Bursting oscillations from a homoclinic tangency in a time delay system

A. Destexhe and P. Gaspard

Université Libre de Bruxelles, CP 231, Campus Plaine, Boulevard du Triomphe, B-1050 Brussels, Belgium
\[
\begin{align*}
\frac{dX}{dt} &= -g_L (X - V_L) - g_{EE} (X - V_E) F(X(t-\tau)) \\
- g_{IE} (X - V_I) F(Y(t-\tau)), \\
\frac{dY}{dt} &= -g_L (Y - V_L) - g_{EI} (Y - V_E) F(X(t-\tau)) \\
- g_{II} (Y - V_I) F(Y(t-\tau)),
\end{align*}
\]

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 mem-

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 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 \( \Omega_2 = \Omega_3 = 5 \) 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

point values...
which appear from an infinite period bifurcation ($\Omega^f$ 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 $\Omega^f$. 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 oscillations have been observed in chemical systems [13].

A closer scrutiny of fig. 2 reveals that, during the approach to the critical point $\Omega^f$, the period continuously increases together with the number of pseudocycles of the fast oscillation, while the intermediate segment remains essentially unchanged. At the critical point $\Omega^f$, 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
least squares fitting is $\lambda = 0.1299 \pm 0.0014$ 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,

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

(3)

where $X_{\text{max}}$ and $t_0$ are constants. If we assume that $X_{\text{max}}$ represents the amplitude of LC2, then the argument of the exponential constitutes an estimation of the eigenvalue corresponding to the unstable direction of LC2. The value obtained from least squares fitting (fig. 5) is $\lambda = 0.128 \pm 0.002$ ms$^{-1}$. A similar value is also obtained from the same procedure applied to the variable $Y$.

The value of $\lambda$ obtained from this first return map

---

Fig. 3. Schematic representation of a homoclinic tangency to an unstable limit cycle. The limit cycle (LC1) approaches progressively an unstable limit cycle (LC2) and tends to a homoclinic orbit (H) at the critical point when LC1 and LC2 are merging. A two-dimensional Poincaré section is schematized. This section is transverse to the limit cycle LC2 and includes the two lowest directions of the stable (S) and unstable (U) manifolds of LC2.

(a) Close to the critical point, bursting oscillations are seen. The successive iterates of the trajectory of LC1 (black dots) approach LC2. (b) At the critical point, the limit cycle tends to a homoclinic orbit and the period is infinite. (c) Successive iterates represented in the $XY$ plane, for each maximum of the variable $X$ during one cycle of the oscillation of fig. 2d. The successive iterates approach and accumulate near LC2 before escaping (U).

---

Fig. 4. Logarithmic scaling of the period near the critical point. The period $T$ is represented as a function of the parameter $\Omega_z$. The values $T_0 = 282.3 \pm 0.8$ ms, $\lambda = 0.1299 \pm 0.0014$ ms$^{-1}$ and $\Omega_z^* = 6.7186215 \pm 1.2 \times 10^{-3}$ were estimated from least squares fitting. Integration step $10^{-3}$ ms.

---

Fig. 5. Successive maxima of the variable $X$ during the end of the active phase. The maxima of $X$ are represented as a function of time for a value of $\Omega_z = 6.718617$ close to the critical point $\Omega_z^*$. The exponential least squares fitting of these points was realized and the following parameters were obtained: $X_{\text{max}} = -7.85 \pm 0.63$ mV, $t_0 = 1180 \pm 2.6$ ms and $\lambda = 0.128 \pm 0.002$ ms$^{-1}$. Integration step $10^{-3}$ ms.
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 intrinsic currents, and therefore is typically a property of the single cell. On the other hand, the oscillations 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 scaling of the period near the critical point allows an identification of homoclinic phenomena from the analysis of ex-


