A MATHEMATICAL MODEL OF THE CIRCADIAN ACTIVITY INDUCED BY THE PRESENCE OF SEXUAL HORMONES IN MALE CRAYFISH

Miguel Lara-Aparicio, Santiago López de Medrano,
Carolina Barriga-Montoya and Beatriz Fuentes-Pardo

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Abstract. The circadian activity in crayfish has been extensively studied, in particular in reference to the organization of oscillators underlying the circadian systems (Fuentes-Pardo et al., 1995; Lara-Aparicio et al., 1993). In this point, it is important to emphasize some theoretical studies about the mathematical modeling of the main elements involved in the ontogeny of both electrical response to light (electroretinogram, ERG) of retinular cells and motor circadian rhythms (Fuentes-Pardo et al., 2001 and Lara-Aparicio et al., 1993).

When the ERG circadian rhythm of an adult, male crayfish is recorded, and in the bath is put either a female crayfish or a solution of a hormone, the ecdysterone (which has been proposed as a pheromone or sexual hormone), the ERG rhythm shows a disturbance in amplitude, excitation level and noise level which is highly increased.

The analysis of the time series before and after the disturbance shows qualitative and quantitative differences between them. The spectral density suggests that the time series are not stationary series. In this analysis is present too a noise level notoriously higher after the disturbance, particularly over some finite frequency ranges. Lastly, it is also detected that the changes induced by the disturbance are irreversible during all the time of the experiment (about 20 days).

On the basis of both experimental results and frequency analysis of the ERG circadian rhythm in the crayfish, before and after the presence of the sexual hormone, we have incorporated some modifications in the original mathematical model about the ERG circadian rhythm which, in essence, consists of two coupled oscillators (Lara-Aparicio et al., 1993). The present mathematical model has three main oscillators. From these, two of them are coupled for describing the generation of the ERG circadian rhythm (Fuentes-Pardo et al., 2001 and Lara-Aparicio et al., 1993) , and the third one has also a circadian frequency but with a period slightly larger than those of the first oscillator. A noisy component has been also incorporated in this model.

1 Introduction

1.1 Biological Antecedents Circadian rhythms have been recognized as a fundamental feature in the organization of living systems. The main characteristics of circadian systems is the presence of an endogenous oscillator with a period different but close to 24 h; a dependence on light in accordance with Aschoff's rule (the Aschoff´s rule says that frequency, excitation level and cycles amplitude of circadian rhythms, increase in diurnal species, when the light intensity increases and decrease in nocturnal species under the same circumstance (Aschoff, 1960)); the presence of temperature compensatory mechanisms; and the existence of synchronization mechanisms which allow to the organism to adjust the period of

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its natural oscillation to the period of some external oscillation (Pittendrigh, 1960, 1965, 1981).

Other temporal scales have been reported in living systems, namely infradian as a circalunar rhythm or ultradian as a circatidal rhythm. The main characteristics of this last class of rhythm are that they are endogenous; show mechanisms of temperature compensation; can be synchronized; appear very early in ontogeny and phylogeny; and frequently underlie to circadian rhythms (Lloyd, 1992). Probably the rhythms of all the temporal scales exhibit an inter-relation in the whole animal, however there is no enough information relating these different classes of rhythms.

In crustaceans, circadian rhythmicity has been documented many years ago. It is expressed in physiological functions as diverse as locomotor activity (Fuentes-Pardo et al., 1997a), tegumentary and retinal shielding pigment position (Welsh, 1930; Bennitt, 1932; Thurman, 1988; Aréchiga et al., 1993; Verde et al, 2007), neuro-hormonal concentrations (Aréchiga and Mena, 1975; Hernández-Falcón et al., 1987), heart rate (Pollard and Larimer, 1977), sensory inputs (Sánchez and Fuentes-Pardo, 1976; Aréchiga and Rodríguez-Sosa, 1998), etcetera.

Particularly in crayfish, a circadian rhythm in sensitivity to light, recorded by means of the electrical response to light from visual photoreceptors (electroretinogram, ERG), has been well characterized (Aréchiga and Fuentes, 1970; Fuentes-Pardo and Ramos-Carvajal, 1983).

With the aim to understand the origin of these oscillations, a lot of investigation both, in intact animal and in isolated eyestalk has been done (Sánchez and Fuentes-Pardo, 1976; Fuentes-Pardo et al., 1987; Fuentes-Pardo and Hernández-Falcón, 1998; Aréchiga and Rodríguez-Sosa, 1998). However, the basis of this rhythm is still undefined because the localization and identification of the main components of the circadian system, namely the pacemaker and the entrainment pathways, have been not clearly established. From ablations and lesions experiments (Barrera-Mera, 1976, 1978; Page and Larimer, 1975; Moreno-Sáenz et al., 1987; Moreno-Sáenz et al., 1992), it was suggested that the ERG rhythm is controlled by neural and endocrine mechanisms localized in the supraesophageal ganglion and the X-organ-sinus gland complex. The fact that the ERG circadian rhythm can be entrained by light (Fuentes-Pardo et al, 1997b) indicates the existence of an afferent via that begins in the visual photoreceptors and finalizes in the circadian pacemaker. The existence of other synchronization pathways is also clear because of the generation of phase response curves with chemical substances (non-photic) as the pigment dispersing hormone (Verde et al., 2007) or melatonin (Solís-Chagoyán et al., in press), as well as the demonstration of ERG phase shifting produced by direct illumination in the sixth abdominal ganglion (Fuentes-Pardo and Inclán-Rubio, 1987).

Ecdysterone has been proposed as a pheromone or sexual hormone in invertebrates. It is also involved in the molting cycle (Hopkins, 1986; Durliat et al., 1988; Walgrave et al., 1988), in the development of the nervous system (Fahrbach, 1992), in programmed neuron death (Fahrbach et al., 1994) and in many other physiological functions (for a review see De Loof, 2008). In crayfish, its synthesis takes place in the Y-organ and is regulated by the molting-inhibiting hormone (MIH), a polypeptide secreted by the X-organ-sinus gland complex in the eyestalk. There are findings that suggest that ecdysteroid secretion from the Y-organ may be regulated not only by changes in the hemolymph of molting inhibitory hormone (MIH) titer, but also by changes in the responsiveness of the Y-organ to MIH (Nakatsuji and Sonobe, 2004).

The interference of pheromones in circadian rhythms has been demonstrated in some invertebrate species (Vafopoulu and Steel, 1991). It is well known that pheromone-dependent mating is under strict circadian control although it is not clear where the circadian control

is exerted. For example, behavioral responses to the pheromone in the turnip moth Agrotis segetum male are under control of an endogenous oscillator and the circadian regulation of the rhythmic behavior occurs at the central nervous system level (Rosén et al., 2003). In other species, however, the circadian regulation occurs in periphery level (Flecke et al., 2006; Merlin et al., 2007). Regarding to the entrainment mechanism, in the male Egyptian cotton leafworm, Spodoptera littoralis, it has been demonstrated that pheromones are able to synchronize circadian behavioral rhythms in absence of other external zeitgebers (Silvegren et al., 2005).

In this work we present a non-canonical example of the effect of the ecdysterone over the ERG circadian rhythm: a single stimulus of ecdysterone applied to male crayfish is able to modify the period, amplitude, excitation level and noise level of the ERG circadian rhythm. In order to understand how and where these changes were produced, we modeled them mathematically.

1.2 Mathematical Antecedents To model mathematically the main experimental results , we have recourse and adapted a model previously built to simulate some experimental results in crayfish namely the ontogeny of the ERG circadian rhythm (Lara-Aparicio et al., 1993), the main properties of this rhythm expressed in adult animals (Fuentes-Pardo et al., 1995) and the motor circadian rhythm (Fuentes-Pardo et al., 2001). The model let us to understand several biological characteristics of circadian rhythms and proposed new experiments and biological hypotheses.

To build the mathematical model we considered, as a basic oscillator, one of the van der Pol type with a circular limit cycle in two dimensional phase space given by a system of differential equations of the form:

$$\dot{\boldsymbol{x}} = F(\boldsymbol{x}, k, c, r).$$

Here $\boldsymbol{x} = \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$ represents a point in phase space and the system depends on following parameters: k is the frequency of the oscillator, r (bifurcation parameter) corresponds to the square of the radius of the limit cycle and c is the first coordinate of the center of the limit cycle. The explicit equations of this system are:

$$\begin{aligned} \dot{x_1} &= -kx_2 + e\,(x_1 - c)\left(r - (x_1 - c)^2 - x_2^2\right) \\ \dot{x_2} &= -k\,(x_1 - c) + ex_2\left(r - (x_1 - c)^2 - x_2^2\right). \end{aligned}$$

If $r > 0$ there is an attracting cycle with radius $\sqrt{r}$ and centre in 0. If $r < 0$, the origin is a point of stable equilibrium. At $r = 0$ an Andronov-Hopf bifurcation occurs.

When the value of c grows, the output x_1 of the system would oscillate around a higher value.

Furthermore, e represents the speed, given the initial conditions, with which the system reaches the steady state.

In this manner for modelling the experimental results of the ERG and motor circadian rhythms we considered two coupled non-linear oscillators, one of them of relatively high frequency namely an ultradian oscillator (biologically identified as a neural oscillator) governed by another oscillator of lower frequency, or circadian one (biologically identified as a hormonal oscillator).

For each oscillator we considered a maturation regime given by a logistic equation of the following type:

$$\dot{x_3} = ux_3 - vx_3^2$$

In Figure 1 appear the corresponding Cartesian equations.

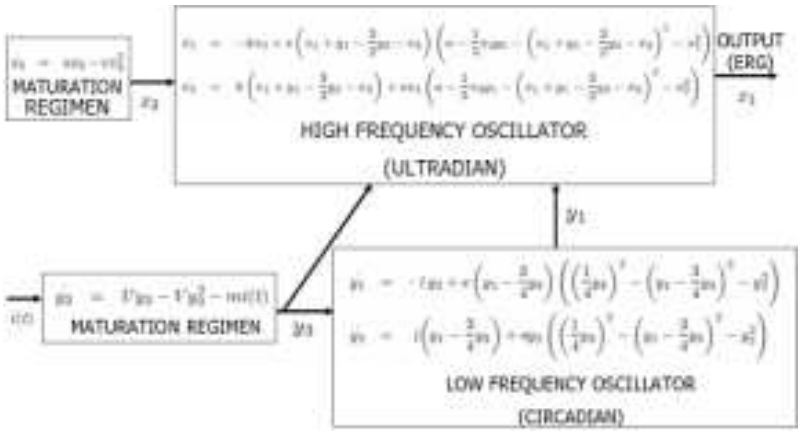


Figure 1. Equations of mathematical model (Lara-Aparicio et al., 1993).

As an example of the mathematical simulation obtained with this model, in Figure 2 appears the phase response curve of the electroretinogram (ERG) circadian system of the crayfish to light pulses applied at different hours of the day.

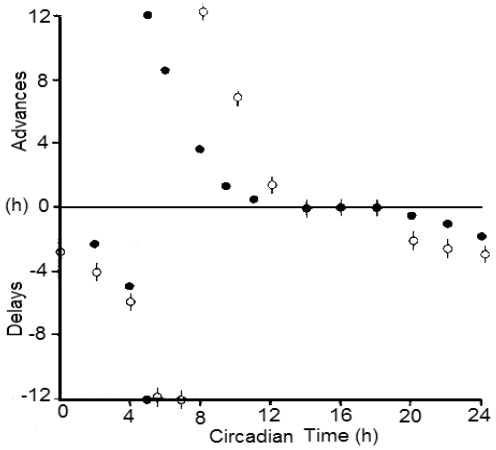


Figure 2. The amplitude and direction of the phase shifts of the ERG circadian rhythm produced by single light pulses of light given to crayfish in constant darkness, plotted against the circadian phase of simulation. Black points correspond to biological measures and white points correspond to the mathematical model.

As another example, in Figure 3 it is compared the experimental response curve of the ontogeny of the ERG circadian rhythm in crayfish with its mathematical simulation.

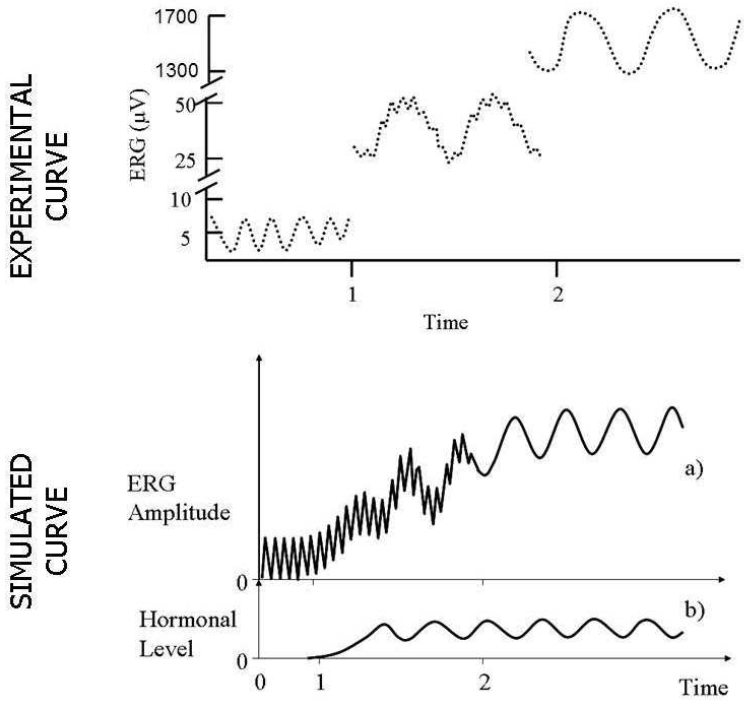


Figure 3. The lower curve corresponds to a hypothetical hormonal curve suggested by the mathematical model which let us to formulate a hypothesis about the oscillators underlying the circadian rhythm.

In the present mathematical model we have employed a third circadian oscillator similar to the hormonal oscillator (circadian) mentioned above but with a slightly different frequency. This oscillator affects the hormonal oscillator, obtaining in such a manner an accuracy simulation of the experimental results.

2 Material and Methods

2.1 Biological material Adult crayfish Procambarus clarkii in intermolt stage (between A and C molt stages) were used. Animals were obtained from a local supplier and kept in an aerated aquarium at controlled temperature (16°C). They were fed three times a week with commercial food and maintained under light-dark cycles (LD 12:12 with light turned on at 7:00 and turned off at 19:00 h).

2.2 Recording of ERG circadian rhythm By means of a cork glued to its dorsal surface, an adult male crayfish remained partially immersed in water during the experiment. An electrode (5μm in the tip diameter) on the cornea surface detected the photoreceptor electrical response to light (electroretinogram, ERG) to flashes (1.8 lux, 10 μs) sent to the eye each 3 min during at least 10 days. To measure the effect of the hormone ecdysterone on the ERG circadian rhythm, in the 5th day of recording either an adult female crayfish (which could not be seen for the male) or an ecdysterone solution was introduced in the bath during 20 min. The recording continued during 5 days more.

There were two kinds of control experiments: in one group, the female crayfish was substituted by a male one. In a second group, previously to long-term ERG recordings the male crayfish was operated to injure or eliminate the deutocerebrum (structure of the cerebroid ganglion where the chemical signals are processed).

2.3 Data analysis From each experiment we measured the period, oscillation amplitude (measured as de ERG voltage from valley to peak), excitation level (which corresponds to the average value of the oscillation) and activity/rest ratio ($\alpha : \rho$ ratio , which corresponds to the quotient between the time when the cycle amplitude is of 50% or more of maximum, and the time when the cycle amplitude is under 50% of amplitude).

By means of Fast Fourier Transform (using the software Mathematica® 5) it was made a frequency analysis of the ERG rhythm recorded from the male crayfish, before and after the introduction of either a female crayfish or an ecdysterone solution.

3 Results Figure 4 depicts a typical recording (from a total of 15) of amplitude changes in the ERG of a male crayfish before and after the presence of a female in the same bath. ERG voltage was measured at 3-min interval. During the first 4 days of recording, before the perturbation by the female or the ecdysterone solution occurred at 5^{th} day, ERG amplitude showed daily fluctuations corresponding to a typical circadian rhythm of a nocturnal animal (with the greatest ERG voltage occurring by midnight). The average period, obtained by measuring the time interval peak-to-peak was of 23.4 ± 2.1h; the cycle amplitude was of 23.4 ± 0.4h; the cycles amplitude was of $546 \pm 28 \mu V$; the excitation level was of $1.4 \pm 0.03 mV$; and the $\alpha : \rho$ ratio was of 1.1 ± 0.57. After the presence of a female crayfish in the bath (signaled by the arrow), important quantitative and qualitative changes could be observed in the recording: cycles amplitude was reduced to $415 \pm 31 \mu V$; excitation level was notoriously reduced to $1.2 \pm 0.04 mV$ showing moments when the ERG voltage was clearly higher or lower than the average; and $\alpha : \rho$ ratio diminished to $1.1 \pm 0.05 mV$. Circadian periods did not shown great differences respecting the values before the disturbance, although the appearance of high frequency (ultradian) oscillations was evident.

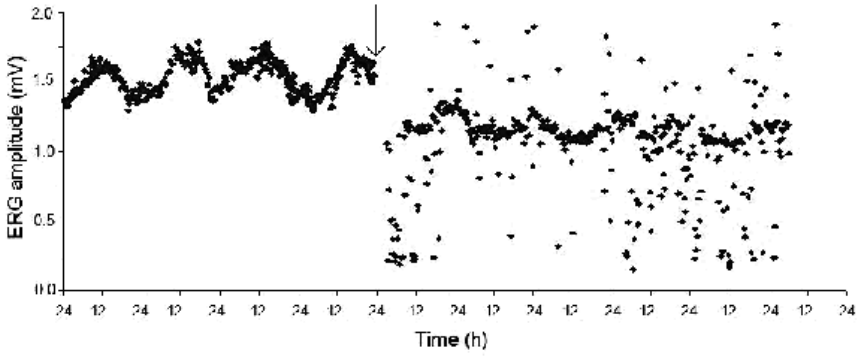


Figure 4. ERG circadian rhythm of an adult, male crayfish recorded in presence of a female crayfish (point by the arrow).

All these data show that the time series is not stationary and that the disturbances of the rhythm were irreversible.

Figure 5 shows the results of the analysis of the time series: a shortening of the length of the circadian period (typically of a half hour) and the apparition of ultradian periods about 16, 12, 6 and 3 h superimposed on the circadian oscillation.

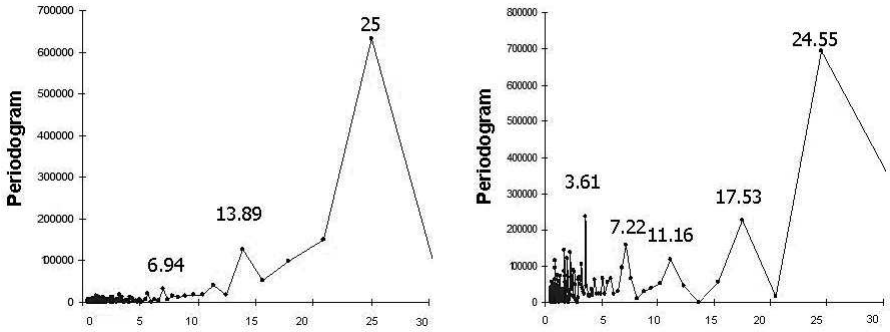


Figure 5. The left graph shows the frequency analysis of the ERG circadian rhythm recorded from a male crayfish during the first four days of recording. The right graph shows the frequency analysis of the same rhythm during and after the presence of a female crayfish. Note the apparition of high frequency cycles.

In Figure 6, it is shown the recording of the ERG circadian rhythm during 8 of the 10 days of a control experiment. The recording shows the periodic voltage changes obtained from a male crayfish before and after (signaled by the arrow) the introduction in the bath of other male crayfish instead a female one. During all days of the experiment it was not detected any change in the characteristics of ERG circadian rhythm.

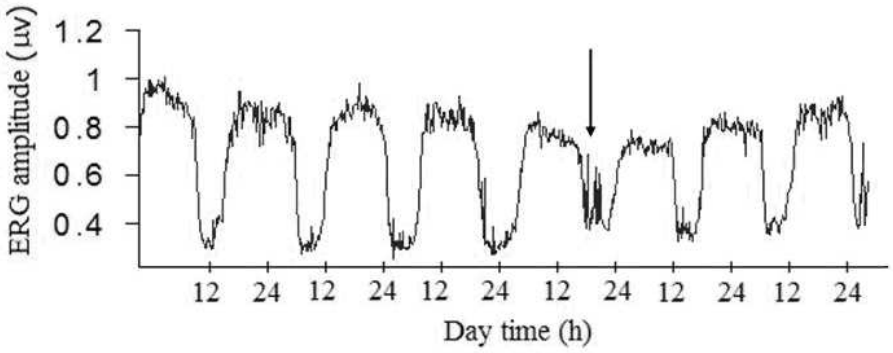


Figure 6. ERG recording. In this case we put a male crayfish instead a female crayfish (point by the arrow).

Something similar was observed when the crayfish's deutocerebrum was removed or injured before the ERG recording: the presence of either a female or a male in the bath, as well as the application of a solution of ecdysterone, did not produce the modifications observed in the intact crayfish in presence of a female or the application of an ecdysterone solution (not shown).

4 The Mathematical Model In base to experimental results we proceeded to modify and to adequate the original mathematical model in order to simulate the changes in the ERG circadian rhythm of a male in presence of a female crayfish.

The most important modification to the previous mathematical model consisted in to aggregate another circadian oscillator with a slightly smaller frequency and slightly noisier than the first circadian one, affecting the hormonal oscillator. That oscillator is identified as one deutocerebrum oscillator.

In Figure 7 we show in blocks the complete system corresponding to the mathematical model.

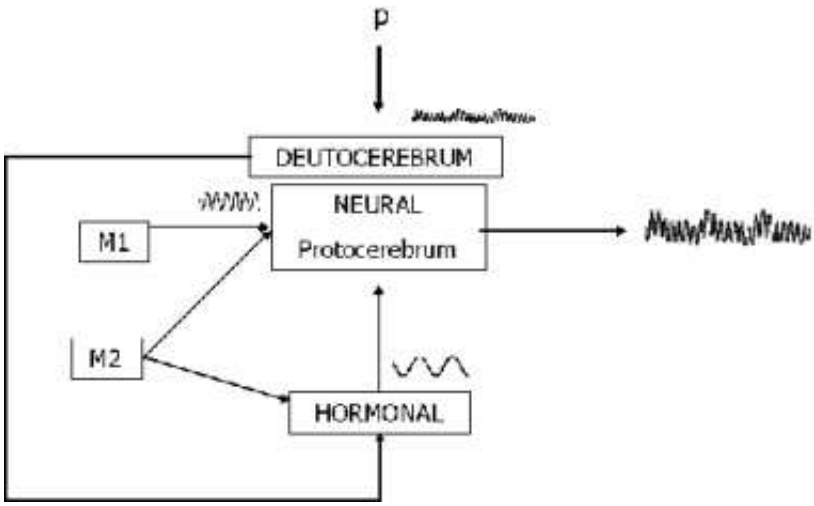


Figure 7. Where M_i =maturation, $i = 1, 2$; p =chemical perturbation.

The corresponding system of differential equations is as follows:

$$
\begin{aligned}
\dot{x_1} &= -kx_2 + e\left(x_1 + y_1 - \frac{3}{2}y_3 - x_3\right)\left(a - \frac{1}{5}x_3y_1 - \left(x_1 + y_1 - \frac{3}{2}y_3 - x_3\right)^2 - x_2^2\right)\\
\dot{x_2} &= k\left(x_1 + y_1 - \frac{3}{2}y_3 - x_3\right) + ex_2\left(a - \frac{1}{5}x_3y_1 - \left(x_1 + y_1 - \frac{3}{2}y_3 - x_3\right)^2 - x_2^2\right)\\
\dot{x_3} &= c_1x_3 - c_2x_3^2\\
\dot{y_1} &= -\left(l + \frac{z_1}{4}\right)y_2 + f\left(y_1 - \frac{3}{4}y_3 - \frac{z_1}{9}\right)\left(\frac{3}{2}y_1y_3 - \frac{z_1}{4} - \frac{y_3^2}{2} - \left(y_1 - \frac{z_1}{9}\right)^2 - y_2^2\right)\\
\dot{y_2} &= \left(l + \frac{z_1}{4}\right)\left(y_1 - \frac{3}{4}y_3 - \frac{z_1}{9}\right) + fy_2\left(\frac{3}{2}y_1y_3 - \frac{z_1}{4} - \frac{y_3^2}{2} - \left(y_1 - \frac{z_1}{9}\right)^2 - y_2^2\right)\\
\dot{y_3} &= d_1y_3 - d_2y_3^2\\
\dot{z_1} &= -mz_2 + g\left(z_1 + c\right)\left(s - \left(z_1 + c\right)^2 - z_2^2\right)\\
\dot{z_2} &= \left(mz_1 + c\right) + gz_2\left(s - \left(z_1 + c\right)^2 - z_2^2\right).
\end{aligned}
$$

In this equation system, x_1 and x_2 correspond to neural oscillator (protocerebrum), and x_3 is its maturation regime; y_1 and y_2 correspond to hormonal oscillator (X-organ-sinus gland system) and y_3 is its maturation regime; z_1 and z_2 correspond to deutocerebrum oscillator.

In Figure 8 we show the corresponding curve obtained from the mathematical model.It is worthwhile to mention that the mathematical model is of qualitative type, that is, it simulates adequately the behavior observed in the experiments.

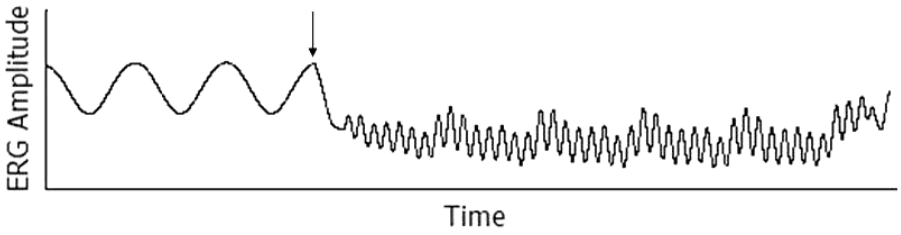


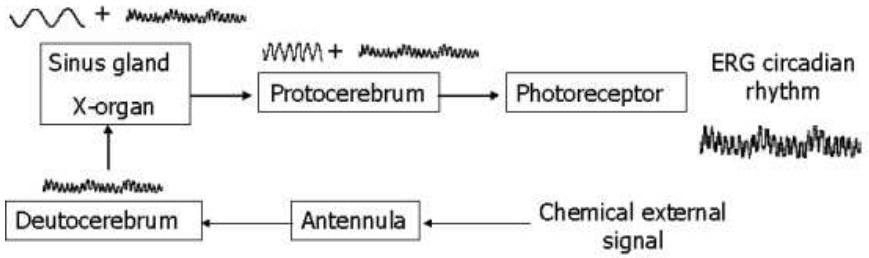
Figure 8. Mathematical simulation of ERG circadian rhythm of an adult, male crayfish recorded in presence of a female crayfish (point by the arrow).

Moreover, we have observed that the model is quite robust, in the sense that the qualitative features that were sought to be simulated are retained when small alterations of the parameters and the initial conditions are tried. However, this stability does not correspond to the classical concept of structural stability, from which point of view, our model in the region considered, is equivalent to a simple attracting limit cycle.

At the present time we are working with problems relative to existence and uniqueness of the limit cycles.

5 Discussion Biological results show the alteration of the main characteristics of the ERG circadian rhythm in male crayfish resulting from the presence of a female crayfish. It is worthwhile that the changes in the rhythm persist during all the time the ERG response is obtained (about 10 days) despite the female was retired from the bath after no more than 20 minutes after initiated the experiment. Something similar happens when instead the female crayfish, an ecdysterone solution is added (and 20 minutes after retired) to the bath where the ERG of the male crayfish is recorded. These findings together the absence of effect when the female crayfish is substituted by a male one, or when the deutocerebrum of the male crayfish has been injured or removed, strongly point to a decisive influence of pheromones (the ecdysterone has been recognized as well) on the circadian system responsible of the ERG circadian rhythm in this species.

A summary of experimental results and the possible interrelations among the putative structures derived from mathematical model is shown in following diagram. Once the chemical signals (coming from chemical receptors in antennula) have been analyzed in the deutocerebrum, a periodical (circadian) and noisy signal is sent from here to X-organ-sinus gland axis affecting the circadian hormonal release that regularly is sent from sinus gland to neural oscillator (protocerebrum). It is important to note that all these facts are encrypted in the system of differential equations that we used to model the experimental results. Another important fact to remark is that the mathematical model (Figure 7) proposed a communication, presumably a neural communication, between deutocerebrum and the hormonal oscillator located in the X-organ-sinus gland axis. At present, we are working in the biological probes.



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Miguel Lara-Aparicio
Departamento de Matemáticas, Facultad de Ciencias, Universidad Nacional Autónoma de México
México DF, CP 04510, México
E-mail: aparicio@servidor.unam.mx

Santiago López de Medrano
Instituto de Matemáticas, Universidad Nacional Autónoma de México
México DF, CP 04510, México

Carolina Barriga-Montoya, Beatriz Fuentes-Pardo
Departamento de Fisiología, Facultad de Medicina, Universidad Nacional Autónoma de México
México DF, CP 04510, México
E-mail: carolina@mmc.igeofcu.unam.mx, bfpardo@servidor.unam.mx