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A path integral approach to the Hodgkin–Huxley model

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HIGHLIGHTS

- We need to develop stochastic models describing the neuronal dynamics.
- Stochastic systems can be expressed in terms of path integrals.
- Noise processes are induced by the neural network/feedforward correlations.
- We obtain path integral solutions driven by a non-Gaussian colored noise q.
- Allows us to investigate the underlying dynamics of the neural system.

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ABSTRACT

To understand how single neurons process sensory information, it is necessary to develop suitable stochastic models to describe the response variability of the recorded spike trains. Spikes in a given neuron are produced by the synergistic action of sodium and potassium of the voltage-dependent channels that open or close the gates. Hodgkin and Huxley (HH) equations describe the ionic mechanisms underlying the initiation and propagation of action potentials, through a set of nonlinear ordinary differential equations that approximate the electrical characteristics of the excitable cell. Path integral provides an adequate approach to compute quantities such as transition probabilities, and any stochastic system can be expressed in terms of this methodology. We use the technique of path integrals to determine the analytical solution driven by a non-Gaussian colored noise when considering the HH equations as a stochastic system. The different neuronal dynamics are investigated by estimating the path integral solutions driven by a non-Gaussian colored noise q. More specifically we take into account the correlational structures of the complex neuronal signals not just by estimating the transition probability associated to the Gaussian approach of the stochastic HH equations, but instead considering much more subtle processes accounting for the non-Gaussian noise that could be induced by the surrounding neural network and by feedforward correlations. This allows us to investigate the underlying dynamics of the neural system when different scenarios of noise correlations are considered.

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1. Introduction

To understand how information is transported in cerebral cortex we need to investigate first the input and output characteristics of a given neuron. The membrane potential is the difference in electric potential between the interior and exterior of the cell, where the surrounding extracellular fluid is located. The resting potential tells us what happens when a neuron is at rest, at a voltage of −70 mV. The voltage in the membrane of a neuron depends on currents from a diverse collection of ion channels, many of which have nonlinear voltage-dependent dynamics [1–5]. General forms for the dynamics of many of the major families of ion channels have been characterized [2,6], but the kinetic parameters vary according to the neuron where the ion channels are located. A spike occurs when a neuron sends information down an axon, away from the cell body as an explosion of electrical activity that is created by a depolarizing current. At the single neuron level neurophysiology recordings allow to accurately measure the membrane potential showing that neurons exhibit rich dynamical behaviors, including rhythmic bursting and patterned sequence generation [5,7–9]. These dynamics derive from the intrinsic properties of individual neurons and from the connections among them within the network. That is neurons, under the current framework, behave similarly to nonlinear oscillators [10].

The path integral method provides us with the means to estimate unmeasured states and parameters conditioned on measurements of some subset of the variables. Moreover, the method is exact, as an exact statement of the information transfer at each measurement comes from an identity on conditional probabilities [11,12]. It has the advantage of combining the local uncertainty in state to state transitions with the global trajectory of the system. This provides an integral representation of the linear partial differential equation for the conditional probability distribution. As such delivers a global view of the solution to the underlying stochastic physical problem and permits going beyond the local view of other methodologies [11–15]. The path integral also takes into account the paths of a stochastic system through its state space as they are influenced by observations. Thus, we have to focus first on the formulation of the questions one wants to answer using the path integral formulation to then developing a methodology to perform the integrals that answer those questions avoiding the limitations of other methods [12]. Stochastic differential equations can be used to model the phenomena of the neuronal firing [16]. Importantly, any stochastic and even deterministic system can be expressed in terms of path integrals that provide a convenient tool to compute quantities such as transition probabilities [11–16].

HH equations allows us to explain how action potentials are generated through the electrical excitability of neuronal membranes [17–21]. The path integral methodology can provide us an alternative approach to determinate the analytical solution of the membrane potential when considering the stochastic HH equations. In this paper we consider the path integral solution driven by a non-Gaussian colored noise of the HH equations as a stochastic system. We develop a path integral formulation for characterizing the different states of a neuron as non-linear dynamical system considering colored noise that could account for the possible effects of the surrounding background activity, correlated activity, feedforward correlations, and the ephaptic coupling [22], as they might alter the functioning of individual neurons and neural assemblies under different physiological conditions. In order to do it so we use a variational method to minimize the action of the path integral formulation [11,12,23]. We apply the methodology of path integrals developed by Wio et al. considering a colored noise within the q-Gaussian formalism [11–13]. More specifically, we investigate the solutions of HH equation as a particular case of the Fokker–Planck equation driven by a non-Gaussian colored noise q that is better suited to be investigated within the path integral approach. We analyze the causality entropy–complexity plane $H \times C$ and causal Fisher information versus statistical complexity/Shannon entropy, $F \times C$ and $F \times H$, considering the solution of the path integral formulation driven by different levels of noise q. This allows us to investigate the underlying dynamics of the neural system, quantifying the degree of correlations in the neural responses.

2. Methodology

2.1. Model

Let us consider first the biophysical model for the membrane potential V of a section of a spatially homogeneous neuron, the HH model reads as [17]:

$$C_m \frac{dV}{dt} = -I_{Na} - I_K - I_M - g_L(V - E_L) - \frac{1}{A} I_{syn} \tag{1}$$

where

$$\begin{aligned} I_{Na} &= \bar{g}_{Na} P_{Na}(V,t)(V - E_{Na}), \\ I_K &= \bar{g}_K P_K(V,t)(V - E_K), \\ I_M &= \bar{g}_M P_M(V,t)(V - E_M). \end{aligned}$$

Here C_m is the membrane capacitance, g_X is the maximal conductance of channels of type X, P_X is the probability that a channel of type X is open, E_X is the reversal potential for channel type X and the subscripts Na, K and M refer to sodium, potassium and M-type potassium channels respectively. A leak current is included with conductance g_L and reversal potential E_L, A is the membrane area, while I_{syn} is the current resulting from synaptic background activity. This model is capable of generating action potentials. Background activity in this case is modeled as a colored non-Gaussian noise, to take care of the