Physica D 295 296 (2015) 30 45

Contents lists available at ScienceDirect

Physica D

journal homepage: www.elsevier.com/locate/physd

# 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.

## article info

Article history:
Received 25 September 2014
Received in revised form
23 December 2014
Accepted 23 December 2014
Available online 2 January 2015
Communicated by S. Coombes

Keywords:
Neural field equations
Delay differential equations
Effective diffusion

## 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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http://dx.doi.org/10.1016/j.physd.2014.12.011

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:

$$du_1(x,t) = \left[ -u_1(x,t) + \int_{-\pi}^{\pi} w(x-y) f(u_1(y,t))\,dy + \int_{-\pi}^{\pi} w_{12}(x-y) f(u_2(y,t-\tau_{12}(x,y)))\,dy \right] dt + \varepsilon\, dW_1(x,t), \tag{1a}$$

$$du_2(x,t) = \left[ -u_2(x,t) + \int_{-\pi}^{\pi} w(x-y) f(u_2(y,t))\,dy + \int_{-\pi}^{\pi} w_{21}(x-y) f(u_1(y,t-\tau_{21}(x,y)))\,dy \right] dt + \varepsilon\, dW_2(x,t), \tag{1b}$$

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 $j$th 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

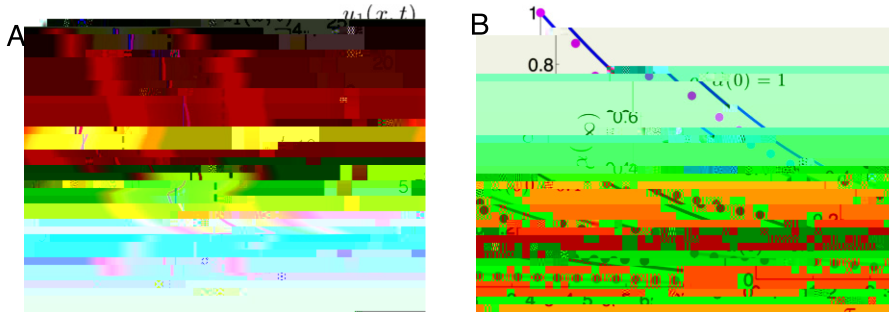

Fig. 2. (A) Response of bump solution (8) of the system (1) to an instantaneous shift perturbation (dashed line) α

Identifying the nullspace $(q_1(x), q_2(x))$ of $L^*$, we can ensure (23) is solvable by taking the inner product of [redacted] this vector to yield the equation

$$\langle q_1, \varepsilon^{-1} d\Delta U_1^{0\prime} + dW_1 + \varepsilon^{-1} \int_{-\pi}^{\pi} w_{12}(x-y) f'(U_2(y)) U_2^{0\prime}(y) (\Delta(t) - \Delta(t-\tau_{12}(x,y))) dy dt$$ [redacted]

$$+ \langle q_2, \varepsilon^{-1} d\Delta U_2^{0\prime} + dW_2 + \varepsilon^{-1} \int_{-\pi}^{\pi} w_{21}(x-y) f'(U_1(y)) U_1^{0\prime}(y) (\Delta(t) - \Delta(t-\tau_{21}(x,y))) dy$$ [redacted]

defining the $L^2$ inner product $\langle u, v \rangle = \int_{-\pi}^{\pi} u(x) v(x) dx$ for any $L^2$ integrable functions $u(x)$ and $v($ [redacted] bump position $\Delta(t)$ obeys the delayed stochastic process:

$$d\Delta(t) = \kappa_{12}(\Delta(t - \tau_{12}(x,y)))dt + \kappa_{21}(\Delta(t - \tau_{21}(x,y)))dt - (\kappa_{11} + \kappa_{22})\Delta(t)$$ [redacted]

### 4.3. Calculating nullspace: dual layers

To compute the effective variance

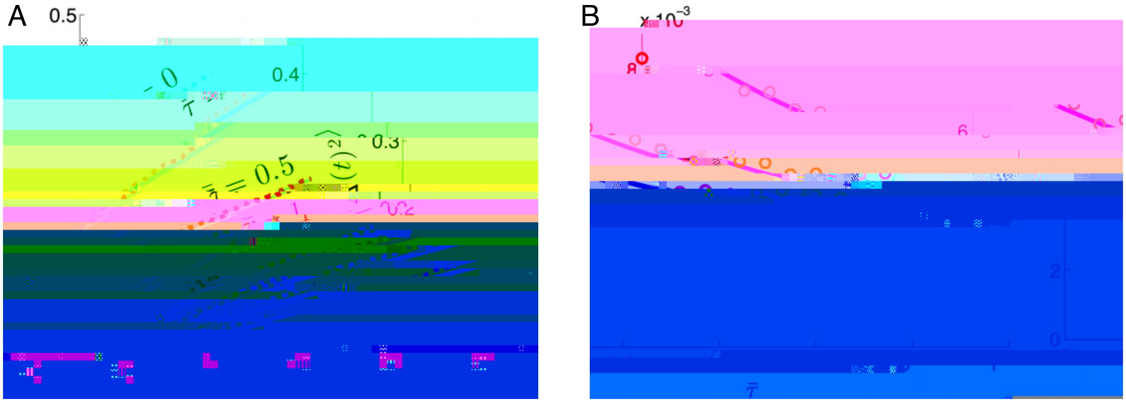

Fig. 4. Effective diffusion $D$ approximated for hard delays $\tau_{12} = \tau_{21} \equiv \bar{\tau}$ and symmetric coupling $w_{12}(x) = w_{21}(x) = \cos(x)$. (A) Variance $\langle \Delta(t)^2 \rangle = Dt$ in the position of coupled bumps in a dual layer network coupled with delays (1) is calculated assuming weak noise and a small delay expansion (38). Both our theoretical prediction (solid lines) and numerical simulations (dashed lines) reveal that the effective variance increases more slowly for longer propagation delays $\bar{\tau}$. (B) Effective diffusion $D$ decreases as a function of hard delay $\bar{\tau}$ in our asymptotic theory (solid line) and numerical simulations (circles). Threshold $\theta = 0.5$, no noise correlations ($c_c \equiv 0$), noise amplitude $\varepsilon = 0.5$. Variances are computed from numerical simulations using 5000 realizations each.

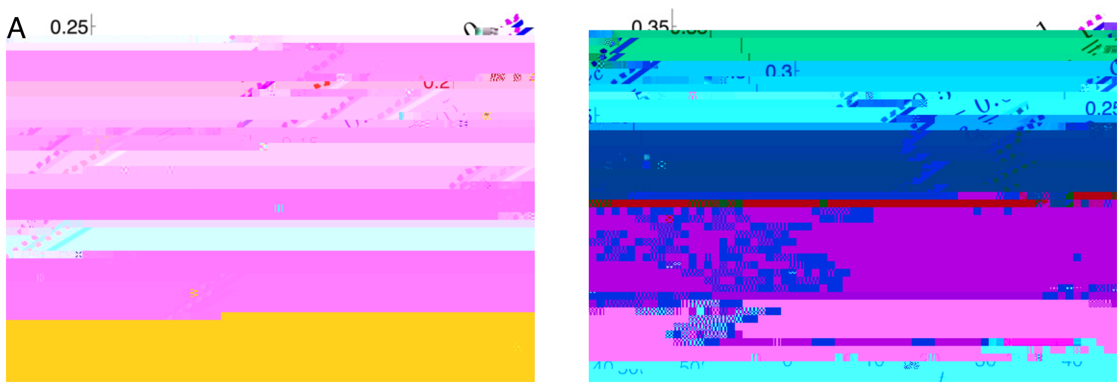

Fig. 5. (A) The impact of asymmetric hard delays $\bar{\tau}_{21} \neq \bar{\tau}_{12} = 1$ on the variance $\langle \Delta(t)^2 \rangle$ is still well characterized by our theoretical prediction (solid lines) given by (32) as matched by numerical simulations (dashed lines). (B) Our theory (solid lines) predicts variance increases as the amplitude of noise correlations $c_c$ between layers increases (38). Threshold $\theta = 0.5$; noise amplitude $\varepsilon = 0.5$; baseline delay $\bar{\tau} = 0$; interlaminar connectivity $w_{12}(x) = w_{21}(x) = \cos(x)$. Variances are computed from 5000 realizations each.

We consider a few different cases of the distance- and layer-dependent delay function $\tau_{jk}(x, y)$. We begin by considering the case where delays are homogeneous in space (hard delays), so $\tau_{jk} \equiv \bar{\tau}_{jk}$, and (37) reduces to

$$T_{jk} = \frac{2 \sin a \sin b \, \bar{\tau}_{jk}}{M_1^{-1}[1 - \cos(2a)] + 2 \sin a \sin b + M_2^{-1}[1 - \cos(2b)] + 2 \sin a \sin b}.$$

To compare our theory to numerical simulations, we begin by focusing on the symmetric case where coupling $M_1 = M_2 \equiv M$, noise $c_1 = c_2 = 1$, and delays $\bar{\tau}_{12} = \bar{\tau}_{21} = \bar{\tau}$ so that $a = b$ and $T_{12} = T_{21} \equiv T$ with

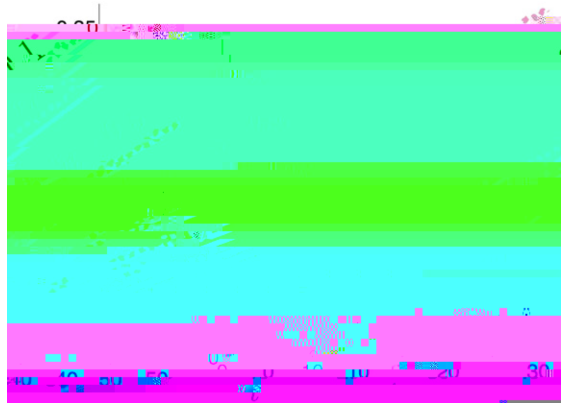

Fig. 6. Distance-dependent delays $\tau_{jk}(x,y) = \tau_d[1 - \cos(x - y)]$ between layers, $(j,k) = (1,2)$ or $(2,1)$, also can stabilize bumps to noise perturbations. Our theoretical calculations (solid lines) suggest that increasing the maximal delay $\tau_d$ further reduces the effective diffusion (39), which compares well with numerical simulations (dashed lines). Threshold $\theta = 0.5$; noise amplitude $\varepsilon = 0.5$; baseline delay $\bar{\tau} = 0$; interlaminar connectivity $w_{12}(x) = w_{21}(x) = \cos(x)$. Variances are computed from 5000 realizations each.

baseline delay $\bar{\tau}$ and delay increases with distance $|x - y|$. In this case, (37) reduces to

$$T_{jk} = \frac{2(\bar{\tau} + \tau_d(1 - \cos a \cos b)) \sin a \sin b}{M_1^{-1}[1 - \cos(2a)] + 2 \sin a \sin b + M_2^{-1}[1 - \cos(2b)]}, \quad j = 1, 2, \; k \neq j.$$

Now, for simplicity, we again focus on the symmetric case ($M_1 = M_2 = M$ so $a = b$) to make the effects of distance-dependent delay most transparent in resulting formulas. In this case $T_{12} = T_{21} = T$, and

$$T = \frac{M(\bar{\tau} + \tau_d \sin^2 a)}{2(}$$

1.9.5641 Tf 3.724 1.45 [(d)]l109.5641 Tf 4.418 7641 Tf
230[(745 r-2160 [(b6230[(745 R(mo[)t4929.5 6 8.28nt)-216(delao[)t492ex6(et)t4921 Tdt492(fet)t492absefecnct492oft)t492noiset)t4929.5 d.56
8 TJ/F121a.9265 9.586 0 Td [(a7)]TJ/F5J/F23 j9.5641Tf51 -3.777 Td2.1757 TJ/F121a.9265 9.586 0 Td [( a)]]TJ

In the symmetric case $M_{jk} = M, \forall j, k$, then $a_j = a, \forall a$, and

$$\theta = 2(1 + (N - 1)M)\cos(a)\sin(a),$$

which can be solved to yield a wide ($a_w$) and narrow ($a_n$) bump pair

$$a_w = \frac{\pi}{2} - \frac{1}{2}\sin^{-1} \qquad \theta$$

8j

delays are inherited by the stochastic variable $\Delta(t)$ for the bump's position. We enforce solvability of (54) by requiring the right hand side is orthogonal to the null space of the adjoint linear operator

$$\mathcal{L}^* \mathbf{p}(x) = \begin{pmatrix} p_1 + f'(U_1)\left[\int_{-\pi}^{\pi} w(x-y)p_1(y)dy + \sum_{k\neq 1}\int_{-\pi}^{\pi} w_{k1}(x-y)p_k(y)dy\right] \\ \vdots \\ p_j + f'(U_j)\left[\int_{-\pi}^{\pi} w(x-y)p_j(y)dy + \sum_{k\neq j}\int_{-\pi}^{\pi} w_{kj}(x-y)p_k(y)dy\right] \\ \vdots \\ p_N + f'(U_N)\left[\int_{-\pi}^{\pi} w(x-y)p_N(y)dy + \sum_{k\neq N}\int_{-\pi}^{\pi} w_{kN}(x-y)p_k(y)dy\right] \end{pmatrix}, \tag{55}$$

for any $L^2$-integrable vector $\mathbf{p}(x) = (p_1(x), \dots, p_N(x))^T$, derived using the inner product definition (26). Upon computing the nullspace $\mathbf{q}(x) = (q_1(x), \dots, q_N(x))^T$ of $\mathcal{L}^*$, we can generate the solvability condition by taking the inner product of both sides of (54) with $\mathbf{q}(x)$ to yield

$$\sum_{j=1}^{N}\left\langle q_j, \epsilon^{-1} d\Delta U_j' + dW_j + \epsilon^{-1}\sum_{k\neq j}\int_{-\pi}^{\pi} \dots\right.$$

Keeping only terms larger than $O(\tau_{jk}^2)$, we find (57) becomes

$$d(t) = \left( \sum_{j=1} \sum_{k \neq j} T_{jk} \right) d(t) + \sum_{j=1} dW_j.$$

Simplifying, we find

$$d(t) = \frac{\sum_{j=1} dW_j}{1 + \sum_{j=1} \sum_{k \neq j} T_{jk}};$$

so the mean $\langle (t) \rangle = 0$ and the variance

$$\langle (t)^2 \rangle = \frac{\sum_{j=1} \sum_{k=1} D_{jk}}{\left( 1 + \sum_{j=1} \sum_{k \neq j} T_{jk} \right)^2} t. \tag{59}$$

As before, delays will rTd [(1)]TJ/F123 6.6948 Tf 3.017 0 TdJ/F42 pg 0 G42 plong/F42 pgTo5641 Tf -2.704 -2.019 Td [(P)]TJ/F42 5.8022 Tf -0.132 -15.7

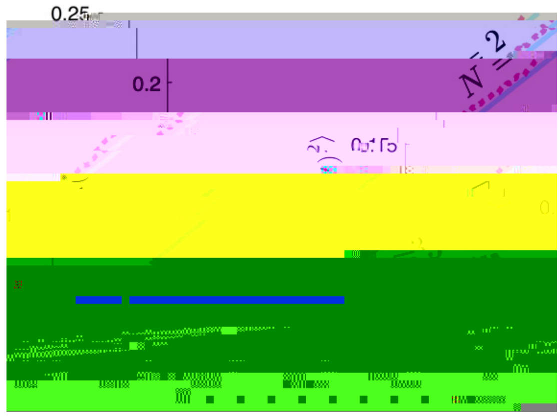


Fig. 7. Effective variance $\langle \Delta(t)^2 \rangle$ in the stochastic motion of bumps in the multilayer stochastic neural field (6). We demonstrate how the variance decreases with the number of layers $N$. Our theory (solid lines) reveals that $N$ reduces variance in a divisive way, also scaling the impact of hard delays $\tau$ (64), which matches well with numerical simulations (dashed lines). Threshold $\theta = 0.5$; noise amplitude $\varepsilon = 0.5$; delay $\tau = 0.5$; interlaminar connectivity $w_{jk} = \cos(x)$, $\forall j, k \neq j$. Variances are computed from 5000 realizations.

Utilizing the formula for $\gamma_j$ given by (46), we can write (62) as

$$A_j \sum_{k \neq j} (w_{jk} * a_k)(a_j$$

have also extended our previous work by addressing the impact of strong interlaminar coupling upon the stochastic dynamics of bumps, rather than utilizing perturbation theory to explore weak coupling [17].

Our work here could be extended in a number of contexts, particularly those concerning the impact of delays on spatial patterns in stochastic neural field equations. First, we plan to explore how propagation delays impact stability of bumps and other patterns in the vicinity of bifurcations. As we have shown here, lateral inhibitory deterministic neural fields tend to support two co-existent branches of stationary bump solutions, a stable wide bump and an unstable narrow bump, which annihilate in a saddle node bifurcation [22,9]. Delays may extend the region in which a stable stationary bump exists in the deterministic system, lengthening the amount of time it would take for noise to generate a rare event whereby the bump is extinguished as in [27]. We will likely need to develop a stochastic amplitude equation approach to study this problem as in [46,47]. In addition, we plan to explore the impact of delays on propagating patterns, such as traveling waves [45]. It is questionable whether or not delays will make wave propagation more reliable, since it may lead to instabilities, as in [12,13].

## Acknowledgment

This publication was based on work supported in part by the National Science Foundation (DMS-1311755).

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