Wandering Bumps in Stochastic Neural Fields*

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Abstract. We study the effects of noise on stationary pulse solutions (bumps) in spatially extended neural fields. The dynamics of a neural field is described by an integrodifferential equation whose integral term characterizes synaptic interactions between neurons in different spatial locations of the network. Translationally symmetric neural fields support a continuum of stationary bump solutions, which may be centered at any spatial location. Random fluctuations are introduced by modeling the system as a spatially extended Langevin equation whose noise term we take to be additive. For nonzero noise, bumps are shown to wander about the domain in a purely diffusive way. We can approximate the associated diffusion coefficient using a small noise expansion. Upon breaking the (continuous) translation symmetry of the system using spatially heterogeneous inputs or synapses, bumps in the stochastic neural field can become temporarily pinned to a finite number of locations in the network. As a result, the effective diffusion of the bump is reduced, in comparison to the homogeneous case. As the modulation frequency of this heterogeneity increases, the effective diffusion of bumps in the network with spatially homogeneous weights.

Key words. neural field, stationary bumps, noise, effective diffusion, heterogeneity

AMS subject classifications. 92C20, 35R60

DOI. 10.1137/120877106

1. Introduction. Spatially localized patterns of persistent neural activity (bumps) are well-studied phenomena thought to subserve a variety of processes in the brain [77]. Working (short term) memory tasks are the best known examples of brain functions that may exploit the fact that bumps are localized in feature or physical space [38, 16]. For example, in oculomotor delayed-response tasks, monkeys preserve knowledge of a visual cue location using prefrontal cortical neurons with elevated activity that is correspondingly tuned to the cue location for the duration of the delay [36, 35]. There has been a great deal of discussion concerning the relative role of various classes of prefrontal cortical neurons in maintaining persistent activity [38]. One strongly supported claim is that slow recurrent excitation is the operant synaptic mechanism for preserving this localized activity during the retention period [76].

Experimentalists have suggested that prefrontal cortical circuitry consisting of local recurrent excitation and lateral inhibition may underlie the formation of the observed tuning of neurons to particular cue locations [38]. Networks with such synaptic architecture have long been studied as a theoretical framework for neural pattern formation, with seminal studies of spatially extended neural fields carried out by Wilson and Cowan [79] and Amari [1]. A

^{*}Received by the editors May 5, 2012; accepted for publication (in revised form) by B. Sandstede October 9, 2012; published electronically January 17, 2013.

http://www.siam.org/journals/siads/12-1/87710.html

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distinct advantage of such networks is that they display bistability, where stable spatially localized bumps can coexist with a spatially homogeneous "off" state. Another common feature of these models is that they tend to be (continuously) translationally symmetric, since they are spatially continuous dynamical systems whose symmetry is preserved under reflections and arbitrary translations [27, 9]. Stationary localized bump solutions arising in these models have been used as theoretical descriptions of tuning to visual input [4, 10], head direction [82], and working memory [14]. These studies demonstrate that neural field models are a useful tool for understanding the dynamical mechanisms necessary to sustain the neural substrates of a variety of sensory and motor processes.

Since stationary bumps are an idealized description of encoding location in networks representing feature space, many neural field studies have examined more deeply how model modifications affect the dynamics of bump solutions [17, 9]. Many studies have also probed the effects of persistent inputs on the dynamics of neural fields with feedback inhibition [1, 5, 42]. For sufficiently strong inhibition, networks can generate spontaneous traveling waves, so activity fails to lock to stationary [5, 33, 24, 28] or traveling [5, 34, 46] inputs. This can lead to breathing instabilities where the activity pattern oscillates regularly [33, 34]. Axonal delays can also substantially alter the dynamics of bumps in models with lateral inhibition, leading to multibumps [19], oscillatory bumps [69], and antipulses [50]. Multibump solutions can also be generated by introducing synaptic connectivity that is oscillatory in space [56, 55]. Aside from the connectivity function, the form of the firing rate function, which converts local synaptic inputs to an output firing rate, can also affect the shape and stability of stationary bumps [39, 75]. Many studies of bumps have also explored the effect of auxiliary negative feedback variables like spike frequency adaptation [64, 21, 28] or synaptic depression [81, 45]. Substantially strong negative feedback can generate a drift instability, where the bump propagates as a traveling pulse [54, 64, 21, 81, 45, 28], or a breathing instability, where the edges of the bump oscillate [65, 21, 22]. Recently, it was shown that an auxiliary synaptic facilitation variable can serve to curtail the tendency of bumps in neural fields with heterogeneous connectivity to wander [44]. Thus, there is a veritable wealth of dynamic instabilities of bumps that have been examined in deterministic neural fields.

Beyond these studies, there have been several analyses of spiking neuron models of stationary bumps [14, 16, 52]. Spiking models have the advantage of capturing finer timescale dynamics—for example, spike time synchrony—than those of which neural fields are capable. Another major difference is that spiking models are often chaotic, leading to dynamics that can appear random. This is much more akin to the environment of networks of neurons in the brain, seething with fluctuations. As a result, a basic behavior that has been revealed in numerical simulations of bumps in spiking networks is wandering of the bump's mean position [14, 16, 52]. There has been very limited investigation of such dynamics in neural field equations [14, 44]. Nonetheless, in both spiking models and neural fields with noise, the variance of the bump's position scales linearly with time, suggesting its position as a function of time behaves as a purely diffusive process [14, 16, 67, 15]. This is due in part to these systems often being translationally symmetric [16, 52, 12]. While this symmetry allows bumps to be initially nucleated at any point in the network, the inherent marginal stability means bumps are never firmly pinned to any particular location over time [14, 16, 52]. Thus, a bump's position is sensitive to noise and perturbations of the evolution equations of the underlying

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dynamical system, whose phase space contains a line attractor.

The wandering of bumps in noisy models of working memory corresponds well with existing data concerning the dependence of recall error on delay time [78, 66]. In spite of the relatively reliable correspondence between the elevation of neural activity and the cue location in prefrontal cortical networks [38], there is inevitably some error made in reporting the original cue location [78]. Interestingly, the amplitude of this error scales linearly in time [66], suggesting that it may be generated by some underlying diffusive process. Thus, improving the accuracy of stored memories in a network requires reducing the effects of this diffusion as much as possible. This invites the question of how networks for working memory may exploit dynamics that are close to line attractors to improve memory recall accuracy. Some computational studies have suggested that relaxing the translation symmetry of line attractors by introducing multiple discrete attractors may make dynamics more resilient [71, 49, 12]. However, others have viewed spatial heterogeneity in networks as a detriment to working memory that must be overcome [67, 44]. Therefore, to make the theory of bump attractors for working memory more robust, we must consider the effects of noise and network heterogeneity and any new phenomena they bring.

We propose performing an in-depth analysis of the diffusion of stationary bump solutions in neural field equations with noise. In doing so, we wish to understand how parameters of the model affect the degradation of the bump's initial position. Since oculomotor delayedresponse tasks usually require recalling the location of an object on a circle, this suggests using a neural field model whose spatial domain is finite and periodic [5, 14, 10, 75]. Thus, to accompany our analysis of stochastic neural fields, we review and extend some of the results for bump existence and stability in section 2 for deterministic ring model [72, 4, 10]

(1.1)
$$\frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\pi}^{\pi} w(x,y) f(u(y,t)) \mathrm{d}y + I(x),$$

where u(x, t) is the total synaptic input to spatial location $x \in [-\pi, \pi]$ at time t. The term I(x) represents an external, time-independent, spatially varying input. The integral term represents synaptic feedback from the entirety of the network so that the kernel w(x, y) encodes the strength of connections from y to x. In many studies of the ring model, $w(x, y) = \overline{w}(x - y)$, so the network is spatially homogeneous [5, 14, 40, 10, 75, 46], making (1.1) continuously translation symmetric. The simplest possible spatially structured kernel of this type is the pure cosine weight kernel

(1.2)
$$w(x,y) = \bar{w}(x-y) = \cos(x-y).$$

Neural fields with spatially homogeneous synaptic weights are known to have spatially structured solutions that are continuously translationally invariant, lying on a line attractor [1, 4, 71, 17, 9]. We also study the effect of periodically heterogeneous synaptic connections, where

(1.3)
$$w(x,y) = (1 + \sigma w_1(ny))\bar{w}(x-y),$$

and w_1 is a 2π -periodic function, which provides spatially heterogeneous, yet periodic, synaptic modulation whose frequency is set by the $n \in \mathbb{N}$. As a specific example, we will analyze (1.1)

using an idealized version of (1.3) where

(1.4)
$$w(x,y) = (1 + \sigma \cos(ny)) \cos(x - y).$$

Such symmetry breaks in the synaptic landscape of a network could originate from Hebbian plasticity reinforcing regions that have received more input during, for example, working memory training [25]. Periodic spatial heterogeneities in the weight functions of neural fields have been shown to alter the propagation of traveling fronts [7, 18] and pulses [47]. We will study how periodic heterogeneities affect the stability and evolution of bumps in the presence of noise.

The nonlinearity f is a firing rate function which converts synaptic inputs u to a resulting fraction of active neurons, between zero and one by definition. In line with experimental observations, this is often taken to be a sigmoidal function [79, 17, 9]

(1.5)
$$f(u) = \frac{1}{1 + e^{-\gamma(u-\theta)}},$$

where γ is the gain and θ is the threshold. We can perform much of our analysis for a general firing rate function f, such as the sigmoid (1.5). One particular idealization that eases mathematical analysis considers the infinite gain $\gamma \to \infty$ limit, so that (1.5) becomes a Heaviside step function [1, 17, 9]:

(1.6)
$$f(u) = H(u - \theta) = \begin{cases} 0 & : u < \theta, \\ 1 & : u \ge \theta. \end{cases}$$

The Heaviside firing rate function (1.6) allows us to explicitly calculate many quantities of interest in our study.

As mentioned, the deterministic neural field equation (1.1) has been studied extensively as a model of neural pattern formation [5, 27, 14, 10, 75]. The main interest of this paper is to consider effects of external fluctuations on stationary bump solutions of (1.1). For the analysis in this paper, we will consider purely additive noise, which has been included in several previous stochastic neural field studies [52, 6, 53, 43, 30, 74, 11]. Thus, in section 3, we analyze the following Langevin equation that describes a noisy neural field:

(1.7)
$$d\mathcal{U}(x,t) = \left[-\mathcal{U}(x,t) + \int_{-\pi}^{\pi} w(x,y)f(\mathcal{U}(y,t))dy + I(x)\right]dt + \varepsilon^{1/2}dW(x,t),$$

where $\mathcal{U}(x,t)$ tracks the sum of synaptic inputs at position $x \in (-\pi,\pi)$ at time t. The term dW(x,t) is the increment of a spatially dependent Wiener process such that

(1.8)
$$\langle dW(x,t)\rangle = 0, \quad \langle dW(x,t)dW(y,s)\rangle = C(x-y)\delta(t-s)dtds,$$

so that ε determines the noise amplitude, which is weak ($\varepsilon \ll 1$). Spatial correlations of the noise are described by the function C(x-y), which is symmetric and depends on the distance between two spatial locations in the network. Recently, some authors have introduced the idea of casting stochastic neural field theory in terms of a neural master equation [13, 8]. In this case, a deterministic neural field is recovered in the limit $N \to \infty$, where N measures the

system size of each local population. For large but finite N, one can truncate a Kramers–Moyal expansion of the master equation to systematically derive a Langevin neural field equation [11], such as (1.7). Furthermore, using stochastic analysis, it is possible to derive neural field models from microscopic models of networks of spiking models, but these are non-Markovian and thus difficult to analyze [30].

It is worth noting that we are considering the Langevin equation (1.7) in the Ito sense. For the purposes of this paper, there will not be any major distinctions between this and the Stratonovich sense. Major differences would begin to appear if the noise term in (1.7)were multiplicative, rather than purely additive [3, 11], due to the fact that the integral of Stratonovich calculus is defined differently than that of Ito calculus (see section 3.3 of [68] for more details). We will not pursue proofs of existence and uniqueness of solutions in this work. In [74], existence and uniqueness of solutions are shown using a contraction argument on an integral form of a discrete version of (1.7). Thus, it may be possible to use a similar method for the analysis of existence and uniqueness in the continuum equation (1.7), but this is outside the scope of the present paper.

The paper is organized as follows. First, in section 2, we present results concerning the existence and stability of bumps in the deterministic neural field equation (1.1). For the spatially homogeneous system $(w(x,y) = \bar{w}(x-y))$ in the absence of inputs $(I(x) \equiv 0)$, the linear stability of translating perturbations has an associated zero eigenvalue. This continuous translation invariance is broken by considering a weak external input $(I(x) \neq 0)$ or synaptic heterogeneity $(w(x,y) \neq \bar{w}(x-y))$. In section 3, the consequences of this bifurcation structure are considered in the presence of noise. Using a perturbative approximation, we predict that bumps wander as a purely diffusive process in the homogeneous network without inputs. In the presence of inputs, bumps are linearly stable to translations, so we find that their position evolves as a mean-reverting stochastic process in the presence of noise, rather than a purely diffusive one. On exponentially long time scales, we expect that bumps can escape from the position to which they are pinned to move to the vicinity of another discrete attractor of the deterministic system. Similarly, in the synaptically heterogeneous network, we predict that bumps are still pinned to a finite number of discrete attractors in the stochastic system (1.7). so their position evolves as a mean-reverting process. Even though bumps can escape from these pinned positions, homogenization theory reveals that they ultimately wander with a smaller effective diffusion coefficient than in the spatially homogeneous network. In section 4, we study the predictions made by our perturbation approximations and make some additional observations by numerically simulating (1.7) in a variety of contexts.

2. Bumps in the deterministic neural field. To begin, we study stationary bump solutions in the deterministic system (1.1). As opposed to the method of construction of Amari [1], we need not presume a Heaviside firing rate function (1.6) to derive explicit bump solutions. We exploit the fact that even-symmetric, 2π -periodic weight functions can be written as the sum of cosines, which are separable through trigonometric identities. Thus, existence and stability problems can be reduced to root-finding problems or linear algebraic systems [27, 40, 75]. Since there are several previous studies of existence and stability of bumps in the deterministic network (1.1), we relegate analysis of the spatially homogeneous network $(w(x, y) = \bar{w}(x - y))$ to the appendix. Derivations for the input-driven and heterogeneous system employ similar methods, so we simply state these subsequently. Our analysis shows the existence of stationary bump solutions by explicitly constructing them. For proofs of the existence and uniqueness of stationary bumps in a variety of neural field models, see [48, 31].

2.1. Spatially homogeneous network. Once we assume $w(x, y) = \overline{w}(x - y)$, it can be shown (see Appendix A) that an even symmetric stationary bump solution takes the form

(2.1)
$$U(x) = \sum_{k=0}^{N} A_k \cos(kx),$$

where N is the highest order Fourier mode in the decomposition of $\bar{w}(x)$. In the case of a purely cosine weight function (1.2) and Heaviside firing rate (1.6), we can write $A_1 = A$ and $A_k = 0$ for $k \neq 1$, so there are up to two solutions of the form

(2.2)
$$U(x) = A\cos x = \left(\sqrt{1+\theta} \pm \sqrt{1-\theta}\right)\cos x,$$

and it can be shown that the wide solution (+) is marginally stable and the narrow solution (-) is unstable, forming a separatrix between the wide bump and the rest state U(x) = 0. Due to the underlying translation invariance of the network with $w(x, y) = \bar{w}(x-y)$, the wide bump is marginally stable to translating perturbations (see Appendix A). We explore this fact in the presence of noise in section 3, showing that noise causes the bump to purely diffuse. However, by introducing small heterogeneities into the network (1.1) such as an external input or spatially heterogeneous kernel \bar{w} , this degeneracy can be broken so that bumps are pinned to a few discrete positions on the ring $x \in [-\pi, \pi]$. For (2.2), as θ is increased through unity, the two branches annihilate in a saddle-node bifurcation. We probe the effects of noise on bumps in the vicinity of this bifurcation in section 4, showing that bump extinction can occur.

2.2. Stabilizing bumps with inputs. Several studies of the ring model (1.1) have considered it to be an idealized model for the visual processing of oriented inputs [40, 5, 10, 75]. Breaking the underlying translation invariance by introducing a nonzero input I(x) to the network (1.1) stabilizes stationary bump solutions to translating perturbations [33, 75]. In particular, we study bumps that arise in the case of the *n*-modal cosine input

$$I(x) = I_0 \cos(nx).$$

Using arguments along the lines of the input-free case in Appendix A, we can derive the form for bumps centered at x = 0 as

(2.4)
$$U(x) = A\cos x + I_0\cos(nx),$$

so self-consistency of the solution (2.4) yields an implicit equation for the amplitude:

(2.5)
$$A = \int_{-\pi}^{\pi} \cos y f(A \cos y + I_0 \cos(ny)) \mathrm{d}y.$$

To demonstrate this analysis, we consider the case of a Heaviside firing rate function (1.6). It is straightforward to evaluate the integral (2.5) under the assumption that I_0 is small enough



Figure 1. Input-locked bumps in the deterministic neural field (1.1) with input (2.3). (a) The bump halfwidth a for a unimodal (n = 1) and bimodal (n = 2) input calculated using (2.7) and (2.9), demonstrating the dependence of the stable (black) and overlapping unstable (grey) branches on the input strength I_0 . (b) The stable (black) and unstable (grey) bump solutions in the case of a bimodal stimulus (dashed) of strength $I_0 = 0.4$. Threshold is fixed at $\theta = 0.5$.

that $U(x) > \theta$ for |x| < a and $U(x) < \theta$ for |x| > a. Essentially, we need to guard against multibump solutions arising [56, 55, 47], as this would complicate our analysis. In light of this, we restrict our study to small values of n and I_0 . Assuming this is the case, we can compute the amplitude A in terms of the bump width and then prescribe the threshold equation for self-consistency:

(2.6)
$$U(\pm a) = \sin 2a + I_0 \cos na = \theta.$$

In the special case n = 1, our equation for the bump half-width (2.6) becomes

$$(2.7) \qquad (2\sin a + I_0)\cos a = \theta.$$

We demonstrate the dependence of the bump half-width a upon the input strength I_0 in Figure 1(a). The implicit equation for the n = 2 case is more interesting:

$$\sin 2a + I_0 \cos 2a = \theta.$$

Equation (2.8) is explicitly solvable for the half-width a in terms of parameters θ and I_0 , using trigonometric identities, to find

(2.9)
$$a = \tan^{-1} \left[\frac{1 \pm \sqrt{1 - \theta^2 + I_0^2}}{I_0 + \theta} \right],$$

where we restrict the range of \tan^{-1} to yield $a \in [0, \pi]$. We demonstrate the dependence of the half-width a on the input strength I_0 in Figure 1(a). In addition, we show how the profile is altered by a bimodal input in Figure 1(b). Now we turn to analyzing how inputs alter the stability of stationary bumps in the network.

External inputs have previously been shown to produce bumps that are linearly stable to translating perturbations, even though the input-free system is marginally stable to such perturbations [5, 10, 33, 75]. To illustrate this, we show linear stability results for the case of a cosine weight function (1.2). Following reasoning similar to that of the input-free case (see Appendix A), the eigenvalue associated with odd perturbations to the bump can be computed as

(2.10)
$$\lambda_o = -\frac{nI_0}{A}\mathcal{I}(\sin x \sin(nx)),$$

where $\mathcal{I}(r(x))$ is given by (A.14). We are mainly interested in the fact that infinitesimal changes in I_0 can alter the linear stability of the bump with respect to these perturbations, since $\lambda_o \to 0$ in the limit $I_0 \to 0$. To employ the linear stability theory we have developed, we study the case of a Heaviside firing rate function (1.6). In this case, we know $A = 2 \sin a$ and we can compute the integrals so that the eigenvalue formula (2.10) reduces to

(2.11)
$$\lambda_o = -\frac{nI_0 \sin(na)}{2\sin^2 a + I_0 n \sin(na)}.$$

Studying specific cases will help us understand how the input changes the stability of the bump (2.4). In particular, if we start with the n = 1 case, we have

(2.12)
$$\lambda_o = -\frac{I_0}{2\sin a + I_0} < 0,$$

since $a \in [0, \pi]$ by definition. Thus, an arbitrarily weak input will pin the bump (2.4) to the position x = 0 so that it is linearly stable to odd perturbations. Moving to the n = 2 case, the odd eigenvalue will be

(2.13)
$$\lambda_o = -\frac{I_0 \sin(2a)}{\sin^2 a + I_0 \sin(2a)},$$

so that $\lambda_{-} < 0$ for sure when $a \in [0, \pi/2]$. In our analysis of the stochastic network (1.7) with input (2.3) found in section 3, the stabilization of odd perturbations to the bump allows it to remain pinned to a position, determined by the bump's original center. This contrasts with the input-free system $(I(x) \equiv 0)$, in which the bump diffuses freely in the presence of noise.

2.3. Discrete attractors due to synaptic heterogeneity. Synaptic connectivity that is patchy and periodic has been identified in anatomical studies of prefrontal cortex [57] and visual cortex [2] using fluorescent tracers. Motivated by these findings, several mathematical analyses of stationary bumps in neural fields have employed synaptic connectivity that is decaying and oscillatory [56, 55] but still translationally invariant. Such synaptic weights can lead to multiple bump solutions, where several disjoint subdomains of the network are active. On the other hand, some studies have examined the effects that synaptic weight heterogeneities have upon the propagation of traveling waves [7, 47, 18], showing they can slow traveling waves or even cause propagation failure. In light of this, we study the effects of periodically heterogeneous synaptic weight functions on the stability of bump attractors in the network (1.1). As we show, the set of bump solutions has a bifurcation structure that is a chain of saddle-node pairs rather than a line attractor.



Figure 2. A finite number (2n) of bump locations in the network (1.1) having heterogeneous synaptic connectivity (1.4) with modulation frequency n. (a) A plot of several bump center locations along $x \in (-\pi, \pi]$ for various values of n have an alternating pattern of locations with a stable bump (blue filled) and only unstable bumps (red circles). This creates a dynamic landscape of alternating stable nodes and saddles in space. (b) The associated bumps determined by implicit equation (2.17) when n = 3. Stable bumps with amplitude A_+ (2.15) centered at $x = 0, \pm \frac{2\pi}{3}$ (blue solid). The unstable bump with amplitude A_- (2.15) centered at $x = \pi, \pm \frac{\pi}{3}$ (red dashed). There are six other unstable bumps (not shown) that accompany each displayed bump. Other parameters are $\theta = 0.5$ and $\sigma = 0.2$. The firing rate function is Heaviside (1.6).

We first show that the network (1.1) with a modified weight kernel (1.3) supports stationary bump solutions. There are 2n locations $x = m\pi/n$ ($m \in \{-n, \ldots, n-1\}$) at which bumps can reside, rather than a continuum (centered at $x \in [-\pi, \pi]$), as in the network with a translationally symmetric kernel like (1.2). To start, we construct two different classes of bump solutions—those centered at $x = 2m\pi/n$ and those centered at $x = (2m + 1)\pi/n$. Stationary solutions u(x, t) = U(x) of (1.1) in the case of periodic heterogeneous weight kernel (1.3) are

(2.14)
$$U(x) = \int_{-\pi}^{\pi} (1 + \sigma w_1(ny)) \bar{w}(x - y) f(U(y)) dy.$$

Following our previous methods, we can use (2.14) along with the weight function (1.4) to find the amplitudes A_{\pm} of bumps centered at x = 0 (A_{\pm}) and $x = \pi/n$ (A_{\pm}) as

(2.15)
$$A_{\pm} = \int_{-\pi}^{\pi} \cos x (1 \pm \sigma \cos(nx)) f(U(x)) dx.$$

We demonstrate how the number and stability of bumps depend on n by plotting the bump centers on the domain $x \in [-\pi, \pi]$ for various values of n in Figure 2(a). As n is increased, the x = 0 bump reverses its stability at particular values of n. This result will be computed in our analysis of linear stability.

For a more illustrative analysis, we study the case of a Heaviside firing rate function (1.6). Under this assumption, we can compute bump solutions by requiring $U(x) > \theta$ for |x| < a and $U(x) < \theta$ for |x| > a, so we can compute the bump amplitudes A_{\pm} (2.15), which differ only in the sign of σ . First, we analyze the special case n = 1, so we integrate (2.15) and invoke the threshold condition $U(\pm a) = \theta$ to generate an implicit equation for the bump half-width



Figure 3. Bumps in the ring network (1.1) using heterogeneous synaptic connectivity (1.4) with modulation frequency n = 1. (a) A plot of the bump half-width a as it depends on amplitude of heterogeneity amplitude σ . A wide bump centered at $x = \pi$ (red dashed) separates the wide stable bump at x = 0 (blue solid) from itself on the periodic domain. A narrow bump at x = 0 (grey solid) separates the stable bump from homogeneous "off" state. (b) The profile of each bump for $\sigma = 0.2$. The threshold parameter is $\theta = 0.5$. The firing rate function is Heaviside (1.6).

a given by

(2.16)
$$\theta = \sin 2a \pm \sigma \left[a \cos a + \frac{\sin a + \sin(3a)}{4} \right]$$

Per our general analysis of the symmetry of bump solutions, we expect there to be only one peak location for each sign of σ (x = 0 and $x = \pi$), since the period of w_1 in this case is 2π , the length of the domain. However, as in the case of the homogeneous weight function, there can be two half-widths a at each location. As we can compute using linear stability, a maximum of one bump at each position of these will be linearly stable. This is demonstrated in Figure 3.

In the case that n > 1, we can integrate (2.15) and require the threshold crossing conditions $U(\pm a) = \theta$ to implicitly specify the bump half-width with the equation

(2.17)
$$\theta = \sin(2a) \pm \frac{\sigma}{2} \left[\frac{\sin((n-2)a)}{n-1} + \frac{2n\sin(na)}{n^2-1} + \frac{\sin((n+2)a)}{n+1} \right].$$

Since $\cos x$ is a unimodal function, its sole maximum will occur at x = 0 ($x = \pi/n$), when $A_+ > 0$ ($A_- > 0$). Therefore, we do not expect the appearance of multibump solutions in this context. We would expect this only if the heterogeneity in (1.4) were in the x variable. We now proceed to study the linear stability of the bump solutions specified by (2.16) and (2.17).

We now study the stability of bumps in the network (1.1) with heterogeneous synaptic weights. As we observed in our existence analysis, switching the sign of σ will lead to the two classes of bumps changing places. Therefore, we study only the stability of bumps centered at x = 0, as simply flipping the sign of σ will provide us with stability of the complementary bump. To compute the eigenvalue associated with odd perturbations of the bump in network (1.1) with the weight function (1.4), we follow reasoning similar to that of the homogeneous



Figure 4. Eigenvalue λ_o associated with odd perturbations of the bump centered at x = 0 given by (2.14) with amplitude A_+ specified in (2.15). (a) The eigenvalue λ_- as a function of heterogeneity amplitude σ becomes negative, indicating linear stability, when n = 1 and n = 2, but becomes positive, indicating linear instability, when n = 4. (b) The eigenvalue λ_o as a function of synaptic modulation frequency n as determined by the formulae (2.19) for n = 1 and (2.20) for n > 1. The heterogeneity amplitude is fixed $\sigma = 0.2$. The threshold parameter $\theta = 0.5$.

case (see Appendix A) to find

(2.18)
$$\lambda_o = -1 + \int_{-\pi}^{\pi} \sin^2 x (1 + \sigma \cos(nx)) f'(U(x)) dx$$

In the case of a Heaviside firing rate function (1.6), we can compute eigenvalues, starting with the special case n = 1. By evaluating the integral term, the eigenvalue associated with odd perturbations is given as

(2.19)
$$\lambda_o = -1 + \frac{2\sin a + 2\sigma\sin a\cos a}{2\sin a + \sigma a + 2\sigma\sin a\cos a} = -\frac{\sigma a}{2\sin a + \sigma a + \sigma\sin 2a} < 0,$$

since a > 0. Thus, we can be certain that the bump is linearly stable to shift perturbations when n = 1 and $\sigma > 0$. In a complementary way, bumps in the network where $\sigma < 0$ will be linearly unstable to shift perturbations when n = 1. For n > 1, the eigenvalue associated with odd perturbations will be

(2.20)
$$\lambda_o = \frac{\sigma n [n \sin a \cos(na) - \cos a \sin(na)]}{(n^2 - 1) \sin a + \sigma [n \cos a \sin(na) - \sin a \cos(na)]}$$

which will, in general, not be zero. We plot the eigenvalue λ_o as a function of σ and of n in Figure 4. As we have mentioned, the eigenvalue λ_o oscillates as a function of n so that the bump at x = 0 reverses its stability. This simply means that we would expect the bump at $x = \pi/n$ to be stable in this case, rather than the bump at x = 0.

3. Diffusion of bumps in stochastic neural fields. We now study the effects of additive noise on bumps in the network (1.7). Previous studies of traveling fronts in reaction-diffusion equations and neural fields have found that noise can cause fronts to wander diffusively [3, 63, 70, 6, 11]. Analyzing (1.7) reveals that noise leads to dynamics whose mean is given by a bump with a position that wanders diffusively. Our analysis allows us to approximate the diffusion coefficient of the bump, estimating the error a network may make in a working memory task that relies on the position of the bump center [78, 66, 14, 15].

3.1. Pure diffusion of bumps in a homogeneous network. We begin by studying approximate solutions to the Langevin equation (1.7) with a spatially homogeneous weight function $w(x, y) = \bar{w}(x - y)$. We are primarily interested in how the bump's position changes. Wandering of bumps was first observed numerically in modeling studies of working memory that employed rate [14] and spiking models [16]. These authors observed that such pure diffusion was due to the potential landscape of the deterministic dynamical system being a line attractor [14, 12]. We show that we can use a linear expansion to approximate the influence of spatially correlated noise on the position of bumps in a neural field. The bump's motion can be approximated as pure diffusion, whose associated coefficient we can derive from our asymptotic analysis.

To start, we assume that the additive noise in (1.7) generates two phenomena that occur on disparate time scales. Diffusion of the bump from its original position occurs on long timescales, and fluctuations in the bump profile occur on short timescales [60, 3, 11]. Thus, we express the solution \mathcal{U} of (1.7) as the sum of a fixed bump profile U displaced by $\Delta(t)$ from its mean position x, and higher order time-dependent fluctuations $\varepsilon^{1/2}\Phi + \varepsilon\Phi_1 + \varepsilon^{3/2}\Phi_2 + \cdots$ in the profile of the bump

(3.1)
$$\mathcal{U}(x,t) = U(x - \Delta(t)) + \varepsilon^{1/2} \Phi(x - \Delta(t), t) + \cdots,$$

so $\Delta(t)$ is a stochastic variable indicating the displacement of the bump U. To a linear approximation, the stochastic variable $\Delta(t)$ undergoes pure diffusion with associated coefficient $D(\varepsilon) = \mathcal{O}(\varepsilon)$, as we show. By substituting (3.1) into (1.7) and taking averages, we find that U still takes the form (2.1), as computed in Appendix A. Proceeding to next order, we find $\Delta(t) = \mathcal{O}(\varepsilon^{1/2})$ and

(3.2)
$$\mathrm{d}\Phi(x,t) = \mathcal{L}\Phi(x,t) + \varepsilon^{-1/2} U'(x) \mathrm{d}\Delta(t) + \mathrm{d}W(x,t),$$

where \mathcal{L} is the non–self-adjoint linear operator

(3.3)
$$\mathcal{L}p(x) = -p(x) + \int_{-\pi}^{\pi} \bar{w}(x-y)f'(U(y))p(y)dy$$

for any function $p(x) \in L^2[-\pi, \pi]$. We can ensure that a bounded solution to (3.2) exists by requiring that the inhomogeneous part be orthogonal to all elements of the nullspace of the adjoint operator \mathcal{L}^* . The adjoint is defined with respect to the L^2 inner product

$$\int_{-\pi}^{\pi} \left[\mathcal{L}p(x) \right] q(x) \mathrm{d}x = \int_{-\pi}^{\pi} p(x) \left[\mathcal{L}^*q(x) \right] \mathrm{d}x,$$

where $p(x), q(x) \in L^2[-\pi, \pi]$. Thus,

(3.4)
$$\mathcal{L}^*q(x) = -q(x) + f'(U(x)) \int_{-\pi}^{\pi} \bar{w}(x-y)q(y) \mathrm{d}y$$

There is a single function $\varphi(x)$ spanning the one-dimensional nullspace of \mathcal{L}^* , which we can compute explicitly for a general firing rate function f. Thus, we impose solvability of (3.2) by taking the inner product of both sides of the equation with respect to $\varphi(x)$ yielding

(3.5)
$$\int_{-\pi}^{\pi} \varphi(x) \left[U'(x) \mathrm{d}\Delta(t) + \varepsilon^{1/2} \mathrm{d}W(x,t) \right] \mathrm{d}x = 0$$

WANDERING BUMPS IN STOCHASTIC NEURAL FIELDS

Isolating $d\Delta(t)$, we find that $\Delta(t)$ satisfies the stochastic differential equation (SDE)

(3.6)
$$d\Delta(t) = -\varepsilon^{1/2} \frac{\int_{-\pi}^{\pi} \varphi(x) dW(x,t) dx}{\int_{-\pi}^{\pi} \varphi(x) U'(x) dx}.$$

With the SDE (3.6) in hand, we can compute the effective diffusivity of the bump to a linear approximation. First, note that the mean position of the bump averaged over realizations does not change in time $(\langle \Delta(t) \rangle = 0)$ since the additive noise is white in time $(\langle W(x,t) \rangle = 0)$. Computing the variance of the stochastic variable $\Delta(t)$, we find it evolves according to pure diffusion since

(3.7)
$$\begin{split} \langle \Delta(t)^2 \rangle &= \varepsilon \frac{\int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \varphi(x) \varphi(y) \langle W(x,t) W(y,t) \rangle \mathrm{d}y \mathrm{d}x}{\left[\int_{-\pi}^{\pi} \varphi(x) U'(x) \mathrm{d}x \right]^2} t, \\ \langle \Delta(t)^2 \rangle &= D(\varepsilon) t, \end{split}$$

and using the definition of W(x,t) in (1.8) yields

(3.8)
$$D(\varepsilon) = \varepsilon \frac{\int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \varphi(x)\varphi(y)C(x-y)\mathrm{d}y\mathrm{d}x}{\left[\int_{-\pi}^{\pi} \varphi(x)U'(x)\mathrm{d}x\right]^2}.$$

Therefore, we can calculate the effective diffusion for a bump in the network (1.7) with a homogeneous weight function $w(x, y) = \overline{w}(x - y)$. To calculate the diffusion coefficient $D(\varepsilon)$ for specific cases, we need to compute the constituent functions U'(x) and $\varphi(x)$. It is straightforward to calculate the form of these constituent functions for a general homogeneous weight kernel. First, differentiating (2.1), we have

(3.9)
$$U'(x) = -\sum_{k=1}^{N} kA_k \sin(kx).$$

Thus, upon applying (A.2) in the adjoint equation (3.4), we can write

(3.10)
$$\varphi(x) = f'(U(x)) \left[\sum_{k=0}^{N} C_k \cos(kx) + \sum_{l=1}^{N} S_l \sin(lx) \right],$$

where

(3.11)
$$C_k = w_k \int_{-\pi}^{\pi} \cos(kx)\varphi(x)dx, \qquad S_l = w_l \int_{-\pi}^{\pi} \sin(lx)\varphi(x)dx$$

for k = 0, ..., N and l = 1, ..., N. Thus, we could solve for $\varphi(x)$ by determining its coefficients, using techniques for linear algebraic systems.

For simplicity, in the subsequent analysis, we employ the cosine weight kernel (1.2). First, we compute the spatial derivative of the bump profile in this case,

$$(3.12) U'(x) = -A\sin x,$$

where A is defined by (2.2). To find $\varphi(x)$, we write (3.10) using (1.2), so

(3.13)
$$\varphi(x) = Cf'(U(x))\cos x + Sf'(U(x))\sin x,$$

where we set $C_1 = C$ and $S_1 = S$. Requiring self-consistency of (3.13) with the coefficient equations (3.11) and applying the identities (A.16), (A.17), and (A.18), we find

(3.14)
$$\varphi(x) = f'(U(x))\sin x,$$

up to the scaling S. Thus, for a general sigmoid (1.5), we can use our formula for the spatial derivative (3.12) along with (3.14) to compute the term in the denominator of the diffusion coefficient (3.8) given

(3.15)
$$\int_{-\pi}^{\pi} \varphi(x) U'(x) dx = -A \int_{-\pi}^{\pi} \sin^2 x f'(U(x)) dx = -A,$$

applying (A.16). Thus, the effective diffusion coefficient is given:

(3.16)
$$D(\varepsilon) = \frac{\varepsilon}{A^2} \int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \sin x \sin y f'(U(x)) f'(U(y)) C(x-y) \mathrm{d}y \mathrm{d}x.$$

To determine the diffusion coefficient (3.16), we must specify correlation function C(x-y). Two limits, spatially homogeneous and spatially uncorrelated noise, will help us understand how the spatial profile of the noise affects diffusion. In the limit of spatially homogeneous correlations $(C(x - y) \equiv C_0)$, the neural field specified by (1.7) is driven by a spatially homogeneous Wiener process $dW_0(t)$. In this case, the bump will not diffuse at all since (3.16) simplifies to

(3.17)
$$D(\varepsilon) = \frac{\varepsilon C_0}{A^2} \left[\int_{-\pi}^{\pi} \sin x f'(U(x)) \mathrm{d}x \right]^2 = 0,$$

since f'(U(x)) is even. Therefore, by widening the spatial correlation length of external noise, the diffusion of the bump is limited. Only the width of the bump will fluctuate in this case, which is not tracked by our first order approximation. In the limit of no spatial correlations $(C(x - y) \rightarrow \delta(x - y))$, every spatial point receives noise from an identically distributed independent Wiener process.¹ In this case, we can simplify (3.16) to find

(3.18)
$$D(\varepsilon) = \frac{\varepsilon}{A^2} \int_{-\pi}^{\pi} \sin^2 x \left[f'(U(x)) \right]^2 \mathrm{d}x,$$

which is nonzero for $\varepsilon > 0$.

¹One important fact to note is that if we attempt to numerically simulate (1.7) with spatially uncorrelated noise on a spatial mesh of width Δx , a nonzero correlation length Δx arises from the discretization [3, 9].

3.2. Bumps locking to inputs. Now, we study how well the network (1.7) locks to a stationary stimulus in the presence of additive noise. In the context of networks that encode working memories, an external input could be interpreted as feedback projections from another participating layer of neurons that may mirror the storage of (1.7). As shown in the deterministic network, the *n*-modal input (2.3) turns the potential landscape of the network from a line attractor (with continuous translation symmetry) to a chain of multiple attractors, such that the network now has dihedral D_n rather than circular O(2) symmetry. As we will show, inputs can pin bumps in place so they do not wander freely. In particular, we find that the stochastic variable describing bump location can be approximated with a mean-reverting (Ornstein–Uhlenbeck) process on moderate timescales. In section 4, we show that on very long timescales, large deviations occur where the bump can escape from the vicinity of the stimulus peak at which it originally resided.

Our analysis proceeds similarly to that of bumps evolving in the input free network $(I(x) \equiv 0)$. We substitute the expansion (3.1) into (1.7), and, taking averages, we find the leading order deterministic equation (1.1), giving us the input-driven bump solution (2.4). Proceeding to the next order, we find $\Delta(t) = \mathcal{O}(\varepsilon^{1/2})$ and

(3.19)
$$\mathrm{d}\Phi(x,t) = \mathcal{L}\Phi(x,t)\mathrm{d}t + \varepsilon^{-1/2}U'(x)\mathrm{d}\Delta(t) + \mathrm{d}W(x,t) + \varepsilon^{-1/2}I'(x)\Delta(t)\mathrm{d}t,$$

where \mathcal{L} is the non-self-adjoint operator (3.3). Notice that the last term on the right-hand side of (3.19) arises due to the input. Since U and Φ are functions of $x - \Delta(t)$, we have made the approximation $I(x) = I(x - \Delta(t) + \Delta(t)) \approx I(x - \Delta(t)) + I'(x - \Delta(t))\Delta(t)$. Now, we can ensure that a bounded solution exists by requiring the inhomogeneous part of (3.19) to be orthogonal to the nullspace $\varphi(x)$ of the adjoint operator \mathcal{L}^* defined by (3.4). Taking the L^2 inner product of both sides of (3.19) with $\varphi(x)$ then provides a solvability condition that we can rewrite to find that $\Delta(t)$ satisfies the Ornstein–Uhlenbeck-type SDE

(3.20)
$$d\Delta(t) + \kappa \Delta(t) dt = d\mathcal{W}(t),$$

where

(3.21)
$$\kappa = \frac{\int_{-\pi}^{\pi} \varphi(x) I'(x) \mathrm{d}x}{\int_{-\pi}^{\pi} \varphi(x) U'(x) \mathrm{d}x}, \qquad \mathcal{W}(t) = -\varepsilon^{1/2} \frac{\int_{-\pi}^{\pi} \varphi(x) W(x,t) \mathrm{d}x}{\int_{-\pi}^{\pi} \varphi(x) U'(x) \mathrm{d}x}.$$

The white noise term $\mathcal{W}(t)$ has zero mean and the same diffusion coefficient as we computed in the input-free case, so $\langle d\mathcal{W}(t)d\mathcal{W}(t)\rangle = D(\varepsilon)dt$, where $D(\varepsilon)$ is given by (3.8). The mean and variance of the Ornstein–Uhlenbeck process (3.20) can be computed using standard techniques [37],

(3.22)
$$\langle \Delta(t) \rangle = 0, \qquad \langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{D(\varepsilon)}{2\kappa} \left[1 - e^{-2\kappa t} \right],$$

assuming $\Delta(t)$ starts at a stable fixed point. Thus, as opposed to the case of the freely diffusing bump, whose position's variance scales linearly with time as (3.7), the stimulus-pinned bump's variance saturates at $D(\varepsilon)/2\kappa$ in the large t limit, according to (3.22). Variance saturation of bump attractors in networks with inputs has been demonstrated previously in simulations of spiking networks [80]. Here, we have analytically demonstrated the mechanism by which this can occur in a neural field. **3.3. Bumps pinned by synaptic heterogeneity.** Now, we explore the effect synaptic heterogeneities have on the diffusion of bumps. Noise causes bumps to wander freely in the translationally symmetric network, so the memory of the initial condition deteriorates over time. However, previous studies of bumps in spiking networks with some spatially dependent heterogeneity in model parameters have shown that the bump will become pinned to a few discrete positions in the network [82, 67]. Here, we study a periodic heterogeneity in the synaptic weight w(x, y), as in section 2, which allows us to predict the most likely position for bumps. Interestingly, as the frequency of this heterogeneity is increased, so too does the effective diffusion of the bump.

To analyze the effect that noise has upon bump solutions, we can make a small noise assumption and perform an asymptotic expansion as we did for the homogeneous network. Due to spatial heterogeneities, noise causes the center of the bump to move as a meanreverting stochastic process on short timescales, rather than as a purely diffusive process. Synaptic heterogeneities, however subtle, can trap neural activity in basins of attraction whose widths are defined by the period of the heterogeneity (1.3). We start by applying the same perturbation expansion (3.1) as before, substituting it into (1.7), and studying the hierarchy of equations generated by expanding in powers of $\varepsilon^{1/2}$. To leading order, we find the deterministic equation (2.14) for the mean bump profile U(x). To next order, we find that $\Delta(t) = \mathcal{O}(\varepsilon^{1/2})$ and

(3.23)
$$\mathrm{d}\Phi(x,t) = \mathcal{L}\Phi(x,t)\mathrm{d}t + \varepsilon^{-1/2}U'(x)\mathrm{d}\Delta(t) + \mathrm{d}W(x,t) + \varepsilon^{-1/2}B(x)\Delta(t)\mathrm{d}t,$$

where \mathcal{L} is the non–self-adjoint linear operator (3.3), and

(3.24)
$$B(x) = \sigma n \int_{-\pi}^{\pi} w'_1(ny) \bar{w}(x-y) f(U(y)) dy.$$

The last term on the right-hand side of (3.23) is generated by integrating the heterogeneous contribution from the weight function (1.3) by parts and linearizing in $\Delta(t)$. Since B(x) scales with n, this approximation will be valid only for small enough n values. Thus, we consider only the effect of low modulation frequencies n in this subsection. Now, we can ensure that a bounded solution to (3.23) exists by requiring the inhomogeneous part to be orthogonal to the nullspace $\varphi(x)$ of the adjoint operator \mathcal{L}^* defined by (3.4). Thus, we find that $\Delta(t)$ satisfies the Ornstein–Uhlenbeck process (3.20), as in the input-driven case, but here the mean-reversion rate is

(3.25)
$$\kappa = \frac{\int_{-\pi}^{\pi} \varphi(x) B(x) \mathrm{d}x}{\int_{-\pi}^{\pi} \varphi(x) U'(x) \mathrm{d}x}$$

and the noise process $\mathcal{W}(t)$ is given by (3.21). Here the bump is pinned by internal bias generated by the heterogeneous contribution of the weight kernel $w_1(ny)$.

3.4. Reduced effective diffusion due to synaptic heterogeneity. We also consider a perturbative approximation that takes into account the nonlinearity of the synaptic heterogeneity (1.3), rather than linearizing it to yield the Ornstein–Uhlenbeck approximation (3.20). To do so, we note that, as *n* becomes large, the contribution made by the heterogeneous part of (1.3) becomes small. Thus, it is not necessary to perform an expansion of this portion in $\Delta(t)$ in order to truncate the integral term in (1.7). In fact, doing so would cause ever worse approximation, due to the slope of the linearization (3.24) becoming steeper and steeper, as it scales with n. This is related to the fact that as n increases, the bump begins to escape from the vicinity of individual discrete attractors more often (see Figure 10). However, even for weak heterogeneities, escape rates are low enough such that the movement of the bump away from its initial condition can occur more slowly than in the homogeneous case.

Carrying out a small-noise expansion, we find that we can derive a nonlinear SDE (see Appendix B) that describes the evolution of the position $\Delta(t)$ of the bump in the network (1.7) with periodically heterogeneous synaptic weight

(3.26)
$$d\Delta(t) + K(n\Delta)dt = d\mathcal{W}(t),$$

where K(x) is a 2π -periodic function, given by formula (B.4) in Appendix B, depending on the heterogenous part w_1 of the weight function (1.3). Therefore, we have reduced the problem of a bump wandering in a neural field with periodic synaptic microstructure to that of a particle diffusing in a periodic potential. This is a well-studied problem for which it is possible to derive an effective diffusion coefficient [68]. To do so, we must derive the profile of the associated periodic potential well V(x) governing the dynamics (see Appendix B for the formula for the well (B.5)). With the $2\pi/n$ -periodic potential well V(x) in hand, we can derive the effective diffusion coefficient

(3.27)
$$D_{eff} = \lim_{t \to \infty} \frac{\langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2}{t}$$

of the stochastic process defined by (3.26). As the definition of D_{eff} (3.27) suggests, the approximation is valid in the limit of large time. However, we do find that it works quite well for reasonably short times, too. This is contingent upon the modulation frequency n being substantially large. As many authors have found, this approximation arises from the fact that the density of trajectories tends asymptotically to [58, 59]

(3.28)
$$P_{as}(\Delta, t) = P_0(\Delta) \frac{\exp[-\Delta^2/4D_{eff}t]}{\sqrt{4\pi D_{eff}t}}$$

where P_0 refers to the stationary $(2\pi/n\text{-periodic})$ solution of (3.26). This function is responsible for the microstructure of the density, whereas the Gaussian is responsible for its macrostructure. Usually, this structure is numerically extracted by evolving the Fokker– Planck formalism of the Langevin equation (3.26), so the approximation (3.28) can be made as an ansatz. In this case, we can approximate using the Lifson–Jackson formula [58, 32, 68]

(3.29)
$$D_{eff} = \frac{D(\varepsilon)(2\pi/n)^2}{\int_0^{2\pi/n} \int_0^{2\pi/n} \exp\left[\frac{2(V(x) - V(y))}{D(\varepsilon)}\right] \mathrm{d}y \mathrm{d}x},$$

where we have used the diffusion coefficient $D(\varepsilon)$ of the white noise source and the $2\pi/n$ periodicity of the potential well V(x). As we will show, the heterogeneity introduced in the synaptic weight (1.3) tends to decrease the effective diffusion coefficient. In other words, we usually find that $D_{eff} < D(\varepsilon)$. Thus, in some sense, having a chain of discrete attractors appears to provide better memory of the initial condition than a line attractor. Of course the trade-off is that only a finite number of initial conditions, specifically n, can be represented in our network (1.7) with the weight (1.3) with modulation frequency n.

4. Numerical simulations. In this section, we study specific examples for the asymptotic formulae we derived in section 3. Doing so, we can compare the results of averaging over a large number of numerical simulations of (1.7) to our small-noise expansion approximations. In general, we find reasonably good agreement. Simulating (1.7) also allows us to observe phenomena which we did not capture in our asymptotic approximation. In particular, we study rare events that can occur on exponentially long timescales and cannot be captured by regular perturbative expansions.

4.1. Pure diffusion in the homogeneous network. Now, to compare our asymptotic analysis to numerical simulations of the homogeneous network, we study the effect of a cosine spatial correlation function

(4.1)
$$C(x-y) = \pi \cos(x-y),$$

so the formula for the diffusion coefficient (3.16) becomes

(4.2)
$$D(\varepsilon) = \frac{\varepsilon\pi}{A^2} \left[\left(\int_{-\pi}^{\pi} \sin^2 x f'(U(x)) \mathrm{d}x \right)^2 + \left(\int_{-\pi}^{\pi} \sin x \cos x f'(U(x)) \mathrm{d}x \right)^2 \right] = \frac{\varepsilon\pi}{A^2},$$

where we have applied the identities (A.2), (A.16), and (A.18). In the case of a Heaviside firing rate function (1.6), we can use the explicit expression (A.8) for the amplitude of the stable bump to write (4.2) simply in terms of the noise amplitude ε and network threshold θ as

(4.3)
$$D(\varepsilon) = \frac{\varepsilon \pi}{2 + 2\sqrt{1 - \theta^2}}.$$

Thus, we have an asymptotic approximation for the effective diffusion coefficient $D(\varepsilon)$ of a stable bump (2.2) in the ring network (1.7) driven by additive noise. We compare (4.3) to diffusion coefficients computed from numerical simulations in Figure 5. As predicted by our theory, averaging across numerical realization the Langevin equation (1.7) shows that the variance of the bump's position scales linearly in time.

4.2. Extinction of bumps near a saddle-node. In general, there are few analyses that approximate the waiting times of large deviations in spatially extended systems with noise [29, 73]. Recently, the approach of calculating the minimum energy of the potential landscape of such systems has been used as a means of approximating the path of least action, along which a rare event is most likely to occur [26]. Here, we show an example of a large deviation in the stochastic neural field (1.7) where the dynamics escapes from the basin of attraction of the stationary bump solution (2.1).

We find that noise can cause trajectories of $\mathcal{U}(x,t)$ to cross through a separatrix of the deterministic system (1.1). This unstable manifold separates stable bump solutions from the



Figure 5. Wandering of bumps due to noise with cosine correlation function (4.1) in ring model (1.7) with Heaviside firing rate function (1.6) and cosine weight kernel (1.2). (a) A single realization of neural activity $\mathcal{U}(x,t)$ driven by additive noise with amplitude $\varepsilon = 0.001$, using stable stationary bump (2.2) as initial condition. The superimposed line tracks the center position (peak) of bump. Threshold $\theta = 0.5$. (b) The bump wanders more for higher amplitude noise $\varepsilon = 0.01$. (c) The variance $\langle \Delta(t)^2 \rangle$ of the bump's center position $\Delta(t)$ computed across 1000 realizations (red dashed) scales linearly with time, as predicted by theory (blue solid). Diffusion coefficient $D(\varepsilon)$ is computed using (4.3). The parameters are $\theta = 0.5$ and $\varepsilon = 0.01$. (d) The dependence of the diffusion coefficient on the network threshold θ for $\varepsilon = 0.001$ and $\varepsilon = 0.01$ is computed using asymptotic approximation (4.3) (blue line) and is computed numerically (red circles) across 1000 realizations run for 50 time units. Numerical simulations of (1.7) are performed using Euler-Maruyama with a trapezoidal rule for the integral with the discretization $\Delta x = 0.01$ and $\Delta t = 0.01$.

homogeneous "off" state. In Figure 6(a), we show the results of simulations where we take a Heaviside firing rate function (1.6) and the threshold $\theta = 0.95$, so the system is operating near the saddle-node bifurcation of the deterministic system at $\theta_{SN} = 1$ (see (A.25)), and additive noise causes the bump to temporarily wander and then extinguish. Relating this to oculomotor delayed-response tasks, such an event would cause major error in the recall of a cue location. In Figure 6(b), we show the mean time to extinction $T_{extinct}$ depends exponentially on the distance of the system to the saddle-node bifurcation, as described by the function $b \exp(\gamma | \theta - \theta_{SN} |)$. While we do not have a derivation of this formula per se, it stands to reason that the dynamics escapes some potential well whose height can be characterized by the distance $|\theta - \theta_{SN}|$. Thus, a Kramer's escape rate calculation could give the desired result [37]. We will leave such analysis to future studies.



Figure 6. Extinction of bumps in the network (1.7) with Heaviside firing rate function (1.6) and additive noise with cosine spatial correlations (4.1). (a) A single numerical simulation of (1.7) with threshold $\theta =$ 0.95 and noise amplitude $\varepsilon = 0.01$, where noise causes bump extinction at $t \approx 65$. (b) A plot of numerical approximations (red circles) to the mean bump extinction time $T_{extinct}$ across 1000 realizations, given by when the bump's peak crosses below threshold θ . This is fit to the exponential function $b\exp(\gamma|\theta - \theta_{SN}|)$ of the distance to the saddle-node at $\theta = \theta_{SN}$ using least squares (blue line). Specifically, $b \approx 10$ and $\gamma \approx 33$. The noise amplitude is $\varepsilon = 0.01$. The numerical scheme is the same as that in Figure 5.

4.3. Bumps locking to inputs. In the case of a Heaviside firing rate function (1.6), cosine synaptic weight (1.2), and cosine input (2.3), we have an approximation of the diffusion coefficient $D(\varepsilon)$ of the white noise $\mathcal{W}(t)$ given by the formula (4.3), and the mean-reversion rate will be given by

(4.4)
$$\kappa = \frac{nI_0 \sin(na)}{2\sin^2 a + nI_0 \sin(na)}.$$

Not surprisingly, up to a scaling factor, this is the same as the eigenvalue (2.11) associated with linear stability of odd perturbations to the bump in the deterministic system. With the formula for κ in hand, we can approximate the variance of the stochastic process $\Delta(t)$ by the formula (3.22). We compare this theory to an average across realizations in Figure 7 for the cases n = 1 and n = 2, showing that it captures the saturating nature of the variance.

4.4. Long-time switching between input-generated attractors. On substantially long waiting times, we would not necessarily expect $\Delta(t)$ to stay close to a fixed point of the deterministic system (1.1) generated by an external input (2.3), even though we have made this assumption in our perturbation analysis. The bump will eventually escape to a neighboring fixed point (see Figure 8(a)). Analogous to this, studies of mutually inhibitory neural networks have shown that including additive noise can cause transitions between two winner-take-all states of a network [61]. To our knowledge, this is the first study to examine such phenomena in the context of a spatially extended neural field equation. However, there have been studies of the switching times between wave propagation directions in a neural field with local adaptation that employed numerically derived forms of an effective potential [54, 53].

We find that additive noise causes trajectories of $\mathcal{U}(x,t)$ to cross through a separatrix of the deterministic system. Similar to our study of extinction in the input-free network, this separatrix is an unstable bump. Rather than separating a stable bump from a homogeneous



Figure 7. Bumps pinned by stationary inputs (2.3) in the stochastic neural field (1.7) with cosine correlated noise (4.1). (a) Numerical simulation for unimodal inputs (n = 1). The bump stays in the vicinity of the stable fixed point at x = 0. (b) The variance of the bump's position is computed across 1000 realizations (red dashed) saturates, rather than growing linearly. The theoretical curve (blue solid), given by the Ornstein–Uhlenbeck calculation (3.22) with (4.4), compares nicely. (c) A numerical simulation for bimodal inputs (n = 2). The bump is initiated and stays in the vicinity of the fixed point at x = 0, although there is another equilibrium at $x = \pi$. (d) The variance of the bump's position for n = 2. Other parameters are $\theta = 0.5$ and $\varepsilon = 0.01$.



Figure 8. Escape of a pinned bump solution from the vicinity of one stable equilibrium to another. (a) Numerical simulation of the stochastic neural field (1.7) in the case $I(x) = I_0 \cos 2x$. After a waiting time, the bump hops from $x \approx 0$ to $x \approx \pi$, the two stable fixed points of the underlying deterministic system. (b) Mean waiting time to a switch as a function of the strength of the input I_0 to the network as computed using numerical simulations (red circles). This is fit using least squares to an exponential bexp(γI_0) (blue solid), where b = 750 and $\gamma = 30$. Other parameters are $\theta = 0.5$ and $\varepsilon = 0.01$.

"off" state, here it separates two stable bumps, centered at x = 0 and $x = \pi$. In Figure 8(a), we show one such transition. In this case, our approximation using an Ornstein–Uhlenbeck process (3.20) will clearly break down, since the bump is now attracted to a completely different stable state. In Figure 8(b), we show that the mean time until a switch T_{switch} depends exponentially on the strength of the input I_0 , given $b \exp(\gamma I_0)$. Essentially, we are controlling the depth of a bistable potential well in which the dynamics of the bump's position will evolve. The stronger the input, the deeper the well will be. As in the case of bump extinction, we might expect that a Kramer escape rate calculation could give us such a result [68, 37]. However, we will leave such calculations to future studies of rare events in neural fields.

4.5. Pinning of bumps by synaptic heterogeneity. Now to compare our asymptotic analysis of the synaptic heterogeneity case to numerical simulations, we specify a Heaviside firing rate function (1.6), cosine (1.2) for \bar{w} and w_1 , and cosine spatial noise correlations (4.1). Here, the diffusion coefficient $D(\varepsilon)$ is given by the formula (4.3). In addition, we restrict our modulation frequency to be greater than unity, n > 1. Then the function B(x), which leads to pinning, can be computed using the formula (3.14) for $\varphi(x)$ and substituted into our formula for the mean reversion rate, so

(4.5)
$$\kappa = \frac{\sigma n [\cos a \sin(na) - n \sin a \cos(na)]}{(n^2 - 1) \sin a \pm \sigma [n \cos a \sin(na) - \sin a \cos(na)]},$$

which, not surprisingly, is simply the eigenvalue λ_{-} associated with odd perturbations (2.20), up to a sign switch. The sign of the σ portion of the denominator is ambiguous because we must select the stable bump, which could have either A_{+} or A_{-} as its amplitude. Using these specific formulae, we can compute the variance of the Ornstein–Uhlenbeck process (3.20) with the formula (3.22). We show an example of this in Figure 9 for n = 2 and n = 3. In particular, we observe that the variance of the bump, computed by averaging across many realizations of (1.7), saturates after a substantial amount of time. However, as the number of attractors n is increased, the Ornstein–Uhlenbeck approximation (3.20) does not do as well at approximating the variance, since the bump can begin to escape from the starting pinned location to a neighboring one.

4.6. Reduced effective diffusion due to synaptic heterogeneity. Now, we compare the asymptotic approximation of D_{eff} (3.29) to numerical simulations. We thus consider the case of a Heaviside firing rate function (1.6), cosine (1.2) for \bar{w} and w_1 , and cosine spatial correlations (4.1). In this case, the diffusion coefficient $D(\varepsilon)$ is given by the formula (4.3). After some calculations (see Appendix B), we find that the formula (3.29) for the effective diffusion coefficient yields

(4.6)
$$D_{eff} = \frac{D(\varepsilon)}{[\mathcal{I}_0(2\mathcal{V}(n)/D(\varepsilon))]^2}$$

where $\mathcal{I}_0(x)$ is the modified Bessel function of the zeroth kind. As shown in Appendix B, $\lim_{n\to\infty} D_{eff} = D(\varepsilon)$. Previous studies of traveling waves in periodically modulated neural fields have also found that wavespeed tends to that of the homogeneous network in the limit of



Figure 9. Pinning of bumps in the network (1.7) with synaptic weight (1.4) for low frequency n synaptic heterogeneity. (a) Numerical simulation of (1.7) using synaptic weight (1.4) for n = 2, $\sigma = 0.1$, and $\varepsilon = 0.01$ shows that the bump remains pinned to the stable attractor at x = 0. (b) The variance of the bump's position plotted against time computed numerically (red dashed) across 1000 realizations saturates after a moderate amount of time when n = 2, as predicted by the Ornstein–Uhlenbeck approximation (3.20) (blue solid). (c) Numerical simulation for n = 3, $\sigma = 0.1$, and $\varepsilon = 0.01$ shows that the bump remains pinned to the stable location at x = 0. (d) The variance of the bump's position plotted against time computed numerically (red dashed) does not match the prediction of the Ornstein–Uhlenbeck approximation (blue solid) quite as well for long times. The threshold parameter is $\theta = 0.5$.

high frequency modulation [7, 47, 18]. Using the formula (4.6) along with the definition (B.9), we approximate the diffusion of a bump in a network with synaptic modulation frequency n = 8 in Figure 10(b). Notice that the linear approximation of the variance's scaling with time matches averages over realizations fairly well. Thus, the variance no longer saturates in time, as in the case of low frequency modulation n. As evidenced by our plots of the probability density $P(\Delta, t)$, in Figure 10(c), the stochastic process $\Delta(t)$ behaves diffusively with microperiodic modulation, as suggested by the asymptotic formula (3.28). Finally, we compare our theoretical effective diffusion (4.6) across a span of modulation frequencies n to that approximated using numerical simulations in Figure 10(d). We find reasonable agreement. In particular, we see that synaptic heterogeneity substantially reduces the effective diffusion of the bump for lower values of n. We plan to pursue this result much more deeply in future studies.



Figure 10. The effective diffusion is reduced in a network with high frequency modulation in synaptic weights. (a) A single numerical simulation of (1.7) with synaptic weight (1.4) in the case n = 8 where the bump frequently moves between locations of stable attractors (cyan) of the deterministic system. (b) The variance of the bump's position scales linearly with time, rather than saturating as in the case of lower frequency modulation of synaptic weights. (c) The probability density $P(\Delta, t)$ of the bump position computed across 5000 realizations evaluated at time t = 400 reveals microperiodic structure of diffusion. Vertical lines (cyan) indicate the location of the n = 8 attractors. (d) Asymptotic approximation of effective diffusion D_{eff} (blue line) computed using theory (4.6) as compared with that computed using numerical simulations (red dashed dot). For small values of n, effective diffusion is considerably reduced as compared to diffusion (4.3) in the homogeneous system (black line). Other parameters are $\theta = 0.5$, $\sigma = 0.1$, and $\varepsilon = 0.01$.

5. Discussion. We have analyzed the effects of external noise on stationary bumps in spatially extended neural field equations. In a network with spatially homogeneous synaptic weights, we found that noise causes bumps to wander about the spatial domain according to a purely diffusive process. We can asymptotically approximate the diffusion coefficient of this process using a small-noise expansion, which assumes that the profile of the activity variable is still a bump to first order. Following this analysis, we study the effects of breaking the translation symmetry of the spatially homogeneous network in two ways, using external inputs and using spatially heterogeneous synaptic weights. Effectively, this alters the dynamic landscape of the network from a line attractor to a chain of discrete attractors. External inputs with multiple peaks serve to pin the bump to one of multiple discrete attractors of the network, so that the bump's position evolves as a mean-reverting process. Periodic synaptic heterogeneity also leads to pinning at low modulation frequencies. At high modulation frequencies, the bump can escape from being pinned to a single location in the network, leading to effective

diffusion in the limit of long time. We can approximate this effective diffusion using methods for studying a particle diffusing in a periodic potential.

We see the main contribution of this work as introducing the notion of reliability, in the presence of noise, to stationary bumps in neural fields. The specific location of a bump in a neural field carries important information about the stimulus that formed it [1, 14, 56]. Noise can degrade this memory, so it is very useful to understand how the architecture and parameters of a neural field model affect how easily this deterioration takes place. This has specific applications in the realm of oculomotor delayed-response tasks in prefrontal cortex, where it is clear there are networks of neurons that can encode visuospatial location during the retention period of such tasks [35, 38, 12]. Since our work shows that breaking the translation symmetry of neural fields can serve to decrease noise-induced diffusion of bumps, it is worth pursuing how well this improves the overall memory process. The advantage of a network that is a line attractor is that, in the absence of noise, it can represent a continuum of initial conditions. Since all of these positions are marginally stable, noise easily degrades memory of the initial condition due to diffusion along the line attractor. On the other hand, when symmetry is broken so a network behaves as a chain of discrete attractors, there is a trade-off between initial representation errors versus long term robustness to noise. Interestingly, we also found that increasing the spatial correlation length of the noise can serve to decrease the resulting diffusion of the bump. Therefore, working memory networks may better maintain a bump's initial condition by spatially averaging incoming external noise.

Neural fields are known to generate a variety of spatially structured solutions other than bumps, such as traveling waves [79, 1, 5, 7, 23], stationary periodic patterns [42, 24, 69], and spiral waves [41, 51, 9]. It would be interesting to study more about how these structures are affected by external noise. It seems that the form of the spatially structured solution markedly contributes to the the way in which noise affects its form and position. Neural fields that support spatially periodic patterns can have the onset of the associated Turing instability shifted by the inclusion of spatially structured noise [43]. In recent work on traveling fronts in stochastic neural fields, it was found that the bifurcation structure of the neural field determined the characteristic scaling of front location variance with time [11]. In particular, pulled fronts have subdiffusive variance scaling, as opposed to diffusive variance scaling of a front in a bistable system. We plan to study the effects of noise on bumps in planar neural fields [62]. In this case, the spatial correlations of the noise will be in two dimensions. Therefore, dimensional bias in the synaptic weight or noise correlations could lead to asymmetric diffusion of the bump in the plane. In addition, it is possible that this analysis could be extended to a two component system, such as a model with local adaptation that generates traveling pulses [64]. If there is a separation of timescales between the activity and adaptation, variable, fast-slow analysis might be paired with the small-noise expansion (3.1) to derive the effective variance in position of the traveling pulse. Finally, it would be quite interesting to study the effects of noise on spiral waves in neural fields [41, 51]. Doing so may provide us with some experimentally verifiable measure of whether long-time deviations of the spiral center arise from deterministic meandering or noise.

Appendix A. Bumps in the homogeneous network. In this appendix, we review the analysis of existence and stability of bumps in a ring model with an even symmetric, spatially

homogeneous weight function [27, 40, 75] so that $w(x, y) = \bar{w}(x - y)$. Upon assuming a stationary solution u(x, t) = U(x), the scalar equation (1.1) requires that it satisfy the integral equation

(A.1)
$$U(x) = \int_{-\pi}^{\pi} \bar{w}(x-y) f(U(y)) dy,$$

which we can interpret by expanding the even, 2π -periodic, spatially homogeneous weight function

(A.2)
$$\bar{w}(x-y) = \sum_{k=0}^{N} w_k \cos(k(x-y)) = \sum_{k=0}^{N} w_k [\cos(kx)\cos(ky) + \sin(kx)\sin(ky)],$$

where N is the maximal mode of the weight function, so that (A.1) becomes

(A.3)
$$U(x) = \sum_{k=0}^{N} A_k \cos(kx) + \sum_{l=1}^{N} B_k \sin(kx),$$

where

(A.4)
$$A_k = w_k \int_{-\pi}^{\pi} \cos(kx) f(U(x)) dx, \qquad B_l = w_l \int_{-\pi}^{\pi} \sin(lx) f(U(x)) dx$$

for k = 0, ..., N and l = 1, ..., N. We look specifically for even stationary bump solutions, as is often done in analyses of localized solutions in neural fields [1, 17, 75, 9]. Thus, $B_l = 0$ for all l, so

$$U(x) = \sum_{k=0}^{N} A_k \cos(kx),$$

and we can solve for the coefficients A_k by requiring self-consistency of the solution $U(x) = \sum_{k=0}^{N} A_k \cos(kx)$ such that (A.4) becomes

(A.5)
$$A_k = \int_{-\pi}^{\pi} \cos(kx) f\left(\sum_{k=0}^{N} A_k \cos(kx)\right) dx, \qquad k = 0, \dots, N.$$

For a general sigmoidal firing rate function (1.5), one could determine the coefficients A_k using a numerical root finding method [75].

For a Heaviside firing rate function (1.6) and cosine weight function (1.2), we can solve exactly for the bump amplitude $A_1 = A$. Equation (2.1) shows that U(x) is unimodal and symmetric, since $A_k = 0$ for $k \neq 1$, so it will cross above and below θ at locations x = -aand x = a, respectively. This provides us with the threshold conditions $U(\pm a) = \theta$ for (2.1), which can be written equivalently as

(A.6)
$$a = \cos^{-1}\frac{\theta}{A}.$$

Thus, we know that $U(x) > \theta$ for $x \in (-\cos^{-1}(\theta/A), \cos^{-1}(\theta/A))$, so the k = 1 self-consistency condition (A.5) becomes

(A.7)
$$A = 2 \int_0^{\cos^{-1} \theta/A} \cos x \, \mathrm{d}x = 2 \sin \left(\cos^{-1} \frac{\theta}{A} \right) = 2 \sqrt{1 - \frac{\theta^2}{A^2}}.$$

Solving (A.7) for the scaling factor of the bump $U = A \cos x$ gives

(A.8)
$$A = \sqrt{1+\theta} \pm \sqrt{1-\theta},$$

which generates the formula (2.2). Applying (A.6), half-widths *a* can be easily computed:

(A.9)
$$a_{\pm} = \cos^{-1}\left(\frac{\sqrt{1+\theta} \mp \sqrt{1-\theta}}{2}\right).$$

The network with a cosine weight kernel (1.2) is translationally symmetric, so that we could construct a bump solution centered at any position $x \in [-\pi, \pi]$. This would simply lead to a system of two equations for A and B associated with (A.3), but the width of such a bump would be the same as that of (2.1). We can also show this by calculating the linear stability of bumps in the network (1.1), revealing marginal stability of a shift perturbation.

Linear stability of bumps (2.1) can be computed by analyzing the evolution of small, smooth, separable perturbations such that $u(x,t) = U(x) + \psi(x)e^{\lambda t}$ for $|\psi(x)| \ll 1$. Substituting this expansion into the evolution equation (1.1), Taylor expanding, applying (A.1), and studying the first order equation yields [10, 20, 75]

(A.10)
$$(\lambda+1)\psi(x) = \int_{-\pi}^{\pi} \bar{w}(x-y)f'(U(y))\psi(y)\mathrm{d}y$$

Applying the expansion (A.2), we can write

(A.11)
$$(\lambda+1)\psi(x) = \sum_{k=0}^{N} \mathcal{A}_k \cos(kx) + \sum_{l=1}^{N} \mathcal{B}_l \sin(lx)$$

where

(A.12)
$$\mathcal{A}_k = w_k \int_{-\pi}^{\pi} \cos(kx) f'(U(x))\psi(x) \mathrm{d}x, \qquad \mathcal{B}_l = w_l \int_{-\pi}^{\pi} \sin(lx) f'(U(x))\psi(x) \mathrm{d}x$$

for k = 0, ..., N and l = 1, ..., N. Thus, we reduce the infinite dimensional equation (A.10) to a $(2N) \times (2N)$ linear spectral problem (A.11). Such a technique was recently shown for a general class of weight functions in [75].

To demonstrate this analysis further, we proceed with the case of a unimodal cosine weight function (1.2), so $\mathcal{A}_1 = \mathcal{A}$, $\mathcal{B}_1 = \mathcal{B}$, and $\mathcal{A}_k = \mathcal{B}_k = 0$ for $k \neq 1$. Upon substituting the form of $\psi(x)$ given by (A.11) into the system of equations (A.12), we have

(A.13)
$$(\lambda+1)\begin{pmatrix} \mathcal{A}\\ \mathcal{B} \end{pmatrix} = \begin{pmatrix} \mathcal{I}(\cos^2 x) & \mathcal{I}(\cos x \sin x)\\ \mathcal{I}(\cos x \sin x) & \mathcal{I}(\sin^2 x) \end{pmatrix} \begin{pmatrix} \mathcal{A}\\ \mathcal{B} \end{pmatrix},$$

where

(A.14)
$$\mathcal{I}(r(x)) = \int_{-\pi}^{\pi} r(x) f'(U(x)) \mathrm{d}x.$$

First, note that the essential spectrum is $\lambda = -1$ and thus does not contribute to any instabilities. Upon integrating (A.5) by parts, we see

(A.15)
$$A = \int_{-\pi}^{\pi} \cos x f(A\cos x) dx = A \int_{-\pi}^{\pi} \sin^2 x f'(A\cos x) dx.$$

Therefore, as long as $A \neq 0$, the equality (A.15) tells us

(A.16)
$$\mathcal{I}(\sin^2 x) = \int_{-\pi}^{\pi} \sin^2 x f'(U(x)) dx = 1.$$

Using this identity (A.16) and the fact that (A.14) is linear, we can then compute

(A.17)
$$\mathcal{I}(\cos^2 x) = \mathcal{I}(1 - \sin^2 x) = \mathcal{I}(1) - \mathcal{I}(\sin^2 x) = \mathcal{I}(1) - 1.$$

Finally, we can use integration by parts to show

(A.18)
$$\mathcal{I}(\cos x \sin x) = \int_{-\pi}^{\pi} \cos x \sin x f'(U(x)) dx = -\int_{-\pi}^{\pi} \sin x f(U(x)) dx = 0,$$

since U(x) is even. Using the identities (A.16), (A.17), and (A.18), it is straightforward to compute the eigenvalues that determine the stability of the bump (2.1). We do so by finding the roots of the associated characteristic equation

(A.19)
$$\lambda^2 + (2 - \mathcal{I}(1))\lambda = 0,$$

which reveals the zero eigenvalue $\lambda_o = 0$, associated with the constant \mathcal{B} , defined in (A.12), which means it reveals the linear stability of bumps in response to odd (shifting) perturbations. The fact that λ_o is zero arises due to the underlying translation symmetry of (1.1) when w(x, y)is the cosine weight function (1.2). In addition, the stability of the bump (2.1) is determined by the sign of the other eigenvalue

(A.20)
$$\lambda_e = 2 \int_0^\pi f'(U(x)) \mathrm{d}x - 2$$

associated with \mathcal{A} , defined by (A.12), and thus even (expanding or contracting) perturbations of the bump.

In the limit of infinite gain $\gamma \to \infty$, f becomes the Heaviside (1.6), and

(A.21)
$$f'(U(x)) = \frac{\mathrm{d}H(U(x))}{\mathrm{d}U} = \frac{\delta(x-a)}{|U'(a)|} + \frac{\delta(x+a)}{|U'(a)|},$$

in the sense of distributions, so (A.20) will be

(A.22)
$$\lambda_e = -2 + \frac{2}{|U'(a)|}$$

for the bump (2.2) of half-width a. Identifying threshold θ values at which (A.22) crosses zero will give the location of a saddle-node bifurcation [1, 20, 33]. Equation (A.22) allows us to compute eigenvalues exactly for the wide and narrow bumps since (A.9) gives the half-widths and the spatial derivative at the edges

(A.23)
$$|U'(a_{\pm})| = \left(\sqrt{1+\theta} \pm \sqrt{1-\theta}\right) \sqrt{\frac{1 \pm \sqrt{1-\theta^2}}{2}}$$

Substituting the expression (A.23) into (A.22) yields

(A.24)
$$\lambda_e = \lambda_{\pm} = -2 + \frac{2\sqrt{2}}{(\sqrt{1+\theta} \pm \sqrt{1-\theta})\sqrt{1\pm\sqrt{1-\theta^2}}},$$

the nonzero eigenvalue associated with the wide (+) and narrow (-) bumps. To identify the threshold θ where the two pulses annihilate in a saddle-node bifurcation, we look for where $\lambda_{\pm} = 0$. Imposing this requirement on (A.24) means

(A.25)
$$\left(\sqrt{1+\theta} \pm \sqrt{1-\theta}\right)\sqrt{1\pm\sqrt{1-\theta^2}} = \sqrt{2}.$$

It can be shown that (A.25) is equivalent to finding zeros of the quartic $\theta^4 + 2\theta^2 - 3$, whose real solutions are $\theta = \pm 1$. Thus, as θ is increased from zero, the stable wide and unstable narrow bump branches will coalesce in a saddle-node bifurcation at $\theta = 1$.

Appendix B. Reduced effective diffusion due to synaptic heterogeneity. In this appendix, we derive the effective diffusion coefficient for a bump in a stochastic neural field with periodically heterogeneous synaptic connectivity. We begin by performing the expansion (3.1), substituting it into (1.7), and studying the $\mathcal{O}(\varepsilon^{1/2})$ equation

(B.1)
$$\mathrm{d}\Phi(x,t) = \mathcal{L}\Phi(x,t)\mathrm{d}t + \varepsilon^{-1/2}U'(x)\mathrm{d}\Delta(t) + \mathrm{d}W(x,t) + \varepsilon^{-1/2}B(x,\Delta(t))\mathrm{d}t,$$

where \mathcal{L} is the non–self-adjoint linear operator (3.3), and

(B.2)
$$B(x,\Delta) = \sigma \int_{-\pi}^{\pi} [w_1(n(y+\Delta)) - w_1(ny)]\bar{w}(x-\Delta-y)f(U(y))dy,$$

which we will show to be small below. To derive the function $B(x, \Delta)$, we have performed the change of variables

$$\int_{-\pi}^{\pi} w(x,y) f(U(y-\Delta)) dy = \int_{-\pi}^{\pi} (1+\sigma w_1(ny)) \bar{w}(x-\Delta-y) f(U(y)) dy + \sigma \int_{-\pi}^{\pi} (w_1(n(y+\Delta)) - w_1(ny)) \bar{w}(x-\Delta-y) f(U(y)) dy$$

in order to make the cancellation

$$U(x - \Delta) = \int_{-\pi}^{\pi} (1 + \sigma w_1(ny))\overline{w}(x - \Delta - y)f(U(y))dy.$$

Since $w_1(ny)$ is a $2\pi/n$ -periodic function, we can also assume that $B(x, \Delta)$ will be $2\pi/n$ -periodic in Δ . To justify the retention of the term $B(x, \Delta)$ in the $\mathcal{O}(\varepsilon^{1/2})$, we note that upon integrating (B.2) by parts, we have

$$B(x,\Delta) = \frac{\sigma}{n} \int_{-\pi}^{\pi} W_d(ny) \frac{\mathrm{d}}{\mathrm{d}y} \left[\bar{w}(x-\Delta-y) f(U(y)) \right] \mathrm{d}y = \mathcal{O}(1/n),$$

which will be small for large n, and we have defined

$$W_d(x) = \int_{-\pi}^{x} [w_1(y + \Delta) - w_1(y)] \, \mathrm{d}y.$$

Note also that since we require $\Delta(t) = \mathcal{O}(\varepsilon^{1/2})$ for our approximation, we can truncate a Taylor expansion of $\bar{w}(x - y - \Delta)$ so that we define

(B.3)
$$B(x,\Delta) = \sigma \int_{-\pi}^{\pi} \left[w_1(n(y+\Delta)) - w_1(ny) \right] \bar{w}(x-y) f(U(y)) \mathrm{d}y.$$

Now, we can ensure that a bounded solution to (B.1) exists by requiring the inhomogeneous part to be orthogonal to the nullspace $\varphi(x)$ of the adjoint operator \mathcal{L}^* defined by (3.4). Doing so, we find that $\Delta(t)$ satisfies the nonlinear SDE (3.26), where

(B.4)
$$K(n\Delta) = \frac{\int_{-\pi}^{\pi} \varphi(x) B(x, \Delta) dx}{\int_{-\pi}^{\pi} \varphi(x) U'(x) dx}$$

is a $2\pi/n$ -periodic function since $B(x, \Delta)$ is $2\pi/n$ -periodic in Δ . The white noise term $\mathcal{W}(t)$ is given by (3.21), so it has zero mean and the same diffusion coefficient as we computed in the input-free case, so $\langle d\mathcal{W}(t)d\mathcal{W}(t)\rangle = D(\varepsilon)dt$, where $D(\varepsilon)$ is given by (3.8). Therefore, to find the periodic potential well V(x) associated with the nonlinear SDE (3.26), we simply integrate the nonlinear function (B.4), which yields

(B.5)
$$V(\Delta) = \int_{-\pi}^{\Delta} K(n\eta) \mathrm{d}\eta = \frac{\int_{-\pi}^{\pi} \varphi(x) \int_{-\pi}^{\Delta} B(x,\eta) \mathrm{d}\eta \mathrm{d}x}{\int_{-\pi}^{\pi} \varphi(x) U'(x) \mathrm{d}x}.$$

To compute the effective diffusion coefficient (3.29) for the specific case of a Heaviside firing rate (1.6), cosine weight (1.2), and cosine correlation (4.1), we start with the function $B(x, \Delta)$ (B.3), which is $2\pi/n$ -periodic in the Δ argument

(B.6)
$$B(x,\Delta) = \sigma \left[\frac{2(\cos(n\Delta) - 1)(n\cos a\sin(na) - \sin a\cos(na))}{n^2 - 1} \right] \cos x$$
$$+ \sigma \left[\frac{2\sin(n\Delta)(n\sin a\cos(na) - \cos a\sin(na))}{n^2 - 1} \right] \sin x.$$

Now, with the formula (B.6) in hand, along with $\varphi(x)$ and A_{\pm} , we can compute the nonlinear function $K(n\Delta)$ using (B.4). Note that the cosine portion of (B.6) vanishes upon integration to yield

(B.7)
$$K(n\Delta) = \left[\frac{2\sigma(n\sin a\cos(na) - \cos a\sin(na))}{(n^2 - 1)\sin a \pm \sigma[n\cos a\sin(na) - \sin a\cos(na)]}\right]\sin(n\Delta),$$

where we select the + or - in the denominator of (B.7), depending on whether the bump centered at x = 0 is stable or not. Now, in order to compute our effective diffusion coefficient D_{eff} (3.29), we must integrate the function $K(n\Delta)$ to yield the potential function governing the dynamics of (3.26). This gives us the potential function

(B.8)
$$V(\Delta) = -\mathcal{V}(n)\cos(n\Delta),$$

where the amplitude (or half-height) of each well is

(B.9)
$$\mathcal{V}(n) = \frac{2\sigma(n\sin a\cos(na) - \cos a\sin(na))}{n(n^2 - 1)\sin a \pm \sigma n[n\cos a\sin(na) - \sin a\cos(na)]}$$

Now, finally, we use the standard formula for the effective diffusion coefficient of a particle in a periodic potential well (3.29). With our particular cosine potential well (B.8), the integrals in (3.29) can be computed and are equal to one another:

$$\int_{0}^{2\pi/n} \exp\left[\frac{2V(x)}{D(\varepsilon)}\right] \mathrm{d}x = \int_{0}^{2\pi/n} \exp\left[-\frac{2V(x)}{D(\varepsilon)}\right] \mathrm{d}x$$
$$= \int_{0}^{2\pi/n} \exp\left[\frac{2\mathcal{V}(n)}{D(\varepsilon)}\cos(nx)\right] \mathrm{d}x = \frac{2\pi}{n}\mathcal{I}_{0}\left(\frac{2\mathcal{V}(n)}{D(\varepsilon)}\right),$$

where $\mathcal{I}_0(x)$ is the modified Bessel function of the zeroth kind. Thus, we find the formula (3.29) for the effective diffusion coefficient yields the formula (4.6). We can also note that in the limit of high frequency modulations $(n \to \infty)$ the formula (4.6) tends to the diffusion coefficient of the homogeneous network since

$$\lim_{n \to \infty} \mathcal{V}(n) = \lim_{n \to \infty} \frac{2\sigma(n \sin a \cos(na) - \cos a \sin(na))}{n(n^2 - 1) \sin a \pm \sigma n[n \cos a \sin(na) - \sin a \cos(na)]} = 0$$

so that we find the limit of (4.6) to be

$$\lim_{n \to \infty} D_{eff} = \lim_{n \to \infty} \frac{D(\varepsilon)}{[\mathcal{I}_0(2\mathcal{V}(n)/D(\varepsilon))]^2} = \frac{D(\varepsilon)}{I_0(0)} = D(\varepsilon).$$

Acknowledgments. We would like to thank Brent Doiron and Robert Rosenbaum for several helpful conversations concerning this work.

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