Verification of Malkin's theorem and report of problem in Figure 10-26, panel $I_{Na} + I_K$-model (Class 2), and in Figure 10-30a, of Izhikevich (2007)

Joaquín Rapela*

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Contents

1 Introduction

Below I state Malkin's theorem, following Theorem 9.2 in Hoppensteadt & Izhikevich (1997) (Section 2), present two succesive simplification and one example of this theorem (Section 3), report a problem in Figure 10-26, panel $I_{Na} + I_K$-model (Class 2), and in Figure 10-30a, of Izhikevich (2007) (Section 4), and verify the validity of Malkin's theorem and that of the repoted problem (Section 5).

2 Malkin's Theorem

The following statement of Malkin's theorem is a modification of that given in Theorem 9.2 of Hoppensteadt & Izhikevich (1997).

*rapela@ucsd.edu

Theorem 1. *Let $\boldsymbol{X}_i(t) \in \Re^m, i = 1, \ldots, n,$ be weakly-connected m-dimensional dynamical systems*

$$\dot{\boldsymbol{X}}_i = F_i(\boldsymbol{X}_i) + \epsilon G_i(\boldsymbol{X}) \tag{1}$$

where $\boldsymbol{X}(t_1, \ldots, t_n) = (\boldsymbol{X}_1(t_1), \ldots, \boldsymbol{X}_n(t_n)) \in \Re^{m \times n}$. Assume that each uncoupled system

$$\dot{\boldsymbol{X}}_i = F_i(\boldsymbol{X}_i) \tag{2}$$

is on a limit cycle of length T parametrized by $\gamma_i : S^1 \to \Re^m$, $\gamma_i(\theta_i) = \boldsymbol{X}_i(\theta_i)$. Define $\gamma(\theta_1, \ldots, \theta_n) = (\gamma_1(\theta_1), \ldots, \gamma_n(\theta_n))$, and let φ_i be the phase deviation of X_i (i.e., $\theta_i = (t + \varphi_i) \mod T$). Then

$$\dot{\varphi}_i = H_i(\boldsymbol{\varphi} - \varphi_i, \epsilon) \tag{3}$$

with $\boldsymbol{\varphi} - \varphi_i = (\varphi_1 - \varphi_i, \ldots, \varphi_n - \varphi_i)$, and

$$H_i(\boldsymbol{\varphi} - \varphi_i, 0) = \frac{1}{T} \int_0^T Q_i(\theta)^T G_i(\gamma(\theta + \boldsymbol{\varphi} - \varphi_i))\, d\theta \tag{4}$$

where $Q_i(\theta)$ is the solution of

$$\dot{Q}_i(\theta) = (DF_i(\gamma_i(\theta)))^T Q_i(\theta) \tag{5}$$

statisfying the normalization condition

$$Q_i(0)^T DF_i(\gamma_i(0))) = 1 \tag{6}$$

3 Two succesive simplifications and one example of Malkin's theorem

Simplification 1

Lemma 1. *If in Eq. 1 the coupling term of oscillator i (G_i) is the sum of coupling terms with other oscillator (g_{ij}) and a self coupling term (g_{ii}):*

$$G_i(X(t)) = \sum_{j=1}^{n} g_{ij}(X_i(t), X_j(t)) \tag{7}$$

then

$$\dot{\varphi}_i = \omega_i + \epsilon \sum_{\substack{j=1 \\ j \neq i}}^{n} H_{ij}(\varphi_j - \varphi_i, 0) \tag{8}$$

with

$$H_{ij}(\varphi_j - \varphi_i, 0) = \frac{1}{T} \int_0^T Q_i(\theta)^T g_{ij}(\gamma_i(\theta), \gamma_j(\theta + \varphi_j - \varphi_i))\ d\theta \tag{9}$$

and

$$w_i = H_{ii}(0, 0) \tag{10}$$

Proof. Using Eq. 7 in Eq. 4 we have

$$\begin{aligned} H_i(\boldsymbol{\varphi} - \varphi_i, 0) &= \sum_{j=1}^{n} \frac{1}{T} \int_0^T Q_i(\theta)^T g_{ij}(\gamma_i(\theta), \gamma_j(\theta + \varphi_j - \varphi_i))\ d\theta \\ &= \sum_{j=1}^{n} H_{ij}(\varphi_j - \varphi_i, 0) \end{aligned} \tag{11}$$

Then

$$\begin{aligned} &\dot{\varphi}_i = H_i(\boldsymbol{\varphi} - \varphi_i, \epsilon) = \epsilon H_i(\boldsymbol{\varphi} - \varphi_i, 0) = \epsilon \sum_{j=1}^{n} H_{ij}(\varphi_j - \varphi_i, 0) \\ &= \epsilon H_{ii}(0, 0) + \epsilon \sum_{\substack{j=1 \\ j \neq i}}^{n} H_{ij}(\varphi_j - \varphi_i, 0) \\ &= \omega_i + \epsilon \sum_{\substack{j=1 \\ j \neq i}}^{n} H_{ij}(\varphi_j - \varphi_i, 0) \end{aligned} \tag{12}$$

The first equality in Eq. 12 follows from Malkin's theorem (Eq. 3), I cannot understand why the second equality holds, the third equality follows from Eq. 11, the right-hand side of fourth inequality separates the constant and non-constant terms in the left-hand side, and the last equality uses Eq. 10.

$\square$

Simplification 1.1

Lemma 1. *If we take $n = 2$ in Eq. 8 we obtain*

$$\dot{\chi} = \epsilon\omega + \epsilon G(\chi) \tag{13}$$

where

$$\chi = \varphi_2 - \varphi_1 \tag{14}$$
$$\omega = \omega_2 - \omega_1 \tag{15}$$
$$G(\chi) = H_{21}(-\chi) - H_{12}(\chi) \tag{16}$$

Proof. Taking $i = 1$ and $i = 2$ in Eq. 8 we obtain

$$\varphi_1(t) = \epsilon\omega_1 + \epsilon H_{12}(\varphi_2(t) - \varphi_1(t), 0) \tag{17}$$
$$\varphi_2(t) = \epsilon\omega_2 + \epsilon H_{21}(\varphi_1(t) - \varphi_2(t), 0) \tag{18}$$

Subtracting Eq. 17 from Eq. 18 and using Eqs. 14-16 we obtain Eq. 13.

□

Note 1 χ is a fixed point of Eq. 13 if and only if $G(\chi) = -\omega$ (Figure 1).

Note 2 If oscillators are not self coupled (i.e., $g_{ii}(\gamma_i(\theta), \gamma_i(\theta)) = 0\ \forall i$), then (from Eq. 9) $H_{ii} = 0\ \forall i$, then (from Eq. 10) $w_i = 0\ \forall i$, and then the fixed points of Eq 13 are the zero crossings of $G(\chi)$.

Example

This example attempts to replicate that in Figure 10.26 of Izhikevich (2007). I simulated two two-dimensional low-threshold INap+IK models of neurons (Izhikevich, 2007) with the same parameters used in Figure 10.26 of Izhikevich (2007). The two models shared the same parameters (as given in Figure 4.1b of Izhikevich (2007) and repeated for reproducibility in Table 1), but had different initial conditions (Table 2). The input current to both models was such that when uncoupled these models were on a stable limit cycle (I=35, INap+IK (Class 2) model on Figure 10.3 of Izhikevich (2007) and blue traces in Figure 2). These models were weakly coulpled with gap junctions (Eq. 19), and the coupling strength was weak enough ($\epsilon = 0.003$ in Eq. 1) so that the coupled models remained on the uncoupled limit cylce (red traces in Figure 2). The model of neuron 1 (Eq. 20), but not that of neuron 2 (Eq. 21), was self coupled, and below we vary the self-coupling strength of neuron 1 (s in Eq. 20) to obtain different patterns of synchronization between neurons 1 and 2.

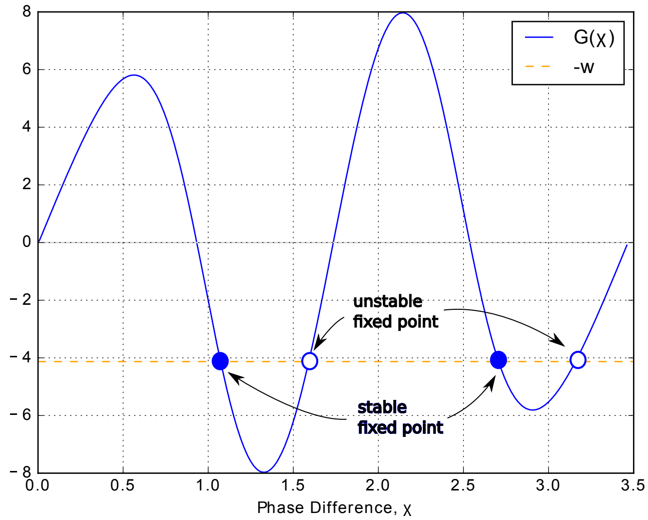


Figure 1: Fixed points of phase model in Eq. 13.

$$g_{ij}(\gamma_i(\theta), \gamma_j(\theta)) = \begin{bmatrix} \gamma_j(\theta)[0] - \gamma_i(\theta)[0] \\ 0 \end{bmatrix}, i \neq j \tag{19}$$

$$g_{11}(\gamma_1(\theta), \gamma_1(\theta)) = \begin{bmatrix} s \times \gamma_1(\theta)[0] \\ 0 \end{bmatrix} \tag{20}$$

$$g_{11}(\gamma_2(\theta), \gamma_2(\theta)) = 0 \tag{21}$$

4 Problem in Figure 10-26 of Izhikevich (2007)

As demonstrated in the next section, the plot of functions H_{ij} and $G(\chi)$ in Figure 10-26 of Izhikevich (2007) are inverted. The correct figure is Fig. 3.

5 Verification of Malkin's Theorem

References

Hoppensteadt, F. C., & Izhikevich, E. M. (1997). *Weakly connected neural networks* (Vol. 126). Springer Science & Business Media.

Izhikevich, E. M. (2007). *Dynamical systems in neuroscience.* MIT press.

Name	Value
C	1.0
g_L	8.0
e_L	-78.0
g_{NA}	20.0
e_{NA}	60.0
g_K	10.0
e_K	-90.0
$mV_{1/2}$	-90.0
mk	15.0
$nV_{1/2}$	-45.0
nk	5.0
τ	1.0

Table 1: Parameters for the the two INap+IK models of neurons, repeated from Figure 4.1b in Izhikevich (2007).

Neuron	Name	Value
1	V_0	-26.30
1	n_0	0.50
2	V_0	-65.01
2	n_0	0.16

Table 2: Initial conditions for voltages, V, and activation gates, n, of the simulated INap+IK models of neurons.

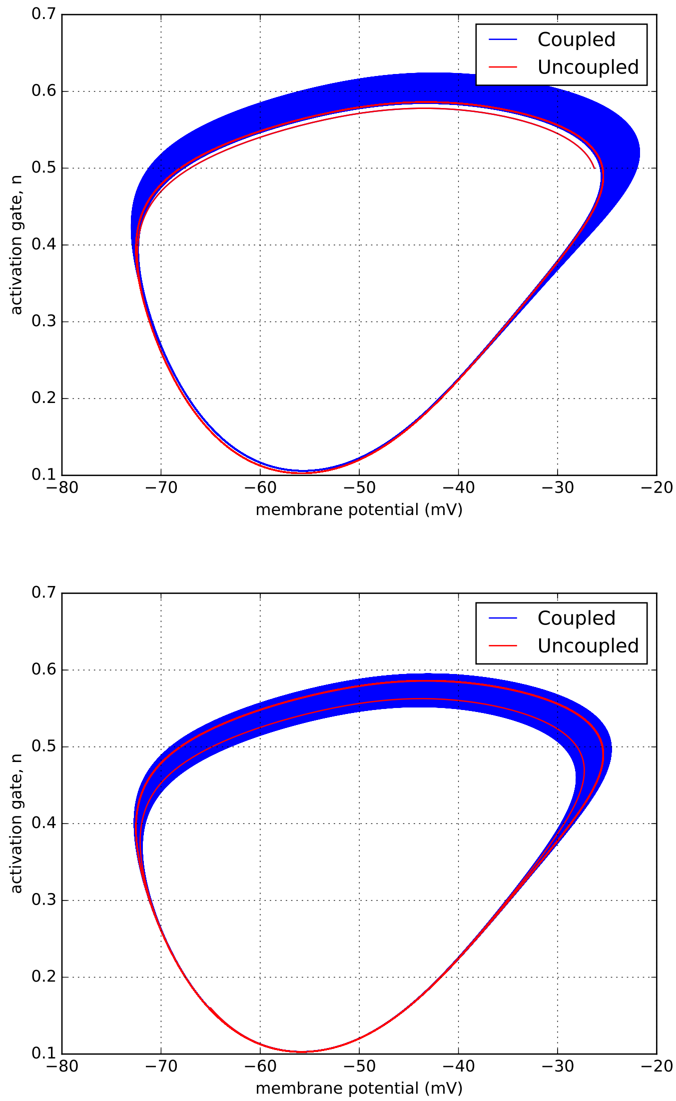


Figure 2: Phase space of the two simulated INap+IK neurons.

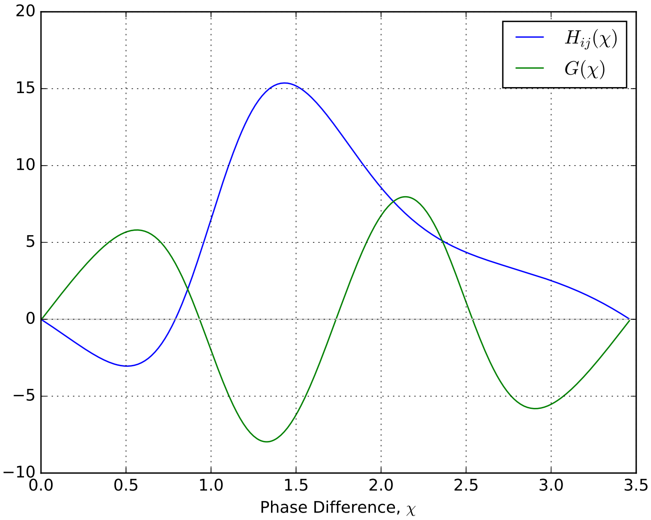


Figure 3:

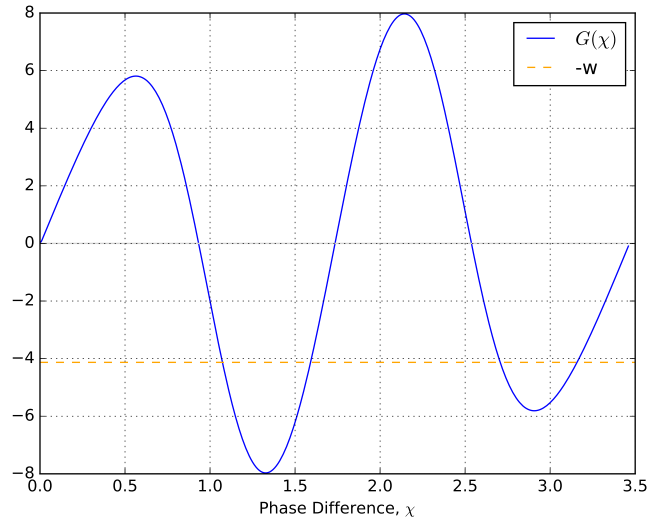


Figure 4:

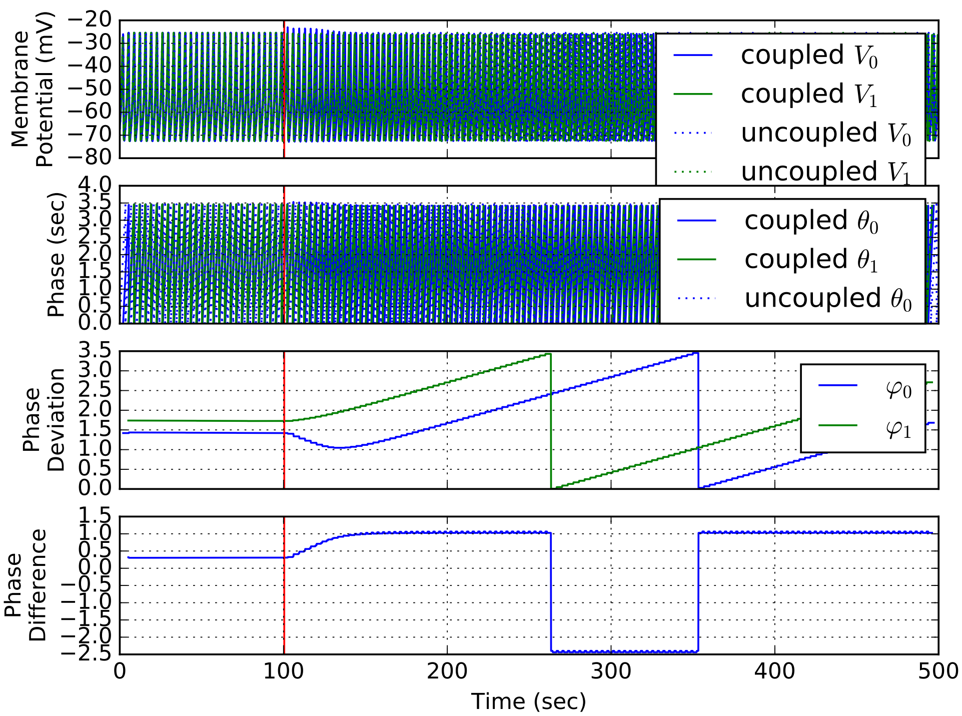
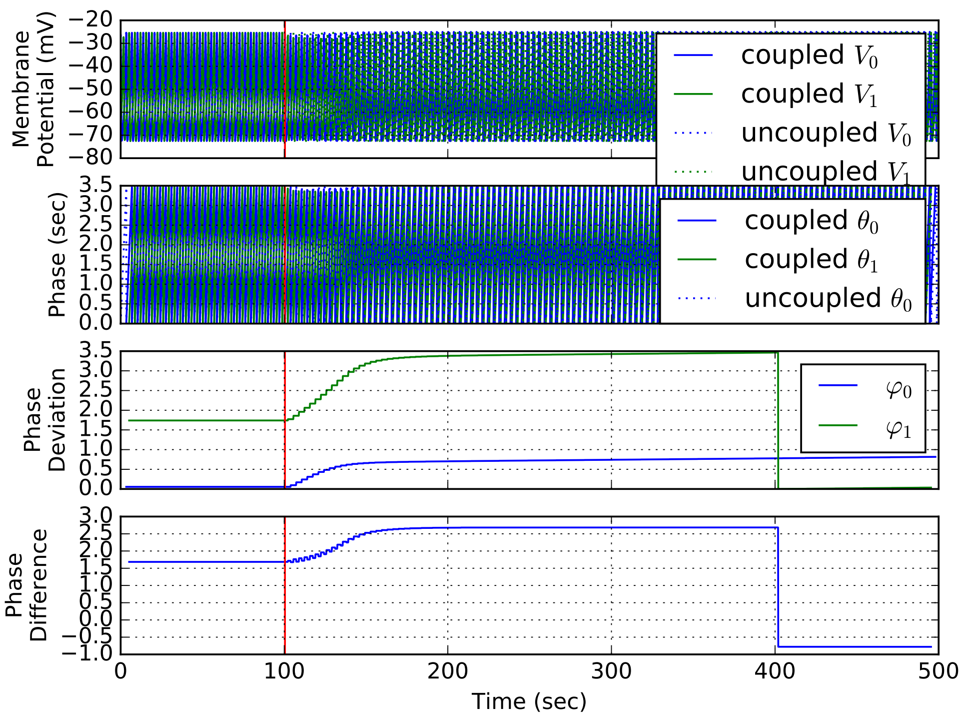
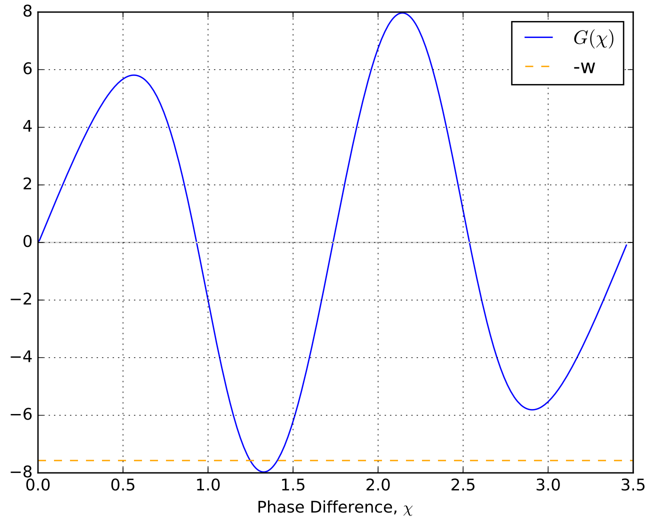

Membrane Potential (mV)
coupled V_0
coupled V_1
uncoupled V_0
uncoupled V_1
Phase (sec)
coupled θ_0
coupled θ_1
uncoupled θ_0
Phase Deviation
φ_0
φ_1
Phase Difference
Time (sec)

Figure 5:

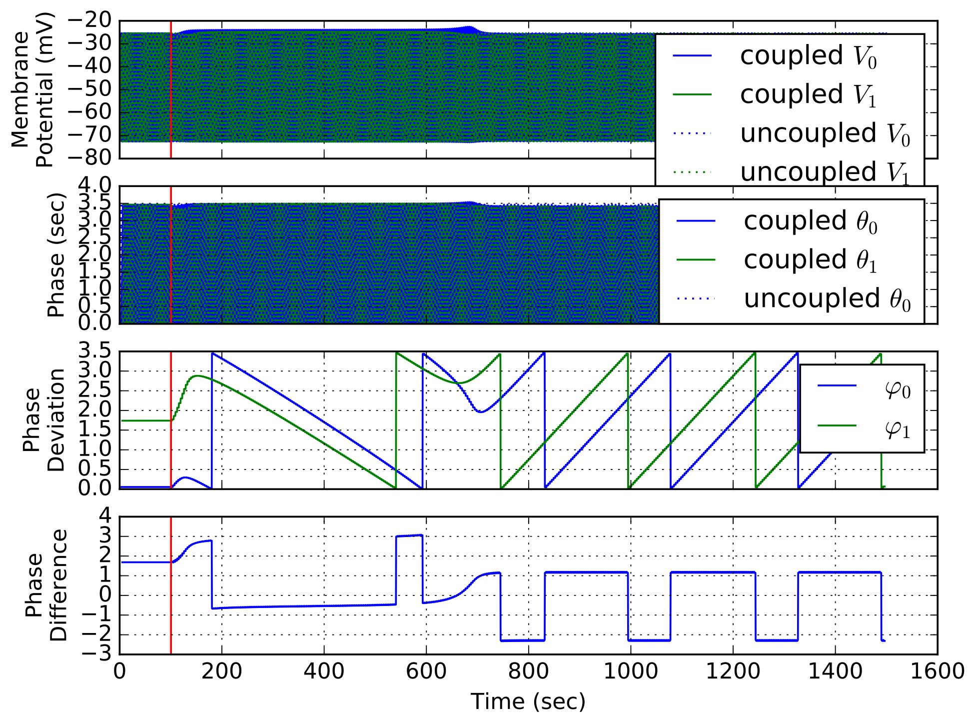


Membrane Potential (mV)
−20
−30
−40
−50
−60
−70
−80
coupled V_0
coupled V_1
uncoupled V_0
uncoupled V_1
Phase (sec)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
coupled θ_0
coupled θ_1
uncoupled θ_0
Phase Deviation
φ_0
φ_1
Phase Difference
−0.5
−1.0
0
100
200
300
400
500
Time (sec)

Figure 6:

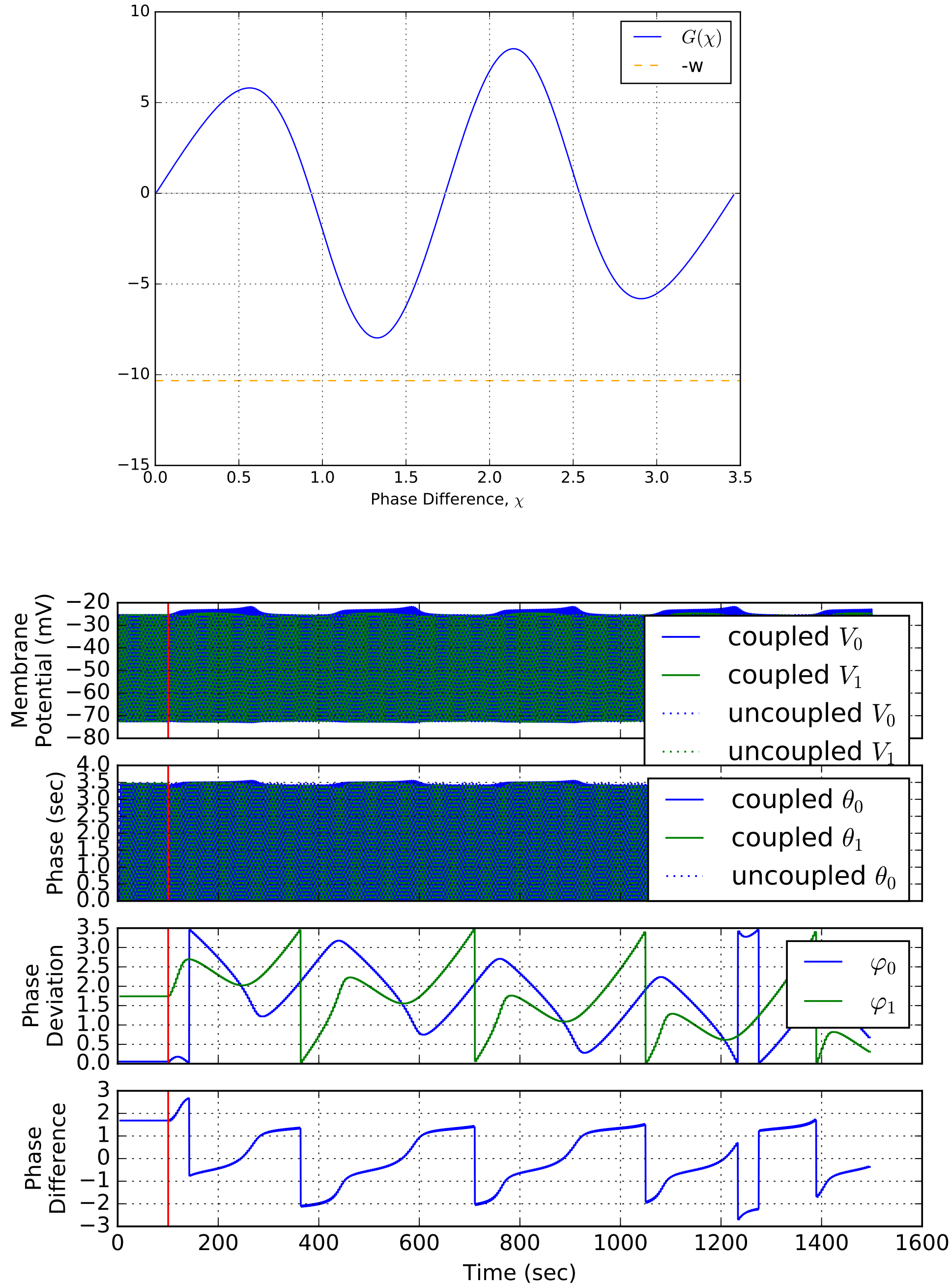


$G(\chi)$
-w
Phase Difference, χ



Membrane Potential (mV)
coupled V_0
coupled V_1
uncoupled V_0
uncoupled V_1
Phase (sec)
coupled θ_0
coupled θ_1
uncoupled θ_0
Phase Deviation
φ_0
φ_1
Phase Difference
Time (sec)

Figure 7:



Phase Difference, χ
$G(\chi)$
-w
Membrane Potential (mV)
coupled V_0
coupled V_1
uncoupled V_0
uncoupled V_1
Phase (sec)
coupled θ_0
coupled θ_1
uncoupled θ_0
Phase Deviation
φ_0
φ_1
Phase Difference
Time (sec)

Figure 8: