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Artificial Hair Cell Integrated with an Artificial Neuron: Interplay between Criticality and Excitability

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We provide a simple dynamical model of a hair cell with an afferent neuron where the spectral and the temporal responses are controlled by the hair bundle's criticality and the neuron's excitability. To demonstrate that these parameters, indeed, specify the resolution of the sound encoding, we fabricate a neuromorphic device that models the hair cell bundle and its afferent neuron. Then, we show that the neural response of the biomimetic system encodes sounds with either high temporal or spectral resolution or with a combination of both resolutions. Our results suggest that the hair cells may easily specialize to fulfil various roles in spite of their similar physiological structures.

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I. INTRODUCTION

The ear is an exquisite mechano-transducer that transforms minute mechanical stimuli into neuronal signals. It can detect sounds at a level close to thermal noise and vibrations as small as one-millionth of the gravitational acceleration. The places where this mechano-transduction occurs are the auditory and the vestibular hair cells. Compared to transduction in olfactory and visual sensory organs, mechano-transduction and its mechanism in auditory organs are relatively less understood on a molecular basis. Transduction is known to be a direct and rapid process that does not need an intermediate molecular process, and only quite recently have scientists started to investigate the detailed process of how hair cells transform the mechanical stimuli into neuronal signals. One of the questions that has attracted attention is how the ear can have sharp frequency selectivity and high temporal resolution at the same time. The human auditory system is capable of detecting the time of arrival of sound at the two ears down to tens of microseconds. In addition, humans can distinguish between two different sounds with a frequency difference of less than one percent.

Here, inspired by hair cells' mechano-transduction in lower vertebrates, we designed, fabricated and integrated an artificial hair cell and an artificial neuron, that mimicked the recently discovered functional principles of hair cells and neurons. In spite of the simplicity of the model, we find that the hair cell-neuron complex mimics the various sound-encoding properties of biological hair cells, such as fine frequency tuning and fast temporal response. We exploit the unique tunability by using our opto-electro-mechanical system to adjust the hair cell's criticality and the neuronal membrane's threshold voltage. When the hair cell is close to its critical point and the neuron's excitability is low, an auditory/vibration signal is encoded in the neuron with a high frequency selectivity, a situation that may possibly occur in auditory neurons. In the opposite case, the hair cell being far from its critical point and the neuron's excitability being low, the system has a broad frequency response that is suitable for a high temporal resolution.

II. THE MODEL

Upon an external stimulus, hair cell bundles are bent toward the tallest stereocilium, and an inward K^+ flow depolarizes the cell body (Fig. 1(a)) [1]. This achieves a fast temporal response in less than a millisecond after the onset of a sufficient stimulus [2,3]. The K^+ influx evokes a receptor potential, which opens voltage-gated calcium channels. These channels drive transmitter release and spontaneous nerve signals even in the absence of sound [4,5]. Hair cells are said to release neurotransmitters continuously through their synaptic junctions. Even with no sound, the hair cell is releasing glutamate because its resting potential is depolarized enough for some of the voltage-gated Ca^{2+} channels. This consideration leads us to assume a steady leakage current μ, which acts as a stimulus current to post-synaptic neurons.

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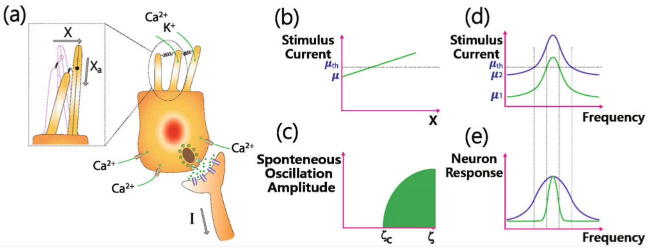

Fig. 1. (Color online) Schematic figures for the proposed sound-encoding mechanism of hair cells: **(a)** The hair cell bundle, synaptic junction, and auditory nerve, **(b)** assumption about the synaptic junction: the neuronal stimulus current I is a function of the bundle displacement X with an offset value of the current (leakage current) μ, **(c)** hair cell bundle as a dynamical system with a Hopf bifurcation in terms of a parameter ζ, **(d)** value of the offset stimulus current μ that determines the size of the frequency range in which the stimulus current goes beyond the neuronal threshold $\mu_{\rm th}$, and **(e)** spectral resolution of the neuronal threshold of hair cells given by μ.

The change in the receptor potential V_X when the bundle is deflected by X from its equilibrium point is assumed to satisfy (Fig. 1(b))

$$I = V_X + \mu, \tag{1}$$

where μ is the synaptic leakage current, which governs spontaneous neuron signals. μ has a certain threshold value μ_{th}, above which afferent neurons generate spontaneous spikes in the absence of external stimuli. In fact, a highly-nonlinear short-term synaptic depression at the synapse is caused by a depletion of the synaptic pool. This effect is important only if the input signal is slowing varying (compared to 30 ms), so the effect is ignored in our model because it is not severe. Because the proximity of μ to $\mu_{\rm th}$ indicates how easily the neuron is excited, we may call the parameter $\mu_{\rm th}$ the excitability.

Dozens of individual afferent neurons, which have different acoustic thresholds and spontaneous rates [6], and might have different excitabilities, contact a single hair cell. When a mechanical stimulus is applied to the stereocilia bundle, a Ca^{2+} influx is also derived (Fig. 1(a)). Although its electric current is significantly less than that of the K^+ influx, the calcium ion causes nontrivial hair-bundle dynamics. An oscillatory instability arises from the interplay between the negative stiffness [7] of the bundle and the Ca^{2+}-regulated molecular motors [8].

Optimal mechanosensitivity and sharp frequency selectivity can be expected when the hair bundle operates near the critical point of the instability (bifurcation) [8, 9]. In Fig. 1(c), the spontaneous oscillation amplitude is schematically described as a function of the parameter ζ that causes a bifurcation. A biomimetic system mimicking this bifurcation was recently realized in an opto-electro-mechanical system [10].

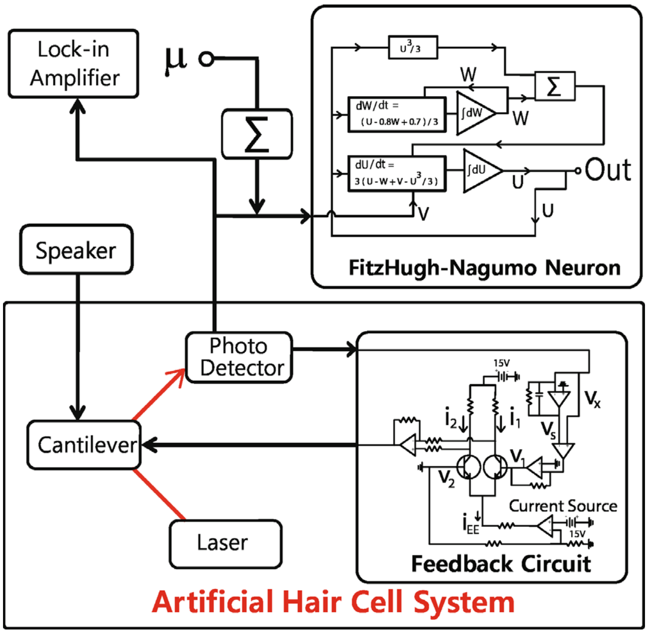

Fig. 2. (Color online) Schematic diagram for the electronic circuit mimicking a neuron in the FitzHugh-Nagumo model. The electronic circuit for the artificial hair cell is from Ref. [10].

As a generic property of this bifurcation phenomenon, the frequency selectivity of the mechanical response of the bundle becomes sharper as the bundle approaches the critical point. One of the key points in our model is that the spectral resolution of the neuron's response to the hair cell is controlled by the criticality parameter ζ and by the excitability parameter μ. When μ gets closer to its neuron threshold value $\mu_{\rm th}$ (compared to the cases of μ_1 and μ_2 in Fig. 1(d)), a neuron stimulus current I above the threshold value is generated over a wider frequency range. This, in turn, causes the neuron to fire in a wider range of the frequencies (Fig. 1(e)). Overall, our hypothesis on the spectral and the temporal precisions of sound coding involves two facts: how close the bundle is to its critical point and how close the synapse leakage current is to its threshold value. The former gives a neuron response over a narrower frequency range as the bundle approaches its critical value, and the latter gives a neuron response over a wider frequency range.

III. EXPERIMENT

A sketch of our experimental setup is shown in Fig. 2. A hair bundle is mimicked by using a cantilever made of a copper loop laminated by polyester sheets [11]. This cantilever is placed in a static magnetic field and is subjected to a time-dependent Lorentz force when a.c. currents are injected through the loop [10,11] . A He-Ne laser beam reflects from the tip of the cantilever. The deflection of the reflected beam is measured by using a photodetector (S3931 Hamamatsu) and recorded as a voltage V_X(t).

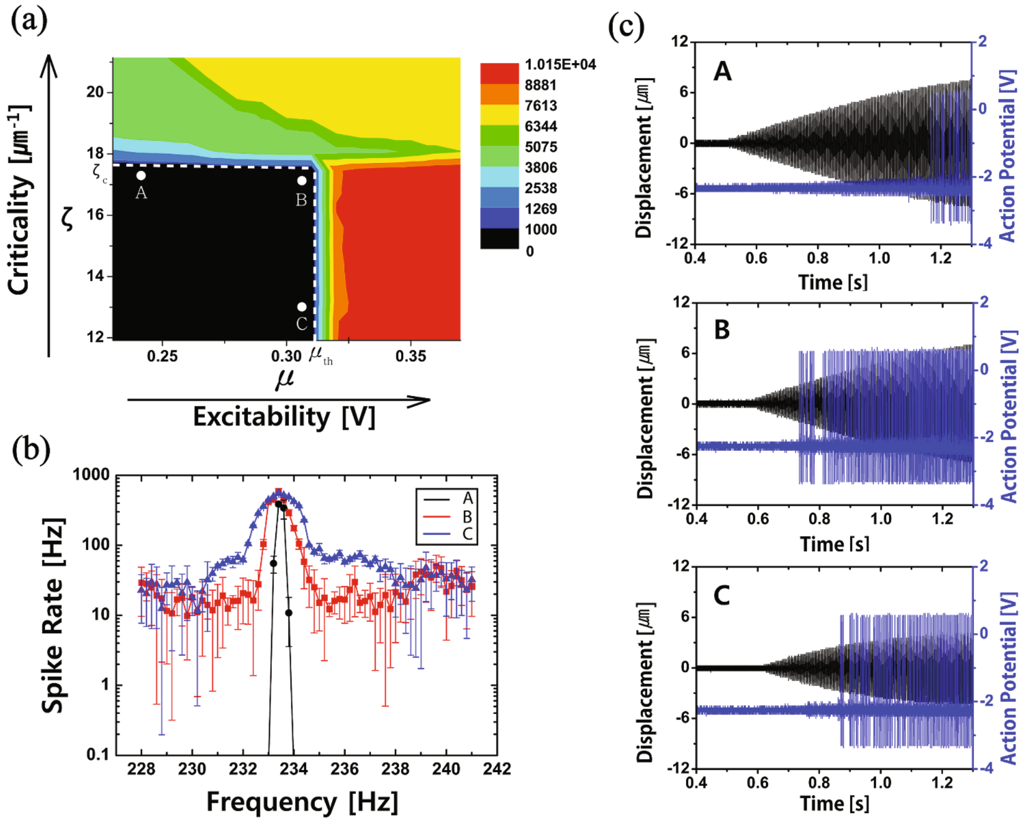

Fig. 3. (Color online) Spectral and temporal precisions of the neuron response of hair cells: **(a)** two-dimensional plot for the spike rates of the neuron in the absence of sound stimuli, **(b)** dependence of the spectral resolution of the sound stimulus on the location (A, B, C) in the parameter space shown in Fig. 3(a), and **(c)** hair bundle displacement in the presence of sound (black) and the corresponding action potential (blue) for the three points A, B, and C in Fig. 3(a).

We integrate an artificial hair cell that shows a Hopf bifurcation [10] with a FitzHugh-Nagumo(FN) neuron that is realized in an electronic circuit. The dynamics of the FitzHugh-Nagumo neuron can be described with the following equations:

$$dU/dt = 3(U - W + V - U^3/3), \quad (2)$$

$$dW/dt = 1/3(U - 0.8W + 0.7), \quad (3)$$

where U is the membrane potential of the neuron, W is a slow recovery variable and V is the input variable. U, V, and W are in units of volts, and time is in units of 0.1 ms. The neuron has a threshold stimulus above which it oscillates. When the neuron input voltage V is beyond the threshold value, the membrane voltage U oscillates. The neuron input variable may generally be written as the sum of the hair cell's output voltage V_X and an offset value μ. In the absence of an input sound, our FN neuron may oscillate spontaneously, depending on the parameters μ and ζ.

The experimental results of the sound coding in our artificial hair cell-neuron system are summarized in Fig. 3. The neuron fires spontaneously either when the amplitude of the hair-bundle oscillation is large enough to excite neurons or the neuron excitability is beyond its threshold value ($\mu > \mu_{\text{th}}$= 0.32 V). We see a rich phase separation in ζ - μ space, where the neuron remains quiet (black). We chose three different interesting regions, which we designated as A, B, and C.

In region A, the hair-cell bundle is close to its critical point, but the neuron-synapse excitability is low. The mechanical response has a high quality factor [10]. The frequency resolution of the neuronal response is the highest among the three cases because the neuron-synapse is not excited by the bundle's oscillation at non-resonant frequencies (Fig. 3(b)). However, the temporal resolution is the worst among the cases (Fig. 3(c)).

In region B, the hair-cell bundle is close to its critical point, and the neuron is easily excitable. The spectral response in this region falls between those in regions A and C. The peak structure occurs at the central frequency, but a neuron response is also shown over a broad frequency range. Interestingly, the temporal response is the fastest among the three cases because both the mechanical amplification and the high excitability help to produce the fast response.

In region C, the hair-cell bundle is far from its critical point and the neuron-synapse excitability is high. The frequency range of the neuron response is the broadest. This might be the case of a vestibular hair cell as the temporal precision is more important than the frequency information in the human vestibular system.

IV. SUMMARY AND DISCUSSION

In summary, we demonstrated that when an artificial hair cell is coupled to a neuron, its spectral resolution can depend on its static leakage current in the synapse. The interplay between the criticality of the hair cell and the excitability of the neuron might contribute to both high spectral resolution and high temporal resolution. Our biomimetic system might be useful for developing smart sensors that detect sound information with high temporal and/or spectral resolution.

Because our model is motivated by the hair cell of lower vertebrates, we need to mention the limits on any application of our results to mammalian hearing. First, the inner hair-cell bundle of the cochlea shows neither a spontaneous oscillation nor a Hopf bifurcation. Second, the FN neuron model is too simple to describe the spike-rate adaptation in post-synaptic ganglion cells in mammalian hearing. A more complex biomimetic system describing realistic synapses and neurons might shed light on the sound-encoding mechanism of hair cells.

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