be resolved at this modulation rate is $\delta f_{\text{min}} \approx 50$ Hz. However, the study reports peak-to-peak modulation magnitudes ranging from 20 to 200 Hz, many of which fall below our calculated limit. This suggests that if mosquitoes are to detect the rapid frequency modulations of each others' wingbeats, then, even in ideal and noiseless conditions, they must circumvent the Gabor limit. This can be achieved through nonlinear operations on the signal [29,30] or by detecting a nonlinear component of the response.

The above calculations consider only the primary tone of the response and only the Fourier transforms for extracting frequency. However, mosquitoes have been shown to use nonlinear distortion products to detect flight tones [23,51]. As shown in Fig. 6, these distortion products modulate at larger amplitudes than the primary tones. The frequencies of the distortion products can be expressed as $f_{p,q} = pf_1 - qf_2$, where f_1 and f_2 are the primary tones, and p and q are integers corresponding to the distortion product order. We can immediately see that the magnitude of the frequency modulations increases with increasing distortion product order. Letting f_1 be the modulated tone, we find that the limit given in Eq. (C4) relaxes with increasing distortion product order:

$$\delta f_{\text{min}} = \frac{4f_{\text{mod}}}{p}. \quad (\text{C5})$$

We therefore speculate that detection of the nonlinear distortion products could allow mosquitoes to circumvent the Gabor limit and extract precise frequency information [52], thereby detecting the rapid frequency modulations.

APPENDIX D: RAPID PHASE SHIFT

We now provide a calculation showing that an acoustic signal measured by a one-dimensional sensor on the receiving insect will undergo a rapid half-cycle phase shift. Consider the flyby event with relative speed, V , and distance of closest pass, d_0 , as defined in the main text. We consider the angular

dependence of the dipole velocity field in Eq. (A9), which has the form $2 \cos \theta \hat{r} + \sin \theta \hat{\theta}$. We orient the sensor at angle ψ in this coordinate system. The scalar projection of the velocity field along the axis of this sensor results in a signal of the form

$$s(t) \propto (3 \cos^2 \theta - 1) \cos \psi - 3 \sin \theta \cos \theta \cos \psi. \quad (\text{D1})$$

Next, we make substitutions $\cos \theta = \frac{-Vt}{\sqrt{d_0^2 + (Vt)^2}}$ and $\sin \theta = \frac{d_0}{\sqrt{d_0^2 + (Vt)^2}}$, thereby parametrizing the flyby event with time, as in the main text. For simplicity, we define the timescale $\tau = d_0/V$, which would be on the order of a few cycles of the acoustic signals when using parameters from the main text. The signal then takes the form

$$s(t) \propto \frac{3 \frac{t}{\tau} \left(\frac{t}{\tau} \cos \psi - \sin \psi \right)}{1 + \left(\frac{t}{\tau} \right)^2} - \cos \psi. \quad (\text{D2})$$

Note that this function has at least one zero crossing in the domain $\frac{t}{\tau} = (-\infty, \infty)$, regardless of our choice for ψ .

In order to study the phase shift independently of the modulations in amplitude and frequency, we choose a forcing term of the form

$$F(t) = A e^{i[\omega t + \phi(t)]}, \quad (\text{D3})$$

where A and ω represent the stimulus amplitude and frequency, respectively. The time-dependent phase offset takes the form

$$\phi(t) = \frac{\pi}{1 + e^{-\frac{t}{\tau_{\text{ps}}}}}, \quad (\text{D4})$$

where τ_{ps} is the time constant associated with the speed of the phase shift. We set $\omega = \omega_0 = 2\pi$, $\mu = -0.1$, $A = 0.01$, and vary τ_{ps} to see the effects of the phase shift on the response amplitude.

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