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Multivariable harmonic balance for central pattern generators☆

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ABSTRACT

The central pattern generator (CPG) is a nonlinear oscillator formed by a group of neurons, providing a fundamental control mechanism underlying rhythmic movements in animal locomotion. We consider a class of CPGs modeled by a set of interconnected identical neurons. Based on the idea of multivariable harmonic balance, we show how the oscillation profile is related to the connectivity matrix that specifies the architecture and strengths of the interconnections. Specifically, the frequency, amplitudes, and phases are essentially encoded in terms of a pair of eigenvalue and eigenvector. This basic principle is used to estimate the oscillation profile of a given CPG model. Moreover, a systematic method is proposed for designing a CPG-based nonlinear oscillator that achieves a prescribed oscillation profile.

1. Introduction

Rhythmic movements in animal locomotion are controlled by a neuronal circuit called the central pattern generator (CPG). A CPG is a group of neurons interconnected in a specific manner so that their membrane potentials autonomously oscillate with particular phase relations, generating a "pattern" to be used for muscle activation. To uncover the biological control mechanism, CPGs have been extensively studied in the neuroscience literature (Cohen, Rossignol, & Grillner, 1988; Orlovsky, Deliagina, & Grillner, 1999). Individual neurons participating rhythmic pattern generation have been identified and their connections determined from physiological experiments. The knowledge on the mechanism of CPGs thus generated has been utilized in engineering applications. For instance, the basic architectures of CPGs are exploited in robotics literature to design feedback controllers that achieve stable limit cycles with desired phase coordination properties (Crepsi, Badertscher, Guignard, & Ijspeert, 2005; Fukuoka, Kimura, & Cohen, 2003). A CPG with sensory feedback may have a potential to provide a new paradigm for nonlinear control theory and applications where the control objective is to achieve robust and adaptable oscillations.

Various theoretical analysis methods for CPGs, or nonlinear oscillators in general, have been developed in the literature, including the Poincaré–Bendixson theorem (Khalil, 1996), Hopf bifurcation theorem (Marsden & McCracken, 1976), perturbation theory and averaging (Guckenheimer & Holmes, 1983), integral quadratic constraints (Jonsson, Kao, & Megretski, 2002), and the Malkin theorem for phase coupled oscillators (Izhikevich, 2006). Most of these results are effective for analysis of dynamical systems, but not directly useful for the problem of our interest — design of (artificial) CPGs to achieve oscillations with a desired profile (frequency, amplitudes, and phases). A rigorous theoretical result has been obtained by Lohmiller and Slotine (1998) using contraction analysis for global convergence, but for a slightly different problem — design of coupled oscillators to achieve prescribed phases (Pham & Slotine, 2007).

The objective of this paper is to develop a systematic method for the analysis and synthesis of CPGs. We consider the class of CPGs modeled by a group of *identical* neuron models. The analysis problem addressed here is to determine whether there is a stable oscillatory trajectory, and if so, predict the oscillation profile. The synthesis problem is to determine appropriate neuronal connections so that the resulting circuit achieves a stable oscillation with a prescribed profile. Our main result shows that the oscillation frequency and overall amplitude are encoded in the "maximal" eigenvalue, while the relative amplitudes and phase information are embedded in the corresponding eigenvector. Thus, both analysis and synthesis of CPGs are essentially reduced to simple eigenvalue problems.

The approach we employed to arrive at these results is the multivariable harmonic balance. The harmonic balance is a classical technique that detects the presence and estimates the profile of oscillations, provided that the shape of the oscillatory signal is close to a sinusoid (Khalil, 1996; Mees, 1981). The method

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has been applied in various engineering fields, including control designs (Berns, Moiola, & Chen, 1998; Tesi, Abed, Genesio, & Wang, 1996), but these results focus on the amplitudes and frequency of oscillations. On the other hand, our focus here is the pattern generation and hence the phase is the most important property of oscillation. To our knowledge, the potential of the harmonic balance idea has not been fully explored in the context of CPG analysis and synthesis. The method is approximate in nature but numerous examples demonstrate that our method works reasonably well for CPGs.

We use the following notation. For a matrix $M \in \mathbb{C}^{n\times n}$, let $\rho(M) \in \mathbb{C}$ be the eigenvalue of M with the largest imaginary part among those eigenvalues with the largest real part. We call $\rho(M)$ the maximal eigenvalue. Let $M^\dagger$ be the Moore–Penrose inverse of M. Denote by $\mathbb{U}$ the set of vectors $u \in \mathbb{C}^n$ such that $|u_i| = 1$ for all $i = 1, \ldots, n$.

2. The CPG model and problem formulation

Let the electrical activity of a neuron be modeled by the dynamical mapping from input u to output v:

$$v = \psi(q), \quad q = f(s)u$$

where ψ is a static nonlinear function and $f(s)$ is a transfer function. The output v is either the cell membrane potential of the neuron or the spike frequency of the membrane potential. The input u is taken as the weighted sum of the output of the presynaptic neurons. The nonlinear function $\psi(q)$ captures the threshold and saturation properties. The transfer function $f(s)$ represents the linear time-invariant part of the neuronal dynamics. Typical choices for $f(s)$ include

$$f_a(s) = \frac{\omega_o}{s+\omega_o}, \qquad f_b(s) = \frac{(\omega_1+\omega_2)s}{(s+\omega_1)(s+\omega_2)}, \tag{1}$$

where $\omega_i > 0$ with $i = o, 1, 2$. The former $f_a(s)$ is a low-pass filter representing the cell membrane time constant $1/\omega_o$, and is one of the simplest and standard choices in many engineering applications of neural network (Hunt, Sbarbaro, Zbikowski, & Gawthrop, 1992). The latter $f_b(s)$ is a band-pass filter with pass band $\omega_1 < \omega < \omega_2$, capturing the adaptation property (impulse adaptation and/or synaptic fatigue) in addition to the time lag. The adaptation is known to be important in the pattern generation of certain CPGs (Futakata & Iwasaki, 2008; Iwasaki & Zheng, 2006; Matsuoka, 1985).

A CPG is a group of neurons interconnected in a specific manner to generate a desired phase pattern. Let us consider a CPG consisting of n neurons where the dynamical behavior of the ith neuron is described by

$$v_i = \psi_i(q_i), \qquad q_i = f_i(s)u_i, \qquad u_i = \sum_{j=1}^{n} \mu_{ij}(s)v_j$$

where $\mu_{ij}(s)$ is the transfer function of the synaptic connection from the jth neuron. If $\mu_{ij}(0)$ is negative/positive, then the connection is said to be inhibitory/excitatory. In the vector form, the CPG can be written

$$v = \Psi(q), \quad q = \mathcal{M}(s)\Psi(q) \tag{2}$$

$$\Psi := \mathrm{diag}(\psi_i), \qquad F(s) := \mathrm{diag}(f_i(s)), \\ \mathcal{M}(s) := F(s)M(s), \tag{3}$$

where $M(s)$ is the transfer matrix whose (i, j) entry is $\mu_{ij}(s)$. We consider the following.

Assumption 1. The CPG described by (2) and (3) consists of identical neurons with static interconnections:

$$M(s) = M, \qquad \Psi = \psi I, \\ F(s) = f(s)I, \quad f(s) = f_a(s) \text{ or } f_b(s), \tag{4}$$

where I is the $n \times n$ identity matrix, the second equation means that the ith entry of $\Psi(q)$ is $\psi(q_i)$, and $f_a(s)$ and $f_b(s)$ are defined in (1) with positive real parameters ω_o, ω_1, and ω_2. Moreover, the nonlinear function $\psi(x)$ is continuous, monotonically increasing, bounded, odd, strictly concave on $x > 0$, and has a unity slope at the origin.

We will propose a method for analyzing the general CPG model in the next section, and then apply the method to the special case under Assumption 1 in the sections that follow. The hyperbolic tangent function $\psi(x) := \tanh(x)$ satisfies the properties indicated in Assumption 1, and will be used for all numerical examples presented later.

In this paper, we will address the following:

Analysis Problem: Determine whether the CPG in (2) has an oscillatory trajectory, and if so, estimate the oscillation profile (frequency, amplitudes, phase) without actually simulating the differential equations.

Synthesis Problem: Given a desired oscillation profile, find the connectivity matrix M in (2) so that the resulting CPG achieves the profile.

Modeling Problem: Given an observed oscillation profile, find the connectivity matrix M in (2) so that the resulting CPG exhibits the profile.

The behavior of a CPG can be analyzed by simulations, but a solution to the analysis problem can be more advantageous in certain aspects. First, it could save time for analysis, especially when the CPG consists of a large number of neurons and its simulation is time consuming. More importantly, theoretical analysis would provide more insights into the pattern generation mechanism; for instance, it would uncover how the neuronal interconnection structure relates to the resulting phase relations. Such result would be useful in neuroscience for understanding the biological control mechanism. The synthesis problem is of importance for engineering applications where artificial CPGs are used to control robotic locomotion systems, whereas the modeling problem is important in neuroscience to understand the neuronal mechanism for generating a particular oscillation pattern. The synthesis and modeling problems are mathematically equivalent and hence we discuss the former only.

3. General framework

In this section, we consider the class of systems described by a feedback connection of general transfer function $\mathcal{M}(s)$ and nonlinear function Ψ as in (2). Throughout this section, $\mathcal{M}(s)$ is an arbitrary stable transfer function matrix of dimension $n \times n$ unless otherwise noted, and Ψ is a diagonal nonlinearity with ψ_i on the ith diagonal, where ψ_i satisfies the properties imposed on ψ in Assumption 1. We will first discuss a method for estimating the profile of oscillation, assuming existence of a periodic orbit. We will then provide a condition for the existence of an oscillatory trajectory.

3.1. Multivariable harmonic balance

We shall develop a multivariable harmonic balance (MHB) equation to characterize the profile of oscillation for (2). The