Stablity Analysis of Entrainment by Two Periodic Inputs With a Fixed Delay

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Abstract

We were able to predict stable entrainments for an open loop neural circuit in which an endogenously rhythmic neuron is driven by two periodic inputs separated by a fixed delay, using linear stability analysis about an assumed entrainment as well as a local linearization of the measured phase resetting curve. An example using Morris Lecar oscillators found multistable entrainments for a fixed delay. A fixed delay could be applicable to interneurons that exhibit postinhibitory rebound bursting. This research is part of an effort to extend the applicability of our previously developed methods to analyse circuits that underlie central pattern generation.

1 Introduction

Central pattern generating circuits often contain endogenous oscillators such as bursting neurons. One technique that is helpful in analysing such circuits utilizes phase resetting curves, which can readily be generated for biological neurons. The existence of entrainment patterns can be predicted using periodicity constraints, and their stability can be determined by linearizing the phase resetting about an assumed entrainment and applying a perturbation analysis. Previous work by others dealt with entrainment by a single periodic input, or by self-entrainment of an oscillator with fixed delay [4, 5, 6].

Previous work from our group focused on circuits composed entirely of endogenously bursting neurons [1, 2, 3], and was restricted to cases in which a single input was received by each neuron per cycle, which is turn limited the circuits analysed to a ring architecture. We would like to extend these analyses to circuits in which the component neurons are not restricted to a single input, and are not restricted to endogenous bursters. As a first step, we examined the simplest possible circuit with two inputs, beginning with an open loop circuit in which one bursting neuron drives another, but adding a nonoscillatory neuron that also synapses on the driven neuron, and produces a burst with a fixed latency after receiving a burst from the driver neuron.

2 Methods

As in our previous analyses, certain assumptions must be made in order to make the problems tractable. First, we contrained the delay plus the total duration of the two input bursts to be less than a cycle period. We assumed that the only effect of a perturbation was to move the limit cycle trajectory backwards or forwards tangentially along its path, producing either an advance or a delay. Specifically, we assumed that by the time the driven oscillator receives the second burst, it has returned suffiently close to its unperturbed limit cycle so that the phase resetting curve still predicts the effect that a burst will produce. We also assumed that a perturbation only affected the cycle in which it received, and therefore did not affect subsequent bursts.

3 Results

The circuit is given at the left of Figure 1 and the stability analysis is illustrated on the right hand side.

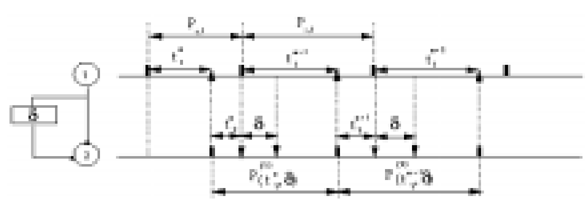

Figure 1: The two neuron circuit (left panel) and the dynamics of the inhibitory perturbations received by the second neuron.

The single-pulse PRC, $F^{(1)}(\varphi)$, which is a measure of the relative temporal advance/delay of the next crossing in the Poincare section when an oscillator is perturbed, can be used to determine the amount of phase resetting induced by two (or more) current pulses acting during the same cycle the PRC writes

$$F^{(2)}(\varphi) = F^{(1)}(\varphi) + F^{(1)}\left(\varphi + F^{(1)}(\varphi) + \frac{\tau_1 + \tau_2}{P_i}\right), \tag{1}$$

where P_i is the intrinsic period of the oscillation and $\frac{\tau_1+\tau_2}{P_i} < 1$ in order to deliver both the current pulses during the same cycle [7].

Based on multiple-inputs per cycle PRC (1) when the delay loop is present (see Figure 1) then the entrainment timing is given by:

$$
\begin{aligned}
t_1^n + t_2^n &= P_{i,1}, &(2)\\
t_2^n + t_1^{n+1} &= P^{(2)}(t_1^n, \delta), &(3)
\end{aligned}
$$

where $P_{i,1}$ is the intrinsic period of the first oscillator and $P^{(2)} = P_{i,2}(1 + F^{(2)})$ is the second-inpust per cycle PRC for the second oscillator in the network. By eliminating t_2 it is possible to determine a first order nonlinear map for the entrainment induced by the first oscillator. The steady phase diference between the two oscillators $\varphi *$ is given by

$$F^{(1)}(\varphi *) + F^{(1)}(\varphi * + F^{(1)}(\varphi *) + \delta) = 0.$$

The Lyapunov exponent for the map derived from (3) is

$$\lambda = 1 - F^{'(1)}(\varphi *) + F^{'(1)}(\varphi * + F^{(1)}(\varphi *) + \delta)(1 + F^{'(1)}(\varphi *)).$$

Two mutually inhibitory Morris Lecar oscillators were used to test the theoretical results described above. Numerical simulations were run for a range of values of fixed delay.Figure 2 illustrates the results of these simulations. The dark curves show stable entrainments.

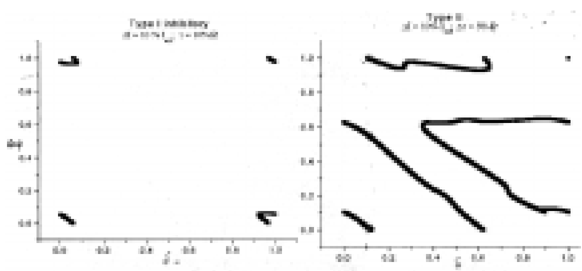

Figure 2: The steady phase difference between the two neurons displays a stable synchronous oscillatory state for the case of two Type I Morris-Lecar model neurons coupled as seen in Figure 1 (left panel). For the case of Type II model neurons the system shows multiple steady phase differences (right panel).

For parameters in the Type I regime, only delays that allowed all three neurons to burst nearly simultaneously were stable. Multistability is evident when there is more than one stable pattern at a fixed delay. The multistability in this case results in part from symmetry, in that the two presynaptic bursts are identical and interchangeable. For Type II, more complex multistability results at a greater range of delay values. Most significantly, the predicted stable modes agreed with the observed stable modes.

4 Discussion

This work is a continuation and extension of a line of research in which phase resetting curves are used to analyse the stability of patterns of entrainment. This circuit is simpler than others we have studied in that there is no feedback. However, it is more complex in that a single neuron receives more than one input in a cycle, and in fact the inputs were allowed to overlap. For perturbations that cause a significant normal departure from the limit cycle, perturbations may not add in this simple fashion, for example if they cause switching to the other side of the limit cycle via a normal path (Soprisan, Thirimulai, Marder, and Canavier 2002).

The next step in our research progression is to incorporate delays into closed circuits with feedback, such as those we have previously analysed without delay, in hopes of extending our methods to real CPGs that contain both endogenously bursting neurons and others that might be simulated as producing a burst after a delay.

References

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