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Entrainment, Arnold tongues, and duality in a periodically driven integrate-and-fire model

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Abstract

We have studied an integrate-and-fire model neuron driven by a periodic sequence of Gaussian-shaped current pulses of width $1/2N$ and amplitude ε. For large N the current is a sequence of delta pulses and for smaller N it approaches a sine. When N is large, the firing rate f vs. ε curve is a staircase of entrainment steps yielding an Arnold tongue structure in the τ vs. ε plane. In the small N limit we find novel entrainment steps in the f vs. τ plane, without Arnold tongue structure. The steps in the two N regimes are related by a *duality transformation*. In the presence of noise in the pulse arrival times, the steps disappear above a critical noise value.

Keywords: Integrate-and-fire model; Entrainment; Arnold tongues; Duality transformation

1. Introduction

An important paradigm in brain studies is to understand the physiological and coding properties of different synchronized neuronal discharges. Neurons are driven by synaptic currents and can become synchronized to the underlying temporal structure. To further understand this generic phenomenon we have studied a driven integrate-and-fire (IF) model. This model has led to a number of interesting generic results for the

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properties of neurons and networks of neurons even when this simple model is not always physiologically relevant. It has been found that globally coupled IF oscillators synchronize under some conditions in the presence of excitatory coupling [1,5]. Therefore, even studying one IF neuron model can provide clues about the behavior of a network of globally connected IF neurons, under the action of periodical pulses. There has been significant interest in the properties of entrainment. For instance, the amount of transduced information measured by mutual information can be significantly increased during entrainment [7]. Entrainment could be a substrate for the regulation of the cortical information processing by neuromodulators. Then, it is important to characterize the parametric regions of entrainment for different types of driving currents. Coombes and Bressloff [2] (see also [4]) studied the mode-locked solutions of IF neurons. They analyzed the parameter space of the "Arnold tongues" (AT) that arise for sinusoidal driving current as well as for a pulse train. The AT are characteristic of nonlinear dissipative systems, and have been observed experimentally in the Aplysia buccal ganglion [3] and cortical neurons [6]. In this paper we analyze the entrainment problem in an IF model that is driven by periodic sequence of Gaussian current pulses. As the variance of the Gaussian pulses is varied there is a crossover from delta-like pulses to a sinusoidal driving current. We analyze the nature of the entrainment in different regimes as N varies including the effect of jitter, or noise, in the timing of these pulses.

2. Model and method

The IF model neuron considered in this paper is defined by the equation

$$\frac{\mathrm{d}V}{\mathrm{d}t} = -\frac{V}{\tau} + \varepsilon \sum_{m=-\infty}^{\infty} \sqrt{\frac{N}{\pi}}\, \mathrm{e}^{-N(t-mT)^2}. \tag{1}$$

Here $V(t)$ is the neuron membrane voltage with associated membrane time constant τ. We have added an infinite train of periodic Gaussian pulses of strength ε and period T. The number N is defined in terms of the width $\sigma_N^2 = 1/2N$ of the Gaussian pulses. When N is large the pulses are sharply peaked tending to a Dirac delta-function comb, while for small N the pulses are broad and extended. When the value of the membrane voltage reaches the threshold $V = 1$, the voltage is instantaneously reset to $V = 0$. The firing times of the IF neuron are $T^i = \inf\{t|V(t) \geqslant 1;\ t > T^{i-1}\}$.

The interspike ith interval is defined by $\Delta^i = T^{i+1} - T^i$. The firing rate is the inverse of their average $f = 1/\langle\Delta\rangle$. Apart from studying the dynamics described by Eq. (1), we also want to consider what happens when noise is introduced in the pulse arrival time. The noise is represented by the random variable ξ in the equation

$$\frac{\mathrm{d}V}{\mathrm{d}t} = -\frac{V}{\tau} + \varepsilon \sum_{m=-\infty}^{\infty} \sqrt{\frac{N}{\pi}}\, \mathrm{e}^{-N(t-mT-\xi)^2}, \tag{2}$$

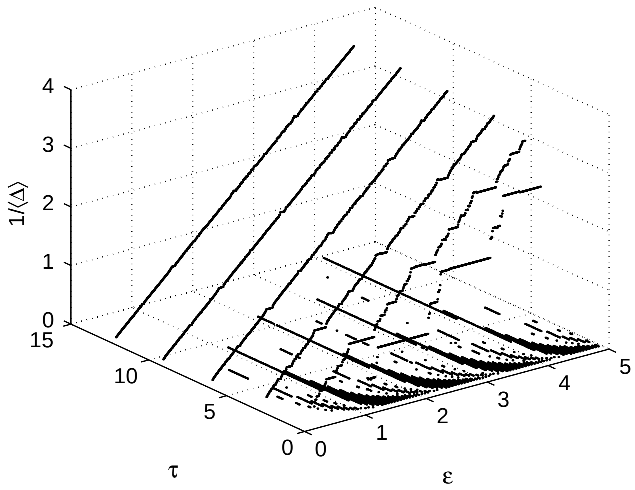

Fig. 1. The frequency $f = 1/\langle \Delta \rangle$ as a function of the membrane time constant τ for sharp Gaussian pulses of strength ε. Here, we only plot a few of the Devil's staircases for clarity. The Arnold tongues are visible in the projection to the τ vs. ε plane.

where ξ has a Gaussian probability distribution $P(\xi)$. The noise average is given by $\langle \cdot \rangle = \int_{-\infty}^{\infty} (\cdot)\, P(\xi)\, \mathrm{d}\xi$. Averaging Eq. (2) over noise, we obtain

$$\frac{\mathrm{d}\langle V \rangle}{\mathrm{d}t} = -\frac{\langle V \rangle}{\tau} + \varepsilon \sum_{m=-\infty}^{\infty} \sqrt{\frac{A}{\pi}}\, \mathrm{e}^{-A(t-mT)^2}, \tag{3}$$

where

$$A = \frac{1}{1/N + 2\sigma_\xi^2}. \tag{4}$$

We integrated Eqs. (1) and (3), between spikes, using a fourth-order Runge–Kutta implemented as a Fortran program. The integration step was $\mathrm{d}t = 0.001$.

3. Results

3.1. Regular input Gaussian pulses

We consider two limiting cases:

- Sharp Gaussian pulses with $N = 100$ and period $T = 1$ (Eq. (1)). In Fig. 1 we show that there are entrainment steps in the plane f vs. ε for fixed values of τ.
- Broad Gaussian pulses with $N = 0.01$, and period $T = 50$. As in the previous case, the Gaussian pulses do not "overlap". In Fig. 2 we show the entrained structure. Here there are no Arnold tongues, but instead there are regular staircases. Furthermore, the entrainment is in the f vs. τ plane for different values of ε. This change can

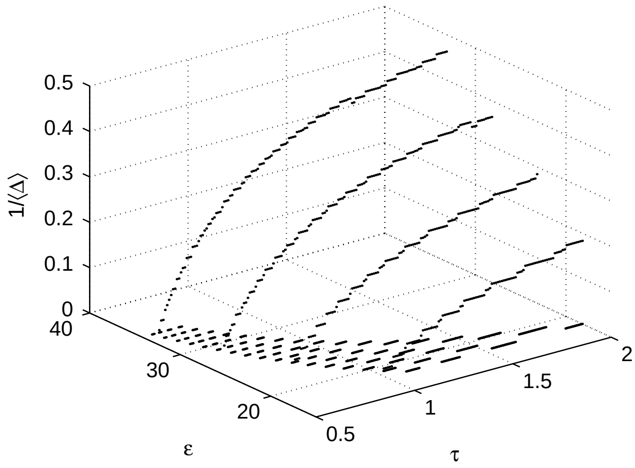

Fig. 2. These curves show the behavior of the averaged firing rate $f = 1/\langle \Delta \rangle$ vs. ε and τ for broad Gaussian pulses. For clarity, we only show a few stairs along the τ-axis. In this case we have a regular structures in the ε vs. τ plane. The segments in this plane represent the projection at frequencies 0.06, 0.10, 0.14, and 0.18, respectively.

be shown to be due to a *duality transformation* between the large and small N regimes. We find that for the case $\varepsilon = 18.2$, the frequency associated with each step is a multiple of $\frac{1}{50}$, and the width of the step increases as τ and the frequency increase.

In both the cases there are entrainment steps. This is by itself an unexpected result, in particular since there is no apparent constant driving current to produce intrinsic oscillation in the firing times. This result can be understood if we consider the following identity:

$$\sum_{m=-\infty}^{\infty} \sqrt{\frac{N}{\pi}}\, e^{-N(t-mT)^2} = \frac{1}{T} + \frac{2}{T} \sum_{m=1}^{\infty} e^{-\pi^2 m^2/NT^2} \sin\left(\frac{2\pi m}{T} t + \frac{\pi}{2}\right), \qquad (5)$$

which can be derived using the Poisson summation formula. We can see that there is a constant term which can be identified as a constant external driving current ($I_0 = \varepsilon/T$) that is responsible for the intrinsic oscillations observed.

3.2. Random input Gaussian pulses

We now consider the previous cases adding noise to the firing times, as given in Eq. (2). We quantitatively found that the width of the entrainment steps decreases until they disappear as σ increases. This is shown in Fig. 3. In this figure we also plot the results from an analytic calculation that explicitly averaged Eq. (2) over noise. The agreement between the two calculations is excellent.

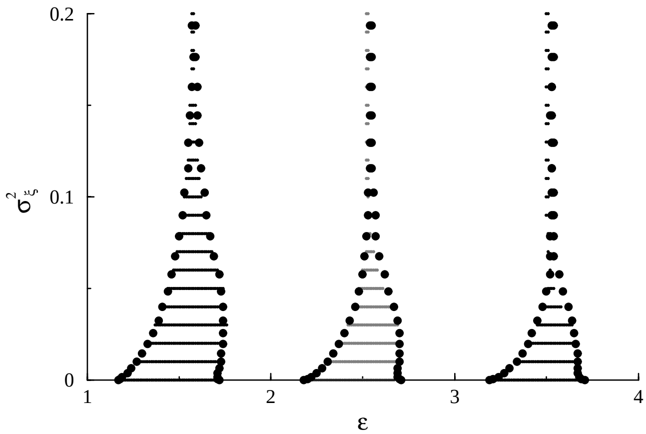

Fig. 3. Entrainment step projections from solving Eq. (2), in the plane for frequencies values of 1, 2, and 3, from left to right. The dotted lines are the results from a numerical stochastic Euler calculation, with time step $dt = 0.0001$. The continuous lines were obtained analytically from the averaged Eq. (3).

4. Conclusions

Here, we found that when the Gaussian pulses are very narrow there are entrainment steps along the ε-axis, with Arnold tongue structure in the τ vs. ε plane. When we considered broader Gaussian pulses, the "dual" regime for small N we found new type of entrainment steps along the τ-axis, with quite different structure from the one found along the ε-axis in the large N regime. This change in entrainment axis properties in both limits was explained in terms of a duality relation between the type of current pulses in both regimes. This duality transformation, its interpretation, and its meaning for the new entrainment steps will be discussed in more detail elsewhere.

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