Synchronization of the Noisy Electrosensitive Cells in the Paddlefish

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Synchronization of electrosensitive cells of the paddlefish is studied by means of electrophysiological experiments. Different types of noisy phase locked regimes are observed. The experimental data are compared with computer simulations of a noise-mediated modified Hodgkin-Huxley neuron model and of a stochastic circle map. [S0031-9007(98)08238-6]

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Since the historical work of Huygens [1], synchronization has attracted much attention. It occurs when a nonlinear oscillator, showing a stable limit cycle [2], is subjected to an external time-dependent force or is coupled with another oscillator. Synchronization has been observed in a wide variety of natural and man-made systems [3]. It is also important in various biological systems, including, most recently, the human heart-respiratory system, as well as certain brain functions revealed by magnetoencephalography [4].

In this Letter we study experimentally the synchronization of electroreceptors of the paddlefish, *Polydon spathula*, which feeds on zooplankton, e.g., the water flea, *Daphnia* [5]. While adult fishes filter feed almost entirely on clouds of zooplankton, small paddlefish are particulate feeders, selecting and capturing zooplankton individually [6,7]. The paddlefish is named for its large rostrum, or "paddle," which is covered with an array of thousands of electrosensory organs (see Fig. 1). Recently it has been demonstrated that paddlefish are sensitive to weak electric fields, which they use for sensing prey electrically in the dark [8]. Both natural zooplankton and artificial electric dipoles were used to stimulate feeding [8].

Each of the electrosensory organs on the rostrum (Fig. 1) consists of a patch of ampullary-type cells, which synapse onto primary afferent (sensory) neurons sending long axons to the brain. The latter will be referred to as "electroreceptor cells" because their spike trains can be recorded, and are modulated by weak electric fields near the rostrum. We present here the first *direct* evidence that each cell contains a noise-mediated oscillator by showing that it can be synchronized with an external signal. In the absence of external stimuli, the cells generate noisy nearly periodic spike sequences. Noise mediated oscillators were previously studied in the electroreceptive cells of the dogfish (a kind of shark) and catfish [9] only indirectly by means of spike interval histograms. They have never been shown to exist in the primitive species of the order acipenseriformes (sturgeons and paddlefish).

Extracellular recordings were obtained *in vivo* from single cells. In our experiments (for details see [8]) a cell was stimulated by a weak electric and/or magnetic field generated by a dipole or a small coil located near the rostrum. The electric field strengths (a few tens of μV/cm) were comparable in magnitude to those generated by the zooplankton. Recordings of the spike train from the cell and periodic signal from the dipole were digitized and analyzed by computer. An example recording is shown in Fig. 1. The synchronized 1:5 mode locking (5 spikes per one stimulus cycle) is clearly seen [10].

In the classical theory of oscillation [2,11], synchronization is understood as instantaneous phase locking or frequency entrainment. When a nonlinear oscillator is subjected to an external periodic force with frequency Ω_0, the condition for phase locking is $|n\Phi(t) - m\Psi(t)| <$ const, where $\Phi(t)$ is the phase of the oscillator, $\Psi(t) = \Omega_0 t$ is the phase of the periodic force, and n and m are integers. The frequency locking condition is $\omega = \langle\dot{\Phi}\rangle = \frac{m}{n}\Omega_0$, where ω is the natural frequency of the oscillator. These requirements are fulfilled within the Arnold tongues [12], for which the $m:n$ resonance limit cycle is stable. Outside, the motion is quasiperiodic and is thus represented by an ergodic torus in the phase space. In the case of 1:1 phase locking, the phase dynamics can be described by a model $\dot{\phi} = \Delta - K\sin\phi$, where Δ represents the mismatch between the system's natural and the driving frequencies, while K is the nonlinearity parameter. The circle map is a generic model, describing higher order resonances, and the quasiperiodic route to chaos [13]:

$$\phi_{n+1} = \Gamma + \phi_n - \frac{K}{2\pi}\sin(2\pi\phi_n) \bmod 1, \qquad (1)$$

where Γ is the unperturbed winding number (at $K = 0$). In this Letter, we focus on the regions of phase locking and quasiperiodicity.

The influence of noise on synchronization is well understood [14]. The phase performs Brownian-like motion in a tilted periodic potential $U(\phi)$, the slope of which is determined by the mismatch Δ. For a time the phase (or "Brownian particle") remains in a well of $U(\phi)$ (phase locking), but can make noise-induced jumps from one potential well to another (phase slips). Thus, the time series

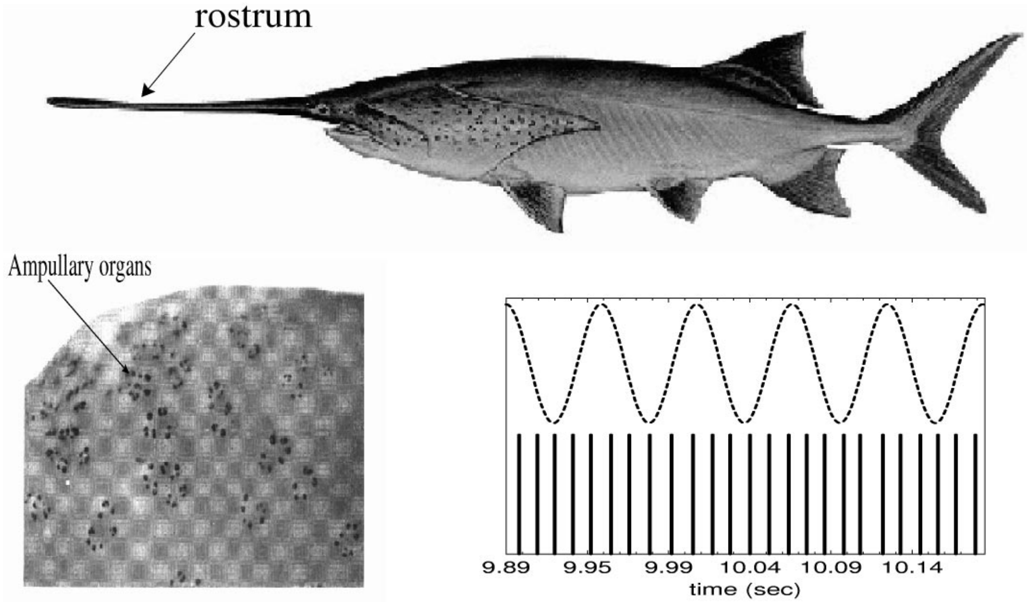

FIG. 1. The paddlefish (upper figure). Magnified fragment of the rostrum (lower left figure; the black patterns are ampullary organs) and an example of recording of spike train from a electroreceptor stimulated by dipole electric field of 17 Hz.

of the phase of a synchronized noisy oscillator contains segments where the phase is nearly constant, interrupted by noise-induced slips, where the phase changes rapidly. A measure of phase coherence is the effective diffusion constant, D_{eff} which describes spreading of an initial distribution,

$$\langle \phi^2(t) \rangle - \langle \phi(t) \rangle^2 \propto D_{\mathrm{eff}} t \,, \tag{2}$$

and $D_{\mathrm{eff}} \propto 1/\langle T \rangle$, where $\langle T \rangle$ is the mean duration of phase locking segments [14]. The region of synchronization in stochastic systems can be defined (somewhat arbitrarily) [15] by requiring that $\langle T \rangle \gg 2\pi/\Omega_0$, or $D_{\mathrm{eff}} \ll \Omega_0$.

We first define the phase as a stroboscopic map, which is closely related to the circle map [16]. Denote the moments of time at which the electroreceptor neuron fires as t_k, $k = 0, 1, 2, \dots, N$. Let τ_i be the zero crossing times of the external stimulus. For sinusoidal stimuli, $\tau_i = 2\pi i/\Omega_0$, $i = 0, 1, 2, \dots, M$. The phase of kth spike is [4,17]

$$\phi(t_k) = \frac{2\pi}{\tau_{i+1} - \tau_i} (t_k - \tau_i), \tau_i < t_k < \tau_{i+1} \,. \tag{3}$$

Defined in this way, the phase varies in the range from 0 to 2π and is determined at discrete moments of time.

In Fig. 2 we present three examples of the phase measured in the experiments. Three different regimes can be clearly distinguished. At a low stimulus frequency (5 Hz) the high-order mode locking of 1:17 is realized during some time segments. The pronounced 1:5 phase locking occurs at $f = 17$ Hz (see also Fig. 1). The five horizontal stripes correspond to phase locking segments, while the inclined lines correspond to phase slips. The phase locking occurs during a few hundreds of stimulus periods. Finally, at higher frequency $f = 21$ Hz we observe quasiperiodic behavior with no synchronization. The probability distributions of the phase shown in Fig. 3 are statistical evidence of synchronization [4]. In the strong synchronization regime (17 Hz) the probability density consists of 5 peaks corresponding to the phase locking patterns in Fig. 2.

The same synchronization patterns can be recovered also from the mathematical model of electroreceptors proposed by Braun [18]. This model is a modification of the well-known Hodgkin-Huxley (HH) neuron: $C_M \dot{V} = I_l - I_d - I_r - I_{sd} - I_{sr} - \sqrt{2D}\,\xi(t) - \epsilon \cos(2\pi f)$, where

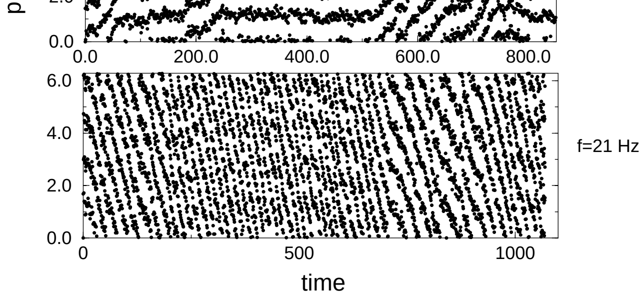

FIG. 2. The phase (3) versus time (in units of the stimulus period) for different values of stimulus frequency measured from electrophysiological experiments with paddlefish.

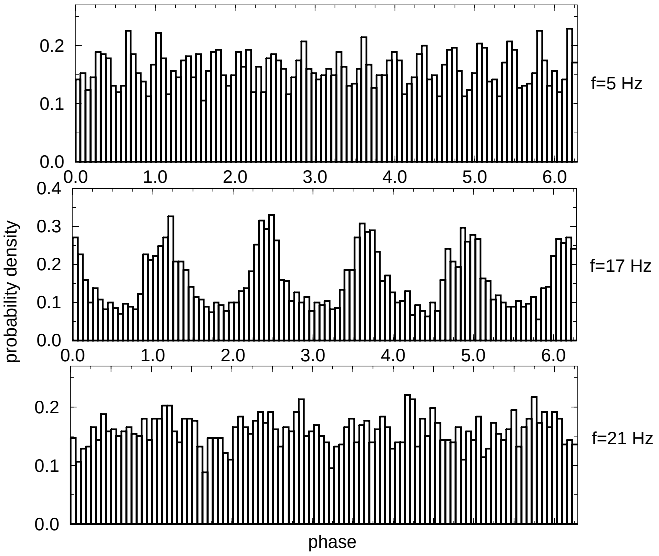

FIG. 3. The probability density of the phase obtained from the same data as in Fig. 2.

I_d and I_r represent the classical HH depolarization and repolarization currents, I_{sd} and I_{sr} are additional slow currents which produce the oscillations, $\xi(t)$ is white Gaussian noise with intensity D, and the last term represents a weak external forcing. For details and definitions of the other quantities, see Ref. [18]. The spontaneous activity of this neuron model is always irregular because of noise. The results of simulations are shown in Fig. 4(a) and are comparable to the experimental data shown in Fig. 2. Again we recognize a high-order resonance at 4.9 Hz, a strong 1:5 phase locking at 18.8 Hz and quasiperiodicity at 21 Hz. These synchronizations demonstrate that an oscillator is clearly present, and therefore the aforementioned slow currents *must* be included in the HH model of electroreceptors.

A simpler model can also capture the features of the observed dynamics. The dynamics of the phase defined by (3) are closely akin to those of a circle map with additive noise [19]. To illustrate this we show in Fig. 4(b) results of iterations of the circle map (1) with additive Gaussian white noise. In the purely deterministic case the phase locking regime of 1:5 is realized. However, with added noise, the phase behaves in the same manner as in the experiment and as in the simulation of the HH model neuron. In fact, remarkably, the synchronization processes in both electroreceptors and in the two simulations closely mimic the behavior of the noisy phase locked loop, a device familiar to electrical engineering [20].

An alternative approach is to define the phase $\phi(t)$ of the spike train instantaneously in time (unwrapped phase) [21],

$$\phi(t) = \rho\left[2\pi\,\frac{t - t_i}{t_{i+1} - t_i} + 2\pi i\right] - \Omega_0 t, \qquad t_i < t < t_{i+1}, \tag{4}$$

where t_i are spike times, Ω_0 is the frequency of external stimulus, and ρ is the winding number. The phase defined in this way is a piecewise linear function of time and, unlike the previous case of Eq. (3), is an unbounded variable. This definition of the phase is more suitable for the calculation of quantitative statistical measures of synchronization, such as the effective diffusion constant (2). In particular, the cases of 1:5 and 1:17 phase locking and the quasiperiodic regime of the electroreceptor are shown in Fig. 5. In the phase locked regimes (5 and 17 Hz) the phase changes slowly compared to the quasiperiodic case (21 Hz). The effective diffusion coefficients from Eq. (2) are 0.076, 0.256, and 2.145 rad^2/s for the stimulus frequencies 5, 17, and 21 Hz, respectively. These numbers are in agreement with estimates of D_{eff} from the mean duration of phase locking segments.

Recordings taken from other electroreceptor cells of the paddlefish rostrum have shown qualitatively similar results. Our results clearly show that noisy oscillations of the electroreceptors of the paddlefish exist, since they can be synchronized by an external electric field.

As mentioned in the introductory part of the paper, small paddlefish use electrosensitivity to feed on individual zooplankton, which generate sinusoidal-like, low

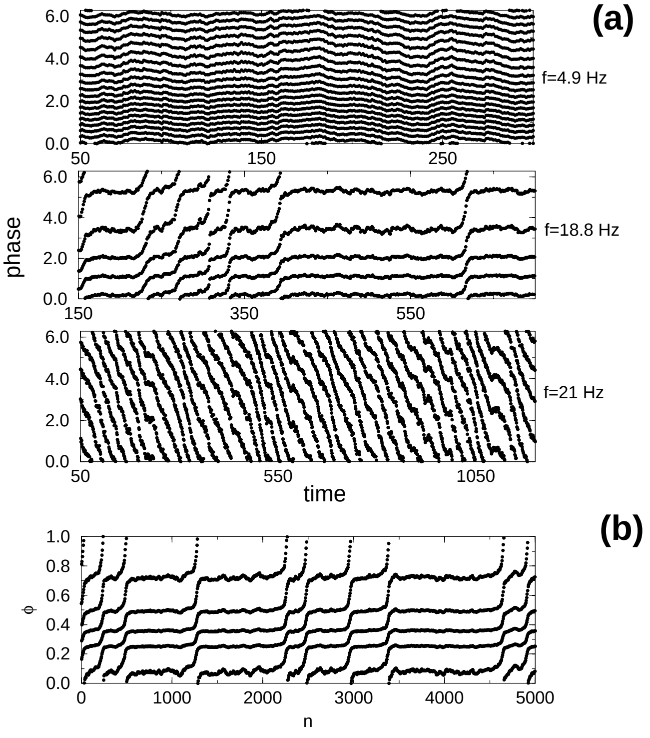

FIG. 4. (a) The phase (3) versus time (in units of stimulus period) for different values of stimulus frequency calculated from the modified Hodgkin-Huxley neuron driven by noise and an external periodic stimulus of indicated frequencies. (b) The sequence generated by circle map (1) with additive Gaussian noise of the variance $\sigma = 10^{-3}$. Other parameters are $\Gamma = 0.2336$ and $K = 0.8$.

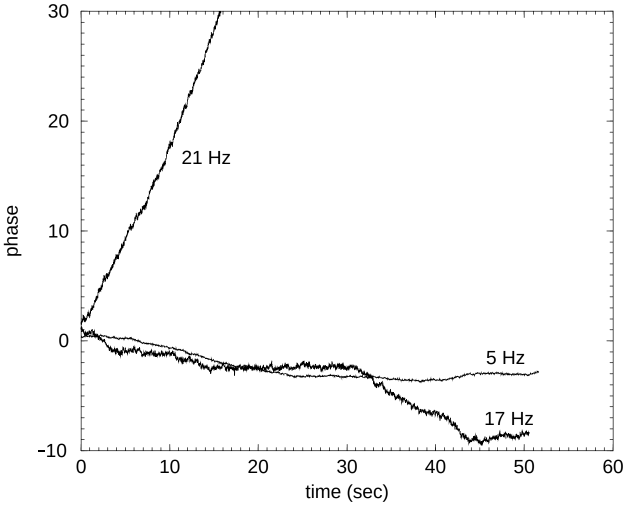

FIG. 5. Instantaneous phase (4) of the spike train generated by a electroreceptor cell of the paddlefish at 5, 17, and 21 Hz stimulus frequency. We used the same records as in Fig. 2.

frequency (8 to 12 Hz) electric fields resulting from muscle activations during their swimming motions. Since the feeding occurs during movements of both the fish and the zooplankton, a synchronization code could be a viable mechanism that the fish uses to track the target prey. This speculation bears directly upon recent and widespread interest in new neural coding schemes, as, for example, recently put forth by Hopfield [22].

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