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Spontaneous dynamics and response properties of a Hodgkin-Huxley-type neuron model driven by harmonic synaptic noise

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Abstract

We study statistical properties, response dynamics, and information transmission in a Hodgkin-Huxley-type neuron system, modeling peripheral electroreceptors in paddlefish. In addition to sodium and potassium currents, the neuron model includes fast calcium and slow afterhyperpolarization (AHP) potassium currents. The synaptic transmission from sensory epithelium is modeled by a Poisson process with a rate modulated by narrow-band noise, mimicking stochastic epithelial oscillations observed experimentally. We study how the interplay of parameters of AHP current and synaptic noise affects the statistics of spontaneous dynamics and response properties of the system. In particular, we confirm predictions made earlier with perfect integrate and fire and phase neuron models that epithelial oscillations enhance stimulus-response coherence and thus information transmission in electroreceptor system. In addition, we consider a strong stimulus regime and show that coherent epithelial oscillations may reduce variability of electroreceptor responses to time-varying stimuli.

1 Introduction

Self-sustained oscillations were observed in several types of peripheral hair cell – primary afferent sensory receptors. Such 2-stage receptors are found in the auditory, vestibular, lateral line, and electrosensory systems and have stimulus-transducing hair cells or similar receptor cells synaptically coupled to sensory neurons (afferents) conveying transduced stimuli to the central nervous system. Recordings of spontaneous firing from auditory afferent fibers in turtles, lizards, and birds showed a series of similarly spaced peaks in interspike interval histograms, indicating “preferred intervals” [1,2]. Some primary vestibular afferents demonstrate extremely regular periodic firing [3,4]. Isolated hair cells of auditory and some vestibular receptors of lower vertebrates undergo ringing (damped membrane potential oscillations) in response to step changes in membrane potential [5,6]. Such hair cells may undergo spontaneous oscillations of membrane potential [7–9], or spontaneous periodic motions of ciliary hair bundles [10–13]. These spontaneous oscillations of hair cells are reflected in periodic sequence of post-synaptic excitatory potentials and, consequently, in periodic firing of primary afferents [9].

Electroreceptors (ERs) in paddlefish are characterized by spontaneous biperiodic activity, as each ER embeds two distinct noisy oscillators [14]. One oscillator (termed as epithelial oscillator, EO) resides in a population of sensory hair cells in epithelium and is coupled via excitatory synapses to primary afferent neuron, which contains another oscillator (afferent oscillator, AO), responsible for generation of periodic sequences of spikes. Thus, single ER system can be viewed as two oscillators coupled unidirectionally, $EO \rightarrow AO$. The fundamental frequency of the AO, represented by the mean firing rate of an afferent, ranges from 30 to 70

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Hz depending on particular ER and can be altered by external stimuli (electric field). On the contrary, the fundamental frequency of the EO is approximately 26 Hz for different ERs and is invariant with respect to weak to moderate stimulation [14,15]. Thus, the EO oscillator sets an internal rhythm for the entire population of ERs. On the other hand, noisy epithelial oscillations can be viewed as a source of internal narrow band or harmonic noise [16].

Multi-modal oscillations may mediate correlations in sequences of action potentials and of receptor responses to external signals. These correlations provide a higher degree of ordering of neural responses and may enhance information transmission and detection performance of receptors. Serial correlations of neuronal interspike intervals have received recently much interest [17–21] as times between sequential spikes of some auditory afferents and electroreceptor afferents tend to not be independent. Instead, a long interspike interval (ISI) tends to follow a short interval, and vice versa. Such anticorrelations are a type of ordering, and imply reduced low-frequency noise in afferent firing. This “noise shaping” yields higher signal-to-noise ratio, increased discriminability and information transfer at low frequencies, as was shown in a number of theoretical [18,18,22] and experimental [17,20] studies. A general theoretical framework for serial inter event correlations is presented in this special issue [Schwalger and Lindner]. Unlike other sensory neurons which exhibit serial ISI correlations propagating to just a few ISIs, paddlefish ER afferents show long-lasting serial correlations extending up to hundreds of ISIs occurring due to specific biperiodic organization of ERs [14,23].

The experimental validation of functional roles of oscillations and correlations in peripheral receptors involves several difficulties. An ultimate experimental test would involve suppression of oscillations and/or correlations and then analyzing how sensitivity, encoding and detection characteristics of a sensor change compared to the original condition, e.g. when oscillations are present. Suppression of oscillations can be achieved by pharmacological blockage of certain ion channels in the cell membrane. Such procedures often change other properties of a receptor, such as the mean firing rate, for example. Moreover, pharmacological procedures are usually performed in *in vitro* preparations which often raises question on the whether receptor system still operates normally. That is why modeling studies and methods of advanced signal processing are crucial in understanding functional significance of coherent rhythmic activity and correlations in sensory systems. These methods allow imposing a clear constraints on a system while varying its parameters and studying responses to various stimuli. For example, to show the role of negative serial ISI correlations in enhancement of information transmission in spiking neurons, theoretical studies [19,22] contrasted two integrate and fire models, a renewal and non-renewal, which differed in ISI autocorrelations, but were constrained to have the same first-order ISI statistics. Similarly, recent theoretical and numerical studies [24,25] used simple phase and perfect integrate and fire models to show that coherent internal fluctuations leading to extended serial ISI correlations can augment the information transfer and discrimination capacity of weak stimuli in a sensory receptor. In this paper, we extend these studies to a conductance-based model and also consider the case of strong stimuli which are known to result in distinct responses in the form of stimulus-induced bursts in paddlefish ERs [15,26]. Although the model is set to mimic paddlefish ERs, it indeed can be viewed in a more general context of a neuron perturbed by stochastic oscillations.

2 Model and methods

We used a modified Hodgkin-Huxley model proposed in [27,28] to study effects of adaptation. The model includes fast sodium current, slow potassium outward current along with fast calcium current, and a calcium-dependent after hyperpolarization potassium current (AHP). AHP currents were found in vestibular afferents [29] and are known to influence variability of spontaneous afferent discharges [30,31,29]. The equation for the membrane potential is

$$C \frac{dV}{dt} = -I_{Na} - I_K - I_L - I_{Ca} - I_{AHP} - I_{syn}. \quad (1)$$

The sodium, potassium, leakage, and calcium currents are given by the Hodgkin-Huxley formalism,

$$I_{Na} = \bar{g}_{Na} h m^3 (V - E_{Na}); \quad I_K = \bar{g}_K n^4 (V - E_K); \quad I_L = g_L (V - E_L); \quad I_{Ca} = \bar{g}_{Ca} m_{\infty} (V - E_{Ca}), \quad (2)$$

where the parameters were the same as in [28]: $E_{Na} = 50$, $E_L = 67$, $E_K = -100$, $E_{Ca} = 120$ mV; $\bar{g}_{Na} = 100$, $g_L = 0.1$, $\bar{g}_K = 80$, $\bar{g}_{Ca} = 1$ mS/cm²; $m_{\infty}(V) = 1/(1 + e^{-(V+25)/5})$; $C = 1$ μF/cm². The gating variables h , m , n obey

$$\begin{aligned} \dot{x} &= \alpha_x(V)[1 - x] - \beta_x(V)x, \quad x = m, h, n; \\ \alpha_m(V) &= \frac{0.32(54+V)}{(1 - e^{-(V+54)/4})}, \quad \beta_m(V) = \frac{0.28(V+27)}{(e^{(V+27)/5} - 1)}; \\ \alpha_h(V) &= 0.128 e^{-(50+V)/18}, \quad \beta_h(V) = \frac{4}{(1 + e^{-(V+27)/5})}; \\ \alpha_n(V) &= \frac{0.032(V+52)}{1 - e^{-(V+52)/5}}, \quad \beta_n(V) = 0.5 e^{-(57+V)/40}. \end{aligned} \quad (3)$$

The AHP current is given by

$$I_{AHP} = \bar{g}_{AHP} \frac{[Ca^{2+}]}{30 + [Ca^{2+}]} (V - E_K), \quad (4)$$

where the slow calcium dynamics follows

$$\frac{d[Ca^{2+}]}{dt} = -0.002 I_{Ca} - 0.0125 [Ca^{2+}]. \quad (5)$$

Excitatory synaptic current modeling transmission from sensory epithelium is

$$I_{syn} = g_s(t)(V - E_{syn}), \quad (6)$$

where $g_s(t)$ is the time-dependent synaptic conductance, and $E_{syn} = 0$ mV is the reversal potential for the synapse. The synaptic conductance follows the equation:

$$\dot{g}_s = -\frac{1}{\tau_s}(g_s - g_0) + b \frac{dP}{dt}, \quad (7)$$

where τ_s is the synaptic time constant, g_0 is a constant contribution and $P(t)$ is a doubly stochastic Poisson process, describing pre-synaptic random release. The rate of this Poisson process is modulated by the activity of sensory epithelium $y(t)$: $\lambda(t) = \lambda_0 \Theta[1 + y(t)]$, where λ_0 is a background constant rate and $\Theta[x]$ is the Heaviside step function. In the following we

assume that the input from epithelial cells is given by the sum of spontaneous (EO) signal $h(t)$, and a time-dependent stimulus $s(t)$, $y(t) = mh(t) + \sigma s(t)$. Both processes are Gaussian with zero means and unit standard deviations, so that the parameters m and σ determine the strength of EO and stimulus, respectively.

The coherent epithelial oscillations, $h(t)$, characterized by the quality factor Q and the peak frequency f_e were modeled by harmonic Gaussian noise with the power spectral density,

$$G_{hh}(f) = \frac{C}{16Q^4(f^2 - f_e^2)^2 + 8(Qf_e)^2(f^2 + f_e^2) + f_e^4}, \quad C = \frac{4Q(1+4Q^2)f_e^3}{\pi} \quad (8)$$

In the absence of stimulus ($\sigma = 0$) and for small m the mean and the variance of synaptic conductance can be calculated as

$$\langle g_s \rangle = g_0 + b\tau_s\lambda_0, \quad \text{var}(g_s) = \frac{\lambda_0\tau_s b^2}{2} \frac{Q^2 + 2Q\tau_s(\pi f_e + m^2 Q\lambda_0) + \pi f_e \tau_s^2 [\pi f_e(1+4Q^2) + 4m^2 Q\lambda_0]}{Q^2 + 2\pi f_e \tau_s + (\pi f_e \tau_s)^2(1+4Q^2)}. \quad (9)$$

Synaptic noise is the only source of randomness in the model. The mean and the variance of synaptic conductance, $\langle g_s \rangle$ and $\text{var}(g_s)$, set the mean firing rate and the coefficient of variation (CV) of the neuron model. In our calculations, we tuned the mean and the variance of the synaptic conductance to values which produced the mean firing rate and CV typical for spontaneous firing of paddlefish ER afferents. Given λ_0 , τ_s , Q , f_e , m , the mean and the variance of synaptic conductance, the parameters g_0 and b in Eq.(7) were calculated using Eq.(9). Thus, in the absence of stimulus, the mean and the variance of synaptic conductance were constant while the parameters of the harmonic noise (Q , f_e , m) were varied. In the following we set $\bar{g}_{\text{AHP}} = 6 \text{ mS/cm}^2$, $\tau_s = 2 \text{ ms}$, $\lambda_0 = 10^4 \text{ Hz}$, $\langle g_s \rangle = 0.081 \text{ mS/cm}^2$, and $\text{var}(g_s) = 3 \times 10^{-5} [\text{mS/cm}^2]^2$. With these parameters the model produced spontaneous (no stimulus) firing with the mean firing rate of 55 Hz and the CVs in the range 0.1 – 0.2, typical for paddlefish ER afferents [14]. The model equations (1 – 7) were integrated numerically using an Euler method with the time step $5 \times 10^{-4} \text{ ms}$. The harmonic noise $h(t)$ was obtained by linear filtering of Gaussian white noise.

A spike train generated by the model was represented as a sequence of delta functions centered

at spike times t_i : $\xi(t) = \sum_{i=1}^N \delta(t - t_i)$, where N is the number of spikes in the train. The first-order statistics of the ISIs, $T_i = t_i - t_{i-1}$, was characterized with the probability density $p(T)$ and by its first two moments combined in the coefficient of variation, $\text{CV} = \sqrt{\text{var}(T)}/\langle T \rangle$. ISI correlations were quantified with the serial correlation coefficient (SCC),

$$C(k) = \frac{\langle T_n T_{n+k} \rangle - \langle T \rangle^2}{\text{var}(T)}. \quad (10)$$

The extension of serial correlations was assessed with the correlation time calculated as

$$t_{cor} = \langle T \rangle \sum_{k=1} |C(k)|, \quad (11)$$

where the sum is taken over lags with SCC significantly different from 0.

We used Gaussian noise bandlimited to a cutoff frequency f_c as a stimulus with the power spectral density, $G_{ss}(f) = 2/f_c, f \leq f_c$. The stimulus variance was invariant with respect to variations of the band (f_c). To estimate the linear response properties and a lower bound of the mutual information rate we applied a long (10 min) realization of such stimulus and calculated the stimulus–response (SR) coherence,

$$\Gamma_{SR}(f) = \frac{|G_{\xi s}(f)|^2}{G_{ss}(f)G_{\xi\xi}(f)}, \quad (12)$$

where $G_{\xi s}(f)$ is the cross-spectral density of the spike train $\xi(t)$ and stimulus $s(t)$, $G_{\xi\xi}(f)$ and $G_{ss}(f)$ are the power spectral densities of the spike train and stimulus, respectively. The lower bound estimate of the mutual information rate is given by [32]

$$\mathcal{I}_{LB} = - \int_0^{f_c} \log_2[1 - \Gamma_{SR}(f)] df, \quad (13)$$

in units of bits per second. We normalized the mutual information rate to the mean firing rate, $\mathcal{I}/\langle f \rangle$ to obtain the information rate in bits per spike [24].

To characterize variability of the model responses to a given stimulus, we repeatedly applied a shorter stimulus segment (120 sec). The cross-trial variability was characterized with the so-called response – response (RR) coherence [33,34]:

$$\Gamma_{RR}(f) = \frac{|\frac{2}{K(K-1)} \sum_{k=1}^K \sum_{j < k} G_{kj}(f)|^2}{\left[\frac{1}{K} \sum_{k=1}^K G_{kk}(f) \right]^2}, \quad (14)$$

where G_{kj} are cross-spectral densities between k -th and j -th responses in the trial sequence, G_{kk} is the power spectral density of k -th response, and K is the total number of stimulus presentations. As seen from Eq.(14), the RR coherence does not involve stimulus power spectra and only characterizes response variability that cannot be accounted for by the stimulus. Like SR coherence, RR coherence is a normalized quantity ranging from 0 (no correlations across responses) to 1 (perfectly synchronized responses) and satisfies the following inequality,

$$\Gamma_{SR} \leq \sqrt{\Gamma_{RR}} \quad [33].$$

To reveal the effect of coherent epithelial oscillations on response properties and information transfer, we contrasted the original model described above with a model where the harmonic noise $h(t)$ was substituted by Gaussian broad band noise. In particular, we used exponentially correlated Ornstein-Uhlenbeck (OU) process, $h(t)$, with the correlation time of 0.5 ms. The variance of $h(t)$ was tuned numerically to match spontaneous mean firing rate and CV of the model with harmonic noise. Then the response properties and information rates were compared for the original model and the model with no oscillations. In the following, we term the model

with harmonic noise as “oscillation” and the model with broad-band OU noise as “no oscillation”.

3 Results

3.1 Spontaneous dynamics

In the absence of synaptic transmission ($g_s = 0$), the system is at a stable equilibrium. In the deterministic case when the variance of synaptic conductance is 0 and $g_s(t) = g_0$, the model demonstrates a saddle-node bifurcation to periodic limit cycle as g_0 increases [28]. Fig. 1 compares statistical properties of oscillation and no oscillation models. The constraint on the CV imposed on the models resulted in the standard deviation (SD) of the broad-band OU noise larger than the SD of harmonic noise. For the example shown in Fig. 1 the SD of OU noise was ≈ 1 , that is, twice larger than the SD of harmonic noise (0.5) in the original model. Although ISI probability densities of both models match, their serial ISI correlations and power spectra differ drastically. We note that both models are non-renewal. Short-lasting negative ISI correlations appear due to self-inhibitory AHP current [27] even in the model with no epithelial oscillations [dotted line in Fig. 1(b)]. The power spectrum of the model with no oscillations showed a peak at $f_a = 55$ Hz corresponding to the mean firing rate of the neuron (afferent oscillator, AO). Because of negative serial correlations the power spectrum decreased towards low frequencies demonstrating the effect of noise shaping discussed in [19,22]. The model with coherent epithelial oscillations showed alternating serial correlations extended to several dozens of ISIs [solid line in Fig. 1(b)]. The power spectrum contained two fundamental frequencies: the fundamental frequency of the EO, f_e , the fundamental frequency of the AO and sidebands, $f_a \pm f_e$. Because of larger magnitudes of SCCs the effect of noise shaping is more pronounced for the model with coherent epithelial oscillations, leading to larger reduction of low-frequency power as compared to the model with no oscillations [Fig. 1(c)]. The structure of SCCs is determined by the ratio of two fundamental frequencies $w = f_e/f_a$ [23]. Experimentally measured value of w for paddlefish ERs is $w = 0.49 \pm 0.08$ [14] indicating that two oscillators embedded into the ER system operates close to 1:2 mode locking regime. The magnitude of the first negative SCC and the correlation time are peaked at $w = 0.5$ as Fig. 2 shows. This is consistent with the previous results obtained with a circle map model [23]. The effect of enhancement and extension of serial correlations is stronger for higher Q -values of epithelial oscillations.

3.2 Response to Gaussian stimuli

The response properties of the model to weak stimuli were characterized with the stimulus-response coherence. Fig. 3 shows SR coherence for two values of the stimulus cutoff frequency, f_c . For the wide-band stimulus [$f_c = 200$ Hz, Fig. 3(a)] the SR coherence of the original model with epithelial oscillations showed a wide peak at ≈ 7 Hz and a notch at the peak frequency of harmonic noise f_e , followed by a smaller maximum. This was expected, since f_e is not affected by external stimuli, consistent with experimental findings [14,35,36]. Therefore epithelial oscillations represented by the harmonic noise in the model act to reduce the coherence at f_e . The model with no oscillations demonstrated a uniform coherence curve with significantly smaller values. As shown in the previous subsection, extended serial correlations induced by harmonic noise lead to significantly smaller values of spectral power at low frequencies, as compared to the model with incoherent epithelial fluctuations of larger intensity [Fig. 1(c)]. This reduction of variability of background spiking resulted in the increased coherence for the model with epithelial oscillations. Similar results were obtained for stimuli with smaller frequency band, $f_c = 20$ Hz, matching the response band of paddlefish ERs [Fig. 3(b)]. SR coherence was used for calculation of the lower bound estimate of mutual information rate, Eq.(13) [32,19]. The dependence of $\mathcal{I}_{LB}$ on the ratio of frequencies of EO to AO, $w = f_e/f_a$ is shown in Fig. 4(a) for the model with harmonic noise. The information rate peaks at $w \approx 0.5$

corresponding to the maximal effect of epithelial oscillations on serial ISI correlations [Fig. 2 (b,c)]. To compare information rates in the model with EO to the model with incoherent epithelial fluctuations we calculated the difference between information rates of these models, $\Delta \mathcal{I} = \mathcal{I}_{\text{osc}} - \mathcal{I}_{\text{nonosc}}$. This information gain [Fig. 4(b)] demonstrated significant enhancement of information transfer due to coherent EO which was maximum at $w \approx 0.5$. The enhancement of information rate increases with the increase of the quality factor of EO. These results confirmed the previous finding made with a toy phase model [24].

The SR coherence Eq.(12) characterizes linear response properties of a system. For a noiseless linear system the SR coherence equals to its maximum value of 1. Internal as well as measurement noise and nonlinearities result in values of SR coherence less than one. In paddlefish ERs strong stimuli result in nonlinear responses in the form of stimulus-induced bursts [15]. Although individual ERs are non-coupled and possess distinct spontaneous firing rates, stimulus-induced bursts can be synchronized across the entire ERs population [37,15]. To study nonlinear response dynamics, we applied identical realization of Gaussian band-limited stimulus repeatedly to the model. This method, known as “frozen noise”, allows characterization of response variability [38]. Fig. 5(b,c) shows raster plots of responses of the ER model with coherent epithelial oscillations to repeated presentations of weak [Fig. 5(b)] and strong [Fig. 5(c)] Gaussian stimulus. Vertical stripes in Fig. 5(c) clearly indicate that strong stimulus synchronized the afferent bursting responses across the trials. Such reliable and precise response dynamics of the model with coherent epithelial oscillations is contrasted to the model with incoherent epithelial fluctuations in Fig. 5(d), which shows significantly lower degree of cross-trial synchrony [see also Fig. 5(f)]. The response-response (RR) coherence is a qualitative measure of cross-trial synchrony in the frequency domain. For the linear response (weak stimuli) the SR and RR coherence functions matched (not shown). For the strong stimulus resulting in a bursting response [Fig. 5(c)] SR and RR coherence functions differ dramatically. Fig. 5(e) shows that while the SR coherence is zero beyond the stimulus cutoff frequency ($f_c = 20$ Hz), non-zero values of RR coherence extend well beyond the stimulus band. Such behavior of cross-trial coherence is typical and indicative of nonlinear neural responses [34]. The effect of epithelial oscillations on cross-trial synchrony is clearly seen in Fig. 5(f) which compares RR coherence for the model with harmonic noise and the model with incoherent epithelial fluctuations. In a wide frequency range of 22 – 120 Hz, the RR coherence is about 3 times larger for the model with epithelial oscillations.

4 Conclusions

We have studied spontaneous and stimulus-induced response dynamics of a Hodgkin-Huxley-type system with stochastic synaptic conductance modulated by harmonic noise. The parameters were tuned to reproduce statistical properties of peripheral electroreceptors in paddlefish, which are characterized by biperiodic background activity of their primary afferents. To elucidate the role of epithelial oscillations observed in paddlefish ERs, we contrasted two models: the original, with harmonic noise served to mimic epithelial oscillations and the model, where harmonic noise was substituted with short-correlated Ornstein-Uhlenbeck noise. The parameters of this second “no oscillations” model were tuned to match the mean firing rate and the coefficient of variation of the original model. We have confirmed previous results obtained with toy models [24,25] that epithelial oscillations induce long lasting serial correlations of interspike intervals leading to significant enhancement of information transmission. Serial ISI correlations may appear due to internal dynamics of a neuron, such as slow adaptation ionic currents [27] or dynamic firing threshold [22,39]. Another source of ISI correlations is an external correlated drive [40–42]. Here we considered a combination of two of these sources: internal dynamics, in the form of an adaptation AHP current, resulting in short-lasting negative ISI correlations and external dynamics, in the form of excitatory synapses modulated by harmonic noise, resulting in long-lasting alternating serial correlations.

We have shown that epithelial oscillations mimicked by harmonic noise, reduce variability of the model responses to strong stimuli enhancing reliability of biperiodic sensor compared to a sensor which possesses the same mean firing rate and CV as biperiodic, but lacks extended serial correlations.

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Fig. 1.

Probability density of ISIs (a), serial correlation coefficients (b) and power spectral density (c) of spontaneous stochastic dynamics. Solid (red) lines correspond to the original model with epithelial oscillations. Dotted (black) lines refer to the model with no epithelial oscillations, whereby a broadband OU noise was used instead of harmonic noise. The intensity of the OU noise was tuned to match the mean firing rate and CV of the original model. The parameters are: $\bar{g}_{AHP} = 6$ mS/cm², $\tau_s = 2$ ms, $\lambda_0 = 10^4$ Hz, $\langle g_s \rangle = 0.081$ mS/cm², $\text{var}(g_s) = 3 \times 10^{-5}$ [mS/cm²]², $m = 0.5$, $Q = 20$, $f_e = 27.5$ Hz. These parameters resulted in the mean firing rate $f_a = 55$ Hz and CV = 0.185.

Fig. 2. First serial correlation coefficient, $C(1)$ (a), and ISI correlation time t_{cor} (b) of spontaneous ISIs sequences versus the ratio of fundamental frequencies of EO to AO, $w = f_e/f_a$ for the indicated Q -values of epithelial oscillations. In these simulations the EO frequency, f_e , was varied. Other parameters are the same as in Fig. 1.

Fig. 3. Stimulus - response coherence for the indicated values of the stimulus cutoff frequency, f_c . In both cases the stimulus standard deviation was $\sigma = 0.5$. Solid (red) lines correspond to the original model with epithelial oscillations (oscil.). Dotted (black) lines refer to the model with incoherent epithelial fluctuations (no oscil.). Both models had identical spontaneous mean firing rates and CVs. The parameters were the same as in Fig. 1.

Fig. 4. Lower bound estimate of the mutual information rate, $\mathcal{I}_{LB}$, (a) and the information gain, $\Delta \mathcal{I} = \mathcal{I}_{osc} - \mathcal{I}_{nonosc}$ (b) versus the ratio of fundamental frequencies of EO to AO, $w = f_e/f_a$. The stimulus parameters were $\sigma = 0.5$, $f_c = 20$ Hz. Other parameters were the same as in Fig. 1.

Fig. 5. Cross-trial response variability. Models with harmonic noise (oscillation) and with broad-band OU noise (no oscillation) were stimulated repeatedly with identical realization of Gaussian noise band-limited to $f_c = 20$ Hz. (a) Short segment of the stimulus. (b–d) Raster plots of models responses to 200 trial presentations of the stimulus. Vertical axis is the trial number; horizontal axis is the time with respect to the stimulus onset. Dots indicate appearance of a spike in a trial relative to the stimulus onset. Panel (b) is for the stimulus standard deviation $\sigma = 0.5$ (weak stimulus). Panels (c,d) is for the case of strong stimulus with $\sigma = 2.0$ applied to the model with harmonic noise (c) and to the model with broad-band OU noise (d). (e) SR (dashed line) and RR (solid line) coherence functions for the model with harmonic noise. (f) RR coherence for the model with harmonic noise (oscil., solid line) and with broad-band OU noise (no oscil., dotted line). Other parameters were the same as in Fig. 1.