Phase synchronization and stochastic resonance effects in the crayfish caudal photoreceptor

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We study the nonlinear response of the crayfish caudal photoreceptor to periodic mechanical stimuli in terms of stochastic synchronization. The amplitude and frequency of the mechanical stimuli and the light level are used as control parameters. The system shows multiple locking regions as the stimulus frequency is varied. We find that the synchronization index increases as the signal-to-noise ratio (SNR) of the periodic drive, in response to increasing light levels; this effect exhibits features similar to stochastic resonance. We demonstrate a nonlinear rectification effect in which the SNR of the second harmonic of the input stimulus increases as the light level is raised, and show that the corresponding synchronization index increases as the SNR of the second harmonic.

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The fundamental nonlinear phenomenon of synchronization has recently received great interest in connection with biomedical systems (for recent books and reviews see Refs. [1,2]). Synchronization as the mechanism of entrainment of a system’s rhythm by an external signal may play a significant role in signal processing by sensory biological systems [3]. Noise is inherently and inevitably present in any dissipative role in signal processing by sensory biological systems. The fundamental nonlinear phenomenon of synchronization is well defined as a phase locking [4,5] or frequency entrainment [4]. Thus, for noisy systems a statistical approach must be used, leading to the notions of effective or stochastic synchronization [4,5], which may be defined using measures derived from (i) phase fluctuations, (ii) frequency fluctuations, and (iii) output signal-to-noise ratio (SNR).

Here, we demonstrate synchronization between the CPR firing and the periodic mechanical stimulus using a variety of quantitative approaches: (i) phase fluctuations characterized by the synchronization index of the probability density of the phase difference [6,7], (ii) the interspike-interval histogram and the standard deviation of the difference between instantaneous period and drive periods, which characterize the frequency fluctuations, and (iii) output SNR, calculated from the spike train power spectrum. We show that multiple locking regions occur in the system, and demonstrate that synchronization, assessed by several methods, increases as light is applied to the photoreceptor cells; this effect exhibits some features characteristic of stochastic resonance. We also discuss a different effect in which light increases the SNR of the second higher harmonic of the input signal, and the corresponding synchronization index.

We consider the synchronization of the CPR firing and the periodic mechanical stimulus using a variety of quantitative approaches: (i) phase fluctuations characterized by the synchronization index of the probability density of the phase difference [6,7], (ii) the interspike-interval histogram and the standard deviation of the difference between instantaneous period and drive periods, which characterize the frequency fluctuations, and (iii) output SNR, calculated from the spike train power spectrum. We show that multiple locking regions occur in the system, and demonstrate that synchronization, assessed by several methods, increases as light is applied to the photoreceptor cells; this effect exhibits some features characteristic of stochastic resonance. We also discuss a different effect in which light increases the SNR of the second higher harmonic of the input signal, and the corresponding synchronization index.

We begin with phase synchronization. If we denote the times at which a neuron fires as \( t_k, \) \( k = 0, \ldots, N \) then we can define the continuous phase of the CPR firing as \( \phi(t) = 2\pi(t-t_k)/(t_{k+1}-t_k) + 2\pi k \), where \( t_k < r < t_{k+1} \) [3,12]. If a neuron fires \( m \) times during \( n \) cycles of the stimulus, then we have \( n:m \) synchronization that can be characterized by the phase difference

\[
\Phi_{nm}(t) = 2\pi n \left[ \frac{t-t_k}{t_{k+1}-t_k} + k \right] - 2\pi m f_0 t. \tag{1}
\]

The degree of synchronization may be quantified using the probability density of the phase differences (1): the existence of well-defined peaks signifies synchronization [4]. Thus, the first Fourier mode of the probability density of the phase difference,

\[
\gamma_{nm}^2 = \langle \cos[\Phi_{nm}(t)] \rangle^2 + \langle \sin[\Phi_{nm}(t)] \rangle^2, \tag{2}
\]

is the phase of oscillator, \( \phi_s(t) = 2\pi f_0 t \) is the phase of periodic drive (stimulus) and \( n,m \) are integers [1]. When noise is
where \( \langle \cdot \rangle \) denotes time averaging, defines the synchronization index \( g_{nm} \), which varies from 0 to 1 and is indicative of the relative strength of \( n:m \) mode locking.

Figure 1 illustrates various synchronization indices \( \gamma_{12}, \gamma_{11}, \gamma_{21}, \gamma_{31}, \) and \( \gamma_{41} \) (triangles), and \( \sigma_{12}, \sigma_{11}, \sigma_{21}, \sigma_{31}, \) and \( \sigma_{41} \) (open circles), as a function of stimulus frequency \( f_o \). Data recorded under dark conditions (5 nW/mm\(^2\)); 120 s of CPR firing was recorded at each stimulus frequency.

The synchronizing effect of the stimulus on the CPR firing can also be graphically illustrated in interspike-interval histograms (ISIHs), shown in Fig. 2. Over the frequency range where \( \gamma_{11} \) is maximal, a sharp ISIH peak occurs at the stimulus period (marked \( T_o \) in the 4.5-Hz panel in Fig. 2). When \( \gamma_{21} \) is maximal, two peaks appear, one at period \( T_o \) and one at period \( 2T_o \) (indicated in the 8.5-Hz panel in Fig. 2). Similarly one would expect a peak at \( T_o/2 \) at the frequency corresponding to maximal \( \gamma_{12} \), and at \( 3T_o \) and \( 4T_o \) for \( \gamma_{31} \) and \( \gamma_{41} \), respectively. However, due to noise in the data clear peaks do not appear at \( 3T_o \) or \( 4T_o \). A sharp peak does not appear at \( T_o/2 \), perhaps due to noise-induced overlapping of nearby Arnold tongues.

FIG. 1. Synchronization indices \( \gamma_{12}, \gamma_{11}, \gamma_{21}, \gamma_{31}, \) and \( \gamma_{41} \) (triangles), and \( \sigma_{12}, \sigma_{11}, \sigma_{21}, \sigma_{31}, \) and \( \sigma_{41} \) (open circles), as a function of stimulus frequency \( f_o \). Data recorded under dark conditions (5 nW/mm\(^2\)); 120 s of CPR firing was recorded at each stimulus frequency.

FIG. 2. ISIHs for data from Fig. 1. Number in top right of each plot indicates the driving frequency in Hertz. Top left plot shows the ISIH for spontaneous firing.
FIG. 3. (a) Power spectra from CPR firing times under dark (left panel) and light (right panel) conditions. (b) SNR for a 10-Hz, 400-nm stimulus (filled circles). Synchronization index $\gamma_{11}$, calculated from the same data, is shown in open circles. Error bars represent standard deviation of two measurements at all light levels except the lowest, where three measurements were made. (c) $\gamma_{11}$ vs SNR at stimulus frequency. Data compiled from experiments on ten photoreceptors from eight crayfish. CPRs were stimulated at a variety of frequencies (2.5, 5, 7.5, 10, 15, and 25 Hz) and amplitudes (0.4, 0.6, 1, 2, 6, and 7 $\mu$m). Symbols show light levels, given in the legend in units of $\mu$W/mm$^2$. Data with SNR > 150 not shown.

Hz) was found to increase as the intensity of light directed onto the sixth ganglion was increased [9]. This effect can be seen dramatically from the power spectra in Fig. 3(a) under dark conditions (5 $\mu$W/mm$^2$, left panel) and under conditions of bright light (22 $\mu$W/mm$^2$, right panel). Note that both power spectra are plotted using identical y scales. For each power spectrum, the tailfan preparation was driven with a 2-$\mu$m stimulus at 10 Hz for 120 s. If the experiment is repeated over a range of light levels, allowing the preparation to recover under dark conditions (5 $\mu$W/mm$^2$) for 300 s between each light application, the SNR at 10 Hz [closed circles in Fig. 3(b)] increases to a maximum at an intermediate light level. This effect exhibits features characteristic of a stochastic resonance response, though we cannot directly determine the input noise generated by the light since the mechanisms of the CPR’s light response are not yet fully understood. The synchronization index $\gamma_{11}$ for these data [open circles, 3(b)] increases with SNR. Summarizing results from experiments on ten photoreceptors from eight different crayfish over a range of conditions, we again find that $\gamma_{11}$ increases with SNR [Fig. 3(c)]. To the best of the knowledge of the authors, this is the first demonstration of the correspondence between a stochastic resonancelike effect and stochastic synchronization in a biological system, a result predicted for physical systems by Neiman et al. [13].

In addition to the stochastic resonancelike effect at low stimulus amplitudes, we observe a different effect of light at larger stimulus amplitudes. In some crayfish, the SNR of the fundamental peak decreased when a large-amplitude stimulus (e.g., 6–7 $\mu$m) was applied, while the peak at the second harmonic of the stimulus frequency increased significantly. The “second harmonic effect” is illustrated in Fig. 4(a). The panel at left shows the power spectrum from a 120-s recording from the CPR axon under dark conditions (5 $\mu$W/mm$^2$), the right panel a power spectrum from the same preparation in the light (22 $\mu$W/mm$^2$).

Now we apply various light levels, as before recording the response to a 10-Hz stimulus for 120 s, and allowing at least 300 s of “rest” in the dark between light applications. The closed circles in Fig. 4(b) show an increase in the SNR of the second harmonic as the light is increased. We observe a cor-
responding drop in $\gamma_{11}$ (open circles) and an increase in $\gamma_{12}$ (closed triangles). Note that the index $\gamma_{12}$ corresponds to two spikes per stimulus cycle, and thus to a doubling of the effective driving frequency as light is increased. In Fig. 4(c) we show the SNR of the second harmonic peak plotted against $\gamma_{12}$ over various light levels, stimulus frequencies and amplitudes. SNR increases as $\gamma_{12}$ over this pooled data set.

We hypothesize that the second harmonic effect may be related to the dual innervation of each mechanosensory hair on the tailfan by two neurons, each of which responds to the opposite half of a sinusoidal displacement cycle [14]: the two neurons respond $\pi$ out of phase with each other. The second harmonic effect may arise from light-enhanced summation of these dual inputs, leading to full-wave rectification of the input signal. However, since each CPR receives input from 70 or so hairs [7–9], the situation is likely to be somewhat more complicated than this speculation suggests.

Both full- and half-wave rectification have been identified in mammalian [15] and invertebrate [16] nervous systems. Whether light accomplishes full-wave rectification in the crayfish system by enhanced summation of antiphase mechanosensory inputs, as we propose in the paragraph above, remains to be verified. If this hypothesis is borne out, then the crayfish system may be the first identified neural system in which full-wave rectification of one type of sensory signal is accomplished by stimulation with a different type of sensory input. Speculations on the “use” of this effect by the crayfish in its daily routine remain open. Light-enhanced mechanical sensitivity may have evolved as a warning mechanism of periodic water motions caused by an oncoming predator when the crayfish is exposed outside its burrow [9]. Rectifying this signal might relate to the sensitivity range of neurons in the higher nervous system upstream of the CPRs; a higher-frequency signal might be easier for some upstream neurons to extract from higher frequency spike trains.

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[11] The crayfish (Procambarus clarkii, Carolina Biological) tailfan and abdominal nerve cord were dissected free of the abdomen, and the connective between the fifth and sixth ganglia was desheathed. Extracellular recordings from the CPR axons between the fifth and sixth ganglia were made with a micropipette filled with 150-mM KCl. The preparation was kept in van Harreveld’s standard crayfish saline solution [10]. Voltage spikes were recorded at 16 667 Hz using a CED 1401 interface (Cambridge Electronic Design). SPIKE 2 software (CED) was used to determine spike times from the recordings. Light was applied as described in Ref. [9]; for variable light levels, light was attenuated with neutral density filters (Oriel, Stamford CT). Light levels were determined using a photometer (Graseby Optronics 371 Optical Power Meter). Mechanical stimuli were applied as in Refs. [8,9], by fixing the tailfan in a vertical configuration to a moveable post within the saline bath. A laser Doppler vibrometer (Polytec) was used to calibrate the actual motions of the post. The preparation was placed within a Faraday cage mounted on a vibration isolation table (TMC, MICRO-g). Experiments were performed at room temperature.