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Liapunov exponents and mode-locked solutions for integrate-and-fire dynamical systems

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Abstract

We discuss the notion of Liapunov exponent for integrate-and-fire (IF) type dynamical systems. In contrast to smooth flows there is a contribution to the IF Liapunov exponent arising from the discontinuous nature of the firing mechanism. Introducing the notion of an IF mode-locked state we are able to show that linear stability is consistent with the requirement of a negative IF Liapunov exponent. We apply our results to IF systems that may be used to study the entrainment of biological oscillators. © 1999 Elsevier Science B.V. All rights reserved.

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1. Introduction

Neurodynamical models based on spiking neurons are playing an increasing role in the interpretation of neurophysiological data. Importantly the precise timing of firing events that can be generated by biological neurons is thought to underly several different forms of sensory processing [1]. Furthermore, it is known that many biological rhythms can be generated in part by neurons or systems of neurons that fire spikes [2]. The simplest and most popular example of a spiking neuron is the so-called integrate-and-fire (IF) model (see for example [3]). The state of an integrate-and-fire neuron changes discontinuously (resets) whenever it crosses some threshold and fires, so that a complete description in terms of smooth differential equations is no longer possible. In this Letter we consider the effect of the resetting and firing mechanisms upon the stability of periodic spike trains. A dynamical systems approach is developed that complements existing studies of IF dynamics (see [4] for a review), since it allows one to classify IF dynamics as periodic, quasi-periodic or chaotic. This is achieved by the explicit construction of (i) mode-locked or bursting spike trains in terms of system parameters and (ii) a Liapunov exponent that incorporates the effects of the firing and resetting mechanism using ideas originally developed for

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the study of impact oscillators. Moreover, a linear stability analysis of the map of firing times is shown to be consistent with the demands of a negative IF Liapunov exponent. To illustrate our results we consider a single driven IF oscillator, relevant to the study of entrainment of biological oscillators and to the generation of mode-locked rhythms. Periodic modulation of a firing threshold is shown to lead only to periodic or quasi-periodic dynamics, whilst periodic modulation of a reset level allows the possibility of chaotic dynamics. In both cases we construct some of the so-called Arnold tongues for mode-locking using our results. Direct numerical simulations of the IF system are performed to support the analysis and to highlight the rich dynamical behaviour that is possible in this particular model of a spiking neuron.

In more detail, the IF mechanism may be regarded as a smooth dynamical system described by a first order ordinary differential equation

$$\frac{\mathrm{d}U}{\mathrm{d}t} = f(U,t), \quad f(U,t) = -\frac{U}{\tau} + A(t) \tag{1}$$

subject to a resetting mechanism

$$U_-(T^n) \equiv \lim_{\epsilon \to 0} U(T^n - \epsilon) = h(T^n),$$

$$U_+(T^n) \equiv \lim_{\epsilon \to 0} U(T^n + \epsilon) = g(T^n) \tag{2}$$

The firing times are defined as

$$T^n = \inf\{t | U(t) \geq h(t); t \geq T^{n-1}\} \tag{3}$$

The state variable $U(t)$ models the membrane potential of a biological neuron with decay constant τ whilst $A(t)$ represents an externally injected current. A detailed model of the refractory process seen in biological neurons is sacrificed in favour of the reset condition (2) which flags firing events as threshold crossing times. The function $h(t)$ is regarded as a firing threshold function whilst $g(t)$, the reset level, is the value that the state variable $U(t)$ takes just after it reaches threshold. Introducing the function

$$G(t) = \int_{-\infty}^{0} \mathrm{e}^{s/\tau} A(t+s)\,\mathrm{d}s \tag{4}$$

and defining $F(t) = \mathrm{e}^{t/\tau}[G(t) - h(t)]$ an implicit map of the firing times may be obtained by integrating (1) between reset and threshold:

$$F(T^{n+1}) = F(T^n) + \mathrm{e}^{T^n/\tau}[h(T^n) - g(T^n)] \tag{5}$$

If F is invertible, $F'(t) \neq 0$ for all t, and defined on the range of $F(t) + \mathrm{e}^{t/\tau}[h(t) - g(t)]$, then we have an explicit map of the form

$$T^{n+1} = \Psi(T^n),$$

$$\Psi(t) = F^{-1}\left[F(t) + \mathrm{e}^{t/\tau}(h(t) - g(t))\right] \tag{6}$$

If F is not invertible then the mapping $T^n \mapsto T^{n+1}$ is defined according to (3). For a theoretical analysis explicit knowledge of the dynamics is desirable which suggests working with the original dynamics (1) and (2) that underlies the map of firing times generated by (3). However, the analysis of IF dynamics is far from trivial owing to the presence of harsh nonlinearities at reset. In the next section we focus on a notion of Liapunov exponent that takes into account these nonlinearities.

2. The Liapunov exponent for integrate-and-fire type dynamics

If $\Psi(t)$ of Eq. (6) is well defined then it is possible to define the Liapunov exponent of an orbit as

$$\lambda = \lim_{N \to \infty} \frac{1}{N} \sum_{n=1}^{N} \ln|\Psi'(T^n)| \tag{7}$$

However, as seen from the last section, the map of firing times is only implicitly defined so that such a definition is not appropriate. The calculation of the Liapunov exponent for the discontinuous dynamical system defined by (1) and (2) is, however, possible using recent ideas developed for the study of impact oscillators [5]. Introduce a perturbed dynamics $\tilde{U}(t)$ and denote the deviation between perturbed and unperturbed trajectories as $\delta U(t)$. Now consider the propagation of an initial perturbation $\delta U(0)$. First consider the case when the unperturbed trajectory reaches threshold first. Denoting the time of the kth threshold crossing of the unperturbed trajectory as

T^k and that of the perturbed trajectory as $T^k + \delta^k$ we have

$$0 = \tilde{U}_-(T^k + \delta^k) - h(T^k + \delta^k)h(T^k) - h'(T^k)\delta^k$$
$$\approx U_-(T^k) + \delta U_-(T^k) + f\big(U_-(T^k)$$
$$+ \delta U_-(T^k), T^k\big)\delta^k - h(T^k) - h'(T^k)\delta^k$$
$$\approx \delta U_-(T^k) + \big[f\big(U_-(T^k), T^k\big) - h'(T^k)\big]\delta^k \tag{8}$$

Hence the perturbation of the firing times is given by

$$\delta^k = -\frac{\delta U_-(T^k)}{f\big(U_-(T^k), T^k\big) - h'(T^k)} \tag{9}$$

The difference between the two trajectories just after the perturbed trajectory reaches threshold is simply

$$\delta U_+(T^k + \delta^k) = g(T^k + \delta^k) - U_+(T^k + \delta^k)$$
$$\approx \big[g'(T^k) - f\big(U_+(T^k), T^k\big)\big]\delta^k \tag{10}$$

Using (9), the perturbations are seen to satisfy

$$\delta U_+(T^k + \delta^k) = \left[\frac{f\big(U_+, T^k\big) - g'(T^k)}{f\big(U_-, T^k\big) - h'(T^k)} \right] \delta U_-(T^k) \tag{11}$$

The same expression is obtained by considering the case when the perturbed trajectory reaches threshold first. In general the Liapunov function for the flow is given by

$$\lambda = \lim_{t\to\infty} \frac{1}{t} \ln \left| \frac{\delta U(t)}{\delta U(0)} \right| \tag{12}$$

where the time evolution of $\delta U(t)$ is obtained from a linearisaton of the dynamics. In the IF case with initial condition $\delta U(t_0)$ at time t_0 we have, between firing events, that $\delta U(t) = \mathrm{e}^{-t/\tau}\delta U(t_0)$ Hence, using (11) the IF Liapunov exponent is given by

$$\lambda = -\frac{1}{\tau} + \lim_{k\to\infty} \frac{1}{(T^k - T^0)} \times \sum_{j=1}^{k} \ln \left| \frac{f\big(U_+, T^j\big) - g'(T^j)}{f\big(U_-, T^j\big) - h'(T^j)} \right| \tag{13}$$

There are two contributions to λ, one from the smooth flow between successive firings and the other from the discontinuous nature of the resetting mechanism.

3. Mode-locked solutions and linear stability

The full map of the firing times specifies the output of the IF oscillator in terms of a spike train. It is of interest to know where spikes occur in relation to preceding spikes, and perhaps more importantly for neural computation, where the spikes occur in relation to any underlying periodic modulation of the system [6]. For simplicity we consider the case of a constant external drive $A(t) = I$ and a simple periodic modulation of the firing and resetting functions so that $h(t+1) = h(t)$ and $g(t+1) = g(t)$. In the limit of zero decay $\tau \to \infty$ the study of a periodic modulation of the threshold has been considered by several authors with regards to biological entrainment of oscillators [7,8]. More general scenarios, such as with $\tau \neq 0$ and periodic variation of the external input, may be handled with the approach outlined below. Restricting attention to periodic spike trains in which p spikes are fired in a period q, the firing times may be written

$$T^n = \left[\frac{n}{p} \right] q - \phi_{n(p)} q, \quad n(p) = n \bmod p, \quad p, q \in \mathbb{Z} \tag{14}$$

where $[\,.\,]$ denotes the integer part and the $\phi_{n(p)} \in [0,1)$ denote a collection of firing phases. In general one wishes to follow the bifurcation sequence of either the inter-spike interval (ISI) $\Delta^n = T^{n+1} - T^n$ or the phase variable $T^n \bmod 1$. Throughout the rest of this paper we concentrate on the former sequence. Construction of the average period $\langle \Delta \rangle$:

$$\langle \Delta \rangle = \lim_{N\to\infty} \frac{1}{N} \sum_{n=1}^{N} \Delta^n \tag{15}$$

shows that the ansatz (14) describe a solution with $\langle \Delta \rangle = q/p$, which we shall call a $q:p$ mode-locked solution. When $\langle \Delta \rangle$ is independent of initial conditions and both $q:p$ and $q':p'$ solutions can be found then another mode-locked solution is expected (in some intermediate region of parameter space) where the entrainment is $q+q':p+p'$ (at least in the regime where the dynamics is described by a circle map – see later).

From Eq. (5) with $G(t)$ given from (4) as $G(t)=I\tau$, the p firing phases are determined by the simultaneous solution of the p equations

$$H_{n(p)}(\Phi,q) \equiv \exp\left[\frac{q}{\tau}\left\{\left[\frac{n+1}{p}\right]-\left[\frac{n}{p}\right]+\phi_{n(p)} - \phi_{(n+1)(p)}\right\}\right] - \frac{I\tau - g(-\phi_{n(p)}q)}{I\tau - h(-\phi_{(n+1)(p)}q)} = 0 \quad (16)$$

where we have used the notation $\Phi \equiv (\phi_0,\ldots,\phi_{p-1})$ to denote the set of phases for a mode-locked state. The stability of a $q:p$ mode-locked solution may be found by perturbing the firing times such that $T^n \to T^n + \delta^n$ and expanding (5) to first order in the δ^ns around the mode-locked solution. In this case we obtain $\delta^{n+1} = \kappa_{n(p)}(\Phi,q)\delta^n$, where

$$\kappa_{n(p)}(\Phi,q) = \exp\left[-\frac{q}{\tau}\left(\left[\frac{n+1}{p}\right] - \left[\frac{n}{p}\right] + \phi_{n(p)} - \phi_{(n+1)(p)}\right)\right] \times \frac{I\tau - g(-\phi_{n(p)}q) - \tau g'(-\phi_{n(p)}q)}{I\tau - h(-\phi_{(n+1)(p)}q) - \tau h'(-\phi_{(n+1)(p)}q))} \quad (17)$$

Note that in deriving (17) we have assumed that $F'(T^n) \neq 0$, which is certainly true in the regime where the map of firing times has an explicit representation. By the implicit function theorem continuation of mode-locked solutions to other regions of parameter space is possible whenever $\partial H_{n(p)}(\Phi,\Delta)/\partial\gamma_a \neq 0$, where the γ_a are system parameters. The persistence of a $q:p$ mode-locked state depends upon the behaviour of the map

$$\delta^{n+1} = \left(\prod_{m=0}^{p-1}\kappa_m(\Phi,q)\right)\delta^{n+1-p} \quad (18)$$

This has solutions of the form $\delta^n = e^{n\nu/p}$ for $\nu \in \mathbb{C}$. Hence, the stability of a mode-locked state is guaranteed for $\mathrm{Re}(\nu(\Phi,q)) < 0$ where $\mathrm{Re}(\nu(\Phi,q)) = \ln|\kappa(\Phi,q)|$ and

$$\kappa(\Phi,q) = \prod_{m=0}^{p-1}\kappa_m(\Phi,q) = e^{-q/\tau}\prod_{m=0}^{p-1}\left[\frac{f(U_+,-\phi_m q) - g'(-\phi_m q)}{f(U_-,-\phi_m q) - h'(-\phi_m q)}\right] \quad (19)$$

Note the condition for stability of a mode-locked solution and the requirement that the Liapunov exponent of such a solution, $\lambda(\Phi,q)$, be negative are consistent, since from (13)

$$\lambda(\Phi,q) = -\frac{1}{\tau} + \frac{1}{q}\ln\prod_{m=0}^{p-1} \left|\frac{f(U_+,-\phi_m q) - g'(-\phi_m q)}{f(U_-,-\phi_m q) - h'(-\phi_m q)}\right| \quad (20)$$

Whenever an explicit map of the form (6) exists and $h(t)$, and $g(t)$ have the form considered above (ie are periodic, with period one) then it is a simple matter to show that $F(\Psi(t)+1) = e^{1/\tau}F(\Psi(t)) = F(\Psi(t+1))$ and hence that $\Psi(t+1) = \Psi(t)+1$. Indeed (6) may now be viewed as the iteration of a circle mapping. Introducing the function $\hat{\Psi}(t) = \Psi(t) - k$ such that $0 \le \hat{\Psi}(0) < 1$ leads to the mapping $T^{n+1} = \hat{\Psi}(T^n)$ with $\hat{\Psi}(t+1) = \hat{\Psi}(t)+1$ so that $\hat{\Psi}$ may be regarded as the lift of a degree one circle map. Introducing

$$\underline{\rho}(t) = \liminf_{n\to\infty}\frac{\hat{\Psi}^n(t)}{n}, \quad \bar{\rho}(t) = \limsup_{n\to\infty}\frac{\hat{\Psi}^n(t)}{n} \quad (21)$$

allows the definition of the rotation interval of $\hat{\Psi}$ as $L(\hat{\Psi}) = [\rho_-,\rho_+]$ where

$$\rho_- = \inf_{t\in\mathbb{R}}\underline{\rho}(t), \quad \rho_+ = \sup_{t\in\mathbb{R}}\bar{\rho}(t) \quad (22)$$

When the rotation interval reduces to a single point, denoted by ρ (so that $\rho_- = \rho_+$), then ρ is called the rotation number of $\hat{\Psi}$ and the lim sup and lim inf in (21) can be replaced by a simple limit. The choice of k ensures $0 \le \rho < 1$ so that ρ measures an average phase rotation per iteration. If ρ exists and is rational then there is an initial T^0 such that the sequence $\{T^n \bmod 1\}$ approaches a periodic sequence asymptotically for large enough n, ie mode-locking occurs. However, if ρ is irrational then every solution is ergodic and the sequence $\{T^n \bmod 1\}$ is dense in the interval [0,1). When a non-trivial rotation interval exists a positive value for the topological entropy is implied. For a detailed account of the possible routes to chaos (or more precisely positive topological entropy) in circle maps see Mackay and Tresser [9]. Typically, for two-parameter non-invertible circle maps, the borders of regions with rational rotation numbers (Arnold tongues) split into two branches in parameter space. Consequently, extension of Arnold tongues can cross, leading to a situation in which two or more different periodic orbits associated with different rotation numbers are found at the same parameter values (multi-stability). The complete Arnold tongue structure is usually complex, with borders defined by tangent and period doubling bifurcations. Beyond the accumulation points of the period doubling sequences chaotic trajectories may exist. Often, the region in parameter space between the border defining a tangent bifurcation and a period doubling one is a narrow one so that the locus of superstable cycles may be used to build a *skeleton* of the Arnold tongue structure [10]. Moreover, it is usual to find a complex sequence of bifurcations within the two branches of the extended tongue structure. Most results concerning the global organization of such bifurcations have been found using a combination of numerical and topological techniques.

For the IF system considered here the borders of the regions where mode-locked solutions become unstable are defined by the conditions $\mathrm{Re}(\nu(\Phi,q)) = 0$, where the set of phases Φ is obtained from the solution of Eqs. (16). Tangent bifurcations are defined by $\kappa(\Phi,q)=1$ whilst period doubling ones (if they exist) satisfy $\kappa(\Phi,q)=-1$. Since a period doubling bifurcation $q{:}p \to 2q{:}2p$ preserves the value of the average firing period, changes in $\langle \Delta \rangle$ are only expected as one crosses borders in parameter space defined by tangent bifurcations. Superstable cycles occur when an extremum of the implicitly defined map in (5) lies on a periodic orbit. In fact we see from (19) and the expression for the Liapunov exponent (20) that $\kappa(\Phi,q)=0$ implies $\lambda(\Phi,q) \to -\infty$ as expected for a superstable cycle. The identification of chaotic orbits, say at the end of a period doubling cascade, is possible by establishing a positive value for the IF Liapunov exponent. Note that for circle map dynamics it should be possible to calculate the first accumulation point of such a period doubling cascade using kneading theory [9]. Other routes to chaos, such as the quasi-periodic route, are also possible. For example, phase-unlocked fully extended chaos for circle map dynamics is expected in a region of parameter space where there is no Arnold tongue structure adjacent to a region where $\rho_- \le p/q < p'/q' \le \rho_+$ [11].

4. Examples

Periodic modulation of either the reset level or firing threshold can lead to surprisingly rich dynamics even in the presence of a simple constant external drive. In the former case we shall demonstrate the possibility of a period doubling route to chaos that can be confirmed by evaluating the IF Liapunov exponent derived in Section 2. Period doubling routes to chaos have also been suggested in other IF type models [8]. In these models the existence of chaotic trajectories is easily verified since the map of firing times reduces to a circle map and the standard notion of Liapunov stability applies. Interestingly, IF type systems with a non-instantaneous reset mechanism and periodically modulated thresholds have been used to model the respiratory rhythm and in particular the entrainment of this rhythm to that generated by a mechanical ventilator. For systems which linearly approach a modulated threshold and then linearly decrease to a modulated reset level one can generate mode-locked behaviour reminiscent of that observed in the periodically forced van der Pol equation [12]. A model with two periodically modulated thresholds has also been used to model the maintenance of the circadian rhythm [13].

In this section we discuss the types of firing map that can arise for periodic modulation of the firing or resetting thresholds and construct regions in parameter space where mode-locked solutions can occur. In particular, numerical continuation of solutions from the situation where the thresholds are constant is practical. For example, when $g(t)=0$ and $h(t)=1$,

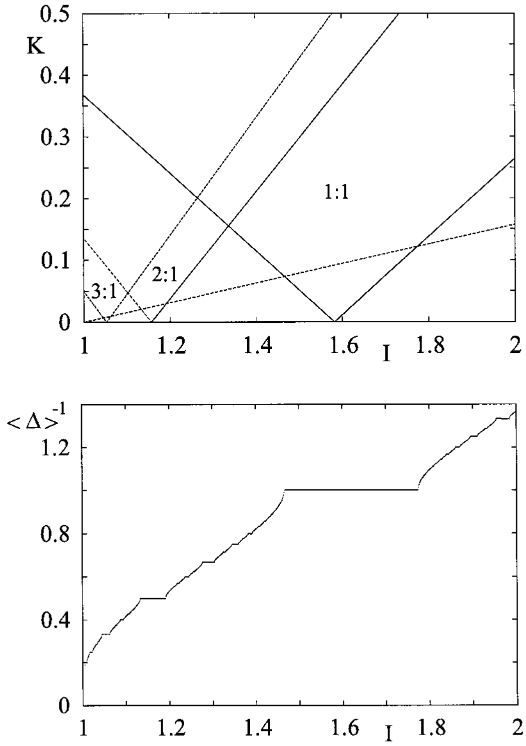

Fig. 1. Arnold tongue structure of q:1 mode-locked states for an IF oscillator with an external drive I, periodically modulated firing threshold $h(t)=1+K\sin 2\pi t$, constant reset level $g(t)=0$ and a decay constant chosen as $\tau=1$. If $I\tau>1$ the map of firing times is described by a circle map for $K<K_c\equiv(I\tau-1)/\sqrt{1+4\pi^2\tau^2}$. Above this line the dynamics is no longer described by a circle map. The borders of the tongues are defined by tangent bifurcations (solid lines with $\kappa(\Phi,q)=1$). In the bottom figure we plot the average firing frequency $\langle\Delta\rangle^{-1}$ as a function of I along the border $K=K_c$ using a direct numerical integration of the IF system. Note that the dominant modes of the Devil's staircase are 1:1 and 2:1, which is consistent with the Arnold tongue structure shown in the top figure.

q:1 mode-locked solutions exist with $I\tau=[1-\exp(-q/\tau)]^{-1}$. Furthermore, we perform direct numerical simulations to show the existence of periodic, quasi-periodic and chaotic spike-trains in parameter regimes that are consistent with those predicted from our analysis.

4.1. Periodic modulation of the firing threshold

Consider the case $g(t)=0$, $h(t)=1+K\sin 2\pi t$. The zero decay limit $\tau\to\infty$ has previously been discussed by Glass and Mackey [7]. For simplicity we assume $I\tau>1$ so that the system can reach threshold when $K=0$. We have $F(t)=e^{t/\tau}[I\tau-1-K\sin 2\pi t]$, so that $F'(t)\neq 0$ whenever $K<K_c\equiv(I\tau-1)/\sqrt{1+4\pi^2\tau^2}$. Since $F(t)+e^{t/\tau}h(t)=e^{t/\tau}I\tau>0$ we see from the discussion of Section 1 that the map of firing times is described by a circle map for $K<K_c$. Moreover, in this parameter regime $(K<K_c)$ the circle map is always invertible since $\Psi'(t)=e^{t/\tau}I/F'(\Psi)\neq 0$. Hence, in this instance the generation of chaotic orbits is not possible and the borders of the Arnold Tongues are defined by tangent bifurcations only. In Fig. 1 we show a region in the (I,K) parameter space where some of the q:1 mode-locked solutions exist as well as a plot of the average firing frequency, for $K=K_c$, that exhibits a typical Devil's staircase structure. In Fig. 2 we show

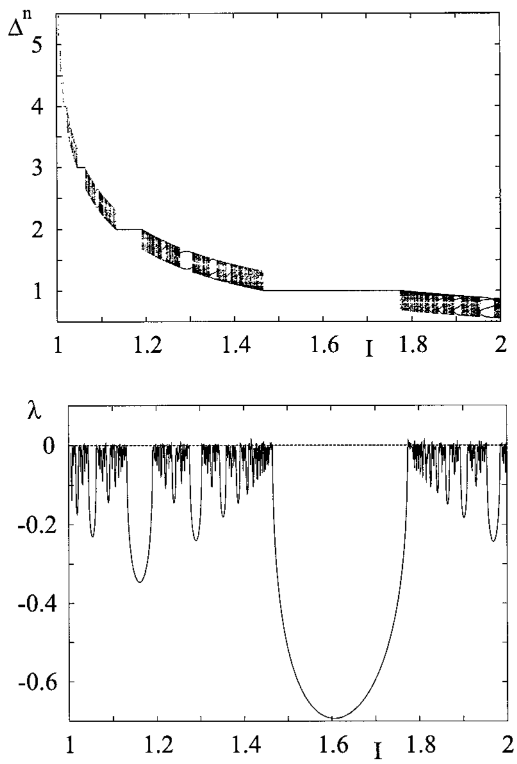

Fig. 2. Bifurcation sequence for the ISIs Δ^n as a function of the external drive I along the critical line $K=K_c$, which defines the border between circle map and non-circle map dynamics. In the bottom figure we show the corresponding IF Liapunov exponent. As expected the dynamics is either periodic or quasi-periodic. There is no parameter regime in which the dynamics can become chaotic for this model.

the bifurcation sequence of the ISIs along the critical curve $K = K_c$. The corresponding construction of the IF Liapunov exponent shows that orbits are either periodic or quasi-periodic as expected.

4.2. Periodic modulation of the reset level

Consider the case $h(t) = 1$, $g(t) = K\sin 2\pi t$. We have $F(t) = e^{t/\tau}[I\tau - 1]$ and $F'(t) = \tau^{-1}F(t)$. Hence, $F'(t) \neq 0$ if $I\tau \neq 1$. For simplicity, we assume $I\tau > 1$, so that when $K = 0$ the oscillator may still reach threshold. Moreover, we shall also restrict attention to the case $K < 1$ so that there is no conflict between the definitions for firing and reset given by (2). The inverse function $F^{-1}(t) = \tau \ln[t/(I\tau - 1)]$ has a natural domain $t > 0$ so that an explicit map of the form (6) is only possible if $g(t) < I\tau$ which is guaranteed for $K < I\tau$. In this case the map Ψ is given by

$$\Psi(t) = t + \tau \ln\left[\frac{I\tau - g(t)}{I\tau - 1}\right] \tag{23}$$

By explicit construction of $\Psi'(t)$ and demanding that $\Psi'(t) \neq 0$ for $\Psi(t)$ to be invertible we find that when the map of firing times is a circle map it is invertible for $K < I\tau/\sqrt{1 + 4\pi^2\tau^2}$). When $K > I\tau/\sqrt{1 + 4\pi^2\tau^2}$ the attractor may exhibit chaotic behaviour punctuated by windows of periodic motion in the (I,K) parameter plane. Moreover, since $\Psi'(t) = 0$ for two or more values of t there exist multiple attractors. In the limit $\tau \to \infty$, $\Psi(t)$ reduces to

$$\Psi(t) = t + \frac{1}{I} - \frac{K}{I}\sin 2\pi t \tag{24}$$

so that the map of firing times is identical in form to the standard two-parameter sinusoidal circle map (see for example [9,14]). As demonstrated by Perez and Glass [15] the threshold crossing times of a dynamical system which instantaneously jumps from a constant reset level to a sinusoidally modulated threshold and then evolves on a straight line trajectory back to the reset level can also be described by the standard two-parameter sinusoidal circle map. In Fig. 3 we show the Arnold tongue structure of the q:1 mode-locked states in the (I,K) parameter plane. Note that in contrast to the previous example, borders are defined by both tangent and period doubling bifurcations. In the regime where the firing map is described by a non-invertible circle map a period doubling route to chaos is possible. Also shown is a plot of the average firing frequency along the locus of points in parameter space defining the border between an invertible and non-invertible circle map for the firing times. Since chaotic trajectories are to be expected at the end of a period doubling cascade

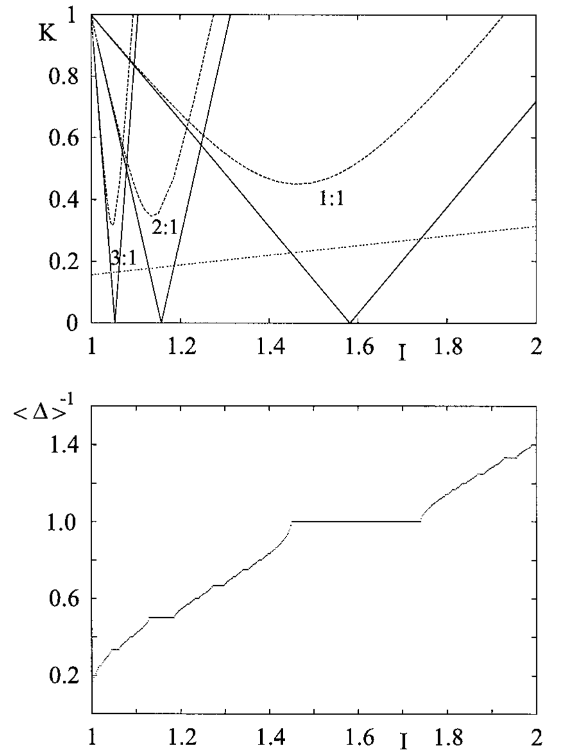

Fig. 3. Arnold tongue structure of q:1 mode-locked states for an IF oscillator with an external drive I, constant firing threshold $h(t) = 1$, oscillatory reset level $g(t) = K\sin 2\pi t$ and a decay constant chosen as $\tau = 1$. If $I\tau > 1$ the map of firing times is described by a circle map for $K < I\tau$ which is invertible below the (dotted) line $K = I\tau/\sqrt{1+4\pi^2\tau^2}$. The lower borders of the tongues are defined by tangent bifurcations (solid lines with $\kappa(\Phi,q) = 1$) whilst the upper ones describe period doubling bifurcations (dashed lines with $\kappa(\Phi,q) = -1$). In the bottom figure we plot the average firing frequency $\langle \Delta \rangle^{-1}$ as a function of I along the border of invertibility for the circle map of firing times using a direct numerical integration of the IF system. Note that the dominant modes of the Devil's staircase are 1:1 and 2:1, which is consistent with the analytical construction of the Arnold tongue structure shown in the top figure.

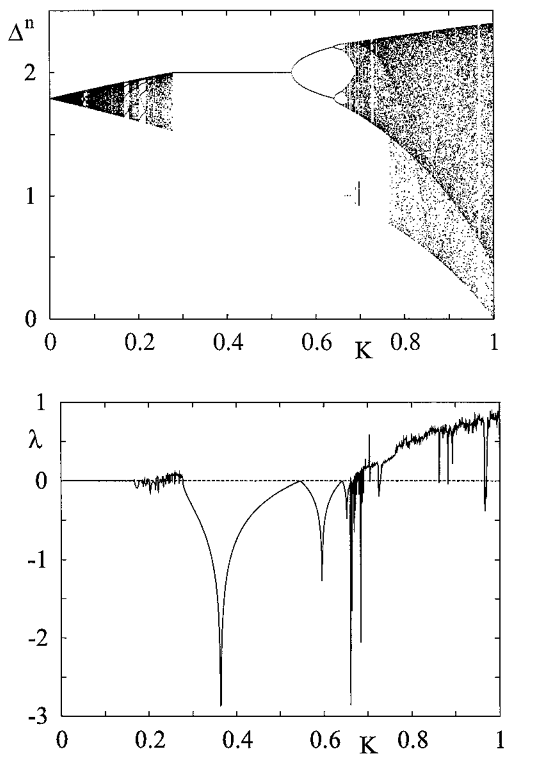

Fig. 4. Bifurcation sequence for the ISIs Δ^n as a function of K with $I = 1.2$. Note the sequence of period doubling bifurcations from the 2:1 mode-locked state starting around $K \approx 0.55$ giving rise to a chaotic state beyond $K \approx 0.7$. Note also the co-existence of the attractors around $K \approx 0.65$ as expected from the Arnold tongue structure shown in Fig. 3 and knowledge that the circle map of firing times is non-invertible in this regime.

Fig. 3 suggests searching for such behaviour in the large K limit. Fig. 4 shows that the bifurcation sequence of ISIs with increasing K does in fact yield a period doubling route to chaos with a corresponding positive value for the IF Liapunov exponent. Hence, theories of neural processing based around the firing phase of a spiking IF type oscillator in comparison to some underlying periodic modulation of the reset level are unlikely to involve any notion of long termforecasting. This is consistent with the recent ideas proposed by Hopfield [6] where only the very first few spikes, in an IF system with subthreshold periodic modulation of the membrane potential, are needed to perform biologically relevant computations. It is worthwhile to note that many mathematical models of biological rhythms consider the effect of pulsatile stimuli on limit cycle oscillators so that a description in terms of circle maps is natural from the outset. In these models chaos may also arise via a period doubling cascade and of course the usual notion of Liapunov exponent applies [15–18].

5. Discussion

In this Letter we have presented a systematic programme for the construction of mode-locked solutions, with rational average firing rate, for periodically driven IF dynamical systems with or without periodic modulation of the thresholds for firing and resetting. Moreover, we have investigated the form that the map of firing times may take in these instances. In certain cases the map of firing times reduces to a circle map and the usual notions of dynamical systems theory are easily applied. In the more general case where the map of firing times is only implicitly defined a revised notion of Liapunov exponent is required. Using ideas first introduced for the study of impact oscillators we have developed a Liapunov exponent for IF systems that is consistent with the notion of stability in the linearised model. The conditions under which chaotic spike trains may be generated in synaptically interacting networks of IF oscillators is an important open question that may be tackled using the notion of an IF Liapunov exponent. Not only may this shed light on the role of chaos in neural computation but will allow a test of the stability of spike-coding strategies. As illustrated in the examples, a further application of this work is to the construction of Arnold tongue structures and to the study of entrainment in driven IF systems such as that considered by Keener et al. [19]. A full study of the tongue structure in sinusoidally driven IF systems including realistic synaptic interactions as well as the issue of chaos in networks of IF oscillators are topics of current investigation.

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