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Self-tuning to the Hopf bifurcation in fluctuating systems

by

Janaki Balakrishnan

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J.Balakrishnan

Max Planck Institute for Mathematics in the Sciences,

Inselstrasse 22, D-04103 Leipzig,   Germany.

Abstract

The problem of self-tuning a system to the Hopf bifurcation in the presence of noise and periodic external forcing is discussed. We find that the response of the system has a non-monotonic dependence on the noise-strength, and displays an amplified response which is more pronounced for weaker signals. The observed effect is to be distinguished from stochastic resonance. For the feedback we have studied, the unforced self-tuned Hopf oscillator in the presence of fluctuations exhibits sharp peaks in its spectrum. The implications of our general results are briefly discussed in the context of sound detection by the inner ear.

1. Introduction

An extensive literature exists on the role of noise in dynamical systems (see, for example, [1]). Critical systems subject to external forces and noise are especially interesting and manifest novel effects in diverse situations — in pattern formation in chemical reaction-diffusion systems, fluid mechanics and turbulence, electrical engineering, lasers and biological systems. In several of these situations, it is desirable to control the operating point at an optimally convenient level to get the desired dynamics. The deceptively simple act of balancing a stick is an example of a situation where one has to continually self-tune the system to the stable point [2].

In this paper we study the problem of self-tuning a dynamical oscillatory system subject to fluctuations from the environment and periodic forcing, to the Hopf bifurcation. This exercise is motivated by examples from biological systems, such as the spiking of neurons and especially by the problem of hearing and sound detection by the inner ear.

We use a general feedback equation in which the control parameter is partly generated by the dynamics of the system. Since the dynamical system we study is very general and generic, one can use our results for specific cases, such as for the system of the hair cell, which is the mechanoreceptor cell in the inner ear, responsible for detecting sound.

The paper is organised as follows. Section 2 consists of two subsections: in the first, we give a brief discussion of a biological example of sound detection by the ear to motivate our study. The second subsection is a small discussion of a generic Hopf oscillator and introduces the form of the feedback we have considered in the paper. Section 3 discusses the dynamics of a resonantly forced self-tuned generic Hopf oscillator in the presence of additive white noise. A solution of the Fokker-Planck equation in a particular frequency regime is given in Section 4, and some ideas and speculations presented on the possible applications of our results in the context of signal detection and hearing.

We obtain several new and interesting results — the system exhibits a highly amplified response which has a non-monotonic dependence on the noise-strength and which is more pronounced for weaker signals. In the biological context, this feature, of sharper sensitivity to weaker signals, is in accord with

observations made of the inner ear [5]. The underlying mechanism seems to be some kind of a stochastic "filtering" effect and is unrelated to stochastic resonance.

The distance of the control parameter from its critical value at the bifurcation for the system is computed as a measure of self-tuning. In the weak-noise limit, for the unforced self-tuned noisy Hopf oscillator, we find that for each noise-strength it is periodically modulated. Also, at certain frequencies, the oscillator makes sudden large departures from the bifurcation point. For the forced oscillator this distance increases with increasing noise strength in the weak noise limit, first very rapidly, and then gradually plateaus off.

We also find that the self-tuned unforced Hopf oscillator subject to fluctuations would exhibit delta peaks in its spectrum. In the context of hearing, we suggest that this could be the origin of the sharp peaks observed in the spontaneous otoacoustic emission spectra.

Finally in the Conclusion, we summarize the main results obtained in the paper. Some of the lengthy derivations have been presented in two Appendices.

2.   Spontaneous oscillations & Hopf bifurcation

A.   An example from biology: Sound detection by the ear

To motivate the study carried out in the paper, we provide here a brief outline of an interesting example found in a recent stream of research in biology which models the mechanotransducer cells in the ear which detect sound, as Hopf oscillators arranged along the cochlea.

The sensory receptors of the inner ear are the hair cells. In the cochlea these are responsible for our sensitivity to sound, and in the vestibule, to our sense of balance. Mechanical stimuli are received by hair bundles — assemblies of 20-300 cylindrical processes called the stereocilia (each consisting of an actin cytoskeleton ensheathed by a plasma membrane) located at the apex of the hair cell, and at their basolateral surfaces the hair cells make synapses with axons. Mechanical stimuli result in the rapid opening of ion channels located in the hair bundles, letting in an influx of current which results in electrical signals being conveyed to the nerve cells (see [3-6] for example, and references therein).

As the ear is able to respond to a wide range of stimuli, varying by several orders of magnitude [5], its responsiveness must therefore be nonlinear. At the lower end, the mammalian cochlea can respond

to sound-driven vibrations of atomic dimensions, even as low as about ± 0.3nm. In order to amplify such low intensity stimuli, it is believed that the ears have developed active force-generating dynamical processes [7-13]. The presence of such elements would also help to understand the recorded otoacoustic emissions (both spontaneous & evoked) from the hearing organ of all organisms [8,9].

Active hair bundle motion can account for many properties of the observed active processes, such as amplification, distortion tone production, spontaneous oscillations, otoacoustic emissions, high frequency selectivity and sharp sensitivity. A recent stream of research in the biophysics literature [10-14] identifies these features with signatures of a dynamical system operating near a Hopf bifurcation. The system acts in the immediate vicinity of the bifurcation as a nonlinear amplifier for sinusoidal stimuli close to the characteristic frequency. As the control parameter is varied, the system changes behaviour from a quiescent state and exhibits self-sustained oscillations. Effective amplification is achieved by tuning the system to operate close to the bifurcation. The concept of a "self-tuned Hopf bifurcation" was invoked in [11], emphasizing that a self-regulatory mechanism exists which enables the hair cell to operate in the proximity of the critical point, whatever its characteristic frequency. This work did not, however, discuss the mechanism of self-tuning. Using two adaptation mechanisms, it was demonstrated in [13] that the hair cell can produce "self-tuned critical oscillations".

In [15], a mathematical study of feedback tuning to the bifurcation was discussed for a neural integrator and for the hair cell in the absence of fluctuations. Their feedback for the system of the hair cell differs from that in [13], and from what is normally found in the biophysically-oriented literature.

In their very interesting work, Jaramillo & Wiesenfeld [16], inspired by the seminal experiments reported in [17] and the work in [18-23], proposed that Brownian motion of the hair bundle enhances the sensitivity of mechanoelectrical transduction by the inner hair cells, overcoming the huge viscous drag force of the fluid in which they are immersed and amplifying limitingly low-amplitude stimuli through stochastic resonance [22-26]. Their mechanism was based on the well-established gating-spring model [3] of mechanotransduction, and they provided as an example, the two-state model, the open and closed states of the transduction channels in the stereocilia representing the two stable states within the framework of the bistable models of stochastic resonance [22,23].

While their conjecture is highly attractive, it is still interesting to see how an active system like a single hair cell as a unit by itself responds to fluctuations and stimuli from outside, since its dynamics is controlled by feedback mechanisms – the calcium dynamics through the transduction channels being one such example. The hypothesis that the activity of the hair-cell is due to the operation of its kinematical constituents at the edge of a Hopf instability, was first worked out explicitly in [10]. If one was to accept this line of thinking, it would be of interest to see how well a generic Hopf oscillator, whose operating point is controlled through a feedback mechanism, would act as a detector. This is our motivation for studying self-tuning in a forced Hopf oscillator subject to noise.

The form of the feedback we have studied, which is partly generated by the dynamics of the system is motivated by the biological system of the hair bundle. Studying a generic system enables us to capture the essential behaviour of the simplified system dynamics and to offer possible explanations of various phenomena without having to deal with the vastly cluttered and often messy equations in complex biological systems. Thus as with all models of biological systems, substitution of actual parameters coming from the mechanoelectrical and chemical properties of a hair cell in the results we have obtained for a generic system could be expected to give better and more realistic estimates of how well a Hopf oscillator models the real biological hair cell.

A model to describe active hair bundle motion has been presented in the past by several authors [4,11,13] in the following way. Let $x(t)$ denote the displacement of the hair bundle to a periodic external stimulus F_{ext} of frequency Ω and $y(t)$ denote the force generated by the active component of the hair bundle arising from the motion of the channel motor complex along an actin filament in the stereocilium. The linear behaviour of the hair bundle displacement may be described by the equation:

$$\begin{aligned}
\lambda\frac{dx}{dt} &= -kx + y + F_{ext}(t) \\
\beta\frac{dy}{dt} &= -y - \bar{k}x
\end{aligned} \tag{1}$$

where λ, k and β stand for the drag coefficient, stiffness of the hair bundle and relaxation time of the active process and $\bar{k}$ has dimensions of a spring constant. The second equation is obeyed by the force generated by the active process within the hair bundle. The model (eqn.(1)) is described in Ref.[4,6] as also in [11,13] and arises from the gating-spring model for regulation of a mechanoreceptive ion

channel in the stereocilia, in which each channel exists within two conformations – the open and the closed states, and opening of a channel shortens the associated gating spring and its tension, lowering the energy of that state in comparison with the closed state.

The nonlinear terms in the equations arise from this swing of the gating spring which depends upon the channel open probability which is a sigmoidal function of the hair bundle displacement.

A linear stability analysis on this system shows that the system exhibits a Hopf bifurcation when $\frac{1}{\beta} = -\frac{k}{\lambda}$. These coupled equations can be rewritten as a single equation for a complex variable z

$$z = x + i\frac{y}{k} \quad . \tag{2}$$

It is possible to rewrite the resulting equation in z in a canonical normal form through a nonlinear transformation of the variable.

B. Generic Hopf oscillator

In the presence of an external driving force $F_{ext} = F_0 \cos \Omega t$, the generic normal form for a system such as eqn.(1) near a Hopf bifurcation has the form [28-31]

$$\frac{dz}{dt} = A(\omega, C)z - B(\omega, C)|z|^2 z + O(|z|^4 z) + F_0 e^{i\alpha_0} e^{i\Omega t} \bar{z}^{s-1} \tag{3}$$

where A and B are complex coefficients which depend upon the characteristic frequency ω of the Hopf oscillator and on the bifurcation parameter C of the system. The additional factor $e^{i\omega_0}$ arises from the transformation of the original equation to the normal form (eqn.(3)) and is independent of z and $\bar{z}$ (for the hair bundle, α_0 depends upon its mechanical parameters).

Equation (3) describes the system at $s : m$ resonance $(s, m$ being coprime integers), $\Omega = \omega(\frac{s}{m} + \gamma)$ where γ is the detuning parameter, and F_0 denotes the amplitude of forcing [29].

In this paper, we consider the situation in which the Hopf oscillator is in 1:1 resonance with the driving frequency, and $\gamma = 0$.

The control parameter, $C(t)$, regulates the dynamics of the oscillating system and tunes it to operate very close to the dynamical Hopf instability. In this paper, we study a Hopf oscillator having a feedback of the form

$$\frac{dC}{dt} = \Gamma(C, x(t)) \tag{4}$$

where $\Gamma(C, x(t))$ is, in general, a nonlinear function of C, and one of the dynamical variables $x(t)$ of the system.

In the case of the hair bundle, the control parameter may be taken as the concentration of the calcium entering the stereocilia, which regulates the opening and closing of ion channels present on them [13]. Here, the dynamics of the control parameter is intertwined with the dynamical motion and displacement of the hair bundle so that $C = C(t, x(t))$. Thus one could apply the results of our analysis for a generic Hopf oscillator having the feedback control (eqn.(4)) we have considered, to the system of the hair bundle.

For a generic Hopf oscillator, a solution of eqn.(3) can be found in terms of its normal modes using Fourier expansions, using the method in [11]. We give the details of this procedure in Appendix-A, stating the result below. A Fourier expansion of the variable x is made and it is assumed that the first Fourier mode x_1 is the dominant one near the bifurcation. In the absence of external forcing, this leads to the equation

$$0 \approx \lambda_6(C_0)x_1 + \lambda_8(C_0)|x_1|^2 x_1 \tag{5}$$

where $\lambda_6(C_0)$ and $\lambda_8(C_0)$ are some functions of C_0. Spontaneous oscillations occur when

$$|x_1|^2 \approx -\frac{\lambda_6(C_0)}{\lambda_8(C_0)} \quad , \tag{6}$$

for nonzero λ_6, when the right hand side of eqn.(6) is positive. This can be rewritten in the form expressed in [11] as

$$|x_1| \approx \Delta\left(\frac{C_c - C}{C_c}\right)^{1/2}, \tag{7}$$

where Δ represents a characteristic saturating value for the x variable and C_c is the critical value of the control parameter. The form expressed in eqn.(7), enables one to keep track of the distance of the control parameter from its critical value.

In this paper we do not restrict ourself to the specific problem of the hair bundle oscillations, but rather, we consider a generic Hopf oscillator system in which the control parameter is dependent upon the dynamics of the system (eqns.(4),(A-3)).

3. Self-tuned Hopf Oscillator in a fluctuating environment

A general two-variable system in the absence of external forcing, containing a Hopf bifurcation and perturbed by an external additive noise $\xi(t)$ has the form [32]

$$
d_t \begin{bmatrix} x \\ y \end{bmatrix} = \begin{bmatrix} \mu & -\omega \\ \omega & \mu \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} + \begin{bmatrix} f_1 x^2 + f_2 xy + f_3 y^2 + f_4 x^3 + f_5 x^2 y + f_6 xy^2 + f_7 y^3 \\ g_1 x^2 + g_2 xy + g_3 y^2 + g_4 x^3 + g_5 x^2 y + g_6 xy^2 + g_7 y^3 \end{bmatrix} + \begin{bmatrix} \sigma_1 \\ \sigma_2 \end{bmatrix} \xi(t) + O(4)
$$

$$(8)$$

before reduction to the normal form. Here, ω, the frequency of the oscillator and μ, which unfolds the bifurcation, are the imaginary and real parts respectively of $A(\omega, C)$. The coefficients f_i and g_i $(i = 1, \ldots n)$ are operators in general – we consider systems which allow for periodic orbits, so the coefficients are such that the system cannot be rewritten in a gradient form.

We start by observing that very close to the Hopf bifurcation, the coefficients A and B in eqn.(3) for the system with self-tuning must be understood as being Taylor expansions around the critical value C_c of the control parameter.

$$
A(\omega, C) = A(C_c) + A'(C_c)(C_0 - C_c) + \frac{1}{2}(C_0 - C_c)^2 A''(C_c) + O(A''')
$$

$$
B(\omega, C) = B(C_c) + B'(C_c)(C_0 - C_c) + \frac{1}{2}(C_0 - C_c)^2 B''(C_p) + O(B''')
$$

$$(9)$$

From eqn.(7) we see that for the system described by eqn.(3), spontaneous oscillations become possible when

$$
C_0 - C_c \approx \frac{C_c}{\Delta^2} |x_1|^2
$$

$$(10)$$

We substitute this into eqn.(9) and use the resulting expressions in eqn.(3) to write down the following normal form equation for a generic Hopf oscillator with a feedback control eqn.(4), and perturbed by an external periodic forcing

$$
\frac{dz}{dt} = \left(A(C_c) + A'(C_c)\frac{C_c}{\Delta^2}|x_1|^2 + \ldots \right) z - \left(B(C_c) + B'(C_c)\frac{C_c}{\Delta^2}|x_1|^2 + \ldots \right)|z|^2 z + O(|z|^4 z) + F_0 e^{i\alpha_0} e^{i\Omega t} \bar{z}^{s-1}
$$

$$(11)$$

As already mentioned, we study only the case of 1:1 resonance with $s = 1$ in this paper.

We introduce the coefficients

$$
\beta = Re(A(C_c)); \quad l = Re(B(C_c)); \quad \beta'(C_c) = Re(A'(C_c))
$$

$$
\omega = -Im(A(C_c)); \quad d = -Im(B(C_c)); \quad \omega'(C_c) = -Im(A'(C_c))
$$

$$(12)$$

In order to study fluctuations in the system close to the bifurcation, we follow the method developed in [33] (see also [35]) for the case of the weak-noise limit. The system of equations (11) are then rewritten in the form

$$\frac{dz}{dt} = f(z, \bar{z}, t) + \epsilon^{1/2} \xi(t) \tag{13}$$

where $f(z, \bar{z}, t)$ includes all the deterministic terms on the right hand side of eqn.(11), $\xi(t) = \xi_1(t) + i\xi_2(t)$ denotes a (complex) white noise and we study the asymptotic behaviour of this stochastic process in the limit $\epsilon \to 0$. We define the noise correlations as

$$\langle \xi_1(t)\xi_1(t') \rangle = Q_a \delta(t - t')$$

$$\langle \xi_2(t)\xi_2(t') \rangle = Q_b \delta(t - t')$$

$$\langle \xi_1(t)\xi_2(t') \rangle = Q_{ab} \delta(t - t') \tag{14}$$

We now write z in polar coordinates

$$z(t) = r(t)e^{i\phi(t)} \tag{15}$$

We are interested in understanding how a Hopf oscillator having a feedback control behaves differently from one without self-tuning. To this end, we combine the Fourier expansion of the variable $x(t)$, its first Fourier mode being the dominant one, with the polar coordinate representation of z in eqn.(15) to express x_1 as

$$2|x_1| \cos(\Omega t + \alpha) = r(t)\cos\phi(t) \tag{16}$$

for nonzero x, to study the approach to criticality.

Equation (11) can then be expressed as a set of coupled Langevin equations

$$
\begin{aligned}
\dot{r} &= \beta r - \left(l - \beta' \frac{C_c}{\Delta^2} \frac{\cos^2\phi(t)}{4\cos^2(\Omega t + \alpha)} \right) r^3 + F_0 \cos(\Omega t + \alpha_0 - \phi(t)) + O(r^5) + \alpha_1 \xi_r \\
\dot{\phi} &= -\omega(C_c) - \left(-d(C_c) + \omega'(C_c)\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2(\Omega t + \alpha)} \right) r^2 + F_0 \frac{\sin(\Omega t + \alpha_0 - \phi(t))}{r} + O(r^4) + \frac{\alpha_2 \xi_\theta}{r}
\end{aligned}
\tag{17}
$$

where

$$\alpha_1 \xi_r = (\cos\phi \xi_1 + \sin\phi \xi_2)\epsilon^{1/2}$$

$$\alpha_2 \xi_\theta = (\cos\phi \xi_2 - \sin\phi \xi_1)\epsilon^{1/2} \tag{18}$$

Thus the noise now becomes process-dependent, as a result of the transformation to polar coordinates.

From here one can write the Fokker-Planck equation equivalent to eqn.(17). We find

$$
\begin{aligned}
\frac{\partial P(r,\phi,t)}{\partial t} &= -\frac{\partial}{\partial r}\Big[\beta r - lr^3 + F_0\cos(\Omega t + \alpha_0 - \phi) + \beta'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2(\Omega t + \alpha)}r^3 + \frac{\epsilon}{2r}Q_{\phi\phi}\Big]P(r,\phi,t) \\
&\quad -\frac{\partial}{\partial\phi}\Big[-\omega + dr^2 + \frac{F_0}{r}\sin(\Omega t + \alpha_0 - \phi) - \omega'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2(\Omega t + \alpha)}r^2 - \frac{\epsilon}{r^2}Q_{r\phi}\Big]P(r,\phi,t) \\
&\quad +\frac{\epsilon}{2}\Big[\frac{\partial^2}{\partial r^2}Q_{rr} + \frac{\partial^2}{\partial\phi^2}\frac{Q_{\phi\phi}}{r^2} + 2\frac{\partial^2}{\partial r\partial\phi}\frac{Q_{r\phi}}{r}\Big]P(r,\phi,t)
\end{aligned}
\tag{19}
$$

where

$$
\begin{aligned}
\frac{1}{2}Q_{rr} &= Q_a\cos^2\phi + 2Q_{ab}\sin\phi\cos\phi + Q_b\sin^2\phi \\
\frac{1}{2}Q_{r\phi} &= -Q_a\cos\phi\sin\phi + Q_{ab}(\cos^2\phi - \sin^2\phi) + Q_b\sin\phi\cos\phi \\
\frac{1}{2}Q_{\phi\phi} &= Q_a\sin^2\phi - 2Q_{ab}\sin\phi\cos\phi + Q_b\cos^2\phi
\end{aligned}
\tag{20}
$$

This is in accordance with Stratonovich calculus.

Let the deterministic part of eqn.(17) have a stable solution $(\bar{r}(t),\bar{\phi}(t))$. In this limit (i.e., with $\epsilon \to 0$), the probability density initially centred around $(\bar{r}(t),\bar{\phi}(t))$ reduces for all times to

$$
\lim_{\epsilon\to 0} P(r,\phi,t) = \delta(r - \bar{r}(t))\delta(\phi - \bar{\phi}(t))
\tag{21}
$$

$\bar{r}(t)$ and $\bar{\phi}(t))$ obey

$$
\begin{aligned}
\frac{d\bar{r}}{dt} &= \beta(C_c)\bar{r} - \Big(l - \beta'(C_c)\frac{C_c}{\Delta^2}\frac{\cos^2\bar{\phi}}{4\cos^2(\Omega t + \alpha)}\Big)\bar{r}^3 + F_0\cos(\Omega t + \alpha_0 - \bar{\phi}) \\
\frac{d\bar{\phi}}{dt} &= -\omega(C_c) - \Big(-d(C_c) + \omega'(C_c)\frac{C_c}{\Delta^2}\frac{\cos^2\bar{\phi}}{4\cos^2(\Omega t + \alpha)}\Big)\bar{r}^2 + \frac{F_0\sin(\Omega t + \alpha_0 - \bar{\phi})}{\bar{r}}
\end{aligned}
\tag{22}
$$

Thus, the equation for the radial variable is not separable from ϕ, except for the special case $\phi = \Omega t + \alpha \pm 2n\pi$, $(n = 0, 1, 2, \ldots)$. For this case, one obtains in the absence of the external force, an orbitally stable periodic solution of circular form with amplitude

$$
\bar{r}_s = \pm\Big[\frac{\beta(C_c)}{\big(l - \frac{\beta'(C_c)C_c}{4\Delta^2}\big)}\Big]^{1/2}, \quad \text{for } C_c < \frac{4\Delta^2 l}{\beta'}, \ \beta > 0,
\tag{23}
$$

when

$$
\bar{\phi}_s = \cos^{-1}\Big(\frac{4d(C_c)\cos^2(\Omega t + \alpha)}{\omega'(C_c)}\frac{\Delta^2}{C_c}\Big)^{1/2}
\tag{24}
$$

in the stationary state limit $t \to 0$.

Thus, when the feedback (eqns.(4),(A-1)) is switched on, the system starts moving on a limit cycle of

a larger radius. The sign and the magnitude of the critical value of the control parameter determines the sense of rotation of the limit cycle.

In order to see how fluctuations affect the regulatory role of the control parameter in bringing the system to operate in the close proximity of the bifurcation, we will define the distance δC of the control parameter at a given operating point from its critical value. The effect of fluctuations on δC can be found by determining its noise average. In order to calculate noise averages, we must first determine the correct form of the probability distribution in the vicinity of the bifurcation. Hence the solution of the Fokker-Planck equation (19) must be found.

In order to do so, we use the singular perturbation technique as developed by Malek Mansour *et al.* [32] for studying fluctuations at the onset of a limit cycle. It was shown by these authors that the asymptotic properties of a stochastic process in the vicinity of the critical point could be studied by an appropriate scaling of the variables. In their procedure rescaled variables are introduced by expanding all quantities in terms of a single noise-smallness parameter ϵ (which is the inverse of the extensivity parameter V which denotes the size of the system). Further they showed that the critical variable exhibits amplified non-Gaussian fluctuations on a slow time scale.

Their arguments stem from their earlier result in the theory of stochastic processes that the stochastic and the macroscopic trajectories converge to a macroscopically steady state for all times, in the limit of weak noise ($\lim \epsilon \to 0$), if the state is unique and globally stable. This is an extension of the well known theorem of Kurtz (see, for instance, reference [34]). For a two-variable system such as described by eqns.(8) and (13), the stochastic variables $x(t)$ and $y(t)$ can then be perturbatively expanded in powers of ϵ^{1-a}, and ϵ^{1-b}, $(0 \le a, b < 1)$ around the deterministic steady state $\bar{x}(t)$, $\bar{y}(t)$. Scaled variables u and v, can then be defined in terms of the deviations: $u = \epsilon^{a-1}(x - \bar{x})$, $v = \epsilon^{b-1}(y - \bar{y})$ and a probability density for the scaled variables helps to study the asymptotic properties of the process [33]. a and b are chosen so that the probability density remains normalizable in the weak noise limit.The values of a and b are further restricted to the range $\frac{1}{2} \le a, b < 1$ by the requirements that the moments of the probability density for the scaled variables, if they exist for $\epsilon \neq 0$, remain finite in the limit $\epsilon \to 0$, and that at least one of them be nonzero. We have $a = b = \frac{1}{2}$ when the initial distribution is Gaussian. The distribution does not depart from Gaussian behaviour if the fluctuations

of the scaled variables do not diverge in the long time limit. The spectral properties of the matrix constructed from the linearization of the deterministic part of the general system presented in eqn.(8), which determines the stability of the macroscopic stationary state, also determines the asymptotic behaviour of the stochastic process.

The description in terms of scaled variables enables one to determine the departure of the probability density for the stochastic process from its initial Gaussian behaviour for the macroscopic state [33]. Therefore, the scaling exponents provide, in a way, a measure of how much the fluctuations are amplified by the marginal stability of the state in the critical regime. We follow this procedure below for the stochastic system in eqns.(17),(19) whose deterministic part $(\bar{r}(t), \bar{\phi}(t))$ satisfies eqns.(21-24).

We consider in this paper only a soft transition leading to a limit cycle. Here also, as in [33], we can perform a linearization of the macroscopic state given by eqns.(21) and (22) around the stable state (eqns.(23,24)) and we are interested in the approach to the stationary state $t \to \infty$. It was argued in [33], that since beyond the critical point, the radius $\bar{r}(t)$ in eqn.(21) may evolve to a constant value $\bar{r}_s$ even though periodicity in the phase variable is retained for all time, one can hence define a scaled variable ρ as

$$r = \bar{r}_s + \rho \epsilon^{1-b} \ , \quad b < 1. \tag{25}$$

As we already discussed before, for $\epsilon = 0$, the probability distribution is a Dirac delta function (eqn.(21)) centred around the macroscopic state $(\bar{r}, \bar{\phi})$. We wish to determine the form of the distribution for $\epsilon \neq 0$.

From eqns.(23) and (24), for $\dfrac{\beta(C_c)}{\left(l - \frac{\beta'(C_c)d(C_c)}{\omega'(C_c)}\right)} < 0$, $\bar{r}_s = 0$; and from eqn.(25) $b = 1/2$, which leads to a Gaussian probability distribution.

We now consider the case $\dfrac{\beta(C_c)}{\left(l - \frac{\beta'(C_c)d(C_c)}{\omega'(C_c)}\right)} \geq 0$ in which eqns.(22) admit an orbitally stable periodic solution as already discussed in eqns.(23) and (24).

In order to facilitate analysis of (19), we rewrite it in an autonomous form by extending the phase space through the transformation

$$\lambda = \Omega t + \alpha \tag{26}$$

so that

$$\dot{\lambda} = \Omega \tag{27}$$

Close to the bifurcation, we scale r as in eqn.(25) and the other quantities as

$$\beta = \tilde{\beta}\epsilon^{2c}$$

$$\bar{r}_s \sim O(\epsilon^c) = \hat{r}_s\epsilon^c \quad , \quad \hat{r}_s \sim \frac{\tilde{\beta}^{1/2}}{l^{1/2}} \quad \text{(because of eqn.(22))}$$

$$\phi = \phi$$

$$F_0 = \hat{\hat{F}}_0\tilde{\beta}^{3/2}\epsilon^c = \hat{F}_0\epsilon^{3c} \qquad , \tag{28}$$

where $\tilde{\beta} > 0$ and is independent of ϵ, $c > 0$, and in the close vicinity of the bifurcation $c > 1 - b$. In terms of the scaled variables, eqn.(19) can be rewritten as

$$
\begin{aligned}
\frac{\partial\wp(\rho,\phi,\lambda,t)}{\partial t} &= -\frac{\partial}{\partial\rho}\Bigg[\frac{\epsilon^{2b-1}Q_{\phi\phi}}{2(\rho+\hat{r}_s\epsilon^{b+c-1})} + \hat{F}_0\epsilon^{b+3c-1}\cos(\lambda-\phi+\alpha_0-\alpha) + \tilde{\beta}\hat{r}_s\epsilon^{b+3c-1} + \tilde{\beta}\rho\epsilon^{2c} \\
&\quad - \rho^3\Big(l - \beta'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2\lambda}\Big)\epsilon^{2-2b} - 3\rho^2\Big(l - \beta'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2\lambda}\Big)\hat{r}_s\epsilon^{-b+c+1} \\
&\quad - 3\rho\Big(l - \beta'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2\lambda}\Big)\hat{r}_s^2\epsilon^{2c} - \Big(l - \beta'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2\lambda}\Big)\hat{r}_s^3\epsilon^{b+3c-1}\Bigg]\wp(\rho,\phi,\lambda,t) \\
&\quad - \frac{\partial}{\partial\phi}\Bigg[-\omega + d\epsilon^{2-2b}\rho^2 + 2d\rho\hat{r}_s\epsilon^{-b+c+1} + d\hat{r}_s^2\epsilon^{2c} + \frac{F_0\sin(\lambda-\phi+\alpha_0-\alpha)\epsilon^{b+3c-1}}{(\rho+\hat{r}_s\epsilon^{b+c-1})} \\
&\quad - \omega'\frac{C_c}{\Delta^2}\frac{\cos^2\phi(t)}{4\cos^2\lambda}\Big(\rho^2\epsilon^{2-2b} + 2\rho\hat{r}_s\epsilon^{-b+c+1} + \hat{r}_s^2\epsilon^{2c}\Big) - \frac{\epsilon^{2b-1}Q_{r\phi}}{(\rho+\hat{r}_s\epsilon^{b+c-1})^2}\Bigg]\wp(\rho,\phi,\lambda,t) \\
&\quad + \frac{1}{2}\Bigg[\epsilon^{2b-1}\frac{\partial^2}{\partial\rho^2}Q_{rr} + \epsilon^{2b-1}\frac{\partial^2}{\partial\phi^2}\frac{Q_{\phi\phi}}{(\rho+\hat{r}_s\epsilon^{b+c-1})^2} + 2\epsilon^{2b-1}\frac{\partial^2}{\partial\rho\partial\phi}\frac{Q_{r\phi}}{(\rho+\hat{r}_s\epsilon^{b+c-1})}\Bigg]\wp(\rho,\phi,\lambda,t) \\
&\quad - \Omega\frac{\partial}{\partial\lambda}\wp(\rho,\phi,\lambda,t) \tag{29}
\end{aligned}
$$

We must now determine the appropriate values of b and c which would lead to a nontrivial form of the probability density of the scaled variables. Following the argument in [33], for $b \leq 1/2$, to dominant order in ϵ, one finds from eqn.(29) that

$$\partial_t\langle\rho^2\rangle = \frac{Q_{rr}}{\epsilon^{1-2b}} > 0 \tag{30}$$

which diverges as $\epsilon \to 0$, so that fluctuations in the long time limit of the radial variable are divergent. This leads to the conclusion that close to the bifurcation the long time regime must be described by $b > 1/2$.

Using this result and integrating eqn.(29) with respect to ϕ we find that

$$\partial_t\wp(\rho,\lambda,t) = O(\epsilon^{2b-1},\epsilon^{2-2b},\epsilon^{1-b+c},\epsilon^{2c},\epsilon^{b+3c-1}) \sim \mathcal{Q}(1) \tag{31}$$

For a given ρ if we denote the conditional probability of ϕ by $\wp(\phi|\rho, \lambda, t)$, then from equations (29)-(31) we see that

$$\partial_t \wp(\phi|\rho, \lambda, t) + \Omega \frac{\partial}{\partial \lambda} \wp(\phi|\rho, \lambda, t) = \omega \frac{\partial}{\partial \phi} \wp(\phi|\rho, \lambda, t) + \mathcal{Q}(1). \tag{32}$$

This has the solution

$$\lim_{\epsilon \to 0} \wp(\phi|\rho, \lambda, t) = \delta(t + \frac{\phi}{\omega} - \frac{\lambda}{\Omega}) \tag{33}$$

for all times, if this is the initial conditional probability. For the non-deterministic case $\epsilon \neq 0$, the probability distribution for the 2+1-dimensional problem approaches a stationary distribution $\wp_{as}(\phi|\rho, \lambda, t)$ for large values of the time. So in this case, the $t \to \infty$ limit is taken before the $\epsilon \to 0$ limit. Then one finds that

$$\lim_{\epsilon \to 0} \lim_{t \to \infty} \wp(\phi|\rho, \lambda, t) = \lim_{\epsilon \to 0} \wp_{st}(\phi|\rho, \lambda) = \frac{1}{2\pi}. \tag{34}$$

Integrating eqn.(29) over ϕ, and using eqn.(34) to calculate the conditional averages, we obtain for the marginal density $\wp(\rho, \lambda, t)$

$$\begin{aligned}
(\partial_t + \Omega \partial_\lambda) \wp(\rho, \lambda, t) = & -\frac{\partial}{\partial \rho} \Big[\frac{\epsilon^{2b-1} Q}{2(\rho + \hat{r}_s \epsilon^{b+c-1})} + \nu \hat{F}_0 \epsilon^{b+3c-1} + \tilde{\beta} \hat{r}_s \epsilon^{b+3c-1} + \tilde{\beta} \rho \epsilon^{2c} \\
& - \rho^3 \Big(l - \beta' \frac{C_c}{\Delta^2} \frac{\mu}{8 \cos^2 \lambda} \Big) \epsilon^{2-2b} - 3\rho^2 \Big(l - \beta' \frac{C_c}{\Delta^2} \frac{\mu}{8 \cos^2 \lambda} \Big) \hat{r}_s \epsilon^{-b+c+1} \\
& - 3\rho \Big(l - \beta' \frac{C_c}{\Delta^2} \frac{\mu}{8 \cos^2 \lambda} \Big) \hat{r}_s^2 \epsilon^{2c} - \Big(l - \beta' \frac{C_c}{\Delta^2} \frac{\mu}{8 \cos^2 \lambda} \Big) \hat{r}_s^3 \epsilon^{b+3c-1} \Big] \wp(\rho, \lambda, t) \\
& + \frac{1}{2} \epsilon^{2b-1} \frac{\partial^2}{\partial \rho^2} Q \wp(\rho, \lambda, t)
\end{aligned} \tag{35}$$

where the constants ν and μ take the values

$$\nu = \begin{cases} 1 & \text{for} \quad \phi(t) = \Omega t + \alpha \pm 2n\pi \\ 0 & \text{otherwise} \end{cases}$$

$$\mu = \begin{cases} 2 \cos^2 \lambda & \text{when} \quad \nu = 1 \\ 1 & \text{otherwise} \end{cases}$$

and

$$Q = Q_a + Q_b. \tag{36}$$

We observe that the integration over ϕ immediately gives rise to an unexpected situation: *the driving term vanishes unless $\phi = \lambda \pm 2n\pi$.* Thus we are led to the important result that for an external periodic

force to have any effect at all on the dynamics of a system with fluctuations near a Hopf bifurcation, the imaginary part (which is the fast variable) of the original two-dimensional Hopf oscillator (eqn.(3)), *must be phase-locked to the frequency of the external periodic force.*

For the system of the hair bundle, this translates to the condition that the "effective active force" of the hair bundle system or "effective phase" of the Hopf oscillator, $(\phi - \alpha)$ is in synchrony with the frequency of the periodic external stimulus:

$$\phi(t) - \alpha = \Omega t \pm 2n\pi \quad . \tag{37}$$

A little reflection shows that this situation stems from the existence of orbitally stable periodic solutions for the phase-locked condition in the absence of noise as in eqn.(23).

The drift and the diffusion terms in eqn.(35) should contribute equally to the probability density in the deterministic limit $(\epsilon \to 0)$ for all values of c and thus should be of the same order in ϵ. This necessitates that $b = 3/4$, from where one finds the value $c = 1/4$ separating the critical regime from the Gaussian one. Substituting these values into eqn.(35), we get

$$\frac{1}{\epsilon^{1/2}}(\partial_t + \Omega\partial_\lambda)\wp(\rho, \lambda, t) = -\partial_\rho\Big[-2\rho\tilde{\beta} - 3\tilde{\beta}^{1/2}l^{1/2}\rho^2 - l\rho^3 + \frac{Q}{2\big(\rho + \frac{\tilde{\beta}^{1/2}}{l^{1/2}}\big)} + \nu\hat{F}_0$$
$$+ \Big(\rho + \frac{\tilde{\beta}^{1/2}}{l^{1/2}}\Big)^3 \frac{\mu\beta' C_c}{8\Delta^2 \cos^2\lambda}\Big]\wp(\rho, \lambda, t) + \frac{1}{2}Q\frac{\partial^2}{\partial\rho^2}\wp(\rho, \lambda, t). \tag{38}$$

The last term in the square bracket is the contribution from self-tuning.

The scaling of the time by $\epsilon^{-1/2}$ on the left hand side shows that the dynamics of the critical, radial variable evolves at a different, slower time scale as compared with the phase variable, representing the reduction of the original system in the presence of noise to the center manifold $\frac{dC}{dt} = 0$ [36].

In general, even if a system is autonomous to begin with, a feedback control can turn it to a non-autonomous one. The normal form reduction for deterministic non-autonomous systems can be carried out as in [37] (see also [38,39]) and in the limit of weak noise, its reduction to the normal form can be done as in [35,40].

Finally, having found the appropriate scaling for the variables, we now re-express eqn.(38) in terms

of the original variables. We obtain

$$
\begin{aligned}
(\partial_t + \Omega\partial_\lambda)\mathcal{P}(r,\lambda,t) &= -\frac{\partial}{\partial r}\Big[\beta r - \Big(l - \frac{\mu\beta' C_c}{8\Delta^2\cos^2\lambda}\Big)r^3 + \nu F_0\Big]\mathcal{P}(r,\lambda,t) \\
&\quad - \frac{\partial}{\partial r}\Big(\frac{Q\epsilon}{2r}\Big)\mathcal{P}(r,\lambda,t) + \epsilon\frac{Q}{2}\frac{\partial^2}{\partial r^2}\mathcal{P}(r,\lambda,t) \\
&= (L_0 + L_I)\mathcal{P}(r,\lambda,t)
\end{aligned}
\tag{39}
$$

where

$$
\begin{aligned}
L_0 &= -\frac{\partial}{\partial r}\Big[\beta r - \Big(l - \frac{\mu\beta' C_c}{8\Delta^2\cos^2\lambda}\Big)r^3\Big] - \frac{\partial}{\partial r}\Big(\frac{Q\epsilon}{2r}\Big) + \epsilon\frac{Q}{2}\frac{\partial^2}{\partial r^2} \\
L_I &= -\nu F_0\frac{\partial}{\partial r}
\end{aligned}
\tag{40}
$$

Using equations (29) to (35), the probability distribution for the full system is given by

$$
P(r,\phi,\lambda,t) = \mathcal{P}(\phi|r,\lambda)\mathcal{P}(r,\lambda,t)
\tag{41}
$$

Thus, as a first step, we have reduced the original 2+1-dimensional autonomous Hopf system (equation 29) to a 1+1-dimensional problem, *i.e.*, to a 1-dimensional system in the slow variables in the extended phase space. The self-tuned system differs from the system without feedback in that the nonlinear part is modified in the drift term.

L_0 denotes the unperturbed Fokker-Planck operator. One would normally expect the periodic time dependence to be visible in the perturbation term L_I, but in the centre-manifold reduction procedure the averaging over the fast variable has eliminated this time-dependence through phase-locking. We observe another interesting phenomenon. The self-tuning term exhibits the periodic time-dependence in the Fokker-Planck equation which is absent only: (i) in the presence of an external force and (ii) when there is no feedback in the system. This is seen by substituting the values of μ and ν from eqn.(36) into eqn.(39) and comes about because of the averaging done over the fast variable which is entrained with the external driving frequency and rotates with it. In the absence of external forcing, the system is oscillatory with intrinsic frequency ω and the $x(t)$ variable has a mode expansion with respect to this intrinsic oscillator frequency. In the unforced system with the kind of feedback we have considered (eqn.(4)), the control parameter has a similar mode expansion (because of eqns.(A-1) and (A-3)). As the fast variable for the unforced system is not phase-locked with any frequency, averaging over the fast variable does not eliminate the time periodicity in the Fokker-Planck equation. *Thus, even in the absence of an external force, the effect of a*

feedback as in equations (4) and (A-3) is felt as a periodic modulation in the full Fokker-Planck equation.

We assume the following physical boundary condition for r: $\mathcal{P}(r \to \infty, \lambda, t) = 0$. Since λ is periodic, $\mathcal{P}_t(r, \lambda) = \mathcal{P}_t(r, \lambda + 2\pi)$, we can perform a Fourier expansion of $\mathcal{P}(r, \lambda, t)$ in λ to find the general asymptotic solution of eqn.(39)

$$\mathcal{P}_{as}(r, \lambda, t) = \sum_{n=-\infty}^{+\infty} W_n(r, \lambda) e^{in\Omega t} = \sum_{n=-\infty}^{+\infty} w_n \mathcal{P}_{st}(r, \lambda) e^{-in(\lambda - \Omega t)} \tag{42}$$

where $\mathcal{P}_{st}$ is the solution of the stationary problem for uniformly distributed phases α and the Fourier coefficients obey

$$\left[L_0 + L_I - \Omega \frac{\partial}{\partial \lambda} - in\Omega \right] W_n(r, \lambda) = 0, \tag{43}$$

w_n denoting the weight of the initial probability $\mathcal{P}(r, \lambda, t = 0)$ on the eigenfunction $e^{-in\lambda}$ with eigenvalue $in\Omega$.

4. Adiabatic limit

We solve for the probability distribution for the simplest case, for very small values of the frequency. In this limit, λ varies very slowly with time so that we can consider the simplified problem

$$\begin{aligned}
\partial_t \mathcal{P}_{ad}(r, \lambda, t) &= -\frac{\partial}{\partial r} \left[\beta r - \left(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda} \right) r^3 + \nu F_0 \right] \mathcal{P}_{ad}(r, \lambda, t) \\
&\quad - \frac{Q\epsilon}{2} \frac{\partial}{\partial r} \left(\frac{1}{r} \right) \mathcal{P}_{ad}(r, \lambda, t) + \frac{Q\epsilon}{2} \frac{\partial^2}{\partial r^2} \mathcal{P}_{ad}(r, \lambda, t).
\end{aligned} \tag{44}$$

For this case, we find that the solution of the stationary problem for this situation is

$$\lim_{t \to \infty} \mathcal{P}_{ad}(r, \lambda, t) = \mathcal{N}_e r \exp \left\{ -\frac{2}{Q\epsilon} \left[(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda}) \frac{r^4}{4} - \beta \frac{r^2}{2} - \nu F_0 r \right] \right\} \tag{45}$$

where the normalization constant $\mathcal{N}_e$ is given by

$$\mathcal{N}_e = \mathcal{N}_0 \left\{ \sum_{n=0}^{\infty} \frac{\Gamma(\frac{n}{2} + \frac{3}{2})}{n!} \left(\frac{2\nu F_0}{(Q\epsilon)^{\frac{3}{4}} \left(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda} \right)^{\frac{1}{4}}} \right)^n \mathcal{D}_{-\frac{n}{2} - \frac{3}{2}} \left(\frac{-\beta}{[Q\epsilon(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda})]^{\frac{1}{2}}} \right) \right\}^{-1}, \tag{46}$$

where

$$\mathcal{N}_0 = 4\pi \left(\frac{(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda})}{Q\epsilon} \right)^{\frac{3}{4}} \exp \left[-\frac{\beta^2}{4Q\epsilon(l - \frac{\mu \beta' C_c}{8\Delta^2 \cos^2 \lambda})} \right] \tag{47}$$

and $\mathcal{D}_{-n}$ are parabolic cylinder functions.

When the fast variable is phase-locked to the external periodic force we obtain the time-independent stationary probability density for the forced system to be

$$\lim_{t\to\infty} \mathcal{P}_{ad}(r,\lambda,t) = \mathcal{N}_F r \exp\left\{ -\frac{2}{Q\epsilon}\left[(l - \frac{\beta'C_c}{4\Delta^2})\frac{r^4}{4} - \beta\frac{r^2}{2} - F_0 r \right] \right\} \tag{48}$$

where

$$\mathcal{N}_F = 4\pi\left(\frac{(l - \frac{\beta'C_c}{4\Delta^2})}{Q\epsilon}\right)^{\frac{3}{4}} \exp\left[-\frac{\beta^2}{4Q\epsilon(l - \frac{\beta'C_c}{4\Delta^2})} \right]\left\{ \sum_{n=0}^{\infty} \frac{\Gamma(\frac{n}{2} + \frac{3}{2})}{n!}\left(\frac{2F_0}{(Q\epsilon)^{\frac{3}{4}}\left(l - \frac{\beta'C_c}{4\Delta^2}\right)^{\frac{1}{4}}} \right)^n \mathcal{D}_{-\frac{n}{2}-\frac{3}{2}}\left(\frac{-\beta}{[Q\epsilon(l - \frac{\beta'C_c}{4\Delta^2})]^{\frac{1}{2}}} \right) \right\}^{-1}$$

.

Thus even in the presence of external driving, the probability density evolving on the time scale of the slower critical variable is stationary because the fast variable over which averaging has been performed is phase locked with the driving frequency and rotates with it.

Fig.1 shows the effect of self-tuning on a plot of the probability distribution as a function of the radial variable. The presence of the self-tuning term increases the width of the distribution, increases the height of its peak and moves it to the right. This is enhanced much more in a forced system since the driving term increases the overall heights of the peaks and shifts these more towards the right (than for the unforced system). This is seen in Fig.2 which is the solution of eqn.(44) for the forced system in the long time limit. The sensitivity of the distribution to the angle is much larger at its decreasing side after the peak, the probability distribution not being symmetric.

The trajectories in the x-y plane for the original system (eqn.11) (written in terms of polar coordinates in eqn.(17)) are shown in a representative simulation (Fig.3). The closed orbit of unforced deterministic Hopf oscillator is shown in the solid line while the dashed orbit is for the deterministic Hopf oscillator perturbed by an external driving force. The dotted curve shows how the path gets completely changed in the presence of a very small additive noise. The effect of the feedback we have considered is seen in the figure (dash-dotted orbit) which "controls" the deviation of the path of the noisy system, bringing it towards the deterministic trajectory.

In the absence of an external driving force (when $\nu = 0$) or when the condition of phase-locking to the external force eqn.(37) is not satisfied, we observe a new feature — *the long-time limit of the probability distribution for the self-tuned unforced system is not stationary:*

$$\lim_{t\to\infty} \mathcal{P}_{ad}(r,t) = \mathcal{N} r \exp\left\{ -\frac{2}{Q\epsilon}\left[(l - \frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)})\frac{r^4}{4} - \beta\frac{r^2}{2} \right] \right\}. \tag{49}$$

In the above expression,

$$\mathcal{N} = \frac{2}{\pi^{\frac{1}{2}}} \left(\frac{(l - \frac{\beta' C_c}{8\Delta^2 \cos^2(\omega t + \alpha)})}{Q\epsilon} \right)^{\frac{3}{4}} \exp\left[-\frac{\beta^2}{4Q\epsilon(l - \frac{\beta' C_c}{8\Delta^2 \cos^2(\omega t + \alpha)})} \right] \left(\mathcal{D}_{-\frac{3}{2}}\left(\frac{-\beta}{[Q\epsilon(l - \frac{\beta' C_c}{8\Delta^2 \cos^2(\omega t + \alpha)})]^{\frac{1}{2}}} \right) \right)^{-1}.$$

(50)

Thus, a stationary probability distribution in the strict sense of time-independence does not exist even in the absence of all external forces for $\nu = 0$, when there is a feedback in the system in which the control parameter is generated by the system dynamics such as in equations (4), (A-1) and (A-3). In the adiabatic limit, the large time distribution is periodically modulated by the self-tuning term, always with $l > \frac{\beta' C_c}{8\Delta^2 \cos^2(\omega t + \alpha)}$, and exhibits peaks close to

$$t \approx < \frac{1}{\omega} \left(\cos^{-1} \left(\frac{\beta' C_c}{8\Delta^2 l} \right)^{1/2} - \alpha \right) \pm \frac{2\pi}{\omega} n \quad, \quad n = 0, 1, 2, 3, \ldots$$

(51)

These features are absent when there is no feedback control on the system.

The time-periodicity of the probability density for the self-tuned system in the absence of external force can be understood if we bear in mind that we are studying the behaviour of a system which can maintain self-sustained oscillations (even in the absence of external driving), at the onset of a limit cycle. The feedback term in the self-tuned system makes the system explicitly non-autonomous even in the absence of external driving and the noise averages of quantities, such as correlation functions are calculated in this case as for a quasistationary process, just as for the case of a driven system. But the unforced self-tuned system differs from the driven system in that the fast variable is not entrained with a particular frequency, in this case with the intrinsic frequency of the limit cycle. Then an averaging performed over the fast variable does not eliminate the temporal periodicity, and this is reflected correspondingly in the probability density.

It is known since the work of [42] that dynamical systems (both autonomous and non-autonomous) showing such periodic behaviour close to instabilities show an enhanced output in the power spectrum from the transient response before the bifurcation due to an increase in the relaxation time when the instability is approached, a phenomenon termed coherence resonance. We elaborate a little more on this for our system, towards the end of this section.

In the adiabatic limit, the mean value $\langle x(t) \rangle_{ad}$ of $x(t)$ for the forced system is given by

$$
\begin{aligned}
\langle x(t, \alpha) \rangle_{ad} &= \cos(\Omega t + \alpha \pm 2k\pi) \frac{(Q\epsilon)^{\frac{1}{4}}}{\left(l - \frac{\beta' C_c}{4\Delta^2}\right)^{\frac{1}{2}}} \\
&\times \frac{\sum_{n=0}^{\infty} \frac{(n+1)(\frac{n}{2}+1)}{\Gamma(\frac{n}{2}+\frac{3}{2})} \left(\frac{F_0}{(Q\epsilon)^{\frac{3}{4}} \left(l - \frac{\beta' C_c}{4\Delta^2}\right)^{\frac{1}{4}}}\right)^n \mathcal{D}_{-\frac{n}{2}-2}\left(\frac{-\beta}{[Q\epsilon(l - \frac{\beta' C_c}{4\Delta^2})]^{\frac{1}{2}}}\right)}{\sum_{n=0}^{\infty} \frac{(n+1)}{\Gamma(\frac{n}{2}+1)} \left(\frac{F_0}{(Q\epsilon)^{\frac{3}{4}} \left(l - \frac{\beta' C_c}{4\Delta^2}\right)^{\frac{1}{4}}}\right)^n \mathcal{D}_{-\frac{n}{2}-\frac{3}{2}}\left(\frac{-\beta}{[Q\epsilon(l - \frac{\beta' C_c}{4\Delta^2})]^{\frac{1}{2}}}\right)}
\end{aligned}
\tag{52}
$$

Details of the derivation of eqn.(52) are given in Appendix B. In the weak noise limit the asymptotic expansions of the parabolic cylinder functions may be used [41]. A few terms of the expansion are displayed below

$$
\begin{aligned}
\langle x(t, \alpha) \rangle_{ad} &= \frac{\bar{r}_s^{\frac{1}{2}}}{\beta^{\frac{3}{4}}} \cos(\Omega t + \alpha \pm 2k\pi) \\
&\times \frac{\left\{\frac{1}{(Q\epsilon)^{\frac{1}{2}}}\left[(\beta^{\frac{1}{2}}\bar{r}_s + \frac{3F_0}{4\beta^{\frac{1}{2}}}) - \frac{F_0^2 \bar{r}_s}{2\beta^{\frac{1}{2}} Q\epsilon} - \frac{F_0 \beta^{\frac{1}{2}} \bar{r}_s^3}{2(Q\epsilon)^2} + \dots\right] + \frac{2F_0}{Q\epsilon}\left(\bar{r}_s + \frac{F_0^2 \bar{r}_s}{4\beta Q\epsilon} + \frac{2F_0^2}{3(Q\epsilon)^2} + \dots\right)\right\}}{\left\{\frac{1}{(Q\epsilon)^{\frac{1}{2}}}\left[(\beta^{\frac{1}{2}}\bar{r}_s + \frac{3F_0^2 \bar{r}_s}{4\beta^{\frac{1}{2}} Q\epsilon}) + \frac{F_0^2 \bar{r}_s \beta^{\frac{1}{2}}}{(Q\epsilon)^2}(2\bar{r}_s^2 + \frac{5F_0^2}{4\beta^2}) + \dots\right] + \frac{2F_0}{Q\epsilon}\bar{r}_s\left(1 - \frac{2F_0^2}{3\beta Q\epsilon} - \frac{2F_0^2 \bar{r}_s^2}{3(Q\epsilon)^2} + \dots\right)\right\}}
\end{aligned}
\tag{53}
$$

where $\bar{r}_s$ is defined in eqn.(23).

We find the response of the system in the weak noise limit following [24,25] by expanding $\langle x(t, \alpha) \rangle_{ad}$ in a Fourier series

$$
\langle x(t, \alpha) \rangle_{ad} = \sum_{-\infty}^{\infty} M_n e^{in(\Omega t + \alpha)} \approx 2|M_1| \cos(\Omega t + \alpha)
\tag{54}
$$

A plot of the response versus the noise strength in the weak noise limit shows a non-monotonic behaviour, with very steep peaks at certain values of the noise strength, reminiscent of stochastic resonance (Fig.4). It is also possible to compute the resulting spectrum in the asymptotic limit following [25], from the phase-averaged asymptotic correlation function $\bar{K}_{as}(t, t')$

$$
\bar{K}_{as}(t, t') = 2 \sum_{n=1}^{\infty} |M_n|^2 \cos n\Omega t
\tag{55}
$$

The asymptotic spectral density which contains the delta spikes is defined from

$$
\bar{S}_{as}(\psi) = \int_{-\infty}^{\infty} d\tau \bar{K}_{as}(\tau) e^{-i\psi\tau} = 2\pi \sum_{n=1}^{\infty} |M_n|^2 \delta(\psi - n\Omega).
\tag{56}
$$

Also as in [25], the spectral power amplification η can be calculated by dividing the power P_n in the nth frequency component by the total input power P_0 in the modulation

$$
\eta = \frac{P_1}{P_0} = \frac{4\pi|M_1|^2}{\pi F_0^2} = 4\left(\frac{|M_1|}{F_0}\right)^2.
\tag{57}
$$

We observe that η depends upon the amplitude for each frequency (Fig.5). Because of phase-locking, the frequency dependence is not apparent in our formalism employing centre-manifold reduction. As the amplitude of the forcing increases, the amplification of the response of the system moves towards increasing values of the noise strength, diminishing rapidly in magnitude (Fig.5). Thus, *a noisy Hopf oscillator amplifies better weak signals.* This is reminiscent of the response of the ear — — the ear is more responsive to weak signals, cochlear amplification being most pronounced at the auditory threshold and falling steeply with increasing stimulus intensity [5,10].

It is very important to note, however, that the underlying phenomenon in a noisy Hopf oscillator with external periodic forcing is completely different from that in stochastic resonance, and rather unrelated to it. In a Hopf oscillator, even though the periodic forcing is imposed from outside, in the 1:1 resonance we have considered here, the oscillator has the same frequency of oscillation as the external periodic force. More important, in the presence of noise, there is phase-locking of the fast variable of the oscillator with the external frequency. Thus, there are no oscillations in the sense of stochastic resonance. However, in this case also, the sharply enhanced response appears to be the consequence of the interaction of the two kinds of perturbations with the stable periodic orbits of the unperturbed system, the noise always trying to kick the system out of the orbit while the applied phase-locked force kicks it back again towards the orbit.

In the presence of noise, the bifurcation point is disturbed (see [1] & references therein). In order to tune the system close to the critical point, the distance of the control parameter from its critical value C_c must be minimal

$$\delta C = C - C_c \approx \frac{C_c}{\Delta^2}|x_1|^2 \to 0. \tag{58}$$

For the system with noise, the quantity of interest is the noise averaged distance $\langle \delta C \rangle$ from the critical point.

In the presence of an external stimulus, we find on using eqn.(16)

$$\langle \delta C \rangle_e \approx \frac{C_c}{4\Delta^2\cos^2(\Omega t + \alpha)}\frac{\mathcal{N}_F}{2\pi}\int_0^{2\pi}d\phi\int_0^\infty dr\, r^4\cos^2\phi\,\delta(\phi - \Omega t - \alpha \pm 2n\pi)\exp\left\{-\frac{2}{Q\epsilon}\left[(l - \frac{\beta'C_c}{4\Delta^2})\frac{r^4}{4} - \beta\frac{r^2}{2} - F_0 r\right]\right\}$$

$$
\begin{aligned}
&\approx \frac{C_c}{4\Delta^2} \frac{(Q\epsilon)^{\frac{1}{4}}}{2(l-\frac{\beta'C_c}{4\Delta^2})^{\frac{1}{2}}} \frac{\sum_{n=0}^{\infty} \frac{(n+1)(n+3)}{\Gamma(\frac{n}{2}+1)} \left(\frac{F_0}{(Q\epsilon)^{\frac{3}{4}}\left(l-\frac{\beta'C_c}{4\Delta^2}\right)^{\frac{1}{4}}}\right)^n \mathcal{D}_{-\frac{n}{2}-\frac{5}{2}}\left(\frac{-\beta}{[Q\epsilon(l-\frac{\beta'C_c}{4\Delta^2})]^{\frac{1}{2}}}\right)}{\sum_{n=0}^{\infty} \frac{(n+1)}{\Gamma(\frac{n}{2}+1)} \left(\frac{\nu F_0}{(Q\epsilon)^{\frac{3}{4}}\left(l-\frac{\beta'C_c}{4\Delta^2}\right)^{\frac{1}{4}}}\right)^n \mathcal{D}_{-\frac{n}{2}-\frac{3}{2}}\left(\frac{-\beta}{[Q\epsilon(l-\frac{\beta'C_c}{4\Delta^2})]^{\frac{1}{2}}}\right)} \\[2mm]
&\approx \frac{C_c\beta}{4\Delta^2(l-\frac{\beta'C_c}{4\Delta^2})^{\frac{3}{2}}} \frac{[1 - \frac{4F_0}{(\beta Q\epsilon)^{\frac{1}{2}}} + 2\frac{F_0^2}{\beta Q\epsilon} - \frac{4}{3}\left(\frac{F_0}{(\beta Q\epsilon)^{\frac{1}{2}}}\right)^3 + \dots]}{[1 + \frac{2F_0}{(\beta Q\epsilon)^{\frac{1}{2}}} + 2\frac{F_0^2}{\beta Q\epsilon} + \frac{4}{3}\left(\frac{F_0}{(\beta Q\epsilon)^{\frac{1}{2}}}\right)^3 + \dots]}.
\end{aligned}
\tag{59}
$$

In this case, the feedback reduces the real part of the cubic term of the original Hopf system by a constant amount. Also $\langle \delta C \rangle_e$ increases with the noise, first rapidly, and then gradually plateaus off for larger values of the noise (Fig.6).

For the unforced self-tuned system, we obtain

$$
\begin{aligned}
\langle \delta C \rangle &\approx \frac{C_c}{4\Delta^2 \cos^2(\omega t + \alpha)} \frac{\mathcal{N}}{2\pi} \int_0^{2\pi} d\phi \int_0^{\infty} dr\, r^4 \cos^2\phi \exp\left\{ -\frac{2}{Q\epsilon}\left[(l - \frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)})\frac{r^4}{4} - \beta\frac{r^2}{2}\right]\right\} \\[2mm]
&\approx \frac{3C_c}{64\pi\Delta^2\cos^2(\omega t + \alpha)} \left(\frac{Q\epsilon}{l-\frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)}}\right)^{\frac{1}{2}} \frac{\mathcal{D}_{-\frac{5}{2}}\left(\frac{-\beta}{[Q\epsilon(l-\frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)})]^{\frac{1}{2}}}\right)}{\mathcal{D}_{-\frac{3}{2}}\left(\frac{-\beta}{[Q\epsilon(l-\frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)})]^{\frac{1}{2}}}\right)} \\[2mm]
&\approx \frac{C_c}{32\pi\Delta^2} \frac{\bar{r}_0^2}{\cos^2(\omega t + \alpha)} \left(1 + \frac{Q\epsilon}{2\beta}\frac{1}{\bar{r}_0^2} + \frac{15}{16}\left(\frac{Q\epsilon}{2\beta}\right)^2\frac{1}{\bar{r}_0^4} + \dots\right)
\end{aligned}
\tag{60}
$$

where

$$
\bar{r}_0 = \left(\frac{\beta}{l-\frac{\beta'C_c}{8\Delta^2\cos^2(\omega t + \alpha)}}\right)^{\frac{1}{2}} \qquad , \tag{61}
$$

and asymptotic expansions of the parabolic cylinder functions have been used in the weak noise limit as before. In this limit, the contributions from higher order noise terms progressively diminish and can be neglected. We observe that the contribution from the feedback equation for a fixed noise strength modulates δC periodically (Fig.7), spiking at specific frequencies. Thus, when one tries to tune the system close to the critical point for a given noise strength, at certain frequencies of the oscillator, it suddenly departs, far from the bifurcation. This behaviour essentially arises because of the dependence of the control parameter on the system dynamics. The large departures at certain frequencies reflect the role of the fluctuations in perturbing the system away from the stable limit cycle.

The sign of $\langle \delta C \rangle$ would determine whether the fluctuations have delayed or advanced the bifurcation. It is known in general that fluctuations smear and advance the bifurcation in an uncoupled system. For a generic resonantly forced Hopf oscillator, we see from eqn.(59) that $\langle \delta C \rangle$ would always be positive.

In an unforced system subject to the feedback in eqn.(4) however, we see from eqn.(60) that the sign of $\langle \delta C \rangle$ would depend upon whether l is greater than or less than $\frac{\beta' C_c}{8\Delta^2 \cos^2(\omega t + \alpha)}$.

To tune any dynamical system to operate close to the Hopf bifurcation in the presence of fluctuations, one would need to adjust the values of the parameters at the operating point so that $\langle \delta C \rangle \to 0$. For a nonlinear system to act as an efficient detector of signals in the presence of noise, it s necessary to choose parameters appropriately so that the system neither gets subject to large oscillations, nor is it far into the quiescent regime, but rather operates as close to the critical point as possible in order to achieve the maximal value of the spectral power amplification for the signal to be amplified effectively. If indeed the mechanotransducers in the inner ear, the hair cells, are Hopf oscillators *in vivo*, then, it appears that Nature has designed the living system in such a way that despite numerous defects and anomalies which occur in the organism, the actual biological parameters — the stiffness of the hair bundle, the length of the stereocilia, the calcium concentration entering them, etc., are all so accurately regulated to operate close to the oscillatory instability, as to achieve optimal efficiency and detect even the faintest whisper.

Finally, we would like to mention that the spectrum of the unforced self-tuned system shows very interesting behaviour. Because of the nature of the feedback in equations (4),(A-1) and (A-3), the self-tuned system is periodic in time and would therefore, in the presence of noise, be expected to exhibit the characteristic precursor of the Hopf instability [42]. Noisy precursors of instabilities in nonlinear systems were first studied and classified systematically in [42] and subsequently noise enhancement of precursors has been demonstrated in [43].

Using the phase-averaged asymptotic correlation function $\bar{K}_{as}(t,t') = \langle\langle x(t)x(t')\rangle\rangle_\alpha$ and after some simplifications, the asymptotic spectral density has the form (to lowest order approximation)

$$
\begin{aligned}
\bar{S}_{as}(\psi) &= \int_{-\infty}^{\infty} d\tau \bar{K}_{as}(\tau) e^{-i\psi\tau} \\
&\approx \int_{-\infty}^{\infty} d\tau \frac{1}{8\pi}\left(\frac{Q\epsilon}{2\beta} + h(t)\right) e^{-i(\psi - n\omega)\tau}.
\end{aligned}
\tag{62}
$$

Here, $\tau = t - t'$ and the time periodicity of $\bar{K}_{as}(\tau)$ arising from the feedback (the self-tuning terms) is used to expand it in Fourier series. The time-dependent periodic part has been represented by $h(t) = h(t + T)$. Approximations such as in eqn.(60) are made in the evaluation of the ratio of

the parabolic cylinder functions $\dfrac{\mathcal{D}_{-\frac{5}{2}}(-u)}{\mathcal{D}_{-\frac{3}{2}}(-u)}$.   We can see from here that the spectrum consists of

delta peaks at frequencies $(\psi - n\omega)$, $n = 0, 1, 2, \ldots$ superimposed on the spectrum of a bounded

time-periodic function. The latter arises because of the oscillatory nature of the feedback.

The delta peaks can be identified with contributions from the nonzero Floquet exponents, with the

real part of the Floquet exponent ($Re(A(C_c)) = \beta$) determining the size and shape of the peaks and

the position of the peaks being determined by the imaginary part of the exponents ($Im(A(C_c)) = \omega$).

The sign of the real part of the Floquet exponents determines the stability of the orbit in phase space,

a stable orbit being characterized by negative values for all the Floquet multipliers [42], a change in

stability being indicated by a change in their sign, the stability of the system therefore being dominated

by the properties of the Floquet exponent with the smallest negative real part. This is captured by the

Lamrey diagrams for the successive iterates of the orbit in phase space, in its corresponding Poincare

return map [44]. A statistical method based on the properties of the behaviour of the return map was

developed in a recent work [45] to detect the onset of bifurcations and their precursors.

Our results and observations above allow us to go a step further and speculate on the implications, in

the biological context of hearing, of feedback for an unforced Hopf oscillator subject to fluctuations.

We suggest that in the context of the Hopf oscillator hypothesis for the sensory hair cells, the self-tuning

mechanism for a noisy Hopf oscillator could be responsible, to a large extent, for the sharp peaks ob-

served in the spectra of otoacoustic emissions emitted spontaneously from the ears of various vertebrates

[8]. This could also be the reason for the corresponding phenomenon of autonomous vibrations observed

in Johnston's organ [9], the hearing organ of insects where the mechanotransducers are sensory neurons,

rather than hair cells.

The effect of the external noise on the self-tuning at the onset of an instability is thus visible as the

sharp peaks in the spectrum of the otoacoustic emissions.

Of course, in order to determine the frequencies at which the spectrum exhibits the delta peaks for a

given hair bundle (or for the sensory neurons in insects), one would need to know all the parameters

describing its mechanical properties – such as the length of the stereocilia, their stiffness, etc.. However,

the range of the otoacoustic spectrum would be determined by various other factors such as the number

of the mechanotransducers (Hopf oscillators), their characteristic frequencies, their arrangement on the

basilar membrane, the length of the basilar membrane, the influence of their attachments if any (such as the tectorial membrane in many organisms), and also, possibly, the influence of the efferent neurons on them. The scope of our study, however, does not extend to working out the biological details of such a system.

5. Conclusion

We have discussed how a Hopf oscillator in the presence of additive noise displays an amplified response in the presence of an external stimulus displaying some kind of a stochastic filtering effect. The effect is more pronounced for weaker signals and diminishes as the magnitude of the stimulus increases.

We have considered the case of a feedback which is generated by the system dynamics and have eliminated the fast oscillations of the system by means of centre manifold reduction, enabling us to solve the associated Fokker Planck equation in the adiabatic limit.

The fast variable of the Hopf oscillator gets phase-locked to the external frequency in the presence of periodic driving.

In the presence of an external periodic force, the distance from the bifurcation increases with increasing noise strength, first very steeply and then plateaus, showing a very gradual but definite increase with the noise. In the absence of external forces it shows a dependence on the frequency of the limit cycle for a fixed noise strength, exhibiting sharp peaks at specific frequencies.

The estimate found in our work for the distance from the bifurcation provides a useful measure for building, for instance, a detector for detecting weak signals in a noisy environment. The parameters of the actual specific dynamical system must be so adjusted as to have a minimal, if not an almost vanishing value for $\langle \delta C \rangle$ so that the system operates with maximal efficiency, and with the largest feasible value of the spectral power amplification so that even the faintest signals can be captured.

Using the actual values of biological parameters from biophysical models of the hair cell in our estimate would be a useful exercise and test to check the applicability of our theoretical treatment of self-tuning a Hopf oscillator, to actual biology.

The phenomenon of stochastic resonance has been proposed as a possible underlying mechanism for amplification of weak signals by the ear [21,16]. Our analysis shows that if the underlying force producing elements in the inner ear are indeed Hopf oscillators as has been proposed by several authors [10-12], then the reason for the amplified response is not because of stochastic resonance, and the totally unrelated stochastic "filtering" effect which we have demonstrated here might be the underlying cause.

The important feature which distinguishes these two phenomena is that of entrainment of the phase of the noisy Hopf oscillator with the stimulus frequency, which does not happen for stochastic resonance. While for the forced Hopf oscillator the peaks in the spectral power amplification diminish in magnitude with increasing stimulus amplitude, they do so moving towards increasing values of the noise strength. In contrast, in the case of stochastic resonance for a bistable potential, this shift is towards decreasing values of the noise strength [25]. These are results which are also amenable to experimental analysis. A key point of course is that stochastic resonance does not occur in the absence of an external stimulus. We found at the end of Section 4 that an unforced Hopf oscillator with feedback, does, however show the expected coherence resonance.

We suggest that within the framework of the Hopf oscillator hypothesis in hearing research, the sharp peaks observed in the spectrum of spontaneous otoacoustic emissions of various organisms could be a signature of the noisy precursor to the Hopf instability for the unforced self-tuned oscillator.

Of course, several alternative views and approaches have been extant in hearing research [46], and various theories have been proposed for the occurrence of otoacoustic emissions (both spontaneous and evoked) — see, for instance, ref.[47] and references therein. The description of the individual hair cells arranged on the cochlea as Hopf oscillators responding to stimulus frequencies resonant with their individual characteristic frequencies is fairly recent and interesting, and a description of the hair cell in a generic way aims to broadly capture the essential dynamics common to that in all organisms — mammals as well as non-mammals. In this framework, our analysis could give useful insight into the effect of fluctuations on regulatory feedback mechanisms at the cellular level.

To our knowledge, our work provides the first theoretical analysis on the consequences of feedback in a Hopf oscillator subject to noise.

A more physically appealing system to consider would be one in which the control parameter fluctuates — the resulting multiplicative noise could give much richer effects. Studies in this direction are under progress and will be reported elsewhere.

On the other hand, we would like to point out that when the system under study is a periodically forced Hopf oscillator, care must be taken to ensure that the correct equation (3) for the normal form [28-31] is employed to model it. This is especially essential when the external forcing contains more than one frequency. Thus it would be instructive to repeat the analysis in [14] using the well-established normal form equation (3) for a periodically forced system near a Hopf bifurcation [28-31].

Appendix A: Normal mode equation for a Hopf oscillator

We state here the essential outline of the steps followed to derive eqn.(5). For a periodic force $F_{ext}(t) = F_{ext}(t + \frac{2\pi}{\Omega})$, x can be expanded in terms of its Fourier modes: $x(t) = \sum_n x_n e^{in\Omega t}$. Since we consider a feedback such as in eqn.(4) which depends upon $x(t)$, we can expand $C(t)$ in Fourier modes

$$C(t) = C_0(t) + \sum_{n \neq 0} C_n e^{in\Omega t} \tag{A-1}$$

where: $C_{-n} = C_n^*$.

As in [11], a solution of eqn.(4) can be found by inverting F and expressing it as a polynomial in the variable $x(t)$ and $C(t)$. In Fourier components, we write this as

$$
\begin{aligned}
F_k &= \mathcal{F}_{kl}^{(1)} x_l + \mathcal{F}_{klm}^{(2)} x_l x_m + \mathcal{F}_{klmn}^{(3)} x_l x_m x_n + G_{kl}^{(1)} C_l + G_{klm}^{(2)} C_l C_m + G_{klmn}^{(3)} C_l C_m C_n \\
&\quad + H_{klm}^{(2)} x_l C_m + H_{klmn}^{(3)} x_l x_m C_n + M_{klmn}^{(3)} x_l C_m C_n + \ldots
\end{aligned} \tag{A-2}
$$

The indices k_i in the expansion coefficients $\mathcal{F}_{k,k_1,\ldots,k_n}^{(n)}$, $G_{k,k_1,\ldots,k_n}^{(n)}$, etc., are constrained by: $k = k_1 + \ldots + k_n$. All expansion coefficients are symmetric with respect to permutations of k_i.

The dependence of the control parameter on the x variable can then be expressed in a general way, as a power series in x

$$C_k = \zeta_{kl}^{(1)} x_l + \zeta_{klm}^{(2)} x_l x_m + \zeta_{klmn}^{(3)} x_l x_m x_n + \ldots \;, \quad k \neq 0 \tag{A-3}$$

where the expansion coefficients $\zeta_{k,k_1,\ldots,k_n}^{(n)}$ are functions of the frequency ω of the limit cycle of the oscillator, and symmetric with respect to permutations of the indices k_i which satisfy: $k = k_1 + \ldots + k_n$. Substituting eqn.(A-3) into eqn.(A-2) leads to a polynomial equation in x_0, x_k, $(k \neq 0)$, and C_0. It is assumed that close to the Hopf bifurcation, the first Fourier mode of the x variable is the dominant one. Equating like harmonics on both sides of the resulting equation, one obtains expressions for F_0, F_1, F_2, etc. In the absence of any external stimulus, the F_i's vanish, enabling one to obtain explicit expressions for x_is. Since the first Fourier mode x_1 is assumed to dominate near the bifurcation, we obtain :

$$x_0 \approx p_4(C_0) + p_5(C_0)|x_1|^2 \tag{A-4}$$

$$x_2 \approx -\frac{\lambda_2(C_0)}{\lambda_1(C_0)}|x_1|^2 \tag{A-5}$$

$$0 \approx \lambda_6(C_0)x_1 + \lambda_8(C_0)|x_1|^2 x_1 \tag{A-6}$$

where p_4 and p_5 are real and λ_l (l= 1, 2, 6, 8) complex, and they are all complicated functions of C_0, and of the expansion coefficients $\zeta_{k,k_1,\ldots,k_n}^{(n)}$, $\mathcal{F}_{k,k_1,\ldots,k_n}^{(n)}$, $G_{k,k_1,\ldots,k_n}^{(n)}$, $H_{k,k_1,\ldots,k_n}^{(n)}$ and $M_{k,k_1,\ldots,k_n}^{(n)}$. The dependence of the stationary part x_0 on $|x_1|$ can be eliminated by an appropriate choice of $p_5(C_0)$ and $p_4(C_0)$. We work with the choice $p_4 = p_5 = 0$. In the case of the hair bundle, where the x variable corresponds to the hair bundle displacement, this choice of p_4 and p_5 would correspond to the elimination of the undesirable dependence of the constant part x_0 on the motion of the system. p_4 and p_5 in this biological example would depend upon the mechanical properties of the hair bundle — however, we do not discuss this issue in our paper.

From eqn.(A-6) we arrive at eqn.(6). In general, eqn.(6) has the structure

$$|x_1|^2 \approx -\frac{a_0 + a_1 C_0 + a_2 C_0^2 + a_3 C_0^3 + \ldots}{b_0 + b_1 C_0 + b_2 C_0^2 + b_3 C_0^3 + \ldots} \tag{A-7}$$

where a_is and b_is depend upon the frequency. Thus, writing eqn.(A-7) in the form of eqn.(7) implies that

$$C_c = C_0 \left\{ 1 + \left[\frac{a_0 + a_1 C_0 + a_2 C_0^2 + a_3 C_0^3 + \ldots}{b_0 + b_1 C_0 + b_2 C_0^2 + b_3 C_0^3 + \ldots} \right]^{-1} \right\}. \tag{A-8}$$

Appendix B : Calculation of noise averages

The mean values of functions $G(z, \bar{z})$ are the noise averages

$$\langle G(z, \bar{z}) \rangle = \int dz d\bar{z} G(z, \bar{z}) P(z, \bar{z}, t) \tag{B-1}$$

which may in general be calculated in the polar coordinate representation using the reduction given by eqn.(41). For instance, the mean value of $x(t)$ can be calculated using eqn.(2) and eqn.(16)

$$\langle x(t) \rangle = \int_0^\infty r dr \int_0^{2\pi} r \cos\phi d\phi P(r, \phi, t). \tag{B-2}$$

From eqn.(41) and eqn.(42) we can calculate its asymptotic mean value

$$\langle x(t) \rangle_{as} = \int_0^\infty dr \int_0^{2\pi} d\phi r^2 \cos\phi \mathcal{P}(\phi|r, \lambda) \mathcal{P}_{as}(r, \lambda, t) \tag{B-3}$$

In the adiabatic limit we can evaluate this using eqn.(45) for the forced system

$$\begin{aligned}
\langle x(t) \rangle_{ad} &= \frac{\mathcal{N}_F}{2\pi} \int_0^\infty dr \int_0^{2\pi} d\phi \delta(\phi - \Omega t - \alpha \pm 2n\pi) \cos\phi \\
&\times r^3 \exp\left\{ -\frac{2}{Q\epsilon}\left[(l - \frac{\beta' C_c}{4\Delta^2})\frac{r^4}{4} - \beta\frac{r^2}{2} - F_0 r \right] \right\}
\end{aligned} \tag{B-4}$$

Performing this integral leads to eqn.(52).

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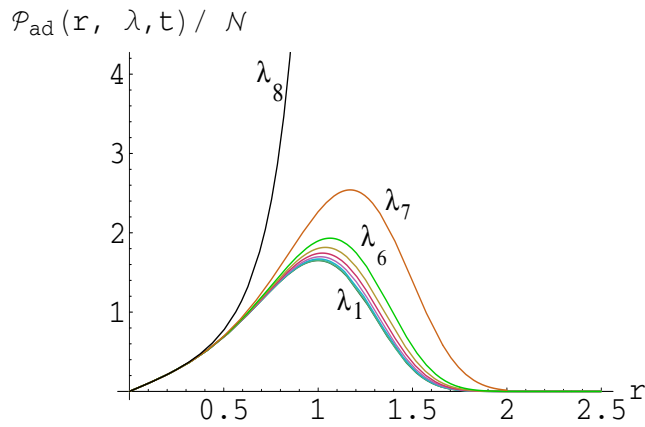
Fig.1.   **Effect of Self-tuning:**   **Un-normalised probability distribution** $\frac{\mathcal{P}_{ad}(r,\lambda,t)}{\mathcal{N}}$ **as a function of the radial variable** r **for increasing values of** λ. $(l = 2.6 \times 10^{-3};\ \beta = 1.5 \times 10^{-3};\ \frac{\beta' C_c}{4\Delta^2} = 1.2 \times 10^{-3};\ Q\epsilon = 1.0 \times 10^{-3};\ \lambda_1 = 0.05,\ \lambda_2 = 0.2,\ \lambda_3 = 0.3,\ \lambda_4 = 0.4,\ \lambda_5 = 0.5,\ \lambda_6 = 0.6,\ \lambda_7 = 0.8,\ \lambda_8 = 1.2).$
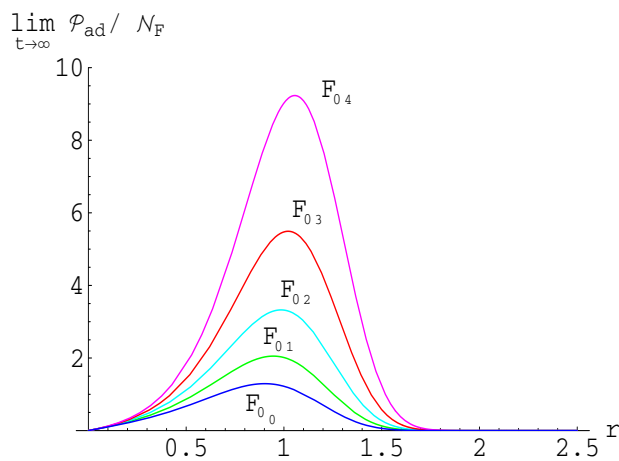

Fig.2.   **Probability distribution for a forced Hopf oscillator for different values of the external forcing** F_0.   ($l = 3.8 \times 10^{-3};\ \beta = 1.5 \times 10^{-3};\ \frac{\beta' C_c}{4\Delta^2} = 1.2 \times 10^{-3};\ Q\epsilon = 1.0 \times 10^{-3};\ F_{00} = 0.0;\ F_{01} = 0.5 \times 10^{-3};\ F_{02} = 1.0 \times 10^{-3};\ F_{03} = 1.5 \times 10^{-3};\ F_{04} = 2.0 \times 10^{-3}).$
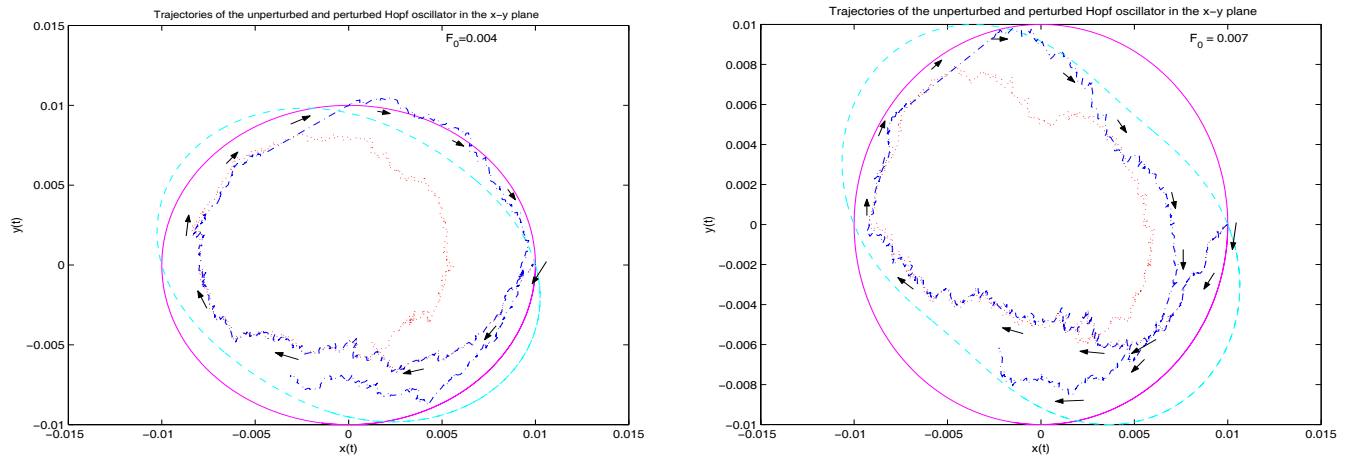
3A.   3B.

Fig.3.   **Trajectories in the x-y plane of the unperturbed and perturbed Hopf oscillators for two different amplitudes of periodic forcing** :   the solid closed curve is the trajectory of the unforced deterministic Hopf oscillator without feedback control;   the dashed trajectory is of the forced deterministic Hopf oscillator without feedback control;   the dotted one is of the noisy forced Hopf oscillator without feedback control;   and the dash-dotted trajectory shows the effect of the feedback control on the noisy forced Hopf oscillator. ($l = 0.1$; $\beta = 0.0$; $\frac{C_e}{4\Delta^2} = 0.3$; $d = 0.4$; $\alpha = 0.2$; $\alpha_0 = 0.2$; $\omega = 1.6$; $\Omega = 1.6$; $\beta' = 0.00001$; $\epsilon = 0.0009$). (**Fig.3A.** $F_0 = 0.004$,   **Fig.3B.** $F_0 = 0.007$.).
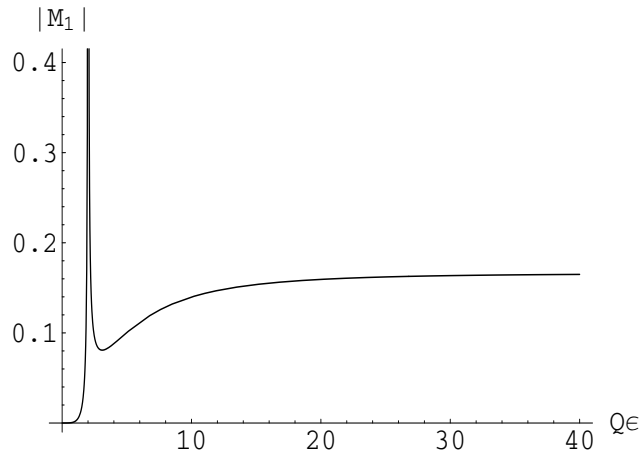
Fig.4. **Response** $|M_1|$ **of a resonantly forced self-tuned Hopf-oscillator in the presence of additive noise** $Q\epsilon$ **(for** $F_0 = 1.5 \times 10^{-3}$, $\beta = 0.1$, $l - \frac{\beta' C_c}{4\Delta^2} = 1.6 \times 10^{-3}$ **).**
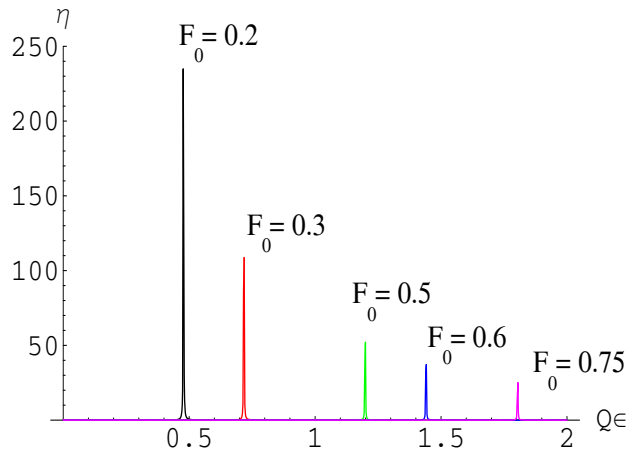
Fig.5. **Spectral power amplification** η **of a resonantly forced self-tuned Hopf oscillator as a function of the noise strength** $Q\epsilon$ **(for** $\beta = 0.1$, $l - \frac{\beta' C_c}{4\Delta^2} = 0.14 \times 10^{-3}$**).**
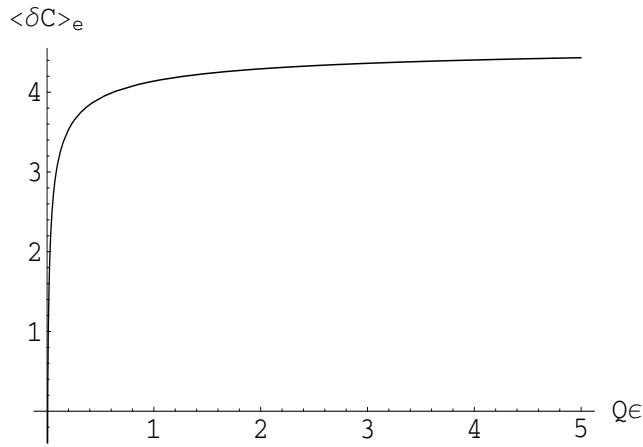
Fig.6.   **Self-tuning in a forced Hopf oscillator subject to additive noise:**   Distance $\langle \delta C \rangle_e$
from the bifurcation as a function of the noise strength $Q\epsilon$ (for $\frac{F_0}{\beta} = 0.02$).
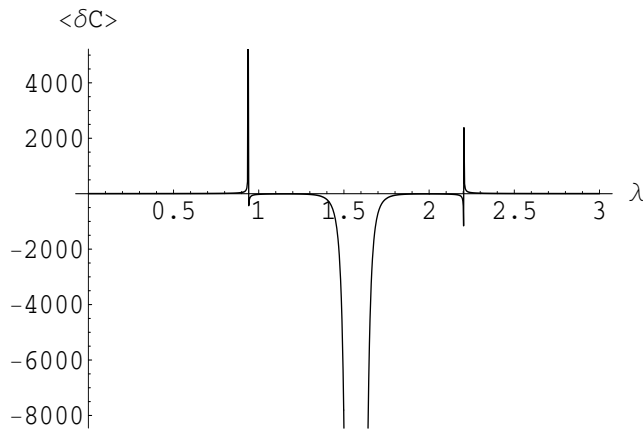
Fig.7.   **Self-tuning in a noisy Hopf oscillator in the absence of external force:**   Distance
$\langle \delta C \rangle$ from the bifurcation is periodically modulated for fixed noise strength, spiking at
specific frequencies $(\beta^2 = 1.5 \times 10^{-6}, \ l = 2.0 \times 10^{-3}, \ \frac{\beta' C_c}{8\Delta^2} = 0.7 \times 10^{-3}, \ Q\epsilon = 1.0 \times 10^{-3}).$