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Complex Oscillations in a Simple Deterministic Neuronal Network

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ABSTRACT. A series of different types of oscillations from low to very high complexity may arise if certain parameters change in a deterministic model describing the activity of a simple network with delayed self- or lateral inhibitory effects. Besides the model we present here some analytical results.

Model considerations. Let $y(t)$ denote either the membrane potential of a single neuron or the averaged potential of a population of neurons coupled by mutual inhibitory synapses. In case of the single neuron a self-inhibitory pathway is assumed mediated either by interneurons or internal refractory mechanisms. The quantity y is conceived as the net effect of excitatory (E) and inhibitory (I) potentials:

$$y = E - I.$$

The excitation E, generated either internally or resulting from external (tonic) input, is supposed to be independent of time. If y changes in time this is only due to the autonomous dynamics of the inhibition described as follows:

Inhibition is generated at a rate proportional to the firing frequency $z(t - \tau)$ a time τ in the past. The feedback time delay τ may be caused by finite conduction velocities, synaptic transmission or other mechanisms (an extraordinary value of $\tau = 0.1$ sec has been measured in the retinal network of Limulus [2], [**10**]). On the other hand I decays at a rate α; hence $dI/dt = K \cdot z(t - \tau) - \alpha I(t)$.

Assume the firing frequency to act via transmitter substance binding to post-synaptic membrane receptors. Under quasi-steady state conditions the fraction of active receptors is an *increasing* function of transmitter concentration which in turn is proportional to the firing

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frequency a time τ ago. The inhibitory coefficient K is assumed here to be proportional to the number of available, i.e. not active receptors, which is a *decreasing* function g of $z(t-\tau)$.

Thus the dynamics of I is governed by

$$\frac{dI(t)}{dt} = g(z(t-\tau)) \cdot z(t-\tau) - \alpha I(t).$$

If, moreover, the firing frequency is an *increasing* function h of membrane potential y, then we arrive at a description of I in its own terms:

$$\frac{dI(t)}{dt} = g(h(E - I(t-\tau))) \cdot h(E - I(t-\tau)) - \alpha I(t),$$

which may be abbreviated by

$$\dot{I} = G(I_\tau) - \alpha I, \tag{1}$$

where $I = I(t)$, $I_\tau = I(t-\tau)$.

We are interested here in the situation where the function G, as a product of a decreasing and an increasing function, turns out to increase on a domain $0 \leqslant I \leqslant I_0$ and to decrease on the domain $I \geqslant I_0$. For other physiological applications of the model see [3], [8].

Mathematical analysis. Equation (1) has been analyzed thoroughly if $G(I_\tau)$ describes delayed negative feedback (in [1] as a model for blood cell production, in [2] as a model for delayed lateral inhibition, in [7] and [9] for rather general G). In all these investigations it is presupposed that there is exactly one steady state solution $\bar{I}$ of (1) and that G obeys a certain sign rule, namely $(I - \bar{I}) \cdot G(I - \bar{I}) < 0$ whenever $I \neq \bar{I}$, expressing that the feedback is of negative type. In this situation the existence of a slowly oscillating periodic solution $I_p(t)$ to equation (1) can be proved, "slowly" meaning the period exceeds 2τ and I_p has at most one minimum within one (smallest) period.

However, numerical simulations ([3], [8]) suggest a much more complex behavior of the solutions if the continuous function G has the following properties:

$$G(0) = 0, \qquad G(\xi) \geqslant 0 \quad \text{if } \xi > 0,$$

$$\lim_{\xi\to\infty} G(\xi) = 0, \qquad G(\bar{I}) = \alpha\bar{I} \quad \text{for some constant } \bar{I} > 0,$$

(note that these assumptions imply a solution to (1) to be nonnnegative, whenever the initial condition is nonnegative).

For such G the analysis of (1) appears extremely difficult. However, as shown in the following, some results may be obtained if the *continuous* function G has the special form

$$G(\xi) = 0 \quad \text{if } 0 \leqslant \xi < a \text{ or } \xi > 1,$$

$$G(\xi) = c \quad \text{if } a + \delta \leqslant \xi \leqslant 1 - \delta,$$

where the constants a, c, δ satisfy $0 < a < 1$, $c > \alpha > 0$, $0 < 2\delta < 1 - a$. On the intervals $(a, a + \delta)$ and $(1 - \delta, 1)$ the function G has to be strictly monotone (but with arbitrary values). Let us denote such a function by G_δ, conceiving the parameters a, c, α as fixed. As $\delta \to 0$, G_δ degenerates to the step function G_0. It is this feature which simplifies the analysis. By means of the following lemma it is possible to generalize results obtained for the case $\delta = 0$ to the class of continuous functions G_δ obeying $0 < \delta < \delta_0$, δ_0 sufficiently small.

Two periodic solutions of equation (1) are said to have the same *degree of complexity* if they share the number of minima within one (smallest) period.

LEMMA 1. *Let a, c, α be fixed. Assume equation* (1) *for $G = G_0$ to have a continuous periodic solution I_0 obeying*

(i) *$I_0(t) > 1$ if $0 \leqslant t \leqslant 1 - \tau$, and*

(ii) *$1 \neq I_0(t) \neq a$ whenever t is an extremum of I_0. Then there is a $\delta_0 > 0$ such that for all $G = G_\delta$, $0 < \delta < \delta_0$, equation* (1) *has a periodic solution I_δ of the same degree of complexity as I_0.*

The proof of this lemma as well as of all other lemmas or theorems is presented elsewhere [6]. Note that δ_0 depends on the set $\{a, c, \alpha\}$.

An initial condition of (1) is a continuous function φ: $[-1, 0] \to \mathbf{R}_+$. The special constant initial condition $\varphi \equiv 1 - \delta$ is denoted by $\varphi(\delta)$. The corresponding solution $I_{\varphi(\delta)}$ of (1) has the following strong stability property.

LEMMA 2. *Let the initial condition φ satisfy $a + \delta \leqslant \varphi(t) \leqslant 1 - \delta$ or $1 \leqslant \varphi(t)$ for all $t \in [-1, 0]$. Then the corresponding solution I_φ of equation* (1) *with $G = G_\delta$ converges to some time-shift of the solution $I_{\varphi(\delta)}$.*

This lemma can be generalized to larger classes of initial conditions [6].

Lemmas 1 and 2 justify concentrating on the special situation where $G = G_0$ (step function) and $\varphi = \varphi(0) \equiv 1$. The corresponding solution is denoted by $I_0 = I_{\phi(0)}$; it depends on the three parameters α, c, a. Since G_0 has only the values 0 and c the solution I_0 is piecewise composed of the following two types of functions (assuming $\tau = 1$):

$$I_0(t) = I_0(t_0)e^{-\alpha(t-t_0)} \quad \text{if } I_0(t'-1) \notin [a, 1] \quad \text{for all } t' \in (t_0, t), \tag{2}$$

$$I_0(t) = c/\alpha - (c/\alpha - x(t_0))e^{-\alpha(t-t_0)} \quad \text{if } I_0(t'-1) \in [a, 1] \quad \text{for all } t' \in (t_0, t). \tag{3}$$

parameter α	period ~	# minima per period	parameter α	period ~	# minima per period
0.3	3.6	1	1.5	4	4
0.4	3.5	1	1.6	8.4	10
0.6	3.3	1	1.65	6.4	7
0.7	3.3	2	1.7	6.3	8
0.75	3.2	2	1.75	10.5	13
0.8	3	2	1.8	21.1	30
0.85	5.8	5	1.9	21.7	32
0.86	5.9	5	2	9.5	13
0.88	5.9	4	2.3	18.5	30
0.9	5.9	5	2.4	5.6	8
0.93	6	6	2.6	11.2	17
0.97	6	6	2.7	72.4	~123
0.99	9.1	9	2.775	20.2	37
1	9.4	10	2.8	28.8	58
1.001	15	16	2.9	12.7	23
1.0015	12.1	13	3.0	10.8	23
1.002	12.3	12	3.2	7.4	14
1.005	6.7	7	3.5	38.5	~87
1.05	7	6	3.6	23.1	~57
1.0625	7	7	3.7	58.3	~142
1.075	9.7	10	3.8	33.5	~80
1.1	4.1	4	6.0	>170	600

TABLE I. For various values of α this table lists the period (in multiples of the delay $\tau = 1$, up to 1 decimal place) and the number of minima within one (minimal) period of *stable* periodic solutions to equation (1) with $G = G_\delta$ as defined in the text, $0 < \delta < \delta_0$, δ_0 sufficiently small. Throughout $a = 0.5$ and $c = 2\alpha$.

Obviously for $0 \leqslant t \leqslant 1$ the solution I_0 satisfies (3) with $t_0 = 0$, $I_0(t_0) = 1$. After $t = 1$, I_0 decays according to (2) with $t_0 = 1$ until the time $t_1 + 1$, where $t_1 > 1$ is defined by $1 = I_0(t_1) = I_0(1)\exp(-\alpha(t_1 - 1))$. During the time interval $[t_1, t_1 + 1]$ the solution I_0 decays exponentially from 1 to $\exp(-\alpha) = I_0(t_1 + 1)$. It is important to note that such a decay (from 1 to $\exp(-\alpha)$) occurs after any time t^* such that $I_0(t) > 1$ for all $t \in (t^* - 1, t^*)$. From these observations the following sufficient criterion for the existence of a periodic solution is easily concluded.

Criterion. Equation (1) with $G = G_0$ has a periodic solution whenever there is a (first) time $t_2 > t_1$ such that $I_0(t) > 1$ for all $t \in (t_2 - 1, t_2)$. The function I_0 restricted to the interval $[t_1, t_2)$ represents just one (minimal) cycle of the periodic solution.

This criterion is generic in the sense that its condition is a property of nonempty open subsets of the 3-dimensional parameter-space $\{\alpha, c, a\}$. Together with Lemmas 1 and 2 it enables one to find periodic oscillations being stable with respect to (small) perturbations both of initial conditions and parameters (including δ).

The reason to write this paper is the fact that the solutions obeying this criterion may be extremely complex (depending on the parameters) in that the period may be very long and within one (smallest) period the solution has a detailed fine structure with many extrema of different amplitudes. The table below gives some examples for a fixed value of $a = 0.5$, but a series of α-values and a fixed relation $c = 2\alpha$. The table holds for continuous nonlinearities $G = G_\delta$ with sufficiently small positive δ, and for $G = G_0$. The evidence of the table's content does not depend on numerical methods but its truth is a consequence of the sketched analytical results and of the fact that for $G = G_0$ equation (1) may be solved exactly. Results on broader regions in parameter space will be published elsewhere [5], [6].

Note added in proof. In [6] it is proved that for certain continuous functions G, equation (1) behaves chaotically in the sense that, depending on the initial conditions, there may be infinitely many periodic solutions with different periods as well as an uncountable number of aperiodic solutions.

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