Phase Characterization of Hyperpolarizing and Depolarizing Currents on a Four Neuron CPG Model

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***Abstract*— This work analyzes eigenvalues for a four neuron central pattern generator (CPG) model with slow sodium dynamics. The developed software finds its equilibrium points, characterizes them, and describes the oscillation without running simulations, allowing for rapid system characterization with new parameters. Different regimes have been identified that produce behavior suitable for different applications: non-oscillating bistability, slow oscillation that is sensitive to perturbations, rapid oscillation that is robust against perturbations, and a single stable node. Oscillatory regimes are numerically characterized by phase response, and suitable parameter sets are selected for use in two distinct robot controllers. Using this analysis, reflexes were designed based on known neural pathways and successfully demonstrated on an insect-like robot with 28 degrees of freedom as well as in a simulation of a rat's hind legs.**

I. INTRODUCTION

CPGs have become an effective tool for locomotion controllers by ensuring phase transitions occur between different rhythmic states. However, using CPGs effectively for locomotion control requires that they can also respond to perturbations in the form of sensory information. To effectively implement CPGs, phase resetting properties are important to understand. Unfortunately, neuron dynamics are nonlinear and transcendental, and the effects of perturbations on detailed models are not feasible to fully test. This has led to simpler, more mathematically tractable models which can easily be reset and examined and has resulted in significant advances in the understanding of the use of sensory input to respond to perturbations and changes in the environment [1].

As more biological data becomes available, more detailed CPG models can be utilized to reproduce more realistic and adaptive behaviors observed in the animals, provided that we have a clear understanding of the CPG dynamics.

II. CPG CHARACTERIZATION

We used numerical methods and eigenvalue analysis to characterize a commonly used computational model of a CPG [2]. The system is composed of two mutually inhibitory neurons called half-centers (HCs), each with a nonlinear ion channel that provides decaying positive reinforcement to activity. The neurons are coupled by linear piecewise synapses, such that a neuron below the conductance threshold cannot inhibit its neighbor. Each inhibitory pathway passes through a nonspiking interneuron, into which external signals may be fed to change the CPG's timing. Depending on the parameters, the entire system may have either two or one distinct equilibrium points. In the two point case, we categorize these points by their current state relative to the other neuron; the excited neuron's equilibrium voltage (ENEV) or the inhibited neuron's equilibrium voltage (INEV).

The proximity of the INEV to the conductance threshold determines the number of equilibrium points and their eigenvalues, making this an important design parameter. The plots in Fig. 1 show the number of equilibrium points, their voltage values, and their eigenvalues as the input drive to the two half centers is increased via an excitatory synapse. When the INEV is below the synaptic threshold, there are two stable equilibrium points. Once the INEV is above the threshold, there are two unstable equilibrium points. This produces slow and easy to control oscillation. Increasing the drive increases the INEV, which causes the two equilibrium points to collapse into one unstable node, a limit cycle requirement [3]. Eventually complex branches appear, and additional drive stabilizes the equilibrium point. Above this point no sustained oscillation can occur. This analysis does not reveal the period of oscillation, but it can immediately inform the designer if the chosen parameters will produce an oscillating system and the nature of that oscillation.

For a number of INEVs above the synaptic threshold (a requirement for sustained oscillation), a numerical phase response analysis was conducted in which stimuli of various phases and durations were injected into one of the interneurons. When the INEV is above but very near the synaptic threshold, oscillation responds linearly to inputs. However, when INEV is larger, the cycles are more robust

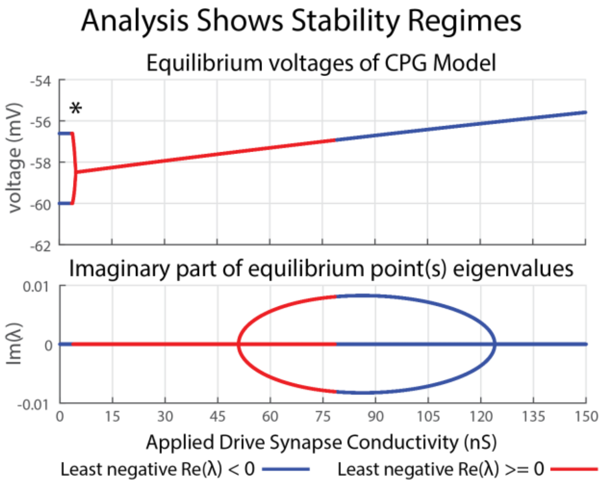

Figure 1. Plots showing the equilibrium voltages of the neurons in a CPG and their eigenvalues as the conductivity of an excitatory pathway to both half-centers is varied. This changes the INEV, resulting in a variety of eigenvalues and thus behaviors. The $*$ denotes the system configuration of the plots in Fig. 3.

This work supported by a NASA Office of the Chief Technologist's Space Technology Research Fellowship (Grant Number NNX12AN24H).

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(and thus less responsive), and the phase shift is harder to predict.

Differences in phase transitions can be readily examined when the external drive to the HC is low and the system is in a bistable configuration. When an excited interneuron is inhibited, the opposite HC is free to activate, inhibiting the other HC. Both HCs will approach their equilibria (INEV and ENEV, respectively). If the interneuron is already inhibited and further inhibition is applied, there is no direct effect; this only prevents the inhibition of the down-stream HC. Signals that prevent a motion (such as unloading a leg while the posterior is unloaded) could take advantage of this mechanism, disallowing a particular reaction but not affecting the system otherwise.

Excitatory current to the interneurons has more interesting effects. If the interneuron is inhibited, the stimulus will advance the phase linearly based on stimulus timing. If the interneuron is already excited, this will introduce more inhibition to the down-stream HC. This excitatory current causes the newly inhibited HC to approach a new equilibrium, below the freely-oscillating INEV. If suppressed for a reasonable amount of time ($t \approx \tau_h$), the Na deactivation variable rises along its nullcline, and when the stimulus is removed, a rapid post-inhibitory rebound occurs due to the positive feedback effects of the sodium activation variable and a CPG transition occurs. This transition can be observed in Fig. 2. Signals that require a new motion after a stimulus is removed (such as loss of load on a leg causing it to enter the swing phase or search for new footholds) can take advantage of this mechanism.

If the drive is increased such that the CPG can transition on its own but is still strongly affected by inputs, each stimulus produces distinct responses in the following cycle. For inhibitory currents, the second cycle after the input is unaffected. However, for excitatory currents, if the excitatory current occurs during the quiescent phase and for a long enough period, its release also triggers a secondary transition (Fig. 3).

III. MANTIS ROBOT

For our robotics work, we took advantage of sensitive CPGs. Sensitve CPGs can quickly respond to changes in environmental conditions, and can be significantly shaped by sensory input. This paradigm was used to design a controller for a robot leg that generates support when the skeleton is strained, but will make the leg "restep" if its load decreases or it becomes too large. This is a technique used by animals to maintain stability under large perturbations [4]. Properly tuned reflexes allow the hexapod robot to make the same reflexive resteps when perturbed. The analysis described in this paper directly informed the design of this controller; understanding the CPG's regime of oscillation and input response not only let sensory information shape the rhythm as necessary, but also take advantage of oscillation without sensory input. Fig. 4 shows data from the robot, and the caption describes the flow of information through the controller.

This kind of restepping reflex is similar to walking, in which decreasing leg loads and posterior leg position signal the end of the stance phase. It is already clear from our experiments that the transition to a locomotion controller may

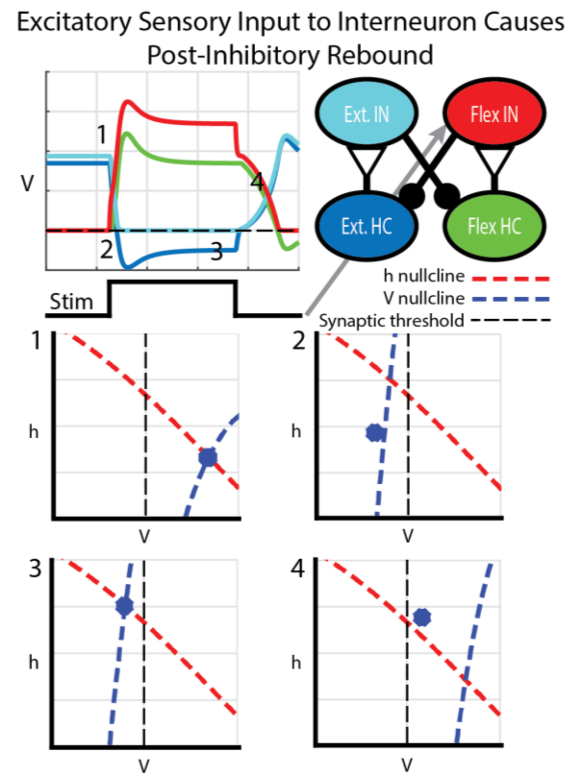
Excitatory Sensory Input to Interneuron Causes Post-Inhibitory Rebound

Figure 2. Examination of bistable CPG response to stimuli. If the Flex IN (red) is given a small excitatory stimulus, the Ext. HC's (blue) stable equilibrium point (1) will change (2). Over time, the state approaches the equilibrium point (3). When the stimulus is removed, the neuron voltage rapidly increases, and the nonlinear dynamics carry the voltage over the synaptic threshold. As the neuron crosses this threshold, it can inhibit the Flex HC (green), and the neurons establish new equilibria (4).

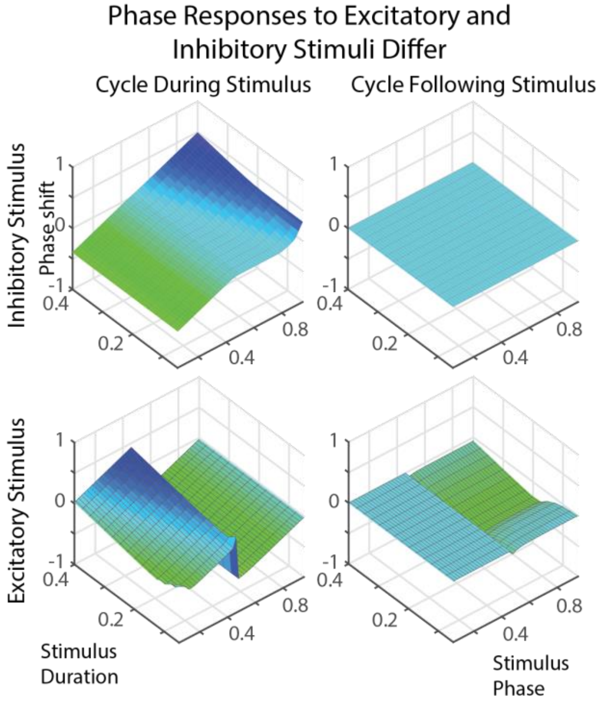
Phase Responses to Excitatory and Inhibitory Stimuli Differ

Figure 3. Plots comparing the phase response of CPGs to inhibitory and excitatory inputs. Inhibitory inputs cause no rebound, resulting in unaffected cycles following stimulus (upper right). Excitatory inputs cause rebound and a second transition, resulting in a non-uniform second cycle response (lower right). The drive corresponds to the ∗ in Fig. 1.

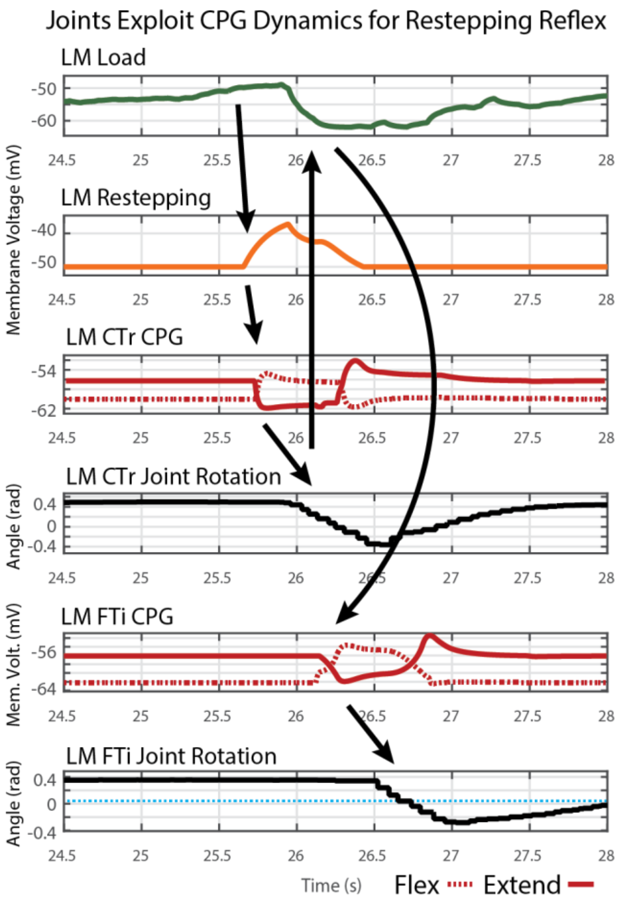

Figure. 4 Restepping reflex as recorded from robot. Load on the leg (green) causes the restepping neuron (orange) to become excited and excite CTr extension via its CPG (red). This flexes the CTr joint, lifting the leg, and reducing the strain. The reduced strain causes the FTi CPG to switch to flex (red dashed). CTr extension, caused by the decaying of the restepping signal, puts the leg back on the ground, increasing the load. Load causes the FTi to extend, supporting the body. The FTi joint is now in a more flexed position (dashed cyan), resulting in lower leg load.

be straightforward, since the adaptive reflexes implemented on the robot produce walking motions when the feet are made to slip. This sharing of reflexes among behaviors, combined with the continuous nature of the control system (Fig. 4) may make design and control more tractable than comparable finite state machine methods.

IV. RAT SIMULATION

This analysis also informed the design a CPG system for a walking rat simulation. The designed CPG is capable of oscillating without feedback and robustly produces transitions from stance to swing and back again. It can also reproduce many behaviors seen in chronic spinal and decerebrate cats.

Two transition mechanisms have been shown to be important in regulating stance to swing transitions in walking mammals [5]. The first mechanism is found in both transition from swing-to-stance and stance-to-swing. Transition from swing-to-stance is affected by hip position via either reduced firing of flexor stretch receptors, or increased firing in extensor stretch receptors. For stance-to-swing, stretching of the hip flexors in the hind leg excite Ia muscle spindles which can cause transitions. Additionally in stance-to-swing, activation of Ib (force sensitive) afferents in the Golgi tendon organ of ankle extensors can inhibit swing, however if there is a decrease in Ib activity a rapid change to swing will occur. These mechanisms reflect the two cases described earlier and are implemented as such in the simulation. Their effect on the CPG can be seen in Fig. 5.

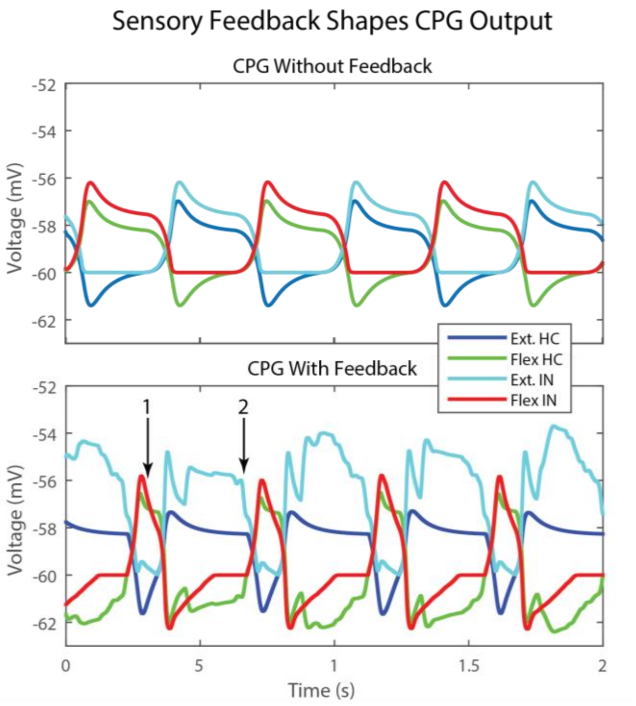

Figure 5. CPG implemented in the rat model with and without walking feedback. A) As the hip flexes, Flex IN is gradually depressed until Ext. HC is able to escape, causing a transition from swing to stance (Mechanism 1). B) Force feedback lengthens stance by exciting Ext. IN. When force is reduced, a quick transition from stance to swing occurs (Mechanism 2). Because noisy feedback acts on the inhibitory interneurons, half-center output (when the HCs are above -60 mV) is minimally affected.

In the above work, Pearson also outlines how the driving sensory influences produce different behaviors between chronic spinal cats and decerebrate cats. In spinal cats, maintained hip flexion prevents rhythmic contraction of muscles, however if the hip is free to move or maintained in the extended position, walking is not inhibited. This is in contrast to decerebrate cats where the driving influence is from inhibition due to Ib ankle extensors. The developed CPG is capable of reproducing the behaviors of both types of cats with the removal external drive to the system to mimic an effect of spinal lesions.

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