Bursting oscillations from a homoclinic tangency in a time delay system

A. Destexhe \(^1\) and P. Gaspard

Université Libre de Bruxelles, CP 231, Campus Plaine, Boulevard du Triomphe, B-1050 Brussels, Belgium

Received 18 May 1992; revised manuscript received 29 November 1992; accepted for publication 11 December 1992
Communicated by A.P. Fordy

We describe a type of bursting oscillations arising in a model of reciprocally connected neurons, where a time delay has been introduced to account for synaptic and propagation delays. We show that in this system bursting oscillations appear at an infinite period bifurcation characterized by a homoclinic tangency to a limit cycle. Such homoclinic bursting phenomena are characterized by a logarithmic lengthening of the period, which could be measured from experimental time series.

The bursting oscillations are among the different types of oscillating behaviors observed in biological systems, such as in the R15 neuron of the Aplysia [1], or in insulin secreting cells [2]. In chemical systems, such as the Belousov–Zhabotinsky reaction [3], this type of oscillations have also been observed. A wide variety of nonlinear systems of first order differential equations also show similar types of oscillations [4–6].

Bursting behavior is characterized by the alternance of a “silent phase” and an “active phase” during each period of the oscillation [2]. The active phase actually consists of the transient apparition of “fast” oscillations of a short period compared to the period of the oscillation, which is referred to as “slow”. The silent phase is usually characterized by a monotonic time evolution.

In some cases, one may separate the dynamical variables of the system into two subsets, the “fast variables” and the “slow variables”. The former allows the system to alternate between active and silent phases.

In many cases of bursting, the treatment of the slow variables as parameters allows one to understand qualitatively the dynamical mechanism underlying the bursting oscillations [5]. According to this singular perturbation approach, the bifurcation diagram of the fast subsystem is studied as a function of the parameters corresponding to the subsystem. In this scheme, a period of the bursting oscillations corresponds to a hysteresis loop. The bursting trajectory jumps alternately between a stable steady branch, characterizing the silent phase, and a limit cycle branch, which underlies the active phase [6].

In the present paper, we present bursting oscillations based on a different mechanism. We introduce first the model of coupled neurons in which this type of oscillations appear. We then show how a homoclinic tangency to an unstable limit cycle may explain the observed properties of these oscillations.
\[ C_m \frac{dX}{dt} = -g_L (X-V_L) - g_{EE} (X-V_E) F(X(t-\tau)) \]
\[ -g_{IE} (X-V_I) F(Y(t-\tau)) \]
\[ \frac{dY}{dt} = \alpha_n (Y_V - Y) - \alpha_{\text{ref}} (Y-V) F(Y(t-\tau)) \]

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\(^{-1}\)): \( \gamma = g_L / C_m \), \( \Omega_1 = g_{EE} / C_m \), \( \Omega_2 = g_{IE} / C_m \), \( \Omega_3 = g_{EE} / C_m \) and \( \Omega_4 = g_{IE} / C_m \). The values used in this paper are \( \Omega_3 = \Omega_4 = 5 \).
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.

Lations have been observed in chemical systems [13]. A closer scrutiny of fig. 2 reveals that, during the approach to the critical point $\Omega^c$, the period continues.
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,

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

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

![Figure 3](image_url)

**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 slowest 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).

![Figure 4](image_url)

**Fig. 4.** Logarithmic scaling of the period near the critical point. The period $T$ is represented as a function of the parameter $\Omega_i$. The values $T_0=282.3 \pm 0.8$ ms, $\lambda=0.1299 \pm 0.0014$ ms$^{-1}$ and $\Omega^{\text{p}}_i=6.7186215 \pm 1.2 \times 10^{-7}$ were estimated from least squares fitting ($\Omega^{\text{p}}=10^{-2}$).

![Figure 5](image_url)

**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 $\Omega_i=6.718617$ close to the critical point $\Omega_i^p$. The exponential least squares fitting of these points was realized and the following parameters were observed: $X_{\text{max}}= -7.85 \pm 0.63$ mV, $t_0=1100 \pm 2.6$ ms and $\lambda=0.128 \pm 0.002$ ms$^{-1}$. Integration with $\Omega_i=10^{-2}$.
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-


