Dynamic aspects of delay activity

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Abstract

The population density equation (PDE) has generated considerable interest, recently. The PDE allows efficient simulation of populations with a large number of neurons. We apply the PDE to an existing model of delay activity, which produces stationary firing rates for delay assemblies. In order to observe transient phenomena, we apply the PDE to this model. Here we present the preliminary results. We find that a novel algorithm to solve the PDE is instrumental for this particular application. Our results agree with stationary rates that can be found using a diffusion approximation.

Key words: delay activity; diffusion approximation; population density; partial differential equation; response curve.

1 Motivation

To allow the modeling of large-scale cortical networks, it is necessary to simulate the behavior of large groups of neurons efficiently. One interesting technique to describe the activity of large groups of neurons is the population density approach. In this approach a large population of neurons is described by a single density function $\rho(v,t)$. The neurons that we consider in this paper are leaky-integrate-and-fire (LIF) neurons, which are point models described by a single dynamical variable v, the (rescaled) membrane potential. The probability for a single neuron in the population to have its membrane potential v in $[v, v + dv]$ is given by $\rho(v,t)dv$. In the mean-field approximation a partial differential equation (PDE) [1] equation can be found (e.g., [5]) that describes the evolution in time of ρ in terms of the population's input. ρ may be used,

[1] We use the abbreviation PDE both for partial differential equation and population density equation. This is unlikely to cause confusion.

for instance, to infer the population's firing rate, in other words, the population's response to input may be calculated. This technique has been applied successfully to a model of orientation tuning [4].

We intend to apply this technique to a model of delay activity, described in [1]. Delay activity is a stimulus induced population response above baseline activity, which persists after the stimulus is removed. It is considered to be an important candidate for the neural substrate of short-term memory. The main reason to consider this model, is that we want to investigate the usefulness of the population density technique to model large-scale cortical networks. The firing rates, that were found in [1], are stationary rates. In order to describe transient phenomena, quite extensive simulations are necessary. These simulations were performed, and therefore it is interesting to see if these results also can be obtained, at lower computational cost, with the population density technique.

Our results, so far, have resulted in a novel algorithm to solve the PDE, which seems to be more stable, and as least as efficient as the finite difference methods that are currently in use. Moreover, it seems that for large-scale cortical networks, it is advantageous to use a single input population, that emulates a Gaussian white noise, rather than to include all input contributions of a population separately.

2 A model for delay activity

In the model of delay activity, formulated by Amit and Brunel [1], a cortical column is modeled with an excitatory population and an inhibitory population. The excitatory population has a substructure: a small part of this population responds with an increased firing rate, with respect to baseline, to specific external stimuli. In [1] it is shown that such a stimulus specific population can retain its increased firing rate after the stimulus that induced it has vanished. Importantly, this firing rate is above baseline, but much lower than the maximal firing rates of the neuron in that population. Amit and Brunel consider LIF neurons in the diffusion approximation, i.e. as an Ornstein-Uhlenbeck process. In this approximation, it is possible to find an output firing rate of a neuron, in terms of the mean and variance of the input current. This approximation is particularly useful, if input rates are high and synaptic efficacies are small, so that the input approximates a Gaussian white noise, which is the case for the parameter range considered by Amit and Brunel. For LIF neurons a response function may be derived, in terms of the first exit time of an Ornstein-Uhlenbeck process. The firing rate ν is given in terms of the mean μ and variance σ of the input: $\nu = \phi(\mu, \sigma)$

$$\phi = [\tau_{ref} + \tau\sqrt{\pi} \int\limits_{(V_r-\mu)/\sigma}^{(\theta-\mu)/\sigma} \exp(u^2) erfc(u) du]^{-1}. \tag{1}$$

Here θ is the threshold potential in mV, and V_r the reset potential in mV. μ and σ are the mean and variance, respectively, of the input current during time τ. For a single neuron with one input with efficacy J, which receives a Poisson distributed input spike train with rate $r(t)$, one has:

$$\begin{aligned} \mu &= \tau J r(t) \\ \sigma^2 &= \tau J^2 r(t). \end{aligned} \tag{2}$$

In the mean-field approximation, where every neuron in a population is assumed to receive similar input, one can replace the entire population by a single neuron, representing the entire population. Amit and Brunel consider a network of four populations. τ is the neuron's time constant in s and τ_{ref} its absolute refractive period. As each population's output contributes to the other population's input, it is possible to find a set of closed equations which describe the stationary rates in the network. It turns out that it is possible to find network parameters, such that both spontaneous and delay activity are stable in the network. As this result depends mainly on the form of the response curve, equation 1, our first goal is to see if the stationary solutions of the PDE are on this curve.

3 The population density equation

LIF neurons are described by a single dynamical equation:

$$\frac{dv}{dt} = -\gamma v. \tag{3}$$

The rescaled membrane potential is defined by $v = \frac{V - V_{rev}}{V_{th} - V_{rev}}$. Here V_{th} is the threshold potential and V_{rev} is the reversal potential, so that for the rescaled potential $-\infty \leq v < 1$ holds. If a neuron has its membrane potential driven past V_{th}, a spike is generated and its potential is reset to a (rescaled) potential value v_{reset}.

In its simplest form, the population density equation for LIF neurons is given by:

$$\frac{\partial \rho(v,t)}{\partial t} - \gamma \frac{\partial}{\partial v}(\rho(v,t)v) = -\sigma(t)\left[\rho(v,t) - \rho(v-\bar{h},t)\right]. \quad (4)$$

A necessary boundary condition is: $\rho(1,t) = 0$, as no decay from $v > 1$ into the system is possible. In this version of the equation we assume a single input synapse, with efficacy $\bar{h}$ which receives a spike train which is Poisson distributed with rate $\sigma(t)$. It is easy to generalize this case to an arbitrary number of inputs, with efficacies distributed according to a given probability density function (PDF), but equation 4 is adequate for this paper.

In this form the flux across the threshold potential, due to input is equal to the (population) firing rate of the population: $r(t) = \sigma(t) \int_{1-\bar{h}}^{1} \rho(v,t)dv$.

As neuron which are driven past threshold spike and then are reset to potential v_r, we add an extra term $r(t)\delta(v - v_r)$ to the right-hand side of equation 4, which reflects that probability density which is lost, due to flux across threshold, is balanced by probability density which appears at $v = v_r$, at the same time. There are various methods available to solve this equation (see e.g., [5], [4]), but for the application of the PDE in this paper, we came up with a novel algorithm, for reasons explained below.

4 A novel numerical method to solve the population density equation

The Gaussian white noise approximation has advantages for the approach presented here. Instead of considering four input populations, we only have to consider one, whose mean and variance are determined by the firing rates of the four input populations and the network parameters. As we consider a white Gaussian noise as an input current for neurons, we can pick the input rate $\sigma(t)$ and the input parameter $\bar{h}$, according to equation 3, which reproduces Gaussian white noise to a good approximation in our parameter range. For the μ and σ considered in this paper (see figure), this means one finds rather small values of $\bar{h}$ (typically in the order of $\bar{h} = 0.01$). This may produce a jagged density profile around $v = 0$, and a finite difference solution of the PDE may be sensitive to the large density gradients that occur there.

In order to avoid the stability problems caused by this, we consider a coordinate transformation:

$$\begin{cases} v \qquad\quad \rightarrow v' = ve^{-\gamma t} \\ \rho(v,t) \rightarrow \rho'(v',t) = e^{-\gamma t}\rho(ve^{\gamma t},t). \end{cases} \tag{5}$$

Equation 4 changes under this transformation equation into:

$$\frac{d\rho'(v',t)}{dt} = \sigma(t)\left\{\rho'(v' - \bar{h}e^{\gamma t}) - \rho(v')\right\}. \tag{6}$$

For a time period $\delta t << \gamma^{-1}$, so that $\bar{h}e^{\gamma t}$ may be considered constant, this corresponds to a set of ordinary differential equations, rather than a PDE, which is insensitive to density gradients. It possible to base an efficient numerical solution on this transformation which is described in detail in [3]. Another option would have been to solve the PDE in the Fokker-Planck approximation, which avoids the jagged profile at $v = 0$. In the Fokker-Planck approximation, however, the PDE still remains sensitive to the density gradient, and stability problems may still occur [2].

5 First results

In the figure, we consider a Gaussian white noise input with variable mean μ and a fixed variance $\sigma = 2$ mV. We consider a excitatory population with membrane time constant $\tau = 10$ ms, absolute refractive $\tau_{ref} = 4$ ms. The figure shows the equilibrium density distribution in the left column, with μ increasing from top to bottom. In the middle column we plot the corresponding response rate as a function of time. The equilibrium values of the response rate are plotted in the right-hand figure using asterisks. The solid curve is the rate given by equation 1. There are two interesting observations: first of all, there is excellent agreement between the diffusion approximation prediction and the PDE solutions at low rates. At higher rates there is a slight disagreement, which can be explained by the somewhat simplistic treatment of the refractive period in equation 1. Secondly, at higher values of μ, the equilibrium rates are reached after substantial transient variation of the signal.

In conclusion, we have used a novel algorithm to solve the PDE. Apart from the replication of earlier results, the good agreement between equilibrium rates given by PDE solutions and diffusion approximation in the description of response curves, provides validation of the new algorithm. Since these response curves are the most important mathematical foundation of Amit and Brunel's model of delay activity, we are confident that we will be able to provide a dynamical description of their model in terms of PDE solutions in the future.

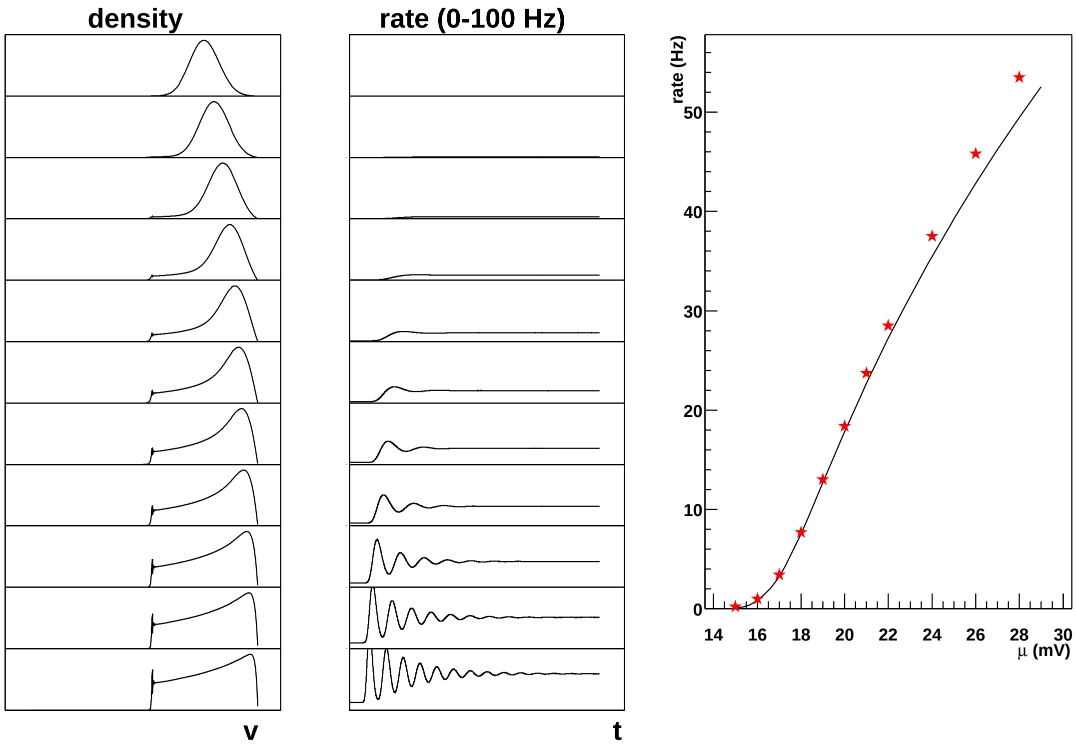

Fig. 1. Comparison between the solutions of the population density equation and the diffusion approximation.

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