

# Dynamics of cochlear nonlinearity: Automatic gain control or instantaneous damping?

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(Received 24 July 2017; revised 2 November 2017; accepted 9 November 2017; published online 12 December 2017)

Measurements of basilar-membrane (BM) motion show that the compressive nonlinearity of cochlear mechanical responses is not an instantaneous phenomenon. For this reason, the cochlear amplifier has been thought to incorporate an automatic gain control (AGC) mechanism characterized by a finite reaction time. This paper studies the effect of instantaneous nonlinear damping on the responses of oscillatory systems. The principal results are that (i) instantaneous nonlinear damping produces a noninstantaneous gain control that differs markedly from typical AGC strategies; (ii) the kinetics of compressive nonlinearity implied by the finite reaction time of an AGC system appear inconsistent with the nonlinear dynamics measured on the gerbil basilar membrane; and (iii) conversely, those nonlinear dynamics can be reproduced using an harmonic oscillator with instantaneous nonlinear damping. Furthermore, existing cochlear models that include instantaneous gain-control mechanisms capture the principal kinetics of BM nonlinearity. Thus, an AGC system with finite reaction time appears neither necessary nor sufficient to explain nonlinear gain control in the cochlea. © 2017 Acoustical Society of America. <https://doi.org/10.1121/1.5014039>

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## I. INTRODUCTION

Much remains unknown about the nonlinearities that expand the dynamic range of hearing by controlling the gain of the delicate mechanical amplifier that evolved within the inner ear.<sup>1</sup> Although measurements of the steady-state harmonic motion of the basilar membrane produced by tonal stimuli indicate that the controlling nonlinearities are compressive, details of their dynamical response to transient or time-varying sounds are less clear. Even if one sets aside the many experimental uncertainties associated with intracochlear measurements, theoretical obstacles to understanding cochlear nonlinearity abound. The mammalian cochlea is a hydro-electro-mechanical network comprising thousands of oscillating elements tuned to different frequencies. Individual oscillators are coupled together by the motion and electrical conductivity of the surrounding fluids, by an intricate anatomical support scaffolding, and by overlying mechanical structures, such as the tectorial membrane. Coupling among the oscillators over distances long and short—and the multiple pathways by which it must occur—greatly complicates the formulation and analysis of the mathematical models needed to interpret experimental data. The difficulty of applying inverse methods to nonlinear systems (e.g., [Zweig, 2016](#)) only exacerbates the problem.

Nevertheless, some basic principles of cochlear nonlinearity are becoming clear. Recent measurements ([Cooper and](#)

[van der Heijden, 2016](#)) of basilar-membrane (BM) responses to amplitude-modulated sounds—a pair of beating tones—demonstrate that the compression evident in the growth of BM motion is both noninstantaneous and temporally asymmetric (i.e., different for the increasing and decreasing portions of the response waveform). In addition to showing mechanical hysteresis, the compression depends on the modulation frequency of the stimulus envelope (see [Fig. 1](#)). As [Cooper and van der Heijden](#) note, the data indicate that the BM nonlinearity resembles that of a compressor with different attack and release times, supporting previous suggestions for the existence of a delayed automatic gain control (AGC) mechanism in the cochlea (e.g., [Zwislocki et al., 1997](#); [van der Heijden, 2005](#); [Recio-Spinoso et al., 2009](#)).<sup>2</sup>

To help clarify the implications of these observations for the kinetics of cochlear nonlinearity, we explore whether a pared-down model, stripped clean of the many complex couplings found in the cochlea, captures any relevant features of the data. The model—an uncoupled harmonic oscillator with variable damping—provides what may be the simplest nontrivial representation of the dynamics of an individual oscillating element. For the harmonic oscillator, the gain and bandwidth of the frequency response are inversely related. Both are controlled by the effective damping—when the damping increases, the maximum gain decreases and the tuning bandwidth increases. Equivalently, both the gain and quality factor ( $Q$ ) of the tuning decrease. This behavior characteristic of an isolated harmonic oscillator resembles that seen in the cochlea, where mechanical transfer functions manifest similar correlations. In the cochlea, both the gain and quality factor of mechanical frequency tuning decrease

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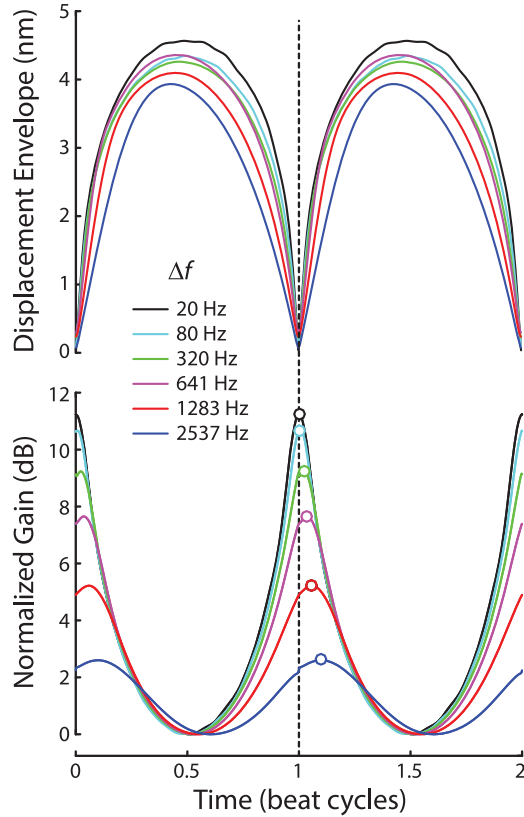


FIG. 1. (Color online) Noninstantaneous distortion measured in basilar-membrane responses to beating tones. The two panels show the envelope (top) and normalized instantaneous gain (bottom) of BM responses to beating tones of different beat rates measured at the 18-kHz place in the base of the gerbil cochlea (Cooper and van der Heijden, 2016). The response envelopes in the top panel become progressively more asymmetric (steeper rise than fall) at higher beat rates. The curves in the bottom panel represent the instantaneous BM gain (i.e., the time-varying ratio between the envelopes of the BM and stapes displacement waveforms) normalized to a minimum value of 1. The data reveal a progressive decrease in gain and increase in phase delay at higher beat rates. Data from Cooper and van der Heijden (2016).

at higher sound levels, suggesting an intensity-dependent increase in the effective damping of the system.<sup>3</sup>

## II. CHANGING THE OSCILLATOR DAMPING

We begin by exploring the effect of inducing a sudden (instantaneous) change in the effective damping of an oscillating system. Because the bandwidth of the system is limited, this sudden change is not immediately apparent in the oscillator response or in measurements of its gain. The response of an oscillatory system to a change of one of its physical parameters always includes a transient component.

### A. The harmonic oscillator

The equation of motion for the simple harmonic oscillator is

$$\ddot{y} + \gamma\dot{y} + \omega_0^2 y = F, \quad (1)$$

where  $y(t)$  is the oscillator displacement,  $\omega_0$  the natural angular frequency,  $\gamma$  the damping coefficient, and  $F(t)$  the external forcing term, with units of acceleration. The

diacritical dot represents a time derivative. If  $\gamma$  and  $\omega_0$  are constant, the oscillator is linear. The response of the linear oscillator to a harmonic force  $F(t) = A\omega_0^2 e^{i\omega t}$  applied at time  $t = 0$  is (e.g., Marion, 1970, Sec. 4.6)

$$y(t) = A\omega_0^2 H(i\omega) e^{i\omega t} + A_{\text{tr}} e^{-\gamma t/2} e^{i(\omega_\gamma t + \phi)}, \quad (2)$$

where  $\omega_\gamma = \omega_0 \sqrt{1 - (\gamma/2\omega_0)^2}$  is the damped resonant frequency and  $H(i\omega)$  is the oscillator transfer function,

$$H(i\omega) = \frac{1}{-\omega^2 + i\gamma\omega + \omega_0^2}. \quad (3)$$

The starting amplitude  $A_{\text{tr}}$  and phase  $\phi$  of the transient term depend on the initial conditions. For simplicity, the solution  $y(t)$  is written as a complex-valued function; the physical solution is its real part,  $\text{Re}\{y(t)\}$ .

### B. Asymmetric responses to a step-change in damping

A simple nonlinearity that arises naturally in many physical systems has the damping coefficient depending instantaneously on the oscillator velocity,  $\dot{y}$ . Because the study of the nonlinear harmonic oscillator requires perturbative or numerical methods, we first illustrate the delayed action of the nonlinear damping using linear analogies and then show examples obtained using numerical simulations.

Consider an oscillator that has been driven at its damped resonant frequency,  $\omega_\gamma$ , since time immemorial, so that its transient response can be considered fully extinguished. At time  $t = 0$ , let the damping coefficient be stepped instantaneously from  $\gamma_1$  to  $\gamma_2$ . When the fractional change in damping is small,  $\omega_\gamma$  can be regarded as a constant. The solution for  $t > 0$  follows from Eq. (2):

$$y(t > 0) = [A_{\gamma_2} + A_{\text{tr}} e^{-\gamma_2 t/2}] e^{i\omega_\gamma t}, \quad (4)$$

where the notation  $A_\gamma$  indicates the complex amplitude of the steady-state solution corresponding to the damping coefficient  $\gamma$  [Eq. (3)]. The amplitude  $A_{\text{tr}}$  can be found by requiring that the displacement be continuous across the step. Just before the step-change, the steady-state solution for the damping coefficient  $\gamma_1$  is

$$y(t \leq 0) = A_{\gamma_1} e^{i\omega_\gamma t}, \quad (5)$$

which leads to

$$A_{\text{tr}} = A_{\gamma_1} - A_{\gamma_2}. \quad (6)$$

Therefore, the solution for a step-change in the damping coefficient is

$$y(t > 0) = [A_{\gamma_2} + (A_{\gamma_1} - A_{\gamma_2}) e^{-\gamma_2 t/2}] e^{i\omega_\gamma t}. \quad (7)$$

After the step, the oscillation amplitude changes smoothly from  $|A_{\gamma_1}|$  to  $|A_{\gamma_2}|$  with a time constant  $2/\gamma_2$ . Note that the time required for the oscillator to converge on its new

steady-state solution depends only on the final damping ( $\gamma_2$ ) and is independent of  $\gamma_1$ .

At frequencies close to the natural frequency, the oscillator gain [ $|H|$  in Eq. (3)] varies inversely with the damping ( $|H(i\omega_0)| = 1/\gamma$ ). Since the time constant of the response to the step-change is also inversely proportional to  $\gamma$ , the duration of the transient varies in proportion to the gain. In other words, the time required to observe a decrease in response amplitude ( $|A_{\gamma_2}/A_{\gamma_1}| < 1$ ) due to an increase in damping ( $\gamma_2 > \gamma_1$ ) is shorter than the time required to observe an increase in amplitude ( $|A_{\gamma_2}/A_{\gamma_1}| > 1$ ) due to a reduction of damping ( $\gamma_2 < \gamma_1$ ).

### C. Generalization of the results to different oscillators

Section II B considered responses to step-changes in the damping coefficient. To simplify the analysis, we approximated the damped frequency,  $\omega_\gamma$ , as constant across the step. For the simple harmonic oscillator, validity of this approximation requires that the fractional change in  $\gamma$  be much less than one. This constraint can be relaxed for oscillators whose resonant frequency is independent of the effective damping. The oscillators in the cochlea appear to belong to this class. The intensity invariance of the fine time structure of basilar-membrane click responses indicates that the local resonant frequencies of the cochlear partition, analogous to  $\omega_\gamma$  in the model, are nearly independent of intensity (Shera, 2001; Zweig, 2016).

We therefore generalize the results for an arbitrary type of oscillator with resonant frequency,  $\omega_r$ , for which one can define an appropriate quality factor,  $Q$ , that determines both the resonant gain and relaxation time constant of the oscillator. Both are assumed proportional to  $Q$ , so that

$$H(i\omega_r) \propto Q \quad (8)$$

and

$$y_{\text{tr}}(t) \propto e^{-\omega_r t/2Q} e^{i\omega_r t}. \quad (9)$$

The simple harmonic oscillator approximately satisfies both conditions when  $Q \gg 1$ , with  $Q = \omega_0/\gamma$ .

If this oscillator is driven at its resonant frequency and its  $Q$  changes from  $Q_1$  to  $Q_2$  at  $t=0$ , then

$$y(t > 0) \propto \left[ Q_2 + (Q_1 - Q_2)e^{-\omega_r t/2Q_2} \right] e^{i\omega_r t}. \quad (10)$$

Thus, it requires roughly  $Q_2$  oscillations to observe a change in gain around the natural frequency. This implies an asymmetry in the time-constants of the transient response to increases and decreases in the oscillator's gain.

### D. Overshoot of the gain trajectory

We now consider the case where both the quality-factor,  $Q$ , of a linear oscillator and its forcing amplitude,  $A$ , are changed instantaneously. This example provides a loose but useful analogy for a nonlinear oscillator whose damping coefficient depends on the oscillator displacement. The example illustrates a simple phenomenon which is then

shown to hold in real nonlinear systems via numerical simulations.

Let the forcing amplitude change from  $A_1$  to  $A_2$  and the quality factor from  $Q_1$  to  $Q_2$  at  $t=0$ . In the steady state, the oscillator gain—defined as the ratio of output to input amplitude—is proportional to  $Q$ ; thus,  $g_1 \propto Q_1$  and  $g_2 \propto Q_2$  for  $t < 0$  and  $t > 0$ , respectively. The form of the solution for  $t > 0$  is given by Eq. (10). To determine how the gain of the oscillator changes over time, we express  $y(t)$  as an envelope  $Q_2 + (Q_1 - Q_2)e^{-\omega_r t/2Q_2}$  multiplied by the carrier  $e^{i\omega_r t}$ . The response for  $t > 0$  is

$$y(t > 0) \propto \left[ Q_2 A_2 + (Q_1 A_1 - Q_2 A_2)e^{-\omega_r t/2Q_2} \right] e^{i\omega_r t}. \quad (11)$$

Defining the instantaneous gain,  $g(t)$ , as the ratio of the envelope of the response to that of the applied force gives

$$g(t > 0) \propto Q_2 + \frac{1}{A_2} (Q_1 A_1 - Q_2 A_2) e^{-\omega_r t/2Q_2}. \quad (12)$$

The terms proportional to  $Q_1 A_1$  and  $Q_2 A_2$  in Eq. (12) represent the steady-state amplitudes for  $t < 0$  and  $t > 0$ , respectively. For future reference, Eq. (12) can be written in the shorter and more transparent form

$$g(t > 0) \propto Q_2 + \Delta Q e^{-\omega_r t/2Q_2}, \quad (13)$$

where  $\Delta Q = (A_1/A_2)Q_1 - Q_2$  is the initial amplitude of the transient component of the change in gain.

When the nonlinearity is compressive, the gain trajectory always overshoots its final value. To see this, consider the two cases

$$\begin{cases} \underbrace{A_2 Q_2 > A_1 Q_1}_{y \uparrow}, \underbrace{Q_2 < Q_1}_{g \downarrow} \Rightarrow \Delta Q < 0, \\ \underbrace{A_2 Q_2 < A_1 Q_1}_{y \downarrow}, \underbrace{Q_2 > Q_1}_{g \uparrow} \Rightarrow \Delta Q > 0. \end{cases} \quad (14)$$

In the first case, the oscillator displacement grows across the step ( $A_2 Q_2 > A_1 Q_1$ ) and the gain decreases ( $Q_2 < Q_1$ ). (To first order, this combination requires that the fractional increase in forcing amplitude exceed the fractional decrease in gain.) In this case, the amplitude of the transient term in Eq. (13) for  $g(t > 0)$  is negative ( $\Delta Q < 0$ ), so that the oscillator gain approaches  $Q_2$ —its new, smaller steady-state value—from *below*. Similarly, when the oscillator displacement decreases across the step ( $A_2 Q_2 < A_1 Q_1$ ) and the gain increases ( $Q_2 > Q_1$ ), then the transient is positive ( $\Delta Q > 0$ ) and the gain approaches  $Q_2$ —its new, larger steady-state value—from *above*. Thus, the gain trajectory always transiently *overshoots* its final value ( $g_{\text{final}} \propto Q_2$ ) when transitioning from its initial state ( $g_{\text{initial}} \propto Q_1$ ).

### E. Responses of nonlinear oscillators

When an oscillator becomes nonlinear, so that one or more of its parameters (e.g., damping) depend on the oscillator response, no simple analytical solutions for the motion can be found. However, the physical intuition of the waving

hand suggests that when the nonlinearities are “weak” (e.g., when the harmonic distortion in the response waveform is small), then the qualitative behavior of the system, averaged over one cycle of the forced oscillation, will be well captured by a linearized analysis. For example, if the damping grows with oscillator displacement, one expects that increasing the forcing amplitude from  $A_1$  to  $A_2$  will increase the time-averaged, steady-state damping ( $\bar{\gamma}$ ), so that  $\bar{\gamma}_2 > \bar{\gamma}_1$ .<sup>4</sup> Furthermore, the analogy with the linear harmonic oscillator suggests that it will take longer to observe a change in  $\bar{\gamma}$  (or, equivalently, in gain or quality factor) when the forcing amplitude decreases than when it increases.

The numerical simulations reproduced in Fig. 2 support this intuitive reasoning. The figure shows the velocity response of a harmonic oscillator with compressive nonlinear damping to a step change in amplitude. The oscillator equation is taken to be

$$\ddot{y} + \frac{\omega_0}{Q_0} \left[ 1 + (\dot{y}/v_{\text{sat}})^2 \right] \dot{y} + \omega_0^2 y = F(t), \quad (15)$$

where the diacritical dot is a time derivative,  $Q_0$  is the quality factor in the linear limit ( $|\dot{y}| \ll v_{\text{sat}}$ ), and the velocity  $v_{\text{sat}}$  sets the scale for the nonlinearity. The oscillator is driven by a sinusoid whose amplitude makes a step increase [Fig. 2(A)] or decrease [Fig. 2(B)] at  $t=0$ . Parameters values were chosen to give  $Q$  values in the range observed experimentally in the gerbil ( $Q_0 = 9$ ,  $v_{\text{sat}} = 0.106$ ). The caption provides additional details of the simulation. Figure 2(C) shows the instantaneous gain, computed as the ratio of the waveform envelopes. The gain curves confirm the qualitative predictions given in Eq. (13). Specifically, the chosen oscillator shows both (i) an overshoot in the gain trajectory and

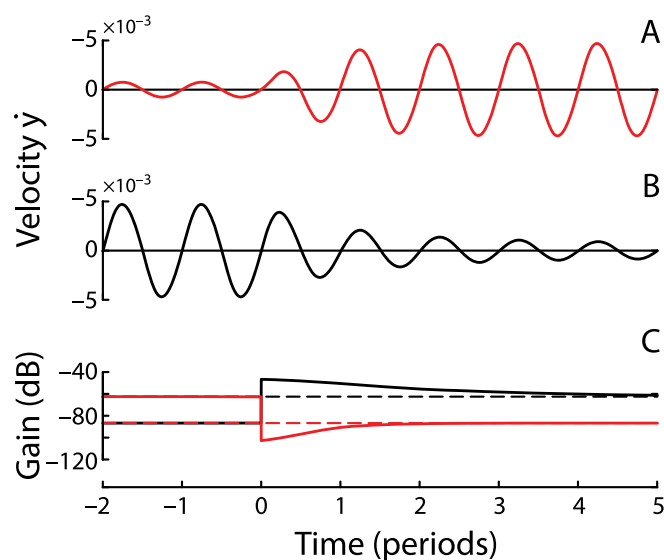


FIG. 2. (Color online) Velocity responses of a compressive, nonlinearly damped harmonic oscillator to a sinusoidal input with a step-change in amplitude. At  $t=0$  the input amplitude  $A$  changes abruptly, either increasing from 10 to 100 (panel A) or decreasing from 100 to 10 (panel B). The oscillator had a natural frequency  $\omega_0 = 18$  kHz. Panel A shows the instantaneous gain for both cases (A, red solid line; B, black solid line). The dashed lines give the asymptotic values of the gain following the step.

(ii) longer relaxation times for decreases in damping than for increases.

## F. High-pass gain-control in nonlinearly damped systems

As predicted by the linear analysis, the time course of the instantaneous gain of a nonlinearly damped oscillator responding to a step-change in forcing amplitude overshoots its steady-state, asymptotic value (see Fig. 2). Because overshoot is typical of systems with high-pass characteristics, these results suggest that the dynamics of the nonlinearity apparent in the oscillator response contains a high-pass component. Once again, we look for insight by considering the linear system. In particular, we obtain an approximate expression for the gain as a function of the modulation frequency of the input envelope by regarding Eq. (13) for  $g(t > 0)$  as the step-response of a linear system. The corresponding frequency response of the system (i.e., the Laplace transform of the impulse response) then becomes

$$G(i\Omega) \propto Q_2 - |\Delta Q| \frac{i\Omega}{1 + i\Omega}, \quad (16)$$

where  $\Omega = \omega/(\omega_r/2Q_2)$  is the modulation frequency normalized by the cutoff frequency of the high-pass filter. Thus, the effective gain and its phase shift depend on the rate at which the envelope of the forcing term is modulated. Furthermore, the bandwidth of the gain signal depends not only on the frequency-tuning of the oscillator, but also on  $|\Delta Q|$ .

## III. CONSISTENCY WITH EXPERIMENTAL DATA

### A. Responses to amplitude-modulated tones

We have shown that the nonlinear effects produced by instantaneous nonlinear damping (or memoryless compressive gain) in a harmonic oscillator do not appear instantaneously in the oscillator’s response. In addition, the oscillator approaches its steady-state amplitude more quickly when the level of the input drive increases than when it decreases. These findings predict that the envelope of the response to amplitude-modulated (AM) tones will be asymmetric about its maximum. Equivalently, the trajectory of the instantaneous gain, defined as the time-varying ratio of the oscillator’s response envelope to that of its drive, exhibits hysteresis. These predictions are consistent with mechanical measurements of BM motion in the gerbil (Cooper and van der Heijden, 2016). Furthermore, the simple, linear analysis culminating in Eq. (16) shows that the nonlinear response to AM tones depends on the modulation frequency. In particular, Eq. (16) predicts that (i) for low-modulation frequencies, the dynamics of the nonlinear gain approaches that of an instantaneous distortion ( $\lim_{\Omega \rightarrow 0} G(i\Omega) = Q_2$ ) and (ii) at higher modulation frequencies, the gain decreases monotonically in magnitude ( $|G(i\Omega)|_{\Omega > 0} < Q_2$ ) and has an increasing phase delay.

We illustrate these predictions in a way that allows easy comparison with motions measured in the cochlea. Figure 3 gives time-domain simulations obtained using a simple

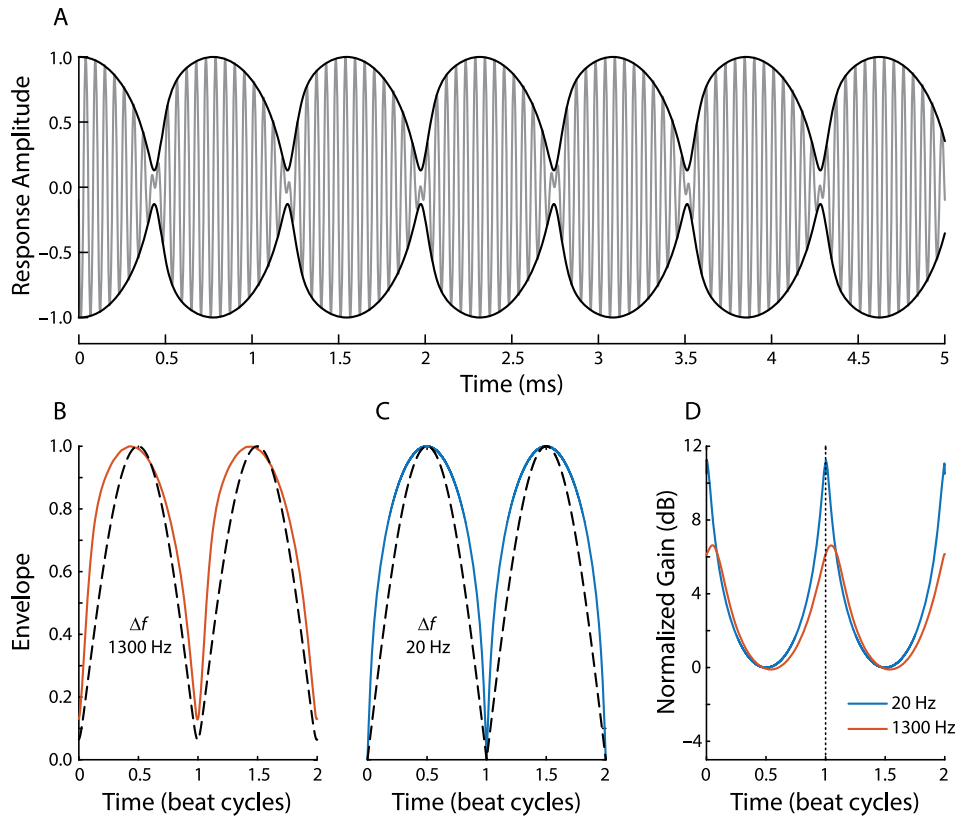


FIG. 3. (Color online) Responses of a nonlinearly damped harmonic oscillator to an AM stimulus created from beating tones. The oscillator, with a natural frequency of 18 kHz, is the same as that used for Fig. 2. Simulations were performed using a fourth-order Runge-Kutta explicit method using a sampling frequency of 1.6 MHz (i.e.,  $\sim 90$  samples per period of the natural frequency). Panel A shows the response to the two beating tones; the stimulus envelope modulates at the frequency difference ( $\Delta f = 1300$  Hz). Panels B and C compare the envelope of the oscillator response to linear predictions (dashed lines) for two different values of  $\Delta f$  (1300 Hz and 20 Hz). The linear predictions were obtained by assuming superposition and summing the responses to the two individual tones. Panel D plots the corresponding instantaneous gain curves, defined as the ratio between the response envelope and the linear prediction. At the higher modulation frequency, the nonlinear damping decreases the RMS gain and shifts its phase. The individual stimulus tones comprising the forcing function  $F(t)$  in Eq. (15) had peak amplitudes of 1000.

harmonic oscillator with nonlinear damping. Comparison with the gerbil data reproduced in Fig. 1 shows that the results closely resemble mechanical responses measured on the basilar membrane (Cooper and van der Heijden, 2016). In particular, Fig. 3 shows that the envelope of the oscillator response to the beating tones is a distorted sinusoid [Fig. 3(A)]. Whereas the response envelope is symmetric about its maxima at low beat frequencies [Fig. 3(C)], the envelope becomes asymmetric at higher modulation frequencies [Fig. 3(B)].<sup>5</sup> Furthermore the envelope of the instantaneous gain depends on the beat frequency, and the peak gain occurs at times delayed relative to the minimum of the stimulus envelope [Fig. 3(D)].

Figure 4 plots the amplitudes and phases of the various harmonic components of the instantaneous gain as a function of the modulation (beat) frequency. The results bear a strong qualitative resemblance to those in Fig. 2 of Cooper and van der Heijden (2016). Figures 4(A) and 4(B) show that the memoryless nonlinear damping preserves the DC component of the gain while reducing the gain at higher modulation frequencies, as predicted by our analysis [Eq. (16)]. Figure 4(C) shows that the phase delays of the gain components increase with the beat frequency, as predicted. When plotted as functions of their own frequency (rather than the beat frequency), the component phase responses appear almost

linear [Fig. 4(D)], with a slightly steeper slope for the higher harmonics. All these features are strikingly similar to those of the reference data (cf. Fig. 2d of Cooper and van der Heijden, 2016).

## B. Responses in a transmission-line cochlear model

Our analysis has thus far been limited to the responses of single, isolated oscillators. As emphasized in the Introduction, however, the mechanics of the mammalian cochlea are somewhat more elaborate—cochlear responses at any one location are shaped by local and nonlocal interactions among scores or more of coupled, nonlinear oscillating elements. Figures 5 and 6 demonstrate that our principal conclusions about the dynamics of instantaneous nonlinear damping extend to oscillators embedded in a more realistic mechanical environment.

Figure 5 plots the responses of an active transmission-line model of the cochlea that incorporates an instantaneous nonlinear gain control designed to yield realistic frequency tuning and compression [Fig. 5(A)], while preserving the intensity invariance of fine-time structure of BM click responses (Shera, 2001). We employed the cochlear model implemented by Sisto *et al.* (2015a), which represents a nonlinear extension of the “double-pole” form of the linear

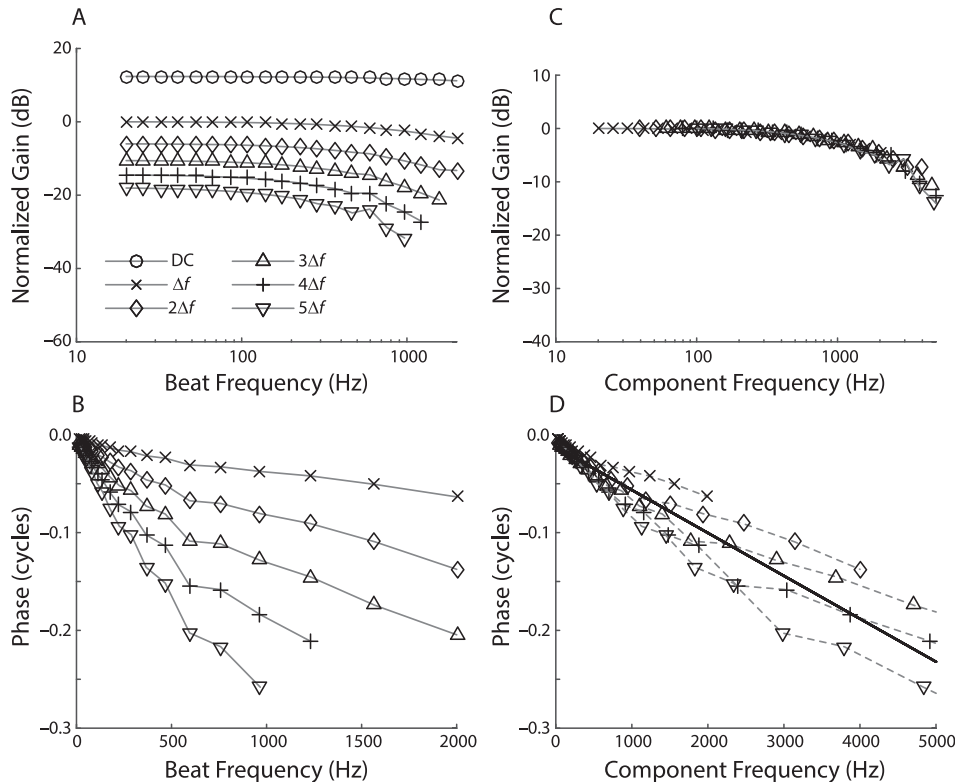


FIG. 4. Spectral analysis of the responses of a nonlinearly damped harmonic oscillator to beating tones. The oscillator is the same as that used for Fig. 2. Panels A and B plot the magnitude and phase of the gain harmonic components as a function of the beat frequency,  $\Delta f$ . Panels C and D replot the same data as functions of their own frequency. The trend line in panel D has a slope of about  $46 \mu\text{s}$ .

model obtained by [Zweig \(1991\)](#) via solution of the inverse problem in squirrel monkey. The oscillators in the model are more complex than simple harmonic oscillators and their parameters vary instantaneously depending on the local BM velocity ([Verhulst et al., 2012](#)).<sup>6</sup> The nonlinearity acts to vary the local gain and tuning bandwidth ( $Q$ -factor) while keeping the resonant frequencies of the underlying oscillators approximately constant. When the model is driven by beating tones, the response envelope becomes more asymmetric at higher beat frequencies [Fig. 5(B)]. Furthermore the maximum instantaneous gain decreases at higher beat frequencies and occurs at times increasingly delayed relative to the minimum of the stimulus envelope [Fig. 5(C)]. These features all strongly resemble the behavior found for both the single nonlinear oscillator (Fig. 3) and the *in vivo* mechanical data (Fig. 1).

Figure 6 presents the spectral analysis of the gain signal in the model. The various panels illustrate both the reduced gain magnitude and the increased phase lag that occur with increasing beat and component frequencies, the same trends noted earlier for the isolated nonlinear oscillator (Fig. 4). In contrast to the behavior of the isolated oscillator, however, the dependence of the gain magnitude and phase on component frequency are slightly different for the lower harmonics than for the higher. We speculate that this difference arises because the model equations include delay terms that introduce additional time scales, rendering the kinetics of the nonlinearity more complex than those of the simple harmonic oscillator.<sup>7</sup> Despite this small difference, the simulations demonstrate that the variation of gain magnitude and phase with beat rate seen in the experimental data do not require the inclusion of AGC mechanisms in cochlear models.

#### IV. DISCUSSION

Nonlinear oscillators whose effective damping depends only on the instantaneous displacement or velocity of the oscillator manifest seemingly history-dependent responses to amplitude-modulated stimuli that are in strong qualitative agreement with those measured in the motion of the basilar membrane ([Cooper and van der Heijden, 2016](#)). Similar results are obtained whether the memoryless nonlinear oscillators are considered in isolation or are coupled together via their embedding in a transmission-line model of the cochlea. Simple analogies based on the transient response of a linear harmonic oscillator to changes in its effective damping elucidate the results and suggest that the findings generalize to broad classes of oscillators with instantaneous nonlinear gain. Our findings indicate that the major qualitative features of the data are consistent with existing models of the cochlea ([Shera, 2001](#); [Verhulst et al., 2012](#); [Sisto et al., 2015a](#)) and can be understood without invoking nonlinearities involving delayed automatic gain control ([Cooper and van der Heijden, 2016](#)).

##### A. Nonlinear damping vs automatic gain control

The dynamics of gain control manifest by nonlinearly damped systems differs dramatically from the AGC strategies typically employed in engineering applications. By definition, AGC systems respond to the recent history of their input by adjusting their gain dynamically. The control process involves a finite time constant, typically longer than the expected oscillation period of the output signal. The design of AGC systems involves a trade-off between the goal of quickly adjusting the gain and the desire to reduce the distortion introduced by rapid gain changes. When confronted

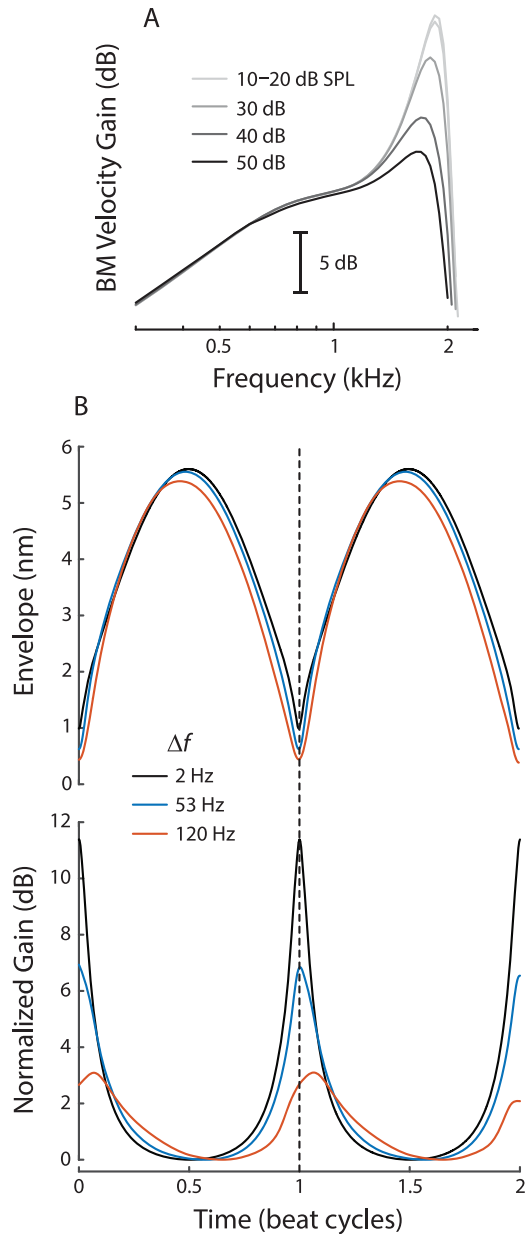


FIG. 5. (Color online) Responses of a cochlear model with instantaneous nonlinear gain. Panel A shows the model's level-dependent tuning at the place tuned to 1.8 kHz. Panel B shows the envelopes (top) and gain signals (bottom) of the response to three pairs of beating tones, computed at the same location. Component frequencies were centered on 1.8 kHz and adjusted to produce the beat frequencies  $\Delta f$  given in the legend. The ratios of beat to center frequency are similar to those of the data in Fig. 1, which were measured at the 18 kHz place. Stimulus amplitudes were 42 and 43 dB sound pressure level (SPL) for the lower and higher frequency tones, respectively. Model parameters  $Q_{\min} = 4$ ;  $Q_{\max} = 12$ ;  $v_{\text{sat}} = 17.6 \mu\text{m/s}$ . Details of the model and its solution are provided elsewhere (Moleti *et al.*, 2009; Sisto *et al.*, 2015a,b; Sisto and Moleti, 2015).

with a step-change in input amplitude, AGC systems ensure a smooth transition in the gain function by allowing for “overshoot” in the amplitude trajectory of the output signal. Figure 7 compares and contrasts the dynamics of three types of compression: instantaneous distortion, automatic gain control, and nonlinear damping. The instantaneous (memoryless) distortion exhibits no transient response to a step-change in the input level. Automatic gain control ensures

smooth transitions in the system's gain at the cost of an overshoot in the response envelope. Nonlinear damping ensures a smooth transition in the response envelope but creates an overshoot in the gain (see Sec. IID).

An important functional difference between AGC and nonlinear damping is that the latter reacts more safely and effectively to variations in the input signal level. For example, in response to a sudden increase in the stimulus level, the AGC reacts “sluggishly” and may only begin to compress the output a few cycles after the increase in its input; nonlinear damping reacts to adjust the output more quickly, avoiding a potentially damaging overshoot in the response. The smooth control of a system's gain provided by AGC systems can be useful in many engineering applications. However, when one wants to avoid damage caused by large response vibrations, smooth gain transitions are highly undesirable, as they allow for significant response overshoots. Nonlinear damping is a fast and effective alternative that provides controlled responses to changes in the input.

## B. Are the mechanical data consistent with an AGC system?

The gain response of an AGC system with finite reaction time to a step change in its input amplitude can be described generically as

$$g_{\text{AGC}}(t > 0) = g_{\text{target}} + (g_{\text{start}} - g_{\text{target}})W(t), \quad (17)$$

where  $g_{\text{target}}$  and  $g_{\text{start}}$  are the target and starting gains, respectively. The function  $W(t)$ , with  $W(0) = 1$ , tapers smoothly to zero in finite time, thereby controlling the system's trajectory between its initial and final gains. Importantly, the gain remains continuous across the step [ $g(0^+) = g_{\text{start}}$ ].

For simplicity, consider the case where the transition is exponential and characterized by a single time constant, so that  $W(t) = e^{-t/\tau_{\text{AGC}}}$ . Computing the frequency response—as we did earlier for the step change in damping [Eq. (16)]—shows that this AGC system provides its most effective gain control at low modulation rates (see bottom panel of Fig. 7).<sup>8</sup> This result can be understood intuitively: the finite reaction time of an AGC system prevents the gain from following rapid modulations in the signal envelope. Thus, reducing the gain of high-frequency components of the envelope requires reducing the gain of *all* components—that is, it requires reducing the overall system gain.

The behavior required of an AGC system is thus exactly the opposite of that observed in the BM mechanical measurements (Cooper and van der Heijden, 2016), which show significant gain reductions and phase shifts for the higher harmonics of the signal envelope while the gain of the DC component remains unchanged. Thus, the gerbil data appear inconsistent with the operation of a classical AGC system with finite reaction time. Of course, the trends seen in the data might be approximated using a more elaborate AGC-based system. But a compressive AGC system that can selectively reduce the gain over some range of envelope frequencies must detect and react to those frequencies. Thus, using an AGC to deliver more compression at high modulation rates than at low requires doing so

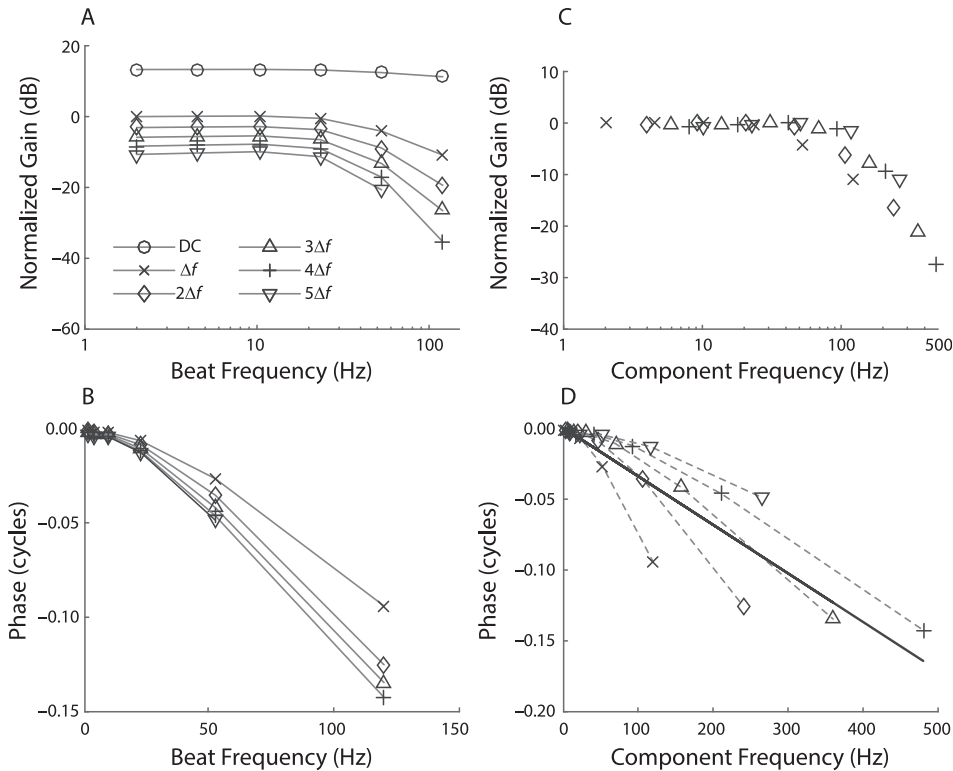


FIG. 6. Spectral analysis of the responses of the nonlinear transmission-line cochlear model to beating tones. The model and parameters are the same as those used for Fig. 5. Panels A and B show the magnitude and phase of the gain harmonic components as a function of the beat frequency,  $\Delta f$ . Panels C and D replot the same data as functions of their own frequency. Note that the ratios of beat to center frequency are similar to those of the reference data (Fig. 1), which were measured at the 18 kHz place.

deliberately—for example, by regulating the target gain in an *ad hoc* fashion or by cascading the AGC gain signal with a low-pass filter to reduce the relative gain at high frequencies.

As emphasized in Sec. III—and in contrast to the responses of the AGC system—the responses of an oscillator with nonlinear damping match the trends seen in the data [cf. Figs. 4(A) and 4(C)]. To reiterate, the gain for the step response of a nonlinearly damped oscillator can be approximated by the

expression given in Eq. (13). Translated into the notation adopted in Eq. (17), the gain becomes

$$g_{\text{NLD}}(t > 0) = g_{\text{target}} - (g_{\text{start}} - g_{\text{target}})e^{-t/\tau}, \quad (18)$$

where  $\tau \sim 2g_{\text{target}}/\omega_r$ . Unlike an AGC, nonlinear damping does not produce a smooth transition in the gain function—the gain is not continuous across the step [ $g(0^+) \neq g_{\text{start}}$ ].

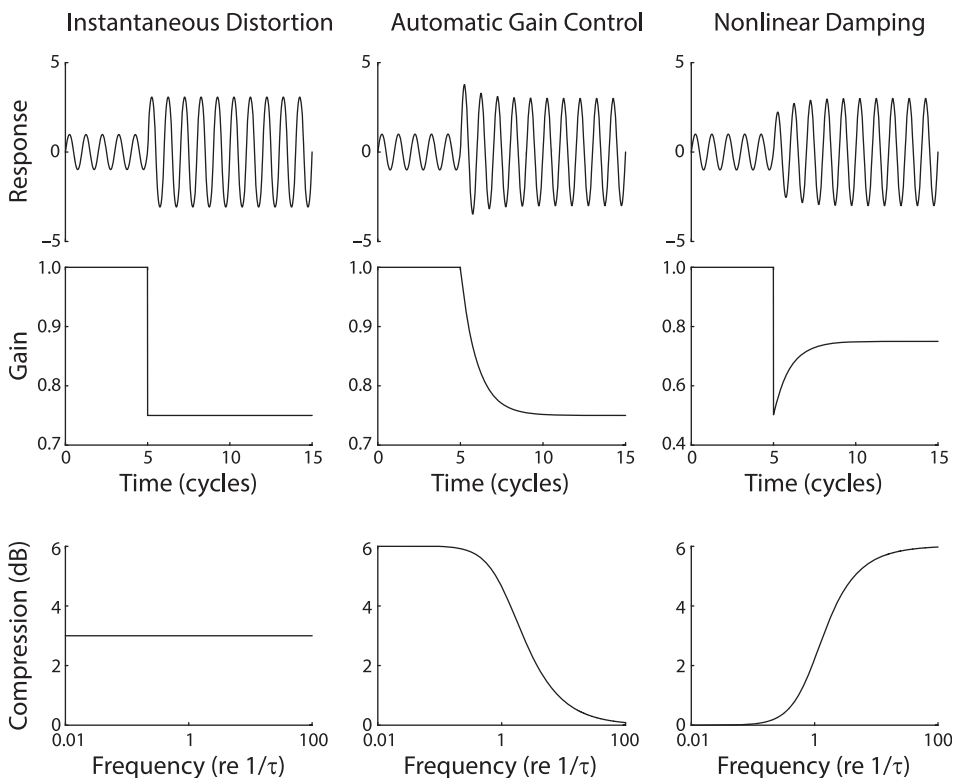


FIG. 7. Illustration of responses to step increases in the input signal level for three different gain control strategies. The three columns represent, from left to right: instantaneous (memoryless) distortion, automatic gain control, and nonlinear damping. The three rows represent, from top to bottom: the output response signal, the envelope gain signal, and the compression vs frequency function derived from the step responses (with frequency measured relative to the time-constant associated with the automatic-gain control or the nonlinear damping). The instantaneous distortion was implemented using the arctangent function.

Rather, by allowing rapid changes in system gain, nonlinear damping ensures a smooth transition in the amplitude of the output signal.

Whereas AGC mechanisms generate little or no harmonic distortion for stationary tones,<sup>9</sup> the same cannot be said of either nonlinear damping or instantaneous distortion. However, because nonlinear damping ensures smooth transitions in response amplitude, the degree of harmonic distortion it introduces remains small. Figure 8 illustrates these remarks by comparing the response spectrum of an oscillator with nonlinear damping with that of an instantaneous distortion. The harmonic distortion produced by the oscillator is considerably smaller. Although nonlinear damping introduces more distortion than an AGC system, its magnitude appears not inconsistent with the distortion measured in intracochlear pressure close to the BM (Olson, 2004).

Although we have focused here on data from BM mechanical measurements, other data sets show features that might be interpreted as evidence for delayed gain control mechanisms in the mammalian cochlea. For example, the suppression curves of human click-evoked otoacoustic emissions (CEOAE) show maximal suppression for masking clicks that precede the test click (Kemp and Chum, 1980). Unfortunately, although the effects in the data are clear, their proper interpretation is less so. As illustrated here, even a single oscillator with instantaneous nonlinear damping exhibits a transient response to fluctuations of its input, creating a form of non-instantaneous gain-control. In an actual cochlea containing thousands of oscillators coupled via the fluids and other structures, responses that appear to reflect the action of delayed gain-control mechanisms may arise as the result of coupled transient responses to broadband sound components (such as clicks or transients produced by the onsets of a complex tonal stimuli). Indeed, for the CEOAE data, Rauffer and Verhulst (2016) show that a one-dimensional cochlear model that implements local instantaneous control of the oscillators' quality factors Verhulst *et al.* (2012) can mimic the presence of local automatic gain

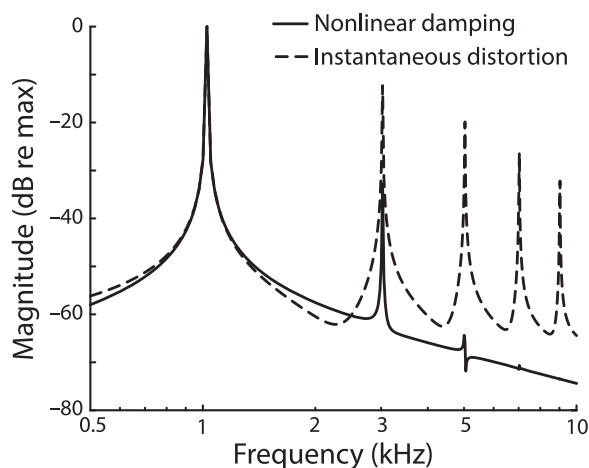


FIG. 8. Comparison between the harmonic distortions produced by an instantaneous distortion and that produced by nonlinear damping. The figure shows the magnitude spectra of the response to a 1 kHz pure tone. The harmonic distortion produced by the nonlinear damping (solid line) is smaller than that produced by an instantaneous distortion (dashed line).

control by producing maximal click suppression on the BM for maskers preceding the test clicks.

### C. Implications for arguments against cycle-by-cycle amplification

Theories of cochlear mechanics that invoke alternatives to cochlear amplification (e.g., the braking action proposed by van der Heijden and Versteegh, 2015) generally posit that the outer hair cells (OHCs) regulate the cochlear gain in a sluggish, “parametric” fashion rather than actively cooperating to amplify the incoming traveling wave in a phase-locked (cycle-by-cycle) manner. A principal argument adduced to support these alternative theories is that the shunting action of the OHC membrane capacitance (e.g., Cody and Russell, 1987) renders high-frequency cycle-by-cycle somatic amplification by OHCs problematic. Interpreted in light of our results, the data of Cooper and van der Heijden (2016) suggest, however, that cochlear gain is regulated rapidly, so that an instantaneous nonlinear damping approximates the data well. If we assume that the OHCs are the nonlinear elements controlling the cochlear gain, then whatever limits may be imposed by the membrane time constant, they are evidently not so serious that they prevent the OHCs from responding *in vivo* to modulation frequencies of 5 kHz or more (the highest envelope components explored in their data). These conclusions, based on measurements of BM motion, are thus consistent with biophysical measurements suggesting that OHC time constants are small enough to support a significant role for high-frequency somatic motility in cochlear mechanics (e.g., Frank *et al.*, 1999; Johnson *et al.*, 2011). At least in the base of the gerbil cochlea, OHCs appear to react on an apparently cycle-by-cycle basis, regardless of whether their rapid responses serve primarily as mechanical amplifiers or as brakes.

Despite the theoretical potential of delayed automatic gain control as a framework for understanding cochlear nonlinearity (Lyon, 1990; Zwislocki *et al.*, 1997; van der Heijden, 2005), our results indicate that both qualitative and quantitative features of the BM response to beating tones (Cooper and van der Heijden, 2016) agree well with models that incorporate a very different type of gain-control system: instantaneous nonlinear damping. Playing devil’s advocate, we note, however, that our analysis cannot rule out the possibility that the agreement we find is somehow accidental or misleading, that the gain in the gerbil cochlea is actually regulated by a suitably engineered AGC system. But if that is the case, then the engineering specifications for this hypothetical AGC system evidently require that it have little activation delay and the ability to mimic, at least in all respects probed here, the action of an instantaneous nonlinear damping.

### ACKNOWLEDGMENTS

Supported by Aalto ELEC Doctoral School, the Foundation for Aalto University Science and Technology, and NIH grant R01 DC003687. We thank Arturo Moleti and Renata Sisto for providing their model implementation and Nigel Cooper and Marcel van der Heijden for sharing their data and for many provocative discussions.

<sup>1</sup>Some argue that the gain of the cochlear amplifier is always less than one (e.g., van der Heijden and Versteegh, 2015), so that the designation “amplifier” is a misnomer. Agnostic here to the validity of these arguments about the maximum gain, this paper focuses on the dynamics of the controlling nonlinearity. Our conclusions depend little on whether the nonlinearity acts by decreasing the gain of the “cochlear amplifier” or by increasing the braking action of the “cochlear killjoy.”

<sup>2</sup>There appears to be no universal and precise definition of automatic gain control. Lyon’s (1990) use of the term is broad enough to encompass almost any dynamical system that controls its gain automatically, including instantaneous nonlinear damping. Here, we adopt a narrower and more classical definition consistent with most of the literature (e.g., Zwislocki et al., 1997; van der Heijden, 2005; Recio-Spinoso et al., 2009). For our purposes, an AGC system is one whose finite reaction time ensures a smooth variation of the gain signal. With this definition, AGC systems can be distinguished experimentally from those that employ instantaneous nonlinear damping.

<sup>3</sup>Although the gain and quality factor ( $Q$ ) of a simple harmonic oscillator are proportional, the relationship between mechanical gain and frequency-tuning is expected to be different in the cochlea. Indeed, both mechanical data from single locations along the BM (e.g., Robles and Ruggero, 2001) and nonlinear cochlear models (e.g., Sisto et al., 2015a), show that as stimulus amplitude increases, the BM gain decreases more rapidly than the corresponding  $Q$ .

<sup>4</sup>The steady-state response at a specific frequency is described by a constant amplitude and phase, and the distortion in the waveform are caused by higher order harmonics that we are ignoring. The phase of the response at the characteristic frequency  $\omega_0$  does not depend on the damping coefficient [see Eq. (3)].

<sup>5</sup>Numerical simulations of the response of nonlinear “Hopf” oscillators to beating tones also show asymmetries in the envelope (Julicher et al., 2001).

<sup>6</sup>The model described by Sisto et al. (2015a) is essentially that of Moleti et al. (2009), except that the nonlocal feed-forward mechanism is replaced by the double-pole variant of the BM admittance derived by Zweig (1991). Following Verhulst et al. (2012), the parameters of the local oscillators are determined by the instantaneous location,  $\alpha_\times$ , of the double pole of the BM admittance function in the complex frequency plane (Shera, 2001). In the model of Sisto et al. (2015a),  $\alpha_\times$  varies with time (and space) according to the equation (Sisto et al., 2015b)

$$\alpha_\times(x, t) = \frac{1.65}{Q(x, t) + 7.5},$$

where the value of the instantaneous  $Q$  is governed by the equation

$$Q(x, t) = Q_{\min} + (Q_{\max} - Q_{\min})[1 - \tanh(|\dot{\xi}(x, t)/v_{\text{sat}}|^2)].$$

In these equations,  $\dot{\xi}(x, t)$  is the local BM velocity and  $v_{\text{sat}}$  sets the scale for the nonlinearity. The parameters  $Q_{\min}$  and  $Q_{\max}$  are, respectively, the minimum and maximum  $Q$  values (referred to by Sisto et al. as the “passive” and “active” values).

<sup>7</sup>The delay term in the model equations arises via solution of the inverse problem in the squirrel monkey using the long-wavelength approximation Zweig (1991). The solution of the inverse problem using the short-wavelength approximation in the BM peak region (Zweig, 2015) yields a BM admittance function that contains no delay terms but consists instead of an harmonic oscillator driven by the local pressure and its time derivative. We therefore conjecture that the difference between the model and the data may ultimately be a consequence of employing the long-wavelength approximation.

<sup>8</sup>This result, obtained here for a tapering function  $W(t)$  governed by a single exponential, can be generalized (using Bernstein’s theorem on monotone functions and the linearity of the Laplace transform) to arbitrary systems with smooth, monotone transitions in the gain.

<sup>9</sup>An AGC mechanism in which the gain depends only on the envelope of the BM response provides an example of what Zweig (2016) terms a “hi-fi” nonlinearity. For a pure tone, the envelope is constant and there is no distortion.

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