I. INTRODUCTION

Non-equilibrium dynamics are exhibited by numerous living systems, which frequently manifest self-sustained limit cycle oscillations driven by an internal energy-consuming process \[7,10,12,13\]. An example of an active nonlinear system is provided by the inner ear. The auditory system parses pressure waves, ranging over several orders of magnitude in frequency, and detects even Ångström-scale displacements of the mechanically sensitive hair cells \[19\]. While the mechanisms behind this extraordinary sensitivity are not entirely known, previous work suggests that an internal active mechanism amplifies the incoming signal \[16,17\]. The active process is also believed to underlie the phenomenon of otoacoustic emissions, indicating the presence of an internal nonlinear oscillator.

Detection of sound in the inner ear is performed by mechano-electrical transducers - bundles of stereocilia - that protrude from the hair cells \[19\]. The stereocilia contain mechanically gated ion channels that open and close as the bundles are deflected by sound waves \[20\]. The channels are further connected to an internal active motor complex, primarily comprising of Myosin 1c, whose movement along actin filaments regulates tension in the tip links connecting the bundles \[21\]. This interplay of ion-channel gating and myosin motor activity can lead to spontaneous limit cycle oscillations, which have been observed (in vitro) \[22,23\].

Dynamics of individual hair cells, as well as the overall mechanical response of the inner ear, have been modeled with systems of nonlinear differential equations of multiple levels of complexity \[24,53,55\]. A simple two-dimensional mathematical system exhibiting the supercritical Hopf bifurcation, known as the normal form equation, has been shown to reproduce the main aspects of the auditory response \[25,27\]. A benefit of simple numerical models is that they can explain complex phenomena, such as amplification, compressive nonlinearity, etc., with sparse a priori assumptions, and few free parameters. However, for studies that seek a more direct mapping between variables of the model and underlying physiological processes, more complex models are warranted \[28,31\]. As both approaches hold benefits for the understanding of experimental results, we work with simple dynamical systems models based on the Hopf bifurcation, as well as a three-dimensional model that explicitly incorporates stereociliary position, myosin motor activity, and the somatic membrane potential \[56\].

A feature of hair cell oscillators and biological systems in general is the presence of stochasticity in the measurements of their dynamical variables \[35\]. Hair bundle motion is affected by thermal Brownian motion from the surrounding fluid; the myosin motor complex is subject to non-equilibrium noise stemming from its attachment and detachment from the actin filaments, and the membrane potential is affected by ion channel clatter and shot noise in ionic transport \[29,36,37\]. The presence of noise inherently implies the lack of experimental access to the noiseless or zero-temperature system. This implies that experimental observations can study either the noisy spontaneous oscillations, or the mean limit cycle, obtained by averaging over many trajectories. We previously observed a change in the three-dimensional model simulations, with variation in the noise amplitude. Fig. 1 illustrates differences in the zero-temperature limit cycle (red) and the average curve (dashed black) of a hair bundle’s stochastic trajectory (green), modeled using noise values representative of equilibrium fluctuations at room temperature, determined by the fluctuation-dissipation theorem \[50\]. The plot is a mapping of the three-dimensional limit cycle onto the experimentally accessible manifold defined by the bundle deflection and membrane potential measurements \[10\].

In the current work, we explore how the mean limit cycle differs from the zero-temperature one, and hence whether noise can lead to significant discrepancies between the experimentally accessible dynamics and deterministic theoretical models. Specifically, we seek to explore the causes for the rounding of the zero-temperature limit cycle that makes unavailable to experimentalists the
sharper features of the deterministic system. As a simple example, we propose a generalized Hopf oscillator that is derived from the two-dimensional model referred to earlier, with additional features added to the limit cycle. We study the energy landscape of the oscillator, by defining a scalar potential, with the zero-temperature limit cycle as the minimum, as well as a vector potential that reflects the internal active mechanism driving the oscillation. We explore how temperature variation affects the competing effects of these potentials. Under such general conditions, we demonstrate a distortion of the zero-temperature limit cycle, and explore the mechanism of corner-cutting behavior.

We aim to understand the innate limitations on theoretical models that seek to reproduce experimental data, by exploring the energy scale that may be inherently inaccessible under finite-temperature conditions, under any amount of averaging. This may impose an upper bound on the useful level of complexity of numerical models, as any small features in the limit cycle are likely to get rounded off at finite temperatures.

The remainder of this article is organized as follows. In section II we detail a two-dimensional regular Hopf oscillator in the stably oscillating regime. In section III we analyse the generalized version and illustrate the effects of stochasticity and internal active drive. Finally, we conclude in section IV where we review the difference between the experimentally accessible trajectory and the theoretical model.

FIG. 1 (color online). Effects of finite temperature using a hair bundle model: A representative stochastic trajectory (green) with superimposed zero-temperature (red) and mean (dashed black) limit cycle, computed at finite temperature of $2kT\lambda$ determined by Fluctuation-Dissipation theorem. $\lambda$ is the coefficient of viscosity [29].

FIG. 2 (color online). Numerical simulation of the stochastic Hopf oscillator: Calculations were performed using Eq. 1. (A) The finite-temperature (light blue) trajectories and the mean (red) limit cycle. (B) A typical time series (black) of the stochastic dynamics of $x(t)$ and $y(t)$.

FIG. 3 (color online). Scalar Potential map for regular Hopf: The zero-temperature limit cycle (red curve) lies in the minimum potential region of the Mexican hat potential described by Eq. 2. The colour map spans across dark blue (low potential) to light yellow (high potential).

II. REGULAR HOPF OSCILLATOR

The supercritical Hopf oscillator is the lowest dimensional system that admits limit cycle oscillations. The normal form of this dynamical system can be described in terms of the generalized position variable, $z(t) = x(t) + iy(t)$, obeying the differential equation

$$\dot{z} = z(\mu - i\omega) + b|z|^2z + \eta z$$  

The dynamics of the system are determined by parameters $\{\mu, \omega, b\}$. For $\mu > 0$, the stable solution is given by the limit cycle of radius $R_0 = \sqrt{\mu/b}$ and oscillation frequency $\omega$.

For $\langle \eta^2 \rangle > 0$, we characterize the system using a mean
limit cycle. Fig. 2 illustrates the dynamics of the stochastic system, with panel (A) showing a representative trajectory (light blue) with the superposed mean limit cycle (red), and panel (B) showing typical $x,y$ traces. Herein, $\mu = 80, b = 1, \omega = 200$, and the details of the simulation are described in Appendix A. The mean limit cycle for the finite-temperature system is computed by binning the phase space $\{-\pi,\pi\}$ into 200 bins and averaging over multiple trajectories. For this simple model of a Hopf oscillator, the average cycle is similar to the zero-temperature limit cycle, due to the inherent symmetry of the system. The two are distinct in the case of a generalized Hopf system, in which additional features are introduced, a point we address in the next section.

The parameters $\{\mu, \omega, b\}$ also define the scalar ($\phi_s$) and vector ($\phi_v$) potentials of the system, defined as

$$\phi_s = -\frac{\mu(x^2 + y^2)}{2} + \frac{b(x^2 + y^2)^2}{4} + \alpha \cos(n\theta)e^{-\left(\sqrt{x^2+y^2} - \sqrt{\mu/b}\right)^2}$$

$$\phi_v = -\frac{\omega(x^2 + y^2)}{2} \hat{z}$$

Across a range of noise amplitudes, the limit cycle trajectories are constrained to the trough of the scalar potential at $\sqrt{\mu/b}$. An example of this is illustrated in Fig. 3 for the zero-temperature limit cycle. The curl of vector potential lies along the direction of zero-temperature limit cycle tangents. Henceforth, we refer to $\nabla \times \phi_v$ as $f_v$. As these two potentials show similar symmetry, in the presence of stochastic noise, the system exhibits a mean limit cycle identical to its zero-temperature counterpart.

### III. GENERALIZED HOPF OSCILLATOR

In a generalized Hopf system, we introduce features that lead to a difference in symmetries of the two potentials, and demonstrate a distortion in the mean behaviour, with the particle occasionally cutting across certain features in the scalar potential landscape. We explore this phenomenon by modulating $\phi_s$. We use the following model to demonstrate the phenomenon:

$$\phi_s = -\frac{\mu(x^2 + y^2)}{2} + \frac{b(x^2 + y^2)^2}{4} + \alpha \cos(n\theta)e^{-\left(\sqrt{x^2+y^2} - \sqrt{\mu/b}\right)^2}$$

As one may expect, the zero-temperature oscillator occupies the low potential regions at nearly all phases of the oscillation, as observed in Figs. 5(A),(B). However, upon increasing the stochasticity in the system as in panels (C) and (D), one observes trajectories that deviate from the mean curve and cut across sharp features in the average path. While most of these pinch back at locations of the nearest global minimum in the potential, some cross over to the next hill. The number of such deviations increases with temperature.

On calculating the mode values of such corner cuts, one observes that the underlying mean limit cycle path corresponds to the region where $f_v$ has a component normal to the limit cycle. Fig. 6 illustrates one of the mean limit cycle lobes (grey) of the finite-temperature system of Fig. 5(D) and the direction of $f_v$ (orange arrows). The dark blue regions (A,B) correspond to the arclengths where the corner-cutting trajectories respectively exit from and merge into the average stochastic curve. The difference in the number of corner-cutting trajectories from the two possible mean paths is evidence
Scalar Potential map for generalized Hopf: 3d plot of the scalar potential in Eq. 4 for $n = 4$ with the valleys seen in dark blue and hills in between them. The valleys are situated at $\theta = \{\pi/4, 3\pi/4, -\pi/4, -3\pi/4\}$. The color map spans across dark blue (low potential) to light green (high potential). The zero-temperature limit cycle (yellow) for small vector potential skirts around the hills and pinches at the valleys.

Finite temperature plots for oscillator with low vector potential strength: (A) Zero-temperature oscillator occupies minimum potential regions. (B) One lobe of the potential landscape. (C) Oscillator at $\langle \eta^2 \rangle = 10$. (D) Oscillator at $\langle \eta^2 \rangle = 30$. A (black) arrow points to an example of a corner cutting trajectory.

Direction of $f_v$: One of the lobes of the mean limit cycle (grey) of the $\langle \eta^2 \rangle = 30$ stochastic system, with the (blue) regions (A,B) corresponding to arclengths amidst which the corner cutting trajectories deviate from the particle's average behaviour. The direction of $f_v$ is illustrated by (orange) arrows. This lobe corresponds to the marked lobe in the (upper right) inset.

Panels (A)-(D) illustrate potential energies normal to the underlying zero-temperature path corresponding to the arclength A-B of Fig. 6. Positions of the noiseless system are highlighted by (red) crosses. These correspond to points on the (yellow) limit cycle demarcated by (black) cuts.

The mean limit cycle of Fig. 6 is calculated in a similar manner as the regular Hopf oscillator, with an additional calculation at each phase, checking for the presence of one or two maxima in the trajectory density. The peaks are considered distinct if they occur radially separated from $\sqrt{\mu/b} = \sqrt{80}$ by a distance of 0.2 or more. We identify the corner-cutting paths as events that lie at an energy distance of $3kT$ away from the respective mean curve.

To analyze how the angle between $f_v$ and the tangent aids the escaping trajectories, we look at potential energy maps orthogonal to the zero-temperature limit cycle in Fig. 7. In a system driven by a vector potential of low strength, the mean curve shown in Fig. 6 is similar to the zero-temperature curve. However, this does not hold true for high $\omega$s, and the potential maps centered about the zero-temperature curves reflect the effects of both noise and $f_v$.

Panels (A)-(D) illustrate potential energies normal to the underlying zero-temperature path corresponding to the arclength A-B of Fig. 6. Positions of the noiseless system are highlighted by (red) crosses. These correspond to points on the (yellow) limit cycle demarcated by (black) cuts.

The prominent hill in (A) and the valley in (D) are caused by the $\alpha$ modulation in the potential. As the particle traverses along this path, $f_v$ drives it away from the local minimum. Additionally, energy balance in the presence of stochastic forces leads to trajectories that lie at a higher potential energy and consequently deviate from the mean curve. At sufficiently high noise, these trajectories escape the global minima and follow the vector potential symmetry (Fig. 9E).

The presence of such corner cutting trajectories, distorts the mean limit cycle in comparison to the zero-temperature curve. We plot a heat map of distance between the average curve at $\langle \eta^2 \rangle = 2000$ and the underlying noiseless cycle in Fig. 8, where cooler(yellower) colors depict less distance. We notice that the greatest devia-
FIG. 7 (color online). Potential energy maps for low $\omega$: (A-D) Energy landscapes in the $\hat{n}$ direction to the zero-temperature limit cycle, corresponding to the A-B arclength in Fig. 6. The (red) cross is indicative of the noiseless particle position, with negative values pointing towards $(0, 0)$. These positions correspond to the (black) cuts along the (yellow) limit cycle atop.

B. Stochasticity and Internal active mechanism

The nature of the oscillator varies with noise strength and $f_\omega$. As seen in Fig. 6, increasing $\omega$ drives the particle to follow the vector potential symmetry. At sufficiently high values, the resulting zero-temperature circular limit cycle, shown by the panel in (L), is indistinguishable from the standard limit cycle of the simple Hopf oscillator.

Increasing noise variances for the $\omega = 0$ curve, shown in panels (A, D, G, J), leads to the particle occupying more phase space and escaping from the global minimum that it initially resides in. The trajectories defined by $\omega = 101$ tend to avoid the global maxima, leading to curves shown in panels (B, E, H, K). Finally, at higher $\omega = 200$, the trajectories plotted in (C, F, I, L) exhibit behavior reflecting the vector potential symmetry. An analysis of this high vector potential system is elaborated upon in Appendix B. At sufficiently high temperatures, the trajectories fill the available phase space.

IV. SUMMARY

We propose that the fluctuations of a stochastic oscillator with an internal active mechanism change the size and shape of its average limit cycle as a function of noise amplitude. We predict that one of the ways this distortion occurs is through the competing effect of the differing symmetries of the system’s energy landscape and its internal drive. We illustrate this idea through numerical simulations of a generalized Hopf oscillator, spanning across varying noise magnitudes and strengths of the underlying vector potential.

We find that in regions where the scalar potential map is relatively smooth, noise aided by the internal active force results in corner cutting trajectories (Fig. 7). This causes rounding of the theoretical zero-temperature limit cycle. The mean limit cycle of the finite-temperature trajectory consists of two regions (Fig. 8). The (yellow) cooler regions are robust to noise, and well-modelled by...
FIG. 9 (color online). Stochastic trajectories with variation in temperature and $\omega$: Quarter lobes of the trajectories obtained by solving Eq. 4 using $\omega$ values of \{0, 101, 200\} and $\langle \eta^2 \rangle$ values of \{0, 80, 320, 600\}.

ACKNOWLEDGMENTS

DB acknowledges support from NSF PoLS grant 1705139, and NIDCD grant R21DC015035. AJL acknowledges partial support from NSF-CMMI-1300514 and NSF-DMR-1709785.
FIG. 10 (color online). Finite temperature plots for oscillator with high vector potential strength: (A) Zero-temperature oscillator is indistinguishable from the regular example corner cutting trajectory. (B) Oscillator at $\eta^2 = 0.1$. (C) Trajectories at $\eta^2 = 10$, with a (black) arrow pointing at an example corner cutting trajectory. (D) Particle motion at a higher temperature of $\eta^2 > 30$.

Appendix A: Simulation details

The stochastic simulations of Eq. 1 were carried out using the $4^{th}$-order Runge-Kutta method for a duration of 60 s. The corresponding time steps were in the range of $10^{-4} \leftrightarrow 2 \times 10^{-3}$ s.

The noise variances $\langle \eta^2 \rangle$ in the Hopf simulations were varied from $10^{-7} \leftrightarrow 0.4$, with bundle oscillation amplitude fixed at 1; consistent results were obtained over the full span of noise amplitudes. Fig. 2 employs the highest variance value in this range. The stochastic terms driving $\{x(t), y(t)\}$ were assumed to be uncorrelated.

The time steps for the simulations of Eqs. 11 were $6 \times 10^{-7} \leftrightarrow 3 \times 10^{-6}$.

Appendix B: Large $\omega$

We substitute $\omega = 200$ in Eq. 6 with the same values for the other parameters as before. This lends us to a zero-temperature system shown in Fig. 10(A). Panels (B), (C) and (D) exhibit effects of varying stochasticity. In comparison to the small $\omega$ system, we notice that corner cutting trajectories occur at lower noise variances as pointed out by the (black) arrow for $\langle \eta^2 \rangle = 10$. While, noise enables the system to explore the phase space and occupy local low potential regions, $f_x$ forces the particle to move as directed by symmetry of the vector potential. Thus, the trajectories both traverse up the hills, and cut corners at lower noise amplitudes. This is further evident in the panels (C,F,L) of Fig. 9.

Analogous to Fig. 7 we look at the potential energy...
Potential energy maps for high $\omega$:

Panels (A)-(D) span over the zero-temperature and average limit cycles that correspond to the corner cutting trajectories of Fig. 10(C). The (red) cross indicates the noiseless particle position, and the (brown) star indicates the mean curve. The maps are in the counterclockwise order of the (black) cuts across the (red) noiseless trajectory atop.

maps orthogonal to the zero-temperature limit cycle in Fig. [11]. The (red) cross is indicative of the mean limit cycle at $\langle \eta^2 \rangle = 10$ and the (brown) star is the zero-temperature limit cycle. The zero-temperature curve follows the vector potential symmetry. While stochastic forces enable the particle to explore the local minima, $f_v$ drives it to higher potential. These cause trajectories to cut across the sharp features in the scalar potential energy landscape. The panels (A), (D) correspond to the arclengths where the corner cutting trajectories leave and re-enter the average stochastic trajectory respectively.