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Emergent central pattern generator behavior in chemical coupled two-compartment models with time delay

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HIGHLIGHTS

- The modified two-compartment PR model is proved to meet the requirement of CPG and can be used to develop the CPG networks.
- The simplest form of CPG is constructed by two inhibitory chemical coupled PR neurons with delay time.
- Emergent behaviors of CPG affected by ambient noise, sensory feedback signals, morphology features as well as the coupled delay time are investigated.

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ABSTRACT

This paper proposes that modified two-compartment Pinsky–Rinzel (PR) neural model can be used to develop the simple form of central pattern generator (CPG). The CPG is called as 'half-central oscillator', which constructed by two inhibitory chemical coupled PR neurons with time delay. Some key properties of PR neural model related to CPG are studied and proved to meet the requirements of CPG. Using the simple CPG network, we first study the relationship between rhythmical output and key factors, including ambient noise, sensory feedback signals, morphological character of single neuron as well as the coupling delay time. We demonstrate that, appropriate intensity noise can enhance synchronization between two coupled neurons. Different output rhythm of CPG network can be entrained by sensory feedback signals. We also show that the morphology of single neuron has strong effect on the output rhythm. The phase synchronization indexes decrease with the increase of morphology parameter's difference. Through adjusting coupled delay time, we can get absolutely phase synchronization and antiphase state of CPG. Those results of simulation show the feasibility of PR neural model as a valid CPG as well as the emergent behaviors of the particularly CPG.

1. Introduction

Central pattern generators are neuronal circuits found in both invertebrate and vertebrate animals that can produce rhythmic patterns of neural activity such as walking, breathing, flying and swimming [1–4] in the absence of sensory or descending inputs that carry specific timing information. CPGs play an important role in the formation of repeated oscillatory behaviors and are considered central to their basic survival across much of the animal species.

Traditionally, reciprocal synaptic inhibition between two neuronal populations (or two groups of neuronal populations, or two individual neurons [5]) is considered as the standard form of generating CPG behavior in both biological and

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computational systems. The simplest form of CPG is called as a 'half-center oscillator', in which two neurons reciprocally inhibit each other. This network was proposed firstly by Brown [6] to explain alternation of extension and flexion phases in cat locomotion, and have subsequently been studied extensively both theoretically [7,8] and experimentally [2].

The half-center CPGs have found in biological models of lamprey [9], in locomotion models such as stick insect locomotion [10]. In Ijspeert's review [4], several features of CPGs were proposed: (1) typically, CPG models have a few control parameters, which can be used to modulate the rhythmical outputs; (2) CPG models display limit cycles to produce stable rhythmical output and have resistance to noise; (3) CPGs are suitable to integrate sensory feedback signals which provide an opportunity to realize entrainment between CPG and the environment [41]. According to different targets of the research, different neuronal models, such as the Hodgkin–Huxley (HH) model [11], the FitzHugh–Nagumo (FN) model [12,13,42] and Hindmarsh–Rose (HR) neuronal model [14,15], can be used to develop CPG model. Those models are capable of mimicking almost all the behaviors exhibited by real biological neurons, such as spiking, bursting and so on [16]. However, most of neurons forming CPGs are single compartment models. The single compartment model is the simplification of real neurons and do not have physical structures including soma, dendrite, axon et al. In contrast, multi-compartment models have rich firing patterns, and could reflect the spatial location of neural structure. What is more important, the multi-compartment model is built based on physiological data, and is used to mimic physiological experiment and reveal the physiological meaning of simulation results.

PR model is a kind of spiking neuronal models with two-compartments—soma and dendrite [17]. The dynamical equations of PR model consist of eight equations, a dozen of functions and tens of parameters, describing membrane potential, activation of sodium current and potassium current, and inactivation of the sodium current and so on. What is more, there are many theoretical studies on the properties of PR model, such as bifurcation [18], analysis of bursting mechanism [19–21] and so on. However, PR model is rarely used to simulate CPG in comparison with other neuronal models, and its application in practice is even less. There is also little systematic analysis about the properties of PR model in the view of CPG network.

In this paper, we firstly aim to explore the properties of PR model on the aspect of CPG, and construct a half-center CPG network based on two reciprocally inhibitory PR neurons with chemical synapses. Considering the causal relationship between firing properties and dendrite structures [22], we also investigate the effects of morphological feature (the size ratio of soma and dendrite) of single neural model on the output rhythm of CPG network. The coupling delay time is another important factor influencing the output of CPG [23,24], and it is also considered.

The rest of the paper is organized as follows. First, we investigate the spiking properties of modified PR model in the view of CPGs and prove that it can be used to form a CPG network. Then, we construct a half-center CPG network based on modified PR model. Last, we analyze the output rhythm of half-center CPG network affected by ambient noise, sensory feedback signals, and different morphology features of PR neuron as well as the coupled delay time.

2. Model and method

2.1. Mechanism of single neuron

The PR model characterizes a typical pyramidal cell as comprising a somatic and a dendritic compartment. Each PR neuron is characterized by eight time-dependent variables, and the equations of membrane potentials are shown in Eq. (1). There are three currents in somatic compartment: transient sodium I_{Na}, delayed rectifier potassium I_{KDR}, and leak current. The dendritic compartment contains persistent calcium I_{Ca}, calcium activated potassium I_{KCa}, after-hyperpolarisation potassium current I_{KAHP} and leak current. All currents are conductance-based, using the Hodgkin–Huxley formalism [11] of activation and inactivation gates dependent on voltage or intracellular calcium that drive the current. The two compartments are coupled by a coupling current $I_{SD} = -I_{DS} = g_c\,(V_d - V_s)$. The size of dendrite compartment as a proportion of the entire neuron was given by $1 - p$ and that of soma compartment as p. Currents and conductances are expressed as densities with units of $\mu A/cm^2$ and mS/cm^2, respectively. Capacitance C_m is in unit $\mu F/cm^2$; the time unit is ms [17].

$$\begin{aligned} C_m \frac{dV_s}{dt} &= -I_{Leak} - I_{Na} - I_{KDR} - \frac{I_{DS}}{p} + \frac{I_s}{p} \\ C_m \frac{dV_d}{dt} &= -I_{Leak} - I_{Ca} - I_{KCa} - I_{KAHP} - \frac{I_{SD}}{1-p} + \frac{I_d}{1-p}. \end{aligned} \tag{1}$$

The activation and inactivation gates of ionic channel evolve as a function of their steady state x_∞ and time constant τ_x, where V represents the membrane potential V_s or V_d, or the intracellular calcium Ca.

$$\begin{aligned} &\frac{dx}{dt} = \frac{x_\infty(V) - x}{\tau_x}; \quad \frac{dCa}{dt} = -0.13Ca - 0.075Ca \\ &x_\infty(V) = \frac{\alpha_x(V)}{\alpha_x(V) + \beta_x(V)}; \tau_x(V) = \frac{1}{\alpha_x(V) + \beta_x(V)} \end{aligned} \tag{2}$$

In order to make a detailed mathematical analysis of the PR model from the view of dynamical system, Laura A. Atherton and Krasimira Tsaneva-Atanasova modified the original PR model, and approximated the discontinuous functions by fitting continuous functions directly to the steady state and time activation curves [25]. All activation/inactivation function and parameters of modified PR model can be found in Ref [18]. In the following sections, we will discuss the properties of modified PR model in respect of CPG.