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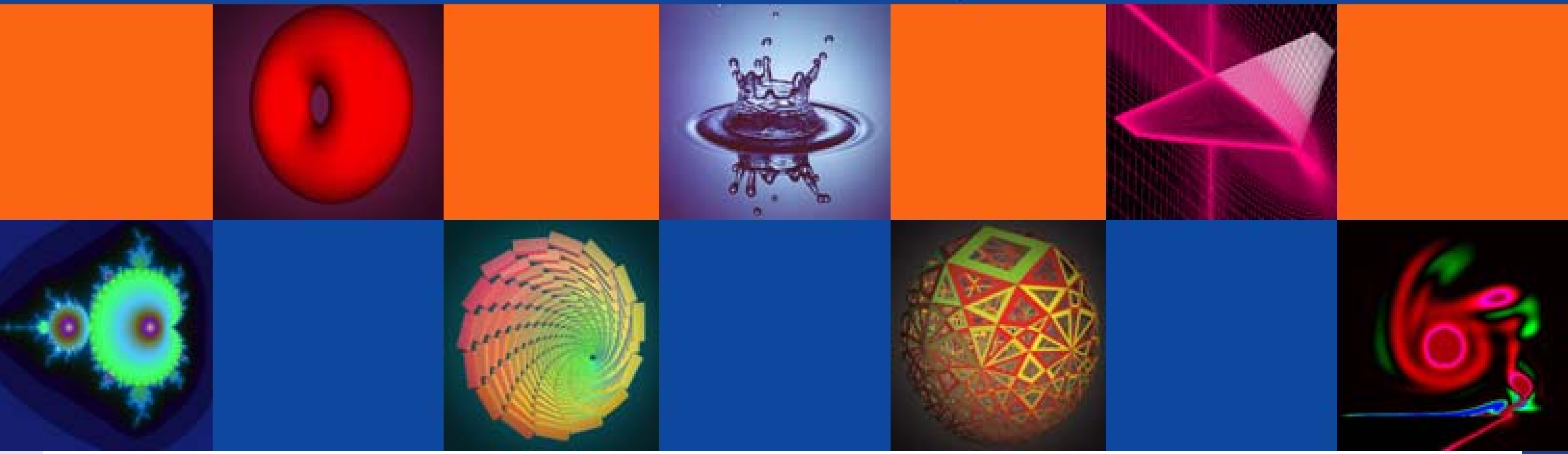

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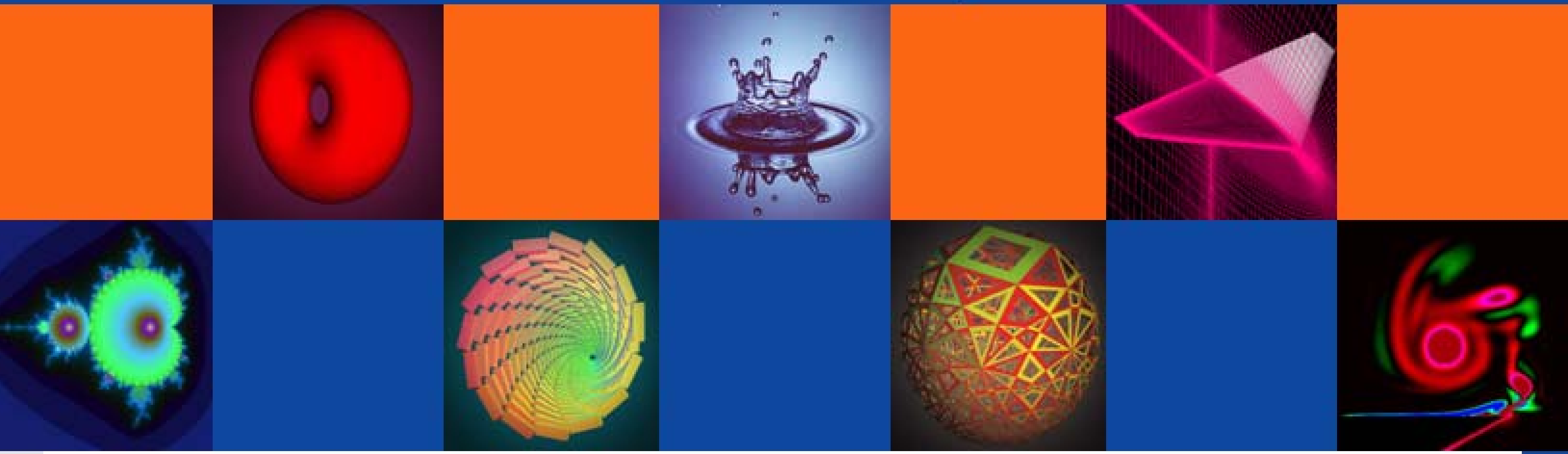

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REGULAR BURSTING EMERGING FROM SYNAPTICALLY COUPLED NEURONS

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Abstract. In this note, we study the change of collective behavior of two synaptically coupled bursting systems as the strength of coupling increases. The two cells present chaotic bursting behavior when uncoupled. But as the strength increases past a certain value, the behavior of two cells becomes synchronized regular bursting motions. It shows that regular oscillations can emerge from connecting intrinsically chaotic oscillators with synapses. The method of analysis is similar to that of Fast Threshold Modulation theory.

1. **Introduction.** We consider a system of two synaptically coupled Hodgkin-Huxley type neurons and we intend to study its dynamical behavior. The system models the collective behavior of two neuron cells coupled through synapses whose actions are due to release of neural transmitters. Quantitatively, the synapse can be approximated by a Heaviside function. Individual cell here presents a chaotic dynamics and has solutions with distinct patterns appear in two time scales, called bursting. The bursting solutions are characterized by an alternating sequence of a chain of intensive large amplitude oscillations in the active phase and then a quite rebound period without oscillation in the inactive phase. In this note, each of the systems is assumed to be identical to other, and individually it presents the typical square bursting as described by Rinzel [7], Terman [14] and Sherman and Rinzel [12]. It was known [14] that at certain parameter range, some chaotic characters of solutions occur. However when two identical chaotic systems are coupled together, there are many possibilities. They could either synchronize into an in-phase solution or a out-of phase solution, or neither, depending on the parameter range and the method of coupling. For example, Sherman and Rinzel [12] showed two neurons with diffusive coupling (gap junction in neuroscience terms) may have a much longer active phase of high frequency oscillations than a single neuron of the same property. There are intensive studies of diffusively coupled regular or chaotic neurons, available in the literature but they are out of the scope of our study. The mathematical study of synaptically coupled cells started from the Fast Threshold

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Modulation Theory, initiated by Somers and Kopell [13]. Rubin and Terman [8] had also described in detail how to analyze the synchronization of neurons by a geometric method for differential equation. Some recent studies can be found in [2] and [9].

We study a synaptically coupled system of two identical Hodgkin-Huxley type neurons in this study. When there is no coupling or weak coupling, the systems appear chaotic and unsynchronized. But when the synaptic coupling strength is large enough, the systems will be regular and synchronized. The phenomenon was observed by Abarbanel et al and was confirmed by calculating their Lyaponov exponents in [1]. Through analyzing its fast and slow manifolds, we provide the underlining mechanism of this phenomenon from a different perspective. Regularizing chaotic cells can also be possible by an averagaed coupling in [10] which is not related to our study.

We organized the paper in the following way. In Section 2, we start with general assumptions and discuss the individual behavior of a single system. In Sections 3 and 4, we consider the dynamical behavior of the systems with a coupling that leads to synchronization. A brief discussion is in Section 5,

2. General Assumptions On Individual Neuron.

For simplicity, we assume that individual neurons are identical in our case. In our model, motivated by Hodgkin-Huxley equation (or its variation such as FitzHugh-Nagumo model, Hindmarsh-Rose model) [7], the intracellular membrane potential and currents of the neuron satisfy the differential equations:

$$v' = f_1(v, w, y) \tag{1a}$$

$$w' = f_2(v, w, y) \tag{1b}$$

$$y' = \varepsilon g(v, w, y). \tag{1c}$$

The sub-system containing the first two equations (1a-1b) is called the fast system (FS). The last equation (1c) is called the slow equation. We assume

- (H1) The set of steady states of (FS) consist of an S-shaped curve of y in (v, y)-plane denoted by S. There exist y_λ and y_ρ such that the number of steady states of (FS) equals to 1 as $y \in (-\infty, y_\lambda)$, equals to 3 as $y \in (y_\lambda, y_\rho)$, equals to 1 as $y \in (y_\rho, \infty)$. Denote the right knee (located on the lower branch) by $P_\rho = (v_\rho, w_\rho, y_\rho)$ and left knee on upper branch $P_\lambda = (v_\lambda, w_\lambda, y_\lambda)$. We also denote the upper, middle and lower branch of S by U, M, L.
- (H2) We further assume that the lower branch L consist of stable steady states for (FS) and the middle branch consist of steady states which are saddles for (FS). The upper branch is more complicated than the cases considered in Terman [14]. For two intervals $y_b \le y < y_h$ and $y_H < y \le y_B$, there exist one-parameter families of periodic solutions of FS, denoted by P_1 and P_2 respectively. Both P_1 and P_2 have a Hopf bifurcation point at one end, and they both terminate at a homoclinic orbit from saddle points at the middle branch. These homoclinic points are denoted as $p_h = (v_h, w_h, y_h)$ and $p_H = (v_H, w_H, y_H)$. See Figure 1. Both P_1 and P_2 are stable for (FS) with y-fixed.
- (H3) For slow dynamics, the y-dependent nullsurface $N \equiv \{(v, w, y) | g = 0\}$ intersect the curve S at a unique point below p_h and further down M towards P_ρ, and N is quite close to P_ρ in distance. As typical, $U \subset \{g < 0\}$, $P_1(t) \subset \{g < 0\}$ and $P_2(t) \subset \{g < 0\}$ while $L \subset \{g > 0\}$. We assure

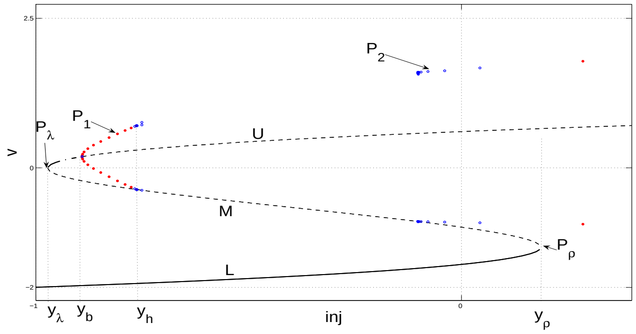

Figure 1. The bifurcation diagram of (FS) for Equation 1

the point P_ρ is nondegenerate described as follows [5]. Let $F = (f_1, f_2)$. Then $DF_x(P_\rho)$ has one negative eigenvalue and one zero eigenvalue. Further, Let η, χ be the eigenvectors corresponding to the zero eigenvalue of $D_xF(P_\rho)$ and $(D_xF(P_\rho))^T$, we have $< \chi, D_xF(P_\rho) > \neq 0$ and $< \chi, D_{xx}F(P_\rho)(\eta, \eta) > \neq 0$. Assumptions on P_λ are similar. Geometrically, it implies that P_ρ and P_λ behave like parabolas. We also assume that there exists a unique stable trajectory r_ρ such that $r_\rho(t) \to P_\rho$ as $t \to -\infty$ and $r_\rho(t) \to P_2(t)$ as $t \to \infty$ for (FS). Similar assumption holds for P_λ.

With the assumptions given above, the behavior of a single cell is well understood by Terman [14] and Lee and Terman [5]. We introduce two basic results.

Theorem 1 (Terman [14] and Lee and Terman [5])**.** *Assume H1-H3 hold for Eq. 1. There exist* $\varepsilon_i \to 0^+$ *as* $n \to \infty$ *and* $\delta_i \leq C_i e^{-k/\varepsilon_i}$*, the periodic bursting solution that alternates between L and* P_2*, is uniquely determined and asymptotically stable for all* $\varepsilon > 0$ *except for* $\varepsilon \in \cup_i(\varepsilon_i - \delta_i, \varepsilon_i + \delta_i)$*.*

The bursting solutions mentioned above are regular solutions without chaotic motions. In cases of our interest, the solutions behave chaotically. In previous study of Terman [14], the null function $g(v, w, y)$ is linearly depedent on a parameter k, that is glucose level in pancreatic model. The parameter k can be adjusted such that when k is small, Eq. 1 gives rise to regular bursting solutions and when k is above a certain value, Eq. 1 has continuous spikes. In the (ε, k)-plane, there is a wedge region where the corresponding Poincare Mapping induced by Eq. 1 presents a Fibonacci dynamics that characterizes the chaotic dynamics.

Theorem 2 (Terman [14])**.** *Assume H1-H3 hold for Eq. 1. The chaotic bursting solutions exist for all* $\varepsilon > 0$ *and for* $k = k(\varepsilon)$*. There exist an integer* $N = N(\varepsilon)$ *and real numbers* $\{k_j\}, 1 \leq j \leq N(\varepsilon)$ *with* $k_j \leq k_{j+1}$ *such that for* $k \in [k_{2j}, k_{2j+1}]$ *the return mapping* $\pi(k, \varepsilon)$ *near the lower branch of the steady state of the fast system at* $y = y_H$ *gives rise to a j-Fibonacci dynamics.*

Several neuron cells have those characters we mentioned above. For example, Morris-Lecar model [14] and Hindmarsh-Ross model (HR) [1] all satisfy the assumptions mentioned earlier. In this study, we will investigate HR (a prototype for Hodgkin-Huxley theory) numerically using XPPAUT software to motivate our study of coupled systems. The biological meaning of the assumptions were carefully explained in [14] and [12]. The variable v represents the voltage, the variable w is recovery variable and y is inward current. The parameter Inj is the injected current into the neuron:

$$\begin{aligned} v' &= w + \phi(v) - y + Inj \\ w' &= \psi(v) - w, \\ y' &= -ry + rS(v - c) \end{aligned} \tag{2}$$

where $Inj = 3.281, r = 0.0021, c = -1.6, S = 4.0$, $\phi(s) = 3s^2 - s^3, \psi(s) = 1 - 5s^2$. The initial values are set at $v = 0, w = 0, y = -2$. Figure 2 shows a chaotic bursting trajectory of Eq. 2.

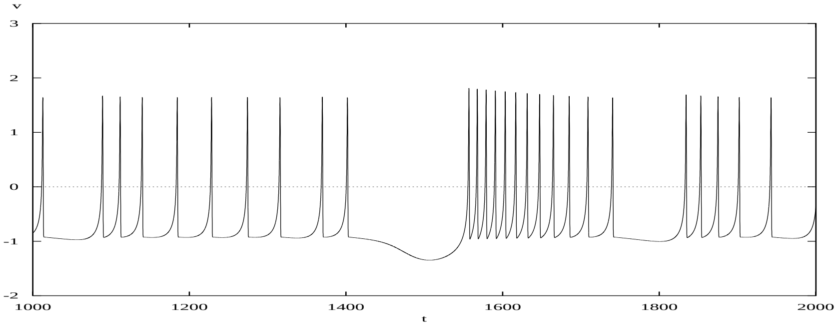

Figure 2. A chaotic trajectory of Equation 2

3. **Coupled Oscillators.** There are a number of ways by which neurons can communicate to each other. Two most common mechanism are diffusive coupling (gap junction) or synaptic coupling through neural transmitters. Roughly speaking, a diffusive coupling models a direct electric connection through two neurons, and synaptic coupling describes the connection through release of neural transmitters when other neurons activate.

Motivated the work of Somers and Kopell [13] and Abarbanel et al[1], we consider the coupled systems:

$$\begin{aligned} v_1' &= f_1(v_1, w_1, y_1) + \alpha(-v_1 - V_c)H(X_c + v_2) \\ w_1' &= f_2(v_1, w_1, y_1) \\ y_1' &= \varepsilon g(v_1, w_1, y_1) \\ v_2' &= f_1(v_2, w_2, y_2) + \alpha(-v_2 - V_c)H(X_c + v_1) \\ w_2' &= f_2(v_2, w_2, y_2) \\ y_2' &= \varepsilon g(v_2, w_2, y_2). \end{aligned} \tag{3}$$

We denote $U_1 = (v_1, w_1, y_1)$, and $U_2 = (v_2, w_2, y_2)$. The constant parameter $\alpha > 0$ represents the strength of the coupling. Reminding that L is the lower branch of the single cell. For $U_1 \in L, U_2 \in L$, we have $(-v_1 - V_c) > 0, (-v_2 - V_c) > 0$ and therefore the couplings are excitatory [13]. The function $H(\cdot)$ is the Heaviside Function and $(-X_c)$ is the threshold. Although the discontinuous Heaviside Function is used, systems with smoothed version of H yield to similar results.

We study first the numerical solutions of the coupled HR model

$$\begin{aligned} v' &= w + \phi(v) - y + Inj - \alpha(v+1.4)H(V+0.85) \\ w' &= \psi(v) - w \\ y' &= -ry + rS(v-c) \\ V' &= W + \phi(V) - Y + Inj - \alpha(V+1.4)H(v+0.85) \\ W' &= \psi(V) - W \\ Y' &= -rY + rS(V-c) \end{aligned} \tag{4}$$

where all conditions in Eq. 2 hold and initial conditions$V = 0, W = 0.2, Y = -3.02$. The coupling strength α is set at 0.2. We find that the solutions will quickly synchronize into a bursting solution that is regular and attracting, as shown in Figure 3. The simulations for Eq. 4 suggested that the behavior of solutions, with a strong coupling $\alpha > \alpha_0$, will result in regular periodical bursting, and solutions of different initial positions will synchronize as t goes to infinity. We denote the family of solutions $S_\alpha(y)$ to be the steady states of (FS) for the synchronized system Eq. 3

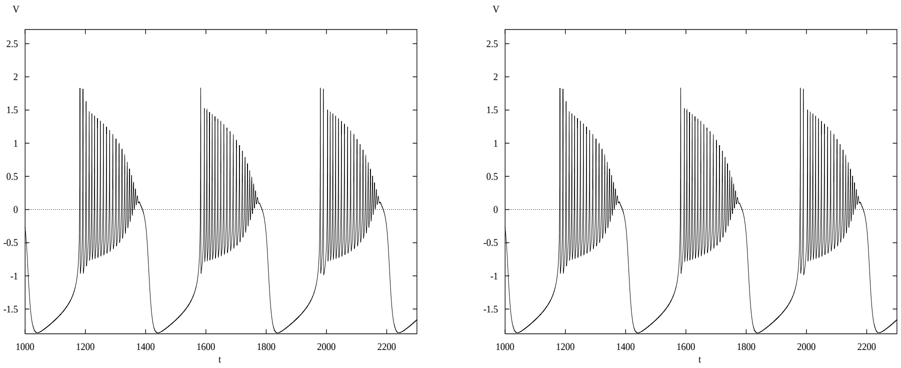

FIGURE 3. The solutions quickly converge to a periodic regular bursting solution

$$\begin{aligned} v' &= f_1(v,w,y) - \alpha(v + X_c) \\ w' &= f_2(v,w,y) \\ y' &= \varepsilon g(v,w,y). \end{aligned} \tag{5}$$

The numerical calculation of the bifurcation for (FS) of Eq. 5 indicated that when $\alpha > \alpha_0^-$, the family of periodic solutions P_1 and P_2 will be detached from the middle branch and will merge into one continuous branch P_α. The periodic family P_α will start from one Hopf bifurcation and terminate at another Hopf-bifurcation at its upper branch at $y = y_b$ and at $y = y_B$, as shown in Graph 4.

We denote the upper branch of the new bifurcation diagram U_α and the lower branch L_α. We now have our final two assumptions.

(H4) Suppose that there exists a unique value α_0 such that as $\alpha \to \alpha_0^-$, both y_h and y_H collapse to each other. If $\alpha > \alpha_0$, then the family of periodic solution P_α will be separated from the middle branch.

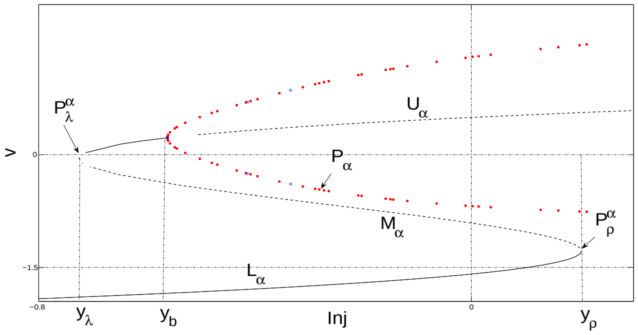

FIGURE 4. The bifurcation diagram of (FS) for Equation 5 for the particular example of (HR), $\alpha = 0.2$

(H5) The coupling strength α is chosen so that the left knee P_λ^α is between the gap of P_1 and P_2 i.e., $y_h < y_\lambda^\alpha < y_H$. This restricts the value α of coupling strength.

4. **Synchronization To Regular Bursting Solutions.** We denote F to be the union of all fast manifolds from L to U or P_2, and from U or P_2 to L for Eq. 2. Similarly, let F_α be the union of all fast manifolds from L_α to U_α or P_α, and from U_α or P_α to L_α for Eq. 5.

Theorem 3 (Main Result)**.** *Suppose H1-H5 hold. There exists a periodic solution $U(t, \varepsilon, \alpha)$ with period $T(\varepsilon, \alpha)$ for Eq. 3 such that*

(1) *dist*$(U(t, \varepsilon, \alpha), L \cup F \cup P_\alpha \cup U_\alpha \cup F_\alpha) = O(\varepsilon)$*, and* $\lim_{\varepsilon \to 0} T(\varepsilon, \alpha) = T_0(\alpha) > 0$.

(2) *there exits $\delta > 0$ such that when any pair of coupled bursting solutions (v_i, w_i, y_i), $i = 1, 2$ with initial conditions satisfying $|(v_1, w_1, y_1) - (v_2, w_2, y_2)| \leq \delta$, $|(v_i, w_i, y_i)(t) - U(t + t_0, \varepsilon, \alpha)| \leq M_0 e^{-c_0 t}$ for some $t_0, i = 1, 2$, i.e. both bursting solutions synchronize to the periodic solution $U(t, \varepsilon, \alpha)$ with a time shift.*

An Outline of Proof for Theorem 3. Analyzing the solutions, we note that the slow manifold L is stable with respect to (FS). Namely, The linearized operator of (FS) near L has two negative real eigenvalues except near the right knee for Eq. 1. For $y_b^\alpha \leq y \leq y_B^\alpha$, the branch $U_\alpha(y)$ is circled by $P_\alpha(y)$ from outside. Along both sections of $U_\alpha(y)$ to the left and to the right of $P_\alpha(y)$, the operator from (FS) of Eq. 5 has a pair of complex eigenvalues of negative real parts, except for the left knee P_λ^α. For the periodic branch P_α, the Floquet multiplier are 1 and $\mu, |\mu| < 1$. We use the classical results from Fenichel [4] to assert the existence of invariant manifolds of Eq. 5 near the slow manifold and only analyze the flows within the neighborhood of the invariant manifolds L, U_α and P_α. Note that the solutions follow L rather than L_α because $H \equiv 0$ when both cells are in lower branch.

We start both solutions of Eq. 3 at different initial points at the lower branch L. Without loss of generality, let $U_1(t)|_{t=0}$ be at the right knee P_ρ and $y_1(t) - y_2(t)|_{t=0} = z > O(\sqrt{\varepsilon})$, $z = O(\alpha)$ is independent of ε. Further $y_2(t)|_{t=0}$ is to the right of P_ρ^α, the right knee of the bifurcation diagram in Eq. 5 with $\alpha > 0$. Because this is a restrictive condition on the initial position difference, our result is a local synchronization.

Since the nature of the coupling there is excitatory, in the terminology of Somers et al [13], both trajectories will move up to the periodic family P_α through the following sequence of events.

(a) For $0 \equiv t_1 \leq t \leq t_2(\varepsilon) = t_1 + O(\frac{1}{\sqrt{\varepsilon}})$, $U_1(t) \in N(F)$ i.e., within the ε-neighborhood of L and $v_1 \leq (-X_c)$ while $U_2(t) \in N(L)$, i.e. the solution U_1 leaves the right knee and moves up along the fast manifold F (discussed earlier, and also see [6]) but it is still below the threshold $(-X_c)$ to influence the second neuron; the second solution U_2 remains the lower branch for the time being.

(b) For $t_2 \leq t \leq t_3(\varepsilon) = t_2 + O(\frac{1}{\sqrt{\varepsilon}})$, $U_1(t) \in N(F \cup P_2)$ and $v_1(t) > -X_c$, while $U_2(t) \in N(F)$ but $v_2(t) < -X_c$ below the threshold i.e., the solution U_1 goes past the threshold and eventually reaches P_2 the family of periodic solutions on the upper branch of unexcited equation. The second solution U_2 leaves from the lower branch to move up to the fast manifold F, because U_2 gets excited after U_1 goes above the threshold.

(c) For $t_3 \leq t \leq t_4(\varepsilon) \leq t_3 + O(1)$, while $U_2(t) \in N(F)$ and $v_2(t) > -X_c$ is above the threshold, $U_1(t)$ jumps away from $N(P_2)$ and goes to $N(P_\alpha)$, the new periodic family of the synchronized system.

(d) For $t_4 \leq t \leq t_5(\varepsilon) \leq t_4 + O(1)$, $U_1(t)$ stays within $N(P_\alpha)$, while $U_2(t) \in N(F_\alpha)$ and $U_2(t_5) \in N(P_\alpha)$ i.e., the solution U_2 jumps to the family of periodic solutions on the upper branch of excited equation.

(e) Finally as $t > t_5$, both $U_1(t)$ and $U_2(t)$ settle on P_α, then $|y_1(t_5) - y_2(t_5)| = z + O(\sqrt{\varepsilon})$. Note $U_1(t)$ and $U_2(t)$ can switch positions during the jump [13].

We remark that when the solutions move along the slow manifolds L, P_α, U_α, the time difference between the solutions is invariant, because the systems are decoupled and the two neurons are identical systems. However the time difference between U_1 and U_2 has certainly changed substantially during the jump up and jump down between slow manifolds via a fast manifold F, even though the phase difference in y-value remain invariant (up to a precision of $O(\sqrt{\varepsilon})$). We now calculate the time difference by tracking the dynamics on slow manifolds (the lower branch, the upper branch as well as the periodic family).

For the lower branch, the slow dynamics satisfies the equation:

$$\begin{aligned} (v, w)(y) &= L(y), \\ y' &= \varepsilon g(L(y), y), \end{aligned} \tag{6}$$

the time difference in the lower branch is $\Delta T = \int_{y_\rho - z}^{y_\rho} \frac{1}{\varepsilon g(L(y),y)} \, d\, y$ where y_ρ is the parameter value for the right knee. Then on the slow manifold along the periodic family P_α, around the upper branch of the excited equations, we use averaging method [11] to get the slow dynamics for y:

$$\begin{aligned} (v, w)(y) =& P_\alpha(t, y) \\ y' =& \varepsilon g(\bar{P}_\alpha(y), y) + O(\varepsilon^2), \end{aligned} \tag{7}$$

where the average motion $\bar{P}_\alpha(y) = \frac{1}{\pi(y)} \int_0^{\pi(y)} P_\alpha(t, y) \, d\, t$ is the averaged over the period $\pi(y)$. Then the time difference on the periodic branch can also be similarly determined as $\Delta T' = \int_{y_\rho}^{y_\rho - z} \frac{1}{\varepsilon g(\bar{P}_\alpha(y),y)} \, d\, y$.

We now consider that both U_1 and U_2 move along P_α while maintaining time difference invariant and eventually enter U_α, the upper branch to the left of Hopf bifurcation point. They will come near the left knee point P_λ^α. Either U_1 or U_2 will lead to the way as they go through the left knee and eventually jump down to the lower branch L in a similar scenario as in the jumping-ups of U_1 and U_2. The reason of jumping downs, however, is different. The couplings there are not excitatory. When one falls below $-X_c$, the other one is near the left knee of U_α and now follows F_α and then F. Because of H3 and H5, both U_1 and U_2 will move down to the only stable steady state L.

Similarly, we can calculate from the invariant time difference $\Delta T'' = \Delta T'$ when traveling along the upper branch U_α to obtain a horizontal phase difference $\tilde{z}$ at the left knee. Also, $\Delta T'''$, the time difference traveling along the lower branch L can be calculated from the horizontal phase difference $\tilde{z}$, becasue the phase difference is invariant during jumping down.

Now, we summarize by calculating the change of time difference between two neurons for one loop. We note that during the jump, the y-difference is invariant (up to an error of $O(\sqrt{\varepsilon})$), and when traveling in upper or lower branches, the t-difference is invariant. Let the initial difference z be sufficiently small, we have $\Delta T = (\frac{1}{\varepsilon g(L(y),y)}|_{y=y_\rho})z + h.o.t$, $\Delta T' = (\frac{-1}{\varepsilon g(\bar{P}_\alpha(y),y)}|_{y=y_\rho})z + h.o.t$, Then the time difference of ΔT will translate into the phase difference of $\tilde{z}$ at the left knee $\Delta T' = \Delta T'' = (\frac{-1}{\varepsilon g(U_\alpha(y),y)}|_{y=y_\lambda})\tilde{z} + h.o.t$ and the final time difference after returning to L is $\Delta T''' = (\frac{1}{\varepsilon g(L(y),y)}|_{y=y_\lambda})\tilde{z} + h.o.t.$ We note here that because of the Heaviside function type coupling, the systems are decoupled if they are both in L or U_α and P_α, $\Delta T' = \Delta T''$, this is simpler than the direct or indirect synapse cases studied by Terman et al [15].

Therefore we drive the ratio of time difference

$$\frac{\Delta T'''}{\Delta T} = \frac{\Delta T'''}{\Delta T''}\frac{\Delta T''}{\Delta T'}\frac{\Delta T'}{\Delta T} = \frac{g(U_\alpha(y),y)|_{y=y_\lambda} g(L(y),y)|_{y=y_\rho}}{g(L(y),y)|_{y=y_\lambda} g(\bar{P}_\alpha(y),y)|_{y=y_\rho}} + h.o.t. \equiv \sigma \qquad (8)$$

When the null surface of g is close to either the right knee of the lower branch L or the left knee of upper branch U_α, the numerator $g(U_\alpha(y),y)|_{y=y_\lambda} g(L(y),y)|_{y=y_\rho}$ is small and $\sigma < 1$. We derive that given any two solutions of initial difference $z \le z_0$, their time difference will decrease and $\Delta T(t) = O(\sigma^{\frac{t}{\pi_\alpha}})$ where $\pi_\alpha = O(1/\varepsilon)$ is the time duration for traveling on slow manifold L, P_α and U_α once.

Remark: We only discussed simplest senario in local synchronizations, while there are other possible cases of synchronizations. However it does not necessary hold global synchronization. It is also possible the two cells are synchronized but the spikes are completely out of phase. On the other hand, the analysis can be carried to a network of N-neurons, the implication there is that all neurons will form several clusters if they are not completely synchronized. The number of cluster will depend on the coupling strength α [16],[8]. □

5. Discussion.

We are interested in the dynamic patterns that arise during the transaction from unsynchronized chaotic actions of neurons to ultimately synchronized regular neuronal activities as we increase the strength of the synaptic coupling. Some numerical experiments suggested the neurons become regular first as we increases the coupling, and then become synchronized. See Figure 5 for a regular but unsynchronized bursting solution, when $\alpha = 0.05$ in Eq. 4. This is partially understandable that as the parameter region for chaotic behavior to occur in a single neuron is relatively narrow. However this behavior involves some transient dynamics that cannot be entirely determined by one neuron alone, the chaotic behavior for coupled systems remains an open question. We plan to further study the transitional range and the evolution of the dynamical behavior of the system of coupled neurons.

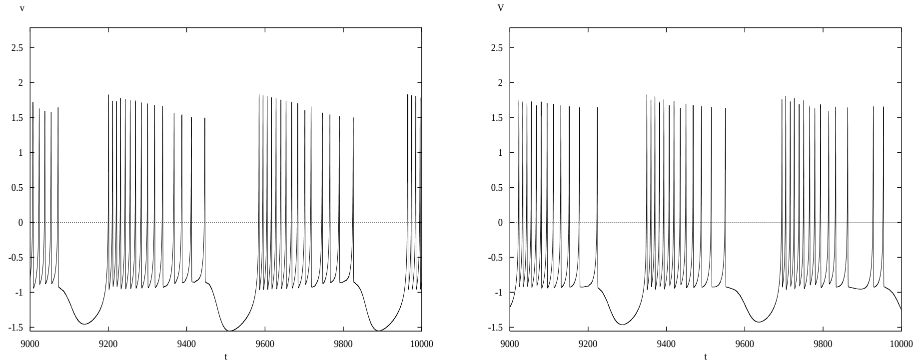

FIGURE 5. For some medium coupling strength, there are regularized bursting solutions of Equation 4. The coupling strength is not strong enough to synchronize the solutions.

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