

Wandering bumps in a stochastic neural field: A variational approach

James N. MacLaurin^b, Paul C. Bressloff^{a,*}

^a Department of Mathematical Sciences, New Jersey Institute of Technology, Newark, NJ, USA

^b Department of Mathematics, University of Utah, Salt Lake City, UT 84112, USA

ARTICLE INFO

Article history:

Received 13 August 2019

Received in revised form 6 February 2020

Accepted 7 February 2020

Available online 12 February 2020

Communicated by K. Josic

Keywords:

Stochastic neural fields

Stationary bumps

Stochastic differential equations

Spatially extended noise

Neural variability

Variational principle

ABSTRACT

We develop a generalized variational method for analyzing wandering bumps in a stochastic neural field model defined on some domain $\mathcal{U}$. For concreteness, we take $\mathcal{U} = S^1$ and consider a stochastic ring model. First, we decompose the stochastic neural field into a phase-shifted deterministic bump solution and a small error term, which is assumed to be valid up to some exponentially large stopping time. An exact, implicit stochastic differential equation (SDE) for the phase of the bump is derived by minimizing the error term with respect to a weighted $L^2(\mathcal{U}, \rho)$ norm. The positive weight ρ is chosen so that the error term consists of fast transverse fluctuations of the bump profile. We then carry out a perturbation series expansion of the exact variational phase equation in powers of the noise strength $\sqrt{\epsilon}$ to obtain an explicit nonlinear SDE for the phase that decouples from the error term. Solving the corresponding steady-state Fokker-Planck equation up to $O(\epsilon)$, we determine a leading-order expression for the long-time distribution of the position of the bump. Finally, we use the variational formulation to obtain rigorous exponential bounds on the error term, demonstrating that with very high probability the system stays in a small neighborhood of the bump for times of order $\exp(C\epsilon^{-1})$.

© 2020 Elsevier B.V. All rights reserved.

1. Introduction

Neural field theory concerns the analysis of nonlinear integro-differential equations arising from a coarse-grained continuum model of spatially-structured neural tissue. The associated integral kernels represent the spatial distribution of neuronal synaptic connections. Neural fields are an important example of spatially extended excitable systems with nonlocal interactions, and exhibit a wide range of self-organizing spatiotemporal patterns analogous to those found in nonlinear partial differential equation (PDE) models of diffusively coupled excitable systems [1,2]. For recent reviews see [3,4]. One topic of current interest is how these patterns are affected by the addition of spatially extended noise terms [5–8]. Much of the recent focus has been on traveling fronts and bumps (stationary pulses) in one-dimensional neural fields. The analysis of stochastic fronts was originally developed using formal perturbation methods [9–11], and was subsequently extended to the case of wandering bumps in single-layer and multi-layer neural fields [12–14]. There have also been a number of more rigorous functional analytic treatments of stochastic neural waves. For example, Faugeras and Inglis [15] addressed the issue of solutions and well-posedness in

stochastic neural fields by adapting results from stochastic partial differential equations (SPDEs). Stannat et al. [16–18] developed a rigorous treatment of the multi-scale decomposition of solutions, Inglis and MacLaurin [19] introduced a variational method that allows one to obtain rigorous bounds on the size of deviations from the underlying deterministic solution, and more recently, Hamster and Hupkes [20] define a wave-position that agrees with the definitions in [16–19] to linear order. A well-written recent review can be found in [21].

A common thread through all of these treatments is that in the case of a homogeneous neural field, a bump or wave solution is marginally stable with respect to uniform spatial translations. This means that one has to treat longitudinal and transverse fluctuations of the bump or wave separately in the presence of noise. This is implemented by decomposing the stochastic neural field into a deterministic bump or wave profile, whose spatial location has a slowly diffusing component, and a small error term. (There is always a non-zero probability of large deviations, but these are assumed to be negligible up to some exponentially long stopping time.) However, this decomposition is non-unique unless an additional mathematical constraint is imposed. Within the context of formal perturbation methods, the latter takes the form of a solvability condition that ensures that the error term can be identified with fast transverse fluctuations, which converge to zero exponentially in the absence of noise. One advantage of formal perturbation theory is that

* Corresponding author.

E-mail addresses: james.n.maclaurin@njit.edu (J.N. MacLaurin), bressloff@math.utah.edu (P.C. Bressloff).

it provides a relatively straightforward method for deriving an explicit stochastic differential equation (SDE) for the diffusive-like wandering of the deterministic component in the weak noise regime. However, it is not rigorous and does not provide bounds on the size of transverse fluctuations. Therefore, in this paper, we show how the explicit results of formal perturbation theory can be derived more rigorously using variational methods. This requires generalizing the analysis of [19] by taking perturbations to belong to the Hilbert space $L^2(U, \rho)$ for an appropriately chosen weight ρ , rather than $L^2(U)$, where U is the spatial domain of the neural field. That is,

$$\langle u, v \rangle_\rho = \int_U u(x)v(x)\rho(x)dx < \infty, \quad u, v \in L^2(U, \rho).$$

Fixing ρ is the additional mathematical constraint necessary to uniquely specify the amplitude-phase decomposition. ρ is chosen to ensure that the dynamics is linearly stable about the bump centered at position β , where β is the bump position that minimizes the norm weighted by ρ . In other words, to leading order in the perturbation, ρ is such that in the absence of any noise, the solution would converge to U_β (the bump centered at β) as $t \rightarrow \infty$. ρ also ensures that the linearized dynamics about U_β is self-adjoint with respect to the weighted inner product. (Note that the idea of using a variational principle with a weighted norm was previously introduced by the authors to study stochastic limit cycle oscillators [22–24]. In the latter case, marginal stability arises from phase-shift invariance around the limit cycle, and the weighted norm ensures that the amplitude is projected on to Floquet vectors.) For concreteness, we develop the theory by considering wandering bumps in a stochastic ring model, which was previously analyzed using perturbation methods in [12,25]. An advantage of the ring model is that the spatial domain $U = S^1$ is compact, which means that the spectrum of the linear operator obtained by linearizing about a bump solution is discrete. As a further generalization of [19], we also include a weak external stimulus h that can pin the location of the peak or phase of the bump in the absence of noise.

The paper is organized in follows. In Section 2 we briefly review the analysis of the deterministic ring model, considering both the existence and stability of bump solutions. In Section 3 we turn to the variational analysis of wandering bumps in a stochastic ring model. We derive an exact, implicit SDE for the phase of the bump by minimizing the error term with respect to a weighted $L^2(U, \rho)$ norm. The positive weight ρ is chosen so that the error term consists of fast transverse fluctuations of the bump profile. We then carry out a perturbation expansion of the exact variational phase equation to obtain an explicit nonlinear SDE for the phase which is accurate to $O(\epsilon)$, where ϵ is the noise strength (Section 4). Taking the homogeneous synaptic weight distribution and external input to be first-order harmonic functions on the ring with $h = O(\sqrt{\epsilon})$, one finds that the leading order phase equation reduces to a von Mises process, see also [25]. The steady-state phase density is given by a classical von Mises distribution [26,27] and the wandering of the bump is unbiased. This result was previously obtained using formal perturbation methods [12,25]. Finally, we use the variational formulation to obtain rigorous exponential bounds on the error term (Section 5). This is a major improvement on our previous result in Corollary 6.4 in [19].

2. Stationary bumps in the deterministic model ring model

Consider the deterministic neural field equation on the ring S^1 :

$$\tau \frac{\partial u(\theta, t)}{\partial t} = -u(\theta, t) + \int_{-\pi}^{\pi} J(\theta - \theta') f(u(\theta', t)) d\theta' + h(\theta) \quad (2.1)$$

where $u(\theta, t)$ denotes the activity at time t of a local population of cells with direction preference $\theta \in [-\pi, \pi)$, $J(\theta - \theta')$ is the strength of synaptic weights between cells with direction preference θ' and θ , and $h(\theta)$ is an external stimulus expressed as a function of θ . (Most applications of the ring model take $\theta \in [0, \pi]$ and interpret θ as the orientation preference of a population of neurons in primary visual cortex, see for example [28,29].) The weight distribution is a 2π -periodic and even function of θ and thus has the cosine series expansion

$$J(\theta) = \sum_{n=0}^N J_n \cos(n\theta). \quad (2.2)$$

For analytical simplicity, we assume that there are a finite number of terms in the series expansion. Finally, the firing rate function is taken to be a sigmoid

$$f(u) = \frac{1}{1 + e^{-\gamma(u-\kappa)}}, \quad (2.3)$$

with gain γ and threshold κ .

The existence and stability of deterministic bump solutions has been analyzed elsewhere [12], so we just state the main results here. We fix the time-scale by setting the time constant $\tau = 1$. First, suppose that there are no external inputs ($h \equiv 0$) and consider an even stationary solution

$$u(\theta, t) = U(\theta) = \sum_{n=0}^N A_n \cos(n\theta). \quad (2.4)$$

The latter $U(\theta)$ satisfies the integral equation

$$U(\theta) = \int_{-\pi}^{\pi} J(\theta - \theta') f(U(\theta')) d\theta'. \quad (2.5)$$

with $U(\theta) = U(-\theta)$. Expanding the weight function as a cosine Fourier series one obtains the self-consistency conditions

$$A_n = J_n \int_{-\pi}^{\pi} \cos(n\theta) f\left(\sum_{l=0}^N A_l \cos(l\theta)\right) d\theta. \quad (2.6)$$

For the general sigmoid function, the coefficients A_n could be obtained using a numerical root finding method. One way to ensure a unimodal direction tuning curve (stationary bump) is to take $J(\theta) = \cos(\theta)$ so that $A_1 = A$, $A_l = 0$ for all $l \neq 1$ and $U(\theta) = A \cos(\theta)$ with

$$A = \int_{-\pi}^{\pi} \cos(\theta) f(U(\theta)) d\theta. \quad (2.7)$$

The amplitude A can be calculated explicitly in the large gain limit $\gamma \rightarrow \infty$, for which $f(u) \rightarrow H(u - \kappa)$, where H is the Heaviside function [12]. One finds a pair of bumps, a marginally stable large amplitude wide bump and an unstable small amplitude narrow bump, consistent with the original analysis of Amari [30].

Linear stability of the stationary solutions can be determined by considering weakly perturbed solutions of the form $u(\theta, t) = U(\theta) + \psi(\theta)e^{\lambda t}$ for $|\psi(\theta)| \ll 1$. Substituting this expression into Eq. (2.5) and Taylor expanding to first order in ψ yields the equation [12]

$$(\lambda + 1)\psi(\theta) = \int_{-\pi}^{\pi} J(\theta - \theta') f'(U(\theta')) \psi(\theta') d\theta'. \quad (2.8)$$

This can be reduced to a finite-dimensional eigenvalue problem using Eq. (2.2). In the specific case $J(\theta) = \cos \theta$, we have [12]

$$(\lambda + 1)\psi(\theta) = \mathcal{A} \cos(\theta) + \mathcal{B} \sin(\theta), \quad (2.9)$$

where

$$\mathcal{A} = \int_{-\pi}^{\pi} \cos(\theta) f'(U(\theta)) \psi(\theta) d\theta, \quad \mathcal{B} = \int_{-\pi}^{\pi} \sin(\theta) f'(U(\theta)) \psi(\theta) d\theta. \quad (2.10)$$

Substituting Eq. (2.9) into (2.10) yields a matrix equation for the coefficients $\mathcal{A}$ and $\mathcal{B}$, from which one obtains the pair of eigenvalues

$$\lambda_0 = 0, \quad \lambda_e = 2 \int_0^\pi f'(U(\theta)) d\theta - 2. \quad (2.11)$$

The zero eigenvalue is a consequence of the fact that the bump solution is marginally stable with respect to uniform shifts around the ring; the generator of such shifts is the odd function $\sin \theta$. The other eigenvalue λ_e is associated with the generator, $\cos \theta$, of expanding or contracting perturbations of the bump. Thus linear stability of the bump reduces to the condition $\lambda_e < 0$. This can be used to determine the stability of the pair of bump solutions in the high-gain limit [12]. (Note that there also exist infinitely many eigenvalues that are equal to -1 , which form the essential spectrum. However, since they lie in the left-half complex λ -plane, they do not affect stability.)

A variety of previous studies have shown how breaking the underlying translation invariance of a homogeneous neural field by introducing a nonzero external input stabilizes wave and bump solutions to translating perturbations [12,31–34]. For the sake of illustration, suppose that $h(\theta) = h_0 \cos(\theta)$ in the deterministic version of Eq. (2.1). This represents a θ -dependent input with a peak at $\theta = 0$. Extending the previous analysis, one finds a stationary bump solution $U(\theta) = A \cos \theta + h_0 \cos \theta$, with A satisfying the implicit equation

$$A = \int_{-\pi}^\pi \cos \theta f(A \cos \theta + h_0 \cos \theta) d\theta. \quad (2.12)$$

Again, this can be used to determine both the width and amplitude of the bump in the high-gain limit. Furthermore, it can be established that for weak inputs, the bump is stable (rather than marginally stable) with respect to translational shifts [12]. The pinning of bumps can also occur in the presence of heterogeneous weights; this also provides a mechanism of restricting the diffusion of noisy bumps at the cost of some information loss [35].

3. Stochastic ring model and the variational method

Consider a stochastic version of the ring model given by

$$\tau du(\theta, t) = \left[-u(\theta, t) + \int_{-\pi}^\pi J(\theta - \theta') f(u(\theta', t)) d\theta' + \eta h(\theta) \right] dt + \sqrt{\epsilon} \Phi(u(\theta, t)) dW(\theta, t), \quad (3.1)$$

where $u(\theta, t)$ now denotes the stochastic activity at time t of a local population of cells with direction preference $\theta \in [-\pi, \pi]$, and we have rescaled $h(\theta)$ by the parameter η which determines the amplitude of the input. The final term on the right-hand side represents external multiplicative noise in the Ito sense, with $W(\theta, t)$ a Q-Wiener process and ϵ the noise strength. In particular, we write

$$\mathbb{E}[W(\theta, t)] = 0, \quad \mathbb{E}[W(\theta, t)W(\theta', s)] = q(\theta, \theta') s \wedge t, \quad (3.2)$$

$q : \mathbb{S}^1 \times \mathbb{S}^1 \rightarrow \mathbb{R}$ is continuous (with units of inverse time) and such that $\int_{\mathbb{S}^1} \int_{\mathbb{S}^1} q(\theta, \theta') a(\theta) a(\theta') d\theta d\theta' \geq 0$ for any continuous $a : \mathbb{S}^1 \rightarrow \mathbb{R}$, and $s \wedge t$ denotes $\min\{s, t\}$. The noise is thus colored in θ (which is necessary for the solution to be spatially continuous) and white in time. We also require that $q(\theta, \theta') = q(\theta', \theta)$ for it to be a well-defined covariance. (One could also take the noise to be colored in time by introducing an additional Ornstein–Uhlenbeck process.) We write the integral operator on $L^2([-\pi, \pi])$ corresponding to q as

$$Qz(\theta) = \int_{-\pi}^\pi q(\theta, \theta') z(\theta') d\theta', \quad (3.3)$$

noting that Q must be positive semi-definite. We will assume throughout that the input amplitude $\eta = O(\epsilon^p)$ for some $p > 0$. As we will see later, the choice of p will determine whether the network is noise or stimulus dominated in the weak noise regime ($0 \leq \epsilon \ll 1$).

Introducing the notation

$$u(\cdot, t) = u_t, \quad dW_t = dW(\theta, t),$$

we rewrite Eq. (3.1) in the more compact form

$$du_t = [-u_t + \mathcal{F}(u_t) + \eta h] dt + \sqrt{\epsilon} \Phi(u_t) dW_t, \quad t \geq 0, \quad (3.4)$$

where

$$\mathcal{F}(u_t)(\theta) = \int_{-\pi}^\pi J(\theta - \theta') f(u_t(\theta')) d\theta'. \quad (3.5)$$

Introduce the Hilbert space $H = \mathbb{L}^2(\mathbb{S}^1, \rho)$ of periodic functions on $[-\pi, \pi]$ with generalized inner product

$$\langle g, k \rangle_\rho = \int_{-\pi}^\pi g(\theta) k(\theta) \rho(\theta) d\theta, \quad g, k \in H \quad (3.6)$$

where ρ is a positive periodic function. For the moment we will keep ρ arbitrary. Later on we will determine ρ uniquely by considering the weak noise limit. In the following we will denote the inner product for $\rho = 1$ by $\langle g, k \rangle$.

In the presence of noise we wish to decompose the solution u_t into two components: the ‘closest’ point of the marginally stable manifold to u_t for a stochastic phase β_t , and a periodic error term v_t :

$$u_t = U_{\beta_t} + \sqrt{\epsilon} v_t, \quad U_a(\theta) := U(a - \theta). \quad (3.7)$$

We emphasize that this decomposition is well-defined for strong noise. However in the case of strong noise, the time that the system spends in a neighborhood of the bump is much less. Note that since the bump is symmetric, $U(a - \theta) = U(\theta - a)$. We prefer the above definition because it ensures that $\frac{d}{da} U_a(\theta) = U'_a(\theta)$.

We determine β_t by requiring that it satisfies the following variational problem:

$$\inf_{a \in \mathcal{N}(\beta_t)} \|\mathbb{T}_a^{-1} u_t - U\| = \|\mathbb{T}_{\beta_t}^{-1} u_t - U\|, \quad (3.8)$$

where $\mathbb{T}_a$ is the translation operator $\mathbb{T}_a u_t(\theta) = u_t(\theta - a)$ with $\mathbb{T}_a^{-1} = \mathbb{T}_{-a}$, $\mathcal{N}(\beta_t)$ is a sufficiently small neighborhood of β_t , and for any periodic function $g(\theta)$

$$\|g\|^2 = \langle g, g \rangle_\rho = \int_{-\pi}^\pi \rho(\theta) g(\theta)^2 d\theta. \quad (3.9)$$

There exists an exact analytic expression for the SDE giving the dynamics of the β_t (locally) minimizing (3.8), until when the curvature of the local minimum hits zero and the local minimum might disappear. This expression is exact for all values of ϵ . From the shift invariance of the inner product, we can recast the variational problem as

$$\inf_{a \in \mathcal{N}(\beta_t)} \|u_t - U_a\|_a = \|u_t - U_{\beta_t}\|_{\beta_t}, \quad (3.10)$$

where

$$\|g\|_a^2 = \int_{-\pi}^\pi \rho_a(\theta) g(\theta)^2 d\theta, \quad (3.11)$$

and $\rho_a(\theta) = \rho(a - \theta)$ (we assume that ρ is symmetric in θ). We also write $\langle g, f \rangle_a = \int_{-\pi}^\pi \rho_a(\theta) g(\theta) f(\theta) d\theta$.

We can find an exact SDE for β_t (up to a stopping time τ that we specify precisely in (3.16)) by considering the first derivatives

$$G(z, a) := \frac{\partial}{\partial a} \|z - U_a\|_a^2 = -2 \langle z - U_a, U'_a \rangle_a$$

$$+ \int_{-\pi}^{\pi} \rho'_a(\theta)(z(\theta) - U_a(\theta))^2 d\theta. \quad (3.12)$$

Define $\mathcal{M} \in \mathbb{R}$ according to

$$\mathcal{M}(z, a) = \frac{1}{2} \frac{\partial}{\partial a} G(z, a).$$

The shift invariance of the system implies

$$0 = \frac{\partial}{\partial a} \langle U_a, U_a \rangle_a = 2 \langle U_a, U'_a \rangle_a + \int_{-\pi}^{\pi} \rho'_a(\theta) U_a(\theta)^2 d\theta,$$

which means that

$$\begin{aligned} G(z, a) &= -2 \langle z, U'_a \rangle_a + \int_{-\pi}^{\pi} \rho'_a(\theta)(z(\theta)^2 - 2z(\theta)U_a(\theta)) d\theta \\ &= -2 \frac{\partial}{\partial a} \langle z, U_a \rangle_a + \int_{-\pi}^{\pi} \rho'_a(\theta) z(\theta)^2 d\theta. \end{aligned} \quad (3.13)$$

Hence,

$$\mathcal{M}(z, a) = -\frac{\partial^2}{\partial a^2} \langle z, U_a \rangle_a + \frac{1}{2} \int_{-\pi}^{\pi} \rho''_a(\theta) z(\theta)^2 d\theta. \quad (3.14)$$

It can be seen that $\mathcal{M}$ is the curvature at the local minimum. At the local minimum, it is necessary that

$$G(u_t, \beta_t) = 0. \quad (3.15)$$

Assume that initially $\mathcal{M}(u_0, \beta_0) > 0$, which is sufficient for β_0 to be a strict local minimizer of (3.10). We then seek an SDE for β_t that holds for all times less than the stopping time τ

$$\tau = \inf\{s \geq 0 : \mathcal{M}(u_s, \beta_s) = 0\}. \quad (3.16)$$

The implicit function theorem guarantees that β_t exists until this time. To see why this is the case, for any particular β_s , as long as $\mathcal{M}(u_s, \beta_s) > 0$, then since $\mathcal{M}(u_s, \beta_s)$ is the derivative of $G(u_t, \beta_t)$ in the second variable, the implicit function theorem implies. Thus we can find a β_t satisfying (3.15) in some neighborhood of u_t .

In order to derive the SDE for β_t , we apply Ito's lemma to the identity

$$dG_t \equiv dG(u_t, \beta_t) = 0, \quad (3.17)$$

with du_t given by Eq. (3.4). We take $d\beta_t$ to satisfy an SDE of the form

$$d\beta_t = V(u_t, \beta_t)dt + \sqrt{\epsilon} \langle B(u_t, \beta_t), \Phi(u_t) dW_t \rangle, \quad (3.18)$$

for functions V and B that we determine below. (Since β_t is independent of $\theta \in (-\pi, \pi]$, V is a functional of u_t .) Using Eq. (3.13), dG_t is found to be

$$\begin{aligned} dG_t &= -2 \frac{\partial}{\partial a} \langle du_t, U_a \rangle_a \Big|_{a=\beta_t} + 2 \int_{-\pi}^{\pi} \rho'_{\beta_t}(\theta) u_t(\theta) du_t(\theta) d\theta \\ &\quad + 2\mathcal{M}(u_t, \beta_t) d\beta_t \\ &\quad + \frac{1}{2} \frac{\partial^2 G_t}{\partial a^2} \Big|_{a=\beta_t} d\beta_t d\beta_t + \int_{-\pi}^{\pi} \rho'_{\beta_t}(\theta) du_t(\theta) du_t(\theta) d\theta \\ &\quad + 2d\beta_t \int_{-\pi}^{\pi} \rho''_{\beta_t}(\theta) u_t(\theta) du_t(\theta) d\theta - 2 \frac{\partial^2}{\partial a^2} \langle du_t, U_a \rangle_a \Big|_{a=\beta_t} d\beta_t \end{aligned} \quad (3.19)$$

Note that we only include the dt contributions from the quadratic differential terms involving the products $du_t d\beta_t$ and $d\beta_t d\beta_t$, which are also known as cross-variations. For example,

$$d\beta_t d\beta_t \hat{=} \epsilon \langle \Phi(u_t) \widehat{B}(u_t, \beta_t), Q \Phi(u_t) \widehat{B}(u_t, \beta_t) \rangle dt, \quad (3.20)$$

where $\widehat{B}(u_t, \beta_t) = B(u_t, \beta_t) \rho_{\beta_t}$. Substituting Eqs. (3.4) and (3.18) into Eq. (3.19) yields an SDE of the form

$$dG_t = \mathcal{V}(u_t, \beta_t)dt + \sqrt{\epsilon} \langle B(u_t, \beta_t), \Phi(u_t) dW_t \rangle. \quad (3.21)$$

In order that (3.17) is satisfied, we require both terms on the right-hand side of the above equation are zero, which will determine V and B .

First, we have

$$\begin{aligned} 0 &:= \frac{1}{2} \langle B(u_t, \beta_t), \Phi(u_t) dW_t \rangle_{\beta_t} \\ &= \mathcal{M}(u_t, \beta_t) \langle B(u_t, \beta_t), \Phi(u_t) dW_t \rangle - \frac{\partial}{\partial a} \langle \Phi(u_t) dW_t, U_a \rangle_a \Big|_{a=\beta_t} \\ &\quad + \langle \rho'_{\beta_t} u_t, \Phi(u_t) dW_t \rangle. \end{aligned}$$

Since for all times less than τ , $\mathcal{M}(u_t, \beta_t) > 0$, we have

$$B(u_t, \beta_t) = \mathcal{M}^{-1}(u_t, \beta_t) X_t, \quad (3.22)$$

where

$$X_t = (\rho_{\beta_t} U_{\beta_t})' - \rho'_{\beta_t} u_t. \quad (3.23)$$

Second,

$$0 := \mathcal{V}(u_t, \beta_t)dt = 2 [\mathcal{M}(u_t, \beta_t)V - \kappa(u_t, \beta_t)] dt, \quad (3.24)$$

with

$$\begin{aligned} \kappa &= \langle -u_t + \mathcal{F}(u_t) + \eta h, X_t \rangle dt \\ &\quad - \frac{1}{2} \int_{-\pi}^{\pi} \rho'_{\beta_t}(\theta) du_t(\theta) du_t(\theta) d\theta - \frac{1}{4} \frac{\partial^2 G_t}{\partial a^2} \Big|_{a=\beta_t} d\beta_t d\beta_t \\ &\quad - d\beta_t \int_{-\pi}^{\pi} \rho''_{\beta_t}(\theta) u_t(\theta) du_t(\theta) d\theta + \frac{\partial^2}{\partial a^2} \langle du_t, U_a \rangle_a \Big|_{a=\beta_t} d\beta_t. \end{aligned} \quad (3.25)$$

The cross-variations in Eq. (3.25) can now be evaluated using Eqs. (3.4), (3.18) and (3.22):

$$d\beta_t d\beta_t \hat{=} \epsilon \mathcal{M}^{-2}(u_t, \beta_t) \langle \Phi(u_t) X_t, Q \Phi(u_t) X_t \rangle dt, \quad (3.26a)$$

$$\int_{-\pi}^{\pi} \rho'_{\beta_t}(\theta) du_t(\theta) du_t(\theta) d\theta = \int_{-\pi}^{\pi} q(\theta, \theta) \rho'_{\beta_t}(\theta) \Phi(u_t(\theta))^2 d\theta, \quad (3.26b)$$

$$d\beta_t \int_{-\pi}^{\pi} \rho''_{\beta_t}(\theta) u_t(\theta) du_t(\theta) d\theta = \epsilon \mathcal{M}^{-1}(u_t, \beta_t) \langle \Phi(u_t) \rho''_{\beta_t} u_t, Q \Phi(u_t) X_t \rangle, \quad (3.26c)$$

$$\frac{\partial^2}{\partial a^2} \langle du_t, U_a \rangle_a \Big|_{a=\beta_t} d\beta_t = \epsilon \mathcal{M}^{-1}(u_t, \beta_t) \left\langle Q \Phi(u_t) X_t, \Phi(u_t) \frac{\partial^2}{\partial a^2} (\rho_a U_a) \Big|_{a=\beta_t} \right\rangle. \quad (3.26d)$$

It follows that the drift term V is given by

$$V(u_t, \beta_t) = \mathcal{M}^{-1}(u_t, \beta_t) \kappa(u_t, \beta_t) \quad (3.27)$$

We thus obtain the following SDE for the phase shift β_t :

$$d\beta_t = \frac{1}{\mathcal{M}(u_t, \beta_t)} (\kappa(u_t, \beta_t) + \sqrt{\epsilon} \langle X_t, \Phi(u_t) dW_t \rangle), \quad (3.28)$$

where κ can be decomposed as

$$\kappa(u_t, \beta_t) = \langle -u_t + \mathcal{F}(u_t) + \eta h, X_t \rangle + \epsilon \kappa_1(u_t, \beta_t), \quad (3.29)$$

with κ_1 containing all of the cross variation terms in (3.25). Eq. (3.28) is an exact SDE for β_t , which holds for arbitrary levels of noise ϵ up to some stopping time that depends on ϵ (assuming $\eta = O(\epsilon^p)$) [19,22]. One can also derive a corresponding equation for the amplitude v_t using the fact that $\sqrt{\epsilon} v_t = u_t - U_{\beta_t}$, so from Ito's lemma

$$\sqrt{\epsilon} dv_t = du_t - U'_{\beta_t} d\beta_t - \frac{1}{2} U''_{\beta_t} d\beta_t d\beta_t. \quad (3.30)$$

Of course, as they stand, Eqs. (3.28) and (3.30) are implicit equations, since they assume that the full solution u_t is known. Moreover, the weight ρ of the modified L^2 norm has not yet been specified. In the following, we will use the implicit equations to

obtain two important results, and in the process determine an appropriate choice for ρ . First, in Section 4 we will derive an explicit closed SDE for the phase in the weak noise limit, which recovers the results of formal perturbation theory [12,25] within a more rigorous setting. Second, we will then derive a higher order closed SDE for the phase, which is necessary in situations where the magnitude of the noise is at least of the order of the stimulus. Third, we will derive rigorous bounds on the expected time of transverse fluctuations to escape a neighborhood of the bump solution, based on a modification of the analysis of [19], see Section 5.

4. Weak noise limit

The derivation of the variational phase equation does not require ϵ (and hence $\eta = O(\epsilon^p)$) to be small. However, in order to ensure that the amplitude-phase decomposition remains valid for exponentially long time-scales, the noise and inputs have to be sufficiently weak, see Section 5. In this section, we use perturbation theory to derive an explicit, closed SDE for the phase in the weak noise regime. The form of the phase equation will depend on the choice of p . We will consider the simplest case for which $\eta = \sqrt{\epsilon}$ so that $O(\epsilon)$ contributions to the drift can be dropped. In particular, we can neglect the cross-variation terms arising from Ito's lemma and terms coupling the amplitude and phase.

4.1. Perturbation expansion to leading order in $\sqrt{\epsilon}$

Set $\eta = \sqrt{\epsilon}$. Substituting the decomposition $u_t = U_{\beta_t} + \sqrt{\epsilon}v_t$ into the left-hand side of Eq. (3.29), Taylor expanding in $\sqrt{\epsilon}$, and using the stationary condition (2.5) gives $X_t \approx \rho_{\beta_t} U'_{\beta_t}$ and

$$\kappa(u_t, \beta_t) = \sqrt{\epsilon} \langle \mathbb{L}_{\beta_t} v_t, U'_{\beta_t} \rangle_{\beta_t} + \sqrt{\epsilon} \langle h, U'_{\beta_t} \rangle_{\beta_t} + O(\epsilon(1 + \|v_t\|^2)),$$

where $\mathbb{L}_{\beta}$ is the following linear operator acting on $L^2(S^1)$:

$$\mathbb{L}_{\beta} v(\theta, t) = -v(\theta, t) + \int_{-\pi}^{\pi} J(\theta - \theta') f'(U(\beta - \theta')) v(\theta', t) d\theta', \quad (4.1)$$

It can be shown that the operator $\mathbb{L}_0$ has a 1D null space spanned by $U'(\theta)$. The fact that $U'(\theta)$ belongs to the null space follows immediately from differentiating Eq. (2.5) with respect to θ . Moreover, $U'(\theta)$ is the generator of uniform translations around the ring, so that the 1D null space reflects the marginal stability of the bump solution. (Marginal stability of the bump means that the linear operator $\mathbb{L}_0$ has a simple zero eigenvalue while the remainder of the discrete spectrum lies in the left-half complex plane. The spectrum is discrete since S^1 is a compact domain.) The corresponding adjoint operator with respect to $\langle \cdot \rangle$ is

$$\mathbb{L}_{\beta}^{\dagger} v(\theta, t) = -v(\theta, t) + f'(U(\beta - \theta)) \int_{-\pi}^{\pi} J(\theta - \theta') v(\theta', t) d\theta'. \quad (4.2)$$

It follows that $\langle \mathbb{L}_{\beta_t} v_t, U'_{\beta_t} \rangle_{\beta_t} = \langle v_t, \mathbb{L}_{\beta_t}^{\dagger} U'_{\beta_t} \rho_{\beta_t} \rangle$.

Next, to leading order, Eq. (3.14) reduces to

$$\begin{aligned} \mathcal{M}(z, a) &\simeq - \int_{-\pi}^{\pi} U_a(\theta) \frac{\partial^2}{\partial a^2} \{ \rho_a(\theta) U_a(\theta) \} d\theta + \frac{1}{2} \int_{-\pi}^{\pi} \rho_a''(\theta) U_a(\theta)^2 d\theta \\ &= \int_{-\pi}^{\pi} U_a'(\theta) \frac{\partial}{\partial a} \{ \rho_a(\theta) U_a(\theta) \} d\theta - \int_{-\pi}^{\pi} \rho_a'(\theta) U_a(\theta) U_a'(\theta) d\theta \\ &= \int_{-\pi}^{\pi} \rho_a(\theta) U_a'(\theta)^2 d\theta = \int_{-\pi}^{\pi} \rho(\theta) U'(\theta)^2 d\theta \equiv \Gamma_{\rho}, \end{aligned} \quad (4.3)$$

after integrating by parts and using translation invariance, and

$$\begin{aligned} B(u_t, \beta_t) &= \mathcal{M}^{-1}(u_t, \beta_t) \{ \rho(\beta_t) U'_{\beta_t} - \rho'(\beta_t) (u_t - U_{\beta_t}) \} \\ &\simeq \mathcal{M}^{-1}(u_t, \beta_t) \rho(\beta_t) U'_{\beta_t}. \end{aligned}$$

Hence, the leading order form of Eq. (3.28) becomes

$$d\beta_t = \frac{\sqrt{\epsilon}}{\Gamma_{\rho}} \left[\langle v_t, \mathbb{L}_{\beta_t}^{\dagger} U'_{\beta_t} \rho_{\beta_t} \rangle + \langle h, U'_{\beta_t} \rangle_{\beta_t} \right] dt + \sqrt{\epsilon} d\widehat{W}_t, \quad (4.4)$$

where

$$\begin{aligned} d\widehat{W}_t &= \Gamma_{\rho}^{-1} \langle \Phi(U_{\beta_t}) dW_t, U'_{\beta_t} \rangle_{\beta_t} \\ &= \Gamma_{\rho}^{-1} \int_{-\pi}^{\pi} \Phi(U(\beta_t - \theta)) dW_t(\theta) U'(\beta_t - \theta) \rho(\beta_t - \theta) d\theta. \end{aligned} \quad (4.5)$$

It follows that

$$\mathbb{E}[d\widehat{W}_t] = 0, \quad \mathbb{E}[d\widehat{W}_t d\widehat{W}_{t'}] = 2D(\beta_t) \delta(t - t') dt' dt,$$

with state-dependent diffusivity

$$\begin{aligned} D(\beta) &= \frac{1}{2\Gamma_{\rho}^2} \int_{-\pi}^{\pi} \int_{-\pi}^{\pi} U'(\theta) U'(\theta') \rho(\theta) \rho(\theta') \\ &\quad \times \Phi(U(\theta)) \Phi(U(\theta')) q_{\beta}(\theta, \theta') d\theta' d\theta, \end{aligned} \quad (4.6)$$

where

$$q_{\beta}(\theta, \theta') = q(\beta - \theta, \beta - \theta').$$

Hence, for a general correlation function $q(\theta, \theta')$, the noise is multiplicative (in the Ito sense). Note that if $q(\theta, \theta') = q(\theta - \theta')$ with q an even, periodic function, then $q_{\beta}(\theta, \theta') = q(\theta - \theta')$ and D is a constant.

Now suppose that we take the weight of the inner product to be defined according to

$$U'(\theta) \rho(\theta) = \nu(\theta), \quad (4.7)$$

where ν is the (unique) null vector of the adjoint operator $\mathbb{L}_0^{\dagger}$, that is, $\mathbb{L}_0^{\dagger} \nu = 0$. Within the context of the variational method, this choice of weight ensures there is a spectral gap for the linear operator $\mathbb{L}_0$, which can be used to obtain rigorous bounds on the growth of the error $\|v_t\|$, see Section 6.

4.2. Homogeneous noise

In the case that $q(\theta, \theta') = q(\theta - \theta')$, the law of the phase equation in (4.4) corresponds to the law of the following SDE that was previously obtained using formal perturbation methods [9,12,25]:

$$d\beta_t = \sqrt{\epsilon} H(\beta_t) dt + \sqrt{2\epsilon D} dW_t, \quad (4.8)$$

where

$$H(\beta) = \Gamma^{-1} \int_{-\pi}^{\pi} \nu(\theta) h(\theta - \beta) d\theta, \quad (4.9)$$

for $H(\beta + 2\pi) = H(\beta)$, with

$$\Gamma = \int_{-\pi}^{\pi} \nu(\theta) U'(\theta) d\theta, \quad (4.10)$$

$W(t)$ is a Wiener process,

$$\mathbb{E}[dW_t] = 0, \quad \mathbb{E}[dW_t dW_{t'}] = \delta(t - t') dt' dt,$$

and the diffusivity is

$$D = \frac{1}{2\Gamma^2} \int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \nu(\theta) \nu(\theta') q(\theta - \theta') d\theta' d\theta. \quad (4.11)$$

Note that D has units of radians² per unit time.

For the sake of illustration, let $J(\theta) = \cos \theta$ and $h(\theta) = h_0 \cos(\theta - \bar{\beta})$. In this particular case, one finds that, up to scalar multiplications, [12,25]

$$\nu(\theta) = f'(U(\theta)) \sin \theta, \quad U(\theta) = \cos \theta. \quad (4.12)$$

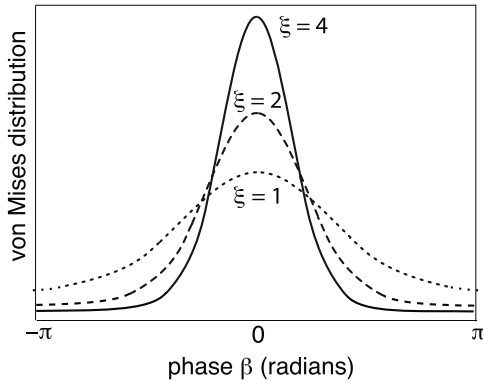


Fig. 1. Sample plots of the von Mises distribution $M(\beta; 0, \xi)$ centered at zero for various values of κ .

It can now be shown that the SDE (4.8) reduces to [25]

$$d\beta_t = -\sqrt{\epsilon} \Lambda \sin(\beta_t + \bar{\beta}) dt + \sqrt{2\epsilon D} dW_t, \quad \Lambda = \frac{h_0}{A} > 0. \quad (4.13)$$

The latter SDE is known as a von Mises process, which can be regarded as a circular analog of the Ornstein–Uhlenbeck process on a line, and generates distributions that frequently arise in circular or directional statistics [26,27]. Introduce the probability density

$$p(\beta, t | \beta_0, 0) d\beta = \mathbb{P}[\beta < \beta(t) < \beta + d\beta | \beta(0) = \beta_0].$$

This satisfies the forward Fokker–Planck equation (dropping the explicit dependence on initial conditions)

$$\frac{\partial p(\beta, t)}{\partial t} = \frac{\partial}{\partial \beta} [\sqrt{\epsilon} \Lambda \sin(\beta + \bar{\beta}) p(\beta, t)] + \epsilon D \frac{\partial^2 p(\beta, t)}{\partial \beta^2} \quad (4.14)$$

for $\beta \in [-\pi, \pi]$ with periodic boundary conditions $f(-\pi, t) = f(\pi, t)$. It is straightforward to show that the steady-state solution of Eq. (4.14) is the von Mises distribution $p(\beta) = M(\beta; \bar{\beta}, \xi/\sqrt{\epsilon})$ for $\xi = h_0/AD$, where

$$M(\beta; \bar{\beta}, \xi) = \frac{1}{2\pi I_0(\xi)} \exp(\xi \cos(\beta - \bar{\beta})), \quad (4.15)$$

where $I_0(x)$ is the modified Bessel function of the first kind and zeroth order ($n = 0$). Sample plots of the von Mises distribution are shown in Fig. 1. One finds that $p(\beta) \rightarrow 1/2\pi$ as $\xi \rightarrow 0$; since $\xi \sim h_0$ this recovers the uniform distribution of pure Brownian motion on the circle. On the other hand, the von Mises distribution becomes sharply peaked as $\xi \rightarrow \infty$. More specifically, for large positive κ ,

$$p(\beta) \approx \frac{1}{\sqrt{2\pi\sigma^2}} e^{-(\beta + \bar{\beta})^2 / 2\sqrt{\epsilon}\sigma^2}, \quad \sigma^2 = \xi^{-1}. \quad (4.16)$$

We thus have an explicit example of the noise suppression of fluctuations by an external stimulus, since $\sigma^2 \propto 1/h_0$. This particular issue is explored further elsewhere [25].

5. Bounding the growth of the error $\|v_t\|$

Recall that the error term is defined to be $\sqrt{\epsilon} v_t := u_t - U_{\beta_t}$. Extending previous analyses [19,22], the variational method can be used to derive bounds on the growth of the error $\|v_t\|_{\beta_t}$ for the $L^2(\mathcal{U}, \rho)$ norm, given that the linear operator $\mathbb{L} = -1 + \mathcal{F}'$ is linearly stable with respect to transverse perturbations that are orthogonal to the tangent space of the manifold. The main aim of this section is to demonstrate that the probability of the system leaving a neighborhood of width a of the bump scales as $\exp(-Ca^2\epsilon^{-1})$, for a constant C , which is formally stated in

(5.9). This means that, in the limit of small noise, one expects the system to stay close to the manifold of translated bumps for exponentially long periods of time. Our result is essentially a ‘Large Deviations’ estimate. We show that as long as the cumulative stochastic perturbations over a time interval of $O(b^{-1})$ are not too large, then the stability of the manifold of bump solutions will always damp down the stochastic perturbations. For simplicity, we assume that there is no external stimulus ($h = 0$) in Eq. (3.1).

We proceed by deriving an SDE for $\|v_t\|_{\beta_t}$ using repeated use of Ito’s Lemma. First, we have

$$\begin{aligned} d\|v_t\|_{\beta_t}^2 &= 2\langle v_t, dv_t \rangle_{\beta_t} + d\beta_t \int_{-\pi}^{\pi} \rho'(\beta_t - \theta) v_t(\theta)^2 d\theta \\ &\quad + \frac{1}{2} d\beta_t d\beta_t \int_{-\pi}^{\pi} \rho''(\beta_t - \theta) v_t(\theta)^2 d\theta \\ &\quad + 2d\beta_t \int_{-\pi}^{\pi} \rho'(\beta_t - \theta) v_t(\theta) dv_t(\theta) d\theta + \langle dv_t, dv_t \rangle_{\beta_t}, \end{aligned} \quad (5.1)$$

with dv_t given by Eq. (3.30), that is,

$$\sqrt{\epsilon} dv_t = du_t - U'_{\beta_t} d\beta_t - \frac{1}{2} U''_{\beta_t} d\beta_t d\beta_t, \quad (5.2)$$

and du_t satisfying equation (3.1). The latter can be re-expressed in terms of v_t so that (5.2) becomes

$$\begin{aligned} \sqrt{\epsilon} dv_t &= \{\sqrt{\epsilon} \mathbb{L}_{\beta_t} v_t + K(\sqrt{\epsilon} v_t, \beta_t)\} dt \\ &\quad + \sqrt{\epsilon} \Phi dW_t - U'_{\beta_t} d\beta_t - \frac{1}{2} U''_{\beta_t} d\beta_t d\beta_t \end{aligned} \quad (5.3)$$

where

$$K(w, \alpha) := \mathcal{F}(U_\alpha + w) - \mathcal{F}(U_\alpha) - \mathcal{F}'(U_\alpha)w. \quad (5.4)$$

and $\mathbb{L}_\alpha$ is the linear operator (4.1). Substituting Eq. (5.3) into the first term on the right-hand side of Eq. (5.1), and using the fact that

$$2\langle v_t, U'_{\beta_t} \rangle_{\beta_t} = \sqrt{\epsilon} \int_{-\pi}^{\pi} \rho'(\beta_t - \theta) v_t(\theta)^2 d\theta, \quad (5.5)$$

which follows from the equation $G(u_t, \beta_t) = 0$ as noted in (3.15), we obtain the following result:

$$\begin{aligned} d\|v_t\|_{\beta_t}^2 &= \{2\langle v_t, \mathbb{L}_{\beta_t} v_t \rangle_{\beta_t} + \frac{2}{\sqrt{\epsilon}} \langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t} + \Sigma_t\} dt \\ &\quad + 2\langle v_t, \Phi(u_t) dW_t \rangle_{\beta_t}, \end{aligned}$$

where

$$\begin{aligned} \Sigma_t dt &= \frac{1}{2} d\beta_t d\beta_t \int_{-\pi}^{\pi} \rho''(\beta_t - \theta) v_t(\theta)^2 d\theta + \langle dv_t, dv_t \rangle_{\beta_t} \\ &\quad - \frac{1}{\sqrt{\epsilon}} \langle v_t, U''_{\beta_t} \rangle_{\beta_t} d\beta_t d\beta_t + 2d\beta_t \int_{-\pi}^{\pi} \rho'(\beta_t - \theta) v_t(\theta) dv_t(\theta) d\theta. \end{aligned} \quad (5.6)$$

Since $d\beta_t d\beta_t = O(\epsilon)$, $d\beta_t dv_t = O(\epsilon^{1/2})$ and $dv_t dv_t = O(1)$, one can readily see that $\Sigma_t = O(1)$. Applying Ito’s identity to the map $x \rightarrow \sqrt{x}$, we find that

$$\begin{aligned} d\|v_t\|_{\beta_t} &= \left\{ \|v_t\|_{\beta_t}^{-1} \langle v_t, \mathbb{L}_{\beta_t} v_t \rangle + \epsilon^{-1/2} \|v_t\|_{\beta_t}^{-1} \right. \\ &\quad \times \langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t} + \frac{1}{2} \|v_t\|_{\beta_t}^{-1} \Sigma_t \\ &\quad \left. - \|v_t\|_{\beta_t}^{-3} \langle \Phi(u_t) v_t, Q \Phi(u_t) v_t \rangle_{\beta_t} \right\} dt \\ &\quad + \|v_t\|_{\beta_t}^{-1} \langle v_t, \Phi(u_t) dW_t \rangle_{\beta_t}. \end{aligned}$$

Taking ρ to be given by Eq. (4.7) ensures that there is a spectral gap, see also [16,18]. That is, the deterministic bump is linearly stable with respect to perturbations that are orthogonal to the

tangent space of the marginally stable manifold. In other words, if $v \in L^2(\mathbb{R}, \rho)$ with $\langle v, U' \rangle_\rho = 0$, then

$$\langle v, \mathbb{L}v \rangle_\rho \leq -b \|v\|_\rho^2 \quad (5.7)$$

for some $b > 0$. Using the spectral gap inequality, and the fact that

$$\langle \Phi(u_t) \rho_{\beta_t} v_t, Q \Phi(u_t) \rho_{\beta_t} v_t \rangle \geq 0,$$

we find that

$$\begin{aligned} d \|v_t\|_{\beta_t} &\leq \{-b \|v_t\|_{\beta_t} + \epsilon^{-1/2} \|v_t\|_{\beta_t}^{-1} \langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t} \\ &\quad + \frac{1}{2} \|v_t\|_{\beta_t}^{-1} \Sigma_t\} dt \\ &\quad + \|v_t\|_{\beta_t}^{-1} \langle v_t, \Phi(u_t) dW_t \rangle_{\beta_t}. \end{aligned} \quad (5.8)$$

The above SDE facilitates the following powerful probability bound on the magnitude of $\|v_t\|_{\beta_t}$ exceeding some threshold. We will establish that there exists $c, A > 0$, such that for any $p > \frac{1}{2}$, for all $a \in (\epsilon^p, A]$ and all ϵ sufficiently small, if $\sqrt{\epsilon} \|v_0\|_{\beta_0} \leq \frac{a}{2}$, then for all $T > 0$,

$$\mathbb{P}\left(\sup_{t \in [0, T]} \|v_t\|_{\beta_t} \geq a \epsilon^{-1/2}\right) \leq (Tb + 1) \exp\left(-\frac{cba^2}{\epsilon}\right). \quad (5.9)$$

Our first step towards the above probability bound is to outline a set of events that, together, imply that $\sqrt{\epsilon} \sup_{t \in [0, T]} \|v_t\|_{\beta_t} \leq a$. Afterwards, we will show that the probability of any of the events failing to hold scales as $\exp(-cTa^2\epsilon^{-1})$ for asymptotically small ϵ . To this end, we now discretize time: for $i \in \mathbb{Z}^+$, define $t_i = ib^{-1}$. Define the event

$$\mathcal{A}_i = \left\{ \sup_{t \in [t_i, t_{i+1}]} \sqrt{\epsilon} \int_{t_i \wedge \tau}^{t \wedge \tau} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \leq \frac{a}{12} \right\} \quad (5.10)$$

Define

$$\tau = \inf \left\{ t \geq 0 : \|v_t\|_{\beta_t} = a \epsilon^{-1/2} \right\} \quad (5.11)$$

$$\mathcal{B}_1 = \left\{ \|v_t\|_{\beta_t}^{-1} \Sigma_t \leq \frac{ba}{4\sqrt{\epsilon}} \text{ whenever } \sqrt{\epsilon} \|v_t\|_{\beta_t} \in [a/2, a] \right\} \quad (5.12)$$

$$\mathcal{B}_2 = \left\{ \sup_{t \leq \tau} \left| \|v_t\|_{\beta_t}^{-1} \langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t} \right| \leq \frac{ba}{8} \right\}. \quad (5.13)$$

Our next step is to establish that, writing $\mathcal{I} = \lfloor Tb \rfloor$,

$$\left\{ \sqrt{\epsilon} \sup_{t \in [0, T]} \|v_t\|_{\beta_t} \leq a \right\} \subseteq \mathcal{B}_1 \cap \mathcal{B}_2 \cap \bigcap_{i=0}^{\mathcal{I}} \mathcal{A}_i \quad (5.14)$$

Let us suppose for a contradiction that $\tau < T$. Letting i be such that $\tau \in (t_i, t_{i+1}]$, define

$$x = \max \left\{ t_{i-1}, \sup \{s \in [0, \tau) : \|v_s\|_{\beta_s} = \frac{a}{2\sqrt{\epsilon}}\} \right\}.$$

Since $\|v_s\|_{\beta_s} \geq \frac{a}{2}$ for all $s \in [x, \tau)$, it follows from (5.8) that

$$a = \sqrt{\epsilon} \|v_\tau\|_{\beta_\tau} \leq \sqrt{\epsilon} \|v_x\|_{\beta_x} + (\tau - x) \left(-\frac{ba}{2} + \frac{ab}{8} + \frac{ab}{8} \right) + \frac{a}{4} \quad (5.15)$$

since

$$\sqrt{\epsilon} \int_x^\tau \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \leq \frac{a}{4} \quad (5.16)$$

for the following reason. If $x \in [t_i, \tau]$, then

$$\left| \sqrt{\epsilon} \int_x^\tau \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \leq \left| \sqrt{\epsilon} \int_{t_i}^\tau \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right|$$

$$+ \left| \sqrt{\epsilon} \int_{t_i}^x \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \leq \frac{a}{12} + \frac{a}{12} < \frac{a}{4}.$$

If $x \in [t_{i-1}, t_i]$, then

$$\begin{aligned} &\left| \sqrt{\epsilon} \int_x^\tau \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \\ &\leq \left| \sqrt{\epsilon} \int_{t_i}^\tau \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \\ &\quad + \left| \sqrt{\epsilon} \int_{t_{i-1}}^{t_i} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \\ &\quad + \left| \sqrt{\epsilon} \int_{t_{i-1}}^x \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right| \\ &\leq \frac{a}{12} + \frac{a}{12} + \frac{a}{12} = \frac{a}{4}. \end{aligned}$$

Either way, it is clear that (5.16) holds.

Rearranging (5.15), we obtain that

$$\frac{3a}{4} \leq \sqrt{\epsilon} \|v_x\|_{\beta_x} - \frac{ba(\tau - x)}{4}. \quad (5.17)$$

From the definition of x , there are two cases. The first case is that $\sqrt{\epsilon} \|v_x\|_{\beta_x} \in (\frac{a}{2}, a)$ and $x = t_{i-1}$. In this case, we find that

$$\tau - x \leq \frac{4}{ba} \left(\sqrt{\epsilon} \|v_x\|_{\beta_x} - \frac{3a}{4} \right) < b^{-1}. \quad (5.18)$$

This contradicts the fact that $\tau - x \geq b^{-1}$. The other case is that $\sqrt{\epsilon} \|v_x\|_{\beta_x} = \frac{a}{2}$ and $x \geq t_{i-1}$. In this case, we obtain from (5.17) that

$$0 \leq -\frac{(\tau - x)}{4}, \quad (5.19)$$

which is a contradiction since $\tau - x > 0$.

We have thus established that $\tau \geq T$ and therefore that (5.14) holds. We must now bound the probability of the events (5.10), (5.12) and (5.13) not holding. Eq. (5.13) holds with probability one, as long as A is sufficiently small. This is because, thanks to the Cauchy-Schwarz Inequality,

$$|\langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t}| \leq \|v_t\|_{\beta_t} \|K(\sqrt{\epsilon} v_t, \beta_t)\|_{\beta_t} \leq C \epsilon \|v_t\|_{\beta_t}^3,$$

for some constant C and u_t being in some neighborhood of U_{β_t} by Taylor's Theorem. Hence

$$\sup_{t \leq \tau} \left| \|v_t\|_{\beta_t}^{-1} \langle v_t, K(\sqrt{\epsilon} v_t, \beta_t) \rangle_{\beta_t} \right| \leq C \epsilon a^2 < \frac{ba}{8}, \quad (5.20)$$

for small enough ϵ . Turning to (5.12), it can be shown that there exists a constant C_2 such that

$$|\Sigma_t| \leq C_2 (1 + \|u_t\|_{\beta_t}^2).$$

In turn,

$$\begin{aligned} \|u_t\|_{\beta_t}^2 &\leq (\|U_{\beta_t}\|_{\beta_t} + \sqrt{\epsilon} \|v_t\|_{\beta_t})^2 \\ &= (\|U_0\| + \sqrt{\epsilon} \|v_t\|_{\beta_t})^2 \\ &\leq (\|U_0\| + a)^2 \end{aligned}$$

for all $t \leq \tau$, as long as $\sqrt{\epsilon} \|v_t\|_{\beta_t} \leq a$. We thus see that if $\sqrt{\epsilon} \|v_t\|_{\beta_t} \geq \frac{a}{2}$, then since $\Sigma_t = O(1)$,

$$\|v_t\|_{\beta_t}^{-1} |\Sigma_t| \leq \frac{ba}{4\sqrt{\epsilon}},$$

for sufficiently small ϵ . It thus remains for us to show that for some constant $c > 0$,

$$\mathbb{P}\left(\bigcap_{i=0}^{\mathcal{I}} \mathcal{A}_i\right)^c \leq (Tb + 1) \exp(-cba^2 \epsilon^{-1}). \quad (5.21)$$

Clearly

$$\mathbb{P}\left(\left\{\bigcap_{i=0}^{\mathcal{I}} \mathcal{A}_i\right\}^c\right) \leq \sum_{i=0}^{\mathcal{I}} \mathbb{P}(\mathcal{A}_i^c).$$

It therefore suffices for us to show that

$$\mathbb{P}(\mathcal{A}_i^c) \leq \exp(-cba^2\epsilon^{-1}). \quad (5.22)$$

Fix i and define $y_t = \int_{t_i \wedge \tau}^{t \wedge \tau} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s}$. Clearly y_t is identically zero if $\tau < t_i$. If $\tau \in [t_i, t_{i+1}]$, then

$$y_t = \int_{t_{i+1}}^{t \wedge \tau} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s}.$$

The Optional Stopping Theorem implies that y_t is a Martingale [36]. For a constant $\kappa > 0$, define $z_t = \exp(\kappa y_t)$. The convexity of $\exp$, together with the fact that y_t is a martingale, implies (through Jensen's Inequality) that z_t is a submartingale. We now find that

$$\begin{aligned} \mathbb{P}\left(\sup_{t \in [t_i, t_{i+1}]} y_t \geq \frac{a}{12\sqrt{\epsilon}}\right) &= \mathbb{P}\left(\sup_{t \in [t_i, t_{i+1}]} z_t \geq \exp\left(\frac{\kappa a}{12\sqrt{\epsilon}}\right)\right) \\ &\leq \mathbb{E}[z_{t_{i+1}}] \exp\left(-\frac{\kappa a}{12\sqrt{\epsilon}}\right), \end{aligned}$$

through Doob's submartingale inequality [37, Page 54]. Now, by assumption, Φ is bounded. It follows from the Cauchy-Schwarz Inequality that

$$\phi_s := \|v_s\|_{\beta_s}^{-2} \langle \Phi(u_s) \rho_{\beta_s} v_s, Q \Phi(u_s) \rho_{\beta_s} v_s \rangle$$

is also bounded by (say) C_3 for all $s \leq \tau$. To see this, observe that

$$\begin{aligned} |\langle \Phi(u_s) \rho_{\beta_s} v_s, Q \Phi(u_s) \rho_{\beta_s} v_s \rangle| &\leq \|Q\| \|\Phi(u_s) \rho_{\beta_s} v_s\|^2 \\ &\leq \|Q\| \|\Phi(u_s)\|^2 \|v_s\|_{\beta_s}^2. \end{aligned}$$

Hence

$$\begin{aligned} \mathbb{E}[z_{t_{i+1}}] &= \mathbb{E}\left[\exp\left(\kappa \int_{t_i \wedge \tau}^{t_{i+1} \wedge \tau} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right. \right. \\ &\quad \left. \left. - \frac{\kappa^2}{2} \int_{t_i \wedge \tau}^{t_{i+1} \wedge \tau} \phi_s^2 ds + \frac{\kappa^2}{2} \int_{t_i \wedge \tau}^{t_{i+1} \wedge \tau} \phi_s^2 ds \right)\right] \\ &\leq \mathbb{E}\left[\exp\left(\kappa \int_{t_i \wedge \tau}^{t_{i+1} \wedge \tau} \|v_s\|_{\beta_s}^{-1} \langle v_s, \Phi(u_s) dW_s \rangle_{\beta_s} \right. \right. \\ &\quad \left. \left. - \frac{\kappa^2}{2} \int_{t_i \wedge \tau}^{t_{i+1} \wedge \tau} \phi_s^2 ds \right)\right] \exp\left(\frac{\kappa^2}{2b} C_3^2\right) \\ &\leq \exp\left(\frac{\kappa^2}{2b} C_3^2\right), \end{aligned}$$

since the content of the expectation is a supermartingale (one can use Ito's Lemma to show that the time-derivative of the expectation is zero). We thus find that

$$\mathbb{P}\left(\sup_{t \in [t_i, t_{i+1}]} y_t \geq \frac{a}{12\sqrt{\epsilon}}\right) \leq \exp\left(\frac{\kappa^2}{2b} C_3^2 - \frac{\kappa a}{12\sqrt{\epsilon}}\right).$$

To optimize the above bound we choose $\kappa = \frac{a}{12\sqrt{\epsilon}} \frac{b}{C_3^2}$, and obtain that

$$\mathbb{P}\left(\sup_{t \in [t_i, t_{i+1}]} y_t \geq \frac{a}{12\sqrt{\epsilon}}\right) \leq \exp\left(-\frac{ca^2b}{\epsilon}\right),$$

for a constant c . We have thus proved (5.22).

6. Discussion

In this paper we developed a generalized variational method for analyzing wandering bumps in a stochastic ring attractor

model. We decomposed the stochastic neural field into a phase-shifted deterministic bump solution and an error term. We derived an exact, implicit stochastic differential equation (SDE) for the phase of the bump by minimizing the error term with respect to a weighted $L^2(\mathcal{U}, \rho)$ norm. The positive weight ρ was chosen so that the error term consists of fast transverse fluctuations of the bump profile. We then carried out a perturbation expansion of the phase equation to obtain an explicit nonlinear SDE on the circle. Finally, we used the variational method to derive rigorous bounds on the error term, establishing that the latter remains small up to some exponentially large stopping time.

There are a number of possible extensions of the current analysis. First, one could consider separate excitatory and inhibitory populations (E-I neural fields), as well as different classes of interneuron. One major difference between scalar and E-I neural fields is that the latter can also exhibit time-periodic solutions, which would add an additional phase variable associated with shifts around the resulting limit cycle. The effects of noise on limit cycle oscillators can be analyzed in an analogous fashion to wandering bumps [22]. A second extension would be to consider higher-dimensional neural fields. For example, one could replace the ring attractor on $\mathbb{S}^1$ by a spherical attractor on $\mathbb{S}^2$, which has been proposed as a model of orientation and spatial frequency tuning in primary visual cortex [38–40]. Marginally stable modes would now correspond to rotations of the sphere. (Mathematically speaking, these are generated by the action of the Lie group $SO(3)$ rather than $SO(2)$ for the circle.)

CRediT authorship contribution statement

James N. MacLaurin: Conceptualization, Formal analysis, Writing - review & editing. **Paul C. Bressloff:** Conceptualization, Formal analysis, Writing - review & editing.

Acknowledgment

PCB was supported by the National Science Foundation (DMS-1613048 and IOS-1755431).

References

- [1] A. Keane, P. Gong, Propagating waves can explain irregular neural dynamics, *J. Neurosci.* 35 (2015) 1591–1605.
- [2] A. Byrne, D. Avitabile, S. Coombes, Next-generation neural field model: The evolution of synchrony within patterns and waves, *Phys. Rev. E* 99 (2018) 012313.
- [3] P.C. Bressloff, Spatiotemporal dynamics of continuum neural fields. Invited topical review, *J. Phys. A* 45 (2012) 033001.
- [4] P.C. Bressloff, Waves in neural media: from single neurons to neural fields, in: *Interdisciplinary Applied Mathematics*, Vol. 41, Springer, New York, 2014.
- [5] M. del Mar Quiroga, A.P. Morris, B. Krekelberg, Adaptation without plasticity, *Cell Rep.* 17 (2016) 58–68.
- [6] J. Jukes, Y. Yu, J.D. Victor, B. Krekelberg, Recurrent network dynamics; a link between form and motion, *Front. Syst. Neurosci.* 11 (2017) 12.
- [7] J. Rankin, F. Chavane, Neural field model to reconcile structure with function in primary visual cortex, *PLoS Comput. Biol.* 13 (2017).
- [8] N.V.K. Medathati, J. Rankin, A.I. Meso, P. Kornprobst, G. Masson, Recurrent network dynamics reconciles visual motion segmentation and integration, *Nat. Sci. Rep.* 7 (2017).
- [9] P.C. Bressloff, M.A. Webber, Front propagation in stochastic neural fields, *SIAM J. Appl. Dyn. Syst.* 11 (2012) 708–740.
- [10] M. Webber, P.C. Bressloff, The effects of noise on binocular rivalry waves: a phys. neurosci., 3 (2013) P03001.
- [11] P.C. Bressloff, Z.P. Kilpatrick, Nonlinear Langevin equations for the wandering of fronts in stochastic neural fields, *SIAM J. Appl. Dyn. Syst.* 14 (2015) 305–334.
- [12] Z.P. Kilpatrick, G.B. Ermentrout, Wandering bumps in stochastic neural fields, *SIAM J. Appl. Dyn. Syst.* 12 (2013) 61–94.
- [13] Z.P. Kilpatrick, Interareal coupling reduces encoding variability in multi-area models of spatial working memory, *Front. Comput. Neurosci.* 7 (2013) 82.

- [14] Z.P. Kilpatrick, Coupling layers regularizes wave propagation in stochastic neural fields, *Phys. Rev. E* 89 (2014) 022706.
- [15] O. Faugeras, J. Inglis, Stochastic neural field theory: a rigorous footing, *J. Math. Biol.* 71 (2014) 259–300.
- [16] M. Kruger, W. Stannat, Front propagation in stochastic neural fields: a rigorous mathematical framework, *SIAM J. Appl. Dyn. Syst.* 13 (2014) 1293–1310.
- [17] E. Lang, W. Stannat, L2-stability of traveling wave solutions to nonlocal evolution equations, *J. Differential Equations* 261 (2016) 4275–4297.
- [18] E. Lang, A multiscale analysis of traveling waves in stochastic neural fields, *SIAM J. Dyn. Syst.* 15 (2016) 1581–1614.
- [19] J. Inglis, J.N. MacLaurin, A general framework for stochastic traveling waves and patterns, with application to neural field equations, *SIAM J. Appl. Dyn. Syst.* 15 (2016) 195–234.
- [20] C.H.S. Hamster, H.J. Hupkes, Stability of traveling waves for reaction-diffusion equations with multiplicative noise, *SIAM J. Appl. Dyn. Syst.* 18 (2019) 205–278.
- [21] C. Kuehn, Travelling waves in monostable and bistable stochastic partial differential equations archiv, 2019.
- [22] P.C. Bressloff, J.N. MacLaurin, A variational method for analyzing stochastic limit cycle oscillators, *SIAM J. Appl. Dyn.* 17 (2018) 2205–2233.
- [23] P.C. Bressloff, J.N. MacLaurin, A variational method for analyzing limit cycle oscillations in stochastic hybrid systems, *Chaos* 28 (2018) 063105.
- [24] P.C. Bressloff, J.N. MacLaurin, Synchronization of stochastic hybrid oscillators driven by a common switching environment, *Chaos* 28 (2018) 123123.
- [25] P.C. Bressloff, Stochastic neural field model of stimulus-dependent variability in cortical neurons, *PLoS Comput. Biol.* 15 (2019) e1006755.
- [26] K.V. Mardia, P.E. Jupp, Directional Statistics, second ed., in: *Wiley Series in Probability and Statistics*, John Wiley and Sons, Chichester, 2000.
- [27] E. Codling, N. Hill, Calculating spatial statistics for velocity jump processes with experimentally observed reorientation parameters, *J. Math. Biol.* 51 (2005) 527–556.
- [28] R. Ben-Yishai, D. Hansel, H. Sompolinsky, Traveling waves and the processing of weakly tuned inputs in a cortical network module, *J. Comput. Neurosci.* 4 (1997) 57–77.
- [29] P.C. Bressloff, J.D. Cowan, An amplitude approach to contextual effects in primary visual cortex, *Neural Comput.* 14 (2002) 493–525.
- [30] S. Amari, Dynamics of pattern formation in lateral inhibition type neural fields, *Biol. Cybernet.* 27 (1977) 77–87.
- [31] S. Folias, P.C. Bressloff, Breathing pulses in an excitatory neural network, *SIAM J. Dyn. Syst.* 3 (2004) 378–407.
- [32] S.E. Folias, P.C. Bressloff, Stimulus-locked traveling pulses and breathers in an excitatory neural network, *SIAM J. Appl. Math.* 65 (2005) 2067–2092.
- [33] G.B. Ermentrout, J.Z. Jalic, J.E. Rubin, Stimulus-driven traveling solutions in continuum neuronal models with a general smooth firing rate function, *SIAM J. Appl. Math.* 70 (2010) 3039–3064.
- [34] R. Veltz, O. Faugeras, Local/global analysis of the stationary solutions of some neural field equations, *SIAM J. Appl. Dyn. Syst.* 9 (2010) 954–998.
- [35] Z.P. Kilpatrick, G.B. Ermentrout, B. Doiron, Optimizing working memory with heterogeneity of recurrent cortical excitation, *J. Neurosci.* 33 (2013) 18999–19011.
- [36] P. Protter, *Stochastic Integration and Differential Equations*, second ed., Springer-Verlag Berlin-Heidelberg, 2005.
- [37] D. Revuz, M. Yor, *Continuous Martingales and Brownian Motion*, Springer, 2005.
- [38] P.C. Bressloff, J.D. Cowan, SO(3) symmetry breaking mechanism for orientation and spatial frequency tuning in visual cortex, *Phys. Rev. Lett.* 88 (2002) 078102.
- [39] P.C. Bressloff, J.D. Cowan, Spherical model of orientation and spatial frequency tuning in a cortical hypercolumn, *Phil. Trans. R. Soc. B* 358 (2003) 1643–1667.
- [40] P.C. Bressloff, Stochastic neural field theory of wandering bumps on a sphere, *Physica D* 399 (2019) 138–152.