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Analysis of Synchronization in a Neural Population by a Population Density Approach

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Abstract. In this paper we deal with a model describing the evolution in time of the density of a neural population in a state space, where the state is given by Izhikevich's two - dimensional single neuron model. The main goal is to mathematically describe the occurrence of a significant phenomenon observed in neurons populations, the *synchronization*. To this end, we are making the transition to phase density population, and use Malkin theorem to calculate the phase deviations of a weakly coupled population model.

Key words: single neuron model, population density approach, synchronization
AMS subject classification: 92C20, 92D25, 34D10, 35L65

1. Introduction.

It is usually a very complex and tedious task to figure out the population coding and information processing modalities of neuronal populations in experimental contexts involving living models. Thanks to the existing electrophysiological tools and setups, we now have reliable and real-time

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access to various parts of the nervous system signalling activity like isolated spikes or local field potentials recordings. These signals reveal significant but minor fractions of the whole brain (or brain regions) electrical activity and most of the information stream dynamics which are yet essential to a global understanding of its intrinsic properties remain out of sight. Among these network-scale properties, the synchronization mechanisms in large neuronal assemblies is one of the most widely investigated by the neuroscientists since it is known to play key roles in physiological as well as in pathological processes (Dejean et al., 2008; Sheeba et al., 2008). A widespread method to deal with this problem, and more generally to investigate complex biological structures and having a full access to all their components, consists in building their most reliable possible computational model. Its qualitative and quantitative properties are thus made available through the adequate numerical implementation. The validated computer model can then be used by the experimenter as a comprehension and prediction tool and exploited to corroborate, invalidate or foresee working hypotheses. In practical terms, the implementation of these mathematical neuronal models mainly confronts two major issues: (i) the computation power required by neuronal modelling usually involves a drastic trade-off between the network size and model refinement degree (Meunier and Segev, 2002; Izhikevich, 2004) and (ii) the mathematical formalism potentialities of the equations are lost and scaled-down to their numerical schemes (Chauvet, 2005; Bennani et al., 2009). To overcome these two difficulties and to provide innovative tools and formalism to neuroscientists, a population density approach is presented here.

The population density approach has been successfully used until now to describe the evolution of structured populations in the context of demography, epidemiology, economy etc. In these cases, the theoretical framework has been very well developed and certain properties of the solutions - such as stability for example - have been intensively studied. Since we devoted our attention to the study of a population of neurons having an internal structure given by their physiological properties, we find appropriate to use the same method to describe the evolution of neural populations. The main advantage of it lies in the fact that it allows us to obtain an analytical expression that describes the synchronization of the neurons regardless the number of neurons in the population, and consequently, offering us a way of understanding the mechanisms that leads to the occurrence of the phenomenon, and, perhaps, a way of controlling it. The long time behavior of the solution expressing the synchronized state and the conditions under which the stability of such a solution can be achieved represents our next point of interest. In particular, we are interested to highlight the effect of different type of synaptic couplings on the stability of the synchronized solution.

Synchronization of neurons has made the object of investigations, both analytically and numerically, of a number of papers, as [4], [7], [10], [9], to remind just few of them.

We start by considering a neural population composed by a *large* number of neurons, each of them being characterized by a state vector denoted by $w = (v, u)$. The evolution of the state of a

single neuron is described by:

$$\begin{cases} \dot{v}(t) = F^v(v,u), \\ \dot{u}(t) = F^u(v,u), \end{cases} \tag{1.1}$$

where v denotes the *membrane potential* and u is the so-called *recovery variable*. It is assumed that every time membrane's potential v reaches a critical value denoted by v_f, a spike is emitted, v is reset to a reset potential value v_r and u is increased by a fixed value d (v_r, v_f and d are known). Therefore, the reset mechanism is formally described by:

$$v > v_f \Rightarrow v_r \leftarrow v \text{ and } u + d \leftarrow u. \tag{1.2}$$

For the sake of simplicity we are using general notations for the functions that give the evolution of the two state variables, and we will assume regularity properties such that certain behaviors to be obtained. In particular, choosing

$$\begin{cases} F^v(v,u) = 0.04v^2 + 5v + 140 - u + I(t), \\ F^u(v,u) = a(bv - u), \end{cases}$$

we arrive to the *Izhikevich model*, where $\{a, b, v_r, d\}$ are parameters and I is an applied current. For more details about this model see [6].

The Izhikevich model has been proven to admit different behaviors for different choice of parameters, in particular the existence of a periodic limit cycle attractor, which is of a particular interest for us.

The method we are using in this paper (*Population Density Approach*) is based on the following assumptions: the number of neurons in the population is considered large and all the neurons have the same dynamics given by (1.1) and the same coupling pattern. Then, the evolution of the population is described by the dynamics of the *population density function*, $p(t,v,u)$, which satisfies:

$$\int p(t,v,u)\,\mathrm{d}v\,\mathrm{d}u = N,$$

where N is the number of neurons in the population. We are dealing therefore with a population structured by the state variables (v,u). The evolution of $p(t,v,u)$ is given by the conservation law:

$$\frac{\partial}{\partial t} p(t,v,u) = -\mathrm{div} J(t,v,u), \tag{1.3}$$

where J is the neural flux flowing through the state (v,u). It is considered that the flux is divided in two components, a *streaming flux*, $J_s(t,v,u)$, and an *interaction flux*, $J_i(t,v,u)$. The streaming flux is thought as the flux of $p(t,v,u)$ neurons flowing through the state (v,u) at time t, with the

velocity $F(w) = \dot{w}(t)$, where we have denoted $F = (F^v, F^u)$ and $w = (v, u)$. On the other hand, the interaction flux stands for the interactions between a neuron and the rest of the population, and depends on the synaptic afferents from other neurons in the population. We consider it in the form

$$J_i(t, v, u) = \sigma(t)\bar{e}_v \int_{v-\epsilon}^{v} p(t, \tilde{v}, u)\, \mathrm{d}\tilde{v}, \tag{1.4}$$

where σ represents the *average individual spike reception rate* of a single neuron in the population, $\bar{e}_v$ is the unit vector in the direction v, and ϵ is the amplitude of a jump in potential of a neuron when receiving a spike. The variable σ can have various forms, depending on the parameters related to the neural connectivity which can be taken into account. If synaptic delays are considered, then one way to express σ is

$$\sigma(t) = \frac{G}{N} \int_{\tau_-}^{\tau_+} r(t - \tau)\alpha(\tau)\, \mathrm{d}\tau, \tag{1.5}$$

where G is the average number of afferents, N is the number of neurons in the population, $\tau_{\tau_-/+}$ are the extremum values for spike conduction delays, and α is a spike conduction delay kernel. In the following we assume that there is no conduction delay.
The *firing rate* $r(t)$ is given by the flux in the direction $\bar{e}_v$ at the boundary $v = v_f$, i.e.

$$r(t) = \int_{u_{min}}^{u_{max}} J(t, v_f, u)\, \mathrm{d}u\, \bar{e}_v. \tag{1.6}$$

The reset mechanism (1.2) is naturally translated here to the following boundary condition

$$J_v(t, v_r^+, u + d) = J_v(t, v_r^-, u + d) + J_v(t, v_f, u), \tag{1.7}$$

where J_v denotes the component of the flux in the direction $\bar{e}_v$.
The model described above has been introduced by J. Modolo in his Ph.D thesis; a full description of the model as well as extensions of it and numerical results can be found in [12], [13], [14], [15].

2. The weakly-coupled neurons case

In what follows we will assume that the amplitude of the jump in the potential of a neuron which receives a spike satisfy

$$\epsilon \ll 1,$$

and we approximate

$$\int_{v-\epsilon}^{v} p(t, \tilde{v}, u)\, \mathrm{d}\tilde{v} \approx \epsilon p(t, v, u)$$

by ignoring the second order terms in ϵ. Then, the conservation law simplifies to

$$\frac{\partial}{\partial t} p(t, v, u) = -\mathrm{div}\left[\left(F(v, u) + \epsilon\sigma(t)\bar{e}_v\right) p(t, v, u)\right]. \tag{2.1}$$

As we argued at the beginning, our main goal is to derive the phase density model in the case of weakly coupled neurons via specific tools of weakly perturbed systems theory. Therefore we start by considering the uncoupled case of the population density approach model, i.e. the conservation law is given by:

$$\frac{\partial}{\partial t}p(t,v,u) = -\text{div}\left[F(v,u)p(t,v,u)\right], \tag{2.2}$$

which can be written equivalently along the trajectories as

$$\frac{\mathrm{d}}{\mathrm{d}t}p(t,v(t),u(t)) = -\text{div}\left[F(v(t),u(t))\right]p(t,v(t),u(t)), \tag{2.3}$$

where the evolution of (v,u) is given by (1.1) together with initial conditions and the reset mechanism described by (1.2).

We assume in the following the existence of a stable limit cycle attractor C for (1.1) and that it has an attractive normally hyperbolic compact invariant manifold. In the Izhikevich model's case, it has been shown (see [6]) that there exists I such that the model admits a stable limit cycle corresponding to periodic spiking. Then we suppose that the neural population is distributed along this periodic trajectory, and consider next the weakly coupled case. Note that the evolution of weakly-coupled population densities is also given by (2.3) but now along the weakly perturbed trajectories described by

$$\begin{cases} \dot{v}(t) = F^v(v(t),u(t)) + \epsilon\sigma(t), \\ \dot{u}(t) = F^u(v(t),u(t)). \end{cases} \tag{2.4}$$

Then (see for example [5], Theorem 4.1), the perturbed system has an attractive normally hyperbolic invariant manifold ω_ϵ which is an ϵ-perturbation of the original one. For ϵ small enough we take a stable neighborhood W of ω_ϵ such that it includes C in it, and then fix the domain $D = [v_{min}, v_f] \times [u_{min}, u_{max}]$ such that $W \subset D$. Therefore, considering the dynamics of (2.3) in the domain D, we can see that the active part of the boundary ∂D is $(\{v_f\} \times (u_{min}, u_{max})) \bigcap W$, and, we can assume without loss of generality that $p = 0$ for the rest of the boundary.

Then, the evolution of the weakly coupled population is given by:

$$\begin{cases} \frac{\partial}{\partial t}p(t,v,u) = -\text{div}\left[(F(v,u)+\epsilon\sigma(t))p(t,v,u)\right], & t>0, (v,u)\in D, \\ J_v(t,v_r^+,u+d) = J_v(t,v_r^-,u+d) + J_v(t,v_f,u), & t \geq 0 \\ p(0,v,u) = p_0(v,u), & (v,u)\in W \\ \text{with } p_0(u,v) = 0 & (v,u)\in D\setminus W \\ p(t,v,u) = 0, & t\geq 0, (v,u)\in \partial D\setminus \Gamma_l, \end{cases} \tag{2.5}$$

with $\Gamma_l = (\{v_f\} \times (u_{min}, u_{max})) \bigcap W$.
Under these conditions the support of $p(t, u, v)$ remains in W. Correspondingly, the evolution of an uncoupled population is given by

$$\begin{cases} \frac{\partial}{\partial t} p(t, v, u) = -\text{div}\left[F(v, u)p(t, v, u)\right], & t > 0, (v, u) \in D, \\ J_v(t, v_r^+, u + d) = J_v(t, v_r^-, u + d) + J_v(t, v_f, u), & t \geq 0 \\ p(0, v, u) = p_0(v, u), & (v, u) \in W \\ \text{with } p_0(u, v) = 0 & (v, u) \in D \setminus W \\ p(t, v, u) = 0, & t \geq 0, (v, u) \in \partial D \setminus \Gamma_l, \end{cases} \tag{2.6}$$

Let us look more closely at the problems we defined above. Since we consider in the uncoupled case (2.6) the neural population distributed along the limit cycle, solving the problem means integrating the differential equation (2.3) on the limit cycle given by (1.1). Note that a discontinuity occurs at the time of the spike t_s, but, the problem is well defined also after the time t_s since we can solve the same equation starting with an initial condition at time t_s^+, initial condition which is given by $(2.6)_2$. Since the trajectory we integrate on is periodic, then $(v(t), u(t))$ remain bounded for all $t \geq 0$, which makes the problem to be well-posed for all $t \geq 0$.
In the weakly coupled case, the equation $(2.5)_1$ can be written also in the form (2.3), with the only difference that the trajectories on which we integrate are given now by (2.4). So, we can argue in the same way the extension of the solution after the times of spikes, but, in this case, the integration along the trajectories is restricted for the case when the trajectories defined by (2.4) do not cross.

3. Phase equations. Malkin theorem.

The first step we take in this section is to derive a phase density model corresponding to the uncoupled population in the specific case we mentioned, i.e. when the population is distributed along the limit cycle. We consider next the weakly perturbed trajectories with respect to the limit cycle, which will correspond to the weakly connected population, and see how the model changes in this case. We mention that in the case of discrete neural networks, an adapted model of Malkin theorem has been given in [5].

Let us consider thus first the case of a uncoupled neural population, therefore the conservation law is given by:

$$\frac{\partial}{\partial t} p(t, v, u) + \text{div}\left(F(v, u)p(t, v, u)\right) = 0, \quad t > 0, \ (v, u) \in D, \tag{3.1}$$

or, equivalently (2.3), and the evolution of the state of a single neuron is given by the system (1.1) introduced in the first section. In order to avoid confusion, we will denote by $(\tilde{v}, \tilde{u})$ the stable limit

cycle attractor. Obviously, $(\tilde{v}, \tilde{u})$ is a periodic solution to the system (1.1), and we denote by T its period. We want to describe next the activity on the limit cycle in terms of its *phase* of oscillation. To this end, let us denote by $\theta(t) = \theta_0 + t$, $t \geq 0$, the *natural phase* of the limit cycle, where $\theta_0 \in [0, T)$ denotes the initial phase; then

$$\dot{\theta} = 1.$$

Without loss of generality, we can choose θ such that the next spike arrival corresponds to the phase $\theta = T$. The parametrization of the curve is given by the mapping $(\tilde{v}, \tilde{u}) : [0, T) \mapsto \mathbf{R}^2$,

$$(\tilde{v}, \tilde{u})(\theta(t)) = (v(\theta(t)), u(\theta(t))),$$

and $(\tilde{v}, \tilde{u})(\theta(t))$ is a solution to:

$$\begin{aligned} \frac{\mathrm{d}\tilde{v}(\theta(t))}{\mathrm{d}t} &= F^v(\tilde{v}, \tilde{u})\dot{\theta}, \quad t \in [0, t_s), \\ \frac{\mathrm{d}\tilde{u}(\theta(t))}{\mathrm{d}t} &= F^u(\tilde{v}, \tilde{u})\dot{\theta}, \quad t \in [0, t_s). \end{aligned}$$

The reset mechanism will take place at $\theta = T(= \theta(t_s))$ and is described by $(\tilde{v}(T), \tilde{u}(T)) \mapsto (v_r, \tilde{u}(T) + d) = (v_r, \tilde{u}_0)$, due to the periodicity of $(\tilde{v}, \tilde{u})$.

The next step is to make the transition from the population densities in the state space, to phase densities populations. Let us denote by $\tilde{p}(t, s)$ the distribution at moment t along the periodic trajectory, i.e., denoting by $C = trace(\gamma)$,

$$p = \tilde{p}(t, s)\delta_C,$$

where δ is the Dirac function and s is the arclength. Since p satisfies (3.1), it follows that, for $\zeta \in \{f \in C^\infty([0, \infty) \times [0, T] \times [0, T]); f -$ periodic function in the last two arguments and with compact support w.r.t. first argument$\}$,

$$\begin{aligned} &\int_0^T \int_D \left(\frac{\partial}{\partial t} p(t, v, u) + \frac{\partial}{\partial u}(F^u(v, u)p(t, v, u)) + \frac{\partial}{\partial v}(F^v(v, u)p(t, v, u)) \right) \zeta(t, v, u)\, \mathrm{d}u\, \mathrm{d}v\, \mathrm{d}t \\ &= -\int_0^T \int_D p(t, v, u) \left(\frac{\partial}{\partial t}\zeta(t, v, u) + F(v, u) \cdot \nabla\zeta \right) \mathrm{d}u\, \mathrm{d}v\, \mathrm{d}t \\ &= -\int_0^T \int_C \tilde{p}(t, s) \left(\frac{\partial \zeta}{\partial t} + F \cdot \nabla\zeta \right) \mathrm{d}s\, \mathrm{d}t. \end{aligned}$$

We choose the test function ζ such that:

$$\begin{aligned} \zeta(v, u) &= \psi(s), \\ \nabla\zeta &= \frac{\mathrm{d}\psi}{\mathrm{d}s}(\tau_v, \tau_u), \end{aligned}$$

where $\tau = (\tau_v, \tau_u)$ is the tangent unit vector. Then

$$\int_0^T \int_C \tilde{p}(t,s) \left(\frac{\partial \zeta}{\partial t} + F \cdot \nabla \zeta \right) \mathrm{d}s \, \mathrm{d}t =$$
$$= \int_0^T \int_C \psi(s) \left(\frac{\partial \tilde{p}(t,s)}{\partial t} + \frac{\partial}{\partial s}[(F \cdot \tau)\tilde{p}(t,s)] \right) \mathrm{d}s \, \mathrm{d}t.$$

Taking

$$\tau = \left(\frac{\mathrm{d}\tilde{v}}{\mathrm{d}s}, \frac{\mathrm{d}\tilde{u}}{\mathrm{d}s} \right) = \left(\frac{\mathrm{d}\tilde{v}/\,\mathrm{d}t}{\mathrm{d}s/\,\mathrm{d}t}, \frac{\mathrm{d}\tilde{u}/\,\mathrm{d}t}{\mathrm{d}s/\,\mathrm{d}t} \right) = \left(\frac{F^v}{\dot{s}}, \frac{F^u}{\dot{s}} \right),$$

then

$$F \cdot \tau = \frac{F^2}{\dot{s}} = \dot{s}.$$

Therefore, on the periodic trajectory $(\tilde{v}, \tilde{u})$, the evolution of population density is given by the following equation:

$$\frac{\partial}{\partial t}\tilde{p}(t,s) + \frac{\partial}{\partial s}\left(\tilde{p}(t,s)\dot{s}\right) = 0, \quad t \in [0, t_s), \tag{3.2}$$

and since the population is distributed on the limit cycle, we can extend it by periodicity to $t > 0$ (we use the same argument in the following computations) . We define the *phase density* $q(t,\theta)$ such that the following relation holds:

$$q(t,\theta)\,\mathrm{d}\theta = \tilde{p}(t,s)\,\mathrm{d}s, \tag{3.3}$$

which implies that

$$q(t,\theta) = \tilde{p}(t,s)\frac{\mathrm{d}s}{\mathrm{d}\theta} = \tilde{p}(t,s)\frac{\mathrm{d}s}{\mathrm{d}t}\frac{\mathrm{d}t}{\mathrm{d}\theta}.$$

Let us compute now the total derivative of q defined as above with respect to t:

$$\begin{aligned}
\frac{\mathrm{d}}{\mathrm{d}t}q(t,\theta(t)) &= \frac{\mathrm{d}}{\mathrm{d}t}\left(\tilde{p}(t,s)\dot{s}\right) \\
&= \dot{s}\frac{\partial}{\partial t}\tilde{p}(t,s) + \ddot{s}\tilde{p}(t,s) + \dot{s}^2\frac{\partial}{\partial s}\tilde{p}(t,s) \\
&= \dot{s}\left(\frac{\partial}{\partial t}\tilde{p}(t,s) + \frac{\ddot{s}}{\dot{s}}\tilde{p}(t,s) + \dot{s}\frac{\partial}{\partial s}\tilde{p}(t,s)\right) \\
&= \dot{s}\left(\frac{\partial}{\partial t}\tilde{p}(t,s) + \frac{\partial}{\partial s}\left(\tilde{p}(t,s)\dot{s}\right)\right) \\
&= 0.
\end{aligned}$$

We obtained thus

$$\frac{\mathrm{d}}{\mathrm{d}t}q(t,\theta(t)) = 0, \quad t > 0,$$

which is equivalent to

$$\frac{\partial}{\partial t}q(t,\theta) + \dot{\theta}\frac{\partial}{\partial \theta}q(t,\theta) = 0, \quad t > 0, \quad \theta \in (0,T), \tag{3.4}$$

and, since $\dot{\theta} = 1$,

$$\frac{\partial}{\partial t} q(t,\theta) + \frac{\partial}{\partial \theta} q(t,\theta) = 0, \quad t > 0, \quad \theta \in (0,T). \tag{3.5}$$

The boundary condition reads:

$$q(t,0) = q(t,T), \quad t \geq 0.$$

Let us consider next the weakly connected system, i.e. (2.5), where

$$\sigma(t) = c_0 \int_{u_{min}}^{u_{max}} J_v(t, v_f, u)\, \mathrm{d}u,$$

(c_0 is a constant), and in our case:

$$J_v(t,v,u) = (F^v(v,u) + \epsilon\sigma(t))p(t,v,u).$$

We remind that, in this case, the evolution of a single neuron is given by:

$$\begin{cases} \dot{v}(t) = F^v(v,u) + \epsilon\sigma(t), & t \in [0,t_s), \\ \dot{u}(t) = F^u(v,u), & [0,t_s), \end{cases} \tag{3.6}$$

and, at the spike moment t_s the reset condition takes place. The solution to the above system will be denoted by (v^ϵ, u^ϵ).

We consider next the corresponding phase density to the perturbed system, $q^\epsilon(t,\tau,\theta^\epsilon)$, i.e. the population density having at time t the phase θ^ϵ, where by θ^ϵ we denote the *perturbed* phase. The dependence of q^ϵ on the variable τ will be explained later. The goal is to derive the phase density equation for q^ϵ, as in the uncoupled case. For that, we shall look first at the changes produced in the evolution of the perturbed phase. For every $\theta_0 \in [0,T)$ an initial phase, the corresponding perturbed phase at time t will be given by

$$\theta^\epsilon = \theta_0 + t + \varphi(\tau,\theta_0),$$

with φ slow phase deviations due to the weak connections, and τ the slow time.

Then, for any $t \in [0,t_s)$ such that $\theta^\epsilon < T$, the corresponding perturbed trajectory can be written in terms of phase deviation and small perturbation with respect to the unperturbed trajectory as:

$$\begin{cases} v^\epsilon(t) = \tilde{v}(\theta_0 + t + \varphi(\tau,\theta_0)) + \epsilon y_1(\theta_0 + t + \varphi(\tau,\theta_0)), \\ u^\epsilon(t) = \tilde{u}(\theta_0 + t + \varphi(\tau,\theta_0)) + \epsilon y_2(\theta_0 + t + \varphi(\tau,\theta_0)). \end{cases} \tag{3.7}$$

In the above expression, (v^ϵ, u^ϵ) are evaluated at time t which corresponds to an unperturbed state $(\tilde{v}, \tilde{u})$ on the orbit C with phase $\theta_0 + t + \varphi(\tau,\theta_0)$. We choose the functions (y_1, y_2) periodic with

the same period as $(\tilde{v}, \tilde{u})$, and since $\tilde{v}$, $\tilde{u}$ satisfy the reset relations, (u^ϵ, v^ϵ) will satisfy the reset relations (up to an $O(\epsilon)$ correction.)

The following theorem is the main result of this section.

Theorem 1. (Malkin)

Consider the uncoupled system (2.6) and suppose that the corresponding single neuron dynamics given by (1.1) have an exponentially orbitally stable periodic solution $(\tilde{v}, \tilde{u})$. Let us consider next the weakly coupled system (2.5) with the corresponding single neuron dynamics given by (3.6), and denote $\tau = \epsilon t$ the slow time, and φ the slow phase deviations from the natural oscillation $(\tilde{v}(t), \tilde{u}(t))$. Then φ is a solution to

$$\frac{\mathrm{d}\varphi(\tau, \theta_0)}{\mathrm{d}\tau} = H(\varphi), \quad \forall \theta_0 \in (0, T), \quad \forall \tau > 0, \tag{3.8}$$

where

$$H(\varphi) = \frac{c_0 \dot{s}(T)}{T} \int_0^T q^\epsilon(t - \theta_0 - \varphi(\tau, \theta_0), \tau, T) \lambda_1(t) \, \mathrm{d}t, \tag{3.9}$$

and λ is the unique nontrivial periodic solution to the adjoint system

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}t}\lambda_1(t, \varphi) = -\dfrac{\partial F^v}{\partial v}(\tilde{v}, \tilde{u})\lambda_1(t, \varphi) - \dfrac{\partial F^u}{\partial v}(\tilde{v}, \tilde{u})\lambda_2(t, \varphi), & t \in [0, T), \\ \dfrac{\mathrm{d}}{\mathrm{d}t}\lambda_2(t, \varphi) = -\dfrac{\partial F^v}{\partial u}(\tilde{v}, \tilde{u})\lambda_1(t, \varphi) - \dfrac{\partial F^u}{\partial u}(\tilde{v}, \tilde{u})\lambda_2(t, \varphi), & t \in [0, T), \end{cases} \tag{3.10}$$

satisfying the normalization condition

$$\lambda(0) \cdot F(\tilde{v}(0), \tilde{u}(0)) = 1.$$

Proof. In the following, wherever there are missing arguments of a variable, it should be understood that it is calculated in $(\theta_0 + t + \varphi(\tau, \theta_0))$; this in done in order to avoid overnotation.

We linearize first the functions in (3.6) with respect to $(\tilde{v}, \tilde{u})$, and obtain:

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}t} v^\epsilon(t) = F^v(\tilde{v}, \tilde{u}) + \epsilon \nabla F^v(\tilde{v}, \tilde{u}) \cdot y + \epsilon \sigma(t), & t \in [0, T), \\ \dfrac{\mathrm{d}}{\mathrm{d}t} u^\epsilon(t) = F^u(\tilde{v}, \tilde{u}) + \epsilon \nabla F^u(\tilde{v}, \tilde{u}) \cdot y, & t \in [0, T), \end{cases} \tag{3.11}$$

where we denoted $y = (y_1, y_2)$. We remind that the expression of σ is given by:

$$\sigma(t) = c_0 \int_{u_{min}}^{u_{max}} J_v(t, v_f, u) \, \mathrm{d}u,$$

where J_v was the flux in the direction v calculated at the firing threshold v_f; we want thus to express σ in terms of phase densities and to approximate it with respect to the periodic trajectory

$(\tilde{v}, \tilde{u})$, as we have done with the rest of the functions. First notice that, for each trajectory, the firing threshold v_f corresponds to the phase T. Then we can write the flux at the firing threshold as the speed on each perturbed trajectory calculated in the phase T multiplied by the phase densities population on the corresponding trajectory. Linearizing it with respect to the periodic trajectory, and keeping into account that, since the perturbation is small (of the order ϵ), then the perturbation of the periods of the perturbed trajectories are of the same order, therefore we can approximate the speed on each trajectory at phase T with the speed on the periodic trajectory at the same phase, by neglecting the terms of second order in ϵ. Then the total flux is given by:

$$\sigma(t) = c_0 \dot{s}(T) q^\epsilon(t, \tau, T), \tag{3.12}$$

where $\dot{s}(T) = ((F^v(\tilde{v}(T), \tilde{u}(T)))^2 + (F^u(\tilde{v}(T), \tilde{u}(T))^2))^{1/2}$.

Differentiating now (3.7) with respect to t, we obtain:

$$\begin{cases} \dfrac{\mathrm{d}v^\epsilon}{\mathrm{d}t}(t) = \dfrac{\mathrm{d}\tilde{v}}{\mathrm{d}t}\left(1 + \epsilon \dfrac{\mathrm{d}}{\mathrm{d}\tau}\varphi(\tau, \theta_0)\right) + \epsilon \dfrac{\mathrm{d}y_1}{\mathrm{d}t}, & t \in [0, T), \\ \dfrac{\mathrm{d}u^\epsilon}{\mathrm{d}t}(t) = \dfrac{\mathrm{d}\tilde{u}}{\mathrm{d}t}\left(1 + \epsilon \dfrac{\mathrm{d}}{\mathrm{d}\tau}\varphi(\tau, \theta_0)\right) + \epsilon \dfrac{\mathrm{d}y_2}{\mathrm{d}t} & t \in [0, T). \end{cases} \tag{3.13}$$

Here and in the following φ is taken as a parameter.

Taking into consideration (3.11) and (3.13) it follows (after dividing by ϵ):

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}t} y_1 = \nabla F^v(\tilde{v}, \tilde{u}) \cdot y + b_1, \\ \dfrac{\mathrm{d}}{\mathrm{d}t} y_2 = \nabla F^u(\tilde{v}, \tilde{u}) \cdot y + b_2. \end{cases} \tag{3.14}$$

We are looking for (y_1, y_2) periodic of period T satisfying these equations. In the above expressions we have denoted:

$$b_1 = c_0 \dot{s}(T) q^\epsilon(t, \tau, T) - F^v(\tilde{v}, \tilde{u}) \frac{\mathrm{d}}{\mathrm{d}\tau}\varphi(\tau, \theta_0),$$

and

$$b_2 = -F^u(\tilde{v}, \tilde{u}) \frac{\mathrm{d}}{\mathrm{d}\tau}\varphi(\tau, \theta_0).$$

The above system is a linear nonhomogeneous one, and to study the existence and uniqueness of the solutions one must consider the *adjoint* linear homogeneous system for the adjoint variable $\lambda(\theta_0 + t + \varphi) := \lambda(t, \varphi)$, with $\lambda = (\lambda_1, \lambda_2)$:

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}t}\lambda_1(t, \varphi) = -\dfrac{\partial F^v}{\partial v}\lambda_1(t, \varphi) - \dfrac{\partial F^u}{\partial v}\lambda_2(t, \varphi), & t \in [0, T), \\ \dfrac{\mathrm{d}}{\mathrm{d}t}\lambda_2(t, \varphi) = -\dfrac{\partial F^v}{\partial u}\lambda_1(t, \varphi) - \dfrac{\partial F^u}{\partial u}\lambda_2(t, \varphi), & t \in [0, T), \end{cases} \tag{3.15}$$

where the functions with missing arguments are calculated in $(\tilde{v}(\theta_0 + t + \varphi(\tau, \theta_0)), \tilde{u}(\theta_0 + t + \varphi(\tau, \theta_0)))$.

We take the following normalization condition:

$$\frac{1}{T}\int_0^T (F^v(\tilde{v}, \tilde{u})\lambda_1(t, \varphi) + F^u(\tilde{v}, \tilde{u})\lambda_2(t, \varphi))\,\mathrm{d}t = 1.$$

We impose the condition $\lambda(T) = \lambda(0)$, and using Fredholm's alternative, the system (3.14) has a unique periodic solution if and only if the orthogonality condition

$$\frac{1}{T}\int_0^T \lambda(t, \varphi(\tau, \theta_0)) \cdot b(\theta_0 + t + \varphi(\tau, \theta_0))\,\mathrm{d}t = 0 \tag{3.16}$$

is satisfied. Replacing b in the above expression and taking into account the normalization condition, we get:

$$\frac{\mathrm{d}\varphi(\tau, \theta_0)}{\mathrm{d}\tau} = \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(t, \varphi(\tau, \theta_0))q^\epsilon(t, \tau, T)\,\mathrm{d}t.$$

The above result was obtain for the time interval $[0, T)$, and it allows us to compute the evolution in slow time of the phase deviations during an inter-spike interval. The results can be extended for all intervals $[nT, (n+1)T)$, $n \in \mathbf{N}$ by taking the initial values $\lambda(nT^+) = \lambda(0)$, $y(nT^+) = y(0)$, $n \in \mathbf{N}^*$.

Notice now that the solutions to the adjoint system satisfy $\lambda(\theta_0 + t + \varphi, 0) = \lambda(t, \varphi)$, therefore it suffices to find a solution to the adjoint system corresponding to $\theta_0 + \varphi = 0$.

Thus we can write

$$\begin{aligned}\frac{\mathrm{d}\varphi(\tau, \theta_0)}{\mathrm{d}\tau} &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(\theta_0 + t + \varphi(\tau, \theta_0), 0)q^\epsilon(t, \tau, T)\,\mathrm{d}t \\ &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(s, 0)q^\epsilon(s - \theta_0 - \varphi(\tau, \theta_0), \tau, T)\,\mathrm{d}s \\ &:= H(\varphi(\tau, \theta_0)).\end{aligned}$$

Moreover, it is obvious that $F(\tilde{v}, \tilde{u})$ is a solution to the homogeneous linear problem

$$\dot{z}(t) = \nabla F(\tilde{v}(t), \tilde{u}(t))z(t),$$

and $\lambda(t, 0)$ is a solution to the adjoint linear system

$$\dot{\lambda} = -(\nabla F(\tilde{v}(t), \tilde{u}(t)))^\top \lambda.$$

Any such solution satisfies

$$\lambda(t, 0) \cdot z(t) = \text{const}, \quad \forall t \geq 0,$$

and from the normalization condition we get that

$$\lambda(t, 0) \cdot z(t) = \lambda(t, 0) \cdot F(\tilde{v}(t), \tilde{u}(t)) = 1, \quad \forall t \geq 0,$$

and in particular for $t = 0$, which allows us to rewrite the normalization condition as

$$\lambda(0) \cdot F(\tilde{v}(0), \tilde{u}(0)) = 1.$$

□

We remind that

$$\theta^\epsilon = \theta_0 + t + \varphi(\tau, \theta_0),$$

and the phase on the limit cycle was given by

$$\theta = \theta_0 + t.$$

Since the density along the perturbed trajectory should satisfy

$$q(t, \theta)\, \mathrm{d}\theta = q^\epsilon(t, \tau, \theta^\epsilon)\, \mathrm{d}\theta^\epsilon,$$

it follows that

$$q(t, \theta) = q^\epsilon(t, \tau, \theta^\epsilon) \frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}\theta}.$$

Differentiating with respect to t the above equality, and taking into account that $\frac{\mathrm{d}}{\mathrm{d}t} q(t, \theta) = 0$, we obtain that the following relation holds:

$$\frac{\mathrm{d}}{\mathrm{d}t} \left[q^\epsilon(t, \tau, \theta^\epsilon) \frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}\theta} \right] = 0.$$

Writing

$$\frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}\theta} = \frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}t} \frac{\mathrm{d}t}{\mathrm{d}\theta} = \frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}t},$$

and since $\frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}t} := g(\theta^\epsilon)$, it follows that

$$\begin{aligned} \frac{\mathrm{d}}{\mathrm{d}t} \left[q^\epsilon(t, \tau, \theta^\epsilon) \frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}\theta} \right] &= g(\theta^\epsilon) \frac{\mathrm{d}}{\mathrm{d}t} q^\epsilon(t, \tau, \theta^\epsilon) + q^\epsilon(t, \tau, \theta^\epsilon) \frac{\mathrm{d}}{\mathrm{d}t} g(\theta^\epsilon) \\ &= g(\theta^\epsilon) \left[\frac{\mathrm{d}}{\mathrm{d}t} q^\epsilon(t, \tau, \theta^\epsilon) + g'(\theta^\epsilon) q^\epsilon(t, \tau, \theta^\epsilon) \right] \\ &= 0. \end{aligned}$$

Dividing the last expression by g, we get

$$\frac{\mathrm{d}}{\mathrm{d}t} q^\epsilon(t, \tau, \theta^\epsilon) + g'(\theta^\epsilon) q^\epsilon(t, \tau, \theta^\epsilon) = 0,$$

or, equivalently

$$\frac{\partial}{\partial t} q^\epsilon(t, \tau, \theta^\epsilon) + \frac{\partial}{\partial \theta^\epsilon} (\dot{\theta}^\epsilon q^\epsilon(t, \tau, \theta^\epsilon)) = 0.$$

Having in mind the expression of θ^ϵ, we get:

$$\begin{aligned}\frac{\mathrm{d}\theta^\epsilon}{\mathrm{d}t} &= 1+\epsilon\frac{\mathrm{d}\varphi}{\mathrm{d}\tau}\\ &= 1+\epsilon H(\varphi),\end{aligned}$$

where $H(\varphi)$ is given by (3.9).

Therefore we arrived to the following system of equations for the phase densities of the perturbed system:

$$\begin{cases}\dfrac{\partial}{\partial t}q^\epsilon(t,\tau,\theta^\epsilon)+\dfrac{\partial}{\partial\theta^\epsilon}\left[(1+\epsilon H(\varphi(\tau,\theta_0)))q^\epsilon(t,\tau,\theta^\epsilon)\right]=0, & t\geq 0,\ \theta^\epsilon\in(0,T),\\ q^\epsilon(t,\tau,0)=q^\epsilon(t,\tau,T), & t\geq 0,\\ q^\epsilon(0,\tau,\theta^\epsilon)=q_0^\epsilon(\theta^\epsilon), & \theta^\epsilon\in[0,T).\end{cases}\tag{3.17}$$

Actually, since q^ϵ evolves in two different time-scales, the *slow* and *fast* times, we are looking for an expression of q^ϵ in the following form:

$$q^\epsilon(t,\tau,\theta^\epsilon)=\bar{q}^\epsilon(\tau,\theta^\epsilon)+\tilde{q}^\epsilon(t,\tau,\theta^\epsilon),\tag{3.18}$$

where $\bar{q}^\epsilon$ is the *mean* part of q^ϵ and $\tilde{q}^\epsilon$ is its *oscillating* part. For the sake of generality we choose in the following $t\in[nT,(n+1)T)$, i.e. an inter-spike interval. We make the choice of oscillating and mean part such that, the evolution of the oscillation part, $\tilde{q}^\epsilon$, to describe the periodic behavior of the phase-densities in every inter-spike interval, therefore we will impose the periodicity in t (the fast time), but also the periodicity in θ^ϵ which is due to (3.17).
On the other hand, $\bar{q}^\epsilon$ will describe the phase density evolution in slow time, and again, we have the periodicity of $\bar{q}^\epsilon$ with respect to θ^ϵ given by the original system.
We must choose then $\tilde{q}^\epsilon$ such that to be periodic with respect to t and to have the mean equal to zero, i.e.

$$\int_{nT}^{(n+1)T}\tilde{q}(t,\tau,\theta^\epsilon)\,\mathrm{d}t=0.\tag{3.19}$$

If we replace the expression of q^ϵ (3.18) in (3.17) and regroup the terms with ϵ, we obtain two equations for $\tilde{q}^\epsilon$ and $\bar{q}^\epsilon$ respectively. The equation for $\tilde{q}^\epsilon$ is

$$\frac{\partial}{\partial t}\tilde{q}^\epsilon(t,\tau,\theta^\epsilon)+\frac{\partial}{\partial\theta^\epsilon}\tilde{q}^\epsilon(t,\tau,\theta^\epsilon)=-\frac{\partial}{\partial\theta^\epsilon}\bar{q}^\epsilon(\tau,\theta^\epsilon),\tag{3.20}$$

Let us assume more that $\tilde{q}(nT,\tau,\theta^\epsilon)=0$ for $n\in\mathbf{N}$. Then, integrating (3.20) along the characteristics $\theta^\epsilon=t+const.$, we obtain for $0<t-nT<\theta^\epsilon$ that

$$\tilde{q}^\epsilon(t,\tau,\theta^\epsilon)=\bar{q}^\epsilon(\tau,\theta^\epsilon-t)-\bar{q}^\epsilon(\tau,\theta^\epsilon).$$

Actually, using the periodicity in θ^ϵ of $\bar{q}^\epsilon$, the same expression holds true for $\theta^\epsilon < t - nT < T$. Taking in the above expression $t = (n+1)T$ and using again the periodicity in θ^ϵ of $\bar{q}^\epsilon$, we obtain that $\tilde{q}^\epsilon((n+1)T, \tau, \theta^\epsilon) = 0$, therefore the function defined in this way satisfies the periodicity condition in t and one can verify directly that (3.19) is satisfied.

Therefore it remains to analyze the evolution of $\bar{q}^\epsilon$. Note that, by finding the evolution of $\bar{q}^\epsilon$, the evolution of $\tilde{q}^\epsilon$, and thus that of q^ϵ, is fully determined. Taking the terms in ϵ obtained by replacing (3.18) in (3.17), we get:

$$\frac{\partial}{\partial \tau}\bar{q}^\epsilon(\tau, \theta^\epsilon) + \frac{\partial}{\partial \theta^\epsilon}\left(H(\varphi)(\bar{q}^\epsilon(\tau, \theta^\epsilon) - \tilde{q}^\epsilon(t, \tau, \theta^\epsilon))\right) = 0, \tag{3.21}$$

and, taking into account the expression of $\tilde{q}^\epsilon$

$$\frac{\partial}{\partial \tau}\bar{q}^\epsilon(\tau, \theta^\epsilon) + \frac{\partial}{\partial \theta^\epsilon}\left(H(\varphi)\bar{q}^\epsilon(\tau, \theta^\epsilon - t)\right) = 0.$$

Since here t is considered fixed, making the change of variable $\theta^\epsilon \mapsto x := \theta^\epsilon - t$ we obtain

$$\frac{\partial}{\partial \tau}\bar{q}^\epsilon(\tau, x) + \frac{\partial}{\partial x}\left(H(\varphi)\bar{q}^\epsilon(\tau, x)\right) = 0. \tag{3.22}$$

The periodicity condition in θ^ϵ implies the periodicity in x:

$$\bar{q}^\epsilon(\tau, 0) = \bar{q}^\epsilon(\tau, T).$$

Now, due to the expression of q given by (3.18) and the expression of x, we can rewrite H in terms of the new independent variables (τ, x) as follows:

$$\begin{aligned} H(\varphi(\tau, \theta_0)) &= \frac{c_0 \dot{s}(T)}{T}\int_0^T \lambda_1(t) q^\epsilon(t - \theta_0 - \varphi(\tau, \theta_0), \tau, T)\,\mathrm{d}s \\ &= \frac{c_0 \dot{s}(T)}{T}\int_0^T \lambda_1(t)\bar{q}^\epsilon(\tau, T - t + x)\,\mathrm{d}t. \end{aligned}$$

Therefore, we arrived to the following integro-differential system:

$$\begin{cases} \dfrac{\partial}{\partial \tau}\bar{q}^\epsilon(\tau, x) + \dfrac{\partial}{\partial x}\left(H(\tau, x)\bar{q}^\epsilon(\tau, x)\right) = 0, & \tau > 0, \quad x \in (0, T), \\ H(\tau, x) = \dfrac{c_0 \dot{s}(T)}{T}\displaystyle\int_0^T \bar{q}^\epsilon(\tau, x - t)\lambda_1(t)\,\mathrm{d}t, & \tau \geq 0, \quad x \in [0, T), \\ \bar{q}^\epsilon(\tau, 0) = \bar{q}^\epsilon(\tau, T), & \tau > 0, \\ \bar{q}^\epsilon(0, x) = q_0^\epsilon(x), & x \in [0, T). \end{cases} \tag{3.23}$$

4. Special solutions. Some stability results.

We remind that the method we have used to derive the form of the system describing the evolution in time of phase densities is based on the assumption that the characteristics given by $\theta^\epsilon(t)$, and consequently $x(\tau)$, are not crossing. Actually we will show in the following that this is not happening in finite time.

We define the characteristic lines in the following way: for every τ fixed, $\forall x \in [0, T)$, we denote by $c[x_0](\tau)$ (to avoid confusion) the characteristic line starting from x_0 that satisfies:

$$c[x_0](\tau) = x,$$

and is solution to

$$\begin{cases} \frac{\mathrm{d}}{\mathrm{d}\tau} c[x_0](\tau) = H(\tau, c[x_0](\tau)), \quad \tau > 0, \\ c[x_0](0) = x_0. \end{cases} \tag{4.1}$$

Actually for τ fixed, $\forall x \in [0, T)$, the characteristic line which passes trough (τ, x) start either from a point $(0, x_0)$ in the down boundary (putting x on the abscissa axis), or from a point $(\tau', 0)$ (or (τ', T), depending on the sign of H); but due to the periodicity of x the second case can be extended to the first one.
Then, along the characteristic lines defined by (4.1), the first equation in (3.23) writes as

$$\frac{\mathrm{d}}{\mathrm{d}\tau} \bar{q}^\epsilon(\tau, c[x_0](\tau)) = -\frac{\partial H}{\partial c}(\tau, c[x_0](\tau)) \bar{q}^\epsilon(\tau, c[x_0](\tau)). \tag{4.2}$$

Or, equivalently:

$$\bar{q}^\epsilon(\tau, x) = \bar{q}^\epsilon(\tau, c[x_0](\tau)) = \bar{q}_0^\epsilon(x_0) \exp\{-\int_0^\tau \frac{\partial H}{\partial c}(\tau', c[x_0](\tau'))\, \mathrm{d}\tau'\}.$$

Here, as before, the solution on a characteristic that starts from the left or right boundary can be written as above due to the periodicity condition $q(\tau, 0) = q(\tau, T)$.

We want to see the way the characteristic lines depend on their initial state; to do that we calculate

$$\frac{\mathrm{d}c[x_0](\tau)}{\mathrm{d}x_0} = 1 + \int_0^\tau \frac{\partial H}{\partial c} \frac{\mathrm{d}c[x_0](\tau')}{\mathrm{d}x_0}\, \mathrm{d}\tau',$$

which yields

$$\frac{\mathrm{d}c[x_0](\tau)}{\mathrm{d}x_0} = \exp\{\int_0^\tau \frac{\partial H}{\partial c}(\tau', c[x_0](\tau'))\, \mathrm{d}\tau'\}.$$

Let us look closely to the expression of H; due to the commutativity of the convolution product,

we can write:

$$\begin{aligned} H(\tau,x) &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(x-\xi)\bar{q}^\epsilon(\tau,\xi)\,\mathrm{d}\xi \\ &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(x-c[x_0](\tau))\bar{q}^\epsilon(\tau,c[x_0](\tau)\,\mathrm{d}c \\ &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(x-c[x_0](\tau))\bar{q}_0^\epsilon(x_0)\exp\{-\int_0^\tau H_x(\tau',c[x_0](\tau'))\,\mathrm{d}\tau'\}\,\mathrm{d}c \end{aligned}$$

and due to the expression of $\frac{\mathrm{d}c[x_0](\tau)}{\mathrm{d}x_0}$, we obtain:

$$\begin{aligned} H(\tau,x) &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(x-c[x_0](\tau))\bar{q}_0^\epsilon(x_0)\,\mathrm{d}x_0 \\ &= \frac{c_0\dot{s}(T)}{T}\int_0^T \lambda_1(x-c[x_0](\tau))\bar{q}_0^\epsilon(x_0)\,\mathrm{d}x_0. \end{aligned}$$

Then, the following relation holds:

$$\frac{\partial H}{\partial x}(\tau,x) = \frac{c_0\dot{s}(T)}{T}\int_0^T \frac{\partial\lambda_1}{\partial x}(x-c[x_0](\tau))\bar{q}_0^\epsilon(x_0)\,\mathrm{d}x_0.$$

Now, since λ_1 is given by the adjoint linear system (3.15) and depends intrinsically on the functions of Izhikevich model computed along the limit cycle, we have that the derivative of λ_1 in the above expression exists and is bounded. Therefore the derivative of H with respect to x stays bounded and it implies that the characteristics starting from different initial points will not cross. In this way the solution defined along the characteristics is well defined for every τ.

The stationary solution.

Let us consider now the stationary problem:

$$\begin{cases} \dfrac{\partial}{\partial x}\left(H^0(x)\bar{q}(x)\right) = 0, & x\in(0,T) \\ H^0(x) = \dfrac{c_0\dot{s}(T)}{T}\displaystyle\int_0^T \lambda_1(t,0)\bar{q}(x-t)\,\mathrm{d}t, & x\in[0,T) \\ \bar{q}(0) = \bar{q}(T). \end{cases} \tag{4.3}$$

From the first equation of (4.3) we get that

$$H^0(x)\bar{q}(x) = \text{constant}. \tag{4.4}$$

In the case when $H \neq 0$, the obvious solution to the the above equation is given by

$$\bar{q}(x) = \bar{q}, \quad \forall x\in[0,T]$$

where $\bar{q} = constant$. Replacing in H^0, we obtain

$$H^0 = k_0 \int_0^T \lambda_1(t,0)\,\mathrm{d}t,$$

where $k_0 = c_0\dot{s}(T)\bar{q}$. This solution corresponds to the *a constant repartition* of neurons with respect to their phase.
If we denote by $\hat{q}^\epsilon := \bar{q}^\epsilon - \bar{q}$, with $\bar{q}^\epsilon$ solution to (3.23) and $\bar{q}$ solution to (4.3), we get that $\hat{q}^\epsilon$ is a solution to the following problem:

$$\begin{cases} \dfrac{\partial}{\partial\tau}\hat{q}^\epsilon(\tau,x) + \dfrac{\partial}{\partial x}\left(H(\tau,x)\hat{q}^\epsilon(\tau,x)\right) = -\dfrac{\partial H}{\partial x}(\tau,x)\bar{q}, & \tau > 0, \quad x \in (0,T), \\ \hat{q}^\epsilon(\tau,0) = \hat{q}^\epsilon(\tau,T), & \tau > 0, \\ \hat{q}^\epsilon(0,x_0) = \bar{q}_0^\epsilon(x_0) - \bar{q}, & x_0 \in [0,T). \end{cases} \tag{4.5}$$

Let us assume now that $\bar{q}_0^\epsilon$ has the support included in the region of $[0,T)$ where λ_1 is increasing. We can write the problem (4.5) as before along the characteristic line defined by (4.2):

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}\tau}\hat{q}^\epsilon(\tau,c[x_0](\tau)) = -\dfrac{\partial H}{\partial c}(\tau,c[x_0](\tau))\left(\hat{q}^\epsilon(\tau,c[x_0](\tau)) + \bar{q}\right), & \tau > 0, \quad x_0 \in [0,T), \\ \hat{q}^\epsilon(\tau,0) = \hat{q}^\epsilon(\tau,T), & \tau > 0, \\ \hat{q}^\epsilon(0,x_0) = \bar{q}_0^\epsilon(x_0) - \bar{q}, & x_0 \in [0,T), \end{cases} \tag{4.6}$$

where the expression of H is given by:

$$\frac{\partial H}{\partial c}(\tau,c[x_0](\tau)) = \frac{c_0\dot{s}(T)}{T}\int_{supp\, q_0^\epsilon} \frac{\partial\lambda_1}{\partial x}(c[x_0](\tau) - c[\xi_0](\tau))\bar{q}_0^\epsilon(\xi_0)\,\mathrm{d}\xi_0.$$

Under our hypothesis it follows that $\dfrac{\partial H}{\partial c}(\tau,c[x_0](\tau)) \geq 0$.
Taking now into account that $\bar{q} \geq 0$ (being a density of population) and using a comparison result, we obtain that the solution $\hat{q}^\epsilon \leq z$, with z solution to the following problem:

$$\begin{cases} \dfrac{\mathrm{d}}{\mathrm{d}\tau}z(\tau,c[x_0](\tau)) = -\dfrac{\partial H}{\partial c}(\tau,c[x_0](\tau))z(\tau,c[x_0](\tau)), & \tau > 0, \quad x_0 \in [0,T), \\ z(\tau,0) = z(\tau,T), & \tau > 0, \\ z(0,x_0) = \bar{q}_0^\epsilon(x_0) - \bar{q}, & x \in [0,T). \end{cases} \tag{4.7}$$

In fact

$$z(\tau,c[x_0](\tau)) = z(0,x)\exp\{-\int_0^\tau \frac{\partial H}{\partial c}(\tau',c[x_0](\tau'))\,\mathrm{d}\tau'\},$$

and, making $\tau \to +\infty$, we get that, in this case

$$z(\tau, x) \to 0, \quad \text{as } \tau \to +\infty,$$

which implies that

$$\hat{q}^\epsilon(\tau, x) \to 0, \quad \text{as } \tau \to +\infty,$$

or, equivalently,

$$\bar{q}^\epsilon(\tau, x) \to \bar{q}, \quad \text{as } \tau \to +\infty.$$

Then, it follows also that

$$H(\tau, x) \to H_0, \quad \text{as } \tau \to +\infty$$

(and, therefore $c[x_0](\tau) \to x_0 + H_0\tau$ as $\tau \to +\infty$), therefore the solution of our problem will converge toward a constant repartition under the special hypothesis that we reminded earlier.

The synchronized solution.

As we stressed at the beginning, we have a special interest in the existence of a solution to (3.23) that expresses the synchronized state of the neural population. We will look for the solution in the following form

$$\bar{q}^\epsilon(\tau, x) = q^0 \delta(x - h\tau - x_0) \tag{4.8}$$

where δ the Dirac function and h will be determined later. Such a solution will express the fact that all the neurons in the population will be "concentrated" in the phase state $x = h\tau + x_0$, therefore the synchronization of the population. Let us check first that $\bar{q}(\tau, x)$ defined by (4.8) satisfies (3.23). First of all, the corresponding expression of H is given by

$$\begin{aligned} H(\tau, x) &= \frac{c_0 \dot{s}(T)}{T} \int_0^T \lambda_1(t) \bar{q}^\epsilon(\tau, x - t)\, \mathrm{d}t \\ &= \frac{c_0 \dot{s}(T)}{T} q^0 \lambda_1(x - h\tau - x_0). \end{aligned}$$

Using the fact that $\lambda_1(x - h\tau - x_0)\bar{q}^\epsilon(\tau, x) = q^0 \lambda_1(0) \delta(x - h\tau - x_0)$ one can check directly that, indeed, $\bar{q}^\epsilon$ satisfies

$$\frac{\partial}{\partial \tau} \bar{q}^\epsilon(\tau, x) + \frac{\partial}{\partial x} \left(H(\tau, x) \bar{q}^\epsilon(\tau, x) \right) = 0,$$

with $H(\tau, h\tau + x_0) = h = \dfrac{c_0 \dot{s}(T)}{T} \lambda_1(0) q^0$.

We consider that the Dirac mass is concentrated at the initial moment in the initial state ξ_0, and suppose that $\bar{q}_0^\epsilon$ has the support included in the interval $[\xi_0 - \beta, \xi_0 + \beta]$.

We take next two initial points such that $\xi_0 - \beta \le x_0^1 \le x_0^2 \le \xi_0 + \beta$; we are interested to see how it evolves in time the distance between the characteristic lines that start from x_0^1 respectively x_0^2. We will show that if λ_1 is decreasing in the neighborhood of the origin, we have the convergence

of the distance between the two characteristics to zero when τ tends to infinity.
First of all, due to the fact that $\frac{\mathrm{d}c[x_0](\tau)}{\mathrm{d}x_0} > 0$, we have that

$$c[x_0^1](\tau) < c[x_0^2](\tau).$$

If we denote $\zeta(\tau) = c[x_0^2](\tau) - c[x_0^1](\tau)$, ζ is a solution to

$$\begin{aligned} \frac{\mathrm{d}\zeta}{\mathrm{d}\tau} &= H(\tau, c[x_0^2](\tau)) - H(\tau, c[x_0^1](\tau),) \\ \zeta(0) &= x_0^2 - x_0^1. \end{aligned}$$

Writing H explicitly as before, it follows that:

$$\begin{aligned} \frac{\mathrm{d}\zeta}{\mathrm{d}\tau} &= H(\tau, c[x_0^2](\tau)) - H(\tau, c[x_0^1](\tau)) \\ &= k_0 \int_{\xi_0-\beta}^{\xi_0+\beta} \lambda_1(c[x_0^1](\tau) - c[x_0](\tau)) - \lambda_1(c[x_0^2](\tau) - c[x_0](\tau))\bar{q}_0^\epsilon(x_0)\,\mathrm{d}x_0, \end{aligned}$$

and one can see that under our assumptions we have that $\lambda_1(c[x_0^1](\tau) - c[x_0](\tau)) - \lambda_1(c[x_0^2](\tau) - c[x_0](\tau)) \leq 0$, therefore $\zeta(\tau) \to 0$ as $\tau \to \infty$. Moreover, from the expression of the solution along the characteristics it follows also:

$$\bar{q}^\epsilon(\tau, c[x_0](\tau)) \to \infty,$$

Therefore, if there exists a $\beta > 0$ such that

$$\lambda_1(t) > \lambda_1(0) \quad \text{for} \quad T - \beta < t < T,$$

$$\lambda_1(t) < \lambda_1(0) \quad \text{for} \quad 0 < t < \beta,$$

the synchronized solution is stable, that is any initial condition with support in that phase interval will converge to a synchronized solution for some x_0 chosen as above. So the quantity $\epsilon\lambda_1(0)$ characterizes the speed at which the phase is changed or in other words $\epsilon\lambda_1(0)T$ is the variation of period due to the coupling.

The mechanisms leading to occurrence of such a solution as well as a more general result of the stability of it makes the object of further investigations in our future work.

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