Fastest strategy to achieve given number of neuronal firing in theta model

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ABSTRACT

We investigate the constrained optimization of excitatory synaptic input patterns to fastest generate given number of spikes in theta neuron model. Optimal input timings and strengths are identified by using phase plane arguments for discrete input kicks with a given total magnitude. Furthermore, analytical results are conducted to estimate the firing time of given number of spikes resulting from a given input train. We obtain the fastest strategy as the total input size increases. In particular, when the parameter $-b$ is large and total input size G is not so large, there are two candidate strategies to fastest achieve given number of spikes, which depend on the considered parameters. The fastest strategy for some cases of $G \gg -b$ to fire m spikes should partition m spikes into $m - n + 1$ spikes for the highest band, with largest g, and one spike for each subsequent $n - 1$ band. When G is sufficiently large, big kick is the fastest strategy. In addition, we establish an optimal value for the dependent variable, θ, where each input should be delivered in a non-threshold-based strategy to fastest achieve given output of subsequent spikes. Moreover, we find that reset and kick strategy is the fastest when G is small and $G \gg -b$. The obtained results can lead to a better understanding of how the period of nonlinear oscillators are affected by different input timings and strengths.

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1. Introduction

Notably, understanding how neurons respond to synaptic inputs has been a potential topic in the field of computational neuroscience. Chemical synaptic transmission offers a specific mechanism for encoding of the neuronal information that an organism can sense from the external environment, which is filtered by the internal state of the organism. Thus, understanding neuronal input–output transformation is a centrally important scientific goal (Wang, Costello, & Rubin, 2011). Neurons make use of action potentials or, more simply, spikes, brief and uniform pulses of electrical activity, to transmit and process information. It is well known that an action potential is generated when the membrane potential of a neuron reaches a threshold value. And then, it travels down the axon toward synapses terminating at postsynaptic neurons, where it initiates postsynaptic currents that summate to trigger (or inhibit) new action potentials. An action potential sequence, or spike train may contain information with diverse coding schemes.

Previous study of Morris and Hooper (1997) has shown that slow muscle contraction amplitude should depend on spike number when burst duration is brief relative to muscle summation time, and on spike frequency when the duration is long relative to this time. In this work, difference between spike number and spike frequency dependence on two slow muscles is clarified in the lobster stomatogastric system. It is shown that, functionally, one muscle is spike number dependent, whereas the other is primarily spike frequency dependent. Thus, both of these parameters can determine slow muscle output. Previous results have shown that input fluctuations can establish a regime of high spike-time reliability (Galán, Ermentrout, & Urban, 2008) or high sensitivity of firing frequency to input current strength (Arsiero, Luscher, Lundstrom, & Giugliano, 2007; Higgs, Slee, & Spain, 2006). Although the framework for incorporating synaptic inputs into computational models is well established, and the computational implications of such inputs have received significant attention, optimization problems involving synaptic inputs are not well represented in existing literatures. In this paper, the optimal way to tailor synaptic inputs that is subject to a certain constraint is explored to fastest generate given number of spikes.

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There are several reasons that minimizing time of given numbers of spikes may be a biologically relevant goal for normal activities of neurons. As neurons operate with the efficient resource being utilized, it could be helpful if, subject to some constraint on the amount of input, the synaptic input time course could be tailored to fastest achieve given number of spikes. Certainly, there exist some brain areas, including areas of somatosensory cortex and visual cortex, where firing intensity encodes stimulus information with neurons showing maximal firing under optimally preferred stimulus conditions (Simons, 1978). Similarly, a sufficiently high firing rate within a given time window may be needed to overcome inhibition or to outcompete activity of other neurons to influence a downstream readout neuron (Abeles, Bergman, Margalit, & Vaadia, 1993; Pinto, Brumberg, Simons, & Ermentrout, 1996). Input time courses that need minimal time to yield given number of spiking can depend on the intrinsic properties of a neuron model, and characterizing optimal input time courses for models can provide some useful information about neuronal coding function. Interestingly, optimal spikes have been explored in neuronal networks as some key factors of the neuronal systems are changed (Ozer, Perc, & Uzuntarla, 2009; Perc, 2009).

Moehlis, Shea-Brown, and Rabitz (2006) used a calculus of variations approach to determine the input current of minimal amplitude that causes a neuron to spike at a specified target time. That work considered a phase model for a spiking neuron, with the evolution of phase $x \in [0, 2\pi)$ given by

$$dx/dt = f(x) + Z(x)I(t),$$

where the impact of the input current $I(t)$ is modulated by the phase sensitivity function $Z(x)$. In addition, Forger and Paydarfar (2004) give optimal weak inputs to start or stop repetitive spiking in a general biological oscillator, with dynamics expressed in polar coordinates as

$$dr/dt = \epsilon I(t) \sin(\phi), \qquad d\phi/dt = 1 + \epsilon I(t) \cos(\phi)/r \qquad (1)$$

with ϵ small. Particular biology systems, whose dynamics is qualitatively equivalent to those of (1), were also considered as examples to illustrate a calculus of variations approach to this problem. This involves numerical solution of a set of ordinary differential equations, which is obtained through the introduction of Lagrange multipliers.

To extend the existing results, we consider input optimization in the well-known mathematical model for single neuron, the theta model (Hoppensteadt & Izhikevich, 1997), which allows us to use certain analytical methods, rather than relying only on numerics. Initially, the neuron is tuned to be silent in the absence of inputs. One approach that we follow is to treat synaptic inputs as the events with discrete onset time, which yields a phase plane representation of the co-evolution of an intrinsic variable of the neuron and a synaptic input variable, as introduced previously in Rubin and Bose (2006) and Wang et al. (2011) for the LIF and theta model. Our results extend this idea, which can provide information about specific time courses that are optimal, not just for the generation of a single spike or maximizing spike outputs but for minimizing time of the given spikes. The theta model can be rigorously derived as a normal form for Type I spiking neurons (Ermentrout, 1996; Hoppensteadt & Izhikevich, 1997; Izhikevich, 2007), which features a transition from silence to oscillations through a SNIC bifurcation (Rinzel & Ermentrout, 1998). Thus, consideration of the theta model allows us to explore how our results extend to a case with additional biological relevance.

The remainder of this paper is organized as follows. In Section 2, we analyze the theta model with discrete synaptic kicks, whose cumulative sizes are constrained. We introduce phase plane structures to analyze the resulting optimization problem and discuss some strategies for controlling the timing of inputs before moving on to prove some results about these structures and optimal strategies. In Section 3, we define band in theta model and estimate firing time of a band. We find that the firing time decreases as input increases by analyzing the band time. We also estimate the time of strategies by using the band time. In Section 4, we analyze the fastest strategy for large $-b$ and small G. When $G \gg -b$, and the input size G is fixed, the fastest strategy is studied to fire m spikes for the given n bands in advance. We show that strategy with minimum time for some area of G to fire m spikes should partition G into an initial input, which should be as large as possible, and $m - n$ kicks of the highest band size for each time of the first $m - n$ spikes fired. We also show that when G is sufficiently large, big kick is the fastest strategy. Further, we establish an optimum value for the dependent variable, θ, where each input should be delivered in a non-threshold-based strategy to fastest achieve given subsequent spike output. We find that reset and kick strategy is the fastest when $G \gg -b$ is small. We conclude with a discussion in Section 5, where we summarize the results and discuss the novelty and relevance of our findings in the neuroscience setting.

2. Model

We consider the dynamics of an theta model receiving positive synaptic excitatory inputs, whose dynamics can be governed by the equations (Wang et al., 2011),

$$\theta' = 1 - \cos\theta + (b + g)(1 + \cos\theta), \qquad (2)$$

$$g' = -\beta g, \qquad (3)$$

where $b < 0$ is a parameter and $\theta \in [-\pi, \pi] \mod 2\pi$. The neuron is said to fire when θ increases through π and is effectively reset to $-\pi$. With $g = 0$, corresponding to the absence of excitatory inputs, and $b < 0$, which is the case we consider, the theta model (2) has two critical points, namely an unstable given point at $\theta_U = \arccos \frac{1+b}{1-b} > 0$ and a stable given point at $\theta_S = -\arccos \frac{1+b}{1-b} < 0$. Furthermore, we represent the excitatory input by the equations

$$g(t_n^+) = g(t_n^-) + s_n, \qquad (4)$$

$$\sum_{n=1}^{N} s_n = G \qquad (5)$$

for $s_n \in (0, G)$, $n = 1, 2, \ldots$ with $N \geq 1$ finite and $G > 0$ given in **R**. Eqs. (3) and (4) state that each input kick can be chosen to arrive at any time and instantaneously updates the value of g when it arrives and that the synaptic conductance g always decays exponentially between kicks. Eq. (5) shows that the sum of all inputs, however they may be divided, is always equal to a given input allowance G. In the subsequent subsections, we assume that b and β are fixed, and then consider the suitable partition and time to input G to yield at least m of threshold crossings, or spikes fastest. First, we discuss a phase plane representation of this problem and consider some strategies.

2.1. Phase plane structures and strategies

We illustrate some key structures in the phase plane for system (2), (3) in Fig. 1 (also see Wang et al., 2011). The *theta*-nullcline, based on Eq. (2), is the curve $\Gamma_0 := \{g = -(1 - \cos\theta + b(1 + \cos\theta))/(1 + \cos\theta)\}$. Denote the minimal value, as $\hat{g}$, such that a trajectory starting from $(-\pi, g)$ will result in a spike if and only if $g > \hat{g}$. To do this analytically, we seek $\hat{g}$ such that the trajectory from $(-\pi, \hat{g})$ reaches $(0, -b)$ and thus crosses the θ-nullcline and converges to θ_S (see Fig. 1). Although there are other trajectories with initial values g above $\hat{g}$ that also converge to θ_S by crossing the θ-nullcline at points with $\theta > 0$ and $g < -b$, this approach nonetheless gives a reasonable approximation to $\hat{g}$ (see Fig. 1).