Local Exponents of Nonlinear Compression in Periodically Driven Noisy Oscillators

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Nonlinear compression of periodic signals is a key feature of the active amplifier in inner ear organs of all vertebrates. Different exponents $\alpha_0 \in [-0.88, -0.5]$ of the sensitivity vs forcing amplitude $|\chi| \sim f^{\alpha_0}$ have been observed. Here we calculate analytically the local exponent for a generic oscillator, the normal form of a Hopf bifurcation driven by noise and a periodic signal. For weak noise and sufficient distance from the bifurcation on the unstable side, the exponent may be close to -1 for moderate forcing amplitudes beyond linear response. Such strong compression is also found in a model of hair bundle motility.

One of the most prominent features of our sense of hearing is the ability to perceive sound stimuli that differ by 6 orders of magnitude in sound pressure [1,2]. Sound waves that hit our ear elicit a traveling wave propagating along the basilar membrane (BM) in the cochlea. Starting at the base, this wave gradually builds up and reaches a maximal amplitude at a characteristic place which depends on frequency. Vice versa, at each place a characteristic frequency ω_0 exists. The extraordinary properties of the hearing organ stem from nonlinear amplification by active processes boosting the BM vibrations. Properties of the cochlear amplifier can be characterized by observing the BM vibration amplitude at a fixed place as a function of sound pressure amplitude p and detuning $\Delta\omega = \omega - \omega_0$ where ω is the stimulus frequency.

The sensitivity, defined as the ratio $|\chi| = |x_{\mathrm{BM}}|/p$ where x_{BM} is the Fourier amplitude of vibration, is highest for weak stimuli if $\Delta\omega = 0$. Beyond linear response, it decreases in this case with growing signal amplitude; experimental data from a guinea pig cochlea [3] are shown in Fig. 1(a). As a result, a large range of input amplitudes is compressed into a smaller range of output amplitudes. This nonlinear compression can often be well described by a power law $|x_{\mathrm{BM}}| \sim p^{1+\alpha_0}$ or $|\chi| \sim p^{\alpha_0}$ with values reported in different animals and for different frequencies in the range $-0.88 < \alpha_0 < -0.5$ [4]; for the data shown in Fig. 1(a) $\alpha_0 \simeq -0.75$ for intermediate amplitudes. The transition from linear response to nonlinear compression at smaller amplitudes is highlighted by plotting the *local* exponent $\alpha = d\ln(|\chi|)/d\ln(p)$ [see Fig. 1(a), lower panel]. It starts with $\alpha \simeq 0$ (linear response) and drops for intermediate amplitudes. Typically, α increases again for sufficiently large stimulus amplitudes (not shown) [4].

It has been suggested that nonlinear amplification is based on the physics of dynamic oscillators. For a system operating at a supercritical Hopf bifurcation, mean-field theory implies $\alpha_0 = -2/3$ [5,6] [gray line in Fig. 1(a)]. The precise nature of the oscillatory modules underlying the amplification in the cochlea is still a matter of debate [7]. Active hair bundle motility is a candidate to provide

the oscillatory modules with a compressive nonlinearity. However, individual hair bundles are subject to significant noise which limits their sensitivity [8]. Recently, we demonstrated numerically that coupling of hair bundles enhances nonlinear amplification because of noise reduction [9], suggesting that coupling small groups of hair bundles is essential for the cochlear amplifier [10]. Depending on the number of coupled hair bundles, α_0 varied between -0.6 and -0.9 and can thus be below the mean-field value of $-2/3$, as is also the case for the experimental data shown in Fig. 1(a).

In this Letter, we describe an oscillatory module by a generic oscillator subject to a weak noise and a periodic driving. We calculate the sensitivity curve and its local exponent analytically in the oscillatory regime. It is shown that the local exponent can be below $-2/3$, corresponding to an even more compressive nonlinear response than expected from mean-field theory. We determine the range
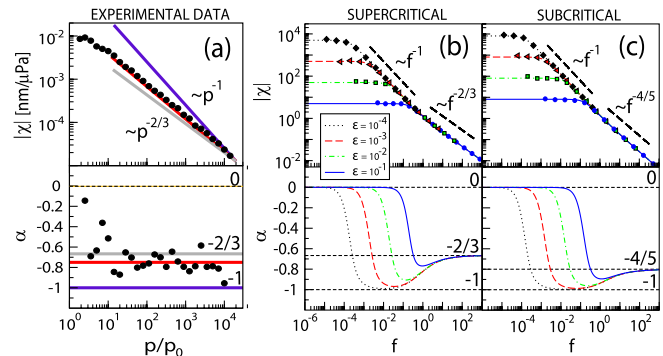

FIG. 1 (color online). Sensitivity (top) and local exponents of compression (bottom) vs input amplitude. Shown: in (a) data from [3] for the basilar membrane vibration amplitude with respect to sound pressure vs normalized sound pressure ($p_0 = 20\ \mu$Pa); in (b) for the Hopf oscillator ($r = -1$, $\omega = \omega_0 = 1$) for the supercritical [in (b) with $B = 1$, $C = 0$] and subcritical case [in (b) with $B = -1$, $C = 1$]; simulations (symbols) compared to theory [Eq. (4) and (5)], lines]. Selected exponents (0, $-2/3$, $-4/5$, and -1) are indicated; enclosed straight lines in (a) are power laws and exponents with $\alpha = -0.75$.

of input amplitudes where the exponent can be close to its lower limit $\alpha \gtrsim -1$ and derive conditions on the noise strength and the detuning to obtain strong nonlinear compression. Finally, we consider a hair bundle model with reduced noise intensity representing a system of coupled hair bundles. The main features of nonlinear compression found in the generic oscillator are faithfully reproduced by this specific system. Periodically driven noisy oscillators appear naturally also in laser physics [11], neuroscience [12], and synchronization in general [13]. The response of such oscillators is generically nonlinear and thus our analysis is relevant for a wide range of nonlinear systems.

We consider the normal form of a Hopf bifurcation driven by a complex-valued white Gaussian noise $\xi(t)$ with $\langle \xi(t)\xi^*(t + \tau)\rangle = 2\delta(\tau), \langle \xi(t)\xi(t + \tau)\rangle = 0$ and a periodic stimulus with amplitude f:

$$\dot{z} = -(r + i\omega_0)z - B|z|^2 z - C|z|^4 z + \sqrt{2\varepsilon}\xi(t) + fe^{-i\omega t}. \tag{1}$$

Here ε is the noise intensity, ω_0 denotes the characteristic frequency, and we assume real coefficients B, C and small detuning $\Delta\omega$. We are interested in the sensitivity $|\chi| = |z_1|/f$ ($z_1 = \langle \tilde{z}(\omega)\rangle$ is the average Fourier amplitude of z at the driving frequency ω) for the supercritical ($B > 0$, $C = 0$) and the subcritical case ($B < 0$, $C > 0$) as well as for tuned ($\omega = \omega_0$) and detuned ($\omega \neq \omega_0$) stimuli in the oscillatory regime ($r < 0$).

Phase and amplitude at weak noise.—We consider the limit of the oscillator dynamics where the variable $z(t)$ can be described by amplitude and phase dynamics separately. The phase difference $\psi(t) = \phi(t) - \omega t$ between the input signal $fe^{-i\omega t}$ and the output signal $z(t) = \rho(t)e^{-i\phi(t)}$ obeys the well-known dynamics [13,14]

$$\dot{\psi} = \Delta\omega - (f/\rho)\sin(\psi) + \sqrt{2\varepsilon/\rho^2}\xi(t). \tag{2}$$

At weak noise, ρ varies only little and can be replaced by the solution ρ_d of

$$0 = r\rho_d + B\rho_d^3 + C\rho_d^5 - f\langle\cos(\psi)\rangle, \tag{3}$$

where $\langle\cos(\psi)\rangle = \text{Re}(\langle e^{i\psi}\rangle)$ is taken over the steady-state ensemble of phases using $\rho = \rho_d$ in Eq. (2). We can self-consistently calculate both ρ_d and $\langle e^{i\psi}\rangle$ invoking the characteristic function for a Brownian particle in an inclined cosine potential [15] and obtain for the sensitivity

$$|\chi| = \frac{\rho_d(f)}{f} \left| \frac{I_{1+i\Delta\omega\rho_d^2/\varepsilon}(f\rho_d(f)/\varepsilon)}{I_{i\Delta\omega\rho_d^2/\varepsilon}(f\rho_d(f)/\varepsilon)} \right|, \tag{4}$$

where $I_a(\cdots)$ is the modified Bessel function of the first kind of complex order a [16]. Although we still have to solve Eq. (3) for $\rho_d(f)$ numerically, limit cases of small and large forces can be explicitly calculated because in those cases, the average $\langle\cos(\psi)\rangle$ is zero or one.

Response at the characteristic frequency ($\Delta\omega = 0$).— The sensitivity of a supercritical and a subcritical oscillator is shown in Fig. 1 for various noise levels ε. For weak

noise, we can distinguish three regimes: at weak force, the sensitivity is constant (linear response), at moderate amplitude it decays as f^{-1} for both sub- and supercritical oscillators. In the asymptotic limit of strong forcing, the exponent of nonlinear compression attains the values of $-2/3$ [supercritical oscillator, Fig. 1(b)] and $-4/5$ [subcritical oscillator, Fig. 1(c)]. The range of moderate forces for which we find an exponent close to -1 depends critically on the noise intensity. Beyond a certain noise intensity, such a range is not observed.

For $\Delta\omega = 0$ the local exponent $\alpha = d\ln(|\chi|)/d\ln(f)$ can be calculated explicitly and reads

$$\alpha = f\frac{\rho_d + \rho_d' f}{\varepsilon}\left(\frac{I_0(f\rho_d/\varepsilon)}{I_1(f\rho_d/\varepsilon)} - \frac{I_1(f\rho_d/\varepsilon)}{I_0(f\rho_d/\varepsilon)}\right) - 2, \tag{5}$$

where $\rho_d' = d\rho_d/df$. The differences of fractions of Bessel functions approaches $2\varepsilon/(\rho_d f)$ for $\rho_d f \ll \varepsilon$, resulting in $\alpha \to 0$ for $f \to 0$ [linear response for which $|\chi| \to \rho_d^2/(2\varepsilon)$]. For strong amplitude ($\rho_d f \gg \varepsilon$), the same difference approaches $\varepsilon/(\rho_d f)$ and $\alpha \simeq f\rho_d'/\rho_d - 1$; in this case the exponent depends on $\rho_d(f)$. For large f, the highest nonlinearity will dominate in Eq. (3) and will result in $\rho_d(f) \sim f^\beta$ with $\beta = 1/3$ and $1/5$ for the super- and the subcritical case, leading to $\alpha = -2/3$ or $-4/5$, respectively. If, however, f is moderately large, more specifically, if it meets the condition

$$\varepsilon/\rho_d \ll f \ll \rho_d(5C\rho_d^4 + 3B\rho_d^2 + r), \tag{6}$$

then α is close to -1 [17]. As a conservative estimate we may use the minimal solution for ρ_d which is $\rho_d(f = 0)$. In the supercritical case, for instance, we find with $C = 0$, $B > 0$, $\rho_d(f) > \rho_d(0) = \sqrt{-r/B}$, that if

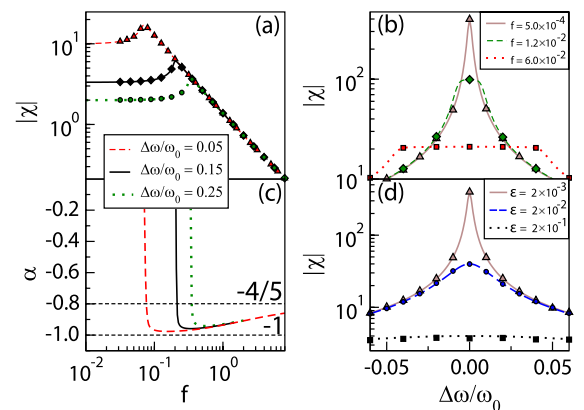$$\varepsilon\sqrt{-B/r} \ll f \ll 2\sqrt{-r^3/B} \tag{7}$$

FIG. 2 (color online). Sensitivity (a) and local exponent (c) vs forcing amplitude for a subcritical Hopf oscillator ($B = -1$, $C = 1$) for relative detuning as indicated; sensitivity vs relative detuning for different values of the force at noise intensity $\varepsilon = 0.002$ (b) and for different ε for forces in the linear response regime (d). Stochastic simulations (symbols) compared to theory [Eq. (4), lines]. Local exponents are determined by numerical differentiation using Eq. (4).

the slope of the sensitivity in a log-log plot will be close to -1. Equation (7) implies that we can always find such a range of f values if we sufficiently reduce the noise ($\varepsilon \to 0$) or increase the distance to the bifurcation (i.e., increase $|r|$). There is no negative slope close to -1 if noise is sufficiently strong: if $\varepsilon \gtrsim 2r^2/B$ one observes a crossover from the zero-exponent linear response into the asymptotics of the deterministic Hopf normal form with $\alpha = -2/3$.

For a subcritical Hopf bifurcation, taking the solution of Eq. (3) at $f = 0$, the inequality (6) turns into

$$\frac{\sqrt{2C}\varepsilon}{\sqrt{|B|+\kappa}} \ll f \ll \frac{\sqrt{|B|+\kappa}(\kappa - B)}{\sqrt{2C^3}}\kappa, \qquad (8)$$

where $\kappa = \sqrt{B^2 - 4Cr}$. In this case, even if the system is right at the bifurcation ($r = 0$), it is still possible to see a strong nonlinear compression if

$$\varepsilon\sqrt{C/|B|} \ll f \ll 2|B|^{5/2}/C^{3/2}, \qquad (9)$$

i.e., essentially for sufficiently weak noise.

Response for $\Delta\omega \neq 0$.—For a finite detuning, the response at weak stimulation is drastically reduced [Fig. 2(a)]. The sensitivity as a function of force amplitude shows a maximum at a finite force f^*. Plotted vs detuning $\Delta\omega$, the sensitivity is strongly peaked for weak driving [Fig. 2(d)] and shows the plateaus characteristic for phase locking [13] at stronger amplitude [Fig. 2(b)].

The value of the force f^* can be estimated for weak noise as the force where a barrier emerges in the inclined periodic potential of Eq. (2), i.e., $f^* = \Delta\omega\rho_d(0)$ where $\rho_d(0)$ is the solution of Eq. (3) for vanishing force [18]. In the supercritical case, $\rho_d(0) = \sqrt{-r/B}$. Because for stronger forces, the sensitivity (and its slope) follows the behavior of the tuned system, we observe an exponent α close to -1 only for sufficiently small detuning, obeying

$$|\Delta\omega|\rho_d(0) \ll f \ll \rho_d(5C\rho_d^4 + 3B\rho_d^2 + r). \qquad (10)$$

Equations (6) and (10) determine critical values of the noise intensity and of the detuning (for a given distance to the bifurcation) below which a strong compression with exponents appreciably larger than the asymptotic values $-2/3$ or $-4/5$, respectively, can be observed.

Stochastic hair bundle dynamics.—We now turn to a model of the essential transduction element in vertebrate hearing organs—the hair bundle. We consider a single hair bundle governed by two variables that describe the deflection X of the bundle and an intrinsic molecular motor displacement X_a

$$\lambda\dot{X} = -K_{GS}(X - X_a - DP_o) - K_{SP}X + F(t) + \xi(t),$$
$$\lambda_a\dot{X}_a = K_{GS}(X - X_a - DP_o) + F_{max}(SP_o - 1) + \xi_a(t)$$
$$(11)$$

where λ and λ_a are friction coefficients, K_{GS} and K_{SP} are elastic coefficients, D is the gating swing, $P_o = (1 + \exp\{[N_e\Delta G + K_{GS}D^2/2 - K_{GS}D(X - X_a)]/(N_e k_B T)\})^{-1}$ is

the open probability of transduction channels, F_{max} is the maximal force of adaptation motors, and S denotes the strength of a calcium-mediated feedback on motors; for model details and parameter values, see [8,19,20]. The system is stimulated by a force $F(t) = f\cos(\omega t)$. The Gaussian white noise terms have the correlation functions $\langle\xi(t)\xi(t + \tau)\rangle = 2\varepsilon\lambda k_B T\delta(\tau)$, $\langle\xi_a(t)\xi_a(t + \tau)\rangle = 2\varepsilon\lambda_a k_B T_a\delta(\tau)$ where T and T_a are the ambient and an effective temperature, respectively [8]. Here we consider the strength of the fluctuations to be tunable by the noise-reduction factor $\varepsilon \leq 1$. This is motivated by the observation that the main effect of a strong mechanical coupling of N hair bundles is a noise reduction, resulting in $\varepsilon \simeq 1/N$ [9].

Without noise and forcing ($\varepsilon = 0$, $f = 0$), this model can exhibit monostable, bistable, and oscillatory behavior. Varying the feedback strength S and the maximal motor force F_{max}, the transition from monostable to oscillatory behavior occurs via a sub- or a supercritical Hopf bifurcation, depending on the exact choice of parameters. The operation point of an experimental cell was close to the subcritical Hopf bifurcation, however, parameters may vary when other cells are considered. In the following, we study the local exponents and frequency tuning at two operation points within the oscillatory region [21]: the operation point OP1 is close to a supercritical Hopf bifurcation, while OP2 is a standard parameter set (fitted to an experimentally studied hair bundle) discussed previously [8,9].

Hair bundle response at the characteristic frequency.—The sensitivities of the hair bundle and the generic oscillator share many features (compare Figs. 1 and 3). A hair bundle operating close to a supercritical Hopf bifurcation, OP1 [Fig. 3(a)], shows a linear response regime at weak
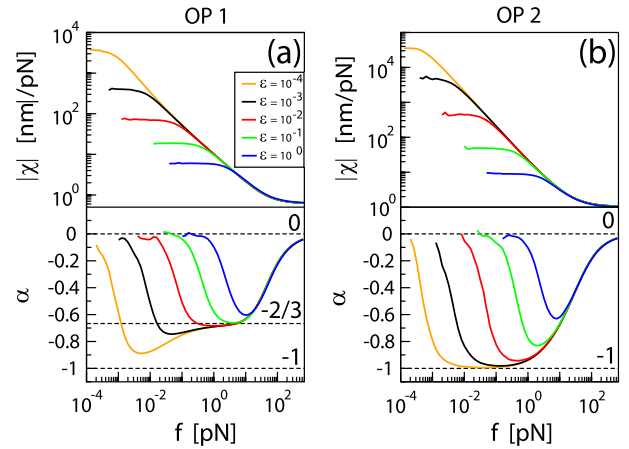

FIG. 3 (color online). Sensitivity (top) and local exponent of compression (bottom) of the hair bundle model vs forcing amplitude at operation points 1 (a) and 2 (b) for various ε as indicated ($\varepsilon = 1$ corresponds to parameters of a single uncoupled hair bundle [8]). Sensitivities and exponent were determined numerically from the response to a driving at the characteristic frequency (peak frequency of the spontaneous power spectrum).
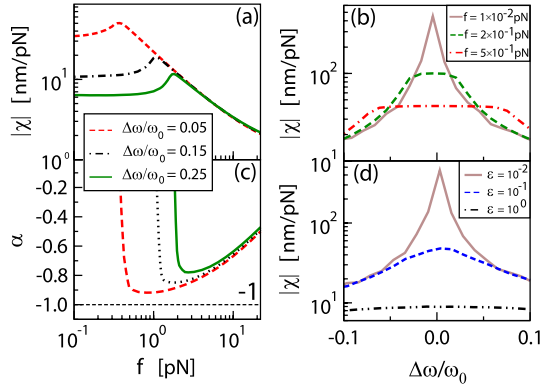
FIG. 4 (color online). Simulation results for the hair bundle model at OP2. Sensitivity (a) and local exponent (c) vs forcing amplitude for different values of the relative detuning as indicated; sensitivity vs relative detuning for different values of the force (b) and in the linear response regime for different ε (d). In (a)–(c), noise-reduction factor $\varepsilon = 0.01$.

force ($|\chi| \sim 1/\varepsilon$ with $\alpha \simeq 0$). For moderate forces, the sensitivity exhibits strong compression and the exponent passes through a noise-level dependent minimum (for the parameters chosen, up to $\alpha \simeq -0.9$). The proximity to the bifurcation reveals itself by a pronounced shoulder with $\alpha \simeq -2/3$. At large forcing, the response becomes linear again ($\alpha \simeq 0$ for large f). This latter property is due to the saturation of the nonlinearity $P_o(X - X_a)$ and is the only feature not shared by the generic oscillator. With standard parameters, OP2 [Fig. 3(b)], we find similarly a linear response at weak and large forcing. For moderate forces, strong compression is observed with α close to -1 over a range of forces that increases with decreasing ε.

Hair bundle response to detuned stimuli.—At weak detuning and small-to-moderate driving amplitude, the hair bundle model at OP2 exhibits similar behavior as a generic oscillator with a detuned stimulus (compare Fig. 2 to Fig. 4). The sensitivity as a function of stimulus amplitude passes through a maximum before approaching the sensitivity to the tuned stimulus [Fig. 4(a)]. As for the generic oscillator, there is a critical detuning below which nonlinear compression with $\alpha \gtrsim -1$ is found [Fig. 4(c)]. Plotted vs detuning [Figs. 4(b) and 4(d)], the sensitivity displays plateaus indicating a phase-locked response in qualitative agreement with the generic oscillator.

Discussion.—Our results illustrate that for noisy oscillators exponents of nonlinear compression may attain values close to -1 if noise and detuning are weak. Upper bounds for the values of noise and detuning sufficient for strong nonlinear compression are set by the oscillator's parameters. One important precondition for strong compression and a fine-tuned response is to be on the oscillatory side, not on the stable side of the Hopf bifurcation. For a supercritical bifurcation, strong compression is found sufficiently far from the bifurcation point. For a subcritical bifurcation, strong compression may already occur at the bifurcation point $r = 0$.

In the mammalian cochlea, different values of the exponent of nonlinear compression were observed ranging between -0.5 and -0.88 [4]. This range includes $\alpha_0 = -2/3$ corresponding to an oscillator close to a supercritical Hopf bifurcation, but also larger magnitudes of α_0 which could result from the strong nonlinear compression regime introduced here. Note, however, that in the cochlea many dynamic oscillators are at work with a graded profile of characteristic frequencies. The traveling wave elicited in this system can affect the features of nonlinear compression seen in the vibrations of the basilar membrane. This will be subject of future studies.

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[17] The right in Eq. (6) follows from $\alpha \simeq f\rho'_d/\rho_d - 1$ being close to -1, i.e., $\rho'_d f \ll \rho_d$. For ρ'_d we use Eq. (3) with $\langle \cos(\psi) \rangle = 1$ [justified by the left in Eq. (6)].
[18] At $f = f^*$, the phase dynamics is dominated by the slow passage around the saddle point, i.e., $\psi \approx \pi/2$ where $\langle \cos\psi \rangle \approx 0$ in Eq. (3).
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[21] At OP1: ($F_{max} = 87.571$ pN, $S = 1.22$); at OP2: $F_{max} = 50.243$ pN, $S = 0.65$).