

SYNCHRONIZATION IN MODEL NETWORKS OF CLASS I NEURONS

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ABSTRACT. We study a modification of the canonical model for networks of class I neurons derived by Hoppensteadt and Izhikevich, in which the ‘pulse’ emitted by a neuron is smooth rather than a δ -function. We prove two types of results about synchronization and desynchronization of such networks, the first type pertaining to ‘pulse’ functions which are symmetric, and the other type in the regime in which each neuron is connected to many other neurons.

1. INTRODUCTION

In the work of Hoppensteadt and Izhikevich [3, 4] a model for networks of class I neurons was derived, which is canonical in the sense that a huge class of detailed and biologically plausible models of weakly-connected neurons near a ‘saddle-node on limit-cycle’ bifurcation can be reduced to it by a piecewise-continuous change of variables. We refer to [4] for the precise conditions under which this reduction is valid, and to [3], chapter 8, for details of the derivation. The canonical model is described by the equations

$$(1) \quad \theta_i' = h(r_i; \theta_i) + \sum_{j=1}^n w(s_{ij}; \theta_j) \delta(\theta_j - \pi), \quad 1 \leq i \leq n,$$

where θ_i is the phase of the i -th neuron, and in which

$$h(r; \alpha) = (1 - \cos(\alpha)) + (1 + \cos(\alpha))r$$

describes the internal dynamics of the i -th neuron (the Ermentrout-Kopell model), which is excitable if $r < 0$ and oscillatory if $r > 0$, $w(s; \alpha)$, which describes the response of neuron i to a pulse from neuron j is the 2π -periodic extension of the function defined for $\alpha \in [-\pi, \pi]$ by

$$(2) \quad w(s; \alpha) = 2 \arctan \left(\tan\left(\frac{\alpha}{2}\right) + s \right) - \alpha,$$

where s is a parameter such that the connection from neuron j to neuron i is excitatory if $s_{ij} > 0$ and inhibitory if $s_{ij} < 0$. An important property of w is that

$$(3) \quad w(s; \pi) = 0 \quad \forall s \in \mathbb{R}$$

which means that the neurons are unaffected by input from other neurons at the moment they are firing. δ is the Dirac delta-function, and the term $\delta(\theta_j - \pi)$ indicates that the neurons fire whenever their phase is π . This δ -term is in fact an approximation of a smooth pulse-like function up to order $O(\sqrt{\epsilon} \log(\epsilon))$, where ϵ is the strength of connections in the ‘unreduced’ model, which is assumed to be small.

A central result of [4], confirming and extending previous numerical and analytical work [2, 1] is that networks of class I neurons *desynchronize*.

In this work we analyze a modified model in which the δ -term is replaced by a smooth 2π -periodic ‘pulse-like’ function $P(\beta)$ satisfying

$$(4) \quad P(\beta) > 0 \quad \forall \beta \in \mathbb{R}.$$

We thus consider networks described by the equations

$$(5) \quad \theta'_i = h(r_i; \theta_i) + \sum_{j=1}^n w(s_{ij}; \theta_j) P(\theta_j), \quad 1 \leq i \leq n$$

In fact the senses in which we shall require P to be ‘pulse-like’ are very weak; indeed a central motivation for investigating the modified model, besides the fact that the model (5), for an appropriate choice of the function P , is actually more precise than (1), is that studying (5) allows us to examine the robustness - and limitations - of the desynchronization results obtained before for the pulse-coupled model. The use of a smooth ‘pulse-like’ function P also requires and allows us to use tools of smooth analysis, leading to interesting mathematical investigations and results. We shall also prove results in which the specific functional forms $h(r; \alpha)$, $w(s; \alpha)$ are replaced by general functions satisfying some of the key qualitative properties of these particular functions. These more general results contribute to elucidating what aspects of the model (1) are responsible for its dynamical behavior.

As in [4], we investigate the issue of synchronization: does there exist a **synchronized oscillation** of the system, *i. e.*, a solution for which $\theta_i(t) = \bar{\theta}(t)$ for all $1 \leq i \leq n$, with

$$(6) \quad \bar{\theta}(t + T) = \bar{\theta}(t) + 2\pi \quad \forall t \in \mathbb{R},$$

for some $T > 0$, and if it exists, is it *stable*? If the answer to both these questions is positive, we say that the network **synchronizes**. Otherwise we say that the network **desynchronizes**.

After some preliminaries in sections 2,3, we present and prove our main results. In section 4 we study the behavior of the model that when the pulse function P is symmetric with respect to π and increasing on $(0, \pi)$, and show that when $r \geq 0$ we have desynchronization. In section 5 we deal with the case of large networks with many connections per neuron, and prove that in this regime, when $P'(\pi) \neq 0$ then synchronization/desynchronization depends only on the local behavior of the ‘pulse-like’ function P near π - if $P'(\pi) > 0$

then desynchronization occurs, while if $P'(\pi) < 0$ the synchronized oscillation is stable.

2. EXISTENCE OF SYNCHRONIZED OSCILLATIONS

In order to ensure existence of a synchronized oscillation, we need to make some assumptions. As in [4], we assume that the internal dynamics of the oscillators are identical, that is,

$$(7) \quad r_i = r, \quad 1 \leq i \leq n$$

In [4] it is assumed that $s_{ij} = s$ for all i, j . In fact less stringent assumptions are sufficient to ensure existence of a synchronized oscillation. We assume that for any i, j ,

$$(8) \quad s_{ij} = 0 \text{ or } s.$$

We note that

$$(9) \quad w(0; \alpha) = 0 \quad \forall \alpha \in \mathbb{R}$$

which means that when $s_{ij} = 0$ neuron j does not influence neuron i . Thus assumption (8) allows for an arbitrary connectivity structure in the network (which can be represented by a directed graph with the neurons as nodes and an arrow from neuron j to neuron i iff $s_{ij} = s$), stipulating only that those connections which exist are identical. This means that we can rewrite (5) in the form

$$(10) \quad \theta'_i = h(r; \theta_i) + \sum_{j=1}^n c_{ij} w(s; \theta_j) P(\theta_j), \quad 1 \leq i \leq n$$

where $c_{ij} = 0$ or 1 for all i, j .

In the case of the ‘delta-coupled’ system (1), under conditions (7), (8), the assumption $r > 0$ is necessary and sufficient to guarantee the existence of a synchronized oscillation; indeed, due to (3), the coupling term vanishes identically if we set $\theta_i = \bar{\theta}$ ($1 \leq i \leq n$), so that the system (1) reduces to

$$\bar{\theta}' = (1 - \cos(\bar{\theta})) + (1 + \cos(\bar{\theta}))r,$$

which has a solution satisfying (6) iff $r > 0$. In the case of the ‘smooth’ system (5), these assumptions are not sufficient, and in order to guarantee that upon substituting $\theta_i = \bar{\theta}$ we get the *same* equation for $\bar{\theta}$ from each of the equations (10) we need to assume further that the number of neurons affecting each neuron is the same, so that the network is ***k*-regular** in the sense that each node in the corresponding directed graph has k incoming arrows, or in other terms that

$$(11) \quad \sum_{j=1}^n c_{ij} = k, \quad 1 \leq i \leq n$$

(note that, in particular, the ‘all-to-all’ coupling case considered in [4] satisfies this assumption). If we assume (11) holds then upon substituting $\theta_i = \bar{\theta}$ ($1 \leq i \leq n$) in any of the equations (10) we obtain

$$\bar{\theta}' = h(r; \bar{\theta}) + kw(s; \bar{\theta})P(\bar{\theta}).$$

This equation will have a solution satisfying (6) iff

$$(12) \quad h(r; \theta) + kw(s; \theta)P(\theta) > 0 \quad \forall \theta \in \mathbb{R}$$

(and this synchronized oscillation is unique up to time-translations). Whether this condition holds depends on the parameters r, s, k . Using the properties of $h(r; \alpha)$, $w(s; \theta)$ and (4), we can easily identify some regimes in which (12) holds or does not hold, so that we have the following result about existence.

Theorem 1. *Consider the network described by (10), and assume that it is k -regular.*

(i) *When $r \geq 0$ and $s > 0$, a synchronized oscillation exists.*

(ii) *When $r \leq 0$ and $s < 0$, a synchronized oscillation does not exist.*

(iii) *When $r > 0$ and $s < 0$:*

(a) *If k is fixed then when $|s|$ is sufficiently small a synchronized oscillation exists.*

(b) *If s is fixed then for k sufficiently large a synchronized oscillation does not exist.*

(iv) *When $r < 0$ and $s > 0$:*

(a) *If k is fixed and $|s|$ sufficiently small a synchronized oscillation does not exist.*

(b) *If s is fixed and k is sufficiently large then a synchronized oscillation exists.*

3. STABILITY OF THE SYNCHRONIZED OSCILLATION

Stability of the synchronized oscillation - in the sense that its Floquet multipliers have modulus less than 1 - is a crucial question: if the synchronized oscillation is unstable we shall never observe synchronization. Since we are dealing here with local stability, even when the synchronized oscillation is stable we cannot guarantee that the network will synchronize whatever the initial conditions, but we do know that it will synchronize for some open set of initial conditions, in particular if these initial conditions are sufficiently close to each other.

In order to investigate the stability of the synchronized oscillation we shall use the following theorem, which is a corollary of theorem 8 of [5], pertaining to networks described by equations of the form

$$(13) \quad \theta_i' = h(\theta_i) + \sum_{j=1}^n c_{ij} f(\theta_i, \theta_j), \quad 1 \leq i \leq n.$$

A network is said to be **irreducible** if it is *not possible* to partition the neurons into two disjoint sets S_1, S_2 so that $c_{ij} = 0$ for all $i \in S_1, j \in S_2$ (in other words, in such a way that neurons in S_2 do not influence neurons in S_1).

Theorem 2. *Consider a network described by equations of the form (13), where h is 2π -periodic and $f(\alpha, \beta)$ is 2π -periodic in both variables. Assume that $c_{ij} \geq 0$ for all i, j , that the network is irreducible and satisfies (11) and that*

$$(14) \quad h(\theta) + kf(\theta, \theta) > 0 \quad \forall \theta \in \mathbb{R}.$$

Then a synchronized oscillation, unique up to time-translations, exists and:

(i) The synchronized oscillation is stable if $\chi > 0$, where χ is defined by

$$(15) \quad \chi = \int_0^{2\pi} \frac{\partial f}{\partial \beta}(\theta, \theta) \frac{d\theta}{h(\theta) + kf(\theta, \theta)}.$$

(ii) The synchronized oscillation is unstable if $\chi < 0$.

4. THE CASE OF A SYMMETRIC PULSE

In this section we make the following assumptions on the smooth 2π -periodic ‘pulse-like’ function $P(\beta)$:

$$(16) \quad P(\pi + \theta) = P(\pi - \theta) \quad \forall \theta \in \mathbb{R}$$

$$(17) \quad P'(\beta) > 0 \quad \forall \alpha \in (0, \pi)$$

Assumption (16) means that the pulse is symmetric with respect to π , and we note that by periodicity it is equivalent to

$$(18) \quad P(\beta) = P(-\beta) \quad \forall \theta \in \mathbb{R}$$

Under these assumptions we shall prove:

Theorem 3. *If $r \geq 0$, P satisfies (4), (16), (17) and the network described by (10) is regular and irreducible, then:*

(i) If $s > 0$ the synchronized oscillation of (10) exists and is unstable.

(ii) If $s < 0$ then a synchronized oscillation of (10) may or may not exist, but if it exists, it is unstable.

Theorem 3 is a consequence of the following more general theorem pertaining to networks described by the equations

$$(19) \quad \theta'_i = h(\theta_i) + \sum_{j=1}^n c_{ij} w(\theta_j) P(\theta_j), \quad 1 \leq i \leq n$$

which does not assume the specific functional forms $h(\alpha) = h(r; \alpha)$, $w(\alpha) = w(s; \alpha)$, but rather only some of the qualitative properties of these functions.

Theorem 4. *Assume the smooth 2π -periodic functions h, w, P satisfy (4), (16), (17) and*

$$(20) \quad h(\alpha) > 0 \quad \forall \alpha \in (0, \pi),$$

$$(21) \quad h(\alpha) = h(-\alpha) \quad \forall \alpha \in \mathbb{R},$$

$$(22) \quad w(-\alpha) > w(\alpha) \quad \forall \alpha \in (0, \pi),$$

and that the network described by (19) is regular and irreducible. Then if a synchronized oscillation of (19) exists, it is unstable.

All the assumptions of theorem 4 hold for the case $h(\alpha) = h(r; \alpha)$, $w(\alpha) = w(s; \alpha)$, $r \geq 0$, so that theorem 3 follows. The only assumption which is not immediate to verify is (22). We need to show

Lemma 5. *If $s \neq 0$ then*

$$(23) \quad w(s; -\alpha) > w(s; \alpha) \quad \forall \alpha \in (0, \pi),$$

To prove lemma 5, we note that using the definition of $w(s; \alpha)$ given by (2), (23) is equivalent to the inequality

$$\arctan(s + \tan(\frac{\alpha}{2})) - \arctan(s - \tan(\frac{\alpha}{2})) < \alpha \quad \forall s \neq 0, \alpha \in (0, \pi).$$

Setting $u = \tan(\frac{\alpha}{2})$, this inequality is equivalent to

$$(24) \quad \arctan(s + u) - \arctan(s - u) < 2 \arctan(u) \quad \forall s \neq 0, u > 0.$$

To prove (24), we *fix* an arbitrary $u > 0$ and we define

$$g(s) = \arctan(s - u) - \arctan(s + u) + 2 \arctan(u).$$

We need to show that $g(s) > 0$ for all $s \neq 0$. We note that $g(0) = 0$ so that it suffices to show that $g'(s) > 0$ for $s > 0$ and $g'(s) < 0$ for $s < 0$. But

$$g'(s) = \frac{1}{1 + (s - u)^2} - \frac{1}{1 + (s + u)^2},$$

and it is easy to check that the expression on the right-hand side is positive when $u > 0$, $s > 0$ and negative when $u > 0$, $s < 0$, completing the proof of lemma 5.

We now prove theorem 4. Assume that a synchronized oscillation of (19) exists, which is equivalent to the assumption

$$(25) \quad h(\theta) + kw(\theta)P(\theta) > 0 \quad \forall \theta \in \mathbb{R}.$$

By theorem 2, with $f(\alpha, \beta) = w(\alpha)P(\beta)$, in order to determine the stability of the synchronized oscillation we need to determine the sign of

$$\chi = \int_{-\pi}^{\pi} \frac{w(\theta)P'(\theta)d\theta}{h(\theta) + kw(\theta)P(\theta)}.$$

We define

$$F(\theta) = \frac{w(\theta)}{h(\theta) + kw(\theta)P(\theta)},$$

so that we can write

$$\chi = \int_{-\pi}^{\pi} F(\theta)P'(\theta)d\theta.$$

We claim that

$$(26) \quad F(-\theta) > F(\theta) \quad \forall \theta \in (0, \pi).$$

To show this, we fix an arbitrary $\theta \in (0, \pi)$, and define the function

$$\Lambda(x) = \frac{x}{h(\theta) + kP(\theta)x},$$

it is easy to verify (in view of (20)) that $\Lambda(x)$ is an increasing function on the interval (x_0, ∞) , where

$$x_0 = -\frac{h(\theta)}{kP(\theta)}.$$

By (20),(25) we have $w(\theta) > x_0$, so (22) implies that $\Lambda(w(-\theta)) > \Lambda(w(\theta))$, which, in view of (18) and (21), is equivalent to (26). We also note that, from (18) we have $P'(-\theta) = -P'(\theta)$ for all θ , hence

$$\int_{-\pi}^0 F(\theta)P'(\theta)d\theta = \int_0^{\pi} F(-\theta)P'(-\theta)d\theta = -\int_0^{\pi} F(-\theta)P'(\theta)d\theta$$

so that

$$\chi = \int_{-\pi}^0 F(\theta)P'(\theta)d\theta + \int_0^{\pi} F(\theta)P'(\theta)d\theta = \int_0^{\pi} (F(\theta) - F(-\theta))P'(\theta)d\theta.$$

Using this, (17) and (26), we obtain $\chi < 0$ which concludes the proof of theorem 4.

In theorem 3 we assumed $r \geq 0$. We now examine the case $r < 0$. If also $s < 0$ then by part (ii) of theorem 1, there does not exist a synchronized oscillation. We thus assume $s > 0$ so that a synchronized oscillation may exist, for example by part (iv)(b) of theorem 1 it exists for k sufficiently large. In the case $r < 0$, $s > 0$, in contrast to the result of theorem 3, it is possible for the conditions (4),(16),(17) to hold and for the synchronized oscillation to be stable. An example is $r = -\frac{1}{2}$, $s = 1$, $P(\beta) = 2 - \cos(\beta)$, $k = 1$. One can check that (25) holds by graphing the function on the right-hand side, so that a synchronized oscillation exists. Computing χ numerically one finds $\chi = 0.085.. > 0$, so that the synchronized oscillation is stable. Thus in this example, in which the uncoupled oscillators are excitable and the coupling is excitatory, the coupling induces synchronization - whereas by theorem 3 (under the stated assumptions on P), when the uncoupled oscillators are oscillatory an excitatory coupling induces desynchronization. To add further surprise, if in the above example

we increase k to $k = 2$, a synchronized oscillation still exists, but now $\chi < 0$ so that it is unstable. Thus, in this example, increasing the connectivity of the network *desynchronizes* the network which was synchronized by sparser coupling!

Let us note, in concluding our investigation of the case of a symmetric pulse, that the property (22) is a key element in the proof of the desynchronization result. Indeed, following the same argument, we can see that if the function w satisfies the reverse inequality $w(-\alpha) < w(\alpha)$ ($\alpha \in (0, \pi)$) then, under the same assumptions on P and h , we will have synchronization. In this connection, it is interesting to examine the simplified version of the model (1), as presented in [4], which consists in replacing $w(s; \alpha)$ by

$$(27) \quad \bar{w}(s; \alpha) = s(1 + \cos(\alpha)).$$

This is the first term in the Taylor expansion of $w(s; \alpha)$ with respect to s , so that it is approximately valid for small s . Since $\bar{w}(s; \alpha) = \bar{w}(s; -\alpha)$, it is immediate that whenever the pulse is symmetric the integral defining χ vanishes. This means that all the Floquet multipliers of the synchronized oscillation are 1 (see the formulas in [5]) so that the synchronized oscillation is ‘neutrally stable’. Thus, for the simplified model we have a ‘weak desynchronization’ result, but to obtain the strict desynchronization the full model is necessary.

5. THE CASE OF MANY CONNECTIONS

In this section we consider the network (10), assuming that it is regular and irreducible and that k , the number of inputs to each neuron, is large (since $k \leq n$ this implies that we are dealing with large networks). We note that from parts (ii) and (iii)(b) of theorem 1, if $s < 0$ then when k is large a synchronized oscillation does not exist, so in the following we assume that $s > 0$. We shall prove

Theorem 6. *Fixing r and $s > 0$, and assuming P is a smooth 2π -periodic function satisfying (4) and*

$$(28) \quad P'(\pi) \neq 0,$$

we have the following results for any irreducible k -regular network described by (10), when k is sufficiently large:

- (i) *If $P'(\pi) > 0$, a synchronized oscillation exists and is unstable.*
- (ii) *If $P'(\pi) < 0$, a synchronized oscillation exists and is stable.*

The striking characteristic of theorem 6 is that it shows that when $P'(\pi) \neq 0$ then in the large- k regime only the local behavior of P at π is responsible for determining synchronization/desynchronization (of course the special significance of the value π is that w vanishes there).

Surprisingly, when $P'(\pi) = 0$ (in particular when P has a maximum at π), the stability criterion is of a quite different nature, in that it depends on the ‘global’ behavior of the P :

Theorem 7. *Fix r and $s > 0$, and assume P satisfies (4) and*

$$(29) \quad P'(\pi) = 0.$$

Define the quantity μ by the improper integral

$$(30) \quad \mu = \int_{-\pi}^{\pi} \frac{h(r; \theta)}{w(s; \theta)} \left(\frac{1}{P(\theta)} \right)' d\theta = \lim_{\gamma \rightarrow 0^+} \int_{-\pi+\gamma}^{\pi-\gamma} \frac{h(r; \theta)}{w(s; \theta)} \left(\frac{1}{P(\theta)} \right)' d\theta.$$

Then for any irreducible k -regular network described by (10), when k is sufficiently large:

- (i) If $\mu < 0$, a synchronized oscillation exists and is unstable.*
- (ii) If $\mu > 0$, a synchronized oscillation exists and is stable.*

We note that the integrand in (30) is singular at $\pm\pi$, hence we have to define the integral as an improper integral. It will follow from the proof of the theorem that μ is finite.

Theorems 6,7 follow from more general results about networks of the form (19) where we do not make use of the specific functional forms of $h(r, \alpha)$, $w(s, \alpha)$ in (10), but only need to assume some of their qualitative properties. We note in particular that the simplified model (27) satisfies the assumptions of the theorems below, so that the theorems 6,7 remain valid if $w(s; \alpha)$ is replaced by (27).

Theorem 6 follows from

Theorem 8. *Let h be a smooth 2π -periodic function satisfying*

$$(31) \quad h(\pi) > 0.$$

Let w be a smooth 2π -periodic function satisfying

$$(32) \quad w(\alpha) > 0 \quad \forall \alpha \in (-\pi, \pi),$$

$$(33) \quad w(\pi) = 0, \quad w'(\pi) = 0, \quad w''(\pi) > 0$$

Let $P(\beta)$ be a smooth 2π -periodic function satisfying (4) and (28). Assume that the network described by (19) is k -regular and irreducible. Then, for sufficiently large k :

- (i) If $P'(\pi) > 0$ then the synchronized oscillation is unstable.*
- (ii) If $P'(\pi) < 0$ then the synchronized oscillation is stable.*

Theorem 7 follows from

Theorem 9. *Let h, w, P be smooth 2π -periodic functions satisfying (4), (29), (31), (32) and (33).*

Then, for sufficiently large k , any k -regular irreducible network described by (19) has a synchronized oscillation which is stable if $\mu > 0$ and unstable if $\mu < 0$, where μ is defined by

$$(34) \quad \mu = \int_{-\pi}^{\pi} \frac{h(\theta)}{w(\theta)} \left(\frac{1}{P(\theta)} \right)' d\theta = \lim_{\gamma \rightarrow 0^+} \int_{-\pi+\gamma}^{\pi-\gamma} \frac{h(\theta)}{w(\theta)} \left(\frac{1}{P(\theta)} \right)' d\theta.$$

To prove the above theorems, we need, according to theorem 2, to study the sign of

$$(35) \quad \chi = \chi(k) = \int_0^{2\pi} \frac{w(\theta)P'(\theta)d\theta}{h(\theta) + kw(\theta)P(\theta)}$$

As $k \rightarrow \infty$.

We note at the outset that we may assume, without loss of generality, that we have

$$(36) \quad h(\alpha) > 0 \quad \forall \alpha \in \mathbb{R}.$$

The reason for this is that if (36) does not hold, we can choose k_0 sufficiently large so that

$$\bar{h}(\alpha) \doteq h(\alpha) + k_0 w(\alpha) P(\alpha) > 0 \quad \forall \alpha \in \mathbb{R}$$

(this follows from the assumptions (4),(31),(32)). Thus defining $\bar{k} = k - k_0$ we have

$$\chi = \int_0^{2\pi} \frac{w(\theta)P'(\theta)d\theta}{\bar{h}(\theta) + \bar{k}w(\theta)P(\theta)}.$$

Thus, we shall henceforth assume (36).

Setting $\epsilon = \frac{1}{\bar{k}}$ we can write

$$\chi\left(\frac{1}{\epsilon}\right) = \epsilon I(\epsilon)$$

where

$$I(\epsilon) = \int_0^{2\pi} \frac{w(\theta)P'(\theta)}{h(\theta)} \frac{d\theta}{\epsilon + \frac{w(\theta)P(\theta)}{h(\theta)}}.$$

We need to determine the sign of $I(\epsilon)$ for $\epsilon > 0$ small. We note first that, using periodicity

$$I(0) = \int_0^{2\pi} \frac{P'(\theta)}{P(\theta)} d\theta = \int_0^{2\pi} \frac{d}{d\theta} [\log(P(\theta))] d\theta = 0.$$

Thus, we need a delicate investigation in order to determine the sign of $I(\epsilon)$ for small $\epsilon > 0$. To simplify our notation, we set

$$(37) \quad A(\theta) = \frac{w(\theta)P'(\theta)}{h(\theta)},$$

$$(38) \quad B(\theta) = \frac{w(\theta)P(\theta)}{h(\theta)},$$

so that

$$(39) \quad I(\epsilon) = \int_0^{2\pi} \frac{A(\theta)d\theta}{\epsilon + B(\theta)}.$$

We now consider the case of theorem 8, so that we assume (28) holds. Together with (32), (33) and (36) this implies

$$A(\pi) = A'(\pi) = 0, \quad \text{sign}(A''(\pi)) = \text{sign}(P'(\pi)),$$

$$(40) \quad B(\theta) > 0 \quad \forall \theta \in (-\pi, \pi),$$

$$(41) \quad B(\pi) = B'(\pi) = 0, \quad B''(\pi) > 0.$$

We may therefore write, for $\theta \in [0, 2\pi]$:

$$A(\theta) = a(\theta - \pi)(\theta - \pi)^2,$$

$$B(\theta) = b(\theta - \pi)(\theta - \pi)^2,$$

where $a, b : [-\pi, \pi] \rightarrow \mathbb{R}$ are continuous, and b is everywhere positive, and

$$(42) \quad \text{sign}(a(0)) = \text{sign}(P'(\pi)).$$

We thus have

$$I(\epsilon) = \int_{-\pi}^{\pi} \frac{a(\theta)\theta^2 d\theta}{\epsilon + b(\theta)\theta^2}.$$

Decomposing into partial fractions we have

$$I(\epsilon) = \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} d\theta - \epsilon \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \frac{d\theta}{\epsilon + b(\theta)\theta^2}.$$

We have

$$\int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} d\theta = \int_0^{2\pi} \frac{A(\theta)}{B(\theta)} d\theta = \int_0^{2\pi} \frac{P'(\theta)}{P(\theta)} d\theta = 0,$$

hence

$$I(\epsilon) = -\epsilon \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \frac{d\theta}{\epsilon + b(\theta)\theta^2}.$$

Substituting $\theta = \sqrt{\epsilon}u$ we obtain

$$I(\epsilon) = -\sqrt{\epsilon} \int_{-\frac{\pi}{\sqrt{\epsilon}}}^{\frac{\pi}{\sqrt{\epsilon}}} \frac{a(\sqrt{\epsilon}u)}{b(\sqrt{\epsilon}u)} \frac{du}{1 + b(\sqrt{\epsilon}u)u^2},$$

and by Lebesgue's dominated convergence theorem we have

$$\lim_{\epsilon \rightarrow 0^+} \frac{I(\epsilon)}{\sqrt{\epsilon}} = -\frac{a(0)}{b(0)} \int_{-\infty}^{\infty} \frac{du}{1 + b(0)u^2}.$$

Thus for small $\epsilon > 0$ we have

$$\text{sign}(\chi) = \text{sign}(I(\epsilon)) = -\text{sign}(a(0)) = -\text{sign}(P'(\pi)),$$

and we obtain the result of theorem 8.

We turn to the proof of theorem 9. We now have, from (4),(29),(32),(33) and (36)

$$A(\pi) = A'(\pi) = A''(\pi) = 0,$$

and also (40), (41). We may therefore write, for $\theta \in [0, 2\pi]$:

$$A(\theta) = a(\theta - \pi)(\theta - \pi)^3$$

$$B(\theta) = b(\theta - \pi)(\theta - \pi)^2$$

where $a, b : [-\pi, \pi] \rightarrow \mathbb{R}$ are continuous, and b is everywhere positive. We can thus write $I(\epsilon)$ as

$$I(\epsilon) = \int_{-\pi}^{\pi} \frac{a(\theta)\theta^3 d\theta}{\epsilon + b(\theta)\theta^2}.$$

We decompose into partial fractions, obtaining

$$I(\epsilon) = \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \theta d\theta - \epsilon \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \frac{\theta d\theta}{\epsilon + b(\theta)\theta^2}.$$

We have

$$\int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \theta d\theta = \int_0^{2\pi} \frac{A(\theta)}{B(\theta)} d\theta = \int_0^{2\pi} \frac{P'(\theta)}{P(\theta)} d\theta = 0,$$

so that

$$I(\epsilon) = -\epsilon \int_{-\pi}^{\pi} \frac{a(\theta)}{b(\theta)} \frac{\theta d\theta}{\epsilon + b(\theta)\theta^2}.$$

We now note that for $\epsilon > 0$

$$\begin{aligned} -\frac{I(\epsilon)}{\epsilon} &= \int_0^{\pi} \frac{a(\theta)}{b(\theta)} \frac{\theta d\theta}{\epsilon + b(\theta)\theta^2} + \int_{-\pi}^0 \frac{a(\theta)}{b(\theta)} \frac{\theta d\theta}{\epsilon + b(\theta)\theta^2} \\ &= \int_0^{\pi} \frac{a(\theta)}{b(\theta)} \frac{\theta d\theta}{\epsilon + b(\theta)\theta^2} + \int_{\pi}^0 \frac{a(-\theta)}{b(-\theta)} \frac{\theta d\theta}{\epsilon + b(-\theta)\theta^2} \\ &= \int_0^{\pi} \theta \left[\frac{a(\theta)}{b(\theta)} \frac{1}{\epsilon + b(\theta)\theta^2} - \frac{a(-\theta)}{b(-\theta)} \frac{1}{\epsilon + b(-\theta)\theta^2} \right] d\theta. \end{aligned}$$

Thus if we define

$$(43) \quad J(\epsilon) = \int_0^{\pi} \theta \left[\frac{a(\theta)}{b(\theta)} \frac{1}{\epsilon + b(\theta)\theta^2} - \frac{a(-\theta)}{b(-\theta)} \frac{1}{\epsilon + b(-\theta)\theta^2} \right] d\theta,$$

we have $I(\epsilon) = -\epsilon J(\epsilon)$ for $\epsilon > 0$. The important point now is that $J(\epsilon)$ makes sense for $\epsilon = 0$, indeed

$$(44) \quad J(0) = \int_0^{\pi} \frac{1}{\theta} \left[\frac{a(\theta)}{(b(\theta))^2} - \frac{a(-\theta)}{(b(-\theta))^2} \right] d\theta,$$

so that the function in the square brackets has a zero at $\theta = 0$, which implies that the integrand is continuous on $[0, \pi]$, hence the integral is well-defined. Thus, if we can ensure that

$$(45) \quad \lim_{\epsilon \rightarrow 0^+} J(\epsilon) = J(0)$$

then we will have

$$(46) \quad I'(0) = \lim_{\epsilon \rightarrow 0^+} \frac{I(\epsilon)}{\epsilon} = -J(0).$$

To prove (45) we use Lebesgue's dominated convergence theorem. The fact that the integrand of (43) converges pointwise to the integrand of (44) as $\epsilon \rightarrow 0^+$ is immediate. Let us show that the integrand of (43) is uniformly bounded:

$$\begin{aligned} & \left| \theta \left[\frac{a(\theta)}{b(\theta)} \frac{1}{\epsilon + b(\theta)\theta^2} - \frac{a(-\theta)}{b(-\theta)} \frac{1}{\epsilon + b(-\theta)\theta^2} \right] \right| \\ & \leq \left| \frac{\theta a(\theta)}{b(\theta)} \left[\frac{1}{\epsilon + b(\theta)\theta^2} - \frac{1}{\epsilon + b(-\theta)\theta^2} \right] \right| + \left| \frac{\theta}{\epsilon + b(-\theta)\theta^2} \left[\frac{a(\theta)}{b(\theta)} - \frac{a(-\theta)}{b(-\theta)} \right] \right| \\ & = \left| \frac{a(\theta)}{b(\theta)} \frac{\theta^3(b(-\theta) - b(\theta))}{(\epsilon + b(\theta)\theta^2)(\epsilon + b(-\theta)\theta^2)} \right| + \left| \frac{\theta}{\epsilon + b(-\theta)\theta^2} \left[\frac{a(\theta)}{b(\theta)} - \frac{a(-\theta)}{b(-\theta)} \right] \right| \\ & \leq \left| \frac{a(\theta)}{b(\theta)} \frac{\theta^3(b(-\theta) - b(\theta))}{(b(\theta)\theta^2)(b(-\theta)\theta^2)} \right| + \left| \frac{\theta}{b(-\theta)\theta^2} \left[\frac{a(\theta)}{b(\theta)} - \frac{a(-\theta)}{b(-\theta)} \right] \right| \\ & = \left| \frac{a(\theta)}{(b(\theta))^2 b(-\theta)} \frac{b(-\theta) - b(\theta)}{\theta} \right| + \left| \frac{1}{(b(-\theta))^2 b(\theta)} \frac{a(\theta)b(-\theta) - b(\theta)a(-\theta)}{\theta} \right|. \end{aligned}$$

Both functions on the right-hand side of the inequality are continuous on $[0, \pi]$ since the numerators vanish at $\theta = 0$, so we have the uniform bound, and we have (46), and thus for small $\epsilon > 0$ we have

$$\text{sign}(\chi) = \text{sign}(I(\epsilon)) = \text{sign}(I'(0)) = -\text{sign}(J(0)).$$

To complete the proof of theorem 9 we only need to show that $J(0) = -\mu$ as defined by (34). And indeed

$$\begin{aligned} & - \int_{-\pi+\gamma}^{\pi-\gamma} \frac{h(\theta)}{w(\theta)} \left(\frac{1}{P(\theta)} \right)' d\theta = \int_{-\pi+\gamma}^{\pi-\gamma} \frac{h(\theta)P'(\theta)}{w(\theta)(P(\theta))^2} d\theta = \int_{\gamma}^{2\pi-\gamma} \frac{h(\theta)P'(\theta)}{w(\theta)(P(\theta))^2} d\theta \\ & = \int_{\gamma}^{2\pi-\gamma} \frac{A(\theta)}{(B(\theta))^2} d\theta = \int_{-\pi+\gamma}^{\pi-\gamma} \frac{1}{\theta} \frac{a(\theta)d\theta}{(b(\theta))^2} = \int_0^{\pi-\gamma} \frac{1}{\theta} \left[\frac{a(\theta)}{(b(\theta))^2} - \frac{a(-\theta)}{(b(-\theta))^2} \right] d\theta. \end{aligned}$$

Going to the limit $\gamma \rightarrow 0^+$, we obtain $-\mu$ on the left-hand side and (since the integrand on the right-hand side is a continuous function) $J(0)$ on the right hand side (note that in particular this proves that the improper integral defining μ exists).

REFERENCES

- [1] G.B. Ermentrout, *Type I membranes, phase resetting curves and synchrony*, Neural Comput. **8** (1996), 979-1001.
- [2] D. Hansel, G. Mato and C. Meunier, *Synchrony in excitatory neural networks*, Neural Comput. **7** (1995), 307-335.
- [3] F.C. Hoppensteadt & E.M. Izhikevich, 'Weakly Connected Neural Networks', Springer-Verlag (New-York), 1997.
- [4] E.M. Izhikevich, *Class 1 neural excitability, conventional synapses, weakly connected networks, and mathematical foundations of pulse-coupled models*, IEEE Trans. Neural Networks **10** (1999), 499-507.
- [5] G. Katriel, *Stability of synchronized oscillations in networks of phase-oscillators*, preprint, <http://arxiv.org/abs/nlin.PS/0308031> .

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