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# CLUSTERS IN A CHAIN OF COUPLED OSCILLATORS BEHAVE LIKE A SINGLE OSCILLATOR: RELEVANCE TO SPONTANEOUS OTOACOUSTIC EMISSIONS FROM HUMAN EARS

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## Contributions:

A Study design/planning  
B Data collection/entry  
C Data analysis/statistics  
D Data interpretation  
E Preparation of manuscript  
F Literature analysis/search  
G Funds collection

## Abstract

Spontaneous otoacoustic emissions (SOAEs) provide startling evidence that there is an active process at the core of the mammalian cochlea, but the mechanism involved is unclear. Models involving single, active Van der Pol oscillators have found favor, but here we extend the system to a chain of coupled, active nonlinear oscillators. It is found that the inherent clustering of oscillators in the chain produces an effect in which each cluster, or frequency plateau, behaves just like a single oscillator, most clearly in terms of phase lock to external tones and phase slip in the presence of noise.

**Key words:** acoustics • biophysics • cochlea • hair cells • auditory

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## LOS GRUPOS EN UNA CADENA DE OSCILADORES ACOPLADOS SE COMPORTAN COMO UN OSCILADOR INDIVIDUAL: SIGNIFICADO PARA EMISIONES OTOACÚSTICAS ESPONTÁNEAS DEL OÍDO HUMANO

### Resumen

Emisiones otoacústicas espontáneas (SOAEs) proporcionan pruebas sorprendentes de la existencia de un proceso activo dentro de la cóclea de los mamíferos. Sin embargo, queda poco claro el mecanismo involucrado en dicho proceso. Se han apoyado modelos que abarcan osciladores activos individuales de Van Der Pol, sin embargo en el presente trabajo dicho sistema se ha ampliado a una cadena de osciladores no lineales acoplados y activos. Se constata que el acoplamiento inseparable de osciladores en la cadena resulta en que cada grupo acoplado o bien plateado de frecuencias, se comporta como un oscilador individual, lo cual es particularmente visible en referencia al ajuste de la fase a tonos externos y el traslado de la fase en presencia de ruido.

**Palabras clave:** acústica • biofísica • cóclea • filamentos auditivos

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## ГРУППЫ В ЦЕПИ СВЯЗАННЫХ ОСЦИЛЛЯТОРОВ, ВЕДУЩИЕ СЕБЯ КАК ОДИНОЧНЫЙ ОСЦИЛЛЯТОР: ЗНАЧЕНИЕ ДЛЯ СПОНТАННОЙ ОТОАКУСТИЧЕСКОЙ ЭМИССИИ ИЗ УШЕЙ ЧЕЛОВЕКА

### Изложение

Спонтанная отоакустическая эмиссия (SOAE) предоставляет удивительные доказательства существования активного процесса внутри улитки млекопитающих. Однако остаётся неясным механизм, вовлечённый в данный процесс. Поддерживались модели, включающие одиночные, активные осцилляторы Ван дер Поля, однако в настоящей работе данная система была расширена до цепи связанных и активных нелинейных осцилляторов. Было обнаружено, что неразрывная связь осцилляторов

в цепи приводит к тому, что каждая связанная группа или же плато частот ведёт себя как одиночный осциллятор, что лучше всего видно по отношению к согласованию фазы с внешним тонами и к смещению фазы при наличии шума.

**Ключевые слова:** акустика • биофизика • улитка • слуховые ячейки

## GRUPY W ŁAŃCUCHU SPRZĘŻONYCH OSCYLATORÓW ZACHOWUJĄ SIĘ JAK POJEDYNCZY OSCYLATOR: ZNACZENIE DLA SPONTANICZNYCH EMISJI OTOAKUSTYCZNYCH Z USZU CZŁOWIEKA

### Streszczenie

Spontaniczne emisje otoakustyczne (SOAEs) dostarczają zaskakujących dowodów na istnienie aktywnego procesu wewnątrz ślimaka ssaków. Jednakże niejasnym pozostaje mechanizm zaangażowany w ów proces. Popierano modele obejmujące pojedyncze, aktywne oscylatory Van Der Pola, jednak w niniejszej pracy system ten rozszerzono do łańcucha sprzężonych i aktywnych oscylatorów nieliniowych. Stwierdza się, iż nieodłączne sprzężenie oscylatorów w łańcuchu skutkuje tym, że każda sprzężona grupa, lub też plateau częstotliwości, zachowuje się jak pojedynczy oscylator, co jest najbardziej widoczne w odniesieniu do dopasowania fazy do tonów zewnętrznych oraz przesunięcia fazy w obecności szumu.

**Słowa kluczowe:** akustyka • biofizyka • ślimak • komórki słuchowe

### Introduction

Otoacoustic emissions (OAEs) are weak sounds emitted by the inner ear. They were discovered some 40 years ago by Kemp [1,2]. His startling discovery was soon confirmed by others [3–7]. A review of the different classes of OAEs and their properties can be found in Probst et al. [8].

OAEs are taken to be a by-product of some sort of active (energy-producing) process in the inner ear which assists in the detection of faint sounds near the threshold of hearing. Such a process had already been foreshadowed decades earlier by Gold [9], to explain the high sensitivity and selectivity of human hearing. Nowadays there is overwhelming experimental evidence that the active process amplifies incoming acoustic signals and that it is situated in the hair cells [10,11].

A special class of OAEs are spontaneous otoacoustic emissions (SOAEs). These are pure weak tones emitted by the ear in the absence of any external acoustic stimulation, and can be detected by a sensitive microphone in the ear canal. The existence of SOAEs was first reported by Kemp [12; Figure 4b] and later confirmed by Wilson [13] and Zurek [14,15]. Spectra of human SOAEs typically show a number of narrow peaks on a background of wide-band noise.

It has already been shown that a one-dimensional array or chain of coupled nonlinear oscillators can emulate the properties of human [16] and lizard [17] SOAEs. These simulations were based on a chain of active oscillators graded in frequency, with no external input [18]. Each oscillator was coupled to its two neighbors (except for the oscillators at the ends), which means that neighboring oscillators tended to oscillate at the same frequency, even though their natural oscillation frequencies were slightly different. As a result, the oscillators formed discrete clusters, identified on a frequency plot as frequency plateaus. Distinctive frequency plateaus are well-known properties of coupled oscillator systems [19,20].

Properties of an isolated SOAE (a single peak in an ear-canal spectrum) can be described in terms of a single

limit-cycle oscillator [21–24]. To model the presence of two or more peaks in the spectrum, at least two such oscillators are needed, and these oscillators, when coupled, can explain how two peaks can sometimes “switch” (alternately swap amplitudes [25]).

In this paper, a different approach to describing SOAEs is taken. Here, the SOAEs are taken not to be individual oscillators, but are identified with the clusters of oscillators which make up the frequency plateaus. The properties of the clusters are investigated, notably in terms of their entrainment properties to external tones, in the absence or presence of noise. It is found that in this respect a cluster of oscillators behaves in the same way as does a single peak – an SOAE – in the spectrum of an ear canal recording.

The physical connection between the inner ear dynamics and the ear canal is not explored in this work. Instead, the simplest possible connection is assumed: the sound in the ear canal is taken to be identical to that which would be picked up by a microphone immersed in the cochlear fluids. That is, the pressure signal in the ear canal is taken to be the sum of the activity of all the oscillators, as if each oscillator contributed its own pressure signal in proportion to its displacement. In this way, details of slow wave propagation are not needed, boundary conditions are largely avoided, and a direct inside view of cochlear mechanics is created. Thus, the modeling depicts a local oscillator scenario [16] rather than a global oscillator one [26]. The local oscillator approach has been more usually used to model the inner ears of lizards and frogs rather than humans, but the surprising thing is that the outcome of applying the local model to the frog ear is very similar to what is seen with the human ear [27–29]. This demonstrates the usefulness of the local oscillator approach, even though it is acknowledged that further refinements could be added. A full description of the possible intricacies of cochlear mechanics is given in [30], and an example of how local oscillator models can provide useful information about cochlear mechanics is provided in [31].

As points of comparison, various other time-domain cochlear models have also been used to simulate SOAEs. One

is the nonlinear and active one-dimensional transmission line model of the human cochlea [32], made up of 1000 segments; comparison of the outcomes of simulations with this transmission line model and the oscillator array investigated in this paper shows strong similarities [33,34]. A second model [35] has used an array of spatially disordered active nonlinear oscillators which are coupled both hydro-mechanically and visco-elastically; this approach finds that the oscillators also tend to cluster into frequency plateaus, with statistics resembling the actual cochlea. Most recently, a third approach has been to use a state-space model with a spatially distributed set of nonlinear active micro-mechanical elements coupled via the cochlear fluid, and has been able to predict various features of SOAEs [36].

However, the focus of the present paper is on the clusters, and the main aim is to see whether the dynamics of each frequency plateau is comparable to that of a single self-sustaining oscillator, at least in its entrainment to external tones. Entrainment of SOAEs to an external tone was first documented decades ago [21,23,37–39], and the related property of phase-slip is also well known [22,40]. Entrainment, phase-lock, and phase-slip are strong evidence that SOAEs are generated by (active) oscillators, and, experimentally, it is known that hair bundles exhibit spontaneous oscillations [41]. Entrainment is the phenomenon by which one oscillator becomes synchronized – locked in phase – to the oscillation of another, and phase-slip is the reverse in which one oscillator escapes this condition – it jumps out of its confining potential well and resumes its own independent activity. This energetic sort of behavior has been observed, and modeled, in hair bundles of *in vitro* preparations of the bullfrog sacculus [42–44], and so it is reasonable to consider that oscillations of hair cells or bundles might be the source of SOAEs in the human cochlea [10].

In this paper, the two possible sources of activity – somatic motility of the hair cell body, and driven deflection of the hair cell bundle [30] – are not distinguished as only a single measure (the sum of oscillator displacements) is calculated. The results of the modeling indicate that the inherent clustering which occurs in a chain of coupled oscillators could underlie SOAEs. That is, an SOAE in the ear canal may reflect not a hyperactive individual oscillator in the cochlea but the cooperative activity of multiple oscillators which have, through coupling, come into synchronization with each other.

## Methods

This paper takes a computational approach, first constructing a mathematical model of the cochlea as a one-dimensional array of coupled, oscillating elements and then numerically solving the equations governing their behavior.

We consider a model consisting of a chain of  $n$  coupled oscillators [18], in which  $\chi_j$  is the displacement and  $\dot{\chi}_j$  the velocity of the  $j^{\text{th}}$  oscillator. If  $\chi_j$  and  $\dot{\chi}_j$  are combined using the complex notation  $z_j = \chi_j - \frac{i}{\omega_j} \dot{\chi}_j$ , the differential equation to be solved for the oscillator ( $j=1,2,\dots,n$ ) becomes:

$$\begin{aligned} \dot{z}_j = & (i\omega_j + \varepsilon_j)z_j + (d_R + id_I)(z_{j-1} - 2z_j + z_{j+1}) \\ & - b_j|z_j|^2 z_j \end{aligned} \quad (1)$$

In Eq. (1),  $\omega_j$  is the natural frequency of oscillator  $j$  (the frequency with which it oscillates if not coupled to its neighbors);  $\varepsilon_j$  is a measure of the effective damping (positive for an active oscillator);  $d_R$  and  $d_I$  are dissipative and reactive coupling constants respectively; and  $b_j$  describes the intrinsic nonlinearity of oscillator  $j$  and controls its amplitude. For the first oscillator in the chain ( $j=1$ ), the term  $(z_{j-1} - 2z_j + z_{j+1})$  is replaced by  $(z_2 - z_1)$ , and for the last oscillator ( $j=n$ ) by  $(z_{n-1} - z_n)$ . Coupling between neighbouring oscillators is represented by the term  $(d_R + id_I)(z_{j-1} - 2z_j + z_{j+1})$ .

Equation (1) was numerically solved for  $n=101$  with Mathematica 10 (Wolfram, www.wolfram.com), using its NDSolve routine with Method option Automatic.

The natural frequencies  $\omega_j$  of the oscillators accorded with Greenwood's position-to-frequency map for the human cochlea [45], covering a range of 1 mm in 0.01 mm steps (the width of a hair cell). In the adult human ear, two clear maxima occur in the frequency distribution of SOAEs: at 1.5 kHz and at 3.0 kHz [46]. To take in the frequency range of the first peak, the frequency of the middle oscillator in the chain ( $j=51$ ) was fixed at 1.5 kHz, giving a modeled range of natural frequencies of 1.4 to 1.6 kHz. Frequency steps  $\Delta f$  between adjacent oscillators ranged from 2.1 Hz at the low frequency end of the array to 2.4 Hz at the high frequency end.

To investigate the effect of stimulation with an external sinusoidal force in the presence of noise, additional terms were added to Eq. (1):

$$\begin{aligned} \dot{z}_j = & (i\omega_j + \varepsilon_j)z_j + (d_R + id_I)(z_{j-1} - 2z_j + z_{j+1}) \\ & - b_j|z_j|^2 z_j + F_{ext} \sin(2\pi f_{ext} t) + a_n \zeta(t) \end{aligned} \quad (2)$$

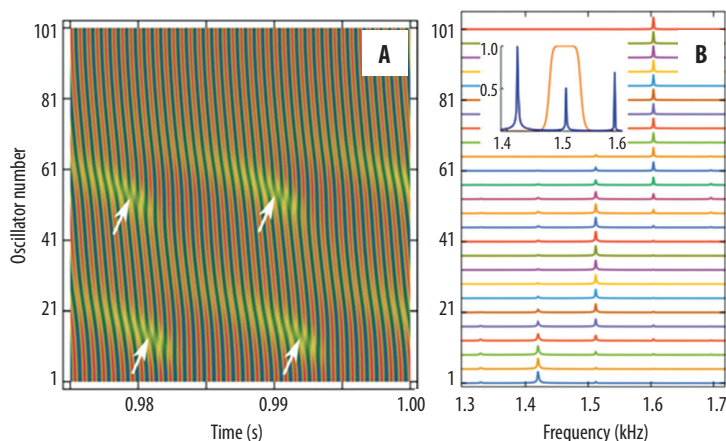
where  $F_{ext}$  is the magnitude of the external force,  $f_{ext}$  its frequency, and  $\zeta(t)$  a gaussian white noise force with mean 0, standard deviation 1, and strength  $a_n$ .

## Results

### Clustering of oscillators

The parameters in Eq. (1) were chosen to be:  $d_R=5$ ,  $d_I=-5$ ,  $\varepsilon_j=1$ , and  $b_j=1$  for all  $j$ . With this parameter choice, solving equation (1) provides the time course of the displacements of all 101 oscillators. The displacements  $\chi_j(t)$  were calculated with a resolution of 0.01 ms for a time interval of 1 s, and the last 25 ms of the interval is shown as a density plot in Figure 1A.

The amplitude spectrum of each oscillator was calculated as the absolute value of the Fourier transform of its displacement  $\chi_j(t)$ , and the result is shown in Figure 1B. Here it is clear that the oscillators cluster into three main frequency plateaus (at 1420, 1512, and 1604 Hz), a characteristic feature of chains of coupled oscillators [19,20]. The separation, about 90 Hz, is typical for human SOAEs around 1.5 kHz [47] and is determined by the strength of the coupling terms. The spectrum for the sum of all displacements  $\sum_j \chi_j(t)$  is shown in the inset. It is suggested that the peaks bear a close resemblance to SOAEs recorded in the ear canal. The hypothesis is made that each



**Figure 1.** (A) Spatiotemporal density plot of normalized displacement  $\chi_j(t) / \text{Max}[\chi_j(t)]$  for all 101 oscillators in the array (red = +1; blue = -1). White arrows mark bifurcations, where the clustering frequency in the array changes. (B) Frequency spectra of each fourth oscillator in the array. The inset shows the spectrum of the sum of the displacements of all oscillators (blue line). The three main peaks are at 1420, 1512, and 1604 Hz. The orange line is the profile of the filter used to isolate a peak and obtain the time signal for a cluster.

SOAE may represent the synchronized activity of a cluster of coupled oscillators. Similar bifurcations to those shown in Figure 1A, can also be seen in Figure 3a of Gelfand et al. [48]. These authors describe SOAEs in the Tokay gecko with a model of coupled oscillators that shares a number of features with the model used in the present paper.

### Entrainment to a periodic external force

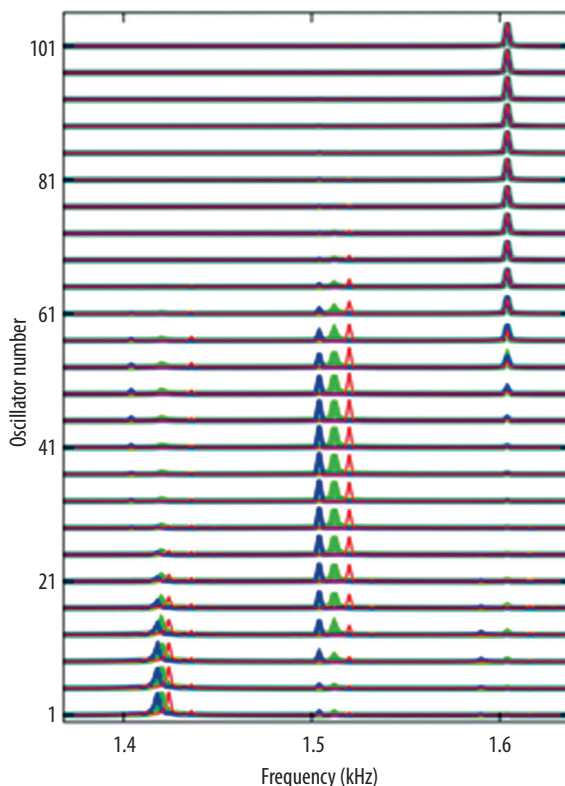
Entrainment to an external tone was simulated by solving Eq. (2) for  $a_n=0$ ,  $F_{ext}=0.02$  and  $f_{ext}=1504$  or  $1520$  Hz, frequencies chosen to be just above or below the cluster frequency for  $F_{ext}=0$ . The other parameters were the same as before. The results are shown in Figure 2.

With zero external force, the central peak in the frequency spectrum of the oscillators occurs at 1512 Hz. However, Figure 2 shows that when the system is stimulated with external tones of 1504 and 1520 Hz, sets of oscillators are forced into synchronization at the imposed frequency. There is a much smaller effect on the 1420 Hz peak, and no effect on the 1604 Hz peak.

### Dynamics of phase-lock and phase-slip

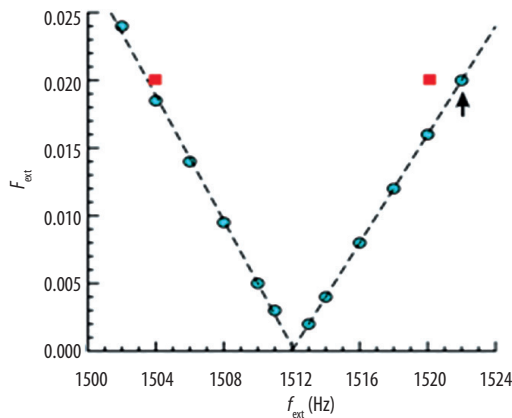
To investigate the way in which a cluster of oscillators becomes entrained – that is, how it gains or loses synchrony with an external tone – Eq. (2) was solved for different combinations of  $F_{ext}$  and  $f_{ext}$ , for  $a_n=0$  (i.e., no noise). Again,  $d_R=5$ ,  $d_I=-5$ ,  $\epsilon_j=1$ , and  $b_j=1$  for all  $j$ . To obtain the time signal for one of the clusters, one spectral peak was isolated. Explicitly, the sum  $x(t) = \sum_{j=1}^{101} x_j(t)$  was filtered with a 5<sup>th</sup>-order Butterworth filter with full width of 60 Hz and center frequency  $f_{ext}$ , which was chosen to be close to the frequency of the central peak in the insert in Figure 1B.

The times of the positive-going zero-crossings  $t_1, t_2, \dots$  of the filtered signal were determined for the time interval 0.2–2.2 s, again with a resolution of 0.01 ms. The positive-going zero-crossings  $\tau_1, \tau_2, \dots$  of the sinusoidal external force were also determined for the same time interval, and delay was calculated as  $(\tau_1 - t_1) / T_d, (\tau_2 - t_2) / T_d, \dots$ , where  $T_d$  is the period of the external force.



**Figure 2.** Amplitude spectra for each fourth oscillator in the array, as in Figure 1B. **Green:** Without external stimulation; the prominent peaks are at frequencies of 1420, 1512, and 1604 Hz (as in Figure 1). **Blue:** With external stimulation, for  $f_{ext}=1504$  Hz and  $F_{ext}=0.02$ . The peaks are now at 1418, 1504, and 1604 Hz. **Red:** With external stimulation, for  $f_{ext}=1520$  Hz and  $F_{ext}=0.02$ . The peaks are now at 1424, 1520, and 1604 Hz.

For different values of  $f_{ext}$ , the minimum value of  $F_{ext}$  with which phase-lock could be achieved (i.e. where there was a fixed delay) was determined. The result is shown in Figure 3.



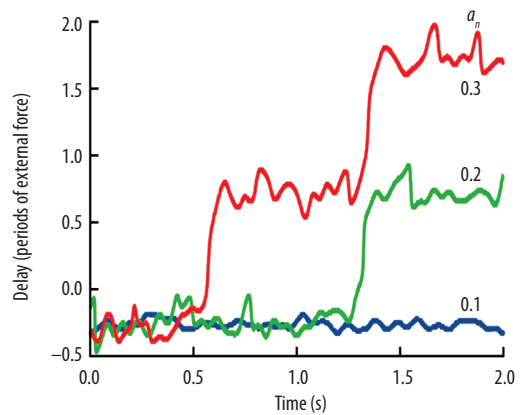
**Figure 3.** How a cluster of oscillators achieves, or loses, lock to an external tone. Circles: minimum values of  $F_{ext}$  with which phase-lock was obtained for different values of  $f_{ext}$ . The dashed straight lines are least squares fits. Red squares: combinations  $\{f_{ext}, F_{ext}\}$  used for Figure 2. Arrow: combination  $\{f_{ext}, F_{ext}\}$  for which phase-lock in the presence of noise was investigated.

To investigate how phase-locking to an external tone was disturbed by random noise, Eq. (2) was again used, but now for  $a_n \neq 0$ .  $F_{ext}$  was set at 0.02 and  $f_{ext}$  at 1522 Hz, and delays were calculated as described above. Results are shown in Figure 4 for three different values of  $a_n$ , each time calculated for a newly generated  $\zeta(t)$ .

The calculation for  $a_n=0.03$  was repeated 10 times, each time with a newly generated  $\zeta(t)$ . The results are shown in Figure 5A, and the corresponding distribution of all 30,422 delay values in Figure 5A is shown in Figure 5B.

## Discussion

Entrainment is a characteristic feature of oscillators [49]. Wit and Van Dijk [16] showed that when oscillators in a chain of coupled self-sustained oscillators cluster into frequency plateaus, such a cluster can be entrained by a periodic external force (that is, change its frequency to that of the external force). The work here confirms and extends

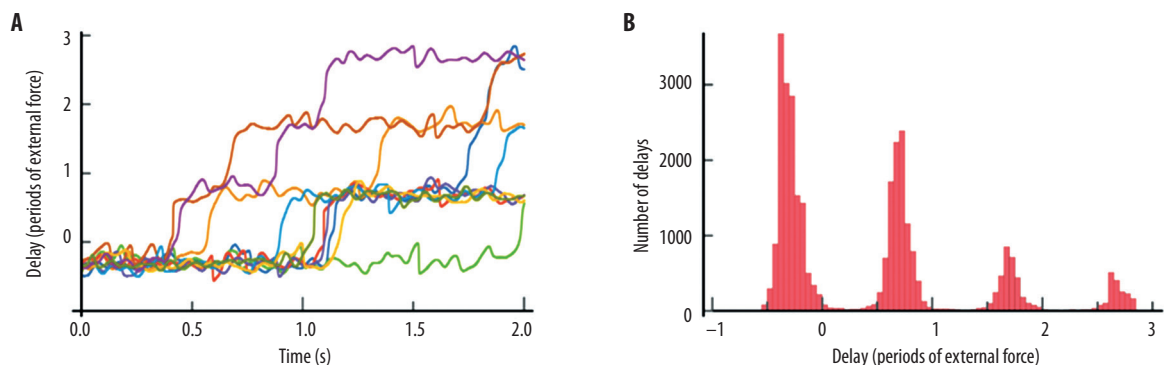


**Figure 4.** Delay of the filtered peak signal in the presence of noise for 3 values of noise strength  $a_n$ . Delay was calculated in terms of zero crossings of the signal with respect to zero crossings of the external force. For  $a_n=0$  phase-lock to the external force is perfect (not shown). Phase-lock occurs for  $a_n=0.1$  over the entire 2-s interval, although the delay fluctuates (blue line). For  $a_n=0.2$  and  $a_n=0.3$ , the filtered peak signal abruptly loses pace with respect to the external force, lagging by one or two cycles over the interval (green and red lines). After each phase jump, phase-lock continues for hundreds of milliseconds.

these findings (Figures 2 and 3). Clustering in frequency groups can even occur when passive and damped harmonic oscillators are coupled [31; Figure 15].

Other characteristic features of oscillators are phase-lock and phase-slip. The first known documented observation of phase-lock is that by Huygens [50], who described how two pendulum clocks phase-locked when they were attached to the same wooden beam.

The findings in the present work can be best understood in terms of the dynamics of a single Van der Pol oscillator, and its entrainment can be most readily appreciated by considering how an external force creates a potential well that the oscillator can fall into. Consider a Van der Pol oscillator exhibiting an almost sinusoidal oscillation



**Figure 5.** Phase delays in a system of coupled oscillators subject to levels of random noise. **(A)** The 10 traces show the calculated delay of zero crossings of the filtered peak signal in the presence of noise. The delay is referred to zero crossings of an external force with a frequency of 1522 Hz and noise strength  $a_n=0.3$ . **(B)** Distribution of all 30,422 delay values in panel A.

with angular frequency  $\omega_0$  (that is, it has an almost circular limit cycle), and subject to a combination of sinusoidal external force  $F_{ext} \sin(\omega_{ext} t)$  and noise force  $a_n \zeta(t)$ . Then the trajectory of its phase with respect to the driving force is the solution of [22,51,52]:

$$\frac{d\varphi}{dt} = -\frac{dV(\varphi)}{d\varphi} + a_n \zeta(t) \quad (3)$$

in which  $V(\varphi)$  is the “phase potential”:

$$V(\varphi) = -\Delta\omega \cdot \varphi - \kappa \cos\varphi, \quad (4)$$

where  $\Delta\omega = \omega_{ext} - \omega_0$  and  $\kappa$  is proportional to  $F_{ext}$ .

Substitution of (4) in (3) gives:

$$\frac{d\varphi}{dt} = \Delta\omega - \kappa \sin\varphi + a_n \zeta(t). \quad (5)$$

Equation (5) allows the theoretical phase dynamics of a Van der Pol oscillator system to be calculated. Numerically, a solution to Eq. (5) could be found using Mathematica’s NDSolve routine for  $\Delta\omega = 20\pi \text{ s}^{-1}$ ,  $\kappa = 1.001 \Delta\omega$ , and  $a_n = 70 \text{ s}^{-1}$ , where  $\zeta(t)$  is white gaussian noise with zero mean and standard deviation 1. The calculation was repeated 10 times, each time with a freshly generated noise force, and the result is shown in Figure 6.

The curves illustrate the way in which a Van der Pol oscillator falls into, and jumps out of, a potential well created by the external force. With no noise ( $a_n = 0$ ), the phase  $\varphi$  is constant, because  $\kappa > \Delta\omega$  (see below). But as noise is added, it pushes  $\varphi$  out of the potential well and the phase jumps into the next valley, where it stays for some time [22,40].

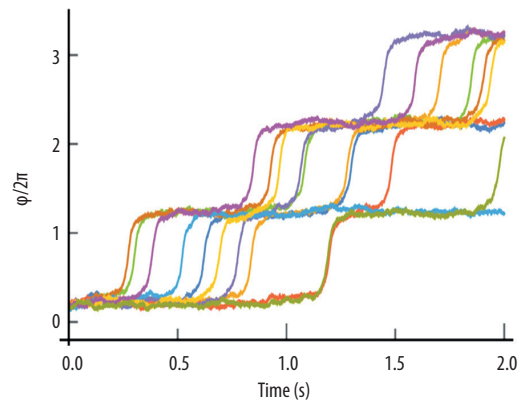
When the responses of the 101-oscillator array (Figure 5A) are compared with the theoretical behavior of a single driven oscillator in the presence of noise (Figure 6), the behaviors are identical. The inference is that the filtered peak signal, representing the behavior of a cluster of multiple oscillators, behaves in the same way as that of a single oscillator (given identical conditions of a sinusoidal external signal having a small frequency offset and disturbed by noise).

The jumps in the delay curves shown in Figures 5A and 6 correspond well with jumps in the phase curve of an otoacoustic emission synchronized by a cubic distortion product and measured in the ear of a human subject (Figure 2 of [22]).

In the absence of any noise force, Eq. (5) reduces to

$$\frac{d\varphi}{dt} = \Delta\omega - \kappa \sin\varphi \quad (6)$$

This is the classical equation obtained by Adler when studying phase-lock in a triode oscillator of the Van



**Figure 6.** Ten traces of the phase of a sinusoidally driven oscillator in the presence of noise, calculated using Eq. (5) for  $\Delta\omega = 20 \text{ s}^{-1}$ ,  $\kappa = 1.001 \Delta\omega$ , and  $a_n = 70 \text{ s}^{-1}$ . Phase is plotted as lag to the external sinusoidal force.

der Pol type [53,54]. For  $\kappa \geq \Delta\omega$ , Eq.(6) has the solution  $\varphi = \text{constant} = \arcsin(\Delta\omega/\kappa)$  and the oscillator is phase-locked to the external force. An explicit solution of Eq. (6) for  $\kappa < \Delta\omega$  is given in the Appendix.

The minimum value of  $\kappa$  for which phase-lock occurs is  $\Delta\omega$ . Because  $\kappa$  is proportional to the magnitude of the external force  $F_{ext}$ , the minimum value of the force required to achieve phase-lock is also proportional to  $\Delta\omega$ , and this is precisely what is seen in Figure 3.

Entrainment, phase-lock, and phase-slip are well-documented properties of both self-sustained (active) oscillators and SOAEs. Previously, SOAE properties have been modeled with a single self-sustained oscillator, usually of the Van der Pol type. The present paper shows that these same properties also arise in groups of oscillators: when mutually coupled, the oscillators inherently cluster into frequency plateaus, and these clusters behave just like a single Van der Pol oscillator.

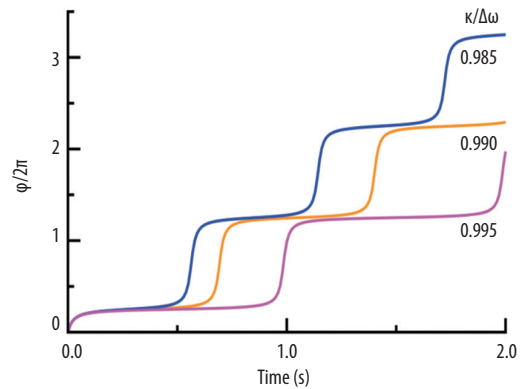
Although the model presented here is by no means a comprehensive model of the human cochlea (the array of oscillators covers just 1 mm of the 35-mm-long basilar membrane [45]), it generally supports the idea that the cochlea can be modeled as a chain of coupled oscillators. Since SOAEs from animals without basilar membranes are remarkably similar to SOAEs from animals that do [27], it is suggested that the oscillator dynamics described here may be usefully applied to describe SOAEs from animals as diverse as lizards and humans. In both cases, SOAEs measured outside the ear might be identified with the activity of oscillators that have clustered into frequency groups or plateaus.

## Appendix

The solution of  $\frac{d\varphi}{dt} = \Delta\omega - \kappa \sin\varphi$ , for  $\varphi(0)=0$  and  $\kappa < \Delta\omega$ , is:  $\varphi(t) = 2 \arctan \left\{ \frac{\kappa + \sigma \tan\{\sigma t/2 - \arctan(\kappa/\sigma)\}}{\Delta\omega} \right\}$ , with

$$\sigma = \sqrt{(\Delta\omega)^2 - \kappa^2}.$$

This solution was found using the DSolve routine of Mathematica. Figure 7 shows solutions for  $\Delta\omega = 20\pi \text{ s}^{-1}$  and three values of  $\kappa$ .



**Figure 7.** Explicit solutions to Adler's [53] equation for phase change in a forced Van der Pol oscillator with no noise, for  $\kappa < \Delta\omega$  (Eq. 6) and for three values of  $\kappa/\Delta\omega$ .

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