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Frequency-dependent response properties of adapting spiking neurons

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Abstract

The dynamics of a population of integrate and fire (IF) neurons with spike-frequency adaptation (SFA) is studied. Using a population density approach and assuming a slow dynamics for the variable driving SFA, an equation for the emission rate of a finite set of uncoupled neurons is derived. The system dynamics is then analyzed in the neighborhood of its stable fixed points by linearizing the emission rate equation. The information transfer properties are then probed by perturbing the system with a sinusoidal input current: despite the low-pass properties of the dynamical variable associated with SFA, the adapting IF neuron behaves as a band-pass device and a phase-lock condition appears at a frequency related to the characteristic time constants of both neuronal and SFA dynamics. When a finite set of neurons is considered, the power spectral density of the pooled firing rates shows for intermediate ω a rich pattern of resonances. Theoretical predictions are successfully compared to numerical simulations.
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Keywords: Spike-frequency adaptation; Stochastic modelling; Resonant properties

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2

G. Gigante et al. / Mathematical Biosciences xxx (2006) xxx–xxx

24 1. Introduction

25 A neuron lowers its firing rate upon receiving sustained stimulation. This behavior, customarily
26 termed spike-frequency adaptation (SFA in the following), is pervasively observed, and is thought to
27 be subserved by complex mechanisms involving several ionic species and characteristic time scales.

28 As a first step towards modelling SFA, the so called I_{AHP} (after-hyperpolarization current)
29 scheme is adopted, by which a calcium-gated potassium current temporarily hyperpolarizes the
30 neuron upon spike emission, with a recovery time of the order of hundreds of milliseconds.
31 Including SFA in integrate and fire (IF) neuron models brings a host of interesting implications,
32 both at the single neuron and the network level [1–4].

33 We approach the dynamics of adapting IF neurons starting from a population density ap-
34 proach [5,6], applying it to a finite set of non-interacting neurons through the formalism intro-
35 duced in [6,7], which provides an “emission rate equation” for the time-dependent firing rate of
36 the neurons, and incorporating SFA via an adiabatic approximation.

37 The behavior of the system is investigated in the neighborhood of its stable fixed points, by lin-
38 earizing the emission rate equation, and the power spectral density of the neurons firing rate is
39 computed, exhibiting a non-trivial pattern of resonances.

40 The information transfer properties of the adapting neuron are then analyzed; specifically, we
41 derive from the theory the phase-locking properties which have been experimentally observed and
42 described through a phenomenological model in [3].

43 2. Theoretical framework

44 The standard IF neuron model is endowed with an extra (inhibitory) potassium input current,
45 proportional to the instantaneous calcium concentration c through a (potassium) conductance g .
46 In turn, c undergoes an upward jump α upon spike emission, after which it decays with a charac-
47 teristic time τ_c :

$$49 \begin{cases} \frac{dv}{dt} = -f(v) - gc + I_{\text{ext}} \\ \frac{dc}{dt} = -\frac{c}{\tau_c} + \alpha \sum_k \delta(t - t_k) \end{cases} \quad (2.1)$$

50 The input external current I_{ext} is assumed to be a Gaussian memoryless noise with infinitesimal mo-
51 ments μ_{ext} and σ_{ext}^2 , which may depend on time. I_{ext} models both the barrage of external spikes re-
52 ceived by the neuron, as argued in the next subsection, and an externally injected deterministic
53 current, as in a hypothetical patch-clamp experiment. t_k is the time of the k th spike emitted when
54 the membrane potential v crosses a threshold θ and is instantaneously reset to the reset potential
55 $v \equiv H$. In what follows we use as the model neuron the VLSI integrate and fire neuron (VIF) intro-
56 duced in [8,9] with a reflecting barrier in $v = 0$ and a constant decay term ($f(v) = \beta$). The collective
57 behavior of interacting VIF neurons has been shown to be similar to those of other IF neurons [9,6].

58 Fig. 1 shows an example time evolution of v and c . As the external current is turned on at $t = 0$,
59 the calcium concentration c increases, and correspondingly the firing rate of the neuron adapts to
60 a lower value with larger inter-spike intervals (ISI). After a transient period c fluctuates around an
61 asymptotic constant value.

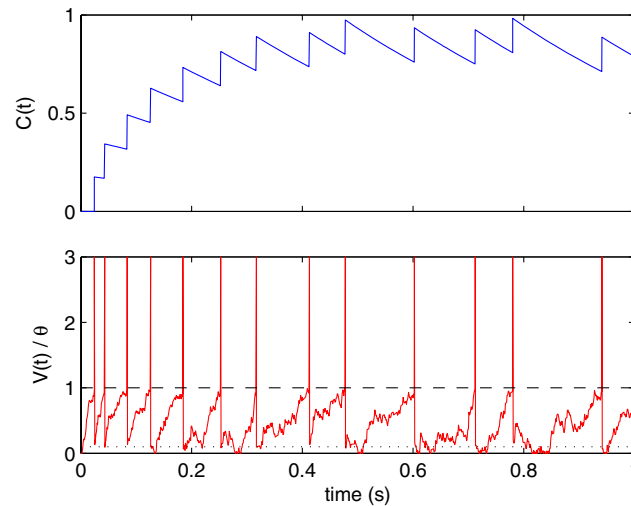


Fig. 1. Numerical integration of Eq. (2.1) for a VIF neuron with SFA receiving at $t = 0$ a noisy afferent current. The parameters set is $\beta = 10/s$, $H = 0.1\theta$, $\mu_{\text{ext}} = 100/s$, $\sigma_{\text{ext}}^2 = 0.5\theta^2/s$, $g = 100/s$, $\tau_c = 0.5$ s and $\alpha = 0.175$, where the calcium concentration is expressed in arbitrary units.

62 2.1. The population density approach

63 Each neuron in the neocortex receives, and projects, a huge number of synaptic contacts, of
64 order some thousands. It is also found experimentally that each pre-synaptic spike induces a small
65 change in the post-synaptic membrane potential, compared to the available dynamic range $\theta - H$.
66 In other words, many afferent spikes are needed in order to depolarize v above the threshold θ and
67 to provoke the emission of a spike (see for instance [10]).

68 Such small ‘efficacy’ of each single synapse allows one, in a first approximation, to consider as
69 uncorrelated the activity of any two neurons, as their mutual influence will be very weak. The
70 independence of spike trains from different neurons and the large number of synaptic contacts,
71 allow then to approximate the barrage of incoming spikes with a Poisson process, possibly
72 non-homogenous in time.

73 Furthermore, under physiological conditions neurons fire on average few spikes per seconds, but
74 due to the large number of afferents the whole incoming Poisson process will have an instantaneous
75 frequency parameter of several thousands Hz. Single neurons integrate the current due to those
76 incoming spikes with a membrane potential time constant of order tens of ms. Since in this time win-
77 dows the membrane potential integrates tens of spikes or more, standard probability arguments al-
78 low us to model the input current I_{ext} as a gaussian white noise with infinitesimal mean μ_{ext} and
79 variance σ_{ext}^2 , which depend both on the total input firing rate and the synaptic efficacies (diffusion
80 approximation) [10].

81 Here we assume an instantaneous synaptic transmission of the afferent spikes, which is a good
82 approximation for AMPA and GABA receptor dynamics [11], while we neglect the non-instanta-
83 neous synaptic transmission mediated by NMDA receptors; this is justified as long as the average
84 membrane potential is low enough to make the removal of the magnesium block unlikely, which is
85 the case for moderate activity regimes [12].

4

G. Gigante et al. / Mathematical Biosciences xxx (2006) xxx–xxx

86 Since we describe the incoming current I_{ext} as a stochastic process, Eq. (2.1) is a bi-dimensional
87 Langevin equation, and the dynamics of the probability density function (*p.d.f.*) $p(v, c, t)$ is given
88 by the deterministic continuity equation:

$$90 \quad \partial_t p(v, c, t) = -\mathbf{V} \cdot \mathbf{S}(v, c, t)$$

91 where $\mathbf{S}(v, c, t)$ is the flux vector of realizations moving from (v, c) at time t , and $\mathbf{V} = \{\partial_v, \partial_c\}$. In
92 the diffusion limit in which I_{ext} is a gaussian white noise, the above equation reduces to the fol-
93 lowing Fokker–Planck (FP) bi-dimensional equation:

$$95 \quad \partial_t p(v, c, t) = \partial_c \frac{c}{\tau_c} p(v, c, t) - \partial_v \mu(v, c, t) p(v, c, t) + \frac{1}{2} \sigma^2 \partial_v^2 p(v, c, t) \quad (2.2)$$

96 where, in our uncoupled neuron case, $\mu(v, c, t) \doteq -f(v) - g c + \mu_{\text{ext}}(t)$ and $\sigma^2 \doteq \sigma_{\text{ext}}^2$ are the infini-
97 tesimal moments of v . The FP equation is complemented by the following boundary conditions:
98 (i) an absorbing barrier at $v = \theta$, where a realization disappears upon spike emission; (ii) a reflect-
99 ing barrier providing a lower bound for v ($v \geq 0$ for VIF neurons); (iii) a source of realizations
100 enforcing the conservation of the probability flux, such that realizations disappeared in θ reappear
101 in $v = H$, the reset potential, after the emission of an action potential, increasing c by α .

102 At a given time the histogram of the membrane potential of the different neurons in the pop-
103 ulation can be seen as a sample of the probability density function $p(v, c, t)$. The FP Eq. (2.2) may
104 be then interpreted as the dynamics of a population of uncoupled neurons with afferent currents
105 sharing the same statistics.

106 The time-dependent variable of interest will be the total emission rate per neuron $v(t)$:

$$108 \quad v(t) = \int_0^\infty v(c, t) dc \quad (2.3)$$

109 where $v(c, t)$ is the firing rate density per neuron, for an instantaneous calcium concentration c ,
110 provided by the flux component parallel to the v direction:

$$112 \quad \begin{aligned} v(c, t) &= \{\mathbf{S}(\theta, c, t)\}_v = \mu(v, c, t) p(v, c, t) - \frac{1}{2} \sigma^2 \partial_v p(v, c, t)|_{v=\theta} \\ &= -\frac{1}{2} \sigma^2 \partial_v p(v, c, t)|_{v=\theta} \end{aligned}$$

113 We set $p(\theta, c, t) = 0$ since $v = \theta$ is an absorbing barrier.

114 Fig. 2 shows an example of the asymptotic *p.d.f.* $p(v, c, t)$ in the phase plane (v, c) . It is seen that
115 $p(v, c, t)$ spans a wide region in both dimensions (v, c) , such that naive strategies for dimensional
116 reduction of the problem, valid when the *p.d.f.* is very concentrated in one or more dimensions,
117 are unlikely to be effective in the case shown.

118 2.2. Dimensional reduction: the adiabatic approximation

119 In order to effectively tackle the problem of solving Eq. (2.2) with its boundary conditions, we
120 exploit the great difference of the time scales of the membrane potential and the calcium concen-
121 tration dynamics, and invoke an adiabatic approximation to reduce the dimensionality of the
122 problem.

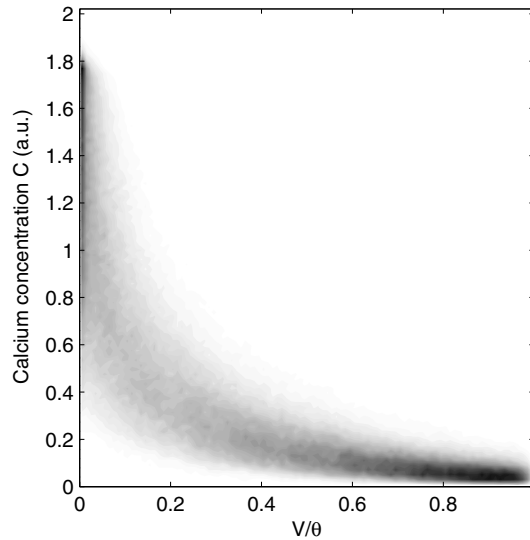


Fig. 2. Asymptotic p.d.f. $p(v, c, t)$ estimated from the numeric integration of Eq. (2.1) over 50 s after a transient period of 1 s needed to forget initial conditions. Darker regions are associated to higher probability densities, white areas correspond to $p(v, c, t) = 0$. The parameters set is the same as in Fig. 1 with the following exceptions: $H = 0$, $\mu_{\text{ext}} = 9 \theta/s$, $\tau_c = 50$ ms and $\alpha = 1.75$.

123 As τ_c is supposed to be much longer than the other time scales in the system (membrane time
 124 constants, average inter-spike interval), the calcium concentration for each neuron is a very effi-
 125 cient integrator filtering almost all the fluctuations in the single neuron activity. Eq. (2.1) for $c(t)$
 126 can be then well approximated by its average on a time window much smaller than τ_c :

$$128 \quad \dot{c}(t) = -\frac{c(t)}{\tau_c} + \alpha v(t) \quad (2.4)$$

129 Furthermore, since the dynamics of c is slow, in the time between two consecutive spike emissions
 130 each neuron sees an approximately constant $I_{\text{AHP}} = -gc(t)$.

131 Such approximation can be better understood considering, in stationary conditions, the relative
 132 width of the $c(t)$ marginal distribution. Consider the case study of a Poissonian emitted spike train
 133 with frequency ν . Both the average and the variance of $c(t)$ can be computed and are respectively
 134 $\alpha\nu\tau_c$ and $\alpha^2\nu\tau_c/2$. The coefficient of variation, given by the ratio between standard deviation and
 135 mean, is then proportional to $1/\sqrt{\nu\tau_c}$. A constant I_{AHP} during an ISI is then a good assumption
 136 provided that $\tau_c \gg 1/\nu$. Such a “slow adaptation” approximation is independent from α . On the
 137 other hand, when the neuron firing is more regular than a Poissonian spike train, as for strong
 138 potassium conductances g bringing the neuron well below the emission threshold for almost
 139 the whole ISI, the relative width of c distribution is independent from $\nu\tau_c$. This is why the limit
 140 of small coefficient of variation of c implies also a not too strong calcium feedback.

141 In such a limit, the density $p(v, c, t)$ then collapses in a one-dimensional subspace parallel to the
 142 v direction in Fig. 2. The flux $\mathbf{S}(v, c, t)$ gets a vanishing c component and the FP equation becomes:

$$144 \quad \partial_t p(v, t) = -\partial_v \mu(v, t) p(v, t) + \frac{1}{2} \sigma^2 \partial_v^2 p(v, t) \quad (2.5)$$

6

G. Gigante et al. / Mathematical Biosciences xxx (2006) xxx–xxx

145 where now $\mu(v, t) = -f(v) - g c(t) + \mu_{\text{ext}}(t)$

146 In this approximation $v(t) = v(c, t)\delta(c - c(t))$:

$$148 \quad v(t) = -\frac{1}{2}\sigma^2\partial_v p(v, t)|_{v=\theta} \quad (2.6)$$

149 As a result of the above dimensional reduction, the relevant boundary conditions will be those
150 appropriate for $p(v, t)$, which are the same as for $p(v, c, t)$ neglecting the jumps α for c . For simplic-
151 ity from now on α is set to 1.

152 2.3. Spectral decomposition of the FP operator

153 We can rewrite Eq. (2.5) as $\partial_t p = \mathcal{L}p$ defining the FP operator:

$$155 \quad \mathcal{L} = -\partial_v \mu(v, t, c) \cdot + \frac{1}{2}\sigma^2\partial_v^2 \quad (2.7)$$

156 Let us suppose a complete set of eigenfunctions for the FP operator \mathcal{L} exists, with their associated
157 eigenvalues:

$$159 \quad \mathcal{L}\varphi_n(v) = \lambda_n\varphi_n(v)$$

160 where φ s and λ s will actually depend on μ , c and σ^2 as \mathcal{L} itself. Defining the following inner
161 product:

$$163 \quad \langle \psi | \varphi \rangle \doteq \int \psi(v)\varphi(v)dv \quad (2.8)$$

164 the adjoint of the FP operator:

$$166 \quad \langle \psi | \mathcal{L}\varphi \rangle = \langle \mathcal{L}^+\psi | \varphi \rangle \quad (2.9)$$

167 will have eigenfunctions and eigenvalues:

$$169 \quad \mathcal{L}^+\psi_n(v) = \lambda_n\psi_n(v)$$

170 \mathcal{L} and \mathcal{L}^+ share the same set of eigenvalues as Eq. (2.9) implies that eigenfunctions with different
171 eigenvalues are orthogonal and because of the assumed completeness of the φ s. With an appro-
172 priate normalization the two sets of eigenfunctions are biorthonormal:

$$174 \quad \langle \psi_n | \varphi_m \rangle = \delta_{nm} \quad (2.10)$$

175 Again because of completeness, φ s will satisfy the same boundary conditions as $p(v, t)$ in Eq. (2.5).

176 Finally, it can be proven that [13,6]:

- 177 • the λ s appear in general in complex conjugate pairs (this comes from the condition of reentering
- 178 flux at H , as, without that condition, \mathcal{L} would admit only real eigenvalues);
- 179 • the λ s have negative real parts;
- 180 • always exists a $\lambda_0 = 0$ that correspond to the stationary solution of Eq. (2.5) (for μ , c and σ^2
- 181 kept fixed);

182 • $\psi_0(v) \equiv 1$.
183

184 2.4. Emission rate equation

185 Knowing the complete spectrum of the FP operator, we can expand every acceptable probabil-
186 ity density function of v as:

188
$$p(v, t) = \sum_n a_n(t) \varphi_n(v) \quad (2.11)$$

189 for adequate coefficients $a_n(t)$. From this equation, using the orthonormality property (Eq. (2.10))
190 and the FP Eq. (2.5), we can derive a dynamics for the infinite set of a s. Starting from:

192
$$a_n(t) = \langle \psi_n | p \rangle$$

193 and taking time derivatives we obtain:

195
$$\begin{aligned} \dot{a}_n(t) &= \langle \psi_n | \partial_t p \rangle + \langle \partial_t \psi_n | p \rangle = \langle \psi_n | \mathcal{L} p \rangle + \sum_k a_k \langle \partial_t \psi_n | \varphi_k \rangle \\ &= \langle \mathcal{L}^\dagger \psi_n | p \rangle + \sum_k a_k \langle \partial_\mu \psi_n | \varphi_k \rangle \dot{\mu} \\ &= \lambda_n a_n + \sum_k a_k \langle \partial_\mu \psi_n | \varphi_k \rangle \dot{\mu} \end{aligned} \quad (2.12)$$

196 We adopt in the following a matrix notation and write a_n for $n \neq 0$ as a vector, \mathbf{a} ; since
197 $\langle \psi_0 | p \rangle = \langle 1 | p \rangle = 1$ at any time (see Section 2.4), $a_0(t) \equiv 1$.

198 Then, we define the three following (infinite) matrices:

200
$$A_{nm} \equiv \delta_{nm} \lambda_n \quad (2.13)$$

200
$$M_{nm} \equiv \langle \partial_\mu \psi_n | \varphi_m \rangle \quad (2.14)$$

201 for $n, m \neq 0$, and the (infinite) vector:

203
$$m_n \equiv \langle \partial_\mu \psi_n | \varphi_0 \rangle \quad (2.15)$$

204 for $n \neq 0$.

205 With the help of these definitions, the set of Eqs. (2.12) can be restated as:

207
$$\begin{cases} \dot{\mathbf{a}} = (A + M \dot{\mu}(t)) \mathbf{a} + \mathbf{m} \dot{\mu}(t) \\ a_0 = 1 \end{cases} \quad (2.16)$$

208 The set of Eq. (2.16) has to be complemented by a dynamic equation for c , which will in turn de-
209 pend on $p(v, t)$ (that is on \mathbf{a}) through v , thus making the FP equation non-linear.

210 In order to close the loop, thanks to Eq. (2.11) we rewrite Eq. (2.6) as:

212
$$v(t) = -\frac{1}{2} \sigma^2(t) \partial_v p(v, t) |_{v=0} = -\frac{1}{2} \sigma^2(t) \sum_n a_n(t) \partial_v \varphi_n(v, t) |_{v=0} \quad (2.17)$$

213 Defining:

215
$$\Phi(\mu, \sigma) \doteq -\frac{1}{2} \sigma^2(t) \partial_v \varphi_0(v, t) |_{v=0} \quad (2.18)$$

216 (Φ is the mean emission rate of the neuron in stationary condition, again for μ , c and σ^2 kept fixed)
217 and:

$$219 \quad f_n(\mu, \sigma) \doteq -\frac{1}{2} \sigma^2(t) \partial_v \varphi_n(v, t)|_{v=0} \quad (2.19)$$

220 for $n \neq 0$ and writing all the f_n as a vector, \mathbf{f} , we can rewrite Eq. (2.17) as:

$$222 \quad v(t) = \Phi + \mathbf{f} \cdot \mathbf{a} \quad (2.20)$$

223 recalling that $a_0 \equiv 1$.

224 Now we are done: we reduced our problem, thanks to an adiabatic approximation and a spec-
225 tral expansion of the FP operator, to the solution of the following dynamical system:

$$227 \quad \begin{cases} \dot{\mathbf{a}} = (A + M\dot{\mu}(t))\mathbf{a} + \mathbf{m}\dot{\mu}(t) \\ v = \Phi + \mathbf{f} \cdot \mathbf{a} \\ \dot{c} = -c/\tau_c + v \end{cases} \quad (2.21)$$

228 The solution of this infinite set of equations is not, generally, easier than that of the original prob-
229 lem; one advantage of this formulation is that Eqs. (2.21) are much more amenable to approxi-
230 mate treatments than Eqs. (2.4) and (2.5).

231 2.5. A finite set of neurons

232 The total emission rate per neuron of a finite *ensemble* of neurons will always present random
233 fluctuations around the average $v(t)$. Such fluctuations have a special interest since, as we will see
234 in a moment, they provide much information about the frequency response of the single neuron.
235 Indeed, even if we are discussing the behavior of a set of independent spiking neurons the emerg-
236 ing spectral properties will be of course single cell properties, but in order to consider the present-
237 ed theoretical framework as a first step toward the analysis of network of neurons with
238 adaptation, we follow the approach introduced in [14,6].

239 Consider a homogeneous population of N independent neurons (that is not connected by syn-
240 aptic couplings). Let us focus our attention on a small time interval dt , and count the number dn_N
241 of spikes emitted by the population in that interval, which will be approximately a Poisson var-
242 iable, with mean and variance $Nv(t)dt$. The instantaneous emission rate of the *finite* population
243 $v_N(t)$ is estimated by:

$$245 \quad v_N(t) \doteq \frac{1}{N} \frac{dn_N(t)}{dt} \quad (2.22)$$

246 As long as $Nv(t)dt \gg 1$, dn_N can be again well approximated by a Gaussian variable; since there
247 are no correlations between successive dn_N , for dt smaller than any time scale of the dynamics, we
248 can write $v_N(t)$ as:

$$250 \quad v_N(t) \doteq v(t) + \sqrt{\frac{v(t)}{N}} \Gamma(t) \quad (2.23)$$

251 where $\Gamma(t)$ is a standard white-noise. As one could expect, for $N \rightarrow \infty$, $v_N(t) \rightarrow v(t)$.

252 In order to describe the dynamics of $v_N(t)$, we recall two main points in the FP description of
 253 our system. First, $v(t)$ represents the probability flux through the emission threshold θ ; second,
 254 this flux reenters instantaneously at the reset potential H : this is the analytical counterpart of
 255 the resetting after the emission of a spike. Thus, fluctuations in $v_N(t)$ will be immediately felt at
 256 H . This effect can be incorporated in the FP description defining a new finite-size, stochastic
 257 FP operator:

$$259 \quad \mathcal{L}_N \doteq \mathcal{L} + \delta(v - H) \sqrt{\frac{v(t)}{N}} \Gamma(t) \quad (2.24)$$

260 which corresponds to an *emission rate equation* for $v_N(t)$, that reads:

$$262 \quad \begin{cases} \dot{\mathbf{a}} = (\Lambda + M\dot{\mu}(t))\mathbf{a} + \mathbf{m}\dot{\mu}(t) + \boldsymbol{\psi} \sqrt{v/N} \Gamma(t) \\ v_N = \Phi + \mathbf{f} \cdot \mathbf{a} + \sqrt{v/N} \Gamma(t) \equiv v + \sqrt{v/N} \Gamma(t) \\ \dot{c} = -c/\tau_c + v_N \end{cases} \quad (2.25)$$

263 where the vector $\boldsymbol{\psi}$ has elements $\psi_k(H)$, where $\psi_k(v)$ is the eigenfunction of \mathcal{L}^+ with eigenvalue λ_k .
 264 The additional term on the r.h.s. in the first equation comes directly from the δ -function appear-
 265 ing in \mathcal{L}_N .

266 2.6. Fixed points and local analysis

267 In the limit $N \rightarrow \infty$ and in absence of non-stationary external stimulations, the system may re-
 268 lax to fixed points such that $\dot{\mathbf{a}} = 0$, $\dot{c} = 0$ and $\dot{v} = 0$, solutions of:

$$270 \quad \{\mathbf{a}_0 = 0, v_0 = \Phi(c_0), c_0 = v_0 \tau_c\} \quad (2.26)$$

271 The non-linear Eq. (2.21) can be then linearized around such fixed points to study small pertur-
 272 bations due to external non-stationary stimulations or the finite-size fluctuations of the emission
 273 rate. To do that we introduce the displacements from the fixed point $v_1(t) \doteq v(t) - v_0$,
 274 $c_1(t) \doteq c(t) - c_0$ and $\mathbf{a}(t)$. Neglecting terms of order higher than the first the emission rate equa-
 275 tion reduces to:

$$277 \quad \begin{cases} \dot{\mathbf{a}} = \Lambda \mathbf{a} + \mathbf{m}_0 \dot{\mu}_1 + \boldsymbol{\psi}_0 \sqrt{v_0/N} \Gamma(t) \\ v_1 = \Phi_\mu \mu_1 + \mathbf{f}_0 \cdot \mathbf{a} + \sqrt{v_0/N} \Gamma(t) \\ \dot{c}_1 = -c_1/\tau_c + v_1 \end{cases} \quad (2.27)$$

278 where all the functions are calculated at the fixed point, including $\Phi_\mu \doteq \partial_\mu \Phi(\mu, \sigma^2)$. In particular
 279 $\mu_1(t) \doteq \mu(t) - g c_0 - \beta + \mu_{\text{ext}}$ is the perturbation of the infinitesimal mean due to the fluctuation
 280 of c and the possible external stimulation.

281 3. Spectral analysis

282 A finite set of uncoupled identical neurons may provide a train of spikes exhibiting a rich rep-
 283 ertoire of resonances. Performing the Fourier transform $v_1(\omega)$ of the population emission rate

284 from the linearized Eq. (2.27), the spectral properties of the system can be studied by means of the
285 power spectrum $P_1(\omega) = |v_1(\omega)|^2$:

$$287 \quad P_1(\omega) = \frac{1 + 2\text{Re}\left[\mathbf{f}_0 \cdot (i\omega I - A_0)^{-1} \boldsymbol{\psi}_0\right]}{\left|1 - \frac{g\tau_c}{1+i\omega\tau_c} \left[\Phi_\mu + i\omega \mathbf{f}_0 \cdot (i\omega I - A_0)^{-1} \mathbf{m}_0\right]\right|^2} \frac{v_0}{N} \quad (3.1)$$

288 where we have considered only the first order term in the finite-size fluctuation size [7]. Some fea-
289 tures emerge: (i) for high ω , $P_1(\omega)$ approaches the white noise flat spectrum due to the superpo-
290 sition of the δs composing the spike train and (ii) when the eigenvalues λ_k are complex conjugate
291 damped resonances appear at frequencies $\omega \simeq \text{Im} \lambda_k$, where $i\omega I - A_0$ attains a local minimum.

292 In Eq. (3.1) are recognizable the different terms due to the finite-size fluctuations (numerator),
293 the membrane potential integration and the self-inhibition related to the calcium dynamics (the
294 product in the denominator). This power spectrum shape is quite general for linear systems with
295 recurrent inhibition. Indeed, similar results has been reported for networks of synaptically con-
296 nected inhibitory neurons [7,15], showing the ability of these kind of systems to distribute the ‘in-
297 put–output channel’ noise on different Fourier frequency bands [16,17,7].

298 In Fig. 3 we plot the estimated power spectrum, averaged over 25 runs of $N = 5000$ independent
299 neurons (diamonds; gray shades indicate standard errors); in this case we have $\tau_c = 500$ ms. On
300 the same plot (solid line) the theoretical prediction Eq. (3.1) is drawn, showing a remarkable
301 agreement with simulation results.

302 The main features of $P_1(\omega)$ are well represented in this plot. For large ω , the power spectrum
303 approaches the asymptotic value v_0/N : from Eq. (2.23) it is seen that, whatever the (inevitably fi-
304 nite) ω -content of v , the flat contribution of the white noise will ultimately dominate for sufficient-
305 ly high ω .

306 $P_1(\omega)$ shows also a clear resonance centered at $\omega/2\pi \simeq 5$ Hz = v_0 ; indeed, when neurons, as in
307 this case, are in a small- σ regime (i.e. when the deterministic component of the afferent current

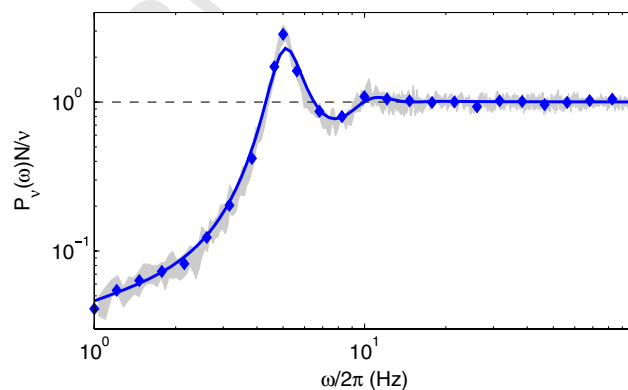


Fig. 3. Power spectrum of finite-size emission rate v_N in stationary state estimated from simulation (diamonds) with errors (gray shades) against the theoretical prediction $P_1(\omega)$ given by Eq. (3.1) (solid line), computed using 2048 couples of eigenfunctions. The neuron parameters are $\beta = 50\theta/s$, $H = 0$, $\mu_{\text{ext}} = 4.87\theta/s$, $\sigma_{\text{ext}}^2 = 0.25\theta^2/s$, $g = 10\theta/s$, $\tau_c = 0.5$ s. The power spectrum was estimated from 25 runs of $N = 5000$ neurons lasting 105 s, neglecting a transient period of 5 s; the sampling frequency was 2 kHz.

308 alone is enough to make the neurons fire), $|\text{Im} \lambda_{\pm 1}| \simeq 2\pi\nu_0$. Under this condition, random clusters
 309 of neurons which happen to fire roughly at the same time evolve together in a quasi-deterministic
 310 way, providing quasi-periodic bumps of activity at the same frequency as the single neuron firing
 311 rate; this accounts for $|\text{Im} \lambda_{\pm 1}|$ being close to $2\pi\nu_0$, and then for the resonances appearing in the
 312 power spectrum, previously described in [18,19,6].

313 Fig. 4 shows $P_1(\omega)$ for increasing levels of SFA and $\tau_c = 250$ ms; markers: simulations results,
 314 continuous lines theoretical predictions. The plot shows that a major effect of SFA on the reso-
 315 nant properties is to decrease power at low frequencies; such decrease is more marked as SFA gets
 316 stronger (increasing g , see Eq. (2.1)). In other words, SFA acts on the emission rate dynamics as a
 317 *high-pass filter* [20].

318 Such behavior is, in a sense, counterintuitive since the calcium dynamics acts exactly as a *low-*
 319 *pass filter* on $v(t)$ (see third equation in (2.21)). The explanation is found in the negative feedback
 320 occurring between the emission rate v and the calcium variable c . Indeed, c will actually filter the
 321 high- ω components of the emission rate; in turn, the power associated with the low- ω components
 322 of v surviving the filter cut, will be available for SFA damping, which will be self-consistently more
 323 efficient on the low- ω components of v , thereby digging a hole in the low- ω part of $P_1(\omega)$.

324 In other words, SFA will not be able to cut off rapid variations of v , because c has not time
 325 enough to build up, and then to inhibit those variations; on the other hand, a slow component
 326 of v will elicit a strong response by calcium dynamics, and therefore a strong inhibitory current
 327 that will tend to shut it off. This same reasoning leads one to conclude that if τ_c is shortened,
 328 the effects of SFA on the power spectrum spread on a wider range of ω , since, roughly speaking,
 329 calcium dynamics is effective for $\omega < 1/\tau_c$.

330 Fig. 4 also shows how, increasing g , the theoretical prediction becomes ever less accurate. In
 331 this plot, the neuron is in a current regime particularly unfavorable for the adiabatic approxima-

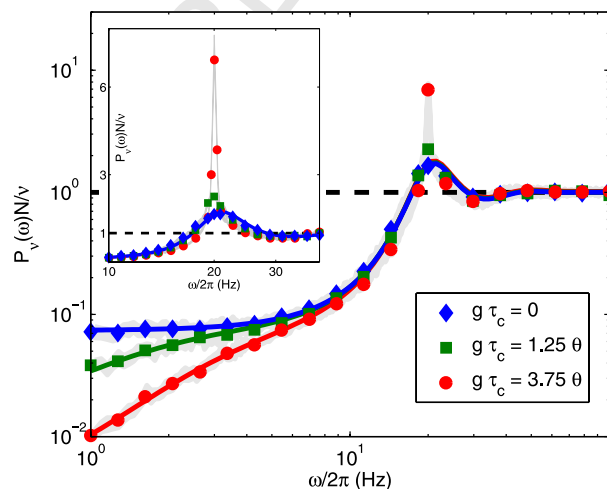


Fig. 4. Theoretical predictions Eq. (3.1) (continuous lines) and simulation results (markers) for the power spectrum of the finite-size emission rate v_N in stationary conditions for different values of g and $\tau_c = 250$ ms. Theoretical predictions have been computed using 2048 couples of eigenfunctions. Inset: zoom, with linear y -scale, around the resonance at about 20 Hz.

332 tion, since in absence of SFA the neuron fires rather regularly, as demonstrated by the resonance
 333 at frequency $f \simeq 20$ Hz, that is about the single neuron emission rate. The greatest differences ap-
 334 pear indeed close to this resonance, and the inset in Fig. 4 shows a zoom of the three power spec-
 335 tra around the peak (note that the y -scale is now linear); the theoretical prediction systematically
 336 undersimates the power of the resonance and is, for this range of ω , actually insensible to varia-
 337 tions of g (blue line: theory for $g = 0$).

338 4. Response to oscillatory input

339 Coming back to the $N \rightarrow \infty$ case, we now undertake to study the adapting neuron dynamics
 340 under the influence of an oscillatory input current.

341 In [3] the authors studied, in experiment and in theory, the emission rate of an IF neuron with
 342 SFA (in a somewhat different model) in response to a gaussian current with a sinusoidally mod-
 343 ulated mean with frequency ω . They found that the oscillatory response exhibits an amplitude
 344 modulation \tilde{A} and phase shift φ with respect to the input, both dependent on ω . In particular,
 345 they demonstrated that the curve $\varphi(\omega)$ crosses the zero-phase-shift line ($\varphi = 0$) twice, one at
 346 $\omega = 0$ the other at a *preferred frequency* ω^* , which, the authors argued, has a leading role in setting
 347 up the frequency of collective global oscillations in networks of interacting adapting neurons.

348 In this section we will recover the results found in [3] using the theoretical framework set up in
 349 Section 2, with no need of additional assumptions. The curve $\varphi(\omega)$ can be computed in an inter-
 350 esting range of ω , ω^* is predicted and successfully checked against simulations.

351 4.1. Small time-scale approximation

352 With reference to Eqs. (2.27), for the sinusoidally modulated input we will have:

$$354 \quad \mu_1(t) = A \sin(\omega t) - g c_1(t) \quad (4.1)$$

355 where A is small enough to fulfill the linear approximation hypothesis. Since we are not interested
 356 here in the finite-size effects, we neglect Γ terms. The solution of the linear, first order equation for
 357 \mathbf{a} in the system Eq. (2.27) has the form:

$$359 \quad \mathbf{a}(t) = \left[\int_{-\infty}^t e^{-A_0(s-t)} \dot{\mu}_1(s) ds \right] \mathbf{m}_0 \quad (4.2)$$

360 The latter equation can be rewritten, using integration by parts, as:

$$362 \quad \int_{-\infty}^t e^{-A_0(s-t)} \dot{\mu}_1(s) ds = -\dot{\mu}_1(t) A_0^{-1} - \dots - \mu_1^{(k+1)}(t) A_0^{-(k+1)} \\ + A_0^{-(k+1)} \int_{-\infty}^t e^{-A_0(s-t)} \mu_1^{(k+2)}(s) ds \quad (4.3)$$

363 Substitution of the above expansion into Eq. (4.2) gives:

$$365 \quad \mathbf{a}(t) = -[\dot{\mu}_1 A_0^{-1} \mathbf{m}_0 + \ddot{\mu}_1 A_0^{-2} \mathbf{m}_0 + \dots] \quad (4.4)$$

366 which, upon insertion into the second of Eqs. (2.27) results in:

368
$$v_1 = \tau_0 \mu_1 - \tau_1 \dot{\mu}_1 + \tau_2 \ddot{\mu}_1 + \dots \quad (4.5)$$

369 having defined:

371
$$\tau_k = (-1)^{k+1} \sum \frac{f_n m_n}{\lambda_n^k} \quad \text{for } k \geq 0 \quad (4.6)$$

372 This definition holds also for $k=0$ since it can be proved that $\Phi_\mu \equiv -\sum f_n m_n$. The series in the
373 above equations converge rapidly and only few couples of eigenfunctions and eigenvalues may
374 be taken into account for good numerical estimates.

375 Now we introduce an approximation by assuming that $\mu_1(t)$ is a ‘slow’ function with a typical
376 time scale τ_μ , much longer than the intrinsic time scales of **a** dynamics (i.e. A_0^{-1}). Under this
377 hypothesis, successive terms in Eq. (4.3) will be decreasing in magnitude, since the n th term of
378 the expansion will be of order $(A_0 \tau_\mu)^{-n}$.

379 In the case of interest of an oscillatory input, $\tau_\mu = \omega^{-1}$. Since λ_1 (calculated at the fixed point) is
380 the eigenvalue with the smallest absolute value, the ‘slowness’ condition for $\mu_1(t)$ will simply read
381 $\omega \ll |\lambda_1|$, which allows us to truncate Eq. (4.5). In this way, using Eqs. (4.1) and the third of Eqs.
382 (2.27), Eq. (4.5) can be transformed to a k th order differential equation for v_1 .

383 In [20] the authors have discussed the implications of SFA on the spectral properties of neu-
384 rons, in a zeroth order approximation, that is assuming the v dynamics instantaneous or, in
385 our notation, keeping only τ_0 terms. Our approach allows to consider higher order terms, and thus
386 to describe the system behavior with greater detail. For example, stopping at $k = 1$ in Eq. (4.5), we
387 have:

389
$$v_1(1 - g\tau_1) = A[\tau_0 \sin(\omega t) - \tau_1 \omega \cos(\omega t)] - g c_1 \left[\tau_0 + \frac{\tau_1}{\tau_c} \right] \quad (4.7)$$

390 Now, deriving both sides:

392
$$\dot{v}_1(1 - g\tau_1) = A[\omega \tau_0 \cos(\omega t) + \omega^2 \tau_1 \sin(\omega t)] - g \dot{c}_1 \left[\tau_0 + \frac{\tau_1}{\tau_c} \right] \quad (4.8)$$

393 Using Eq. (2.27) for $c_1(t)$, the preceding equation becomes:

395
$$\dot{v}_1(1 - g\tau_1) = A[\omega \tau_0 \cos(\omega t) + \omega^2 \tau_1 \sin(\omega t)] - g \left(-\frac{c_1}{\tau_c} + v_1 \right) \left[\tau_0 + \frac{\tau_1}{\tau_c} \right] \quad (4.9)$$

396 Finally, using Eq. (4.7) to substitute c_1 , we get the first-order dynamics, for $g \neq 0$:

398
$$\dot{v}_1 = -\frac{v_1}{1 - g\tau_1} \left(\frac{1}{\tau_c} + g\tau_0 \right) + \frac{A}{1 - g\tau_1} \left[\omega \left(\tau_0 - \frac{\tau_1}{\tau_c} \right) \cos(\omega t) + \left(\tau_1 \omega^2 + \frac{\tau_0}{\tau_c} \right) \sin(\omega t) \right] \quad (4.10)$$

399 which has the asymptotic solution:

401
$$v(t) = v_0 + \tilde{A}(\omega) \sin(\omega t - \varphi(\omega)) \quad (4.11)$$

402 Left panel in Fig. 5 shows the amplitude of the sinusoidal component $\tilde{A}(\omega)$ of v ; a good agreement
403 is achieved on the considered range of ω between simulation result (blue squares) and third order
404 theory (continuous blue line). The plot clearly shows how the neuron acts as a *band-pass filter* on

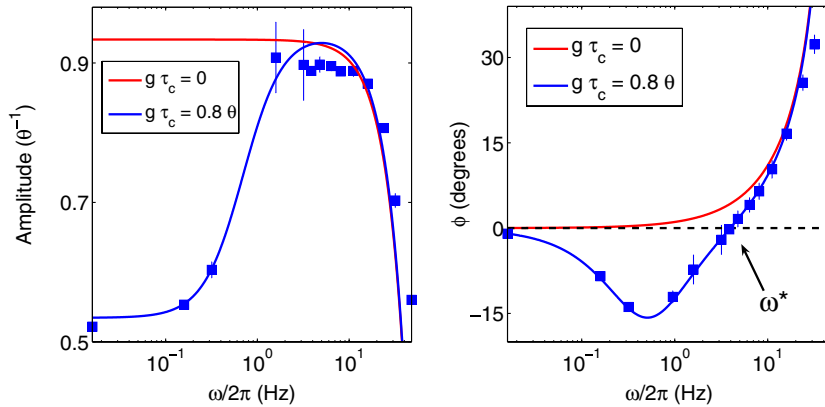


Fig. 5. Band-pass and phase-locking properties of adapting neuron: amplitude (left panel) and phase shift (right panel) of the oscillatory component of $v(t)$. The squares mark the values estimated from simulations (vertical bars represent standard errors), whereas the continuous blue line is the theoretical prediction truncated at order $k = 3$. The red lines show the theoretical prediction for $g = 0$.

405 small sinusoidal inputs [20]. This behavior is mainly due to the interplay between v and c dynam-
 406 ics. The first one accounts for the high frequency cutoff, as discussed above. On the other hand, as
 407 we have seen in Section 3, SFA acts partially as a high pass filter on v , damping any slow com-
 408 ponent of the emission rate. The overall result is a bell-shaped amplitude $\hat{A}(\omega)$ for the neuron re-
 409 sponse. The role of SFA is better understood looking at the red continuous line of Fig. 5 that
 410 shows the neuron response amplitude (theoretical prediction) for $g = 0$, i.e. in absence of adapta-
 411 tion; for low ω , SFA leads to a sensible decrease in power with respect to the $g = 0$ case, whereas,
 412 for higher ω , the two lines tend to overlap, since the slow calcium dynamics is no more effective at
 413 that frequencies.

414 Right panel in Fig. 5 shows the phase shift $\varphi(\omega)$; the agreement between simulation (blue squar-
 415 es) and theory (continuous blue line) is good in the considered range of ω . In particular, the pre-
 416 ferred angular frequency ω^* is well predicted; higher k terms ensure good estimates for higher ω .
 417 The phase shift is negative for $\omega < \omega^*$ and positive for $\omega > \omega^*$; in other words, for low frequencies
 418 of the oscillatory input current, the neuron response is anticipated with respect to the stimulus,
 419 whereas for higher ω it is delayed. For $\omega \rightarrow 0^+$, the stimulus and the emission rate are trivially
 420 phase-locked.

421 The red line, on the other hand, shows the theoretical phase shift for $g = 0$; in this case $\varphi(\omega)$ is
 422 always greater than zero. In order to have phase-locking a finite g is in fact needed. Indeed, deriv-
 423 ing Eq. (4.5), keeping only first order terms, one gets:

$$425 \quad \dot{\mu}_1 = \frac{\dot{v}_1}{\tau_0} - \frac{\tau_1}{\tau_0} \ddot{\mu}_1 \tag{4.12}$$

426 Inserting this result again in Eq. (4.5), and neglecting the $\ddot{\mu}_1$ term, since its order is greater than
 427 one, one obtains:

$$429 \quad \tau^* \dot{v}_1 = -v_1 + \tau_0 \mu_1 \tag{4.13}$$

430 with $\tau^* \doteq \tau_1/\tau_0$. This is a first order differential equation for v_1 ; since it describes a physical system,
431 τ^* (and therefore τ_1 , since $\tau_0 = \Phi_\mu > 0$) must be positive in order not to have exploding solutions
432 for any small (and slow) μ_1 . Such equation implies a positive phase shift for every ω .

433 It is interesting to note that, truncating expansion Eq. (4.5) to τ_1 , ω^* takes a simple explicit
434 form:

$$436 \quad \omega^* = \frac{1}{\tau_c} \sqrt{\frac{g\Phi_\mu^2\tau_c^2 - \tau_1}{\tau_1(1 - g\tau_1)}} \simeq \sqrt{\frac{g\Phi_\mu^2}{\tau_1}} + O(1) \quad \text{for } \tau_1 \rightarrow 0 \quad (4.14)$$

437 This equation clearly shows that for $g \rightarrow 0^+$, ω^* can take imaginary values, that have no physical
438 meaning; in addition, one has that:

$$440 \quad \varphi(\omega) \simeq \frac{\tau^* - g\tau_c^2\Phi_\mu}{1 + g\tau_c\Phi_\mu} \omega \quad \text{for } \omega \rightarrow 0^+ \quad (4.15)$$

441 therefore, for small ω , $\varphi(\omega)$ is negative only if ω^* is real, that is when $g > \tau^*/\tau_0\tau_c^2$. This result
442 strongly suggests that below a given SFA level, v_1 can never ‘anticipate’ its input.

443 The first order approach, thence, allows to predict phase-locking properties of the system, that
444 a zeroth order one (see [20]) cannot derive.

445 The limit $\tau_1 \rightarrow 0^+$ in Eq. (4.14) is relevant since τ_1 is very small for typical parameters. The lead-
446 ing order of the expansion for small τ_1 has the same form as the expression found for ω^* in [3],
447 with the bonus of no free parameters. Writing the leading term in Eq. (4.14) as:

$$449 \quad \omega^* \simeq \sqrt{\frac{1}{\tau^*}} \sqrt{g\Phi_\mu} \quad (4.16)$$

450 we can distinguish in ω^* two contributions. The first one is related to τ^* , the characteristic time
451 scale of the neuron relaxation dynamics; the other term is $g\Phi_\mu = -\partial_c\Phi$, that measures the sensi-
452 tivity of the stationary emission rate to changes in the calcium concentration, and acts as the elas-
453 tic force term of the damped oscillator.

454 5. Conclusions

455 The approach to the population density formalism introduced in [6] has been extended to ac-
456 count for the implications of SFA. In the present work we dealt with (1) the effects of sampling a
457 finite number of identical, adapting neurons, on the structure of the power spectrum of their total
458 measured firing rate; (2) the response properties of (an infinite sample of) adapting neurons to an
459 oscillatory input, with special reference to phase-locking and band-pass properties.

460 The formalism extends naturally to the case of synaptically coupled adapting neurons, which
461 will be reported elsewhere [21].

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