Physica D 239 (2010) 905–911

Contents lists available at ScienceDirect

Physica D

journal homepage: www.elsevier.com/locate/physd

A canonical model for gradient frequency neural networks

Edward W. Large *, Felix V. Almonte, Marc J. Velasco

Center for Complex Systems and Brain Sciences, Florida Atlantic University, 777 Glades Road, Boca Raton, FL 33431-6424, USA

ARTICLE INFO

Article history:
Received 30 October 2008
Received in revised form
7 October 2009
Accepted 4 November 2009
Available online 18 January 2010
Communicated by S. Coombes

Keywords:
Auditory system
Neural oscillation
Canonical model
Network dynamics
Nonlinear resonance

ABSTRACT

We derive a canonical model for *gradient frequency neural networks* (GFNNs) capable of processing time-varying external stimuli. First, we employ normal form theory to derive a fully expanded model of neural oscillation. Next, we generalize from the single oscillator model to heterogeneous frequency networks with an external input. Finally, we define the GFNN and illustrate nonlinear time-frequency transformation of a time-varying external stimulus. This model facilitates the study of nonlinear time-frequency transformation, a topic of critical importance in auditory signal processing.

1. Introduction

Most existing work on neural oscillator networks focuses on the intrinsic dynamics of networks with a homogeneous distribution of oscillator frequencies. The truncated normal form (see, e.g., [1–3]) provides a suitable canonical model for the study of network dynamics in such cases (e.g., [4,5]) because it includes all resonant terms necessary to understand the interactions of oscillators with equal (or ϵ-close) frequencies. We wish to study heterogeneous frequency oscillator networks that process external stimuli because this topic is of critical relevance to understanding auditory processing. A growing body of evidence suggests that the auditory nervous system is highly nonlinear, and that nonlinear transformations of auditory stimuli have important functional consequences [6–10]. Thus, findings and interpretations about the dynamics of heterogeneous networks may have relevance for cochlear modeling [11–14] and brainstem physiology [9,15,10], as well as pitch and music perception [16–18].

Our goal is to develop a model of neural oscillation that facilitates investigations of the nonlinearities that underlie auditory physiology and perception. Our approach involves specifying an appropriate class of oscillators and transforming it to a generic form, known as a *normal form*, via *normal form theory* [3,19,20,2,1]. Normal forms are important analytical tools in the local analysis of dynamical systems in the neighborhood of elementary solutions such as equilibria and periodic orbits. The principal goal of normal form theory is to obtain local coordinates in terms of which a dynamical system near an elementary solution has a "simplest" form or canonical representation which, in turn, can facilitate its analysis. The structures of the normal forms we consider are in terms of "resonances" (e.g., [19,20,1]).

An important issue that arises when considering the external stimulation of an oscillator network is that the structure of the input to any given oscillator is not known in advance. Moreover, at any given time, the stimulus may contain a combination of external and internal (within the network) signals. The key to our approach to obtaining a canonical model is to fully expand the nonlinearities and the resonant terms of the normal form for each oscillator based on its *natural frequency*. Any frequencies in the stimulus that "resonate" with the natural frequency will have significant effects on the canonical oscillator's dynamics. This approach leads us to consider external stimulation at the level of the canonical model instead of at the level of the original class of oscillators, simplifying the analytical nature of the resulting model. In what follows, we define *gradient-frequency neural networks* (GFNN's) and derive a canonical GFNN. We compare the nonlinear time-frequency transformation of an acoustic stimulus by a GFNN based on Wilson–Cowan oscillators and a GFNN based on our canonical model.

2. A truncated canonical model for neural oscillator networks

Consider the general system of coupled neural oscillators modeled by the network equations:

$$\begin{aligned} \dot{u}_i &= f_i(u_i, v_i, \lambda) + \epsilon p_i(u_1, v_1, \ldots, u_n, v_n, \epsilon) \\ \dot{v}_i &= g_i(u_i, v_i, \lambda) + \epsilon q_i(u_1, v_1, \ldots, u_n, v_n, \epsilon). \end{aligned} \quad (1)$$

* Corresponding author. Tel.: +561 2970106; fax: +561 2973634.
E-mail addresses: large@ccs.fau.edu (E.W. Large), almonte@ccs.fau.edu (F.V. Almonte), velasco@ccs.fau.edu (M.J. Velasco).

0167-2789/$ – see front matter © 2010 Elsevier B.V. All rights reserved.
doi:10.1016/j.physd.2009.11.015

In Eq. (1), $\{u_i, v_i\} \subset \mathbb{R}$ represent the coordinates of the state of the ith oscillator. λ represents the set of parameters of the functions f_i and g_i. $\epsilon > 0$ is a connectivity parameter.

Appendix A, briefly reviews one of the standard procedures for obtaining normal forms and clarifies the relationship between a normal form and a canonical model. As discussed in Appendix A, the classical analysis leading to a normal form for Eq. (1) involves a coordinate transformation, dependent on the Jacobian matrix of the system, and an expansion of the nonlinearities. For the class of neural oscillators represented by Eq. (1), normal form theory (see [1,5,2,21,3,22]) leads to a generic form (Eq. (2)) in a new complex valued state variable, z, resulting from the coordinate transformation.

$$\dot{z}_i = z_i(a_i + b_i|z_i|^2) + x_i(t) + h.o.t., \quad i \in \{1, \dots, n \in \mathbb{Z}^+\}$$

where

$$x_i(t) = \sum_{j \neq i}^{n} c_{ij} z_j, \quad \{a_i, b_i, c_{ij}, z_i\} \subset \mathbb{C}. \tag{2}$$

Eq. (2) is also a canonical model representing the local dynamics about an Andronov–Hopf bifurcation for the entire class of neural oscillators given by Eq. (1). It has complex-valued parameters a_i and b_i which can be related, via the coordinate transformation (see [1,5]), to the parameters of the original system (Eq. (1)). In standard complex form, $a_i = \alpha_i + \imath\omega_i$, where ω_i is the *natural frequency* or *eigenfrequency* of the ith oscillator, and $b_i = \beta_i + \imath\delta_i$. The complex coefficients c_{ij} represent the coupling strengths among the oscillators. Note that $x_i(t)$ represents the total combination of input to the ith oscillator, including all coupled inputs from other oscillators. The system given by Eq. (2) is an appropriate model for the study of a system such as Eq. (1) near one of its bifurcation points, e.g., at an Andronov–Hopf bifurcation, where each oscillator will have a specific frequency. Normal form models, with the addition of an external stimulus, i.e., $x_i(t) = s(t) + c_{ij}z_j$, have been proposed to capture some functionally important nonlinearities of the mammalian cochlea [23,13].

Eq. (2) is referred to as a *truncated normal form* because the expansion of the nonlinearities (Eq. (1)) is truncated, effectively ignoring the higher order terms, $h.o.t.$ It is important to realize, however, that any interactions between oscillators of different frequencies in Eq. (1) would be captured in the higher order terms of Eq. (2). But if it is assumed that all oscillators in the network have frequencies that are ϵ-close (see, e.g., [1] Thm. 5.8 Pg. 165), then the higher order terms have a negligible effect on the dynamics of the system, and there is a canonical model given by Eq. (3).

$$\dot{z}_i = z_i(a_i + b_i|z_i|^2) + \sum_{j \neq i}^{n} c_{ij} z_j + \mathcal{O}(\sqrt{\epsilon}), \quad i \in \{1, \dots, n \in \mathbb{Z}^+\}. \tag{3}$$

The behavior of the canonical system Eq. (3) can be further understood by transforming it to polar coordinates (Eq. (4)) by expressing z_i in terms of its amplitude r_i and phase ϕ_i: $z_i(t) = r_i(t)e^{\imath\phi_i(t)}$. The coupled input $x_i(t) = \sum_{j \neq i}^{n} c_{ij}z_j$ can be represented in polar form as well, say, by $F_i(t)e^{\imath\theta_i(t)}$ where F_i and θ_i represent the amplitude and phase, respectively. This polar representation of the model allows for the independent study of amplitude and phase dynamics, and makes the meaning of the parameters explicit.

$$\begin{aligned} \dot{r}_i &= r_i(\alpha_i + \beta_i r_i^2) + F_i \cos(\phi_i - \theta_i) + \mathcal{O}(\sqrt{\epsilon}) \\ \dot{\phi}_i &= \omega_i + \delta_i r_i^2 - \frac{F_i}{r_i} \sin(\phi_i - \theta_i) + \mathcal{O}(\sqrt{\epsilon}). \end{aligned} \tag{4}$$

2.1. Neural oscillator network with input

Because of their theoretical and practical importance, we want to study nonlinear oscillator networks under the influence of complex acoustic stimuli. When external input $(\rho_{u_i}(t), \rho_{v_i}(t)) \in \mathbb{R}^2$ is specified in the original system as shown in Eq. (5) then the transformative procedure employed to obtain the normal form also transforms the external input.

$$\begin{aligned} \dot{u}_i &= f_i(u_i, v_i, \lambda) + \epsilon p_i(u_1, v_1, \dots, u_n, v_n, \rho_{u_i}(t), \epsilon) \\ \dot{v}_i &= g_i(u_i, v_i, \lambda) + \epsilon q_i(u_1, v_1, \dots, u_n, v_n, \rho_{v_i}(t), \epsilon). \end{aligned} \tag{5}$$

This transformation leads to significant complexities in deriving a canonical model. For example, the expressions representing coupling coefficients can involve limits of integrals that are not necessarily convergent, or other complex expressions ([1] Thm. 5.10 p. 176). Moreover, if the input is resonant with the oscillators' natural frequencies, the canonical model may be difficult or impossible to derive. Due to such complexities, known methods for deriving canonical models cannot be applied.

Here we consider a different approach, taking into account the fact that canonical models are generic models for a system's local dynamics about one of its attractors. In this paradigm, the canonical model for a system without external input is considered as the fundamental model representing the intrinsic dynamics of a system. This essentially models a system at one of its behavioral modes. The generic mode of the system and its resonant behavior to input is precisely the case we are interested in as it corresponds to important physical situations (e.g., [5,13]). Thus, Eq. (2) becomes the fundamental model of interest, and additive external input $s(t) \in \mathbb{C}$ to oscillator z_i can be included in the coupling term $x_i(t)$ as follows.

$$x_i(t) = s(t) + \sum_{j \neq i}^{n} c_{ij} z_j. \tag{6}$$

Next, we consider the case in which a network of neural oscillators can have different natural frequencies, perhaps spanning several orders of magnitude. In this case, intrinsic oscillator frequencies do not need to be ϵ-close. Such freedom makes the analysis of such systems more difficult, but the dynamics are more interesting in terms of new behaviors. We then consider an external input whose frequency content is not known a priori. We fully expand the nonlinearities and resonances contained in the higher order terms $h.o.t.$ of Eq. (2), to incorporate the responses to an input of unknown frequency. We then compare the response of the canonical model to the input with that of a particular neural oscillator model.

3. A fully expanded canonical model for a single neural oscillator with an input

In this section we derive a fully expanded canonical model corresponding to the dynamical system Eq. (1) by continuing the expansion of higher order terms ($h.o.t.$) of the normal form near an Andronov–Hopf bifurcation. Higher order terms of the normal form are necessary to capture the response of an oscillator to an input that is not close to its natural frequency. We employ the linear relationship, or *resonance*, given by Eq. (A.2) in terms of the system's eigenvalues. Note that near the Andronov–Hopf bifurcation, the canonical oscillator frequencies $\{\omega_1, \dots, \omega_n\}$ are absolute values of the eigenvalues of the system represented by Eq. (1) (see [1,5]). In this case, the resonance relationship becomes:

$$\begin{aligned} &\omega_{res} = n_1\omega_1 + \cdots + n_m\omega_n \\ &\text{where } \{m, n\} \subset \mathbb{Z}^+, \quad res \in \{n_1, \dots, n_m\} \subset \mathbb{Z}^+. \end{aligned} \tag{7}$$

This relationship leads to *resonant monomials*, which correspond to resonances among the eigenvalues of the original system that cannot be eliminated from the normal form [1]. Resonant monomials capture harmonics, subharmonics, and higher order combinations of the input frequencies. For example, we can expand the normal form for a pair of canonical oscillators having frequencies related by an integer ratio, in terms of resonant monomials (see Appendix A). If the pair of oscillators has frequencies satisfying the resonant relationship $\omega_1 = 2\omega_2$, then we have

$$\begin{aligned}\dot{z}_1 &= z_1(a_1 + b_1|z_1|^2) + \sqrt{\epsilon}c_{12}z_2^2 + O(\epsilon)\\ \dot{z}_2 &= z_2(a_2 + b_2|z_2|^2) + \sqrt{\epsilon}c_{21}z_1\bar{z}_2 + O(\epsilon)\end{aligned} \tag{8}$$

and for a pair of oscillators with resonance $\omega_1 = 3\omega_2$,

$$\begin{aligned}\dot{z}_1 &= z_1(a_1 + b_1|z_1|^2 + \epsilon d_1|z_1|^4) + \epsilon c_{12}z_2^3 + O(\epsilon\sqrt{\epsilon})\\ \dot{z}_2 &= z_2(a_2 + b_2|z_2|^2 + \epsilon d_2|z_2|^4) + \epsilon c_{21}z_1\bar{z}_2^2 + O(\epsilon\sqrt{\epsilon}).\end{aligned} \tag{9}$$

The above analysis can be carried out for pairs of canonical oscillators with any resonant relationship between their natural frequencies.[1] The normal form analysis retains only the resonant monomials by which z_2 will have an effect on the dynamics of z_1 and vice versa, and eliminates all non-resonant higher-order terms.

Now consider the canonical oscillators, $z \in \mathbb{C}$ and $x \in \mathbb{C}$, where the frequency of z is known but the frequency of x is unknown. In this case the above approach is not possible, because we do not know the relationship among the eigenvalues, therefore we do not know which monomials to retain and which can be eliminated. However if we retain all monomials, by including the full expansions of all nonlinearities stemming from normal form analysis (e.g., see [1–3]), then x will have the appropriate effect on the dynamics of z – regardless of its frequency content – in the resulting model.

This leads to an *expanded canonical oscillator model* (e.g., Eq. (10)) for the nonlinear neural oscillator z under the influence of input x. In the expanded model, the resonant terms (RT) include all monomials obtained via the relation Eq. (A.2), given by the *Poincaré–Dulac theorem* (see Appendix A). Including all monomials in RT allows the model to respond appropriately to an external stimulus, regardless of frequency, because only the monomials that are resonant with the stimulus will have a significant effect on the oscillator's dynamics in the long term.

$$\begin{aligned}\dot{z} &= z(a + b_1|z|^2 + b_2\epsilon|z|^4 + b_3\epsilon^2|z|^6\\ &\quad + b_4\epsilon^3|z|^8 + \cdots) + RT.\end{aligned} \tag{10}$$

We can now define a network of n expanded canonical oscillators z_i, with an input $x_i(t)$ for each oscillator z_i, $i = 1, \ldots, n$ as a function of an external stimulus $s(t) \in \mathbb{C}$. The interaction between the network oscillators may also be incorporated through the input, with the definition of an appropriate RT. In other words,

$$x_i(t) = s(t) + \sum_{j\neq i}^{n} c_{ij}z_j. \tag{11}$$

It is possible to derive a general expansion of RT that captures the responses to a complex-valued, multi-frequency input. In this article, we consider a somewhat simpler expansion of RT for a real-valued, sinusoidal external stimulus of unknown frequency.

$$\begin{aligned}RT &= x + \sqrt{\epsilon}x\bar{z} + \epsilon x\bar{z}^2 + \epsilon\sqrt{\epsilon}x\bar{z}^3 + \cdots\\ &\quad + \sqrt{\epsilon}x^2 + \epsilon x^2\bar{z} + \epsilon\sqrt{\epsilon}x^2\bar{z}^2 + \epsilon^2x^2\bar{z}^3 + \cdots\\ &\quad + \epsilon x^3 + \epsilon\sqrt{\epsilon}x^3\bar{z} + \epsilon^2x^3\bar{z}^2 + \epsilon^2\sqrt{\epsilon}x^3\bar{z}^3 + \cdots\\ &\quad + \epsilon\sqrt{\epsilon}x^4 + \epsilon^2x^4\bar{z} + \epsilon^2\sqrt{\epsilon}x^4\bar{z}^2 + \epsilon^3x^4\bar{z}^3 + \cdots\\ &= (x + \sqrt{\epsilon}x^2 + \epsilon x^3 + \epsilon\sqrt{\epsilon}x^4 + \cdots)\\ &\quad \times (1 + \sqrt{\epsilon}\bar{z} + \epsilon\bar{z}^2 + \epsilon\sqrt{\epsilon}\bar{z}^3 + \cdots).\end{aligned} \tag{12}$$

[1] Note that as we expand the higher order terms, we also expand the compressive nonlinearities corresponding to the functions f_i and g_i in Eq. (1) (e.g., the sigmoid function S in Eq. (18), Section 4).

Given this definition of RT, we do not need to know whether the input frequency is resonant with the eigenfrequency of any specific oscillator because only those monomials that are resonant with the eigenfrequency of z_i will affect its behavior in the long term.

Eqs. (10) and (12) both contain infinite geometric series that converge when $|z| < 1/\sqrt{\epsilon}$ and $|x| < 1/\sqrt{\epsilon}$. Thus, the choice of ϵ constrains both the magnitude of the input and the magnitude of the oscillation. Moreover, under certain conditions on the coefficients of the full expansion in Eq. (10), the oscillatory dynamics will follow well known cases. For instance, if $b_1 = b$ and $b_k = d$, $k \in \{2, 3, 4, 5, \ldots\}$ then Andronov–Hopf and Bautin (a.k.a. generalized Hopf) bifurcations are possible [2,24,19,20]. In both cases the dynamics is oscillatory, which is the regime of interest since we are concerned with modeling neural oscillators.[2] Using these ideas, we focus on writing a closed form expression for Eq. (10) which can exhibit Andronov–Hopf and generalized Andronov–Hopf bifurcations. First, rewrite Eq. (10) as:

$$\dot{z} = z(a + b|z|^2) + dz(\epsilon|z|^4 + \epsilon^2|z|^6 + \epsilon^3|z|^8 + \cdots) + RT. \tag{13}$$

Notice the convergence of the geometric series obtained from the nonlinear terms:

$$\begin{aligned}&\epsilon|z|^4 + \epsilon^2|z|^6 + \epsilon^3|z|^8 + \cdots = \epsilon|z|^4(1 + \epsilon|z|^2 + \epsilon^2|z|^4 + \cdots)\\ &\quad = \epsilon|z|^4\sum_{k=0}^{\infty}(\epsilon|z|^2)^k = \frac{\epsilon|z|^4}{1-\epsilon|z|^2},\\ &\quad |\epsilon|z|^2| < 1 \Longrightarrow |z| < \sqrt{1/\epsilon}.\end{aligned}$$

Next, we simplify RT by factoring x from the first series and writing the two resulting series as geometric series which converge when $|\sqrt{\epsilon}x| < 1$ and $|\sqrt{\epsilon}\bar{z}| < 1$. The restriction on the amplitude of x emphasizes that the input to the oscillator cannot be arbitrarily large, it is constrained by ϵ as is the amplitude of z.

$$\begin{aligned}RT &= x\sum_{k=0}^{\infty}(\sqrt{\epsilon}x)^k\sum_{k=0}^{\infty}(\sqrt{\epsilon}\bar{z})^k = \frac{x}{1-\sqrt{\epsilon}x}\cdot\frac{1}{1-\sqrt{\epsilon}\bar{z}}\\ |x| &< \sqrt{1/\epsilon}, \quad |z| < \sqrt{1/\epsilon}.\end{aligned} \tag{14}$$

Combining these results we can write a closed form equation for the *canonical neural oscillator with an input* (Eq. (10))[3] as:

$$\begin{aligned}\dot{z} &= z\left(a + b|z|^2 + \frac{d\epsilon|z|^4}{1-\epsilon|z|^2}\right) + \frac{x}{1-\sqrt{\epsilon}x}\cdot\frac{1}{1-\sqrt{\epsilon}\bar{z}}\\ |x| &< \sqrt{1/\epsilon}, \quad |z| < \sqrt{1/\epsilon}.\end{aligned} \tag{15}$$

Note that if we apply normal form analysis to a network of two oscillators of the kind defined by Eq. (15), with a known frequency relationship, we can obtain normal forms such as Eqs. (8) and (9).

We can write Eq. (15) in polar form by using polar representations for x and z.

$$x = Fe^{\imath\theta}, \qquad z = re^{\imath\phi} \Longrightarrow \bar{z} = re^{-\imath\phi}, \qquad \dot{z} = e^{\imath\phi}\left(\dot{r} + \imath r\dot{\phi}\right).$$

Also let:

$$\begin{aligned}&a = \alpha + \imath\omega, \qquad b = \beta_1 + \imath\delta_1,\\ &d = \beta_2 + \imath\delta_2, \qquad \{\alpha, \omega, \beta_1, \beta_2, \delta_1, \delta_2, F, r, \theta, \phi\} \subset \mathbb{R}.\end{aligned}$$

By substituting into Eq. (15), using *Euler's formula*

$$re^{\imath\theta} = r(\cos(\theta) + \imath\sin(\theta)),$$

[2] Clearly, there are other relationships among the coefficients b_k of Eq. (10) for which we can obtain closed form expressions, as well as those that do not lead to closed form expressions. One such generalization is explored in Appendix B.

[3] Eq. (B.4) in Appendix B is a generalization of Eq. (15).

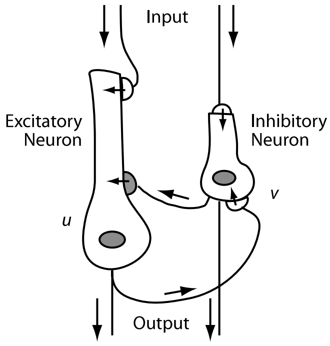

Fig. 1. *Schematic of a neural oscillator:* The variables u and v represent the dynamics of coupled excitatory and inhibitory neuron populations. The various arrows illustrate the input, output, excitatory, and inhibitory flows of information. Adapted from [1].

and equating real and imaginary parts of the left and right hand sides of the equation we obtain the phase and amplitude equations (Eqs. (16) and (17)) of the canonical neural oscillator with a natural frequency ω and an input x. This completes our goal of obtaining a fully expanded canonical model of a neural oscillator with an input which we use in the next section to construct a GFNN.

$$\begin{aligned}\dot{r} &= r\left(\alpha + \beta_1 r^2 + \frac{\beta_2 \epsilon r^4}{1-\epsilon r^2}\right) \\ &\quad + \frac{F(\epsilon F r + \cos(\phi - \theta)) - \sqrt{\epsilon}(F\cos\phi + r\cos\theta)}{(1+\epsilon F^2 - 2F\sqrt{\epsilon}\cos\theta)(1+\epsilon r^2 - 2r\sqrt{\epsilon}\cos\phi)}\end{aligned} \tag{16}$$

$$\begin{aligned}\dot{\phi} &= \omega + \delta_1 r^2 + \frac{\delta_2 \epsilon r^4}{1-\epsilon r^2} \\ &\quad + \frac{F(\sin(\theta - \phi) + \sqrt{\epsilon}(F\sin\phi - r\sin\theta))}{(1+\epsilon F^2 - 2F\sqrt{\epsilon}\cos\theta)(1+\epsilon r^2 - 2r\sqrt{\epsilon}\cos\phi)r}.\end{aligned} \tag{17}$$

4. Gradient frequency networks of neural oscillators

In this section, we consider a model of nonlinear signal processing based on 1-dimensional networks of nonlinear oscillators, tuned to different natural frequencies. Such networks are conceptually similar to banks of band-pass filters, except that the resonating units are nonlinear rather than linear. The frequencies of the oscillators in the network are chosen based on human auditory physiology, and the oscillators are organized by their natural frequency, from the lowest to the highest, and stimulated with a time-varying acoustic signal. We refer to this type of network as a *gradient frequency neural oscillator network*, or GFNN for short. GFNNs have relevance to theories of active cochlear responses [12,13], central auditory physiology [25], and pitch perception [16].

One model for *neural oscillation* is the Wilson–Cowan [26] system, describing the dynamics of excitatory (u) and inhibitory (v) neural populations as illustrated in Fig. 1. We can write the equation for a single Wilson–Cowan oscillator responding to an external input as follows:

$$\begin{aligned}\dot{u} &= -u + S(\rho_u + au - bv + s(t)) \\ \dot{v} &= -v + S(\rho_v + cu - dv).\end{aligned} \tag{18}$$

In Eq. (18), $\{a, b, c, d, u, v, \rho_u, \rho_v\} \subset \mathbb{R}$, S is a sigmoid function, e.g., $S(y) = \frac{1}{1+e^{-y}}$, $S(-\infty) = 0$, $S(\infty) = 1$, and ρ_u, ρ_v are bifurcation parameters. $s(t)$ represents an external input, which in this example is real valued and affects only the excitatory population. The Wilson–Cowan system given by Eq. (18) with $s(t) = 0$ is an instance of the class of systems represented by Eq. (1), whereas with $s(t) \neq 0$ it is an instance of Eq. (19).

We can define a GFNN with an external input (Eq. (19)) as a collection of n Wilson–Cowan oscillators with differing frequencies $\omega_i = 2\pi/\tau_i$, $i = 1, \ldots, n$ forming a gradient whose order satisfies $\omega_1 \leqslant \omega_2 \leqslant \cdots \leqslant \omega_n$. For this example, the other parameters were set to: $a = 10$, $b = 10$, $c = 8.6095$, $d = -1.1429$, $\rho_u = -2.3486$, $\rho_v = -4.2411$, $\epsilon = 0.4$.

$$\begin{aligned}\tau_i \dot{u}_i &= f_i(u_i, v_i, \lambda) + \epsilon p_i(u_1, v_1, \ldots, u_n, v_n, s(t), \epsilon) \\ \tau_i \dot{v}_i &= g_i(u_i, v_i, \lambda) + \epsilon q_i(u_1, v_1, \ldots, u_n, v_n, \epsilon).\end{aligned} \tag{19}$$

We then specify a corresponding *canonical* GFNN (Eq. (20)) as a collection of n canonical oscillators with frequencies, $\omega_i = 2\pi/\tau_i$, $i = 1, \ldots, n$, corresponding to those of Eq. (19).

$$\begin{aligned}&\tau_i \dot{z}_i = z_i\left(a_i + b_i|z_i|^2 + \frac{d_i \epsilon |z_i|^4}{1-\epsilon|z_i|^2}\right) + \frac{x_i}{1-\sqrt{\epsilon}x_i} \cdot \frac{1}{1-\sqrt{\epsilon}\bar{z}_i} \\ &x_i(t) = s(t), \quad |x_i| < \sqrt{1/\epsilon}, \quad |z_i| < \sqrt{1/\epsilon}.\end{aligned} \tag{20}$$

Near the Andronov–Hopf bifurcation, we expect the two networks to respond similarly to an external stimulus. This is illustrated in Fig. 2 which compares the dynamics of a Wilson–Cowan GFNN (using Eq. (18)) to the corresponding canonical GFNN (Eq. (20)).

In this simulation, the network parameters are set such that each oscillator is close to the Andronov–Hopf bifurcation and such that the oscillators will relax to their respective fixed points if the total input they receive is not sufficient to drive them into the oscillatory critical regime [12]. Both networks respond to a high-amplitude sinusoidal stimulus $s(t) = F\sin(2\pi t)$, $F = 0.30$ which is fed to all oscillators in both networks. The complex valued parameters of Eq. (20) were specified as follows where ω_i is the natural frequency of the ith oscillator:

$$\begin{aligned}&a_i = \alpha_i + \imath\omega_i, \qquad b_i = \beta_{1_i} + \imath\delta_{1_i}, \\ &d_i = \beta_{2_i} + \imath\delta_{2_i}, \qquad 0.125 \leqslant \tau_i \leqslant 8 \\ &\{\alpha_i, \omega_i, \beta_{1_i}, \beta_{2_i}, \delta_{1_i}, \delta_{2_i}\} \subset \mathbb{R}\end{aligned}$$

and were set to:

$$a_i = 0 + \imath 2\pi, \qquad b_i = -10 + \imath(-9), \qquad d_i = -10 + \imath(-9).$$

Fig. 2 illustrates that the Wilson–Cowan GFNN and its corresponding canonical GFNN have qualitatively similar dynamics in response to a sinusoidal input. In this simulation there was no internal coupling (i.e., $c_{ij} = 0$) among the network's oscillators; this focuses the response of the networks to the external input. Both networks respond not only at the stimulus frequency, but also at harmonics (2:1, 3:1) and subharmonics (1:2) of this frequency. The frequency response of the two models is highly correlated ($r^2 = 0.946$). We have also observed similar responses in the two networks to other types of external stimuli, and ongoing work is considering the responses to external stimuli and connectivity in detail. In future work, we plan to study the canonical GFNN as a generic system for nonlinear time-frequency transformation.

5. Conclusion

We have derived a canonical model (Eqs. (15)–(17) and (B.4)) of neural oscillation for heterogenous frequency neural networks with an external input. Our approach treats canonical models as being fundamental and proceeds from that level. Within the appropriate constraints the canonical model dynamics is expected to be topologically equivalent to the local dynamics of the original neural network. Formal proof of this theoretical hypothesis is left for future work. However, we demonstrated that a gradient-frequency neural oscillator network and a corresponding canonical GFNN yielded qualitatively similar dynamics in a numerical simulation with an external stimulus. A comprehensive analysis

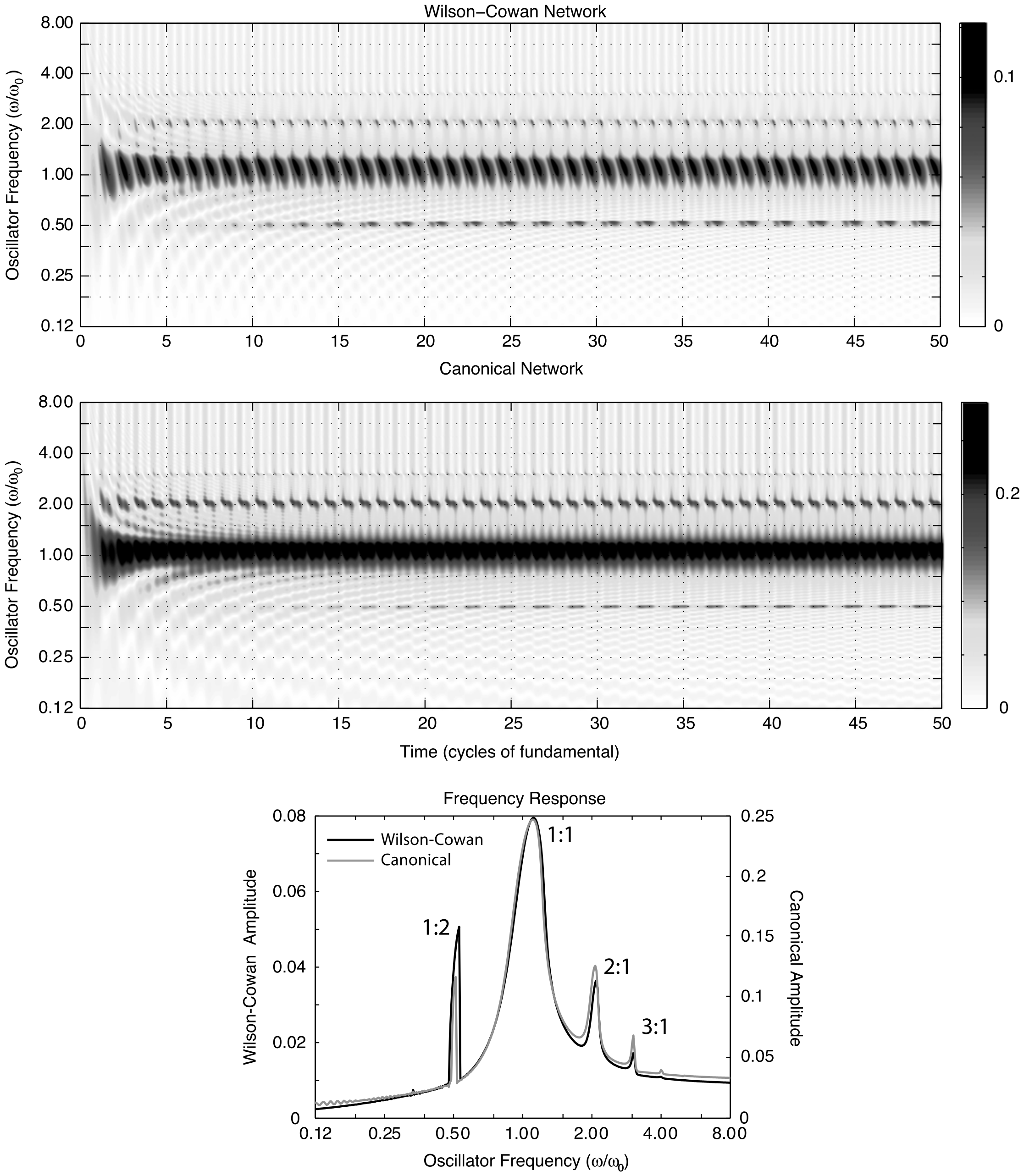

Fig. 2. *Time frequency transformation by a GFNN:* Dynamics of a Wilson–Cowan GFNN and a corresponding canonical GFNN under the influence of a sinusoidal input. Each network consists of 360 oscillators arrayed along a logarithmic frequency gradient of 6 octaves with 60 oscillators per octave. The external input $s(t) = F\sin(\omega_0 t)$, $i = 1, \ldots, 360$, $F = 0.30$, $\omega_0 = 2\pi$ is the same for all oscillators in both networks. The top panels show oscillator amplitude (gray level) as a function of time and frequency for the Wilson–Cowan and canonical models, respectively. Oscillations arise at frequencies that are not present in the stimulus, due to the nonlinear coupling, captured in the higher order monomials of RT. The strongest response is found at the stimulus frequency, but oscillations are also observed at harmonics (e.g., 2:1 and 3:1) and subharmonics (e.g., 1:2) of the stimulus frequency. The bottom panel compares the response amplitude (averaged over the last 5 stimulus cycles) for the Wilson–Cowan model (black line) and the canonical model (gray line). The average amplitudes are highly correlated ($r^2 = 0.946$).

of canonical GFNNs under the influence of external stimulation is currently underway. We are studying the construction of resonant terms and the effect of the connectivity structures (e.g., diffusive nearest neighbor interaction) on system dynamics. We expect fully expanded canonical models to play an important role in our developing understanding of auditory system's function, including nonlinear and multifrequency interactions in the cochlea and central auditory nervous system. Experimental evidence suggests that the auditory system performs nonlinear time-frequency transformations of acoustic stimuli. Because such canonical models enable the study of generic properties of nonlinear time-frequency transformation, they are of potential significance in the study of auditory physiology and psychophysics.

Acknowledgement

Supported by the US Air Force: AFOSR Grant FA9550-07-C0095.

Appendix A. Normal forms and canonical models

Here we briefly consider the well established *Poincaré–Dulac* normal form theory (see, e.g., [1,19,27]) which can be used to reduce a class of dynamical systems to a *normal form* which is a simplified form for the local dynamics of the original system near one of its attractors (see, e.g., [1,3,28,29,2,22,30–36]). The reduction is typically accomplished via a *near identity change of* *variables* of a set of equations representing a class of dynamical systems. To this end, let the system described by Eq. (A.1) be a *smooth dynamical system*.

$$\dot{\mathbf{x}} = F(\mathbf{x}) = A\mathbf{x} + N(\mathbf{x}), \quad \mathbf{x} = (x_1, \ldots, x_m) \in \mathbb{R}^m. \tag{A.1}$$

Assume without loss of generality that Eq. (A.1) has $\mathbf{x} = 0$ as a fixed point, i.e., $F(\mathbf{x} = 0) = 0$. A is the Jacobian matrix of the system evaluated at $\mathbf{x} = 0$, i.e., $A = D_{\mathbf{x}}F$ (where $D =$ the Differentiation Operator) with the corresponding eigenvalues $\lambda_1, \ldots, \lambda_m$ and eigenvectors $v_i \in \mathbb{R}^m, i = 1, \ldots, m$. The vector function $N(\mathbf{x}) = F(\mathbf{x}) - A\mathbf{x}$ represents the nonlinear terms of $F(\mathbf{x})$. For the sake of simplicity and without loss of generality, assume that A is in *Jordan Normal Form*. Then, each polynomial relationship of the form

$$\lambda_i = n_1\lambda_1 + \cdots + n_m\lambda_m; \quad i = 1, \ldots, m; \quad \{n_1, \ldots, n_m\} \subset \mathbb{Z}^+ \tag{A.2}$$

such that

$$\sum n_k \geqslant 2, \quad k \in \{1, \ldots, m\}$$

is said to be a **resonance** or resonant relationship of the system (Eq. (A.1)) in terms of the eigenvalues of A. Each resonance has an associated **resonant monomial** of the form $v_i X_1^{n_1} \ldots X_m^{n_m}$. By the *Poincaré–Dulac theorem* Eq. (A.1) can be reduced to a simpler form (Eq. (A.3))

$$\dot{\mathbf{y}} = A\mathbf{y} + \mathscr{P}(\mathbf{y}) \tag{A.3}$$

via the near identity change of variables:

$$\mathbf{x} = \mathbf{y} + P(\mathbf{y}), \qquad P(\mathbf{y}) = 0, \qquad D_{\mathbf{y}}P(0) = 0$$

where P is a vector function of formal power series without constant and linear terms satisfying the *Poisson* (*or Lie*) *bracket operation* [3,37,1,2] $[A\mathbf{y}, P] = (D_{\mathbf{y}}(A\mathbf{y}))P - (D_{\mathbf{y}}P)(A\mathbf{y})$. $\mathscr{P}$ is a nonlinear homogeneous polynomial vector function in the variables $X_1, \ldots, X_m$ consisting only of resonant monomials of some fixed degree k. The system represented by Eq. (A.3) is called a **normal form** of the system represented by Eq. (A.1). More generally, Eq. (A.3) is simply called a **normal form** when the nonlinear portion of $\mathscr{P}$ lies in the complement of the Poisson/Lie bracket operation of a sum of nonlinear monomials H related to the Jacobian matrix A, i.e., $\mathscr{P}(\mathbf{y}) \bigcap [A, H] = \{0\}$ ([1], pp. 122–124).

The concept of a *canonical model* is independent from that of a normal form. However, normal forms can usually be shown to be canonical models, e.g., for the local dynamics of a dynamical system. Suppose $\mathscr{D}$ is a collection of dynamical systems were each member is a model, say, of some physical system such as the brain. Furthermore, assume that there exists a dynamical system, e.g., $\dot{\mathbf{x}} = \mathbf{f}(\mathbf{x})$ such that any $\mathbf{y} \in \mathscr{D}$ can be transformed into the system $\mathbf{x}$ by a continuous change of variables. Then, the system $\mathbf{x}$ is said to be a **canonical model** for the family of dynamical systems $\mathscr{D}$.

The normal forms Eq. (A.3) can be shown to be local canonical models for the class of models (e.g., Eq. (A.1)) near a bifurcation point. Hoppensteadt & Izhikevich [1,5] derived such a local canonical model for a weakly connected neural network (WCNN) where the frequencies of any given pair of oscillators in the network are ϵ-close. However, in this manuscript we are mainly interested in the case when the frequencies of the oscillators are not necessarily ϵ-close and have arbitrary resonances.

Appendix B. Generalized fully expanded canonical model

Here, we derive a closed form expression for $\dot{z}$ in Eq. (10) similar to Eq. (15) based on specific assumptions on the coefficients b_k of Eq. (10). This generalized equation will capture more of the dynamic effects caused by the nonlinearities and the higher order resonant terms present in Eq. (10). Without loss of generality, assume:

$$\epsilon > 0, \epsilon \in \mathbb{R}$$
$$b_k \in \mathbb{C}, \quad k \in \{1, \ldots, p\}, p \geqslant 1, \; p \in \mathbb{Z}^+$$
$$b_k = b_{p+1} \in \mathbb{C}, \quad k \in \{p+2, p+3, \ldots\}.$$

Following the pattern of steps leading to Eq. (15) rewrite Eq. (10) as:

$$\dot{z} = z(a + b_1|z|^2 + b_2\epsilon|z|^4 + b_3\epsilon^2|z|^6 + b_4\epsilon^3|z|^8 + \cdots) + RT$$
$$\dot{z} = az + z(b_1|z|^2 + b_2\epsilon|z|^4 + \cdots + b_p\epsilon^{p-1}|z|^{2p}) + z(b_{p+1}\epsilon^p|z|^{2(p+1)} + b_{p+2}\epsilon^{p+1}|z|^{2(p+2)} + \cdots) + RT$$
$$\dot{z} = az + z\sum_{k=0}^{p-1} b_{k+1}\epsilon^k|z|^{2(k+1)} + zb_{p+1}\sum_{k=p}^{\infty}\epsilon^k|z|^{2(k+1)} + RT.$$

Note that for $k = p$, $\epsilon^p|z|^{2(p+1)}$ is a factor of $\sum_{k=p}^{\infty}\epsilon^k|z|^{2(k+1)}$ so we can write:

$$\dot{z} = az + z\sum_{k=0}^{p-1} b_{k+1}\epsilon^k|z|^{2(k+1)} + zb_{p+1}\epsilon^p|z|^{2(p+1)}\sum_{k=p}^{\infty}\epsilon^{k-p}|z|^{2(k-p)} + RT$$

Let $m = k - p$ which implies that for $k = p, m = 0$ and for $k = \infty, m = \infty - p = \infty$ thus, we can write:

$$\dot{z} = z\left(a + \sum_{k=0}^{p-1} b_{k+1}\epsilon^k|z|^{2(k+1)}\right) + zb_{p+1}\epsilon^p|z|^{2(p+1)}\sum_{m=0}^{\infty}(\epsilon|z|^2)^m + RT$$

$\sum_{m=0}^{\infty}(\epsilon|z|^2)^m$ is a geometric series with radius of convergence:

$$|\epsilon|z|^2| < 1 \Longrightarrow |z| < \sqrt{1/\epsilon}.$$

Recalling the result for RT from Section 3 we obtain the general case for the *canonical neural oscillator with an input*:

$$\dot{z} = z\left(a + \left(\sum_{k=0}^{p-1} b_{k+1}\epsilon^k|z|^{2(k+1)}\right) + \frac{b_{p+1}\epsilon^p|z|^{2(p+1)}}{1-\epsilon|z|^2}\right) + \frac{x}{1-\sqrt{\epsilon}x}\cdot\frac{1}{1-\sqrt{\epsilon}\bar{z}}$$
$$\text{when } |z| < \sqrt{1/\epsilon}, \quad |x| < \sqrt{1/\epsilon}, \quad p \in \mathbb{Z}^+ \text{ and } p \geqslant 1. \tag{B.4}$$

Notice that if we set $p = 1$ in Eq. (B.4) we obtain Eq. (15) where $b = b_1$ and $d = b_2$. Eq. (B.4) can also be written in polar form as was done for Eq. (15).

To summarize the above procedure, in general, we choose a finite number of the coefficients b_k from Eq. (10) with the constraint that the remaining terms containing b_k's form a convergent series. Clearly, this will yield a closed form expression for $\dot{z}$.

References

[1] F.C. Hoppensteadt, E.M. Izhikevich, Weakly Connected Neural Networks, Springer, 1997.
[2] S. Wiggins, Introduction to Applied Nonlinear Dynamical Systems and Chaos, Springer, 1990.
[3] J.A. Murdock, Normal Forms and Unfoldings for Local Dynamical Systems, Springer, 2003.
[4] D. Aronson, G. Ermentrout, N. Kopell, Amplitude response of coupled oscillators, Physica D 41 (3) (1990) 403–449.
[5] F.C. Hoppensteadt, E.M. Izhikevich, Synaptic organizations and dynamical properties of weakly connected neural oscillators. i. Analysis of a canonical model, Biol. Cybern. 75 (2) (1996) 117–127.

[6] M.A. Ruggero, Responses to sound of the basilar membrane of the mammalian cochlea, Curr. Opin. Neurobiol. 2 (4) (1992) 449–456.
[7] M.A. Ruggero, N.C. Rich, A. Recio, S.S. Narayan, L. Robles, Basilar-membrane responses to tones at the base of the chinchilla cochlea, J. Acoust. Soc. Am. 101 (4) (1997) 2151–2163.
[8] M.L. Sutter, C.E. Schreiner, Physiology and topography of neurons with multipeaked tuning curves in cat primary auditory cortex, J. Neurophysiol. 65 (5) (1991) 1207–1226.
[9] M.A. Escabi, C.E. Schreiner, Nonlinear spectrotemporal sound analysis by neurons in the auditory midbrain, J. Neurosci. 22 (10) (2002) 4114–4131.
[10] D.W. Purcell, B. Ross, T.W. Picton, C. Pantev, Cortical responses to the 2f1–f2 combination tone measured indirectly using magnetoencephalography, J. Acoust. Soc. Am. 122 (2) (2007) 992–1003.
[11] Y. Choe, M.O. Magnasco, A.J. Hudspeth, A model for amplification of hair-bundle motion by cyclical binding of Ca2+ to mechanoelectrical-transduction channels, Proc. Natl. Acad. Sci. USA 95 (26) (1998) 15321–15326.
[12] S. Camalet, T. Duke, F. Julicher, J. Prost, Auditory sensitivity provided by self tuned critical oscillations of hair cells, Proc. Natl. Acad. Sci. 97 (1999) 3183–3188.
[13] V. Eguiluz, M. Ospeck, Y. Choe, A. Hudspeth, M. Magnasco, Essential nonlinearities in hearing, Phys. Rev. Lett. 84 (22) (2000) 5232–5235.
[14] R.D. Rabbitt, S. Clifford, K.D. Breneman, B. Farrell, W.E. Brownell, Power efficiency of outer hair cell somatic electromotility, PLoS Comput. Biol. 5 (7) (2009) e1000444.
[15] G. Langner, Temporal processing of periodic signals in the auditory system: Neuronal representation of pitch, timbre, and harmonicity, Z. Audiol. 46 (2007) 80–21.
[16] J. Cartwright, D. Gonzlez, O. Piro, Nonlinear dynamics of the perceived pitch of complex sounds, Phys. Rev. Lett. 82 (26) (1999) 5389–5392.
[17] E.W. Large, A.E. Tretakis, Tonality and nonlinear resonance, in: G. Avanzini, L. Lopez, S. Koelsch, M. Majno (Eds.), The Neurosciences and Music II: From Perception to Performance, in: Annals of the New York Academy of Sciences, vol. 1060, 2005, pp. 53–56.
[18] I.S. Lots, L. Stone, Perception of musical consonance and dissonance: An outcome of neural synchronization, J. R. Soc. Interface 5 (2008) 1429–1434.
[19] V.I. Arnold, Geometrical Methods in the Theory of Ordinary Differential Equations, 2nd ed., Springer, 1996.
[20] J. Guckenheimer, P. Holmes, F.E. John, J.E.E. Marsden, Nonlinear Oscillations, Dynamical Systems, and Bifurcations of Vector Fields, Springer Verlag, 1990.
[21] P.B. Kahn, Y. Zarmi, Nonlinear Dynamics: Exploration through Normal Forms, Wiley-Interscience, 1997.
[22] J.A. Sanders, Normal form theory and spectral sequences, J. Differential Equations 192 (2) (2003) 536–552.
[23] A. Kern, R. Stoop, Essential role of couplings between hearing nonlinearities, Phys. Rev. Lett. 91 (12) (2003) 128101.
[24] Y.A. Kuznetsov, Elements of Applied Bifurcation Theory, 3rd ed., Springer, 2004.
[25] E. Large, J. Crawford, Auditory temporal computation: Interval selectivity based on post-inhibitory rebound, J. Comput. Neurosci. 13 (2002) 125–142.
[26] H.R. Wilson, J.D. Cowan, A mathematical theory of the functional dynamics of cortical and thalamic nervous tissue, Kybernetik 13 (2) (1973) 55–80.
[27] G. Chen, J. Della Dora, Further reductions of normal forms for dynamical systems, J. Differential Equations 166 (1) (2000) 79–106.
[28] J. Murdock, Hypernormal form theory: Foundations and algorithms, Journal of Differential Equations 205 (2) (2004) 424–465.
[29] A.H. Nayfeh, Method of Normal Forms, Wiley-Interscience, 1993.
[30] P. Yu, A.Y.T. Leung, A perturbation method for computing the simplest normal forms of dynamical systems, J. Sound Vib. 261 (1) (2003) 123–151.
[31] A.Y.T. Leung, Q.C. Zhang, Normal form computation without central manifold reduction, J. Sound Vib. 266 (2) (2003) 261–279.
[32] A.Y.T. Leung, Q.C. Zhang, Higher order normal form and period averaging, J. Sound Vib. 217 (5) (1998) 795–806.
[33] W. Zhang, K. Huseyin, On the relation between the methods of averaging and normal forms, Appl. Math. Model. 24 (4) (2000) 279–295.
[34] L. Hsu, L.J. Min, L. Favretto, Recursive approach to compute normal forms, J. Sound Vib. 243 (5) (2001) 909–927.
[35] P. Yu, Simplest normal forms of hopf and generalized hopf bifurcations, Internat. J. Bifur. Chaos 9 (10) (1999) 1917–1939.
[36] L.M. Perko, Higher order averaging and related methods for perturbed periodic and quasi-periodic systems, SIAM J. Appl. Math. 17 (4) (1969) 698–724. URL: http://www.jstor.org/stable/2099314.
[37] I. Kolar, P.W. Michor, J. Slovak, Natural Operations in Differential Geometry, Springer-Verlag, 1993, URL: http://www.emis.de/monographs/KSM/index.html.