Integrate-and-fire model with threshold fatigue, adaptation and correlations

G. Wainrib - wainrib.gilles@ijm.jussieu.fr

Institut J. Monod - LPMA Univ. Paris 6 - Polytechnique

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Introduction

Biological context

- Key property : adaptation. Transient frequency increase at the onset of stimulation
- Intespike interval (ISI) correlations in experimental recordings
- Correlations influence neural information transfer or signal detection

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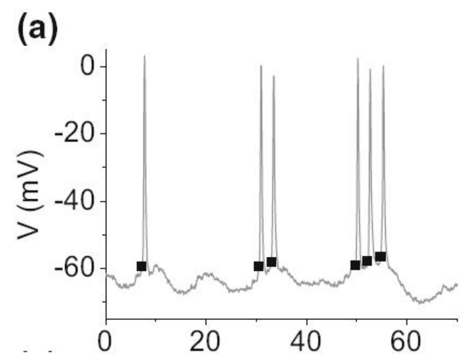
Modeling

- Leaky integrate-and-fire (LIF) : elementary spiking model, reproduces all-or-none response and postdischarge refractoriness
- Analytically tractable : no memory. Analysis with orientation-preserving circle maps. Noisy LIF: renewal process, characterized by the ISI distribution : no correlations.
- Modified LIF : threshold depends on the past spiking history. Memory parameter to adjust the level of fatigue. Leads to adaptation property and ISI correlation.



(Chacron, Lindner, Longtin J. Comput. Neurosci 2007)

References

Interspike interval correlations, memory, adaptation, and refractoriness in a leaky integrate and fire model with threshold fatigue, M.J Chacron, K. Pakdaman, A. Longtin, Neural Computation, 15, 253-278 (2003).

Plan

1. The model
2. The results
   - adaptation
   - ISI correlations
3. Discussion

1.The model

$$\frac{dv}{dt} = -\frac{v}{\theta} + I(t) \text{ if } v(t) < v(t) \quad (1)$$

$$\frac{ds}{dt} = \frac{s_r - s}{\tau_s} \text{ if } v(t) < s(t) \quad (2)$$

$$v(t^+) = v_0 \text{ if } v(t) = s(t) \quad (3)$$

$$s(t^+) = s_0 + W(s(t), \alpha) \text{ if } v(t) = s(t) \quad (4)$$

Notation : v volatge ; s threshold ; $I(t)$ stimulation current ; θ and τ_v time constants for voltage and threshold dynamic ; s_r threshold resting value (without firing)
Reset rule : voltage v_0, threshold $s_0 + W(s(t), \alpha)$, with $v_0 \leq 0 < s_r \leq s_0$. Memory parameter : α ; particular case : $W_1(s, \alpha) = \alpha s$

1.The model

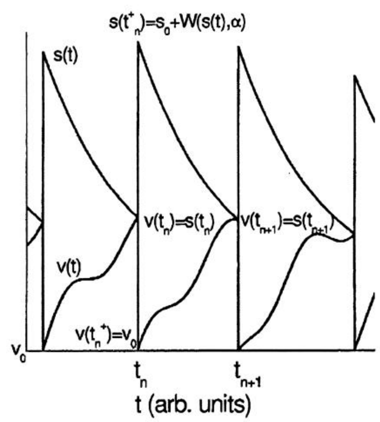


Figure 1: Voltage (black solid line) and threshold (gray solid line) time series obtained with the model. An action potential occurs when voltage and threshold are equal. The firing times t_n thus satisfy $v(t_n) = s(t_n)$. Immediately after an action potential, the voltage is reset to zero while the threshold is set to a value $s(t_n^+) = s_0 + W(s(t_n), \alpha)$.

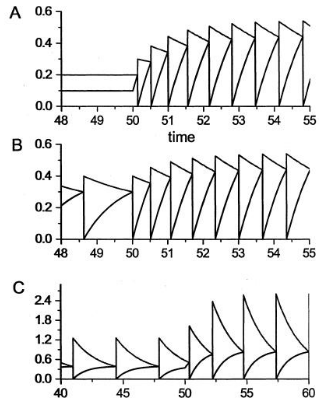


Figure 2: Response of the model to a step increase in current. (A) The current goes from subthreshold ($\mu = 0.1$) to suprathreshold ($\mu = 0.9$) at $t = 50$. Note the adaptation in the threshold and the progressive lengthening of ISIs to the new equilibrium value. Parameter values used were $\tau_s = 2$, $\tau_v = 1$, $\alpha = 1$, $s_r = 0.2$, $s_0 = 0.1$, $v_0 = 0$. (B) The current goes from $\mu = 0.4$ to $\mu = 0.9$ with all other parameters unchanged. (C) Illustration of the effects of increased α. μ goes from 0.4 to 0.9 but $\alpha = 10$ with all other parameters unchanged. Note the increased rate of adaptation.

Assume $W = W_1(s,\alpha) = \alpha s$ and $I(t) = \mu$ constant.
Two cases:

- if $\mu\theta < s_r$: subthreshold stimulus and $v(t)$ stabilizes at $\mu\theta$
- if $\mu\theta > s_r$: generates sustained firing

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Spiking times : $t_n \to$ postdischarge threshold $s(t_n^+) = S_n^+$.
ISI : $\Delta_{n+1} = t_{n+1} - t_n$.
Aim : construct a map F such that $S_{n+1}^+ = F(S_n^+)$.

- Dynamic between discharges:
  Initial conditions $v(0) = v_0$ and $s(0, S) = S$

$$v(t) = (v_0 - \mu\theta)e^{-t/\theta} + \mu\theta$$

$$s(t, S) = (S - s_r)e^{-t/\tau_r} + s_r$$

2.1 Adaptation under constant and step current stimulation

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- ISI Δ_{n+1} is such that:

$$s(\Delta_{n+1}, S_n^+) = v(\Delta_{n+1})$$

$$s(t, S_n^+) > v(t) \text{ for all } 0 \leq t \leq \Delta_{n+1}$$

  This defines Δ_{n+1} as a function of S_n^+

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- Defines a map F by:
  $S_{n+1}^+ = s_0 + \alpha s(\Delta_{n+1}(S_n^+), S_n^+) := F(S_n^+)$
  F concave monotonic increasing function$\longrightarrow$ Unique fixed point S^*

2.1 Adaptation under constant and step current stimulation

Consequences:

- Stabilizes at a periodic firing with constant ISI

$$\Delta^* = \theta \ln\left[\frac{\alpha(v_0 - \mu\theta)}{S^* - s_0 - \alpha\mu\theta}\right]$$

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- Impact of the input current μ:

$$\mu(\Delta^*) = \frac{-s_0 + s_r - s_r e^{\Delta^*/\tau_s} + v_0 e^{\Delta^*/\tau_s} e^{-\Delta^*/\theta} - \alpha v_0 e^{-\Delta^*/\theta}}{\theta(\alpha - e^{\Delta^*/\tau_s} + e^{\Delta^*/\tau_s} e^{-\Delta^*/\theta} - \alpha e^{-\Delta^*/\theta})}$$

$\rightarrow \frac{\partial\mu}{\partial\Delta^*} < 0$: firing frequency increases with μ
$\rightarrow$ if $\alpha > 1$, ISI Δ^* remains greater than $\tau_s \ln(\alpha)$

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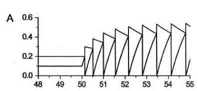
2.1 Adaptation under constant and step current stimulation

Adaptation:

- a modification $\mu \rightarrow \mu + \delta\mu$ with $\delta\mu > 0$ leads to a modification(increase) of the discharge rate : S_n increases from S^* to a new value S^*_δ, resulting in a new ISI value $\Delta^*_\delta < \Delta^*$.



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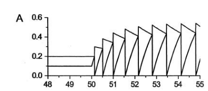
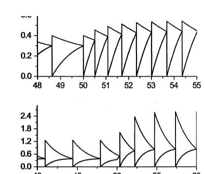


- Impact of parameter α: F is contracting for $\alpha \geq 1$, but not necessarily otherwise
$\rightarrow$ discharge rate adaptation more pronounced when α larger :faster rate of adaptation.



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Adrian and Zotterman, 1926

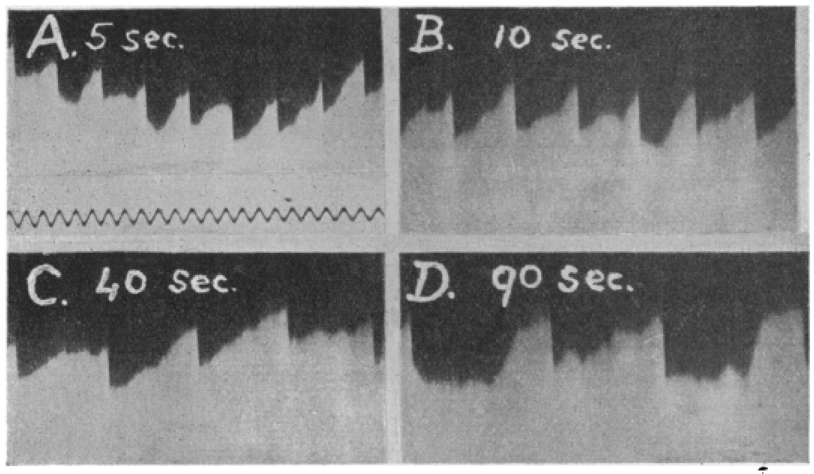

Fig. 6. Exp. 1. Single end-organ. Decrease in frequency of response as duration of stimulus is increased. 1 grm. weight.

2.2 ISI correlations with gaussian white noise stimulation

Assume $W = W_1(s, \alpha) = \alpha s$ and $I(t) = \mu + \sigma\xi(t)$, where μ is constant and $\xi(t)$ is white gaussian noise with unit intensity.
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- when $\alpha = 0$, no threshold fatigue, ISIs are i.i.d random variables, completely determined by their probability density function (pdf) $g(t|s_0)$.
  g is the FTP pdf of the Ornstein-Uhlenbeck (O.U) process η through the threshold $s(t)$ with:

$$\frac{d\eta}{dt} = (-\eta/\theta + \mu) + \sigma\xi(t) \text{ with } \eta(0) = v_0$$

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- when $\alpha > 0$: need to take into account the variation of the post discharghe threshold. Aim: establish a relation between two consequent post discharge threshold thus constructing a Markov chain.

- The conditional pdf of S_{n+1}^+ given S_n^+ can be written as:

$$\Pi_1(u|S_n^+) = \frac{\tau_s}{u - s_0 - \alpha s_r} g\left[\tau_s \ln \frac{\alpha(S_n^+ - s_r)}{u - s_0 - \alpha s_r}|S_n^+\right]$$

where g is the FTP pdf of the O.U process throught $s(t, S_n^+) = (S_n^+ - s_r)\exp(-t/\tau_s) + s_r$.

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- This defines the transition probability of an irreductible Markov chain. Denote $h^*(S)$ its stationary distribution.
- The pdf of the ISI distribution $g^*(t) = \int g(t|S)h^*(S)dS$

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2.2 ISI correlations with gaussian white noise stimulation

ISIs correlations for n large:

- Serial correlation coefficients of ISIs:

$$\rho_p = \frac{<\Delta_n\Delta_{n+p}> - <\Delta_n>^2}{<\Delta_n^2> - <\Delta_n>^2}$$

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- Moments: $<\Delta_n> = \int t g^*(t)dt$ and $<\Delta_n^2> = \int t^2 g^*(t)dt$
- Covariation:

$$<\Delta_n \Delta_{n+p}> = \int \Delta \Delta' \, g[\Delta'|S'] \Pi_{p-1}[S'|f(s,\Delta)] \, g[\Delta|S] \, h^*(S)$$

where $f(S_n^+, \Delta_n) = (S_n^+ - s_r)\exp(-t/\tau_s) + s_r = S_{n+1}^+$ and $\Pi_{k+1}(u|S) = \int_{S'} \Pi_1(u|S')\Pi_k(S'|S)dS'$.
Find $\rho_p = 0$ for $\alpha = 0$. Not a renewal process for $\alpha > 0$.

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2.2 ISI correlations with gaussian white noise stimulation

Simulation results:

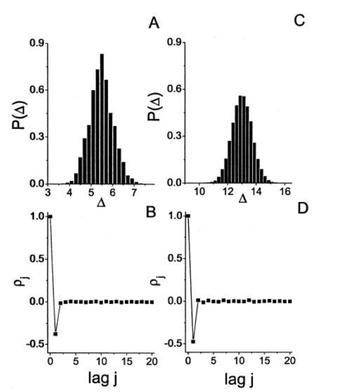

Figure 3: (A) ISI distribution obtained for $\alpha = 1$ in the presence of gaussian white noise of standard deviation 0.1. (B) Correlation coefficients ρ_j as a function of lag. Note that only $\rho_1 = -0.38$ is negative and that all coefficients are zero for higher lags. (C) ISI distribution obtained for $\alpha = 4$. (D) Correlation coefficients. Note that $\rho_1 = -0.48$ is lower than for $\alpha = 1$. Other parameter values were $\tau_s = 8$, $\tau_v = 1$, $\mu = 1$, $s_r = 0$, $s_0 = 1$.

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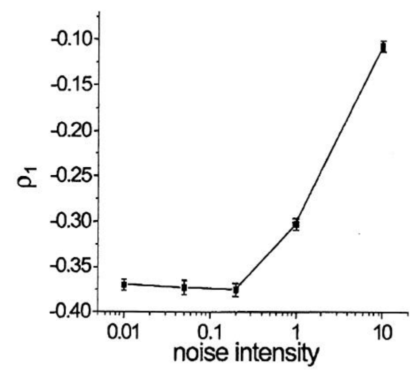

Figure 4: ρ_1 as a function of the noise standard deviation. ρ_1 exhibits a minimum for the noise intensity around 0.2. It is at this noise level that the noise is most effective at perturbing the map without itself destroying the ISI correlations. Parameter values were the same as in Figure 3 with $\alpha = 1$. Twenty thousand ISIs were used in each case.

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Performance enhancement

- Detection of weak signal : reduce variance of pulse number distribution while keeping mean unchanged (signal detection theory) (Ratnam Nelson, J.Neurosci2000 - Chacron, Longtin, Maler, J.Neurosci 2001)
- Information transfer by noise shaping (PSD low frequency) (Chacron Lindner Longtin, PRL, 2004)
- Through short-term synaptic plasticity (Ludtke Nelson, Neural Comp., 2006)

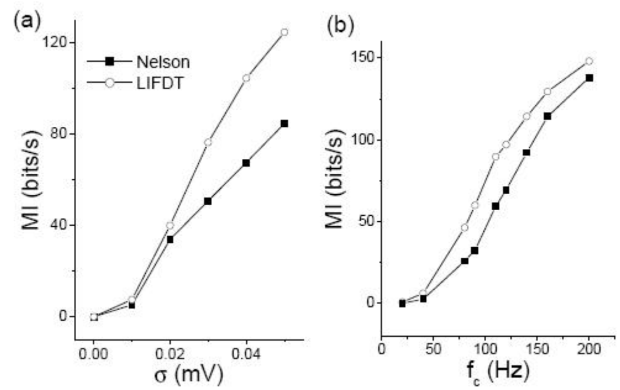

Figure 3. (a): Mutual information rates for the LIFDT and Nelson models as a function of σ and $f_c = 100$ Hz. Mutual information rates as a function of cutoff frequency f_c for $\sigma = 0.03$ mV. The LIFDT model consistently greater information rates than the Nelson model. Parameter values were previously given.[43]

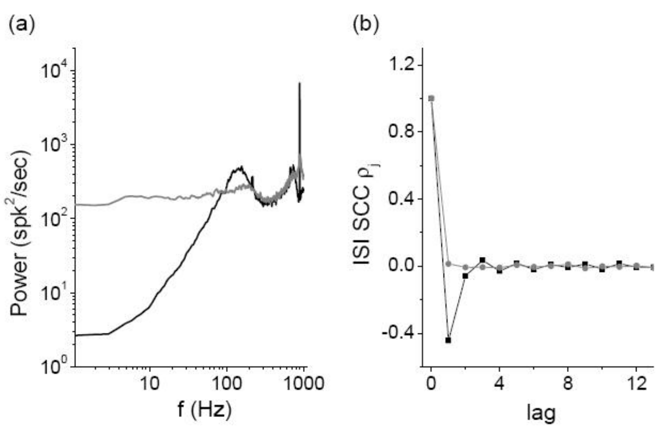

Figure 6. (a): Power spectrum of an experimentally obtained spike train from a receptor afferent under baseline activity (black). We randomly shuffled the ISI sequence and plotted the power spectrum of the resulting spike train (grey). This procedure eliminates ISI correlations and the spike train is now a renewal process. (b) ISI SCC's of the raw data (black squares) and the shuffled data (grey circles) showing that negative ISI correlations are indeed removed by the shuffling procedure.

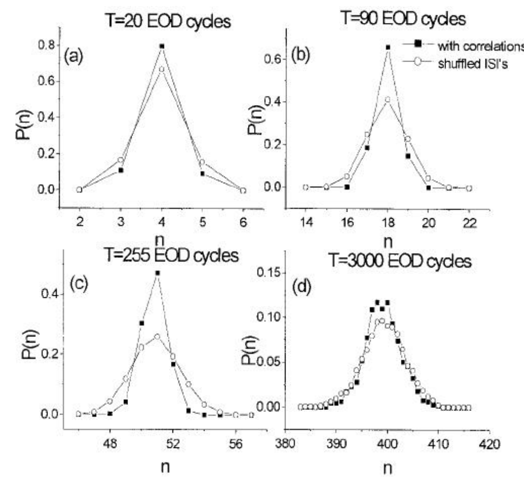

Figure 7. PNDs obtained for both models for various counting times: (*a*) 20, (*b*) 90, (*c*) 255, (*d*) 3000 EOD cycles. ISI correlations reduce the variance of the PND while keeping the mean unchanged. This effect is maximal at counting times in which the Fano factor is minimal.

Neuronal populations and coding : questions about correlations

- Neuron response is sensitive to noise properties : neural coding by correlation? (Holden, Nature, 2004) information in correlations?
- Interplay between spatial correlations and temporal correlations?
- Correlations propagation? Role in percepetion and memory? (Longtin Laing Chacron, 2003)

Develop appropriate measures for coupling/dependance

Periodically forced noisy leaky integrate-and-fire model

G. Wainrib - wainrib.gilles@ijm.jussieu.fr

Institut J. Monod - LPMA Univ. Paris 6 - Polytechnique

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- ISI distribution, autocorrelation, power spectral density of the spike train
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Modeling

- Leaky integrate-and-fire model
- Input : periodic stimulation + noise
- Input phase not reset upon firings

References

- *A first passage time analysis of the periodically forced noisy leaky integrate and fire model*, T.Shimokawa, K.Pakdaman, T.Takahata, S.Tanabe, S.Sato, Biological Cybernetics, 83,327-340 (2000)
- *Time-scale matching in the response of a leaky integrate-and-fire neuron model to periodic stimulus with additive noise.* Shimokawa T, Pakdaman K, Sato S (1999a) Phys Rev E 59: 3427- 3443
- *Stochastic resonance and spike-timing precision in an ensemble of leaky integrate and fire neuron models.*Shimokawa T, Rogel A, Pakdaman K, Sato S (1999b) Phys Rev E 59: 3461-3470
- *Mean discharge frequency locking in the response of a noisy neuron model to subthreshold periodic stimulation.* Shimokawa T, Pakdaman K, Sato S (1999c) Phys Rev E 60: R33-R36

Plan

1. The leaky integrate and fire model
2. Analysis of the model
3. Computation of the spike train characteristics
4. Applications

1.The leaky integrate and fire (LIF) model

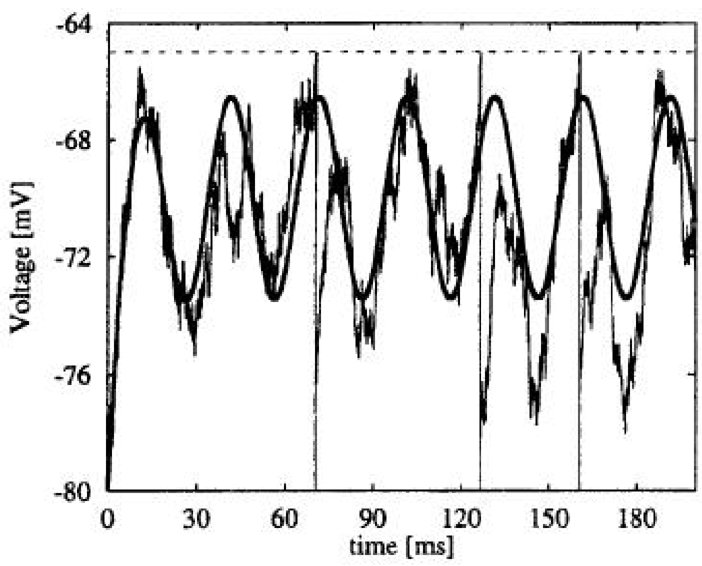
Consider standard LIF model, with a noisy periodic stimulation:

$$dv(t) = \left[-\frac{v(t)}{\tau} + \mu + I(t)\right] dt + \sigma dW(t) \text{ if } v(t) < s_0 \quad (1)$$

$$v(t^+) = v_0 \text{ if } v(t) = s_0 \quad (2)$$

Notation : v volatge ; s_0 threshold (constant) ; v_0 reset potential ; θ membrane time constant ; $I(t)$ deterministic input signal (periodic); σ noise intensity ; $W(t)$ standard Wiener process.
Remark : can also assume a Poisson noise source.

1.The leaky integrate and fire (LIF) model



2. Analysis of the model

We want to derive a stochastic phase transition operator

1. Change of variable $\rightarrow$ Ornstein-Uhlenbeck process with time-dependent boundary
2. First-passage time probability density
3. Phase transition operator : knowing the probability density for the phase at the n-th spike, what is the probability density for the phase at the $n+1$th spike?

2. Analysis of the model

1.Change of variable → Ornstein-Uhlenbeck process with time-dependant boundary
Solution in the absence of noise, given that the last firing occured at time t'. When $I(t)$ is T-periodic, with $u = t - t'$ and $\theta = 2\pi t'/T \bmod 2\pi$:

$$v_m^1(t,t') = v_0 e^{-u/\tau} + \mu\tau(1 - e^{-u\tau}) + \int_0^u I(s + T\theta/2\pi) e^{-(u-s)/\tau} ds$$

→:Intesrpike interval u determined by phase θ at the previous discharge.

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$$X(t) = V(t) - v_m^1(t,t') \quad (3)$$
$$S_m^1(t,t') = s_0 - v_m^1(t,t') \quad (4)$$

New dynamic equations:

$$dX(t) = -\frac{X(t)}{\tau} dt + \sigma dW(t) \text{ if } X(t) < S_m(t,t') \quad (5)$$
$$X(t^+) = 0 \text{ if } X(t) = S_m(t,t') \quad (6)$$

2. Analysis of the model

2.First-passage time probability density
$v_m(u,\theta) = v_m^1(t,t')$ and $S_m(u,\theta) = S_m^1(t,t')$

$$FPT = \inf\{u : X(u) > S_m(u,\theta) \mid X(0) = 0 < S_m(0,\theta)$$

Random variable with coniditional probability density function (pdf) $g(S_m(u,\theta), u | X(0) = 0)$ satisfying:

$$p(x,t|0,0) = \int_0^t g(S_m(u,\theta), u|0) p(x,t|S_m(u,\theta), u) du$$

for $X(t) = x > S_m(t,\theta)$ and $X(0) = 0 < S_m(0,\theta)$, and with p the transition pdf of the O.U process $X(t)$.

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2.First-passage time probability density
$v_m(u,\theta) = v_m^1(t,t')$ and $S_m(u,\theta) = S_m^1(t,t')$

$$FPT = \inf\{u : X(u) > S_m(u,\theta) \mid X(0) = 0 < S_m(0,\theta)$$

Random variable with coniditional probability density function (pdf) $g(S_m(u,\theta), u | X(0) = 0)$ satisfying:

$$p(x,t|0,0) = \int_0^t g(S_m(u,\theta), u|0) p(x,t|S_m(u,\theta), u) du$$

for $X(t) = x > S_m(t,\theta)$ and $X(0) = 0 < S_m(0,\theta)$, and with p the transition pdf of the O.U process $X(t)$.
→ **given that a discharge occured at time t' (phase θ), the following interspike interval u is distributed according to $g(S_m(u,\theta), u|0) := g(u|\theta)$.**

3.Stochastic phase transition operator
Probability density for the discharge phase ϕ knowing that the previous discharge phase was θ:

$$f(\phi|\theta) = \frac{1}{\Omega}\sum_{k=0}^{\infty} g\left(kT + (\phi-\theta)/\Omega \mid \theta\right)$$

with $\Omega = 2\pi/T$.

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The pdf of the phase at the n-th firing is, given h_0 the pdf for the initial phase:

$$h_n(\phi) = \int_0^{2\pi} f(\phi|\theta)h_{n-1}(\theta)d\theta := (Ph_{n-1})(\phi) = (P^n h)(\phi)$$

P : stochastic phase transition operator.

3.Stochastic phase transition operator
Properties of P

- P is a linear operator on $L^1([0, 2\pi])$ (can be restricted to L^2)
- P is a Markov operator (unity preserving positive contraction)

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$\rightarrow$ under the assumption that $\inf_\theta f(\phi,\theta) > 0$, $\{h_n\}$ is asymptotically stable : **there exists a unique $\mathbf{h}_\infty \in L^1$ such that** $h_\infty \geq 0$, $\int_0^{2\pi} h_\infty = 1$, and

$$\mathbf{Ph}_\infty = \mathbf{h}_\infty$$

$P^n h_0 - h_\infty$ converges in L^1 to 0. Better: if f is C^1, uniform convergence.

1.Computation of the phase distribution h_∞
Approximate P by finite ranked linear operators of L^2. Let (u_n) a complete orthogonal family (ex: trigonometric functions) of L^2. if $h(\phi) = \sum \xi_n u_n(\phi)$ and $f(\phi|\theta) = \sum\sum A_{mn} u_m(\phi) u_m(\theta)$ then one can approximate P by

$$P_N h(\phi) = \sum_{m=1}^{N} \sum_{n=1}^{N} A_{mn} \xi_n ||u_n||_2^2 \; u_m(\phi)$$

To compute h_∞, start with h_0 and iterate P_N until convergence criteria.

3.Computation of the spike train characteristics

2.Combining $g(t|\theta)$ and $h_\infty(\theta)$ one can compute:

- ISI distribution: $i_\infty(t) = \int_0^{2\pi} g(t\theta) h_\infty(\theta) d\theta$

G. Wainrib - wainrib.gilles@ijm.jussieu.fr Periodically forced noisy leaky integrate-and-fire model

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- Autocorrelogram : probability $L(t)dt$ for a discharge to occur within a time interval $(t, t + dt)$ from another. $L(t)$ periodic for large t.

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- Power spectral density : $P(\omega) = \frac{1}{\pi < t >}[1 + \tilde{L}(\omega) + \tilde{L}(-\omega)]$ (Bartlett,1978).
- Input-output cross-correlation : input $x(t) = I(t)$ vs. output $y(t) = \sum_i \delta(t - t_i)$ then: $R_{xy}(u) :=$

$$\lim_{t' \to \infty} \frac{1}{t'} \int_0^{t'} x(t+u)y(t)dt = \frac{1}{< t >} \int_0^{2\pi} I(\theta/\Omega + u)h_\infty(\theta)d\theta$$

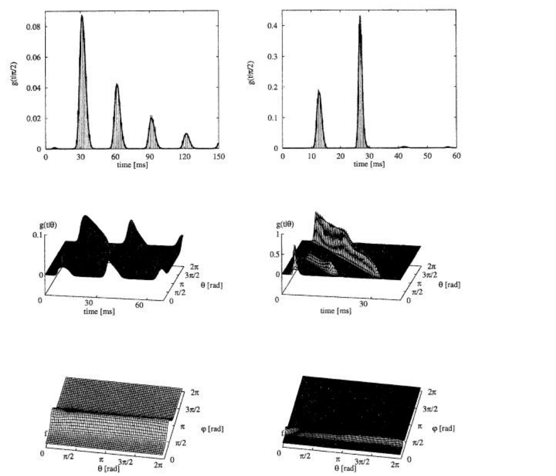


Fig. 2. First-passage time probability density function (FPT pdf) $g(t|\pi/2)$ for fixed initial phase $\theta = \pi/2$ (*upper row*), three-dimensional representation of $g(t|\theta)$ (*middle row*), and the kernel $f(\varphi|\theta)$ of the SPTO $\mathscr{P}$ (*lower row*). In *upper row*, *solid line* is calculated based on the algorithm by Giorno et al. (1989) and the *box* is numerically estimated from the stochastic differential equation. For the *upper left panel*, the number of the bin is 600 and discharges occur 10 000 times during 440 ms with simulation time step 0.005 ms. For the *upper right panel*, the number of the bin is 100 and discharges occur 10 000 times during 40 ms with simulation time step 0.01 ms. Input signal is one sinusoidal function $A\sin(\Omega t + \theta)$ in *left column*, and sum of two sinusoidal functions $A_1 \sin(\Omega_1 t + \theta) + A_2 \sin(\Omega_2 t + (\Omega_2/\Omega_1)\theta)$ in *right column*, where θ is the initial phase for both inputs. In the *lower row*, θ is the phase of the periodic input at the previous firing, and φ is the phase at the next firing. Parameters: $S = 15$ mV, $\mu = 2$ mV, $A = A_1 = 1$ V/s, $A_2 = 3$ V/s, $\tau = 5$ ms, $T = 2\pi/\Omega = 30$ ms, $T_1 = 2\pi/\Omega_1 = 30$ ms, $T_2 = 2\pi/\Omega_2 = 15$ ms

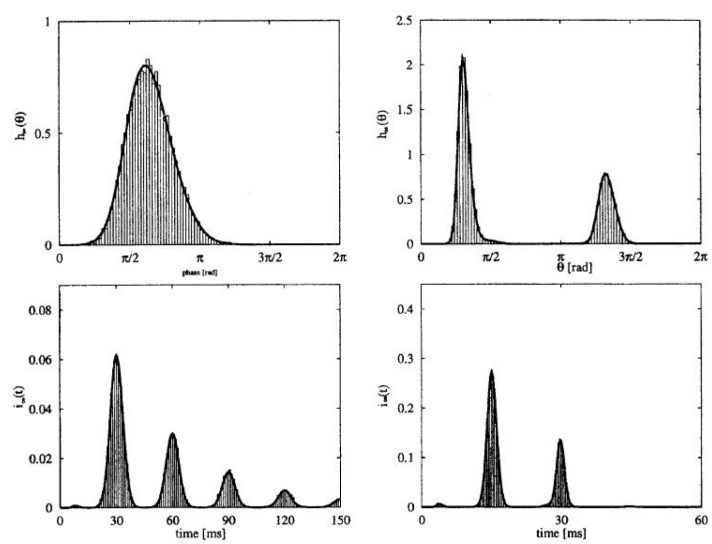


Fig. 3. Phase distribution (*upper panels*) and interspike interval distribution (*lower panels*). *Solid line* is calculated based on the method written in this paper, and we compare it with the numerically estimated phase distribution from the stochastic differential equation. The *box* in the *left column* (or *right column*) is estimated by the same data as in the upper left (or right) panel in Fig. 2. The number of the bin is 100 upper two panels. In the *lower row*, the bin size is 1 ms (*left panel*) and 0.325 (*right panel*). Input signal is one sinusoidal function in left column, and sum of two sinusoidal functions in right column. Both input signals are the same as in Fig. 2. Same parameters as in Fig. 2

3.Computation of the spike train characteristics

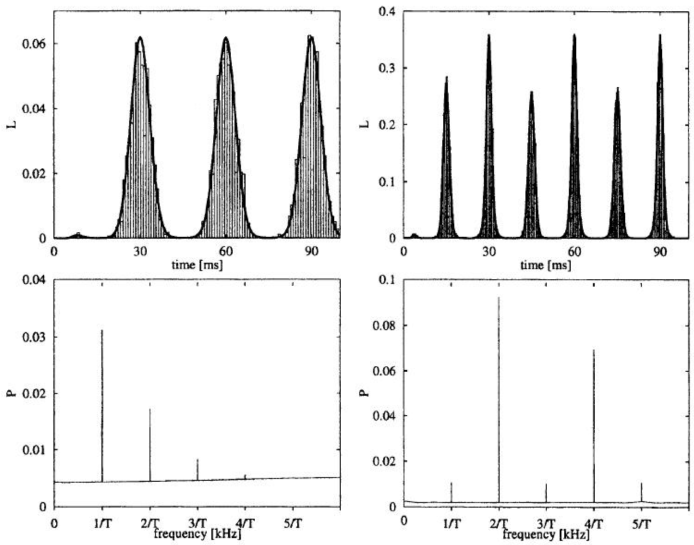


Fig. 4. Autocorrelation function (*upper panels*) and power spectral density of the spike train (*lower panels*). In *upper panels*, *solid line* is calculated based on the method written in this paper, and the *box* is numerically estimated from the stochastic differential equation. We use 2000 units of leaky integrate-and-fire model (LIFM) for the latter case. Input signal is one sinusoidal function in *left column*, and sum of two sinusoidal functions in *right column*. For the *upper left panel*, the number of the bin is 450 and discharges occur 13 302 times during 400 ms with simulation time step 0.01 ms. For the *upper right panel*, the number of the bin is 800 and discharges occur 40 067 times during 400 ms with simulation time step 0.01 ms. In *lower panels*, the Dirac pulses at the harmonics are represented by vertical segments of the height equal to $2q_n$ in Eq. (55). Both input signals are the same as in Fig. 2. Same parameters as in Fig. 2

4.Applications

1. Detection of a weak periodic signal goes through a max. as σ increases ; single LIF or ensembles of LIF.
2. LIF performance improved by adding noise : for weak subthreshold input, matching beween time-scales of the intrinsic noise-induced discharge and modulation period
3. For large subthreshold input : response enhancement depends upon the frequency response to a deterministic suprathreshold signal near threshold.

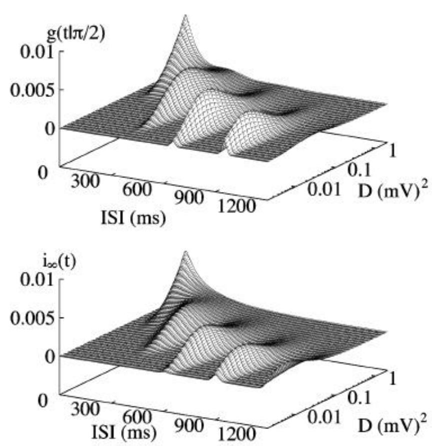
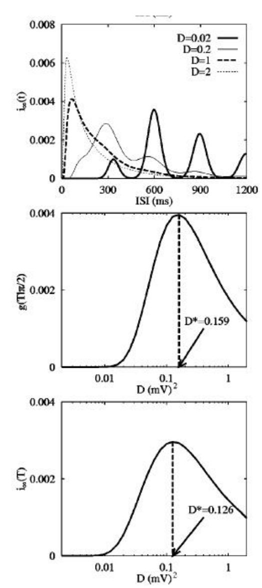
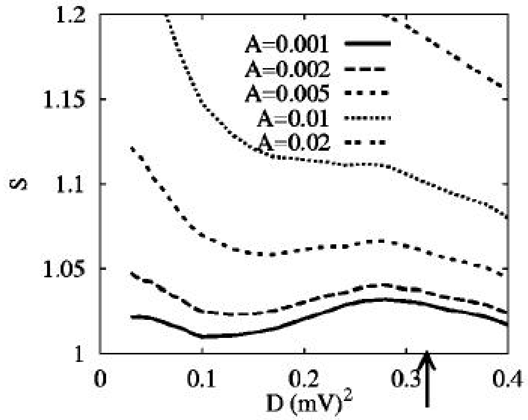


FIG. 11. Three-dimensional representations of the ISI distribution (in kilohertz) as a function of ISI in milliseconds and noise intensity D in (millivolts)^2 for endogenous (upper panel) and exogenous (lower panel). The parameters are the same as in Fig. 10.





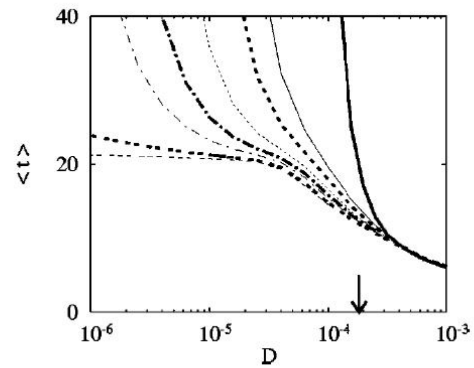


FIG. 2. Mean ISI $\langle t \rangle$ versus noise intensity D in $[(\mathrm{mV})^2/(\mathrm{ms})]$ for exogenous forcing. The lines show $\langle t \rangle$ for forcings with amplitudes $A=0$, 0.0225, 0.025, 0.0275, 0.029, 0.03, 0.0314, and 0.032 V/s from right to left. Only $A=0.032$ V/s is suprathreshold. The arrow indicates the noise intensity yielding $\langle t \rangle = T$ for $A=0$ (where T is the modulation period). Same parameters as in Fig. 1.