

On a Finite-Size Neuronal Population Equation*

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Abstract. Population equations for infinitely large networks of spiking neurons have a long tradition in theoretical neuroscience. In this work, we analyze a recent generalization of these equations to populations of finite size, which takes the form of a nonlinear stochastic integral equation. We prove that, in the case of leaky integrate-and-fire neurons with escape noise and for a slightly simplified version of the model, the equation is well-posed and stable in the sense of Brémaud and Massoulié. The proof combines methods from Markov processes taking values in the space of positive measures and nonlinear Hawkes processes. For applications, we also provide efficient simulation algorithms.

Key words. stability, finite-size fluctuations, nonlinear Hawkes processes, piecewise deterministic Markov processes, Meyn–Tweedie theory, spiking neuron, SPDEs driven by Poisson random measure

MSC codes. 60G55, 60H20, 60K35, 92B20

DOI. 10.1137/21M1445041

1. Introduction. Neuronal population equations describe the dynamics of large networks of neurons in terms of single neuron parameters [31]. As such, they are useful mathematical abstractions for relating microscopic and large-scale brain signals and contribute to the biophysical interpretation of the latter [17]. Their motivation is twofold: on the one hand, they enable the theoretical analysis of emergent phenomena, like collective oscillations [7, 30, 14]; on the other hand, from the data analysis point of view, they constitute the basis of “forward models” of large-scale brain signals [17, 44, 8, 4, 26]. This second motivation requires neuronal population equations to achieve the right balance between accuracy (the equation faithfully captures the dynamics of the population of neurons it represents) and usability (the equation can be efficiently simulated).

An example of such a neuronal population equation is the integral equation (or refractory density equation) for a homogeneous network of spiking neurons (“neuronal population”) [29, 30, 12, 31, 47]. Contrary to standard neural-mass models [52, 17, 35], the integral equation

* Received by the editors September 7, 2021; accepted for publication (in revised form) by J. Moehlis October 31, 2022; published electronically June 12, 2023. All authors contributed equally to the present article.

<https://doi.org/10.1137/21M1445041>

Funding: This work was funded by the Swiss National Science Foundation (grant 200020_184615) and has been conducted as part of the FAPESP project Research, Innovation, and Dissemination Center for Neuromathematics (grant 2013/07699-0) and of the ANR project ANR-19-CE40-0024.

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captures the effect of neuronal refractoriness on the mean population dynamics [12, 31, 47] and is exact in the mean-field limit if neurons are modeled as intensity-based renewal point processes [16, 25, 10]. Specific examples of the integral equation are the time-elapsing neuron network model [39] (or age-structured model [22]) and the voltage-structured model of [16, 25].

Besides capturing the effect of single neuron dynamics (such as postspike refractory effects) on the *mean* population dynamics, there is a second challenge for neuronal population equations: the proper account of *fluctuations*. Fluctuations of the average population activity are present in the case of finite population sizes and vanish in the mean-field limit of infinitely many neurons. From a modeling perspective, an important question arises: Are the relevant neuronal populations large enough so that finite-size fluctuations can be neglected? There is no clear answer to this question, but the anatomical and functional organization of the cerebral cortex into different cortical areas, columns, and layers each containing different cell classes [32, 41, 45, 2] requires a subdivision of a cortical circuit into many relatively small populations. For example, at the scale of a cortical column, empirical data from mouse barrel cortex suggests populations of around 50 to 2000 neurons [36]. For these population sizes, finite-size fluctuations are nonnegligible, and this noise may strongly impact the nonlinear population dynamics [48]. Therefore, modeling cortical circuits at the mesoscopic scale of populations requires a stochastic description, which is in marked contrast to the deterministic integral equation.

Rigorous extensions of the integral equations to account for finite-size fluctuations are subject to an accuracy/usability trade-off. If neuronal refractoriness is neglected, the population equation reduces to that of [19, 20], and finite-size noise can be added by the linear-noise approximation [33] or, granting some Markov embedding, by the diffusion approximation [20], whose numerical implementation is relatively simple [11]. These approaches fail to reproduce the nonstationary dynamics of the mean population activity and the temporal correlation structure of fluctuations for a population of spiking neurons with refractoriness (Figure 1(a)). On the other hand, if one does not neglect refractoriness, central limit theorem-based arguments lead to formal stochastic PDEs (SPDEs) [9, 23], which are computationally expensive to simulate, or to formal integral equations with colored noise [18], for which a simulation algorithm is unknown.

In [48], a heuristic extension of the integral equation with finite-size fluctuations is derived. It can be easily simulated and takes into account the effects of neuronal refractoriness. While this extension is not exact, its numerical implementation gives an accurate approximation to the dynamics of finite-size networks of spiking neurons, such as the broad class of generalized integrate-and-fire neurons [42, 48] and formal renewal-type neurons [30, 40]. Moreover, since it takes the form of an intensity-based point process, the likelihood of a population spike train can be easily computed, which enables efficient data fitting [43, 51]. The intensity function of this point process exhibits a novel type of nonlinear history dependence that goes beyond nonlinear Hawkes processes and has not been studied mathematically so far. In particular, the stability of the process observed in simulations is poorly understood from the theoretical point of view. Therefore, the aim of this work is to give a rigorous foundation to the model of [48] and prove its stability.

Below, we briefly give a review of some standard population equations. We then present the finite-size model of [48] in a slightly simplified form. Finally, we show that the simplified model, in the case of leaky integrate-and-fire (LIF) neurons with escape noise [30, 27], can be written as an SPDE driven by Poisson noise, which will be the main object of study in this work.

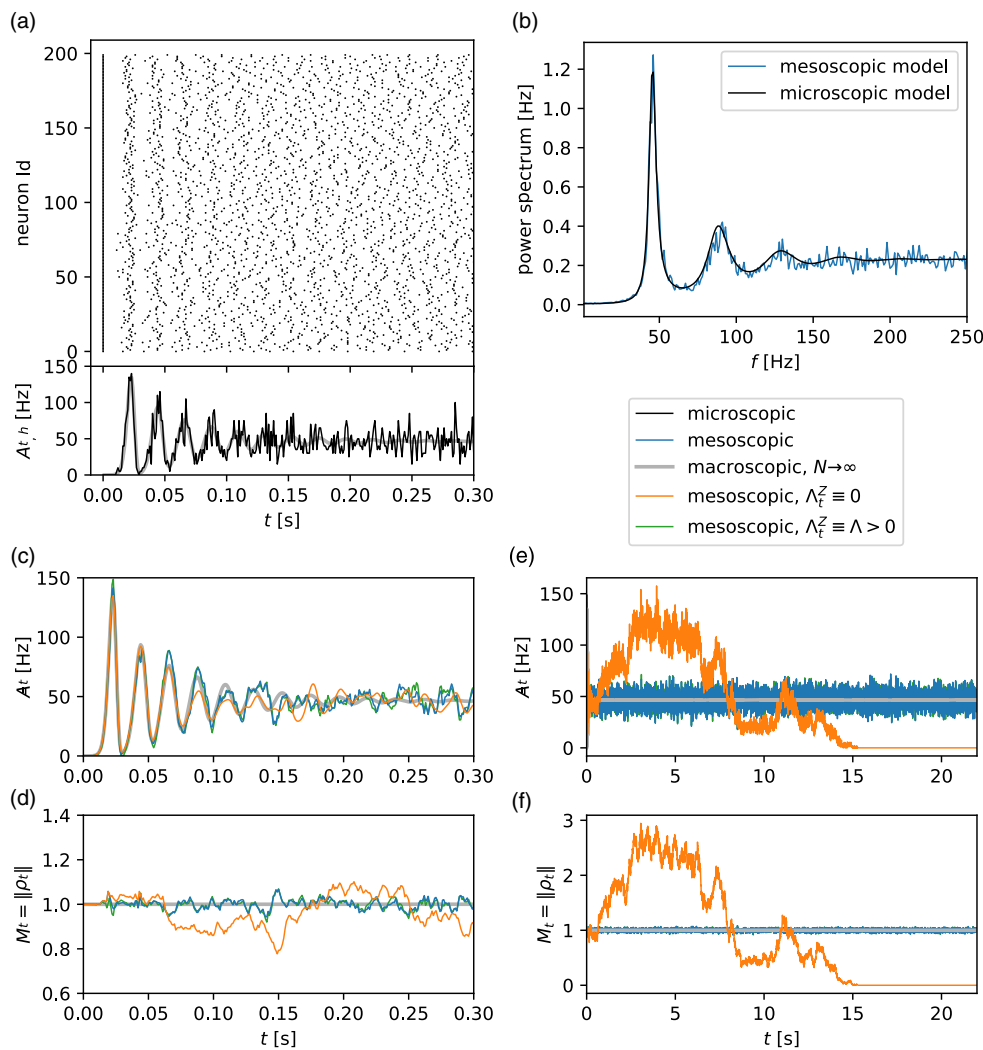


Figure 1. Mesoscopic population dynamics. (a) Top: Spike-raster plot of a microscopic model of $N = 200$ uncoupled leaky integrate-and-fire neurons with escape noise, (1.1) with $J = 0$. Neurons were initialized in a synchronized state, i.e., all neurons spiked at time $t = 0$. Bottom: Empirical population activity measured with temporal bin size $h = 0.001s$ (black line) and macroscopic population activity predicted by the deterministic integral equation (1.7) for $N \rightarrow \infty$ with $\nu_0 = \delta_0$ (gray line). (b) Comparison of the power spectral densities (as defined in Appendix D, see also [48]) of the empirical population activities $A_{t,h}(t)$ of the microscopic model (black line, exact theory [31]) and $\hat{A}_{t,h}(t)$ of the mesoscopic model (blue line, simulation). (c, d) A_t (1.12b) and mass M_t (1.14) for simulations of the mesoscopic model (blue line) and the “naive” mesoscopic model with $\Lambda_t^Z \equiv 0$ (orange line). For comparison, the macroscopic model and the mesoscopic model with fixed $\Lambda_t^Z \equiv 277$ Hz (corresponding to the temporally averaged Λ_t^Z of the mesoscopic model) are shown by gray and green lines, respectively. (e, f) Same as (c, d) but for a longer simulation time. Parameters: $\tau_m = 0.02$ s, $\mu = 20$ mV, $f(u) = ce^{(u-\vartheta)/\Delta_u}$, $c = 10$ Hz, $\vartheta = 10$ mV, $\Delta_u = 1$ mV.

1.1. Neuronal population equations. To give a mathematical introduction to the integral equation formalism, it is useful to consider the special case of LIF neurons with escape noise [30, 27], which is also the main case we will treat in this work. Let us consider a network of

N identical neurons that are all-to-all connected with uniform connection strength J/N for $J \in \mathbb{R}$. Each neuron i has a voltage variable $U^{i,N}$ which evolves according to the system of SDEs: For all $i = 1, \dots, N$,

$$(1.1a) \quad dU_t^{i,N} = \frac{\mu_t - U_t^{i,N}}{\tau_m} dt - U_t^{i,N} dZ_t^{i,N} + \frac{J}{N} \sum_{j=1}^N dZ_t^{j,N},$$

$$(1.1b) \quad Z_t^{i,N} = \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq f(U_{s^-}^{i,N})} \pi^i(ds, dz).$$

Here, $Z_t^{i,N}$ is the spike counting process of the neuron i and has intensity $f(U_{t^-}^{i,N})$, t^- denoting the left limit. Furthermore, μ_t comprises the resting potential and the (possibly time-dependent) external drive, τ_m is the membrane time constant, $f : \mathbb{R} \rightarrow \mathbb{R}_+$ is the intensity function, and $\{\pi^i\}_{i=1, \dots, N}$ is a collection of independent Poisson random measures on $\mathbb{R}_+ \times \mathbb{R}_+$ with Lebesgue intensity measure.

Equation (1.1) is called a *microscopic model* because the neuronal dynamics is modeled with single-cell resolution (Figure 1(a), top). A drastic reduction of the complexity of the model can be achieved by coarse-graining over the population of neurons. To this end, we consider the *empirical population activity*

$$(1.2) \quad A_{t,\mathfrak{h}}^N = \frac{1}{N} \sum_{i=1}^N \frac{Z_{t+\mathfrak{h}}^{i,N} - Z_t^{i,N}}{\mathfrak{h}},$$

where $\mathfrak{h} > 0$ is a small time interval determining the temporal resolution (Figure 1(a), bottom). Neuronal population equations are models of such coarse-grained quantities that describe the neuronal dynamics at the scale of whole populations. If the population is of finite size ($N < \infty$), the dynamics is called a *mesoscopic model*, while the dynamics for an infinitely large population ($N \rightarrow \infty$) is referred to as a *macroscopic model*. In [16, 25], the authors proved that, in the macroscopic limit $N \rightarrow \infty$, if the initial conditions $\{U_0^i\}_{i=1, \dots, N}$ are independent and identically distributed with law ν_0 , the empirical measure of the system (1.1) is characterized by the voltage-structured PDE (with solutions in the sense of measures [14]): For all $u \in \mathbb{R}$ and $t > 0$,

$$(1.3a) \quad \partial_t \rho(du, t) + \partial_u \left(\left(\frac{\mu_t - u}{\tau_m} + J \rho_t[f] \right) \rho(du, t) \right) = -f(u) \rho(du, t) + \rho_t[f] \delta_0(du),$$

$$(1.3b) \quad \rho_0 = \nu_0,$$

where $\rho_t := \rho(\cdot, t)$ and $\rho_t[f] := \int_{\mathbb{R}} f(u) \rho(du, t)$.

The latter can be interpreted as the population activity

$$(1.4) \quad \lim_{\mathfrak{h} \downarrow 0} \lim_{N \rightarrow \infty} A_{t,\mathfrak{h}}^N = A(t) := \rho_t[f].$$

Furthermore, $\rho_t[1] = 1$ for all $t > 0$ expressing the fact that the number of neurons is conserved.

We now transform (1.3) into an integral equation. For all continuous functions $a : \mathbb{R}_+ \rightarrow \mathbb{R}$, we define the time-dependent vector field $b^a(t, u) := (\mu_t - u)/\tau_m + Ja(t)$ and write, for all $0 \leq s \leq t$, $\Phi_{s,t}^a(u)$ the associated flow given by

$$(1.5) \quad \Phi_{s,t}^a(u) := ue^{-\frac{t-s}{\tau_m}} + \int_s^t e^{-\frac{t-r}{\tau_m}} \frac{\mu_r}{\tau_m} dr + J \int_s^t e^{-\frac{t-r}{\tau_m}} a_r dr \quad \text{for all } u \in \mathbb{R}.$$

We can now define, for all $0 \leq s \leq t$,

$$(1.6) \quad \lambda^a(t|s) := f(\Phi_{s,t}^a(0)) \quad \text{and} \quad S^a(t|s) := \exp\left(-\int_s^t \lambda^a(r|s) dr\right).$$

The function $\lambda^a(t|s)$, called the hazard rate, gives the intensity at time t (i.e., the instantaneous probability of emitting a spike) as a function of the time of the last spike s and the past population activity $(a(r))_{s \leq r \leq t}$; the membrane potential dynamics of LIF neurons—leaky integration and spike-triggered reset, (1.1a)—is accounted for in the definition of $\lambda^a(t|s)$. Similarly, the function $S^a(t|s)$, called the survival, gives the probability of not emitting a spike in the time interval $]s, t[$, given that the last spike was emitted at time s . By the method of characteristics, we get that the population activity $A(t)$ solves the integral equation

$$(1.7) \quad A(t) = H^A(t) + \int_0^t \lambda^A(t|s) S^A(t|s) A(s) ds,$$

where

$$(1.8) \quad H^A(t) := \int_{\mathbb{R}} f(\Phi_{0,t}^A(u)) e^{-\int_0^t f(\Phi_{0,r}^A(u)) dr} \nu_0(du).$$

Equation (1.7) is the integral equation of [52, 29, 30]; see also [13]. Note that, traditionally, the integral equation has no explicit initial condition and therefore requires a normalizing condition [31, sect. 14.1]. The integral equation (1.7) is normalized such that

$$(1.9) \quad \tilde{H}^A(t) + \int_0^t S^A(t|s) A(s) ds = 1$$

for all $t > 0$, where we defined

$$(1.10) \quad \tilde{H}^A(t) := \int_{\mathbb{R}} e^{-\int_0^t f(\Phi_{0,r}^A(u)) dr} \nu_0(du).$$

The normalization, (1.9), expresses the fact that the number of neurons is conserved.¹ Note that the integral equation (1.7) is simply the time derivative of the normalizing condition (1.9); this fact has been originally used to derive the integral equation [30].

In the case of LIF neurons with escape noise, the voltage-structured equation (1.3) is equivalent to the integral equation (1.7) if $\lambda^A(t|s)$ is defined by (1.6). However, we could have chosen a different definition for the hazard rate $\lambda^A(t|s)$; the integral equation is therefore more general than (1.3). In fact, (1.7) can be seen as a renewal equation that holds for any

¹The conservation of neuronal mass can be understood as follows: At time t , $\tilde{H}^A(t)$ represents the fraction of neurons ($\#$ neurons divided by N) that had their unique last spike before time 0, while for $s \in [0, t[$ the term $S^A(t|s)A(s)ds$ represents the fraction of neurons that had their unique last spike time in the interval $[s, s+ds[$ (here $A(s)ds$ is the fraction of neurons that fired in that interval and $S^A(t|s)$ is the probability for one neuron of not emitting a spike in $]s, t[$ given a spike at time s). Therefore, $\int_0^t S^A(t|s)A(s)ds$ represents the fraction of neurons that had their unique last spike in $[0, t[$. Hence, (1.9) states that the fraction of neurons at time t that had their unique last spike time before time t (either before time 0 or since time 0) is equal to unity. Since this statement holds for all $t > 0$ and each neuron has exactly one last spike time before time t , the total number of neurons must be conserved.

population of neurons modeled as time-inhomogeneous renewal processes [40]. For example, the Fokker–Planck equation for neuronal networks with diffusive noise (see [31, Chap. 13]) or the time-elapsed neuron network model [39] can also be written as an integral equation with a suitable choice of the hazard rate.

1.2. The finite-size integral equation. In [48], the authors derive a generalization of the integral equation (1.7) which takes into account finite-size noise. For clarity, we will present the equation of [48] in the case of LIF neurons with escape noise. Before presenting the model, we need to extend the definitions (1.6). For all nondecreasing functions $z : \mathbb{R}_+ \ni t \mapsto z_t$ with bounded variation on finite time intervals, we redefine, for all $0 \leq s \leq t$,

$$(1.11) \quad \Phi_{s,t}^z(u) := ue^{-\frac{t-s}{\tau_m}} + \int_s^t e^{-\frac{t-r}{\tau_m}} \frac{\mu_r}{\tau_m} dr + J \int_{]s,t]} e^{-\frac{t-r}{\tau_m}} dz_r \quad \text{for all } u \in \mathbb{R}.$$

We can now extend the definitions (1.6), (1.8), and (1.10), replacing Φ^A by (1.11).

For a finite number of neurons N , the finite-size integral equation of [48] (“mesoscopic model”) can be written as follows: For all $t \geq 0$,

$$(1.12a) \quad Z_t = \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbf{1}_{z \leq N \bar{A}_{s-}} \pi(ds, dz),$$

$$(1.12b) \quad \bar{A}_t = \left[H^Z(t) + \int_{[0,t]} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda_t^Z \left(1 - \tilde{H}^Z(t) - \int_{[0,t]} S^Z(t|s) dZ_s \right) \right]_+,$$

$$(1.12c) \quad \Lambda_t^Z = \frac{G^Z(t) + \int_{[0,t]} \lambda^Z(t|s) \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}{\tilde{G}^Z(t) + \int_{[0,t]} \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s},$$

where π is a Poisson random measure on $\mathbb{R}_+ \times \mathbb{R}_+$ with Lebesgue intensity measure and $[\cdot]_+ = \max(0, \cdot)$. The functions G^Z and \tilde{G}^Z are analogous to H^Z and \tilde{H}^Z :

$$G^Z(t) := \int_{\mathbb{R}} f(\Phi_{0,t}^Z(u)) \left\{ 1 - e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \right\} e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \nu_0(du),$$

$$\tilde{G}^Z(t) := \int_{\mathbb{R}} \left\{ 1 - e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \right\} e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \nu_0(du).$$

The mesoscopic model (1.12) defines a jump process Z_t , where jumps of size $1/N$ occur with intensity $N \bar{A}_{t-}$. The derivation of (1.12), explained in detail in [48, pp. 35–43], involves heuristic arguments and approximations. Consequently, this mesoscopic model is inexact (in contrast to the formal SPDE of [9, 23]). However, extensive numerical simulations have shown that the model is highly accurate in many multiscale modeling applications [48] (see also Figure 1(b)). Moreover, it has the advantage of being an intensity-based and history-dependent point process and, as such, can be efficiently simulated and used for statistical data analysis [43, 51]. A concise derivation of (1.12) is presented in section 4, where we also show that, for some convenient initial condition, the functions H^Z , \tilde{H}^Z , G^Z , and \tilde{G}^Z are trivial.

The finite-size analogue of the population activity $A(t)$ for infinitely large populations (1.7) is the distributional derivative of Z_t ,

$$\dot{Z}_t = \frac{1}{N} \sum_k \delta(t - t_k),$$

where t_k is the jump times of Z_t and $\delta(\cdot)$ denotes the Dirac delta distribution.² We call \dot{Z}_t the population spike train (sum of δ -pulses at spike times t_k). Note that the biologically relevant quantity is the empirical population activity at a finite time resolution, $\bar{A}_{t,h}^N := \mathfrak{h}^{-1} \int_t^{t+\mathfrak{h}^+} \dot{Z}_s ds = [Z(t+\mathfrak{h}) - Z(t)]/\mathfrak{h}$, for some small time interval $\mathfrak{h} > 0$. Furthermore, we will often call the finite-size population model, (1.12), a *mesoscopic model* in contrast to “macroscopic model” that refers to the case $N \rightarrow \infty$. Note that the variables \bar{A}_t and Z_t describe the neuronal activity of the population as a whole, driven by only one single Poisson noise $\pi(dt, [0, N\bar{A}_t^-])$. A time discretization of the mesoscopic model permits an efficient simulation of the neuronal dynamics directly on the population level, without the need to simulate individual neurons (see section 5 and Algorithm A.1). Importantly, even though the mesoscopic model is an approximation, it accurately captures the statistics of the population activity $\bar{A}_{t,h}^N$ of the original microscopic model. In particular, the fluctuation statistics of the population activities $A_{t,h}^N$ and $\hat{A}_{t,h}^N$, as expressed by their power spectral density, are well matched (Figure 1(b), also see [48] for further examples).

A key difference between the macroscopic model for an infinitely large population (1.7) and the mesoscopic model (1.12) is the “correction term” $\Lambda_t^Z(1 - \dots)$ in (1.12b) arising due to finite network size, $N < \infty$. This correction term may seem unexpected in light of the following heuristic argument: in (1.7) for infinite N , the fraction of neurons $A(s)ds$ firing in the past, $s < t$, contribute to the current activity $A(t)dt$ with probability $\lambda^A(t|s)S^A(t|s)dt$. For finite N , the corresponding fraction of neurons is dZ_s , and assuming that the probability to fire their next spike at time t is again given by $\lambda^A(t|s)S^A(t|s)dt$, the expected activity should be given by the much simpler expression $\bar{A}_{t,\text{naive}} = H^Z(t) + \int_0^t \lambda^Z(t|s)S^Z(t|s)dZ_s$. This naive finite-size model is obtained by putting $\Lambda_t^Z \equiv 0$ and thus lacks the “correction term.” Numerical simulations of the naive finite-size model indeed reproduce the transient initial dynamics of the population activity at short times, including damped oscillations caused by refractoriness (Figure 1(c), orange curve). However, longer simulations of the naive model reveal that the population rate \bar{A}_t strongly fluctuates and eventually collapses to the silent solution $\bar{A}_t = 0$. In contrast, the mesoscopic model, (1.12) with $\Lambda_t^Z > 0$, reaches a nonsilent, stationary state consistent with the microscopic model (1.1) (Figure 1(e)). A completely open theoretical question is, Why does the “correction term” in (1.12b) “stabilize” the finite-size neuronal population dynamics?

To address this question mathematically, we focus our analysis on the case where the modulating factor Λ_t^Z is fixed ($\Lambda_t^Z \equiv \Lambda > 0$). This is a simplified version of the finite-size integral equation (1.12), for which we can prove a rigorous stability result. Note that fixing $\Lambda_t^Z \equiv \Lambda > 0$ is for mathematical tractability only; for practical modeling, Λ_t^Z as defined in (1.12c) should be preferred (a detailed simulation algorithm is presented in section 5).

Before presenting our main stability result in subsection 1.4, we provide some additional insights into the mechanisms of the finite-size integral equation (1.12), in particular, why the naive model ($\Lambda = 0$) is expected to fail. First, in subsection 1.2.1, we show a close relationship between the finite-size integral equation and nonlinear Hawkes processes, for which stability properties are well known. Second, in subsection 1.2.2, we propose a heuristic argument for the

²Formally, $\dot{Z}_t dt := dZ_t$, where dZ is the Lebesgue–Stieltjes measure associated with the counting measure Z .

stability in terms of neuronal mass conservation and an analogy with the Cox–Ingersoll–Ross process.

1.2.1. Relationship with nonlinear Hawkes processes. If $J = 0$ (neurons do not interact), $\mu_t \equiv \mu$ (the external drive is constant), and $\Lambda_t^Z \equiv \Lambda$, (1.12) reduces to a nonlinear Hawkes process [5]: For all $t \geq 0$,

$$(1.13a) \quad Z_t = \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N \bar{A}_{s-}} \pi(ds, dz),$$

$$(1.13b) \quad \bar{A}_t = \left[\Lambda + H^0(t) - \Lambda \tilde{H}^0(t) + \int_{[0,t]} \underbrace{(\lambda^0(t|s) - \Lambda) S^0(t|s)}_{=: h^\Lambda(t-s)} dZ_s \right]_+$$

where λ^0 , S^0 , H^0 , and \tilde{H}^0 correspond to the definitions (1.6), (1.8), and (1.10) when Φ^Z (1.11) is replaced by $\Phi_{s,t}^0(u) = ue^{-\frac{t-s}{\tau_m}} + \int_s^t e^{-\frac{t-r}{\tau_m}} \frac{\mu_r}{\tau_m} dr$.

The function $h^\Lambda : \mathbb{R}_+ \rightarrow \mathbb{R}$ in (1.13a) can be interpreted as the self-interaction kernel of the nonlinear Hawkes process. The model (1.13) is not particularly useful in practice since it only approximates the dynamics of a population of noninteracting neurons with constant external input. Nevertheless it sheds light on the role of Λ for the stability of the mesoscopic model, and it helps to see why the theory of nonlinear Hawkes processes [5] will prove to be instrumental in this work. It is easy to verify that $\int_0^\infty h^\Lambda(t)dt = 1$ if $\Lambda = 0$ and $\int_0^\infty h^\Lambda(t)dt < 1$ if $\Lambda > 0$. If $\Lambda = 0$, (1.13) is a critical Hawkes process and has a nontrivial stationary solution only if h^0 is heavy-tailed [6] (which is not the case for the neuron models considered here). On the other hand, if $\Lambda > 0$, (1.13) is a stable nonlinear Hawkes process with a unique stationary solution (Theorem 1 in [5] and see also [15]). Hence, in the time-homogeneous ($\mu_t \equiv \mu$) and noninteracting case ($J = 0$), $\Lambda_t \equiv \Lambda > 0$ is a sufficient condition for the stability of (1.13) in the sense of [5].

To generalize this stability result to the interacting case ($J \neq 0$), we will use a Markov embedding of (1.12) and the Meyn–Tweedie theory [37], in addition to standard techniques for nonlinear Hawkes processes [5].

1.2.2. Approximate conservation of neuronal mass. In contrast to the conservation of neuronal mass in the macroscopic model, (1.9), such a strict conservation law no longer holds for the mesoscopic model, (1.12). However, in analogy to (1.9), we would expect the neuronal “mass”

$$(1.14) \quad M_t := \tilde{H}^Z(t) + \int_{[0,t]} S^Z(t|s) dZ_s$$

to stay close to 1. This feature is supported by simulations of the mesoscopic model showing that M_t fluctuates around unity (Figure 1(d),(f)). Indeed, with the number of neurons in the system (1.1) being obviously constant, the finite-size population model (1.12) should reflect this mass conservation principle.

Let us consider the first hitting time $\tau^* = \inf\{t > 0 : \bar{A}_t = 0\}$. For $0 < t < \tau^*$, the intensity \bar{A}_t is strictly positive; hence (1.12b) can always be written as

$$\bar{A}_t = H^Z(t) + \int_{[0,t]} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda_t^Z (1 - M_t).$$

By formal differentiation of (1.14), we obtain for $0 < t < \tau^*$

$$(1.15) \quad dM_t = -H^Z(t)dt + dZ_t - \left(\int_{[0,t]} \lambda^Z(t|s) S^Z(t|s) dZ_s \right) dt = \Lambda_t^Z(1 - M_t)dt + d\tilde{Z}_t,$$

where $\tilde{Z}_t := Z_t - \int_0^t \bar{A}_s ds$ is the compensated jump process. Equation (1.15) yields some rough insights into the dynamics of the neuronal mass M_t . For simplicity, let us assume $\Lambda_t^Z \equiv \Lambda$ to be constant. First, the conditional mean $\bar{M}_t^c := \mathbb{E}[M_t | \tau^* > t]$ can be obtained by averaging (1.15): $d\bar{M}_t^c = \Lambda(1 - \bar{M}_t^c)dt$. This equation shows that its solution, $\bar{M}_t^c = 1 + (\tilde{H}^Z(0) - 1)e^{-\Lambda t}$, is attracted to unity if $\Lambda > 0$. Conversely, in the naive model, when $\Lambda = 0$, the conditional mean does not drift toward unity but remains constant, $\bar{M}_t^c = \tilde{H}^Z(0)$ for all $t > 0$. Second, in the naive model ($\Lambda = 0$), once M_t hits the boundary 0, it sticks to this boundary forever, i.e., $M_t = 0$ for all $t > \tau^*$ (Figure 1(f)). In fact, if f is upper bounded by $\|f\|_\infty < \infty$, we have $0 \leq \bar{A}_t \leq \|f\|_\infty M_t + \Lambda(1 - M_t)$. Thus, $M_t = 0$ and $\Lambda = 0$ entail that $\bar{A}_t = 0$, and hence the “noise” $d\tilde{Z}$ in (1.15) vanishes.

Third, if the jumps of \tilde{Z}_t are small and frequent enough and if the increments of \tilde{Z}_t are “independent” enough, we may replace $d\tilde{Z}_t$ by its diffusion approximation $\sqrt{\bar{A}_t}/N dW_t$, where W_t is a Wiener process. If we further assume that \bar{A}_t and M_t vary roughly in proportion (as suggested by Figure 1(e),(f) for the naive model), we expect that M_t behaves like a Cox–Ingersoll–Ross process, $d\hat{M}_t = \Lambda(1 - \hat{M}_t)dt + \sigma\sqrt{\hat{M}_t}dW_t$, where σ is the volatility parameter. Due to the drift term, this process fluctuates around its mean $\mathbb{E}[\hat{M}_t] = 1$ if $\Lambda > 0$, consistent with simulations of the model (Figure 1(d),(f)). Such drift force is absent in the naive model, $\Lambda = 0$, in which case $d\hat{M}_t = \sigma\sqrt{\hat{M}_t}dW_t$ describes the critical Feller branching diffusion which goes extinct in the long run (and once it hits 0 remains there forever) with extinction probability $P(\hat{M}_t = 0 | \hat{M}_0 = x) = e^{-\frac{x}{\sigma^2 t}}$.

1.3. Markov embedding of the finite-size integral equation. As the voltage-structured equation (1.3) can be transformed into an integral equation, assuming $\Lambda_t^Z \equiv \Lambda$, we can transform the stochastic integral equation (1.12) back into a voltage-structured SPDE driven by Poisson noise. Denoting \mathcal{M}_+ the space of nonnegative finite measures on \mathbb{R} , for all \mathcal{M}_+ -valued random variables $\hat{\nu}_0$, the SPDE formally writes as the following: For all $t > 0$ and $u \in \mathbb{R}$,

$$(1.16a) \quad \partial_t \rho(du, t) + \partial_u \left(\left(\frac{\mu_t - u}{\tau_m} + J\dot{Z}_t \right) \rho(du, t^-) \right) = -f(u)\rho(du, t) + \dot{Z}_t \delta_0(du),$$

$$(1.16b) \quad Z_t = \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N\bar{A}_{t^-}} \pi(ds, dz) \quad \text{with } \bar{A}_t := [\rho_t[f] + \Lambda(1 - \|\rho_t\|)]_+,$$

$$(1.16c) \quad \rho_0 = \hat{\nu}_0,$$

where $\|\cdot\|$ denotes the total variation norm, that is, the total mass of the measure.

We will give a precise meaning to the SPDE (1.16) and show that it is equivalent to the stochastic integral equation (1.12) in section 2 below. The two jump terms $\partial_u(J\dot{Z}_t\rho(du, t^-))$ and $\dot{Z}_t\delta_0(du)$ have the following interpretation: At each jump time of Z_t , the current mass of the solution $\rho(du, t)$ is shifted by J/N , and a mass $(1/N)\delta_0$ is added to the current value of the solution (emulating the membrane potential reset of LIF neurons, (1.1a)). Although the jump intensity $N\bar{A}_{t^-}$ of Z_t is not a priori bounded, we shall prove in Lemma 2.4 below that a.s. Z

has only a finite number of jumps within each finite time interval such that (1.16) is well-posed as a measure-valued piecewise deterministic Markov process having càdlàg trajectories.

We say that (1.16) is the Markov embedding of the jump process (1.12) (with $\Lambda_t^Z \equiv \Lambda$) and that Z is the jump process associated with the solution ρ .

1.4. Assumptions and main result. The main result of this work concerns the stability of (1.16). We use a notion of stability that is close to that of Brémaud and Massoulié [5] for nonlinear Hawkes processes.

We say that a jump process Z is *stationary* if, for all $\tau > 0$, the time-shifted process $(Z_{t+\tau} - Z_\tau)_{t \geq 0}$ has the same law as $(Z_t - Z_0)_{t \geq 0}$. Then, we say that a solution $\bar{\rho}$ to (1.16) with the \mathcal{M}_+ -valued random initial condition $\bar{\nu}_0$ is stationary if the associated jump process \bar{Z} is stationary.

Since the noise in (1.16) comes from a Poisson random measure, we can naturally construct a *coupling* of two solutions ρ and $\tilde{\rho}$ to (1.16) (for different, possibly random, initial conditions) on the same probability space, using the same underlying Poisson random measure. Writing Z and \tilde{Z} the jump processes associated with ρ and $\tilde{\rho}$, we define T_c the *coupling time* of Z and \tilde{Z} , i.e., the time starting from which Z and \tilde{Z} are identical,

$$(1.17) \quad T_c := \inf \left\{ \tau \geq 0 : (Z_{t+\tau} - Z_\tau)_{t \geq 0} \equiv (\tilde{Z}_{t+\tau} - \tilde{Z}_\tau)_{t \geq 0} \right\},$$

with the usual convention that $T_c = +\infty$ if Z and \tilde{Z} never couple. In other words, T_c is the time starting from which ρ and $\tilde{\rho}$ have the exact same jump times. By abuse of terminology, we will say that T_c is the coupling time of ρ and $\tilde{\rho}$, although it is in fact the coupling time of the associated jump processes. We can now adapt the definition of stability in variation of [5].

Definition 1.1 (stability in variation). *The voltage-structured SPDE (1.16) is stable in variation if there exists a stationary process $\{\bar{\rho}, \bar{\nu}_0\}$ solving (1.16) such that, for all \mathcal{M}_+ -valued random initial conditions $\hat{\nu}_0$, there exists a coupling of $\bar{\rho}$ and ρ (a solution to (1.16) with initial condition $\hat{\nu}_0$) such that the coupling time T_c of $\bar{\rho}$ and ρ is a.s. finite.*

In modeling terms, the stability in variation implies that, for any (random) initial condition $\hat{\nu}_0$, the population spike train \dot{Z}_t relaxes to a unique stationary process in finite time. More specifically, for any initial condition $\hat{\nu}_0 \in \mathcal{M}_+$, if we draw $\bar{\nu}_0$ from a stationary distribution and if we simulate the two corresponding processes with the same Poisson noise, they couple in finite time a.s.. In particular, this implies the uniqueness of the stationary distribution.

To prove that (1.16) is stable in variation, we need the following assumption.

Assumption 1.2. $\mu_t \equiv \mu \in \mathbb{R}$.

This just means that the external drive is time-homogeneous, and it is a natural assumption to make if we want to show relaxation to a stationary process.

The other important assumption concerns the intensity function f .

Assumption 1.3. f is bounded, i.e., $\|f\|_\infty < \infty$, and $\inf_{u \in \mathbb{R}} f(u) =: f_{\min} > 0$.

A simple example of a function satisfying the assumption is the shifted sigmoid. Note that these bounds do not allow taking an exponential function f (or any unbounded function) or having an absolute refractory period (short interval of time following a spike during which

a neuron cannot spike). In other terms, neurons cannot be forced to spike in a finite time interval or be forced to stay silent. Nevertheless, since $\|f\|_\infty$ can be arbitrarily large and f_{\min} can be arbitrarily small, these bounds do not meaningfully alter biological realism.

Finally, to prove that the stationary process exists, we need the following assumption.

Assumption 1.4. f is differentiable, and f' is bounded. Furthermore, there exists a positive constant C such that $|uf'(u)| \leq C$ for all u .

This is a purely technical assumption and is rather innocent since f is anyway bounded.

We can now state our main result.

Theorem 1.5. *Grant Assumptions 1.2–1.4. The voltage-structured SPDE (1.16) is stable in variation.*

The proof is divided into two parts. In the first part, using Meyn–Tweedie theory [37], we show that the solutions of (1.16) satisfy a certain recurrence property which then allows us to prove that the associated jump processes couple, using methods from [5] for nonlinear Hawkes processes. In the second part, we prove the existence of a nontrivial stationary process solving (1.16).

In simulations, the simplified model with fixed Λ , (1.16), has a qualitatively similar behavior (from the stability point of view) to the original model of [48], where Λ_t^Z has an explicit expression in terms of the past Z (see section 4). Hence, the proof of Theorem 1.5 provides an important understanding of the role of the “correction term” $\Lambda_t^Z(1 - \dots)$ in the original model (Figure 1(c)–(f)).

1.5. Plan of the paper. First, in section 2, we prove the well-posedness of the SPDE (1.16) as a measure-valued piecewise deterministic Markov process. The proof of Theorem 1.5 is then presented in section 3.

In section 4, we present a concise derivation of the finite-size integral equation (1.12), and a simple simulation algorithm is provided in section 5. A general simulation algorithm for multiple interacting populations of generalized integrate-and-fire neurons can be found in the appendix.

2. Well-posedness. Although the SPDE (1.16) might look somewhat formal, it can be rigorously formulated in terms of a piecewise deterministic Markov process (PDMP) taking values in the space \mathcal{M}_+ of all positive measures on \mathbb{R} . We endow \mathcal{M}_+ with the topology of weak convergence, which makes \mathcal{M}_+ Polish.

Since Assumptions 1.2 and 1.3 are always imposed in what follows, we will omit their mention. In particular, we will always assume that f is bounded.

For all $\nu \in \mathcal{M}_+$, let us write $(\mathcal{S}(t)\nu)_{t \geq 0} := (\rho(\cdot, t))_{t \geq 0}$ the solution to the transport equation

$$(2.1) \quad \partial_t \rho(du, t) - \partial_u \left(\left(\frac{u - \mu}{\tau_m} \right) \rho(du, t) \right) = -f(u) \rho(du, t) \quad \text{for all } (u, t) \in \mathbb{R} \times \mathbb{R}_+^*,$$

$$\rho_0 = \nu.$$

With the notation of (1.5), take the flow $\Phi_{s,t}^0$ without exterior input, that is, $a \equiv 0$. Then we have the explicit representation

$$(2.2) \quad S(t)\nu = \int_{\mathbb{R}} \delta_{\Phi_{0,t}^0(u)} e^{-\int_0^t f(\Phi_{0,r}^0(u))dr} \nu(du).$$

$(S(t))_{t \in \mathbb{R}_+}$ can be seen as a substochastic \mathcal{C}_0 -semigroup of bounded linear operators on \mathcal{M}_+ . Moreover, we introduce, for any $a \in \mathbb{R}_+$ and any $\nu \in \mathcal{M}_+$, the shifted measure

$$\Delta_a \nu : \mathcal{B}(\mathbb{R}) \ni B \mapsto \nu((B - a)).$$

Putting $\rho_0 = \nu_0$, we can construct a pathwise solution to (1.16) following the procedure:

1. We start from an initial value $\nu_0 \in \mathcal{M}_+$ at time $t = 0$.
2. We consider the counting process

$$Z_t^* = \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N[(S(s)\nu_0)[f] + \Lambda(1 - \|S(s)\nu_0\|)]_+} \pi(ds, dz)$$

together with its first jump time $\tau^1 := \inf\{t \geq 0 : Z_t^* = 1\}$.

3. We put $\rho_t := S(t)\nu_0$ for all $t < \tau^1$.
4. At time τ^1 , we update

$$(2.3) \quad \rho_{\tau^1} := \Delta_{\frac{J}{N}}(S(\tau^1)\nu_0) + \frac{1}{N}\delta_0$$

and we return to step 1, replacing ν_0 by ρ_{τ^1} and time 0 by τ^1 .

Remark 2.1. This construction provides indeed a PDMP taking values in \mathcal{M}_+ ; in between the successive jumps of Z_t only the transport equation acts, and we shall show below that only a finite number of jumps occurs within each finite time interval. We have the explicit representation

$$(2.4a) \quad \rho_t = \int_{\mathbb{R}} \delta_{\Phi_{0,t}^Z(u)} e^{-\int_0^t f(\Phi_{0,r}^Z(u))dr} \nu_0(du) + \int_{[0,t]} \delta_{\Phi_{s,t}^Z(0)} e^{-\int_s^t f(\Phi_{s,r}^Z(0))dr} dZ_s,$$

$$(2.4b) \quad Z_t = \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N[\rho_{t-}[f] + \Lambda(1 - \|\rho_{t-}\|)]_+} \pi(ds, dz).$$

In the above formula, the first term on the right-hand side (RHS) of (2.4a) corresponds to (2.2), except that we have to replace the null exterior input by Z such that, at each jump of Z , the original mass is shifted by J/N , according to the jump term $\Delta_{\frac{J}{N}}$ of (2.3). The second term corresponds to the source term $\frac{1}{N}\delta_0$ which is added at each jump of Z and then transported by $S(t)$.

The above notion of solution is actually equivalent to the notion of a *mild solution* of the SPDE (1.16) driven by Poisson noise (see [24] and [50]). However, since the only underlying noise is Poisson, with finite jump intensity, the notion of a PDMP with values in \mathcal{M}_+ seems to be more natural in this context.

Remark 2.2. Using the representation (2.4a), we can easily make the link between the SPDE (1.16) and the stochastic integral equation (1.12). Taking the definition of \bar{A}_t in (1.16), we have

$$\begin{aligned}\bar{A}_t &= [\rho_t[f] + \Lambda(1 - \|\rho_t\|)]_+ \\ &= \left[\int_{\mathbb{R}_+} f(\Phi_{0,t}^Z(u)) e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \nu_0(du) + \int_{[0,t]} f(\Phi_{s,t}^Z(0)) e^{-\int_s^t f(\Phi_{s,r}^Z(0)) dr} dZ_s \right. \\ &\quad \left. + \Lambda \left(1 - \int_{\mathbb{R}_+} e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \nu_0(du) - \int_{]0,t]} e^{-\int_s^t f(\Phi_{s,r}^Z(0)) dr} dZ_s \right) \right]_+\end{aligned}$$

(using (1.6), (1.8), and (1.10))

$$= \left[H^Z(t) + \int_{[0,t]} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda \left(1 - \tilde{H}_t^Z - \int_{[0,t]} S^Z(t|s) dZ_s \right) \right]_+,$$

showing that (1.16) and (1.12) are equivalent. Also, since

$$\|\rho_t\| = \int_{\mathbb{R}_+} e^{-\int_0^t f(\Phi_{0,r}^Z(u)) dr} \nu_0(du) + \int_{]0,t]} e^{-\int_s^t f(\Phi_{s,r}^Z(0)) dr} dZ_s = \tilde{H}_t^Z + \int_{[0,t]} S^Z(t|s) dZ_s,$$

$\|\rho_t\|$ is equivalent to the neuronal mass M_t defined in (1.14).

In what follows we study *the extended generator* \mathcal{L} of our process in the sense of Meyn and Tweedie [37]. Extended generators are defined by the pointwise convergence and the fact that a fundamental martingale property reminiscent of the Itô formula is verified. For the convenience of the reader we recall its definition: We set $\mathcal{D}(\mathcal{L})$ as the set of all measurable functions $g : \mathcal{M}_+ \rightarrow \mathbb{R}$ for which there exists a measurable function $h : \mathcal{M}_+ \rightarrow \mathbb{R}$ such that $t \mapsto \mathbb{E}_\nu(h(\rho_t))$ is continuous in 0 and such that for all $\nu \in \mathcal{M}_+$, for all $t \geq 0$,

1. $\mathbb{E}_\nu[g(\rho_t)] - g(\nu) = \mathbb{E}_\nu \int_0^t h(\rho_s) ds$;
2. $\mathbb{E}_\nu[\int_0^t |h(\rho_s)| ds] < \infty$.

In this case, we write $\mathcal{L}g := h$.

On a restricted set of test functions, we can explicitly calculate the extended generator \mathcal{L} of the PDMP described above: For all $\varphi \in \mathcal{C}_b^1(\mathbb{R})$ (bounded and continuously differentiable functions), for all $\nu \in \mathcal{M}_+$, and using the abuse of notation $\varphi(\nu) := \nu[\varphi]$, we have that

$$(2.5) \quad \begin{aligned}\mathcal{L}\varphi(\nu) &= - \int_{\mathbb{R}} \frac{u - \mu}{\tau_m} \varphi'(u) \nu(du) - \nu[\varphi f] \\ &\quad + N[\nu[f] + \Lambda(1 - \|\nu\|)]_+ \left(\int_{\mathbb{R}} \varphi \left(u + \frac{J}{N} \right) \nu(du) + \frac{1}{N} \varphi(0) - \nu[\varphi] \right).\end{aligned}$$

We now show that this process is well defined. For that sake, let us define, for all $K > 0$, the exit time

$$(2.6) \quad T^K := \inf\{t \geq 0 : \|\rho_t\| > K\}.$$

Remark 2.3. The T^K are well-defined stopping times since the sets $\{\nu \in \mathcal{M}_+ : \|\nu\| > K\}$ are the preimage of $]K, +\infty[$ by the linear form $\mathbf{1} : \mathcal{M}_+ \rightarrow \mathbb{R}_+$, $\nu \mapsto \nu[\mathbf{1}]$, and we have endowed \mathcal{M}_+ with the topology of weak convergence. For a general treatment of the measurability of hitting times, see [1] and in particular Theorem 2.4 of that article.

Up to time T^K , the overall jump intensity of the process is bounded by $\|f\|_\infty K + \Lambda$ such that the procedure described above is well defined up to the explosion time of the process

$\zeta := \lim_{K \rightarrow +\infty} T^K$. To show that (1.16) is well defined on \mathbb{R}_+ , we need to prove that the PDMP defined above is *nonexplosive* in the sense of [37], i.e., $\zeta = +\infty$ a.s.. We follow the standard “drift condition”-based approach of [37]. Writing $V(\nu) := \|\nu\| = \nu[\mathbf{1}]$, for all $\nu \in \mathcal{M}_+$, we have the following lemma.

Lemma 2.4 (Foster–Lyapunov inequality). *There exist $K^* > 0$, $d > 0$, and $c > 0$ such that*

$$(2.7) \quad \text{for all } \nu \in \mathcal{M}_+, \quad \mathcal{L}V(\nu) \leq d\mathbf{1}_{\|\nu\| \leq K^*} - c(1 + V)(\nu).$$

Proof. Using (2.5) and $V(\nu) = \nu[\mathbf{1}]$, we have $\mathcal{L}V(\nu) = -\nu[f] + [\nu[f] + \Lambda(1 - \|\nu\|)]_+$.

Two cases arise: either $[\nu[f] + \Lambda(1 - \|\nu\|)]_+ > 0$, in which case $\mathcal{L}V(\nu) = \Lambda(1 - \|\nu\|) = \Lambda - \Lambda V(\nu)$, or $[\nu[f] + \Lambda(1 - \|\nu\|)]_+ = 0$, in which case $\mathcal{L}V(\nu) = -\nu[f] \leq -f_{\min} V(\nu)$.

Whence, $\mathcal{L}V(\nu) \leq \Lambda - (f_{\min} \wedge \Lambda)V(\nu)$. We can adapt the constants to obtain (2.7). ■

Arguing as in Theorem 2.1 of [37], Lemma 2.4 guarantees that the PDMP is nonexplosive. Hence, we have proved the well-posedness of (1.16).

Proposition 2.5 (well-posedness). *For all $\nu_0 \in \mathcal{M}_+$, there exists an \mathcal{M}_+ -valued pathwise unique solution to (1.16) on \mathbb{R}_+ .*

3. Stability.

3.1. Coupling. More than nonexplosion, the “drift condition”-based method of [37, 38] allows us to show that the PDMP (1.16) satisfies a certain “recurrence” property.

For all $K > 0$, let us write the hitting time $t_K := \inf\{t \geq 0 : \|\rho_t\| \leq K\}$ and denote by $\mathbb{E}_{\nu_0}[t_K]$ the expected hitting time of the PDMP (1.16) starting in state $\nu_0 \in \mathcal{M}_+$ at time 0.

Lemma 3.1. *Take the constant K^* of Lemma 2.4. For all $\nu_0 \in \mathcal{M}_+$ such that $\|\nu_0\| > K^*$, $\mathbb{E}_{\nu_0}[t_{K^*}] < +\infty$.*

Proof. The proof is standard, but we reproduce it here to highlight the fact that it holds even if the space in which the process evolves is not locally compact.

We use V and the constants of Lemma 2.4. For any $t > 0$ and any $M > K^*$, by Dynkin’s formula (see [37]),

$$\mathbb{E}_{\nu_0}[V(\rho_{t \wedge T^M})] = V(\nu_0) + \mathbb{E}_{\nu_0} \int_0^{t \wedge T^M} \mathcal{L}V(\rho_s) ds \leq V(\nu_0) + dt,$$

where T^M is the exit time defined in (2.6) and where d is given in (2.7).

Since $V(\rho_{t \wedge T^M}) \geq M\mathbf{1}_{T^M \leq t}$, this implies

$$\mathbb{P}_{\nu_0}(T^M \leq t) \leq \frac{V(\nu_0) + dt}{M}.$$

Taking $M \rightarrow \infty$, by monotone convergence, $\mathbb{P}_{\nu_0}(\zeta \leq t) = 0$, which implies nonexplosion.

We now make another use of Dynkin’s formula:

$$\begin{aligned} \mathbb{E}_{\nu_0}[V(\rho_{t \wedge t_{K^*} \wedge T^M})] &= V(\nu_0) + \mathbb{E}_{\nu_0} \int_0^{t \wedge t_{K^*} \wedge T^M} \mathcal{L}V(\rho_s) ds \\ &\leq V(\nu_0) - c\mathbb{E}_{\nu_0} \int_0^{t \wedge t_{K^*} \wedge T^M} (1 + V)(\rho_s) ds. \end{aligned}$$

Whence,

$$\mathbb{E}_{\nu_0} \int_0^{t \wedge t_{K^*} \wedge T^M} (1 + V)(\rho_s) ds \leq \frac{V(\nu_0) - \mathbb{E}_{\nu_0}[V(\rho_{t \wedge t_{K^*} \wedge T^M})]}{c} \leq \frac{V(\nu_0) - K^*}{c}.$$

Taking $t, M \rightarrow \infty$, we get, by monotone convergence,

$$\mathbb{E}_{\nu_0} \int_0^{t_{K^*}} (1 + V)(\rho_s) ds \leq \frac{V(\nu_0) - K^*}{c}.$$

The fact that $\mathbb{E}_{\nu_0}[t_{K^*}] \leq \mathbb{E}_{\nu_0} \int_0^{t_{K^*}} (1 + V)(\rho_s) ds$ concludes the proof. ■

The definition of stability we use involves the notion of coupling of two processes (see subsection 1.4). For ν_0 and $\tilde{\nu}_0 \in \mathcal{M}_+$, a natural way to couple two processes ρ and $\tilde{\rho}$ following (1.16) with initial condition ν_0 and $\tilde{\nu}_0$, respectively, is to construct them with the same Poisson random measure π . With this coupling, the associated jump processes Z and \tilde{Z}_t follow, for all $t \geq 0$,

$$\begin{aligned} Z_t &:= \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N[\rho_s[f] + \Lambda(1 - \|\rho_s\|)]_+} \pi(ds, dz), \\ \tilde{Z}_t &:= \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N[\tilde{\rho}_s[f] + \Lambda(1 - \|\tilde{\rho}_s\|)]_+} \pi(ds, dz). \end{aligned}$$

For all $t \geq 0$, we can now introduce the event

$$E_t := \{Z_{t+s} - Z_t = \tilde{Z}_{t+s} - \tilde{Z}_t \text{ for all } s \geq 0\}$$

on which both jump processes couple after time t . With $(\mathcal{F}_t)_{t \geq 0}$ denoting the natural filtration of the coupled process, we have a lower bound on $\mathbb{P}(E_t | \mathcal{F}_t)$.

Lemma 3.2. *For any $K > 0$, there exists a constant $\varepsilon \in]0, 1[$ such that, for all $t \geq 0$,*

$$(3.1) \quad \mathbb{P}(E_t | \mathcal{F}_t) \geq \varepsilon \mathbb{1}_{\{\|\rho_t\| + \|\tilde{\rho}_t\| \leq K\}}.$$

Proof. We use the shorthand $\bar{A}[\nu] := [\nu[f] + \Lambda(1 - \|\nu\|)]_+$ for all $\nu \in \mathcal{M}_+$. Fix any $t \geq 0$ such that $\|\rho_t\| + \|\tilde{\rho}_t\| \leq K$. Write $\tau_t^1 := \inf\{s > t : (Z_s - Z_t) + (\tilde{Z}_s - \tilde{Z}_t) \geq 1/N\}$ the next jump after time t . Noticing that, for all $t \leq s < \tau_t^1$, $\bar{A}[\rho_s] \vee \bar{A}[\tilde{\rho}_s] \leq \|f\|_\infty K + \Lambda$, we clearly have that $t < \tau_t^1$; that is, there is no accumulation of jumps in finite time.

In what follows, we evaluate the difference $\bar{A}[\rho_s] - \bar{A}[\tilde{\rho}_s]$ for $t \leq s$.

We start by considering the difference $\rho_s[f] - \tilde{\rho}_s[f]$ for all $t \leq s < \tau_t^1$. It is clear that, for all $t \leq s < \tau_t^1$,

$$\rho_s[f] = \int_{\mathbb{R}} \rho_t(du) f(\Phi_{t,s}^0(u)) \exp\left(-\int_t^s f(\Phi_{t,r}^0(u)) dr\right) \leq K \|f\|_\infty e^{-(s-t)f_{\min}},$$

where Φ^0 is the flow of the transport equation (2.1) and where, for the inequality, we use the bounds of f given by Assumption 1.3. Consequently, for all $t \leq s < \tau_t^1$, $|\rho_s[f] - \tilde{\rho}_s[f]| \leq 2K \|f\|_\infty e^{-(s-t)f_{\min}}$. Similarly, $|\|\rho_s\| - \|\tilde{\rho}_s\|| \leq 2K e^{-(s-t)f_{\min}}$.

At the jump time τ_t^1 , two cases arise.

- τ_t^1 is an asynchronous jump, that is, only one of the two processes, say Z , jumps, in which case ρ is shifted to the right by J/N , and a Dirac mass $\frac{1}{N}\delta_0$ is added (see (2.3)). Then, for all $s \in [\tau_t^1, \tau_t^2[$, where $\tau_t^2 := \inf\{s > \tau_t^1 : (Z_s - Z_{\tau_t^1}) + (\tilde{Z}_s - \tilde{Z}_{\tau_t^1}) \geq 1/N\}$, we have

$$\begin{aligned} \rho_s[f] &= \int_{\mathbb{R}} \rho_{\tau_t^1-}(du) f(\Phi_{\tau_t^1, s}^0(u + J/N)) \exp\left(-\int_{\tau_t^1}^s f(\Phi_{\tau_t^1, r}^0(u + J/N)) dr\right) \\ &\quad + \frac{1}{N} f(\Phi_{\tau_t^1, s}^0(0)) \exp\left(-\int_{\tau_t^1}^s f(\Phi_{\tau_t^1, r}^0(0)) dr\right), \end{aligned}$$

while

$$\tilde{\rho}_s[f] = \int_{\mathbb{R}} \tilde{\rho}_{\tau_t^1-}(du) f(\Phi_{\tau_t^1, s}^0(u)) \exp\left(-\int_{\tau_t^1}^s f(\Phi_{\tau_t^1, r}^0(u)) dr\right).$$

As a consequence,

$$\begin{aligned} |\rho_s[f] - \tilde{\rho}_s[f]| &\leq \|f\|_{\infty} e^{-f_{\min}(s-\tau_t^1)} (\|\rho_{\tau_t^1-}\| + \|\tilde{\rho}_{\tau_t^1-}\|) + \frac{\|f\|_{\infty}}{N} e^{-f_{\min}(s-\tau_t^1)} \\ &\leq 2K \|f\|_{\infty} e^{-f_{\min}(s-\tau_t^1)} e^{-f_{\min}(\tau_t^1-t)} + \frac{\|f\|_{\infty}}{N} e^{-f_{\min}(s-\tau_t^1)} \\ &= 2K \|f\|_{\infty} e^{-f_{\min}(s-t)} + \frac{\|f\|_{\infty}}{N} e^{-f_{\min}(s-\tau_t^1)}. \end{aligned}$$

- τ_t^1 is a synchronous jump, in which case we obtain similarly that, for all $s \in [\tau_t^1, \tau_t^2[$,

$$|\rho_s[f] - \tilde{\rho}_s[f]| \leq 2K \|f\|_{\infty} e^{-f_{\min}(s-t)}.$$

Similar estimates hold for $\|\rho_s\| - \|\tilde{\rho}_s\|$. Since the function $x \mapsto x_+$ is Lipschitz with Lipschitz constant 1, this implies that

$$|\bar{A}[\rho_s] - \bar{A}[\tilde{\rho}_s]| \leq |\rho_s(f) - \tilde{\rho}_s(f)| + \Lambda \|\rho_s\| - \|\tilde{\rho}_s\|.$$

Working iteratively with respect to the successive jump times $\tau_t^n, n \geq 2$, and using the above arguments, we deduce that for an appropriate constant $C > 0$, for all $t \leq s$,

$$(3.2) \quad |\bar{A}[\rho_s] - \bar{A}[\tilde{\rho}_s]| \leq C e^{-f_{\min}(s-t)} (\|\rho_t\| + \|\tilde{\rho}_t\|) + C \int_{]t, s]} e^{-f_{\min}(s-r)} dD_r,$$

where $(D_s)_{s \geq t}$ is the process counting the asynchronous jumps of Z and \tilde{Z} . Notice that $(D_s)_{s \geq t}$ has stochastic intensity $(N|\bar{A}[\rho_s] - \bar{A}[\tilde{\rho}_s]|)_{s \geq t}$. In particular, the above upper bound implies that, on $[t, \infty[$, $(D_s)_{s \geq t}$ is stochastically upper bounded by a linear Hawkes process, say $(H_s)_{s \geq t}$, with self-interaction kernel $h(s) = N C e^{-f_{\min}s}$ and with time-inhomogeneous baseline rate $s \mapsto N C e^{-f_{\min}(s-t)} (\|\rho_t\| + \|\tilde{\rho}_t\|)$.

The rest of this proof follows the arguments given in the proof of Theorem 2 of [5, p. 1581] together with their Lemma 1. Here are the details of the argument: As a consequence of the above, we obtain the lower bound

$$\mathbb{P}(E_t | \mathcal{F}_t) = \mathbb{P}(D([t, \infty]) = 0 | \mathcal{F}_t) \geq \mathbb{P}(H([t, \infty]) = 0 | \mathcal{F}_t)$$

since D is stochastically upper bounded by N . But, by the structure of the Hawkes process,

$$\begin{aligned}\mathbb{P}(H([t, \infty]) = 0 | \mathcal{F}_t) &= \exp\left(-\int_t^\infty NC e^{-f_{\min}(s-t)} (\|\rho_t\| + \|\tilde{\rho}_t\|) ds\right) \\ &= \exp(-NC(\|\rho_t\| + \|\tilde{\rho}_t\|)/f_{\min}).\end{aligned}$$

Putting $\varepsilon := \exp(-2NCK/f_{\min})$ concludes the proof. \blacksquare

Theorem 3.3. *Let ρ and $\tilde{\rho}$ be the coupled processes defined above for the initial conditions ν_0 and $\tilde{\nu}_0 \in \mathcal{M}_+$, and write $\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}$ for the associated expectation. Then, the associated counting processes Z and \tilde{Z} couple a.s. in finite time, i.e.,*

$$\mathbb{P}\left(\limsup_{t \rightarrow +\infty} \{(Z_s)_{s \geq t} \neq (\tilde{Z}_s)_{s \geq t}\}\right) = 0.$$

Moreover, the associated coupling time T_c , defined in (1.17) above, admits exponential moments; that is, there exists a positive constant $\bar{\lambda} > 0$ such that, for all initial conditions ν_0 and $\tilde{\nu}_0 \in \mathcal{M}_+$,

$$(3.3) \quad \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_c}] < +\infty.$$

Proof. The beginning of the proof of this theorem is similar to Lemma 5 of [5]. Defining $E_\infty := \cup_{t=0}^\infty E_t$, $(\mathbb{E}[\mathbf{1}_{E_\infty} | \mathcal{F}_t])_{t \geq 0}$ is a uniformly integrable martingale, and we have $\mathbb{E}[\mathbf{1}_{E_\infty} | \mathcal{F}_t] \rightarrow \mathbf{1}_{E_\infty}$ a.s..

However, for all $K > 0$, we have, by Lemma 3.2,

$$\mathbb{E}[\mathbf{1}_{E_\infty} | \mathcal{F}_t] = \mathbb{P}(E_\infty | \mathcal{F}_t) \geq \mathbb{P}(E_t | \mathcal{F}_t) \geq \varepsilon \mathbf{1}_{\{\|\rho_t\| + \|\tilde{\rho}_t\| \leq K\}} \quad \text{for all } t \geq 0.$$

We can easily adapt the proofs of Lemmas 2.4 and 3.1 to discrete times $n \in \mathbb{N}$ and show that there exists $K^* > 0$ such that $\mathbb{P}(\limsup_{n \rightarrow \infty} \{\|\rho_n\| + \|\tilde{\rho}_n\| \leq K^*\}) = 1$. Hence, $\mathbf{1}_{E_\infty} \geq \varepsilon$ a.s., which in turn implies that $\mathbb{P}(E_\infty) = 1$. Since the event E_∞ is the complement of the event $\limsup_{t \rightarrow +\infty} \{(Z_s)_{s \geq t} \neq (\tilde{Z}_s)_{s \geq t}\}$, this concludes the first part of the proof.

The proof of the existence of exponential moments for the coupling time, which is rather classical, is postponed to Appendix B. \blacksquare

3.2. Existence of the stationary process. We construct a stationary process Z following the lines of [5]. The main idea is to show that a construction on the whole line \mathbb{R} , that is, starting from $t = -\infty$, is feasible. If it is so, then intuitively the constructed process is automatically stationary. More precisely, we have the following theorem.

Theorem 3.4. *In addition to the usual assumptions, grant Assumption 1.4. Then there exists a unique stationary process Z solving (1.16).*

Proof. We only need to show that a stationary process Z exists; uniqueness follows then from the coupling property stated in Theorem 3.3 above.

We construct a sequence $Z^{[n]}$ of jump processes in the following way: For any fixed $n \geq 1$, let $(\rho^{[n]}, \tilde{Z}^{[n]})$ be the solution of (1.16) defined on $[-n, \infty[$, starting at time $-n$ from the initial condition $\rho_{-n}^{[n]} = \frac{1}{N}\delta_0$, with

$$\tilde{Z}_t^{[n]} = \frac{1}{N} \int_{[-n,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N \bar{A}_s^{[n]}} \pi(ds, dz) \quad \text{with } \bar{A}_t^{[n]} := \left[\rho_t^{[n]}[f] + \Lambda(1 - \|\rho_t^{[n]}\|) \right]_+ \quad \text{for all } t \geq -n$$

and $\tilde{Z}_t^{[n]} \equiv 0$ for all $t \leq -n$.

In order to obtain a standardized sequence of processes, we put

$$Z_t^{[n]} := \tilde{Z}_t^{[n]} - \tilde{Z}_0^{[n]}.$$

In this way, for all n , $Z^{[n]}$ is an element of the Skorokhod space $D(\mathbb{R}, \mathbb{R})$ with $Z_0^{[n]} = 0$. We shall also consider the associated sequence of processes

$$X_s^{[n]} := \rho_s^{[n]}[f] - \Lambda \|\rho_s^{[n]}\|$$

such that the stochastic intensity of $NZ_s^{[n]}$ is $\lambda^{[n]}(s) := N[X_s^{[n]} + \Lambda]_+$.

Step 1. We first show that the family $(Z^{[n]}, X^{[n]})_{n \geq 1}$ is tight in the Skorokhod space $D(\mathbb{R}, \mathbb{R}^2)$. To do so, we use the criterion of Aldous; see Theorem VI.4.5 of [34]. It is sufficient to prove that

(a) for all $T > 0$, all $\varepsilon > 0$,

$$\lim_{\sigma \downarrow 0} \limsup_{n \rightarrow \infty} \sup_{(\tau, \tau') \in P_{\sigma, T}} \mathbb{P}(|Z_{\tau'}^{[n]} - Z_{\tau}^{[n]}| + |X_{\tau'}^{[n]} - X_{\tau}^{[n]}| > \varepsilon) = 0,$$

where $P_{\sigma, T}$ is the set of all pairs of stopping times (τ, τ') such that $-T \leq \tau \leq \tau' \leq \tau + \sigma \leq T$ a.s.;

(b) for all $T > 0$, $\lim_{K \uparrow \infty} \sup_n \mathbb{P}(\sup_{-T \leq s \leq T} (|Z_s^{[n]}| + X_s^{[n]}) \geq K) = 0$.

To check (a), observe that

$$\mathbb{E}[|Z_{\tau'}^{[n]} - Z_{\tau}^{[n]}|] \leq \frac{1}{N} \mathbb{E} \int_{\tau}^{\tau+\sigma} \lambda^{[n]}(s) ds \leq \frac{1}{N} \sqrt{2T\sigma} \sqrt{\sup_{-T \leq s \leq T} \mathbb{E}[(\lambda^{[n]}(s))^2]}.$$

Note that $(\lambda^{[n]}(s))^2 \leq C \|\rho_s^{[n]}\|^2 + C'$ for some constants C, C' independent of n . By similar arguments as in the proof of Lemma 2.4, we have that $W(\nu) := \|\nu\|^2$ satisfies

$$(3.4) \quad \text{for all } \nu \in \mathcal{M}_+, \quad \mathcal{L}W(\nu) \leq \alpha - \beta W(\nu)$$

for suitable constants $\alpha, \beta > 0$.³ Then, it is straightforward to show that (3.4) implies

$$\sup_n \sup_{-T \leq s \leq T} \mathbb{E}[W(\rho_s^{[n]})] < \infty,$$

implying (a) for the sequence of processes $Z^{[n]}$.

We now turn to the study of the sequence of processes $X^{[n]}$. We show how to control $\rho^{[n]}[f]$; the control of $\|\rho^{[n]}\|$ is obtained similarly by taking $f \equiv 1$. We fix stopping times $\tau < \tau'$ and consider the increment $\rho_{\tau'}^{[n]}[f] - \rho_{\tau}^{[n]}[f]$ on the event $Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} = 0$. On this event,

³See Appendix C.

$$\rho_{\tau'}^{[n]}[f] - \rho_{\tau}^{[n]}[f] = \int_{\mathbb{R}} \rho_{\tau}^{[n]}(du) \left(f(\Phi_{\tau,\tau'}^0(u)) \exp\left(-\int_{\tau}^{\tau'} f(\Phi_{\tau,s}^0(u)) ds\right) - f(u) \right).$$

Then,

$$\begin{aligned} & \left| f(\Phi_{\tau,\tau'}^0(u)) \exp\left(-\int_{\tau}^{\tau'} f(\Phi_{\tau,s}^0(u)) ds\right) - f(u) \right| \\ & \leq |f(\Phi_{\tau,\tau'}^0(u)) - f(u)| + \|f\|_{\infty} \left| \exp\left(-\int_{\tau}^{\tau'} f(\Phi_{\tau,s}^0(u)) ds\right) - 1 \right| \\ & \leq |f(\Phi_{\tau,\tau'}^0(u)) - f(u)| + \|f\|_{\infty} (1 - e^{-\sigma\|f\|_{\infty}}). \end{aligned}$$

Using that $|\Phi_{\tau,\tau'}^0(u) - u| \leq (1 - e^{-\sigma/\tau_m})|u - \mu|$, Taylor's formula implies

$$|f(\Phi_{\tau,\tau'}^0(u)) - f(u)| \leq |f'(\xi)|(1 - e^{-\sigma/\tau_m})|u - \mu|,$$

where $\xi \in [u, \Phi_{\tau,\tau'}^0(u)] \cup [\Phi_{\tau,\tau'}^0(u), u]$.

We first produce an upper bound in the case where $u \geq \mu$ and $\mu \geq 0$. Since $|f'(u)| \leq C/u$ by Assumption 1.4 and since $\xi \geq \Phi_{\tau,\tau'}^0(u)$, we have

$$(3.5) \quad |f(\Phi_{\tau,\tau'}^0(u)) - f(u)| \leq C(1 - e^{-\sigma/\tau_m})C_{\sigma},$$

where

$$C_{\sigma} := \sup_{u \geq \mu} \frac{1}{ue^{-\sigma/\tau_m} + \mu(1 - e^{-\sigma/\tau_m})}(u - \mu).$$

Moreover, it is clear that, for any $\sigma_0 > 0$, $\sup_{\sigma \leq \sigma_0} C_{\sigma} < \infty$.

If $\mu \leq 0$ and $\mu < u \leq 0$, we use that $f'(\xi)$ is bounded on $[\mu, 0]$ to obtain (3.5). The case $u < \mu$ is treated analogously.

As a consequence, we get the global upper bound (on the event $Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} = 0$):

$$\left| \rho_{\tau'}^{[n]}[f] - \rho_{\tau}^{[n]}[f] \right| \leq C(1 - e^{-\kappa\sigma})\|\rho_{\tau}^{[n]}\|, \quad \text{with } \kappa := \|f\|_{\infty} \vee 1/\tau_m.$$

We conclude the control of $\rho_{\tau}^{[n]}[f]$, on the event $Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} = 0$, using the Foster–Lyapunov inequality (Lemma 2.4)

$$\mathbb{E}\|\rho_{\tau}^{[n]}\| \leq \mathbb{E}\|\rho_0^{[n]}\| + dT, \quad \text{with } d \text{ from (2.7),}$$

and the fact that $\sup_n \mathbb{E}\|\rho_0^{[n]}\| < \infty$.

To deal with the event $Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} > 0$, observe that

$$\mathbb{E} \left[\left| \rho_{\tau'}^{[n]}[f] - \rho_{\tau}^{[n]}[f] \right| \mathbb{1}_{\{Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} > 0\}} \right] \leq \|f\|_{\infty} \mathbb{E} \left[\left(\|\rho_{\tau'}^{[n]}\| + \|\rho_{\tau}^{[n]}\| \right) \mathbb{1}_{\{Z_{\tau'}^{[n]} - Z_{\tau}^{[n]} > 0\}} \right].$$

Moreover, for any stopping time τ taking values in between $-T$ and T , we have

$$\mathbb{E} \left[\|\rho_\tau^{[n]}\| \mathbb{1}_{\{Z_\tau^{[n]} - Z_\tau^{[n]} > 0\}} \right] \leq \sqrt{\mathbb{E}\|\rho_\tau^{[n]}\|^2} \sqrt{\mathbb{P}(Z_\tau^{[n]} - Z_\tau^{[n]} > 0)}.$$

Using similar arguments as above but now with the Lyapunov function $W(\nu) = \|\nu\|^2$, we obtain

$$\sup_n \mathbb{E}\|\rho_\tau^{[n]}\|^2 < \infty.$$

Finally, using the already established control over $Z^{[n]}$, we get that

$$\limsup_{\sigma \downarrow 0} \sup_n \mathbb{P}(Z_\tau^{[n]} - Z_\tau^{[n]} > 0) = 0,$$

which concludes the proof of (a).

(b) Let us first observe that $\sup_{-T \leq s \leq T} |Z_s^{[n]}| \leq Z_T^{[n]} - Z_{-T}^{[n]}$, and

$$\sup_{-T \leq s \leq T} |X_s^{[n]}| \leq C \sup_{-T \leq s \leq T} \|\rho_s^{[n]}\| \leq C \left(\|\rho_{-T}^{[n]}\| + Z_T^{[n]} - Z_{-T}^{[n]} \right).$$

We can then conclude using the moment estimates established above.

Step 2. By tightness we can extract a subsequence n_k such that $(Z^{[n_k]}, X^{[n_k]})$ converges, in $D(\mathbb{R}, \mathbb{R}^2)$, to a limit process that we shall denote (Z, X) . We now show that Z is necessarily stationary. For that sake, take a test function $\varphi : D(\mathbb{R}, \mathbb{R}) \rightarrow \mathbb{R}_+$ which is continuous (with respect to the Skorokhod topology) and bounded and which does only depend on $Z \in D(\mathbb{R}, \mathbb{R})$ within a finite time interval $[a, b] \subset \mathbb{R}_+$. We have to show that, for every $t \geq 0$,

$$\mathbb{E}[\varphi(Z)] = \mathbb{E}[\varphi(\theta_t Z)],$$

where $\theta_t Z$ is the shifted counting process defined by $(\theta_t Z)_s = Z_{t+s} - Z_t$ for all $s \geq 0$.

By weak convergence, we have that

$$\mathbb{E}[\varphi(Z)] - \mathbb{E}[\varphi(\theta_t Z)] = \lim_{k \rightarrow \infty} \mathbb{E}[\varphi(Z^{[n_k]})] - \mathbb{E}[\varphi(\theta_t Z^{[n_k]})].$$

Now we use the coupling property proven in Theorem 3.3 above. For any fixed k and t we realize $Z^{[n_k]}$ and $\theta_t Z^{[n_k]}$ according to the construction used in the proof of Theorem 3.3.

This means the following: Let $\pi(dt, dz)$ be a Poisson random measure on $\mathbb{R} \times \mathbb{R}_+$ which has intensity $dt dz$ on $\mathbb{R} \times \mathbb{R}_+$. We construct $Z^{[n_k]}$ using the atoms of π within $[-n_k, \infty[\times \mathbb{R}_+$, starting from $\frac{1}{N} \delta_0$ at time $-n_k$. Then we choose, independently of π , a random measure $\tilde{\rho}_{-n_k} \sim \mathcal{L}(\rho_{-n_k+t}^{[n_k]})$. Note that this law does not depend on n_k ; it only depends on t . Finally, we realize the process $\theta_t Z^{[n_k]}$ letting it start at time $-n_k$ from the initial condition $\tilde{\rho}_{-n_k}$ and using the same underlying Poisson random measure π . Let $T_{coup}^{n_k}$ be the finite coupling time of the two processes. Notice that, once again, $\mathcal{L}(T_{coup}^{n_k})$ does not depend on n_k .

Using this coupling, we obtain

$$\left| \mathbb{E}[\varphi(Z^{[n_k]})] - \mathbb{E}[\varphi(\theta_t Z^{[n_k]})] \right| \leq \|\varphi\|_\infty \mathbb{P}(T_{coup}^{n_k} \geq n_k + a) = \|\varphi\|_\infty \mathbb{P}(T_{coup} > n_k + a) \rightarrow 0$$

as $n_k \rightarrow \infty$, implying that $\mathbb{E}[\varphi(Z)] - \mathbb{E}[\varphi(\theta_t Z)] = 0$. Since the test functions φ form a separating-class (see Theorem 1.2 in [3, p. 8]), we have that Z and $\theta_t Z$ have the same law, whence stationarity.

Step 3. Now, we verify that the process Z , where Z is taken from the stationary limit process (Z, X) constructed above, is a jump process where jumps of size $1/N$ occur with intensity $\lambda_t := N[X_{t^-} + \Lambda]_+$.

To ease the notation, in what follows, we rename the subsequence n_k by n . Using the Skorokhod representation theorem, we may assume that the above weak convergence is almost sure for a particular realization of the couples $(Z^{[n]}, X^{[n]})$. Hence, we know that, a.s., $(Z^{[n]}, X^{[n]}) \rightarrow (Z, X)$ and $\lambda^{[n]} \rightarrow \lambda$. Moreover, let \bar{Z} be the process having intensity λ for the same underlying Poisson random measure as (the realization of) Z . Then, by Fatou's lemma, for any $t \geq 0$,

$$\mathbb{E}|Z_t - \bar{Z}_t| \leq \liminf_n \mathbb{E}|Z_t^{[n]} - \bar{Z}_t| \leq \frac{1}{N} \liminf_n \mathbb{E} \int_0^t |\lambda^{[n]}(s) - \lambda(s)| ds = 0,$$

where we used the uniform integrability of the $\lambda^{[n]}$, namely, that $\sup_n \sup_{s \in [0, t]} \mathbb{E}[\lambda_s^{[n]}] < \infty$. The same argument shows that $\mathbb{E}|Z_t - \bar{Z}_t| = 0$ for all $t \leq 0$. Hence $Z = \bar{Z}$ a.s., implying that Z has the limit intensity λ .

Step 4. Finally, we show that the limit process Z has the right dynamic; i.e., its intensity λ_t is equal to $\bar{\lambda}_t$ given by

$$(3.6) \quad \bar{\lambda}_t := N \left[\sum_{k: T_k < t} \frac{1}{N} \exp \left(- \int_{T_k}^t f(\Phi_{T_k, s}^Z(0)) ds \right) (f(\Phi_{T_k, t}^Z(0)) - \Lambda) + \Lambda \right]_+ \quad \text{for all } t \in \mathbb{R},$$

where T_k denotes the jump times of Z and Φ^Z is given in (1.11).

The goal of this step is to show that $\lambda \equiv \bar{\lambda}$. Fix some time $t \geq 0$ and a truncation level $K > 1$. Since, a.s., Z does not jump at time t or time $-K$ for all $K \geq 1$, Proposition VI.2.2.1 of [34] implies that $Z_t^{[n]} - Z_{-K}^{[n]} \rightarrow Z_t - Z_{-K}$. Therefore, we may choose n_K to be such that $Z_t^{[n]} - Z_{-K}^{[n]} = Z_t - Z_{-K}$ for all $n \geq n_K$. By the continuity properties of the Skorokhod topology, as $n \rightarrow \infty$, we have that $T_k^{[n]} \rightarrow T_k$ as $n \rightarrow \infty$ for all $Z_{-K} \leq k \leq Z_t$ (Proposition VI.2.2.1 of [34]). Hence,

$$\begin{aligned} & \sum_{k: -K \leq T_k^{[n]} < t} \frac{1}{N} \exp \left(- \int_{T_k^{[n]}}^t f \left(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0) \right) ds \right) \left(f \left(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0) \right) - \Lambda \right) \rightarrow \\ & \sum_{k: -K \leq T_k < t} \frac{1}{N} \exp \left(- \int_{T_k}^t f \left(\Phi_{T_k, s}^Z(0) \right) ds \right) \left(f \left(\Phi_{T_k, t}^Z(0) \right) - \Lambda \right). \end{aligned}$$

Notice that the expression on the left-hand side corresponds to the terms contributing to $X_{t^-}^{[n]}$, issued by jumps happening after time $-K$. Since we know that $X_t^{[n]}$ converges to X_t for almost all t , this implies that, for all K ,

$$\begin{aligned}
 X_{t^-} &= \sum_{k: -K \leq T_k < t} \frac{1}{N} \exp\left(-\int_{T_k}^t f(\Phi_{T_k, s}^Z(0)) ds\right) (f(\Phi_{T_k, t}^Z(0)) - \Lambda) \\
 &\quad + \lim_{n \rightarrow \infty} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) (f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)) - \Lambda),
 \end{aligned}$$

where this last limit is necessarily finite. Letting $K \rightarrow \infty$ we deduce that

$$\begin{aligned}
 X_{t^-} &= \sum_{k: T_k < t} \frac{1}{N} \exp\left(-\int_{T_k}^t f(\Phi_{T_k, s}^Z(0)) ds\right) (f(\Phi_{T_k, t}^Z(0)) - \Lambda) \\
 &\quad + \lim_{K \rightarrow \infty} \lim_{n \rightarrow \infty} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) (f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)) - \Lambda).
 \end{aligned}$$

Next, we shall prove that

$$(3.7) \quad \lim_{K \rightarrow \infty} \lim_{n \rightarrow \infty} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)) = 0 \quad \text{a.s.},$$

a similar argument proving that

$$\lim_{K \rightarrow \infty} \lim_{n \rightarrow \infty} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) \Lambda = 0 \quad \text{a.s.},$$

to obtain that, indeed, $\lambda_t = N[X_{t^-} + \Lambda]_+ = \bar{\lambda}_t$.

Let us now prove (3.7). Using Fatou's lemma, we get

$$\begin{aligned}
 (3.8) \quad &\mathbb{E} \lim_{K \rightarrow \infty} \lim_{n \rightarrow \infty} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)) \\
 &\leq \liminf_{K \rightarrow \infty} \liminf_{n \rightarrow \infty} \mathbb{E} \sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)).
 \end{aligned}$$

Using the same arguments as those leading to (3.2), we have

$$\sum_{k: T_k^{[n]} < -K} \frac{1}{N} \exp\left(-\int_{T_k^{[n]}}^t f(\Phi_{T_k^{[n]}, s}^{Z^{[n]}}(0)) ds\right) f(\Phi_{T_k^{[n]}, t}^{Z^{[n]}}(0)) \leq \|f\|_\infty \|\rho_{-K}^{[n]}\| e^{-\min(f)(t+K)}.$$

Therefore, the RHS of (3.8) is upper bounded by

$$\|f\|_\infty \liminf_{K \rightarrow \infty} \liminf_{n \rightarrow \infty} \mathbb{E}(\|\rho_{-K}^{[n]}\|) e^{-\min(f)(t+K)} = 0$$

since $\sup_n \sup_K \mathbb{E}(\|\rho_{-K}^{[n]}\|) < \infty$. This concludes the proof. ■

Corollary 3.5. *Under the same assumptions as in Theorem 3.4, there exists a unique stationary process $\{\rho, \hat{v}_0\}$ solving (1.16).*

Proof. Taking the process $Z \in D(\mathbb{R}, \mathbb{R})$ constructed in Theorem 3.4 and using the same notations as in (3.6), the stationary process $\{\bar{\rho}, \bar{\nu}_0\}$ corresponding to Z is simply

$$\bar{\nu}_0 = \sum_{T_k \leq 0} \exp\left(-\int_{T_k}^0 f(\Phi_{T_k, s}^Z(0)) ds\right) \frac{1}{N} \delta_{\Phi_{T_k, 0}^Z(0)},$$

and for all $t \geq 0$,

$$\bar{\rho}_t = \sum_{T_k \leq t} \exp\left(-\int_{T_k}^t f(\Phi_{T_k, s}^Z(0)) ds\right) \frac{1}{N} \delta_{\Phi_{T_k, t}^Z(0)}. \quad \blacksquare$$

4. Background on the finite-size population equation. In this section, we first present a concise derivation of the stochastic integral equation (1.12), which synthesizes the arguments of the original derivation [48]. Following the integral equation convention [29, 30] and as in [48], we formally put the initial condition at time $-\infty$, and (1.12) reads as follows: for all $t \in \mathbb{R}$,

$$(4.1a) \quad dZ_t = \frac{1}{N} \pi(dt, [0, N\bar{A}_t^-]),$$

$$(4.1b) \quad \bar{A}_t = \left[\int_{]-\infty, t]} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda_t^Z \left(1 - \int_{]-\infty, t]} S^Z(t|s) dZ_s \right) \right]_+,$$

where π is a Poisson random measure on $\mathbb{R} \times \mathbb{R}_+$ having Lebesgue intensity and λ^Z and S^Z are defined by (1.6) with replacement (1.11). Furthermore, the time-dependent modulating factor Λ_t^Z is given by

$$(4.1c) \quad \Lambda_t^Z = \frac{\int_{]-\infty, t]} \lambda^Z(t|s) \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}{\int_{]-\infty, t]} \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}.$$

Note that, in the original formulation of the model (see equations (11) and (12) in [48]), the expression for the time-dependent modulating factor Λ_t^Z involved a “variance function” v . Integrating equation (12) in [48] gives $v(t|s) = \{1 - S^Z(t|s)\} S^Z(t|s) \dot{Z}_s$. As a consequence, equation (11) in [48] can be written as (4.1c), eliminating v .

To understand the reasoning behind the derivation of (4.1), one needs to keep in mind that the goal is to obtain an intensity-based and history-dependent point process (i.e., that only depends on the past Z) approximating the empirical population activity of the microscopic model (1.1).

Let $(Z_s)_{s < t}$ denote the past population activity. In terms of $(Z_s)_{s < t}$, the stochastic intensity of the empirical population activity (of the microscopic model), at time t , can be expressed as

$$(4.2) \quad N \int_{]-\infty, t[} \lambda^Z(t|s) \mathfrak{S}^Z(t|s) dZ_s,$$

where, for all past spike times s , $\mathfrak{S}^Z(t|s)$ denotes the “microscopic survival processes”: if there was a spike at time s , $\mathfrak{S}^Z(t|s) = 1$ if the neuron which has fired at time s has not fired a spike in

$]s, t[$, and $\mathfrak{G}^Z(t|s) = 0$ if it has. We need to approximate (4.2) by an expression which does not involve the microscopic $\mathfrak{G}^Z(t|s)$ but only the past Z . Writing $\Delta\mathfrak{G}^Z(t|s) := \mathfrak{G}^Z(t|s) - S^Z(t|s)$, we have

$$(4.3) \quad \int_{]-\infty, t[} \lambda^Z(t|s) \mathfrak{G}^Z(t|s) dZ_s = \int_{]-\infty, t[} \lambda^Z(t|s) S^Z(t|s) dZ_s + \int_{]-\infty, t[} \lambda^Z(t|s) \Delta\mathfrak{G}^Z(t|s) dZ_s.$$

Note that, since the number of neurons N is strictly preserved (in the microscopic model),

$$(4.4) \quad \int_{]-\infty, t[} \Delta\mathfrak{G}^Z(t|s) dZ_s = 1 - \int_{]-\infty, t[} S^Z(t|s) dZ_s.$$

To replace the microscopic $\Delta\mathfrak{G}^Z(t|s)$ on the RHS of (4.3), we introduce a family of conditionally independent (conditioned on Z) survival processes $\{(\widehat{\mathfrak{G}}^Z(t'|s))_{t' \geq s}\}_s$ —one for each past spike time $s < t$ —defined by

$$\widehat{\mathfrak{G}}^Z(t'|s) = \begin{cases} 1 & \text{if } t' < T_s, \\ 0 & \text{if } t' \geq T_s, \end{cases}$$

where $\{T_s\}_{\text{past spike time } s < t}$ is accessory random variables satisfying the following conditions: (i) the variables $\{T_s\}_{\text{past spike time } s < t}$ are conditionally independent given Z and (ii), for all past spike time $s < t$, T_s takes values in $[s, +\infty[$ and satisfies $\mathbb{P}(T_s > t' | Z) = S^Z(t'|s)$ for all $t' \in [s, t[$ (T_s can therefore be interpreted as a “death” time given by the survival S^Z). Importantly, the processes $\{(\widehat{\mathfrak{G}}^Z(t'|s))_{t' \in [s, t[}\}_s$ are close but not exactly equivalent to the microscopic $\{(\mathfrak{G}^Z(t'|s))_{t' \in [s, t[}\}_s$; e.g., the conservation equation (4.4) does not hold for the processes $\Delta\widehat{\mathfrak{G}}^Z(t|s) := \widehat{\mathfrak{G}}^Z(t|s) - S^Z(t|s)$. However, the conditional independence of the processes $\{(\widehat{\mathfrak{G}}^Z(t'|s))_{t' \in [s, t[}\}_s$ will allow us to close the system of equations (see below), and this is the reason why they are introduced.

We make the approximation

$$(4.5) \quad \int_{]-\infty, t[} \lambda^Z(t|s) \Delta\mathfrak{G}^Z(t|s) dZ_s \approx \Lambda_t^Z \int_{]-\infty, t[} \Delta\widehat{\mathfrak{G}}^Z(t|s) dZ_s,$$

where

$$(4.6) \quad \begin{aligned} \Lambda_t^Z &:= \arg \min_{\Lambda} \mathbb{E} \left[\left(\int_{]-\infty, t[} (\lambda^Z(t|s) - \Lambda) \Delta\widehat{\mathfrak{G}}^Z(t|s) dZ_s \right)^2 \middle| Z \right] \\ &= \arg \min_{\Lambda} \mathbb{E} \left[\int_{]-\infty, t[} (\lambda^Z(t|s) - \Lambda)^2 \Delta\widehat{\mathfrak{G}}^Z(t|s)^2 dZ_s \middle| Z \right] \\ &= \arg \min_{\Lambda} \int_{]-\infty, t[} (\lambda^Z(t|s) - \Lambda)^2 \mathbb{E} \left[\Delta\widehat{\mathfrak{G}}^Z(t|s)^2 \middle| Z \right] dZ_s. \end{aligned}$$

Note that, in the definition of Λ_t^Z , (4.6), we have used $\widehat{\mathfrak{G}}^Z(t|s)$ instead of the microscopic $\mathfrak{G}^Z(t|s)$, which would have defined the minimum conditional mean squared error of the

approximation (4.5). While this replacement cannot be rigorously justified, it allows us to approximate the conditional mean squared error and, in particular, the position of its minimum. Since $\mathbb{E}[\Delta \widehat{\mathfrak{S}}^Z(t|s)^2 | Z] = \{1 - S^Z(t|s)\}S^Z(t|s)$ and taking the derivative with respect to Λ in (4.6), we get

$$\Lambda_t^Z = \frac{\int_{]-\infty, t[} \lambda^Z(t|s) \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}{\int_{]-\infty, t[} \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}.$$

We have obtained an approximation of the stochastic intensity (4.2) which only involves the past Z :

$$\begin{aligned} & N \int_{]-\infty, t[} \lambda^Z(t|s) \mathfrak{S}^Z(t|s) dZ_s \\ & \approx N \left[\int_{]-\infty, t[} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda_t^Z \left(1 - \int_{]-\infty, t[} S^Z(t|s) dZ_s \right) \right]_+. \end{aligned}$$

(Taking the positive part on the RHS simply guarantees that the intensity is nonnegative.)

In practice, we can deal with the ill-defined initial condition at time $-\infty$ by assuming that $Z_t = 0$ for all $t < 0$ and $Z_0 = 1$ (all neurons spike at time 0). Consistently, we also put $\Lambda_0^Z = 0$. Then, the model (4.1) can be written as follows: For all $t > 0$,

$$(4.7a) \quad Z_t = 1 + \frac{1}{N} \int_{]0, t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N \bar{A}_s} \pi(ds, dz),$$

$$(4.7b) \quad \bar{A}_t = \left[\int_{]0, t[} \lambda^Z(t|s) S^Z(t|s) dZ_s + \Lambda_t^Z \left(1 - \int_{]0, t[} S^Z(t|s) dZ_s \right) \right]_+,$$

$$(4.7c) \quad \Lambda_t^Z = \frac{\int_{]0, t[} \lambda^Z(t|s) \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}{\int_{]0, t[} \{1 - S^Z(t|s)\} S^Z(t|s) dZ_s}$$

with the initial condition $Z_0 = 1$ and $\Lambda_0^Z = 0$. Assuming that the original model (4.1) has the same stability property as the simpler model (1.16), this practical choice of initial condition is acceptable as it will be “forgotten” after some time.

5. Simulation algorithm. Here, we present a simple simulation algorithm for (4.7). The algorithm presented below can be easily adapted to the more realistic case of multiple interacting populations for generalized integrate-and-fire neurons [48], as we show in Appendix A.

To ease the notation, here, we drop all the superscripts Z . We can rewrite (1.5) and (1.6) as the solution of an SDE: for any $s > 0$,

$$(5.1a) \quad \frac{dS(t|s)}{dt} = -\lambda(t|s)S(t|s),$$

$$(5.1b) \quad du(t|s) = \frac{\mu t - u(t|s)}{\tau_m} dt + J dZ_t$$

with $\lambda(t|s) = f(u(t|s))$ and initial conditions $S(s|s) = 1$ and $u(s|s) = 0$.

Finite history. For all $t \geq 0$, let us define the free membrane potential $h(t)$ as the solution of

$$(5.2) \quad dh_t = \frac{\mu_t - h_t}{\tau_m} dt + J dZ_t$$

with initial condition $h_0 = 0$ (cf. (5.1b)). It is clear that, for fixed $s > 0$, $|u(t|s) - h_t| \rightarrow 0$ when $t \rightarrow \infty$. In practice, there exists a sufficiently large time $T \gg \tau_m$ such that, for $t - s > T$, the initial condition for (5.1b) will be forgotten, and the membrane potential $u(t|s)$ with last reset time s can be well approximated by the free membrane potential h_t . We call T the history length. Associated with the free membrane potential is the free hazard rate defined as $\lambda_{free}(t) := f(h_t)$. The free hazard rate can be interpreted as the firing intensity of neurons that have fully recovered from refractoriness because the last spike of those neurons happened before time $t - T$ and thus has been approximately forgotten. For the numerical implementation, it is useful to consider the slightly modified model, in which we use the above approximation, i.e., where $\lambda(t|s)$ is set to $\lambda_{free}(t)$ if $t - s > T$. For the sake of notational simplicity, we will use the same symbols for this approximate model. For $0 < t < T$, there is no difference between the approximate and the original model. Hence, the solution of the approximate model is governed by (4.7) and (5.1). However, for $t > T$, the integrals in (4.7b) and (4.7c) do not need to be evaluated over the whole history from 0 to t but reduce to integrals over $]t - T, t[$:

$$(5.3a) \quad \bar{A}_t = \left[\int_{]t-T,t[} \lambda(t|s) S(t|s) dZ_s + \lambda_{free}(t) x_t + \Lambda_t \left(1 - \int_{]t-T,t[} S(t|s) dZ_s - x_t \right) \right]_+,$$

$$(5.3b) \quad \Lambda_t = \frac{\int_{]t-T,t[} \lambda(t|s) \{1 - S(t|s)\} S(t|s) dZ_s + \lambda_{free}(t) z_t}{\int_{]t-T,t[} \{1 - S(t|s)\} S(t|s) dZ_s + z_t}.$$

These expressions depend on the additional variables $x_t := \int_{[0,t-T]} S(t|s) dZ_s$ and $z_t := \int_{[0,t-T]} \{1 - S(t|s)\} S(t|s) dZ_s$ that solve the following SDEs [48]:

$$(5.4a) \quad dx_t = -\lambda_{free}(t) x_t dt + S(t|t - T) dZ_{t-T}, \quad x_T = 0,$$

$$(5.4b) \quad dz_t = -2\lambda_{free}(t) z_t dt + \{1 - S(t|t - T)\} S(t|t - T) dZ_{t-T}, \quad z_T = 0.$$

Time discretization. The model with finite history length (5.3) with the SDEs (5.1) and (5.4) suggests a straightforward update scheme in discrete time. To this end, we consider an equally spaced partition of the time-axis with mesh Δt and time points $t_{\hat{t}} = \hat{t} \Delta t$, $\hat{t} = 0, 1, 2, \dots$. Furthermore, we partition the co-moving history frame $]t - T, t[$ in discrete time points $s_{r,\hat{t}} = (\hat{t} - \mathcal{T} + r) \Delta t$, $r = 1, \dots, \mathcal{T}$, with $\mathcal{T} = T/\Delta t$. On the discrete time points, we define the following quantities:

$$\begin{aligned} n_{r,\hat{t}} &:= Z_{s_{r,\hat{t}}+\Delta t} - Z_{s_{r,\hat{t}}}, & S_{r,\hat{t}} &:= S(\hat{t} \Delta t | s_{r,\hat{t}}), & u_{r,\hat{t}} &:= u(\hat{t} \Delta t | s_{r,\hat{t}}), \\ P_{r,\hat{t}} &:= 1 - \exp \left[-\frac{\Delta t}{2} \left(\lambda(\hat{t} \Delta t | s_{r,\hat{t}}) + \lambda((\hat{t} + 1) \Delta t | s_{r,\hat{t}}) \right) \right], \\ h_{\hat{t}} &:= h(\hat{t} \Delta t), & x_{\hat{t}} &:= x(\hat{t} \Delta t), & y_{\hat{t}} &:= y(\hat{t} \Delta t), & z_{\hat{t}} &:= z(\hat{t} \Delta t) \\ \bar{P}_{\hat{t}} &:= 1 - \exp \left[-\frac{\Delta t}{2} \left(\lambda_{free}(\hat{t} \Delta t) + \lambda_{free}((\hat{t} + 1) \Delta t) \right) \right]. \end{aligned}$$

Using these quantities, the mesoscopic model can be simulated with the following update rule [48]: For $r = 1, \dots, \mathcal{T} - 1$,

$$\begin{aligned}
(5.5a) \quad & n_{r,\hat{t}+1} = n_{r+1,\hat{t}}, \\
(5.5b) \quad & S_{r,\hat{t}+1} = \left(1 - P_{r+1,\hat{t}}\right) S_{r+1,\hat{t}}, \\
(5.5c) \quad & u_{r,\hat{t}+1} = u_{r+1,\hat{t}} + \left(\frac{\mu_{\hat{t}\Delta t} - u_{r+1,\hat{t}}}{\tau_m} + J \frac{n_{\mathcal{T},\hat{t}}}{\Delta t}\right) \Delta t, \\
(5.5d) \quad & h_{\hat{t}+1} = h_{\hat{t}} + \left(\frac{\mu_{\hat{t}\Delta t} - h_{\hat{t}}}{\tau_m} + J \frac{n_{\mathcal{T},\hat{t}}}{\Delta t}\right) \Delta t, \\
(5.5e) \quad & x_{\hat{t}+1} = (1 - \bar{P}_{\hat{t}}) x_{\hat{t}} + S_{1,\hat{t}+1} n_{1,\hat{t}+1}, \\
(5.5f) \quad & z_{\hat{t}+1} = (1 - \bar{P}_{\hat{t}})^2 z_{\hat{t}} + P_{\hat{t}} x_{\hat{t}} + \left(1 - S_{1,\hat{t}+1}\right) S_{1,\hat{t}+1} n_{1,\hat{t}+1}
\end{aligned}$$

with boundary conditions $S_{\mathcal{T},\hat{t}} = 1$ and $u_{\mathcal{T},\hat{t}} = 0$ for all $\hat{t} > 0$, and

$$\begin{aligned}
(5.5g) \quad & n_{\mathcal{T},\hat{t}+1} = \frac{\xi_{\hat{t}}}{N}, \quad \xi_{\hat{t}} \sim \text{Binomial}(N, \bar{n}_{\hat{t}}), \\
(5.5h) \quad & \bar{n}_{\hat{t}} = \bar{P}_{\hat{t}} x_{\hat{t}} + \sum_{r=2}^{\mathcal{T}} P_{r,\hat{t}} S_{r,\hat{t}} n_{r,\hat{t}} + P_{\Lambda,\hat{t}} \left(1 - x_{\hat{t}} - \sum_{r=2}^{\mathcal{T}} S_{r,\hat{t}} n_{r,\hat{t}}\right), \\
(5.5i) \quad & P_{\Lambda,\hat{t}} = \frac{\bar{P}_{\hat{t}} z_{\hat{t}} + \sum_{r=2}^{\mathcal{T}} P_{r,\hat{t}} (1 - S_{r,\hat{t}}) S_{r,\hat{t}} n_{r,\hat{t}}}{z_{\hat{t}} + \sum_{r=2}^{\mathcal{T}} (1 - S_{r,\hat{t}}) S_{r,\hat{t}} n_{r,\hat{t}}}.
\end{aligned}$$

The independent, identically distributed binomial random variables $\xi_{\hat{t}}^k$ represent the total number of neurons that fire in the time interval $(\hat{t}\Delta t, (\hat{t} + 1)\Delta t]$. Therefore, the empirical population activity, (1.2), and the corresponding population rate (intensity) are finally obtained as $A_{\hat{t}\Delta t, \Delta t} = n_{\mathcal{T},\hat{t}+1}/\Delta t$ and $\bar{A}_{\hat{t}\Delta t} = \bar{n}_{\hat{t}}/\Delta t$, respectively. A pseudocode implementation of the mesoscopic model, (5.5), is given in Algorithm 5.1. A Julia-code implementation of the

Algorithm 5.1. Mesoscopic neuronal population model.

Data: External stimulus at grid points $\mu_{\hat{t}\Delta t}$, $\hat{t} = 1, \dots, t_{sim}$

Result: Population activities $A_{\hat{t}\Delta t, \Delta t}$ and rates $\bar{A}_{\hat{t}\Delta t}$, $\hat{t} = 1, \dots, t_{sim}$

```

1  $\mathcal{T} = \lfloor 5\tau_m/\Delta t \rfloor + 1$   $x = 0, z = 0, h = 0$   $n_{\mathcal{T}} = 1, n_{1:\mathcal{T}-1} = 0$   $A_{0,\Delta t} = 1/\Delta t$   $S_{1:\mathcal{T}} = 1, u_{1:\mathcal{T}} = 0$ 
    $\lambda_{free} = f(h), \lambda_{1:\mathcal{T}} = f(h)$ ;
2 for all times  $\hat{t} = 1, \dots, t_{sim}$  do
3    $h \leftarrow h + [(\mu_{\hat{t}\Delta t} - h)/\tau_m + JA_{(\hat{t}-1)\Delta t, \Delta t}] \Delta t$   $P_{\lambda} = \text{Pfire}(f(h), \lambda_{free})$   $W = P_{\lambda} x, X = x,$ 
    $Y = P_{\lambda} z, Z = z$   $x \leftarrow x - W$   $z \leftarrow (1 - P_{\lambda})^2 z + W$  for  $r = 2, \dots, \mathcal{T}$  do
4      $u_{r-1} = u_r + [(\mu_{\hat{t}\Delta t} - u_r)/\tau_m + JA_{(\hat{t}-1)\Delta t, \Delta t}] \Delta t$   $P_{\lambda}, \lambda_{r-1} = \text{Pfire}(f(u_{r-1}), \lambda_r)$   $m = S_r n_r$ 
      $v = (1 - S_r) m$   $W \leftarrow W + P_{\lambda} m$ ; //  $W := \int_{[0,\hat{t}]} \lambda(t|s) S(t|s) dZ_s$ 
5      $X \leftarrow X + m$ ; //  $X := \int_{[0,\hat{t}]} S(t|s) dZ_s$ 
6      $Y \leftarrow Y + P_{\lambda} v$ ; //  $Y := \int_{[0,\hat{t}]} \lambda(t|s) \{1 - S(t|s)\} S(t|s) dZ_s$ 
7      $Z \leftarrow Z + v$ ; //  $Z := \int_{[0,\hat{t}]} \{1 - S(t|s)\} S(t|s) dZ_s$ 
8      $S_{r-1} = (1 - P_{\lambda}) S_r$   $n_{r-1} = n_r$ 
9   end
10   $x \leftarrow x + S_1 n_1$   $z \leftarrow z + (1 - S_1) S_1 n_1$  if  $Z > 0$ :  $P_{\Lambda} = Y/Z$ , else  $P_{\Lambda} = 0$   $\bar{n} = \min(\max(0, W +$ 
    $P_{\Lambda}(1 - X)), 1)$ ; // expected spike count  $N\bar{n} = N\bar{A}_{\hat{t}\Delta t}$ 
11  draw  $n_{\mathcal{T}} = \text{Binomial}(N, \bar{n})/N$   $\bar{A}_{\hat{t}\Delta t} = \bar{n}/\Delta t$   $A_{\hat{t}\Delta t, \Delta t} = n_{\mathcal{T}}/\Delta t$ 
12 end

```

extended model (Appendix A, Algorithm A.1) is publicly available at the following GitHub link: <https://github.com/schwalger/mesodyn-LIF>.

<p>Function Pfire(λ, λ_{old})</p> <p>1 $P_\lambda = (\lambda + \lambda_{old})\Delta t/2;$</p> <p>2 if $P_\lambda > 0.01$ then $P_\lambda \leftarrow 1 - e^{-P_\lambda};$</p> <p>3 return P_λ, λ</p>

6. Conclusions. We have proven that a simplified version of the model proposed in [48] is well-posed and stable in variation in the sense of Brémaud and Massoulié [5]. The simplified model is a Markov embedding of an intensity-based and history-dependent point process where the history dependence is, loosely speaking, more “nonlinear” than in nonlinear Hawkes processes (in the sense that the past filtering function is updated at each jump event such that, even in the argument of the intensity function $f(\cdot)$, the dependence on the past is not linear any more, that is, not given by convolution over the past events). To deal with this difficulty in the proofs, we combined arguments for Markov processes taking values in the space of positive measures and nonlinear Hawkes processes. From this point of view, the finite-size population equation (1.12) is even more “nonlinear,” which makes its mathematical analysis challenging. The simplified model and the original model of [48] could therefore be seen as examples of general intensity-based and history-dependent point processes, extending nonlinear Hawkes processes. Despite their mathematical complexity, these general point processes are rather practical for applications since they can be efficiently simulated and, as intensity-based processes, can be easily fitted to empirical data using likelihood-based methods [43, 51]. We hope that this work will stimulate further mathematical research on these general intensity-based processes, which have already proven to be useful in neuroscience.

Appendix A. Multipopulation model. The only difference between the neuron model in (1.1) and the generalized integrate-and-fire model considered in [48] is the addition of a synaptic filtering kernel ϵ and an absolute refractory period $\Delta_{abs} \geq 0$. Accordingly, (1.1a) is replaced by

$$dU_t^{i,N} = \left[\frac{\mu t - U_t^{i,N}}{\tau_m} dt - U_{t^-}^{i,N} dZ_t^{i,N} + \left(\frac{J}{N} \sum_{j=1}^N \int_{]-\infty, t]} \epsilon(t-s) dZ_s^{j,N} \right) dt \right] \mathbf{1}_{T_t^{i,N} > \Delta_{abs}},$$

where $T_t^{i,N}$ is an additional “age”-variable defined by the stochastic dynamics $dT_t^{i,N} = dt - T_{t^-}^{i,N} dZ_t^{i,N}$, which clocks the time elapsed since the last spike of neuron i . Then, the definitions for the hazard rate λ and the survival S can be easily adapted replacing Φ in (1.11) by

$$\Phi_{s,t}^z(u) := ue^{-\frac{t-s}{\tau_m}} + \int_s^t e^{-\frac{t-r}{\tau_m}} \left(\frac{\mu r}{\tau_m} + J \int_{]-\infty, r]} \epsilon(r-s') dz_{s'} \right) dr \quad \text{for all } u \in \mathbb{R}$$

and replacing λ in (1.6) by $\lambda^z(t|s) = f(\Phi_{s+\Delta_{abs},t}^z(0)) \mathbf{1}_{t \geq s+\Delta_{abs}}$.

As explained in [48], it is straightforward to generalize (4.7) (with the aforementioned extensions) to multiple interacting populations. Importantly, the multipopulation model allows

us to coarse-grain microscopic models of large biological networks of neurons, like a cortical column.

Again, we will henceforth drop the superscripts Z . Let us consider a system of K interacting (homogeneous) populations, each consisting of N^1, \dots, N^K neurons, with parameters

$$\{N^k, \tau_m^k, \Delta_{\text{abs}}^k, f^k, \epsilon^k, (\mu_t^k)_{t \geq 0}\}_{k=1, \dots, K}$$

and average connectivity matrix \mathbf{J} , where J^{kl} is the average connection strength from population l to population k . The multipopulation version of (4.7) is the following: For all $k = 1, \dots, K$ and $t > 0$,

$$(A.1a) \quad Z_t^k = 1 + \frac{1}{N} \int_{[0,t] \times \mathbb{R}_+} \mathbb{1}_{z \leq N \bar{A}_s^k} \pi^k(ds, dz),$$

$$(A.1b) \quad \bar{A}_t^k = \left[\int_{[0,t]} \lambda^k(t|s) S^k(t|s) dZ_s^k + \Lambda_t^k \left(1 - \int_{[0,t]} S^k(t|s) dZ_s^k \right) \right]_+,$$

$$(A.1c) \quad \Lambda_t^k = \frac{\int_{[0,t]} \lambda^k(t|s) \{1 - S^k(t|s)\} S^k(t|s) dZ_s^k}{\int_{[0,t]} \{1 - S^k(t|s)\} S^k(t|s) dZ_s^k},$$

with the initial condition $Z_0^1 = \dots = Z_0^K = 1$ and $\Lambda_0^1 = \dots = \Lambda_0^K = 0$, where $\{\pi^k\}_{k=1, \dots, K}$ is independent Poisson random measures on $\mathbb{R}_+ \times \mathbb{R}_+$ with Lebesgue intensity measure and

$$(A.2a) \quad S^k(t|s) = \exp\left(-\int_s^t \lambda^k(r|s) dr\right),$$

$$\lambda^k(t|s) = f^k(u^k(t|s)) \mathbb{1}_{t \geq s + \Delta^k},$$

$$(A.2b) \quad u^k(t|s) = \mathbb{1}_{t \geq s + \Delta^k} \int_{s + \Delta^k}^t e^{-\frac{t-r}{\tau_m^k}} \left(\frac{\mu_r^k}{\tau_m^k} + \sum_{l=1}^K J^{kl} \int_{[s,r]} \epsilon^k(r-s') dZ_{s'}^l \right) dr.$$

For simplicity, we have presented here a version of the multipopulation model without spike-frequency adaptation or short-term synaptic plasticity, but these features can be included [48, 46].

In the following we choose a delayed exponential synaptic filter $\epsilon^k(t) = \frac{1}{\tau_s^k} \exp\left(-\frac{t-d^k}{\tau_s^k}\right) \mathbb{1}_{t \geq d^k}$, where τ_s^k is the synaptic decay time constant and $d^k > 0$ denotes the transmission delay associated with the presynaptic population k . This choice allows us to rewrite (A.2a) and (A.2b) as the solution of an SDE (with delay): for any $s > 0$,

$$\begin{aligned} \frac{dS^k(t|s)}{dt} &= -\lambda^k(t|s) S^k(t|s), \\ \tau_m^k \frac{du^k(t|s)}{dt} &= -u^k(t|s) + \mu_t^k + \tau_m^k \sum_{l=1}^K J^{kl} y_t^l, \\ \tau_s^k dy_t^k &= -y_t^k dt + dZ_{t-d^k}^k, \end{aligned}$$

with initial conditions $S^k(s|s) = 1$, $u^k(s|s) = 0$, and $y_0^k = 0$.

As in the case for a single population (section 5), the infinite history of (A.1) can be approximated by a finite history. The method is completely analogous to that described in

Algorithm A.1. Mesoscopic multipopulation model with $\Delta_{abs}^k \geq 0, d^k \geq 0, \tau_s^k \geq 0$.

Data: External stimulus at grid points $\mu_{i\Delta t}^k, \hat{t} = 1, \dots, t_{sim}, k = 1, \dots, K$
Result: Population activities $A_{i\Delta t, \Delta t}^k$ and rates $\bar{A}_{i\Delta t}^k, \hat{t} = 1, \dots, t_{sim}, k = 1, \dots, K$

4 **for** all populations $k = 1, \dots, K$ **do**
5 $\mathcal{T}^k = \lfloor (5\tau_m^k + \Delta_{abs}^k) / \Delta t \rfloor + 1, \hat{\Delta}_{abs}^k = \lfloor \Delta_{abs}^k / \Delta t \rfloor, \hat{d}^k = \lfloor d^k / \Delta t \rfloor$ $x^k = 0, y^k = 0, z^k = 0,$
 $h^k = 0, n_{\mathcal{T}^k}^k = 1, n_{1:\mathcal{T}^k-1}^k = 0, S_{1:\mathcal{T}^k}^k = 1, u_{1:\mathcal{T}^k}^k = 0, \lambda_{free}^k = f(h^k), \lambda_{1:\mathcal{T}^k}^k = f(h^k);$
6 **end**
7 **for** all times $\hat{t} = 1, \dots, t_{sim}$ **do**
8 **for** all populations $k = 1, \dots, K$ **do** $I_{syn}^k = \sum_{l=1}^K J^{kl} y^l$ **for** all populations $k = 1, \dots, K$
 do
9 $h^k \leftarrow h^k + [(\mu_{\hat{t}\Delta t}^k - h^k) / \tau_m^k + I_{syn}^k] \Delta t$ $P_\lambda, \lambda_{free}^k = \text{Pfire}(f(h^k), \lambda_{free}^k)$ $W = P_\lambda x^k, X =$
 $x^k, Y = P_\lambda z^k, Z = z^k$ $x^k \leftarrow x^k - W$ $z^k \leftarrow (1 - P_\lambda)^2 z^k + W$ **for** $r = 2, \dots, \mathcal{T}^k - \hat{\Delta}_{abs}^k$
 do
10 $u_{r-1}^k = u_r^k + [(\mu_{\hat{t}\Delta t}^k - u_r^k) / \tau_m^k + I_{syn}^k] \Delta t$ $P_\lambda, \lambda_{r-1}^k = \text{Pfire}(f^k(u_{r-1}^k), \lambda_r^k)$ $m = S_r^k n_r^k$
 $v = (1 - S_r^k) m$ $W \leftarrow W + P_\lambda m;$ $// \mathcal{W} := \int_{[0, \hat{t}]} \lambda^k(t|s) S^k(t|s) dZ_s^k$
11 $X \leftarrow X + m;$ $// \mathcal{X} := \int_{[0, \hat{t}]} S^k(t|s) dZ_s^k$
12 $Y \leftarrow Y + P_\lambda v;$ $// \mathcal{Y} := \int_{[0, \hat{t}]} \lambda^k(t|s) \{1 - S^k(t|s)\} S^k(t|s) dZ_s^k$
13 $Z \leftarrow Z + v;$ $// \mathcal{Z} := \int_{[0, \hat{t}]} \{1 - S^k(t|s)\} S^k(t|s) dZ_s^k$
14 $S_{r-1}^k = (1 - P_\lambda) S_r^k$ $n_{r-1}^k = n_r^k$
15 **end**
16 $x^k \leftarrow x^k + S_1^k n_1^k$ $z^k \leftarrow z^k + (1 - S_1^k) S_1^k n_1^k$ **for** time points in refractory period $r =$
 $\mathcal{T}^k - \hat{\Delta}_{abs}^k + 1, \dots, \mathcal{T}^k$ **do**
17 $X \leftarrow X + n_r^k$ $n_{r-1}^k = n_r^k$
18 **end**
19 if $Z > 0$: $P_\lambda = Y/Z$, else $P_\lambda = 0$ $\bar{n} = \min(\max(0, W + P_\lambda(1 - X)), 1);$ $//$ expected
 spike count $N\bar{n} = N\bar{A}_{\hat{t}}^k \Delta t$
20 draw $n_{\mathcal{T}^k}^k = \text{Binomial}(N^k, \bar{n}) / N^k$ $y^k \leftarrow y^k e^{-\Delta t / \tau_s^k} + (1 - e^{-\Delta t / \tau_s^k}) n_{\mathcal{T}^k - \hat{d}^k}^k / \Delta t$ $\bar{A}_{\hat{t}}^k =$
 $\bar{n} / \Delta t$ $A_{\hat{t}}^k = n_{\mathcal{T}^k}^k / \Delta t$
21 **end**
22 **end**

section 5 except that, now, each population k has its own free membrane potential $h^k(t)$ following

$$\tau_m^k \frac{dh^k(t)}{dt} = -h^k(t) + \mu_t^k + \tau_m^k \sum_{l=1}^K J^{kl} y_t^l,$$

with initial condition $h^k(0) = 0$, and its own history length $T^k \gg \tau_m^k$.

For the discrete time dynamics, being also completely analogous to the single population case, we get the generalized algorithm.

Appendix B. Exponential moments for T_c (end of the proof of Theorem 3.3). Introducing $\bar{V}(\nu, \tilde{\nu}) := \frac{1}{2}(\|\nu\| + \|\tilde{\nu}\|)$ and \bar{L} as the generator of the coupled processes $(\rho_t, \tilde{\rho}_t)$, we obtain as a direct consequence of (2.7) the control

$$\bar{L}\bar{V}(\nu, \tilde{\nu}) \leq \Lambda - (f_{\min} \wedge \Lambda)\bar{V}(\nu, \tilde{\nu}),$$

implying that, for any $0 < c < f_{\min} \wedge \Lambda$, there exists a suitable constant K^* such that, with $C := \{\bar{V} \leq K^*\}$,

$$(B.1) \quad \bar{L}\bar{V} \leq -c\bar{V} + \Lambda \mathbf{1}_C.$$

Fix some $\delta > 0$, and introduce the sequence of hitting times

$$T_1(\delta) = \inf\{t \geq \delta : (\rho_t, \tilde{\rho}_t) \in C\}, \quad T_{n+1}(\delta) = \inf\{t \geq T_n(\delta) + \delta : (\rho_t, \tilde{\rho}_t) \in C\}, \quad n \geq 0.$$

Adapting the arguments of Theorem 3.1 of [21] to our frame, we deduce from (B.1) that there exist positive constants $c_1, \bar{\lambda}$ and $c(\delta, \bar{\lambda}), c_2(\delta)$ with

$$\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_1(\delta)}] \leq c_1 \bar{V}(\nu_0, \tilde{\nu}_0) + c_2(\delta)$$

and

$$\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}(T_{n+1}(\delta) - T_n(\delta))}] \leq c(\delta, \bar{\lambda}) \text{ for all } n \geq 1.$$

Relying on (3.1), we may associate with each $T_n(\delta)$ a Bernoulli random variable $U_n \sim \mathcal{B}(\varepsilon)$, independent of $\mathcal{F}_{T_n(\delta)}$, such that

$$U_n = 1 \text{ implies that, at time } T_n(\delta), \text{ the coupling has succeeded.}$$

In particular,

$$T_c \leq \inf\{T_n(\delta) : U_n = 1\}$$

and

$$\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_c}] \leq \sum_{n=1}^{\infty} \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_n(\delta)} \mathbf{1}_{\{U_1 = \dots = U_{n-1} = 0\}}]$$

for any $\bar{\lambda} > 0$. We are now ready to conclude. Since, by monotone convergence,

$$\lim_{\bar{\lambda} \rightarrow 0} \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}(T_{n+1}(\delta) - T_n(\delta))}] = 1,$$

we choose $\lambda_c > 0$ such that, for all $0 < \bar{\lambda} < \lambda_c$,

$$\sup_{n \geq 1} \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{2\bar{\lambda}(T_{n+1}(\delta) - T_n(\delta))}] \cdot (1 - \varepsilon) =: \kappa^2 < 1.$$

Using that, by successive conditioning,

$$\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{2\bar{\lambda}T_n(\delta)}] \leq \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{2\bar{\lambda}T_1(\delta)}] \cdot \left(\frac{\kappa^2}{1 - \varepsilon}\right)^{n-1},$$

this implies, using the Cauchy–Schwarz inequality,

$$\begin{aligned} \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_c}] &\leq \sum_{n=1}^{\infty} \mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{\bar{\lambda}T_n(\delta)} \mathbf{1}_{\{U_1 = \dots = U_{n-1} = 0\}}] \\ &\leq \sum_{n=1}^{\infty} \sqrt{\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{2\bar{\lambda}T_n(\delta)}] (1 - \varepsilon)^{(n-1)/2}} \leq \sqrt{\mathbb{E}_{(\nu_0, \tilde{\nu}_0)}[e^{2\bar{\lambda}T_1(\delta)}]} \sum_{n=1}^{\infty} \kappa^{n-1} < \infty, \end{aligned}$$

which concludes the proof.

Appendix C. Proof of (3.4). Using (2.5), we have $\mathcal{L}W(\nu) = -2\|\nu\|\nu[f] + [\nu[f] + \Lambda(1 - \|\nu\|)]_+(2\|\nu\| + \frac{1}{N})$. Whenever $[\nu[f] + \Lambda(1 - \|\nu\|)]_+ > 0$, this yields, for a suitable constant C ,

$$\mathcal{L}W(\nu) \leq -2W(\nu) + C(\|\nu\| + 1),$$

which implies the claim. The easier case $[\nu[f] + \Lambda(1 - \|\nu\|)]_+ = 0$ follows simply from the fact that $\nu[f] \geq f_{\min}\|\nu\|$.

Appendix D. Power spectral density. In Figure 1(b), we have characterized the stationary population activity by the power spectral density (PSD) defined for a wide-sense stationary process $X(t)$ and $f > 0$ as [28]

$$(D.1) \quad \tilde{C}_X(f) := \lim_{T \rightarrow \infty} \frac{|\tilde{X}_T(f)|^2}{T}, \quad \tilde{X}_T(f) := \int_0^T e^{-2\pi i f t} X(t) dt.$$

For the mesoscopic model, we estimated the PSD from the simulated, empirical population activity $\hat{A}_{t,\mathfrak{h}}^N(t)$, (1.2) with $\mathfrak{h} = 0.001$ s, using the averaged periodogram (Bartlett's method without windowing). Specifically, for the PSD shown in Figure 1, we segmented a 50-s-long realisation of the empirical population activity (sampled with time step $\mathfrak{h} = 0.001$ s) into 50 nonoverlapping segments of length $T = 1$ s, computed the squared absolute values of the fast Fourier transform for each segment, divided the result by T (as in (D.1)), and averaged the resulting periodograms over all 50 segments.

For the microscopic model with $J = 0$ (as in Figure 1), the neuronal population consists of N independent renewal processes generated by the LIF model with escape noise. Therefore, the PSD of $A_{t,\mathfrak{h}}^N(t)$ in the limit $\mathfrak{h} \rightarrow 0$ is well known from the renewal formula [49, 18]

$$(D.2) \quad \tilde{C}_A(f) = \frac{r}{N} \frac{1 - |\tilde{P}_{ISI}(f)|^2}{|1 - \tilde{P}_{ISI}(f)|^2}.$$

Here, $\tilde{P}_{ISI}(f) = \int_{\mathbb{R}} P_{ISI}(t) e^{-2\pi i f t} dt$ is the Fourier transform of the interspike-interval density of single neurons $P_{ISI}(t) = \lambda^0(t|0)S^0(t|0)\mathbf{1}_{t \geq 0}$, and $r = [\int_0^\infty S^0(t|0) dt]^{-1}$ is their firing rate. In Figure 1, these quantities were calculated numerically.

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