Bursting oscillations from a homoclinic tangency in a time delay system

A. Destexhe and P. Gaspard
\[ \frac{dX}{dt} = -g_L(X - V_L) - g_{EE}(X - V_E)F(X(t - \tau)) - g_{IE}(X - V_I)F(Y(t - \tau)) \]
\[ \frac{dY}{dt} = -g_L(Y - V_L) - g_{EI}(Y - V_E)F(X(t - \tau)) - g_{II}(Y - V_I)F(Y(t - \tau)) \]

where \( X \) and \( Y \) represent the membrane potential of an excitatory and an inhibitory neuron respectively, \( C_m=1 \mu F/cm^2 \) is the specific membrane capacitance, \( g_L=0.25 \) mS/cm\(^2\) is the leakage conductance and \( V_L=-60 \) mV is the leakage potential. The values chosen for this model are in the range of values measured experimentally in a neuronal membrane (cf., for example, ref. [7]). \( g_{EE}, g_{IE}, g_{EI} \) and \( g_{II} \) are respectively the synaptic conductances for excitatory-to-excitatory (EE), inhibitory-to-excitatory (IE), excitatory-to-inhibitory (EI) and inhibitory-to-inhibitory (II) interactions. \( V_E=50 \) mV and \( V_I=-80 \) mV are the equilibrium potentials for synaptic excitation and inhibition. Synaptic interaction is taken into account by the use of the transfer function

\[ F(V) = \frac{1}{1+\exp\left[-\frac{1}{25}(V+25)\right]} \]

This sigmoidal function gives the output activity of the neuron as a function of its potential \( V \). For the most negative values of the potential, the neuron is silent and \( F \approx 0 \). Above the threshold value of \( V=50 \) mV, the output activity of the neuron increases, and the fraction of excitatory or inhibitory cells active per unit of time.

Renormalizing the conductances by \( C_m \) leads to the following set of parameters (in \( \text{ms}^{-1} \)): \( \gamma=g_L/C_m \), \( \Omega_1=g_{EE}/C_m \), \( \Omega_2=g_{IE}/C_m \), \( \Omega_3=g_{EI}/C_m \) and \( \Omega_4=g_{II}/C_m \). The values used in this paper are \( \Omega_2=\Omega_3=5 \) \( \text{ms}^{-1} \) and \( \Omega_4=0 \). \( \Omega_1 \) is the main parameter of the model. It is important to note that similar behavior is observed for a very wide range of these parameters and the values given here are therefore representative of the system.

As indicated by fig. 1, this model exhibits multiple steady states. The lower steady branch corresponds to the resting membrane potential and is around the value of \( V_L \). For higher values of \( \Omega_1 \), other fixed points appear. In this case the upper steady branch is stable whereas the intermediate branches are unstable (cf. fig. 1). It is to be noticed that the upper branch corresponds to a stable state where both neurons stay permanently above the threshold.

For the values of \( \Omega_1, ..., \Omega_4 \) considered, the lower steady branch gives rise to limit cycle oscillations via a supercritical Hopf bifurcation (\( \Omega^H \) in fig. 1). We focus here on the complex oscillatory phenomena...
which appear from an infinite period bifurcation ($\Omega^E_1$ in fig. 1). As shown in fig. 1, a very similar diagram is seen for different values of the time delay.

Figure 2 shows the oscillating patterns seen at the approach of the point $\Omega^E_1$. For increasing values of $\Omega$, the limit cycle oscillations turn into bursting behavior.

We emphasize that the presence of the delay is necessary to observe this type of oscillations. Very similar behavior is observed for a very wide range of the parameters provided the delay is not too small, and the synaptic coefficients $\Omega_2$ and $\Omega_3$ are large enough. However, bursting oscillations disappear for time delays close to zero.

Figure 2 also shows that a bursting oscillation period is composed of an intermediate segment (the silent phase) and a burst of faster oscillatory behavior (the active phase). Very similar bursting oscillations have been observed in chemical systems [13].

A closer scrutiny of fig. 2 reveals that, during the approach to the critical point $\Omega^E_1$, the period continuously increases together with the number of pseudo-cycles of the fast oscillation, while the intermediate segment remains essentially unchanged. At the critical point $\Omega^E_1$, the oscillatory active phase lasts an infinite time, which leads us to assume the existence of a second limit cycle LC2 corresponding to the active phase fast oscillations. Since this limit cycle LC2 does not exist alone without the intermediate segment of the silent phase, we conclude that LC2 must be an unstable limit cycle of saddle type because trajectories like LC1 can enter the vicinity of LC2 before escaping from it. We now show that this behavior can be accounted for by the presence of a homoclinic tangency to the limit cycle LC2 as schematically illustrated in fig. 3.

As $\Omega$ increases, fig. 2 shows that the amplitude of the limit cycle LC1 increases with its period. Bursting oscillations appear when the limit cycle LC1 approaches the region of phase space where the unstable limit cycle LC2 exists (cf. fig. 3). A homoclinic tangency to LC2 can explain the properties of these oscillations. When the trajectory of LC1 is forced to pass in the vicinity of LC2, the limit cycle is distorted and fast oscillations appear transiently. In fig. 3a, a Poincaré section illustrates how the successive iterates of LC1 approach LC2. At the critical point, the trajectory of LC1 coalesces with LC2. The resulting homoclinic orbit is represented schematically in fig. 3b.

In such a homoclinic tangency to an unstable cycle, the increase of the period follows a logarithmic law of the form [15,16]

$$ T = T_0 - \frac{1}{\lambda} \ln |\Omega_1 - \Omega^E_1| , $$

where $\lambda > 0$ is the positive eigenvalue of the unstable limit cycle, $\Omega^E_1$ is the critical value of $\Omega_1$ and $T_0$ is a constant. Such a logarithmic lengthening of the period constitutes a characteristic feature of infinite-period bifurcations based on homoclinic orbits [15–19].

The period $T$ was estimated numerically for values of $\Omega_1$ very close to the critical point. Figure 4 indi-

Fig. 2. Appearance of bursting oscillations as $\Omega_1$ is increased. The variable $X(t)$ is represented as a function of time $t$, as well as the phase space projection $X(t)$–$Y(t)$. The values of $\Omega_1$ are 6.5 (a), 6.625 (b), 6.65 (c) and 6.675 (d). The symbols $\times$ represent the coordinates of the fixed points in the plane $X(t)$–$Y(t)$. Numerical integration was performed using a Runge–Kutta algorithm.
least squares fitting is \( \lambda = 0.1299 \pm 0.0014 \text{ ms}^{-1} \)
(other parameters are given in the caption of fig. 4).

If we refer to the scheme of the Poincaré section of the system (fig. 3), then one can deduce that, close to the critical point, the successive iterates follow the unstable direction of the limit cycle (indicated by U in fig. 3c). These particular iterates correspond to the escape from the unstable limit cycle. The distance between each iterate and the unstable cycle should evolve exponentially, with an argument approaching \( \lambda t \). Therefore, sufficiently close to the critical point, studying the successive iterates of LC1 on a Poincaré section should allow one to estimate the positive eigenvalue \( \lambda \) of LC2. This value must be compared with that obtained from relation (2).

We realized a first return map of the system by considering the successive maxima \( X_m(t) \) of the variable \( X \) (fig. 5). This quantity seems to obey the following relation,

\[
X_m(t) = X_{\text{max}} - \exp[\lambda(t-t_0)] ,
\]

where \( X_{\text{max}} \) and \( t_0 \) are constants. If we assume that \( X \) represents the amplitude of LC2, then the eq-
of the system is remarkably close to that obtained from period measurements using relation (2). The coincidence of these two values confirms that the bursting oscillations are based here on a homoclinic tangency to an unstable limit cycle.

As a conclusion, we have described a novel type of bursting oscillations which appear in a model of coupled neurons with time delay. Neuronal bursting, such as in the R15 neuron of the Aplysia [1], usually results from the combination of several active in previously described mechanisms [6] shows that, here also, a "slow" oscillatory process is associated to the stable limit cycle LC1, whereas the unstable limit cycle LC2 is characterized by a faster time scale. On the other hand, in this system, the "fast" oscillation characterizing the active phase of the bursting oscillation is not associated to a stable oscillating branch in the fast subsystem. It rather corresponds to an approach to an unstable oscillating state.

The characteristic logarithmic period of the


