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Delay stabilizes stochastic motion of bumps in layered neural fields

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HIGHLIGHTS

- We study bumps in multilayered neural fields with delayed coupling between layers.
- Delayed coupling stabilizes bumps to translating perturbations.
- Delay-induced stabilization of bumps reduces their diffusion, due to stochastic forcing.
- Diffusion reduction due to delays can be approximated using a small delay expansion.

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ABSTRACT

We study the effects of propagation delays on the stochastic dynamics of bumps in neural fields with multiple layers. In the absence of noise, each layer supports a stationary bump. Using linear stability analysis, we show that delayed coupling between layers causes translating perturbations of the bumps to decay in the noise-free system. Adding noise to the system causes bumps to wander as a random walk. However, coupling between layers can reduce the variability of this stochastic motion by canceling noise that perturbs bumps in opposite directions. Delays in interlaminar coupling can further reduce variability, since they couple bump positions to states from the past. We demonstrate these relationships by deriving an asymptotic approximation for the effective motion of bumps. This yields a stochastic delay-differential equation where each delayed term arises from an interlaminar coupling. The impact of delays is well approximated by using a small delay expansion, which allows us to compute the effective diffusion in bumps' positions, accurately matching results from numerical simulations.

1. Introduction

Delays commonly arise in dynamical models of large scale neuronal networks, often accounting for the detailed kinetics of chemical or electrical activity [1]. The finite-velocity of action potential (AP) propagation can lead to delays on the order of milliseconds between AP instantiation at the axon hillock and its arrival at the synaptic bouton [2]. Similar propagation delays have been observed in dendritic APs propagating to the soma [3]. Furthermore, synaptic processing involves several steps including vesicle release, neurotransmitter diffusion, and uptake, so the chemical signal communicating between cells is effectively delayed [4]. However, computational models of large scale networks that describe all these processes in detail are unwieldy, not admitting direct analysis, so one must rely on expensive simulations to study their behavior [5]. An alternative approach is to develop mean field models of spiking networks that incorporate delay that accounts for these microscopic processes [6].

Neural field equations are a canonical model of large scale spatiotemporal activity in the brain [7]. Many studies have explored the impact of delays on the resulting spatiotemporal solutions of these equations [8–10]. One common observation is that the inclusion of delays can lead to oscillations via a Hopf bifurcation in the linear system describing the local stability of solutions to the delay-free system: Turing patterns [10], stationary pulses [11,12], and traveling waves [6,13]. Thus, a major finding across many studies of delayed neural field equations is that delay will tend to contribute to instabilities in stationary states [14]. Recent work has shown that in stochastic neural field models, delay can stabilize the system near bifurcations [15]. This distinction has been explored extensively in control theory literature: delayed negative feedback loops can induce instability while delayed positive feedback can augment stability [16]. In this work, we further

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explore the potential stabilizing impact of delays in neural field models. Specifically, we focus on the case where positive feedback between two layers of a neural field help stabilize patterns to noise perturbations.

We will focus specifically on a multilayer neural field model that supports *bump attractors* [17]. Persistent spiking activity with a “bump” shape is an experimentally observed neural substrate of spatial working memory [18,19]. The position of the bump encodes the remembered location of a cue [20]. Noise degrades memory accuracy over time [21], due to diffusive wandering of bumps across the neutrally stable landscape of the network [22]. Several mechanisms have been proposed to limit such diffusion-induced error: short term facilitation [23,24], bistable neural units [25,26], and spatially heterogeneous recurrent excitation [27,28]. Recently, we showed interlaminar coupling, known to exist between the many brain areas participating in spatial working memory [29], can also help to reduce bump position variability due to noise cancellation. Here, we show that delays in the interlaminar coupling further reduce the long term variability in bump positions. Essentially, this occurs because each layer is constantly coupled to past states of other layers, states that have integrated noise for a shorter length of time than the current state.

The paper is organized as follows. In Section 2, we introduce the multilayer neural field model with delays and noise, showing they take the form of a delayed stochastic integrodifferential equation. Section 3 then explores how delays impact the local stability of stationary bumps in a dual layer neural field, in the absence of noise. Essentially, we demonstrate the delay reduces the impact of translating perturbations to the bump solution, underlying the mechanism of position stabilization. This motivates our findings in Section 4, where we derive effective stochastic equations for the motion of bump solutions subject to noise, showing they take the form of stochastic delay differential equations. A small delay expansion allows us to compute an effective variance, which is shown to be reduced by increasing the delay in coupling between layers. Lastly, we extend our results in Section 5, showing similar results hold in stochastic neural fields with more than two layers, and the effective variance decreases with the number of layers.

2. Laminar neural fields with delays and noise

2.1. Dual layer neural field with delays between layers

We model a pair of reciprocally coupled stochastic neural fields, accounting for the propagation delay between layers as:

$$\mathrm{d}u_1(x,t) = \left[-u_1(x,t) + \int_{-\pi}^{\pi} w(x-y) f(u_1(y,t))\mathrm{d}y + \int_{-\pi}^{\pi} w_{12}(x-y) f(u_2(y, t - \tau_{12}(x,y)))\mathrm{d}y \right] \mathrm{d}t + \varepsilon \mathrm{d}W_1(x,t), \tag{1a}$$

$$\mathrm{d}u_2(x,t) = \left[-u_2(x,t) + \int_{-\pi}^{\pi} w(x-y) f(u_2(y,t))\mathrm{d}y + \int_{-\pi}^{\pi} w_{21}(x-y) f(u_1(y, t - \tau_{21}(x,y)))\mathrm{d}y \right] \mathrm{d}t + \varepsilon \mathrm{d}W_2(x,t), \tag{1b}$$

so $u_j(x,t)$ is the total synaptic input at location $x \in [-\pi, \pi]$ in layer j. The effects of synaptic architecture are given by the convolution terms, so $w(x-y)$ describes the polarity (sign of w) and strength (amplitude of w) of recurrent connectivity within a layer. Typically, bump attractor network models assume spatially dependent synaptic connectivity that is lateral inhibitory [22], such as the cosine

$$w(x-y) = \cos(x-y), \quad j = 1, 2, \tag{2}$$

but our analysis will apply to the general case of any even weight function. Synaptic connections from layer k to j are described by the kernels $w_{jk}(x-y)$. To compare our analysis with numerical simulations, we will use the cosine coupling

$$w_{jk}(x-y) = M_j \cos(x-y), \quad k \neq j, \tag{3}$$

where M_j specifies the strength of coupling projecting to the jth layer.

Another feature of long range coupling is that the activity signals can take a finite amount of time to propagate from one neuron to the next [30,3,31]. Thus, delay is incorporated into the connectivity between layers through the spatially dependent functions $\tau_{jk}(x,y)$ [32,10,9,6], describing the amount of time it takes a signal to propagate from location y in layer k to location x in layer j. Our analysis can be carried out in the case of general functions $\tau_{jk}(x,y)$, but we demonstrate our results using specific cases, such as hard delays $\tau_{jk}(x,y) = \bar{\tau}_{jk}$ (constant) or distance-dependent delays (e.g., $\tau_{jk}(x,y) = \tilde{\tau}_{jk}(x-y)$).

Firing rate functions $f(u)$ are typically nonlinear monotonic functions of the synaptic input u, which we take to be sigmoidal [33]

$$f(u) = \frac{1}{1 + \mathrm{e}^{-\gamma(u-\theta)}},$$

with threshold θ and gain γ. To compute quantities explicitly, we typically take the high gain limit $\gamma \to \infty$ to yield the Heaviside firing rate function [22]

$$f(u) = H(u-\theta) = \begin{cases} 0 & : u < \theta, \\ 1 & : u \geq \theta. \end{cases} \tag{4}$$

Noise in each layer j is described by a small amplitude ($0 \leq \varepsilon \ll 1$) stochastic process $\mathrm{d}W_j(x,t)$ that is white in time and correlated in space so that $\langle \mathrm{d}W_j(x,t) \rangle = 0$ and

$$\langle \mathrm{d}W_j(x,t)\mathrm{d}W_j(y,s) \rangle = C_j(x-y)\delta(t-s)\mathrm{d}t\mathrm{d}s,$$
$$\langle \mathrm{d}W_j(x,t)\mathrm{d}W_k(y,s) \rangle = C_c(x-y)\delta(t-s)\mathrm{d}t\mathrm{d}s,$$

describing both local ($C_j(x-y)$, $j = 1, 2$) and shared ($C_c(x-y)$) noise correlations as a function of the difference in positions. Notice, in the case $C_c \equiv 0$, there are no interlaminar noise correlations, whereas if $C_1 \equiv C_2 \equiv C_c$, noise in each layer is drawn from the same process. In explicit examples, we typically take cosine spatial correlation functions

$$C_j(x) = c_j \cos(x), \qquad C_c = c_c \cos(x). \tag{5}$$