
Supplemental appendix for “Response of Integrate-and-Fire Neurons to Noisy Inputs Filtered by Synapses with Arbitrary Timescales: Firing Rate and Correlations” by Rubén Moreno-Bote and Néstor Parga, *Neural Computation*, Vol. 22, No. 6 (June 2010), pp. 1528–1572.

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Supporting information

Details for the computation of the adiabatic firing rate of LIF neurons

Here, we provide the details of the calculations to derive the adiabatic expression for the firing rate for a LIF neuron shown in the main text.

In Sec. (1) we describe the LIF neuron and linear synaptic model used throughout. Several characteristics like the mean and variance of the current and the voltage are studied as a function of the membrane and synaptic time constants of the model. The problem of finding the firing rate is solved in the long Sec. (2) with the adiabatic approach. The firing rate of a neuron with both fast and slow synaptic linear filters is found in Sec. (3). The case of two and more filters is considered in Sec. (4). In Sec. (5) we study the problem of simultaneous filtering by AMPA and NMDA synaptic receptors. Finally, In Sec. (6) the FPE for the LIF neuron with a single linear synaptic filter is carefully derived and numerical procedures are described in (7).

1 Model

We consider a LIF neuron with a single linear synaptic filter receiving many independent Poisson spike trains. Based on this model, we first study the effect of a single spike on the postsynaptic current and membrane potential. Second, the means and variances of the current and voltage traces are determined when the input is given by Poisson trains. In all cases we carefully analyze how those quantities depend on the two timescales of the problem: the membrane and synaptic time constants. This preliminary exploration will help us to understand the effect of the membrane and synaptic time constants on the statistical

properties of the current, voltage and firing response of the neuron.

The membrane potential V of the model neuron obeys

$$\tau_m \dot{V} = -V + \tau_m I(t), \quad (1)$$

where τ_m is the membrane time constant, and $I(t)$ is the synaptic current. In the model, a spike is evoked when V hits the threshold Θ , and then the voltage is reset to H . Without loss of generality, the resting potential is taken at $V = 0$. We take the absolute refractory period to be zero.

The current $I(t)$ is an exponentially filtered version of the weighted sum of all afferent spikes coming from the presynaptic connections

$$\tau_s \dot{I}(t) = -I(t) + J \sum_{i,k} \delta(t - t_i^k), \quad (2)$$

where τ_s is the decay time constant of the exponential filter. Here t_i^k labels the arrival time of the k th spike from the i th presynaptic neuron. We assume that spikes arrive at exponentially distributed intervals [Softky and Koch, 1993]. The ratio J/τ_s is the size of the postsynaptic current generated by a single spike (see eq. (3) below), while the parameter J is the total injected current per spike. For simplicity, we do not take into account in this example the driving force of the synaptic currents, allowing us to study the effect of temporal synaptic filtering alone. The solution for conductance-based synapses has been presented in [Moreno-Bote and Parga, 2005], and the firing rate in this case can be derived using the general equations provided in Methods in the main text for the general IF neuron.

We first analyze the effect of a single spike on the postsynaptic current and membrane potential generated on the neuron. The postsynaptic current (PSC) is a single exponential with decay time τ_s . Assuming that the spike arrives at

time $t = 0$, this current is

$$I_{PSC}(t) = \frac{J}{\tau_s} e^{-t/\tau_s} \mathcal{H}(t), \quad (3)$$

where $\mathcal{H}(t)$ is the step (Heaviside) function ($\mathcal{H}(t) = 1$ when $t > 0$ and it is zero otherwise). This PSC provokes a postsynaptic potential (PSP) on the neuron, whose rise time and decay time are determined by the synaptic and membrane time constants. Assuming that the neuron is initially at the rest potential ($V = 0$), the time course of the PSP can be obtained integrating the PSC, eq. (3), with the equation for the voltage, eq. (1), leading to

$$V_{PSP}(t) = J \frac{\tau_m}{\tau_m - \tau_s} (e^{-t/\tau_m} - e^{-t/\tau_s}) \mathcal{H}(t). \quad (4)$$

Note that the decay time of the PSP is determined by the longer of these two time constants. Therefore, for synapses with long time constant, τ_s fully controls the decay time of the PSP. In this case, the rise time of the PSP can be approximated by the time needed to reach its peak value,

$$\tau_{rise} \sim \tau_m \ln \left(\frac{\tau_s}{\tau_m} \right). \quad (5)$$

In addition, for long τ_s the amplitude of the PSP is determined by the ratio τ_m/τ_s . Changing the synaptic time constant in eq. (3) maintains fixed the total charge injected by a single spike, J , as it can be seen by integrating the PSC waveform over time. Increasing τ_s decreases the PSC amplitude but at the same time broadens it in such a manner that the total injected charge is kept fixed. Therefore, it is expected that for long τ_s the total synaptic current generated by many input spikes is almost constant in time with very small fluctuations, because each individual PSC spreads over time.

To gain some insight into the problem, we calculate for the model in eqs.

(1 - 2) the mean and variance of both the synaptic current and the membrane potential, disregarding the spiking threshold in the neuron model. All input spike trains are lumped together into a single Poisson spike train with rate ν_{in} . The total current generated by such a train is written as

$$I(t) = \sum_i I_{PSC}(t - t_i), \quad (6)$$

where the t_i 's are the spike arrival times. Its mean and variance are calculated as

$$\mu = \langle I(t) \rangle = \nu_{in} \int_0^\infty dt I_{PSC}(t) = J\nu_{in}, \quad (7)$$

$$\sigma_I^2 = \langle I^2(t) \rangle - \langle I(t) \rangle^2 = \nu_{in} \int_0^\infty dt I_{PSC}^2(t) = \frac{J^2 \nu_{in}}{2\tau_s}. \quad (8)$$

Unlike the mean current, the variance of the current decreases with the synaptic time constant. Each PSC produces an independent PSP, so that

$$V(t) = \sum_i V_{PSP}(t - t_i). \quad (9)$$

Again, the mean and variance of $V(t)$ can be calculated easily:

$$\langle V(t) \rangle = \nu_{in} \int_0^\infty dt V_{PSP}(t) = J\nu_{in}\tau_m, \quad (10)$$

$$\sigma_V^2 = \langle V^2(t) \rangle - \langle V(t) \rangle^2 = \quad (11)$$

$$= \nu_{in} \int_0^\infty dt V_{PSP}^2(t) = \frac{J^2 \nu_{in} \tau_m^2}{2(\tau_m + \tau_s)}. \quad (12)$$

These results show that both current and voltage fluctuations decrease as $1/\tau_s$ for long synaptic time constants. In the subthreshold regime, where the

mean membrane potential is below threshold, voltage fluctuations are required to produce random threshold crossings. However, in the large τ_s limit, these fluctuations are so much smoothed that slow filtering would eventually prevent firing. We will show that the way the firing rate decreases to zero as τ_s grows is faster than any power of $1/\tau_s$, so that a perturbative expansion of the output firing rate in powers of $1/\tau_s$ is not possible. Also we will show how to deal with this mathematical singularity and calculate the output firing rate of the neuron valid for long τ_s .

2 Solution for a single slow synaptic receptor type

In this section we formally find that the adiabatic approach as described in the Results in the main text solves the LIF neuron model with linear synaptic filtering for long τ_s in the diffusion limit. Hence, the adiabatic firing rate represents the exact solution for the firing rate of a LIF neuron for long enough τ_s . As explained in the main text, the adiabatic rate provides also an excellent fit when τ_s is comparable to τ_m . The adiabatic expression for the firing rate of a LIF neuron has been found in [Moreno-Bote and Parga, 2004].

We start by writing down the FPE associated to the LIF neuron with linear synaptic filtering. Then, we show that a naive expansion of the solution in powers of $1/\tau_s$ does not work in the subthreshold regime, and therefore a more general approach is needed. The solution is presented later using the adiabatic approach.

First, we consider the case of a single synaptic receptor type with long time constant in a more rigorous way. Since the number of presynaptic spikes is normally quite large and the evoked PSP's are very small compared to the

firing threshold, the spike trains in eq. (2) can be approximated [Ricciardi, 1977] by a white noise with mean μ and deviation σ as

$$\tau_s \dot{I}(t) = -I(t) + \mu + \sigma \eta(t), \quad (13)$$

($\eta(t)$ satisfies $\langle \eta(t) \rangle = 0$ and $\langle \eta(t)\eta(t') \rangle = \delta(t-t')$). The mean current is μ and the variance of the current is $\sigma_I^2 = \sigma^2/2\tau_s$. The filter introduces exponential correlations in the current with a correlation time τ_s

$$\langle (I(t) - \mu)(I(t') - \mu) \rangle = \frac{\sigma^2}{2\tau_s} e^{-\frac{|t-t'|}{\tau_s}}. \quad (14)$$

Note that the variance of the current can be obtained from the correlation function when $t = t'$. It is worth mentioning the difference between this correlation function and that used to investigate exponentially correlated input spike trains in our previous work [Moreno et al., 2002, Moreno-Bote et al., 2008]. Here the correlation function depends smoothly of the argument $t-t'$ because $I(t)$ has at most finite discontinuities (see the original process defined in eq. (2)). However, when correlated input spike trains without synaptic filtering are considered, a delta function at zero time lag always contributes to the current correlation function, reflecting the fact that now the synaptic current $I(t)$ has infinitely large discontinuities.

Going on with the discussion, it is convenient to perform the linear transformations

$$\begin{aligned} V &= \mu\tau_m + x \sqrt{\frac{\tau_m}{2}} \sigma \\ I &= \mu + z \frac{\sigma}{\sqrt{2\tau_s}} \end{aligned}$$

and rewrite eqs. (1, 13) in terms of x and z as

$$\dot{x} = -\frac{x}{\tau_m} + \frac{z}{\sqrt{\tau_m \tau_s}}, \quad (15)$$

$$\dot{z} = -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}} \eta(t). \quad (16)$$

In these units, the threshold and reset potentials read: $\hat{\Theta} = \sqrt{2}(\Theta - \mu\tau_m)/\sigma\sqrt{\tau_m}$ and $\hat{H} = \sqrt{2}(H - \mu\tau_m)/\sigma\sqrt{\tau_m}$. The stationary Fokker-Planck equation (FPE) [Brunel and Sergi, 1998, Moreno-Bote and Parga, 2004] associated to eqs. (15 - 16), which is derived in detail in Methods, is

$$\left[\frac{\partial}{\partial x} (x - \epsilon z) + \epsilon^2 L_z \right] P(x, z) = -\tau_m J(z) \delta(x - \hat{H}), \quad (17)$$

where $\epsilon = \sqrt{\tau_m/\tau_s}$ and $L_z = \frac{\partial}{\partial z} z + \frac{\partial^2}{\partial z^2}$. $P(x, z)$ is the stationary probability density of having the neuron in the state (x, z) . The source probability current $J(z)$ accounts for the reset effect: the flow of probability escaping at the threshold is reinjected at the reset potential with the same rate and distribution in z that it had when it escaped. The probability current $J(z)$ has to be determined in a self-consistent way, that is, it has to match the escape probability current of the LIF neuron, which is the x -component of the probability current vector evaluated at threshold. The equation relating $J(z)$ and $P(x, z)$ is obtained by writing the left hand side of eq. (17) as the divergence of a probability current vector $\vec{J}(x, z)$ [Risken, 1989] as

$$\frac{1}{\tau_m} \left[\frac{\partial}{\partial x} (x - \epsilon z) + \epsilon^2 L_z \right] P(x, z) = - \left[\frac{\partial}{\partial x} J_x(x, z) + \frac{\partial}{\partial z} J_z(x, z) \right], \quad (18)$$

from where one finds that

$$J_x(x, z) = \frac{1}{\tau_m}(-x + \epsilon z)P(x, z) , \quad (19)$$

$$J_z(x, z) = -\frac{\epsilon^2}{\tau_m} \left(z + \frac{\partial}{\partial z} \right) P(x, z) . \quad (20)$$

After setting $x = \hat{\Theta}$ in $J_x(x, z)$ one obtains that the escape probability current has the expression

$$J(z) = \frac{1}{\tau_m}(-\hat{\Theta} + \epsilon z)P(\hat{\Theta}, z) . \quad (21)$$

The output firing rate is then computed as

$$\nu = \int_{-\infty}^{\infty} dz J(z) . \quad (22)$$

The probability current $J(z)$ cannot be negative because there cannot be probability flow entering from the region $x > \hat{\Theta}$. Then, the integral in eq. (22) only extends from the value of z above which the probability current $J(z)$ is positive (see eq. (21)):

$$z \geq z_{min} = \hat{\Theta}/\epsilon . \quad (23)$$

Below z_{min} , $J(z)$ is made zero by imposing that $P(\hat{\Theta}, z) = 0$ for $z < z_{min}$, and then the firing rate (22) can be written as

$$\nu = \int_{z_{min}}^{\infty} dz J(z) . \quad (24)$$

In the next section we try to find a solution of eqs. (17,21,24) using a perturbative expansion of both the probability density and current probability density in powers of ϵ (see expansion (25) below), and show why this attempt

fails.

2.1 A naive perturbative expansion does not exist in the subthreshold regime

We first perform a naive perturbative expansions of $P(x, z)$ and $J(z)$ in powers of $\epsilon = \sqrt{\tau_m/\tau_s}$ as

$$\begin{aligned} P &= \tilde{P}_0 + \epsilon \tilde{P}_1 + O(\epsilon^2) \\ J &= \tilde{J}_0 + \epsilon \tilde{J}_1 + O(\epsilon^2). \end{aligned} \quad (25)$$

Introducing them into the FPE (17) and eq. (21), we find that the coefficients of the expansion satisfy

$$0 = \frac{\partial}{\partial x}(x\tilde{P}_n - z\tilde{P}_{n-1}) + L_z\tilde{P}_{n-2} + \tau_m\tilde{J}_n(z)\delta(x - \hat{H}), \quad (26)$$

where we define $\tilde{P}_n = 0$ for $n < 0$. Along with this equation the following conditions should hold:

$$i) \tilde{P}_n(\hat{\Theta}, z) = 0 \quad \forall z < z_{min} \equiv \hat{\Theta}/\epsilon \quad (27)$$

$$ii) \tilde{J}_n(z) = \tau_m^{-1}(z\tilde{P}_{n-1}(\hat{\Theta}, z) - \hat{\Theta}\tilde{P}_n(\hat{\Theta}, z)) \quad (28)$$

$$iii) \int_{-\infty}^{\hat{\Theta}} dx \int_{-\infty}^{\infty} dz \tilde{P}_n(x, z) = \delta_{n,0} \quad (29)$$

$$iv) \lim_{z \rightarrow \pm\infty} z \tilde{P}_n \rightarrow 0, \quad \lim_{x \rightarrow -\infty} x \tilde{P}_n \rightarrow 0. \quad (30)$$

Here $\delta_{n,0}$ is the Kronecker's delta ($\delta_{n,0} = 1$ if $n = 0$, otherwise it is zero). Condition i) comes from condition (23); ii) results from eq. (21); iii) just means that $P(x, z)$ is a density function (unit integral); finally, iv) specifies that the

probability currents have to be zero at infinity.

Because the z obeys eq. (16), its stationary marginal probability density is a Gaussian with unit variance. This introduces a useful additional constraint over the coefficients $\tilde{P}_n(x, z)$,

$$\int_{-\infty}^{\hat{\Theta}} dx \tilde{P}_n(x, z) = \delta_{n,0} \frac{e^{-z^2/2}}{\sqrt{2\pi}}. \quad (31)$$

In what follows, crucially, we have to distinguish two different cases: the suprathreshold and the subthreshold regimes.

Suprathreshold regime: In this case, the mean depolarization, $\mu\tau_m$, is above threshold, $\mu\tau_m > \Theta$ ($\hat{\Theta} < 0$). Then, from eq. (28) we obtain

$$\tilde{J}_0(z) = -\tau_m^{-1} \hat{\Theta} \tilde{P}_0(\hat{\Theta}, z), \quad (32)$$

which is positive. Solving the FPE (26) at zero-th order with the conditions (28, 30) leads to

$$\tilde{P}_0(x, z) = -\tau_m \tilde{J}_0(z) \frac{H(x - \hat{H})}{x}. \quad (33)$$

Using conditions (22, 31) for $n = 0$, we find $\tilde{J}_0(z) = \tilde{\nu}_0 e^{-z^2/2}/\sqrt{2\pi}$, from where we obtain that the zero-th order firing rate is

$$\tilde{\nu}_0^{-1} = \tau_m \ln(\hat{H}/\hat{\Theta}) = \tau_m \ln\left(\frac{H - \mu\tau_m}{\Theta - \mu\tau_m}\right). \quad (34)$$

Note that $\tilde{\nu}_0$ is the rate of a LIF neuron driven by a noiseless current with intensity μ . Thus, in the suprathreshold regime and when τ_s is very large, input fluctuations are filtered out and the neuron acts as a noiseless integrator. It is straightforward to carry on with the expansion by using eq. (26) and the conditions (24, 29, 31) for the n -th order. When this is done, one finds that

the first order correction to the rate is zero ($\tilde{\nu}_1 = 0$) and that the firing rate up to second order is

$$\nu \sim \tilde{\nu}_0 + \frac{\tau_m^2 \tilde{\nu}_0^2}{\tau_s} \left[\tau_m \tilde{\nu}_0 (\hat{\Theta}^{-1} - \hat{H}^{-1})^2 - \frac{\hat{\Theta}^{-2} - \hat{H}^{-2}}{2} \right]. \quad (35)$$

This expression has also been obtained in [Moreno-Bote and Parga, 2004, Moreno and Parga, 2004].

Subthreshold regime: Now we prove that in this regime the perturbative expansion of the firing rate does not exist. Here, the mean depolarization is below threshold ($\hat{\Theta} > 0$). Since the probability current $J(z)$ cannot be negative, the zero-th order probability current,

$$\tilde{J}_0(z) = -\tau_m^{-1} \hat{\Theta} \tilde{P}_0(\hat{\Theta}, z), \quad (36)$$

cannot be negative. Then, since $\hat{\Theta} > 0$, the density $\tilde{P}_0(\hat{\Theta}, z)$ has to be zero, and also $\tilde{J}_0 = 0$. This implies that the zero-th order rate is $\tilde{\nu}_0 = 0$ in the subthreshold regime. Assuming that $\tilde{P}_m(\hat{\Theta}, z) = 0$ for all $m < n$, it is easy to prove by induction that $\tilde{P}_n(\hat{\Theta}, z) = 0$: If $\tilde{P}_m(\hat{\Theta}, z) = 0$ for all $m < n$, then (see eq. (28))

$$\tilde{J}_n(z) = -\tau_m^{-1} \hat{\Theta} \tilde{P}_n(\hat{\Theta}, z). \quad (37)$$

Since $J(z)$ cannot be negative and $\tilde{J}_m = 0$ for all $m < n$, the order \tilde{J}_n cannot be negative. But since $\hat{\Theta} > 0$, $\tilde{P}_n(\hat{\Theta}, z)$ has to be zero too and, in fact, at all orders the J_n are zero. This proves that the output firing rate in eq. (22) does not admit an expansion in powers of ϵ in the subthreshold regime.

To go more deeply into the problem, let us write the FPE (26) at zero-th order:

$$0 = \frac{\partial}{\partial x} x \tilde{P}_0 . \quad (38)$$

The solution that satisfies the conditions (27 - 30) is

$$\tilde{P}_0(x, z) = \delta(x) e^{-z^2/2} / \sqrt{2\pi} . \quad (39)$$

Then, the whole probability is placed at $x = 0$, or equivalently, at the equilibrium potential $V = \mu\tau_m$. Being the whole probability far from threshold, the neuron does not fire in the long τ_s limit, because fluctuations have been removed. As we have indirectly showed, the perturbative correction of a delta function is ill-posed in this problem and the next order densities \tilde{P}_n are not defined.

2.2 A regularized adiabatic approach for slow filters

We have found that the coefficients for the expansion of the escape probability current in powers of ϵ are not defined, unless the input parameters are in the suprathreshold regime ($\hat{\Theta} < 0$). This shows that such a perturbative expansion of the output firing rate, eq. (22), is not possible for the full input parameter space.

Investigating in some detail the problem and the analytical expressions involved in it, it can be noticed that in the suprathreshold regime z_{min} in eq. (24) approaches minus infinity for long τ_s , leading to a well behaving output rate when τ_s is large. However, in the subthreshold regime, z_{min} approaches infinity apparently so fast that the firing rate does not admit a perturbative expansion in powers of ϵ . Because an expansion was possible when the integration interval $[z_{min}, \infty)$ did not get empty, that is, in the suprathreshold regime, this suggests maintaining *fixed* z_{min} in eq. (24) as τ_s increases, and at the same time

performing an expansion of $P(x, z)$ and $J(z)$ in powers of a convenient perturbative parameter. This presumably would lead to a well defined expansion of the output rate in both the sub- and suprathreshold regimes. Indeed, this is what happens, as we explain below.

This idea is implemented by defining a new constant γ that replaces ϵ in the FPE (17), while ϵ^2 is left unchanged, to obtain the FPE

$$\left[\frac{\partial}{\partial x} (x - \gamma z) + \epsilon^2 L_z \right] P(x, z) = -\tau_m J(z) \delta(x - \hat{H}). \quad (40)$$

At the same time, we must express the probability current as (see eq. (21))

$$J(z) = \frac{1}{\tau_m} (-\hat{\Theta} + \gamma z) P(\hat{\Theta}, z). \quad (41)$$

Now the key idea becomes apparent: to solve the FPE (40,41) we expand the stationary probability density and the probability current in powers of ϵ^2 as

$$\begin{aligned} P &= P_0 + \epsilon^2 P_1 + O(\epsilon^4) \\ J &= J_0 + \epsilon^2 J_1 + O(\epsilon^4) \end{aligned} \quad (42)$$

maintaining fixed the parameter γ . Only at the end, when the coefficients P_n and J_n have been determined, γ can be given its true value ϵ . Note that the coefficients P_n and J_n depend on γ but not on ϵ^2 . While the FPE (17) is defined in a one-dimensional parameter space (ϵ), the FPE (40) has extended its range to the two dimensional parameter space (γ, ϵ) . The restriction of the new FPE to the case $\gamma = \epsilon$ leads to the original formulation of the problem, although this new FPE is somehow easier to solve. The choice of fixing γ while taking the limit $\epsilon^2 \rightarrow 0$ in the expansion is called *distinguished limit* in singular perturbation theory, since it involves a balance between two terms in the left

side of FPE (40) (see e.g. [Bender and Orszag, 1978]).

It is also possible to understand the physical meaning of the limit $\epsilon \rightarrow 0$ with fixed γ that led us to the FPE (40). For that, let us come back to the stochastic equations defined in (15 - 16) and rewrite them in the new space of parameters (γ, ϵ) as

$$\begin{aligned}\dot{x} &= \frac{1}{\tau_m}(-x + \gamma z), \\ \dot{z} &= -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\eta(t).\end{aligned}\tag{43}$$

The effect of any fluctuation in the normalized current, z , lasts for a time τ_s , and its effect on the normalized voltage, x , is constant as τ_s grows, because γ is now a fixed parameter. This will lead to the possibility of an expansion of the rate in powers of $1/\tau_s$ (or, equivalently, ϵ^2) for fixed γ . Now we proceed to determine the leading order solution for the expansion (42).

Solution of the FPE in the long τ_s limit: we introduce the expansion (42) into the FPE (40) and collect terms according to powers of ϵ^2 . Each order has to be solved along with conditions similar to those in eqs. (29 - 30), but conditions (27 - 28) have to be replaced by

$$i) P_n(\hat{\Theta}, z) = 0 \quad \forall z < \hat{\Theta}/\gamma\tag{44}$$

$$ii) J_n(z) = \tau_m^{-1}(\gamma z - \hat{\Theta})P_n(\hat{\Theta}, z).\tag{45}$$

Because the equation for the normalized current z has not changed, condition (31) still holds. Carrying on with the perturbative analysis we find that in general the n th order density P_n satisfies a differential equation that depends

on the previous order P_{n-1} and the probability current at the same order J_n as

$$0 = \frac{\partial}{\partial x}(x - \gamma z)P_n + L_z P_{n-1} + \tau_m J_n(z)\delta(x - \hat{H}) , \quad (46)$$

where we defined $P_n = 0$ for $n < 0$. The leading order has to be dealt with in two cases. When $z \geq \hat{\Theta}/\gamma$, $J_0(z)$ is positive (see eq. (41)), and then the FPE (46) is

$$0 = \frac{\partial}{\partial x}(x - \gamma z)P_0 + \tau_m J_0(z)\delta(x - \hat{H}) , \quad (47)$$

whose solution, using condition (30), is

$$P_0(x, z) = \frac{\tau_m J_0(z)\mathcal{H}(x - \hat{H})}{\gamma z - x} . \quad (48)$$

When $z < \hat{\Theta}/\gamma$, the equation we have to solve is

$$0 = \frac{\partial}{\partial x}(x - \gamma z)P_0 . \quad (49)$$

Its solution satisfying condition (30) is

$$P_0(x, z) = D(z)\delta(x - \gamma z) , \quad (50)$$

where $D(z)$ depends only on z . The density $P_0(x, z)$ can be written as a single expression:

$$P_0(x, z) = \frac{\tau_m J_0(z)\mathcal{H}(x - \hat{H})}{\gamma z - x} + D(z)\delta(x - \gamma z)\mathcal{H}(\hat{\Theta}/\gamma - z) . \quad (51)$$

Note that if $z \geq \hat{\Theta}/\gamma$, the neuron can fire and the potential is distributed continuously from \hat{H} to $\hat{\Theta}$ (first term in eq. (51)). However, if $z < \hat{\Theta}/\gamma$, the synaptic fluctuations are not high enough to induce firing, and the membrane

potential is held at $x = \gamma z$, which is below threshold (second term in eq. (51)).

To determine the unknowns $D(z)$ and $J_0(z)$ in eq. (51), we introduce P_0 into the constraint (31), giving $D(z) = e^{-z^2/2}/\sqrt{2\pi}$ and

$$J_0(z) = \frac{e^{-z^2/2}}{\sqrt{2\pi}} \nu_0(z), \quad (52)$$

where we have defined

$$\nu_0^{-1}(z) = \tau_m \ln \left(\frac{\hat{H} - \epsilon z}{\hat{\Theta} - \epsilon z} \right). \quad (53)$$

Note that at this point we have replaced γ by $\epsilon = \sqrt{\tau_m/\tau_s}$. Introducing $J_0(z)$ into eq. (24) leads to the adiabatic expression for the output firing rate at zero-th order

$$\nu = \int_{\hat{\Theta}/\epsilon}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-z^2/2} \nu_0(z), \quad (54)$$

as it appears in Results in the main text.

3 One fast and one slow synaptic types

In this section we continue the discussion of slow filters based on the FPE, but this time in the presence of a second, fast filter. In this case, the total current in eq. (1) has two contributions, $I(t) = I_1(t) + I_2(t)$, which in the diffusion limit are

$$\begin{aligned} \tau_s \dot{I}_1(t) &= -I_1(t) + \mu_1 + \sigma_1 \eta(t) \\ I_2(t) &= \mu_2 + \sigma_2 \zeta(t). \end{aligned} \quad (55)$$

The quantities μ_1 , μ_2 and σ_1^2 , σ_2^2 are the means and variances of the inhibitory and excitatory currents, and $\eta(t)$ and $\zeta(t)$ are two independent white noise processes with unit variance. Defining $\mu \equiv \mu_1 + \mu_2$ and performing the linear transformation

$$\begin{aligned} V &= \mu\tau_m + x\sqrt{\frac{\tau_m}{2}}\sigma_2 \\ I_1 &= \mu_1 + z\frac{\sigma_1}{\sqrt{2\tau_s}} \end{aligned}$$

the equations for the voltage and the current are transformed into

$$\begin{aligned} \dot{x} &= \frac{1}{\tau_m}[-x + \sqrt{2\tau_m}\zeta(t) + \sqrt{\alpha}\gamma z], \\ \dot{z} &= -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\eta(t). \end{aligned} \quad (56)$$

Again we write γ in place of ϵ . Here $\alpha \equiv \sigma_1^2/\sigma_2^2$, and the threshold and reset potentials now become: $\hat{\Theta} = \sqrt{2}(\Theta - \mu\tau_m)/\sigma_2\sqrt{\tau_m}$ and $\hat{H} = \sqrt{2}(H - \mu\tau_m)/\sigma_2\sqrt{\tau_m}$.

The current autocorrelation is

$$\langle (I(t) - \mu)(I(t') - \mu) \rangle = \sigma_2^2\delta(t - t') + \frac{\sigma_1^2}{2\tau_s}e^{-\frac{|t-t'|}{\tau_s}}. \quad (57)$$

Note that the autocorrelation has a delta function, something that did not happen with a single slow filter, eq. (14). The stationary FPE reads [Moreno-Bote and Parga, 2004]

$$\left[L_x - \gamma\sqrt{\alpha}z\frac{\partial}{\partial x} + \epsilon^2 L_z \right] P(x, z) = -\tau_m J(z)\delta(x - \hat{H}). \quad (58)$$

As before, γ will be treated as a fixed parameter, and an expansion in the parameter ϵ^2 of both the density $P(x, z)$ and the escape probability current

as in eq. (42) will be employed to find the output firing rate of the neuron. Again, $J(z)$ acts in the FPE (58) as a source term injecting probability current at the reset potential at the same rate and the same distribution that z has when the probability escapes at threshold. It is the probability current vector in the direction of x and evaluated at threshold. The probability density current vector for this FPE is [Risken, 1989]

$$\vec{J}(x, z) = \frac{1}{\tau_m} \left[-\frac{\partial}{\partial x} - x + \gamma\sqrt{\alpha}z, -\epsilon^2 \left(\frac{\partial}{\partial z} + z \right) \right] P(x, z), \quad (59)$$

which obeys the continuity equation

$$\vec{\nabla} \cdot \vec{J}(x, z) + \tau_m \delta(x - \hat{H}) J(z) = 0, \quad (60)$$

with $\vec{\nabla} = [\frac{\partial}{\partial x}, \frac{\partial}{\partial z}]$. The escape probability current is then

$$J(z) = \frac{1}{\tau_m} \left(-\frac{\partial}{\partial x} - x + \gamma\sqrt{\alpha}z \right) P(x, z)|_{x=\hat{\Theta}}, \quad (61)$$

which has to be inserted into the FPE (58).

Solution of the FPE in the long τ_s limit: We start by introducing the expansion in eq. (42) of the density and escape probability current into the FPE (58). Each order $P_n(x, z)$ and $J_n(z)$ must be determined self-consistently using the set of conditions

$$i) P_n(\hat{\Theta}, z) = 0 \quad \forall z \quad (62)$$

$$ii) J_n(z) = -\frac{1}{\tau_m} \frac{\partial}{\partial x} P_n(\hat{\Theta}, z), \quad (63)$$

along with the conditions (29, 30). The first important difference with respect

to the case of a single slow filter is that now condition i) states that the density has to be zero at threshold for all z . Secondly, condition ii) on the probability density flux involves now a derivative of the probability density evaluated at threshold. To obtain the coefficients P_n and J_n , we proceed as with the case with a single synaptic time constant (section (2.2)). At each order n , the density P_n satisfies

$$\left[L_x - \gamma\sqrt{\alpha}z \frac{\partial}{\partial x} \right] P_n + L_z P_{n-1} = -\tau_m \delta(x - \hat{H}) J_n(z). \quad (64)$$

Solving this equation for $n = 0$, we obtain that the zero-th order density is a function of the unknown zero-th order escape probability current of the form

$$P_0(x, z) = \tau_m J_0(z) e^{-\frac{(x - \gamma\sqrt{\alpha}z)^2}{2}} \int_x^{\hat{\Theta}} du e^{\frac{(u - \gamma\sqrt{\alpha}z)^2}{2}} \mathcal{H}(u - \hat{H}). \quad (65)$$

Since the P_n 's solve a equation identical to eq. (31), inserting P_0 into this equation leads to the expression for the zero-th order probability current

$$J_0(z) = \frac{1}{\sqrt{2\pi\tau_m}} e^{-z^2/2} \nu_{fast}(z), \quad (66)$$

where we have defined the quantities

$$\nu_{fast}(z)^{-1} = \sqrt{\frac{\pi}{2}} \tau_m \int_{\hat{H} - \epsilon\sqrt{\alpha}z}^{\hat{\Theta} - \epsilon\sqrt{\alpha}z} dt e^{t^2/2} (1 + \text{erf}(t/\sqrt{2}))., \quad (67)$$

where $\text{erf}(t)$ is the error function. The output firing rate of the neuron up to zero order is obtained by integration over z as

$$\nu = \int_{-\infty}^{\infty} \frac{dz}{\sqrt{2\pi}} e^{-z^2/2} \nu_{fast}(z). \quad (68)$$

The quantity $\nu_{fast}(z)$ in eq. (68) has also an intuitive meaning: it is the rate of a LIF neuron driven by a current with effective mean $\mu_{eff} = \mu + z\sigma_1/\sqrt{2\tau_s}$ and

variance σ_2^2 [Ricciardi, 1977]. As it can be appreciated, the output firing rate is given by the average of $\nu_{fast}(z)$ with the stationary distribution of z , as in the case with a single slow filter. The formula (68) admits an expansion in powers of ϵ , which up to $O(\epsilon^2)$ is

$$\begin{aligned}
\nu &= \mathcal{F}_0 + \frac{C}{\tau_s} & (69) \\
\mathcal{F}_0 &= \nu_{fast}(0) \\
C &\equiv \alpha \tau_m^2 \mathcal{F}_0^2 [\tau_m \mathcal{F}_0 (R(\hat{\Theta}/\sqrt{2}) - R(\hat{H}/\sqrt{2}))^2 \\
&\quad - \frac{\hat{\Theta}R(\hat{\Theta}/\sqrt{2}) - \hat{H}R(\hat{H}/\sqrt{2})}{2}] ,
\end{aligned}$$

where $R(t) = \sqrt{\frac{\pi}{2}} e^{t^2} (1 + \text{erf}(t))$.

At leading order, the rate is just \mathcal{F}_0 , the firing rate of a LIF neuron driven by a white noise input with mean μ and variance of the fast noise σ_2^2 [Ricciardi, 1977]. The firing rate approaches \mathcal{F}_0 as the synaptic time constant increases.

We have approximated the rate using the zero-th order term in the expansion (42). This approximation contains a term $O(\epsilon^2)$ (see eq. (69)). However, other contributions to the total firing rate at order $O(\epsilon^2)$ could also come from the non zero-th order terms of the expansion. In particular, it could come from the first order in the expansion (42). However, it is possible to see that an expansion in powers of ϵ of the probability current J_1 at first order gives a dominant order $O(\epsilon^2)$, that globally leads to a correction $O(\epsilon^4)$ to the firing rate, and therefore it can be neglected (see [Moreno et al., 2002, Moreno-Bote et al., 2008]).

It is also possible to obtain the firing rate for a LIF neuron with a single slow filter, eq. (54), from the expression of the rate in the case of both fast and slow filters, eq. (68). This is done by taking the limit of vanishing fast noise, $\sigma_2^2 \rightarrow 0$, in eq. (68) so that the fast synapse disappears and there is only a single

slow synapse. In this limit, contributions to the integral (68) are different from zero when $z \geq \Theta/\gamma\sqrt{\alpha}$, where we can approximate (see e.g. [Abramowitz and Stegun, 1964])

$$e^{\frac{u^2}{2}} \int_{-\infty}^u dv e^{-\frac{v^2}{2}} \sim \frac{-1}{u}, \quad (70)$$

where u is assumed to be large and negative. Integrating over u and setting $\alpha = \sigma_1^2/\sigma_2^2$ gives the expression (54) where $\sigma = \sigma_1$.

The results found above can be extended to any other IF neuron model. A general formula similar to eq. (68) for the firing rate of an IF neuron with both fast and slow filters is given in the Methods section in the main text.

4 Two and more slow filters

In this appendix we study the case of two (and more) long synaptic time constants, τ_1 and τ_2 . They could correspond to *AMPA* and *GABA* synapses when τ_m is very short ($\tau_m \sim 1 - 5ms$). The membrane potential obeys the equations

$$\begin{aligned} \dot{V} &= -\frac{V}{\tau_m} + \mu + \frac{\sigma_1}{\sqrt{2\tau_1}}z_1 + \frac{\sigma_2}{\sqrt{2\tau_2}}z_2, \\ \dot{z}_1 &= -\frac{z_1}{\tau_1} + \sqrt{\frac{2}{\tau_1}}\eta_1(t), \\ \dot{z}_2 &= -\frac{z_2}{\tau_2} + \sqrt{\frac{2}{\tau_2}}\eta_2(t), \end{aligned} \quad (71)$$

where $\mu = \mu_1 + \mu_2$, is the total current generated by the inputs, σ_1^2 and σ_2^2 are the input variances, and $\eta_1(t)$ and $\eta_2(t)$ are two independent white noise processes with zero mean and unit variance. Using the same techniques described in this work, we find that the output firing rate is

$$\nu = \frac{1}{\sqrt{2\pi\tau_m}} \int_{\Omega} dz_1 dz_2 \frac{e^{-\frac{1}{2}(z_1^2+z_2^2)}}{\int_H^{\Theta} dV \left(\frac{\sigma_1}{\sqrt{2\tau_1}} z_1 + \frac{\sigma_2}{\sqrt{2\tau_2}} z_2 - \frac{V}{\tau_m} + \mu \right)^{-1}}. \quad (72)$$

The region Ω of the plane (z_1, z_2) is defined as $\Omega : \forall z_1 z_2 / \frac{\sigma_1}{\sqrt{2\tau_1}} z_1 + \frac{\sigma_2}{\sqrt{2\tau_2}} z_2 - \frac{V}{\tau_m} + \mu \geq 0, \forall V \in [H, \Theta]$, that is, all those synaptic fluctuations that make the drift positive for all membrane potentials lying between the reset and threshold values. Let us simplify the formula (72) by defining two orthonormal variables

$$\begin{aligned} u &= \frac{1}{\sqrt{2B}} \left[\frac{\sigma_1}{\sqrt{\tau_1}} z_1 + \frac{\sigma_2}{\sqrt{\tau_2}} z_2 \right] \\ v &= \frac{1}{\sqrt{2B}} \left[-\frac{\sigma_2}{\sqrt{\tau_2}} z_1 + \frac{\sigma_1}{\sqrt{\tau_1}} z_2 \right] \\ B &= \sqrt{\frac{\sigma_1^2}{2\tau_1} + \frac{\sigma_2^2}{2\tau_2}}. \end{aligned}$$

Thus, the condition defining Ω reduces to $\Omega : \forall u / Bu - \frac{V}{\tau_m} + \mu \geq 0, \forall V \in [H, \Theta]$, or equivalently $u \geq \frac{\Theta - \mu\tau_m}{B\tau_m}$. We can define the effective reset, threshold and γ values as

$$\begin{aligned} \hat{\Theta}_{eff} &= \frac{\sqrt{2}(\Theta - \mu\tau_m)}{\sqrt{(\sigma_1^2 + \sigma_2^2)\tau_m}} \\ \hat{H}_{eff} &= \frac{\sqrt{2}(H - \mu\tau_m)}{\sqrt{(\sigma_1^2 + \sigma_2^2)\tau_m}} \\ \epsilon_{eff} &= \sqrt{\frac{\sigma_1^2 \frac{\tau_m}{\tau_1} + \sigma_2^2 \frac{\tau_m}{\tau_2}}{\sigma_1^2 + \sigma_2^2}}. \end{aligned}$$

The renormalized threshold and reset, $\hat{\Theta}_{eff}$ and \hat{H}_{eff} , are defined similarly as in the one synaptic type case. With these definitions, formula (72) can be expressed identically to formula (54) as

$$\nu = \int_{\hat{\Theta}_{eff}/\epsilon_{eff}}^{\infty} \frac{du}{\sqrt{2\pi}} e^{-u^2/2} \nu_0(\hat{H}_{eff} - \epsilon_{eff}u, \hat{\Theta}_{eff} - \epsilon_{eff}u), \quad (73)$$

where $\nu_0^{-1}(a, b) = \tau_m \ln(a/b)$. The neuron responds to fluctuations u above a critical value $\hat{\Theta}_{eff}/\epsilon_{eff}$. Then it detects large fluctuations in a combination of both excitatory and inhibitory drive. Additionally, this formula can be generalized to include N synaptic filters, which is done by defining μ as the sum of the individual mean synaptic currents, $\mu = \sum_{i=1}^N \mu_i$, and

$$\begin{aligned} \hat{\Theta}_{eff} &= \frac{\sqrt{2}(\Theta - \mu\tau_m)}{\sqrt{\sum_{i=1}^N \sigma_i^2 \tau_m}} \\ \hat{H}_{eff} &= \frac{\sqrt{2}(H - \mu\tau_m)}{\sqrt{\sum_{i=1}^N \sigma_i^2 \tau_m}} \\ \epsilon_{eff} &= \sqrt{\frac{\sum_{i=1}^N \sigma_i^2 \frac{\tau_m}{\tau_i}}{\sum_{i=1}^N \sigma_i^2}}. \end{aligned}$$

5 The role of NMDA and AMPA synaptic noise.

We move to a relevant situation found in the central nervous system. Spikes arriving at many central neurons can generate at the same time fast and slow unitary currents. Fast AMPA receptors filter presynaptic inputs with a time constant $\tau_{AMPA} \sim 1 - 10ms$, while for NMDA receptors the time constant is longer, $\tau_{NMDA} \sim 50 - 150ms$. Because both receptor types normally coexist in central neuron synapses [Bekkers and Stevens, 1989], the information contained in the inputs is present in the membrane potential at these two timescales. For the sake of clarity, in this section we work directly on the synaptic current variable $I(t)$, without transforming it into the normalized variable z . We first describe the model of simultaneously active AMPA and NMDA receptors, and

then we find by simple arguments an ad hoc formula for the firing rate of this neuron. This section is partly based on the results found in our work [Moreno-Bote and Parga, 2005].

The membrane potential V of the leaky IF neuron obeys

$$\tau_m \dot{V} = -V + \tau_m I(t) \quad (74)$$

$$I(t) = I_{AMPA}(t) + I_{NMDA}(t) , \quad (75)$$

where $I(t)$ is the total afferent current composed by the sum of two contributions generated by AMPA and NMDA filters, $I_{AMPA}(t)$ and $I_{NMDA}(t)$ respectively.

Cortical [Crair and Malenka, 1995, Myme et al., 2003, Fleidervish et al., 1998] and deep cerebellar nuclei [Anchisi et al., 2001] neurons receive a large number of presynaptic spikes through their AMPA and NMDA receptors. We model their contribution to the total input current by two white noise processes with means μ_{AMPA} , μ_{NMDA} , and variances σ_{AMPA}^2 , σ_{NMDA}^2 . In this model, the presynaptic signal generates the following AMPA and NMDA currents

$$\begin{aligned} \tau_{AMPA} \dot{I}_{AMPA}(t) &= -I_{AMPA}(t) + \mu_{AMPA} + \sigma_{AMPA} \eta(t) , \\ \tau_{NMDA} \dot{I}_{NMDA}(t) &= -I_{NMDA}(t) + \mu_{NMDA} + \sigma_{NMDA} \eta(t) , \end{aligned} \quad (76)$$

where $\eta(t)$ is a Gaussian white noise with zero mean and unit variance. Since both filters receive the same spikes, they integrate the same white noise, what introduces a large correlation between the currents. Writing the current without driving forces to model subthreshold dynamics is justified because then V is very far from the reversal potential of excitatory synapses.

We start by providing a qualitative derivation of an expression for the firing

rate of this model neuron valid for $\tau_{NMDA} \gg \tau_m$ and τ_{AMPA} comparable to τ_m , which might be a realistic case [Bernander et al., 1991]. Since the synaptic time constants are either longer (τ_{NMDA}) or at most comparable (τ_{AMPA}) to τ_m , we assume that the current is approximately constant during a time period τ_m , that is, $I(t) = I$. A LIF neuron receiving such a constant current fires with instantaneous rate (see main text and [Tuckwell, 1988])

$$\nu^{-1}(I) = \tau_m \ln \left(\frac{\tau_m I - H}{\tau_m I - \Theta} \right). \quad (77)$$

The current defined in eqs. (75, 76) is a random variable which we describe with a probability density distribution $\rho(I)$. Then, following the reasoning described in the first section of Results, the mean firing rate can be computed by averaging the rate at constant current, eq. (77), with the probability density $\rho(I)$ as

$$\nu = \int_{I_{min}}^{\infty} dI \rho(I) \nu(I), \quad (78)$$

where the integral extends from $I_{min} = \Theta/\tau_m$. This *threshold current* is the minimal current required for the neuron to fire (see eq. (74)). To evaluate the firing rate we still need the distribution $\rho(I)$ for the stochastic process defined in eqs. (75, 76). Since $\rho(I)$ is Gaussian, it is fully determined by its mean μ and variance σ_I^2 . The mean is simply the sum of the AMPA and NMDA mean currents, $\mu = \mu_{AMPA} + \mu_{NMDA}$. To obtain the variance we first solve eqs. (76) with the initial condition $I_k(0) = 0$ ($k = AMPA, NMDA$) to obtain

$$I_k(t) = \mu_k(1 - e^{-t/\tau_k}) + \frac{\sigma_k}{\tau_k} e^{-t/\tau_k} \int_0^t ds e^{s/\tau_k} \eta(s). \quad (79)$$

The variance σ_I^2 is computed as

$$\begin{aligned}\sigma_I^2 &= \lim_{t \rightarrow \infty} \langle (I_{AMPA}(t) + I_{NMDA}(t) - \mu)(I_{AMPA}(t) + I_{NMDA}(t) - \mu) \rangle \\ &= \frac{1}{2} \left(\frac{\sigma_{AMPA}^2}{\tau_{AMPA}} + \frac{\sigma_{NMDA}^2}{\tau_{NMDA}} + 4 \frac{\sigma_{AMPA} \sigma_{NMDA}}{\tau_{AMPA} + \tau_{NMDA}} \right).\end{aligned}\quad (80)$$

The first two terms are the current variances generated by the AMPA and NMDA input fluctuations, while the third positive term arises from the correlations between AMPA and NMDA input fluctuations. If AMPA and NMDA filters were driven by two independent white noises, the third term would not be present. Note also that the effect of combined AMPA and NMDA events is to increase the synaptic noise relative to that provided by independently driven synapses. After determining $\rho(I)$ with μ and σ_I^2 in the way just described and using eq. (77), the firing rate in eq. (78) can be finally written as

$$\nu = \int_{I_{min}}^{\infty} \frac{dI}{\sqrt{2\pi}\sigma_I\tau_m} e^{-\frac{(I-\mu)^2}{2\sigma_I^2}} \ln^{-1} \left(\frac{\tau_m I - H}{\tau_m I - \Theta} \right). \quad (81)$$

This expression generalizes the result found in the previous sections for a current filtered through a single slow synaptic filter. The firing rate for this particular case is readily obtained from eq. (81) by setting to zero the mean and variance of one of the two receptors. The prediction given by eq. (81) has been compared with simulations results of a neuron receiving both AMPA and NMDA currents in [Moreno-Bote and Parga, 2005], providing excellent fits.

6 Derivation of the FPE for the LIF neuron

We consider the LIF neuron defined by eqs. (1, 13). First, we perform the linear transformation

$$V = \mu\tau_m + x \sqrt{\frac{\tau_m}{2}}\sigma, \quad I = \mu + z \frac{\sigma}{\sqrt{2\tau_s}}, \quad (82)$$

to obtain

$$\dot{x} = -\frac{x}{\tau_m} + \frac{z}{\sqrt{\tau_m\tau_s}}, \quad \dot{z} = -\frac{z}{\tau_s} + \sqrt{\frac{2}{\tau_s}}\eta(t). \quad (83)$$

To derive the FPE associated to eqs. (83), we first discretize the time and obtain

$$\begin{aligned} x'(w) &= x + \frac{x}{\tau_m}\delta t - \frac{z}{\sqrt{\tau_m\tau_s}}\delta t, \\ z'(w) &= z + \frac{z}{\tau_c}\delta t - \sqrt{\frac{2}{\tau_c}}w\sqrt{\delta t}, \end{aligned} \quad (84)$$

which relates the initial state $(x'(w), z'(w))$ with the final state (x, z) after a time δt . Note that the initial point coordinates appear on the left side of the equations, whereas the final point coordinates appear on the right side. Here, $w = w(t)$ are i.i.d. random variables defined at each time step t taking values $+1$ and -1 with equal probability $1/2$. Then, $\langle w(t) \rangle = 0$, $\langle w^2(t) \rangle = 1$ and $\langle w(t)w(t') \rangle = 0$ for $t \neq t'$. This means that the quantity $w/\sqrt{\delta t}$, which appears above, approximates the delta function, since $\langle w(t)/\sqrt{\delta t} \rangle = 0$, $\langle w^2(t)/\delta t \rangle = 1/\delta t$, and $\langle w(t)w(t')/\delta t \rangle = 0$ for $t \neq t'$.

The critical point is to understand how to relate the probability density at time $t + \delta t$, $P(x, z, t + \delta t)$, with the density at a previous time t , $P(x', z', t)$. First, note that the probability of finding a neuron within an infinitesimal cell of size $\delta x' \delta z'$ around the state (x', z') at time t has probability $P(x', z', t) \delta x' \delta z'$. Second, the state cell centered at (x', z') with area $\delta x' \delta z'$ will be projected at the successive time $t + \delta t$ into another cell centered at (x, z) with surface $\delta x \delta z$

close to the previous one, obeying the rules defined in eqs. (84). By conservation of the probability, we have that

$$P(x, z, t + \delta t) \delta x \delta z = \sum_{w=\pm 1} p(w) P(x'(w), z'(w), t) \delta x' \delta z'. \quad (85)$$

This is because the two states $(x'(w), z'(w))$ ($w = 1$ and $w = -1$) defined above are the only ones from where one can arrive to the state (x, z) after an infinitesimal amount of time δt . In addition, the box around state (x', z') is compressed to the box around the final state (x, z) by a factor $\delta x \delta y = (1 - \delta t / \tau_m)(1 - \delta t / \tau_c) \delta x' \delta y'$, given by the decaying terms in eqs. (83).

After expanding the densities in eq. (85) in powers of $\sqrt{\delta t}$, we find that all terms $O(\sqrt{\delta t})$ are zero (since $\langle w \rangle = 0$), while the terms $O(\delta t)$ do not vanish. Then, we can equal the terms at $O(\delta t)$ to obtain the FPE

$$\tau_m \frac{\partial}{\partial t} P(x, z, t) = \left[\frac{\partial}{\partial x} (x - \epsilon z) + \epsilon^2 L_z \right] P(x, z, t). \quad (86)$$

For the stationary regime, the time derivative of the probability density is zero. In order to have a stationary FPE, however, whenever a neuron reaches threshold, the state has to be absorbed and reinjected at the reset. This leads to the FPE (17).

7 Numerical procedures

Here we describe the numerical procedures used to simulate the LIF neuron. Analogous procedures have been followed for the other IF neurons considered. The voltage and noise eqs. (83) are solved using Euler's method. This is done by discretizing the time with bins of size $\delta t = 5 \cdot 10^{-4} ms \ll \tau_m$ and use eqs. (84). When $x > \hat{\Theta}$, a spike is emitted and the normalized voltage it is reset to $x = \hat{H}$. The variable z is not reset after a spike, so its value before a spike

rolls over to the next integration interval. The variable $w(t)$ are i.i.d. random variables taking values $+1$ and -1 with equal probability $1/2$. Fortran90 custom programs were used for all simulations and numerical integrations.

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