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Stochastic phase synchronization in the crayfish mechanoreceptor/photoreceptor system

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The two light-sensitive neurons in the crayfish's abdominal sixth ganglion (''caudal photoreceptors,'' or CPRs), are both primary light sensors and secondary neurons in a mechanosensory pathway. Pei *et al.* (1996) demonstrated that light enhances the transduction of weak, periodic hydrodynamic stimuli (measured as an increase in the signal-to-noise ratio at the stimulus frequency in the power spectrum of the recorded neural spikes). This has been interpreted as a stochastic resonance effect, in which added light increases the noise intensity of the input to the photoreceptor (possibly through fluctuations in membrane potential), leading to an enhancement of the signal-to-noise ratio (SNR). Here, we discuss the recent demonstration (Bahar *et al.*, 2002) of the correlation between a stochastic-resonance-like effect and an increase in stochastic phase synchronization between the neural response and a periodic mechanical stimulus. We also discuss a novel effect (Bahar *et al.*, 2002) in which light increases the SNR of the second higher harmonic of a periodic input signal, effectively rectifying the input signal. This ''second harmonic effect'' can also be interpreted in terms of stochastic phase synchronization (Bahar *et al.*, 2002). We review other recent results on the role of stochastic phase synchronization in mediating sensory responses in the crayfish nervous system. © *2003 American Institute of Physics.* [DOI: 10.1063/1.1501899]

Scientific interest in the synchronization of oscillating systems dates back to the legendary work of Christian Huygens (1673). Many systems in biology are oscillatory—circadian rhythms, heart rate, neural firing, calcium oscillations, etc. (Glass and Mackey, 1988; Goldbeter, 1996). But these oscillations do not follow the crisp periodicity a physicist might hope for; they are inherently stochastic as well as oscillatory. Synchronization of noisy biological systems may be critical for many processes, such as neural information processing. The study of synchronization of biological systems was made possible by Stratonovich's pioneering studies of the synchronization of stochastic (''noisy'') oscillating systems (Stratonovich, 1967). This work was later extended with studies of synchronization between the phases of noisy oscillators (Osipov *et al*., 1997; Rosenblum *et al*., 1996, 1997; Neiman *et al*., 1999a; Park *et al*., 1999; Zaks *et al*., 1999; Pikovsky *et al*., 2001; Rosenblum *et al*., 2000), studies of synchronization-like phenomena in coupled bistable systems (Neiman, 1994), and other work (see Pikovsky *et al*., 2001 for review). With a theory now firmly in place, experimental observations of biological synchronization have poured in over the last few years. Schäfer *et al*. (1998) characterized the synchronization between breathing and heartbeat. Tass *et al*. (1998) demonstrated increased synchronization between muscle activity and cortical firing in patients with Parkinson's disease. Anishchenko *et al.* (2000) demonstrated stochastic phase synchronization between human heartbeat and a weak periodic forcing. Neiman *et al.* (1999a, 1999b) observed synchronization in the electrosensitive afferent neurons of the paddlefish. The crayfish mechanoreceptor/photoreceptor system provides a dramatic example of the role of stochastic phase synchronization in the processing of sensory information.

BACKGROUND

The crayfish has two light-sensitive neurons in its sixth abdominal ganglion (Welsh, 1934; Kennedy, 1963; Wilkens and Larimer, 1972; Edwards, 1984; Wilkens, 1988). These caudal photoreceptors, or CPRs, increase their firing rate when illuminated by light in the visible range (Bruno and Kennedy, 1962). The CPRs are also mechanosensory interneurons: mechanosensory hairs on the crayfish tailfan are mechanically coupled to sensory neurons (MRs) whose axons enter the sixth abdominal ganglion and synapse onto the CPRs (Flood and Wilkens, 1978; Wilkens and Douglass, 1994; Douglass and Wilkens, 1998).

In addition to sharing a common pathway (the photoreceptor axon), these two sensory modalities, mechanosensitivity and light sensitivity, interact with one another (Simon and Edwards, 1990). In a particularly striking demonstration of this interaction, Pei *et al.* (1996) showed that light *enhances the signal-to-noise ratio (SNR)* of weak, periodic hydrodynamic stimuli. This has been interpreted as a stochastic reso-

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nance (SR) effect, in which added light increases the noise intensity in the input signal to the photoreceptor, leading to an enhancement of the SNR (Pei *et al.*, 1996). More recently, a light-induced increase in the SNR of the *second higher harmonic* of a periodic input signal was demonstrated, and shown to correlate with light-induced changes in stochastic phase synchronization (Bahar *et al.*, 2002). Light-induced increases in the SNR of the fundamental peak, observed by Pei *et al.* (1996) were *found to correlate with an increase in stochastic phase synchronization* (Bahar *et al.*, 2002), a result predicted by Neiman *et al.* (1998, 1999b). Here, we review these recent results, discuss their biological interpretation, and survey other advances in the study of stochastic phase synchronization in the crayfish sensory system.

METHODS

Experimental

In each experiment, the crayfish (*Procambarus clarkii*, Carolina Biological) tailfan and abdominal nerve cord below the second ganglion were dissected free of the abdomen, and the connective between the fifth and sixth ganglia was desheathed. Recordings were made with a suction micropipette filled with 150 mM KCl, recording extracellularly from the axon of one or both of the photoreceptors between the fifth and sixth ganglia. The preparation was kept in van Harreveld's standard crayfish saline solution (van Harreveld, 1936), at room temperature. Voltage spikes were amplified and recorded using a CED 1401 interface (Cambridge Electronic Design). Spike 2 software (CED) was used to determine spike times from the recordings. The data acquisition rate was 16 667 Hz (i.e., 0.06 ms time steps). Note that at this sampling rate our maximum error in calculating the phase of a spike within a 2π stimulus cycle may be calculated as follows. At the maximum stimulus frequency, 30 Hz, there are 33 ms per cycle, giving a possible error of 0.06 ms/33 ms, which is equivalent to 0.18% of a 2π cycle. Thus, even at this high stimulus frequency, the phase is measured with high accuracy at this sampling rate.

Light was applied to both photoreceptors simultaneously via a halogen bulb (DDL, 20 V, 160 W) passed through a light pipe, with the exit of the pipe approximately 7.5 cm from sixth ganglion. For variable light levels, neutral density filters (Oriel, Stamford, CT) were placed between the bulb and the light pipe. Light levels were determined using a photometer (Graseby Optronics 371 Optical Power Meter) placed as closely as possible to the location of the photoreceptor in the preparation. The spectral sensitivity of the CPR has been shown to have a maximum at 500 nm (Bruno and Kennedy, 1962); the tungsten–halogen bulb used in the present experiments has significant spectral output in this wavelength range. It should be noted, however, that the work of Bruno and Kennedy was performed in excised nerve cords which had been chilled in van Harreveld's solution overnight; in contrast, in the present work the tailfan and nerve cord are placed immediately after dissection into van Harreveld's solution at room temperature. We assume that the overnight chilling in the experiments of Bruno and Kennedy does not significantly change the spectral response function of the CPRs; however, this remains to be experimentally demonstrated.

The CPR cells were positively identified as follows. Once a clear recording was obtained from a single axon in the 5–6 connective, the preparation was allowed to recover in the dark ($5\ \mathrm{nW/mm^2}$) for 5 minutes. A light of moderate intensity ($22\ \mu\mathrm{W/mm^2}$) was then turned on briefly. If the firing rate of the axon increased significantly (e.g., from 5 Hz in the dark to 30 Hz in the light) and then slowed again once the light stimulus was removed, it was determined that a CPR axon had been located.

Mechanical stimuli were applied as described in (Douglass and Wilkens, 1998, Wilkens and Douglass, 1994), by rigidly fixing the tailfan in a vertical configuration, by means of one pin through each of the two outer uropods, to a moveable post within a room-temperature saline bath. The post, attached to an electromechanical vibration transducer (Pasco Scientific, Model SF-9324), could be moved up and down at various frequencies and amplitudes, generating relative motion between tailfan and saline solution. Due to slack in the nerve cord, there was negligible motion at the recording site. A laser Doppler vibrometer (Polytec) was used to calibrate the actual motions of the post to which the tailfan was fixed. Due to the rigid pinning between the tailfan and the post, it is reasonable to assume that there is no phase delay between the motion of the post and the motion of the tailfan.

The preparation was placed within a Faraday cage mounted on a vibration-isolation table (Technical Manufacturing Corporation, *MICRO*-g). Experiments were performed at room temperature ($\sim 18-22\,^\circ\mathrm{C}$). In all experiments described below, unless otherwise indicated, ''dark conditions'' refers to a measured light level of $5\ \mathrm{nW/mm^2}$, and ''light conditions'' refers to a measured value of $22\ \mu\mathrm{W/mm^2}$.

Data analysis

Signal-to-noise ratio. Spike times were obtained from the digitized wave form using Spike 2 software (CED). The power spectra of digitized spike trains were obtained by taking the Fourier transform of a wave form of delta pulses at the spike times (Gabbiani and Koch, 1998). The SNR was approximated from the power spectrum, as the ratio of the peak height at the frequency of interest to the noise level in a 1 Hz band centered at the stimulus frequency. Note that this approximation actually gives us a ratio of (signal +noise)/noise, since the peak at the frequency of interest (stimulus frequency) is offset by the baseline noise. Nevertheless, for our purposes, this gives a close approximation to the actual SNR.

Synchronization indices. If the neural firing times are denoted as at t_k, $k=0,1,2,\ldots,N$, and the upward zero-crossing times of the applied periodic stimulus as τ_i, $i=0,1,2,\ldots,M$, then the phase difference of the kth spike with respect to the stimulus is

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

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where $\tau_i < t_k < \tau_{i+1}$ (Neiman *et al.*, 1999a; Rosenblum *et al.*, 2000; Neiman *et al.*, 1999b; Pikovsky *et al.*, 2001); $\phi(t_k)$ will have values between 0 and 2π. The *continuous* phase difference $\phi(t)$ falls between 0 and infinity, rather than being ''wrapped'' modulo 2π:

$$\phi(t) = 2\pi \frac{(t-\tau_i)}{\tau_{i+1}-\tau_i} + 2\pi i, \tag{2}$$

where i is the stimulus cycle number, and $\tau_i < t < \tau_{i+1}$ (Neiman *et al.*, 1999a; Neiman *et al.*, 1999b; Rosenblum *et al.*, 2000; Pikovsky *et al.*, 2001).

If a neuron fires m times during n stimulus cycles, the *n:m* phase locking condition is

$$|n\phi(t) - m\phi_{\text{stim}}(t) - \delta| < \text{const} \tag{3}$$

in the ideal case where there the system is noise free. Here, $\phi(t)$ is the continuous phase difference defined in (2), $\phi_{\text{stim}}(t) = 2\pi f_0 t$ is the continuous phase of the stimulus, f_0 is the stimulus frequency, and δ is the average phase difference between the two signals (Rosenblum *et al.*, 2000). When condition (3) holds, the oscillator (neuron) and driving stimulus are said to be $n{:}m$ phase locked. The $n{:}m$ phase difference is defined as

$$\Phi_{nm}(t) = \left[2\pi \frac{(t-\tau_i)}{(\tau_{i+1}-\tau_i)} + 2\pi i \right] n - 2\pi m f_0 t. \tag{4}$$

The corresponding frequency entrainment condition is

$$nf = mf_0 \tag{4a}$$

recalling that the frequency f and phase ϕ of a periodic oscillator are related as

$$f = \frac{1}{2\pi} \frac{d\phi}{dt}. \tag{4b}$$

In this case one can make the statement that phase synchronization and frequency entrainment are two different ways of describing the same condition.

In a noisy system, the phase difference (3) becomes unbounded, and we can speak of synchronization only *in a statistical sense*. Frequency entrainment occurs only during the brief intervals where $\phi(t)$ remains constant between phase slips where $\phi(t)$ abruptly changes by $\pm 2\pi$. These phase slips can be caused either by noise or weak coupling (or some combination of both) (Pikovsky *et al.*, 2001). In our system, where the photoreceptor firing is quite noisy, it is likely that noise plays a major role in inducing the observed phase slips, though weak coupling may also play a significant role.

Synchronization may be quantified by plotting the probability density of the phase differences (4). The intensity of the first Fourier mode of this distribution,

$$\gamma_{nm}^2 = \langle \cos(\Phi_{nm}(t)) \rangle^2 + \langle \sin(\Phi_{nm}(t)) \rangle^2, \tag{5}$$

where $\langle \cos(\Phi_{nm}(t)) \rangle^2$ and $\langle \sin(\Phi_{nm}(t)) \rangle^2$ are time averages, defines the *synchronization index* γ_{nm}, which varies from 0 to 1 and indicates the relative strength of $n{:}m$ mode locking (Rosenblum *et al.*, 2000). Thus, for example, if 1:2 synchronization (two responses per stimulus cycle) is dominant in a particular data set, γ_{12} will be maximal.

In addition to the synchronization indices γ_{nm}, we may use a complementary statistical measure of synchronization, the standard deviation σ_{nm} of the difference between the instantaneous period $t_k - t_{k-m}$ and the effective stimulus period nT_0, where $T_0 = 1/f_0$. Thus we have

$$\sigma_{nm}^2 = \langle [(t_k - t_{k-m}) - nT_0]^2 \rangle. \tag{6}$$

The minimal value of σ_{nm} calculated from experimental data corresponds well with the maximal γ_{nm}, as will be discussed below.

RESULTS

Second harmonic effect

For low-amplitude periodic stimuli, Pei *et al.* (1996) found a light-induced SNR increase in the fundamental peak in the power spectrum at the stimulus frequency. Pei *et al.* (1996) found that SNR increases as a function of *light* intensity, just as SNR increases as a function of *noise* intensity in a ''classical'' stochastic resonance effect.

In contrast to the work of Pei *et al.* (1996), a novel effect is observed at higher amplitude periodic stimuli ($\geq 2\ \mu$m) (Bahar *et al.*, 2002). Two examples of this phenomenon are shown in Fig. 1. In the top panel of Fig. 1(a), under dark (5 nW/mm^2) conditions, we observe a peak at the fundamental stimulus frequency (10 Hz) and a smaller peak at the second higher harmonic (20 Hz). In light (22 μW/mm^2), fundamental peak (SNR$_1$) vanishes while the SNR of the second harmonic (SNR$_2$) increases [lower panel, Fig. 1(a)]. In some other animals (data not illustrated here) the fundamental peak does not disappear, though it becomes much smaller than the second harmonic peak.

An interesting but more atypical instance of this effect is shown in Fig. 1(b). In contrast to Fig. 1(a), the second harmonic peak is much larger than the fundamental even in the dark. In the light, the fundamental peak essentially disappears. We define $(\text{SNR}_2/\text{SNR}_1)_{\text{light}} > (\text{SNR}_2/\text{SNR}_1)_{\text{dark}}$ as indicative of this ''second harmonic effect.'' In 25 photoreceptors from 23 crayfish, stimulated with amplitudes ranging from 2 μm to 9 μm and frequencies between 7.5 Hz and 10 Hz, 13 CPRs exhibited $(\text{SNR}_2/\text{SNR}_1)_{\text{light}} > (\text{SNR}_2/\text{SNR}_1)_{\text{dark}}$.

In agreement with the results of Pei *et al.* (1996), Bahar *et al.* (2002) found that the SNR of the fundamental peak increased as the light level was raised, following a traditional stochastic resonance curve, assuming that light level plays the role of ''noise.'' In the case of the second harmonic effect, we find a similar result, in which SNR$_2$ increases as light level is increased, illustrated with the filled circles in Fig. 2. We also observe that γ_{12} increases as does SNR$_2$ (triangles), and γ_{11} (open circles) decreases. Thus 1:1 synchronization weakens as 1:2 synchronization becomes dominant. In other words, *1:2 synchronization, which corresponds to 2 responses per stimulus cycle, i.e., a doubling of the original input frequency, increases as the second harmonic peak increases*.

The correlation between γ_{12} and SNR$_2$ is robust over a range of visible light levels, illustrated in Fig. 3(a). We also find that γ_{11} increases as SNR$_1$, illustrated in Fig. 3(b).

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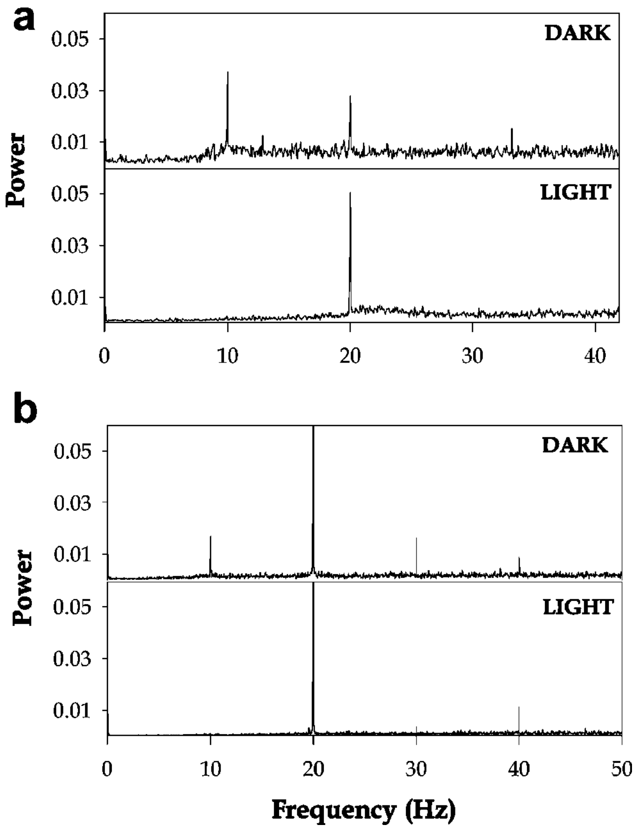

FIG. 1. Two examples of the "second harmonic effect." In (a), CPR power spectra are shown in dark (top panel, 5 nW/mm^2) and light (bottom panel, 22 μW/mm^2). Stimulus amplitude 3 μm, frequency 10 Hz. Stimulus train was delivered for 120 seconds. In (b), CPR power spectra are again shown in dark (top panel, 5 nW/mm^2) and light (bottom panel, 22 μW/mm^2). Stimulus amplitude 9 μm, frequency 10 Hz. In (b), the second harmonic is much larger than the fundamental even in the dark, while in (a) the second harmonic is smaller than the first in the dark. In both cases, the fundamental peak decreases dramatically in the light, and the second higher harmonic increases. In both cases, the ratio SNR$_2$/SNR$_1$ increases in the light.

These correlations between synchronization index and SNR, intuitively satisfying and predicted theoretically by Neiman *et al.* (1998; 1999b), were, to the knowledge of the authors, demonstrated *for the first time experimentally* in the crayfish photoreceptor/mechanoreceptor system (Bahar *et al.*, 2002).

In Fig. 4 we sketch a plausible biological explanation for the "second harmonic effect" based on full-wave rectification of the input sine wave by the photoreceptor. This mechanism, first discussed in Bahar *et al.* (2002), is illustrated in more detail below.

Arnol'd tongues and stochastic synchronization

As discussed above, a hallmark of stochastic phase synchronization is stochastic "entrainment" of an oscillator by a periodic stimulus over a range of stimulus frequencies (Pikovsky *et al.*, 2001). It is necessary to demonstrate this in order to truly show that stochastic phase synchronization occurs in a system (Pikovsky *et al.*, 2001; Rosenblum *et al.*, 2000); we now turn to this problem.

The frequency-detuning plot is a standard demonstration of synchronization between a noisy oscillating system and a periodic driving force, showing the difference (or, alternatively, the ratio), between the oscillator's average frequency and the driving frequency, plotted as a function of the driving frequency (Rosenblum *et al.*, 2000; Pikovsky *et al.*, 2001). However, in noisy biological data, frequency-detuning plots are extremely noisy, due to the inherent variability in the neural firing rate, and flat regions are difficult to observe.

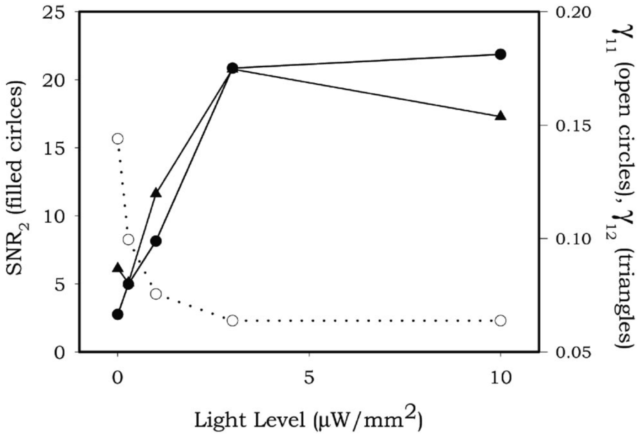

FIG. 2. SNR$_2$ (filled circles) vs light level (stimulus 10 Hz, 7 μm). Note decrease in γ_{11} (open circles) as γ_{12} (triangles) increases. Stimulus trains were delivered for 120 seconds at each light level. CPRs were allowed to recover under dark conditions for >5 minutes between recordings.

Luckily, more quantitative methods than the frequency-detuning plot exist for measuring the synchronization between the photoreceptor firing and the applied stimulus. Syn-

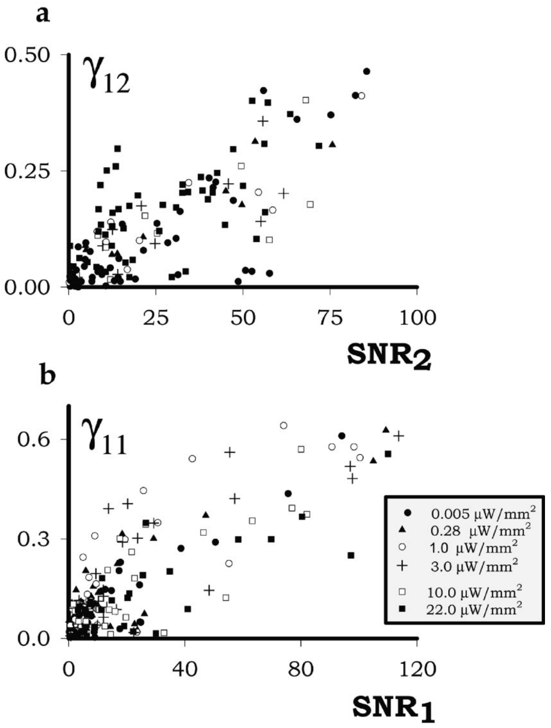

FIG. 3. (a) γ_{12} vs SNR$_2$ (nine photoreceptors in seven crayfish; 2.5, 5, 7.5, 10, 15, 25 Hz; 0.4, 2, 6, 7, 9 μm). SNRs$>$100 not shown. Symbols [legend attached to (b)] indicate light intensity in μW/mm^2. (b) γ_{11} vs SNR$_1$ (10 photoreceptors in eight crayfish; 2.5, 5, 7.5, 10, 15, 25 Hz; 0.4, 0.6, 1, 2, 6, and 7 μm). SNRs$>$150 not shown.

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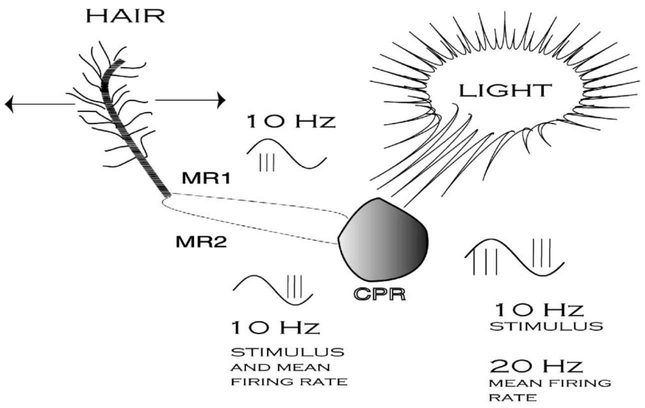

FIG. 4. Possible mechanism of full-wave rectification by the CPR. Each mechanosensory hair is innervated by two mechanoreceptor (MR) neurons, whose directional sensitivities differ by 180 degrees (Wiese, 1976; Wiese *et al.*, 1976). Summation of the MR inputs at the CPR is enhanced by light, accomplishing full-wave rectification of the input signal and doubling the effective stimulus frequency.

chronization behavior as stimulus frequency is changed can be more precisely calculated using γ_{nm} and σ_{nm} as defined above [Eqs. (5) and (6), respectively]. In the experiment shown in Fig. 5, a sinusoidal mechanical stimulus was applied over a range of driving frequencies f_0, under dark conditions. Each stimulus was applied over a period of 2 minutes, resulting in a spike train at each of the driving frequencies. The synchronization measures γ_{nm} and σ_{nm} were calculated for each of these 2 minute data sets, and plotted as a function of driving frequency in Fig. 5. Note that the minimal values of the σ_{nm} correspond well to the maximal values of γ_{nm}.

Critical to note is the *sequence* in which the synchronization index maxima appear. First we find a peak in γ_{12}, then, as the driving frequency is increased, in γ_{11}, γ_{21}, γ_{31} and finally γ_{41}. This sequence of modes should immediately ring a bell for nonlinear dynamicists: our system is passing through a sequence of Arnol'd tongues. Essentially, we are moving from left to right across a standard Arnol'd tongue plot (see, for example, Moon, 1992), at constant amplitude. The observation of a more detailed Arnol'd tongue structure is precluded first by the fact that the system is highly noisy, and second by the limited range of frequencies to which the crayfish MR/CPR system is sensitive. Indeed, of eight crayfish observed driven over this range of frequencies, only one exhibited the five Arnol'd tongues illustrated in Fig. 5; the others showed only the sequence γ_{12}, γ_{11}, γ_{21}.

In Fig. 6 we illustrate the effect of light on the synchronization index γ_{12}. Under both dark (5 nW/mm^2, filled circles) and light conditions (22 μW/mm^2, open circles), peaks occur in γ_{12}. But light shifts the peak toward the right, toward higher frequencies. Similar shifts to higher frequencies are observed for synchronization indices γ_{11} and γ_{21} (data not shown). Essentially, light has the effect of pushing the Arnol'd tongues toward higher frequencies, *indicating a change in the frequency response characteristics of the photoreceptor in the presence of light*. We speculate below on the relation of this effect to the higher baseline firing rate of the CPRs observed in the light.

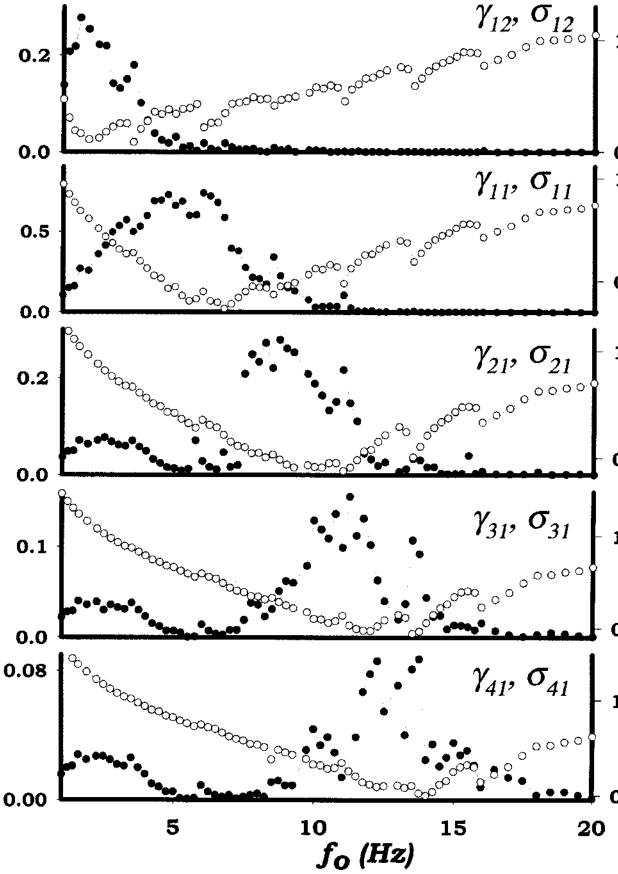

FIG. 5. Synchronization indices γ_{12}, γ_{11}, γ_{21}, γ_{31}, and γ_{41} (filled circles), and σ_{12}, σ_{11}, σ_{21}, σ_{31}, and σ_{41} (open circles) as a function of stimulus frequency (Hz). Data were recorded under dark conditions (5 nW/mm^2), with stimulus amplitude 6 μm. 120 seconds of CPR firing were recorded at each stimulus frequency.

It should also be noted in Fig. 6 that the maximum γ_{12} in the light is greater than the maximum γ_{12} in the dark. Despite this individual result, it is important to note that there is no average increase in the magnitudes of the synchronization indices in light vs dark. For example, in nine photoreceptors

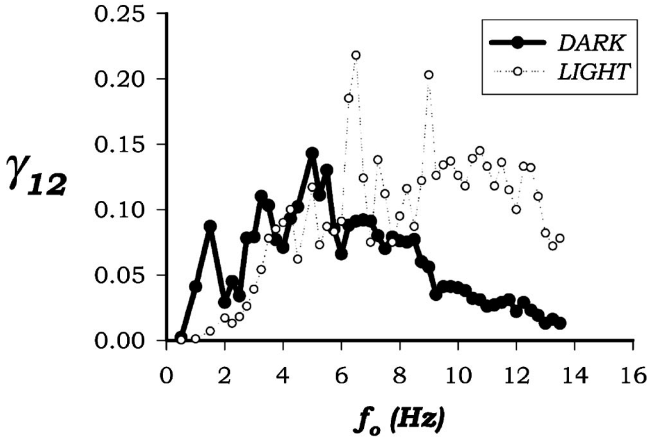

FIG. 6. Synchronization index γ_{12} as a function of driving frequency in dark (filled circles, 5 nW/mm^2) and light (open circles, 22 μW/mm^2). 120 seconds of CPR firing were recorded at each stimulus frequency. After each recording in the light, a minimum of two minutes were allowed in the dark for photoreceptor recovery before the next recording.

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from eight crayfish, we observed an average maximal γ_{12} in the dark of 0.17 ± 0.09. In the light (4 CPRs from four different crayfish), an average maximal γ_{12} of 0.16 ± 0.09 was observed. An unpaired t-test performed on these two data sets indicates that there is no statistically significant difference between the mean value of the synchronization index in the dark compared with the index in the light (p-value 0.678). Similar results were found for γ_{11} and γ_{21}.

DISCUSSION

Second harmonic effect

The second harmonic effect may be interpreted as 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 (Wiese, 1976; Wiese *et al.*, 1976). In other words, the neurons respond π out of phase with each other. Figure 4 shows a simple diagrammatic scheme through which directional rectification of the mechanical stimulus by the two afferents and subsequent light-intensity-mediated summation in the CPR could account for our observations. The net effect is a full-wave rectification of the stimulus sine wave. However, since each CPR receives inputs from ~70 hairs (Wilkens, 1988; Pei *et al.*, 1996), the situation is certain to be far more complex than this speculation would suggest.

An additional puzzle lies in the observation that enhancement of the fundamental peak occurs in the presence of light for a weak (low amplitude) periodic input signal, as described by Pei *et al.* (1996), whereas the light-induced harmonic dominance occurs predominantly for large amplitude, though still physiologically realistic, sinusoidal stimuli. This remains to be explained.

It is also of interest to compare the second harmonic effect to the observation of stochastic resonance at higher harmonics observed by Grigorenko *et al.* (1997) in a magnetic system. Since stochastic resonance is by definition an enhancement of a weak periodic signal (Wiesenfeld and Moss, 1995), and the second harmonic effect occurs only for stimuli which are comparatively large in amplitude, it is doubtful whether we are actually observing an effect similar to that discussed by Grigorenko *et al.*

Both full- and half-wave rectification have been identified in mammalian (e.g., Horst *et al.*, 1990; Solomon and Sperling, 1994; Rowe and Palmer, 1995; Chubb and Nam, 2000) and invertebrate (e.g., Mizunami, 1990; Kondoh *et al.*, 1993; Newland and Kondoh, 1997) sensory systems, and discussed in the context of cortical receptive field models (Spitzer and Hochstein, 1985). *The crayfish system, however, appears to 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.*

Arnol'd tongues, entrainment and stochastic synchronization

We have described the noisy entrainment of the CPR firing by a periodic hydrodynamic signal, leading to the appearance of various phase-locking regimes as a system parameter (driving frequency) is varied. But is this really what we have observed? Can we be sure that a continuous rate change hypothesis would not work equally well? Indeed we can, for several reasons. First of all, there is strong evidence that the CPR is indeed an oscillator. This can be demonstrated in experiments where the sensory afferents (mechanoreceptor roots) are cut, so that there is no external input to the CPRs. The CPRs fire much more regularly under these conditions, indicating that they do contain an intrinsic ''pacemaker'' (Wilkens, 1988). The CPRs are also known to exhibit nonlinear characteristcs, responding to periodic hydrodynamic stimuli only over a narrow, well-defined range of frequencies (Pei *et al.*, 1996).

So the evidence is strong that the CPRs are nonlinear oscillators. But the system is indeed highly noisy, and frequency-detuning plots (not shown) only show vague plateaus as a function of driving frequency. But if the system is too noisy to reveal distinctive plateaus in the frequency-detuning plot, Arnol'd tongues can still be detected by finding maxima of the various synchronization indices (Pikovsky *et al.*, 2001). This is precisely what we have done (Fig. 5). (Note that phase locking regions can also be detected by calculating interspike interval histograms, illustrated for this system in Bahar *et al.*, 2002.) The small values of the synchronization indices (see the left-hand y axes in Fig. 5, recalling that the maximum of each synchronization index is 1) indicate that the synchronization is weak. Nonetheless, Fig. 5 shows that distinct maxima clearly occur as a function of driving frequency, corresponding to different stimulus-response locking ratios. Thus the γ_{nm} (and the σ_{nm}) reveal what the frequency-detuning curve is not sensitive enough to show: Arnol'd tongues and noisy, statistical entrainment between a nonlinear oscillator and a periodic drive.

A role in sensory encoding?

Speculations on the ''use'' of these dynamical effects 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, that is, in the light (Pei *et al.*, 1996). 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 a 20–30 Hz spike train, while a lower frequency input might be more easily extractable from a spike train with a lower average frequency. Once identified, however, these upstream neurons may provide insight into the role of the second harmonic effect within the computational apparatus of the crayfish CNS, and may ultimately suggest mammalian systems which might also use rectification of one sensory input, induced by another, for ''computation.''

Another subject for further research will involve the effect of light on the Arnol'd tongues, illustrated in Fig. 6. The shift in the synchronization index maxima to higher frequencies in the light indicates that the crayfish is sensitive to a higher frequency range in the light. This raises several questions whose answers may bear on fundamental problems of signal encoding. Is the higher frequency range evolutionarily

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related to differences in the natural frequency range of environmental stimuli to which the crayfish is subject in the light, in contrast to lower frequency stimuli it may be exposed to in the dark? Or is sensitivity to a higher frequency a dynamical result of signal encoding against a background of faster CPR firing in the light? This latter possibility can be tested using neural models where the firing rate can be realistically tuned over a 5–30 Hz range.

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