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GHOSTS OF BUMP ATTRACTORS IN STOCHASTIC NEURAL FIELDS: BOTTLENECKS AND EXTINCTION

Zachary P. Kilpatrick

Department of Applied Mathematics, University of Colorado
Boulder, CO 80309, USA
and
Department of Mathematics, University of Houston
Houston, TX 77204, USA

Abstract.

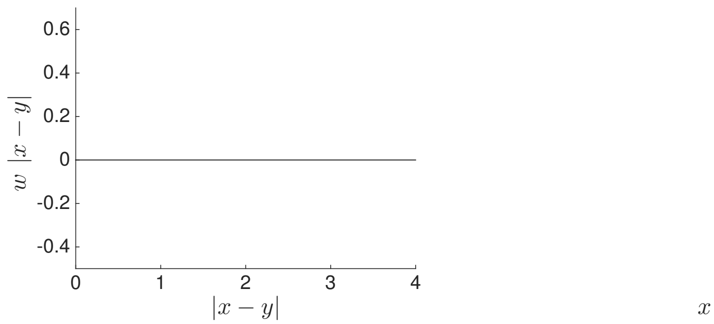

Figure 1. Saddle-node bifurcation of bumps in (1) with a Heaviside firing rate function (3). (A) Difference of Gaussians weight function $w(x) = e^{-x^2} - Ae^{-x^2/\sigma^2}$ has a Mexican hat profile with $A = 0.4 < 1$ and $\sigma = 2 > 1$. The critical bump half-width a_c at the saddle-node satisfies the relation $w(2a_c) = 0$. (B) The weight function integral (4) determines the bump half-widths a. When θ is below the critical threshold θ_c at the saddle-node, there are two stationary bump solutions to (1): one stable a_s and one unstable a_u. When $\theta > \theta_c$, there are zero equilibria, but the dynamics of (1) are slow in the bottleneck near $U_c(x)$.

By utilizing the integral function (4), we can write the even-symmetric solution

$$U(x) = W(x+a) - W(x-a). \tag{7}$$

To determine the half-width a, we require the threshold conditions $U(\pm a) = \theta$ of the solution (7) to yield

$$U(a) = W(2a) = \int_0^{2a} w(y)\mathrm{d}y = \theta.$$

Note that when $\theta < W_{max} = \max_x W(x)$, there will be a stable and unstable bump solution to (1). When $\theta = \theta_c \equiv W_{max}$, there is a single marginally stable bump solution $U_c(x)$ to (1), as illustrated in Fig. 1B. Differentiating $W(2a)$ by its argument yields $W'(2a_c) = w(2a_c) \equiv 0$ as an implicit equation for the half-width a_c at this criticality. Utilizing the notation of Amari condition (i), we have that $a_c = x_0/2$. Note, the relation $w(2a_c) = 0$ is explicitly solvable for a_c for several typical lateral inhibitory type weight functions. For instance, in the case of the difference of Gaussians $w(x) = e^{-x^2} - Ae^{-x^2/\sigma^2}$ on $x \in (-\infty, \infty)$ [1], we have $a_c = \sqrt{\ln(1/A)}/2\sqrt{\sigma^2 - 1}$ and $\theta_c = \frac{\sqrt{\pi}}{2}[\mathrm{erf}(2a_c) - A\sigma\,\mathrm{erf}(2a_c/\sigma)]$. For the "wizard hat" $w(x) = (1 - |x|)e^{-|x|}$ on $x \in (-\infty, \infty)$ [12], we have $a_c = 1/2$ and $\theta_c = e^{-1}$. For a cosine weight $w(x) = \cos(x)$ on the periodic domain $x \in [-\pi, \pi]$ [35], we have $a_c = \pi/4$ and $\theta_c = 1$.

To characterize the stability of bump solutions to (1), we will study the evolution of small smooth perturbations $\varepsilon\psi(x,t)$ ($\varepsilon \ll 1$) to stationary bumps $U(x)$ by utilizing the Taylor expansion $u(x,t) = U(x) + \varepsilon\psi(x,t) + O(\varepsilon^2)$. By plugging this expansion into (1) and truncating to $O(\varepsilon)$, we can derive an equation whose solutions constitute the family of eigenfunctions associated with the linearization of (1) about the bump solution $U(x)$. We begin by truncating (1) to $O(\varepsilon)$ assuming

u is given by the above expansion and that the nonlinearity $f(u)$ is given by the Heaviside function (3), so

$$\frac{\partial \psi(x,t)}{\partial t} = -\psi(x,t) + \int w(x-y)H'(U(y)-\theta)\psi(y,t)\mathrm{d}y, \tag{8}$$

and we can differentiate the Heaviside function, in the sense of distributions, by noting $H(U(x)-\theta) = H(x+a) - H(x-a)$, so

$$\delta(x+a) - \delta(x-a) = \frac{\mathrm{d}H(U(x)-\theta)}{\mathrm{d}x} = H'(U(x)-\theta)U'(x),$$

which we can rearrange to find

$$H'(U(x)-\theta) = \frac{\delta(x+a)-\delta(x-a)}{U'(x)} = \frac{1}{|U'(a)|}\left(\delta(x+a)+\delta(x-a)\right). \tag{9}$$

Upon applying the identity (9) to (8), we have

$$\frac{\partial \psi(x,t)}{\partial t} = -\psi(x,t) + \gamma\left[w(x+a)\psi(-a,t) + w(x-a)\psi(a,t)\right], \tag{10}$$

where $\gamma^{-1} = |U'(a)| = w(0) - w(2a)$. One class of solutions, such that $\psi(\pm a,t) = \psi(\pm a,0) = 0$, lies in the essential spectrum of the linear operator that defines (10). In this case, $\psi(x,t) = \psi(x,0)e^{-t}$, so perturbations of this type do not contribute to any instabilities of the stationary bump $U(x)$ [24]. Assuming separable solutions $\psi(x,t) = b(t)\psi(x)$, we can characterize the remaining solutions to (10). In this case, $b'(t) = \lambda b(t)$, so $b(t) = e^{\lambda t}$ where $\lambda \in \mathbb{R}$, and

$$(\lambda+1)\psi(x) = \gamma\left[w(x+a)\psi(-a) + w(x-a)\psi(a)\right]. \tag{11}$$

Solutions to (11) that do not satisfy the condition $\psi(\pm a) \equiv 0$ can be separated into two classes: (i) odd $\psi(a) = -\psi(-a)$ and (ii) even $\psi(a) = \psi(-a)$. This is due to the fact that the equation (11) implies the function $\psi(x)$ is fully specified by its values at $x = \pm a$. Thus, we need only concern ourselves with these two points, yielding the two-dimensional linear system

$$(\lambda+1)\psi(-a) = \gamma\left[w(0)\psi(-a) + w(2a)\psi(a)\right] \tag{12a}$$

$$(\lambda+1)\psi(a) = \gamma\left[w(2a)\psi(-a) + w(0)\psi(a)\right]. \tag{12b}$$

For odd solutions $\psi(a) = -\psi(-a)$, the eigenvalue

$$\lambda_o = -1 + \gamma\left[w(0) - w(2a)\right] = -1 + \frac{w(0)-w(2a)}{w(0)-w(2a)} = 0,$$

reflecting the fact that (1) is translationally symmetric, so bumps are marginally stable to perturbations that translate their position. Even solutions $\psi(a) = \psi(-a)$ have associated eigenvalue

In anticipation of our derivations of amplitude equations, we define the eigenfunctions at the criticality $\theta = \theta_c$. Utilizing the fact that $|U'(-a_c)| = w(0)$ and the linear system (12a), we have that the odd eigenfunction at the bifurcation is

$$\psi_o(x) = \frac{1}{w(0)} \left[w(x - a_c) - w(x + a_c) \right], \tag{13}$$

and the even eigenfunction is

$$\psi_e(x) = \frac{1}{w(0)} \left[w(x - a_c) + w(x + a_c) \right]. \tag{14}$$

Note, this specifies that $\psi_e(-a) = \psi_o(a) = -\psi_o(-a) = 1$. Furthermore, we will find it useful to compute the derivatives

$$\psi_o'(x) = \frac{1}{w(0)} \left[w'(x - a_c) - w'(x + a_c) \right],$$

which is even ($\psi_o'(-a_c) = \psi_o'(a_c)$), and

$$\psi_e'(x) = \frac{1}{w(0)} \left[w'(x - a_c) + w'(x + a_c) \right],$$

which is odd ($\psi_e'(-a_c) = -\psi_e'(a_c)$). Lastly, we note that we will utilize the fact that, for even symmetric functions $w(x)$, $w'(0) = 0$ and $w'(-x) = -w'(x)$, so $\psi_o'(-a_c) = \psi_e'(-a_c) = -\psi_e'(a_c) = |w'(2a_c)|/w(0) = w'(-2a_c)/w(0) = -w'(2a_c)/w(0)$, noting Amari's conditions (iii) and (iv) [1].

2.2. Saddle-node bifurcation of bumps. Motivated by the above linear stability analysis, we now carry out a nonlinear analysis in the vicinity of the saddle-

The right hand side of (16) vanishes due to the formula for the even (14) eigenfunction associated with the stability of the bump $U_c(x)$. At $O(\varepsilon^2)$, we obtain an equation for higher order term u_2:

$$L\,[A_o\psi_o + u_2] = A_e'\psi_e + A_o'\psi_o + \int w(x-y)H'(U_c(y)-\theta_c)\mathrm{d}y \qquad (17)$$
$$-\frac{A_e^2}{2}\int w(x-y)H''(U_c(y)-\theta_c)\psi_e(y)^2\mathrm{d}y;$$

where L is the non-self-adjoint linear operator

$$Lu(x) = -u(x) + \int w(x-y)H'(U_c(y)-\theta_c)u(y)\mathrm{d}y. \qquad (18)$$

Both $\psi_o(x)$ and $\psi_e(x)$ lie in the nullspace $N(L)$, as demonstrated in the previous section by identifying solutions to (8). Thus, the ψ_o terms on the left hand side of (17) vanish. We can ensure a bounded solution to (17) exists by requiring that the right hand side be orthogonal to all elements of the nullspace of the adjoint operator L^*. The adjoint is defined with respect to the L^2

where we have utilized $_e(\ a_c) = 1$ and $w(2a_c)$

in the equation for A_e, we have

$$\langle \varphi_e, w * H''(U_c - \ )\ _e^2 \rangle = \int\int w(x-y)\varphi_e(x)H''(U_c(y) - \ )\ _e(y)^2 \mathrm{d}y\mathrm{d}x$$
$$= \sum_{a=\pm a_c} \ _e(a) \int w(a-y)H''(U_c(y) - \ )\ _e(y)^2 \mathrm{d}y. \qquad (30)$$

The integrals in (30) are identical to those in (27), so it is straightforward to compute, using (28) and (29), that

$$\langle \varphi_e, w * H''(U_c - \ )\ _e^2 \rangle = \frac{2w'(2a_c)}{w(0)^2} + \frac{2w'(2a_c)}{w(0)^2} = \frac{4w'(2a_c)}{w(0)^3}.$$

Thus, we can at last compute all the terms in (23), specifying that

$$\frac{\mathrm{d}A_o}{\mathrm{d}t} = 0, \qquad (31a)$$
$$\frac{\mathrm{d}A_e}{\mathrm{d}\ } = \ - \frac{|w'(2a_c)|}{w(0)^2} A_e(\ )^2, \qquad (31b)$$

where we have noted the fact that $w'(2a_c) < 0$ due to Amari's conditions (iii) and (iv) on the weight function $w(x)$ [1].

Equation (31a) reflects the translational symmetry of the original neural field equation (1), so bumps are neutrally stable to translating perturbations $\ _o$ regardless of the bifurcation parameter . On the other hand, as the bifurcation parameter is changed, the dynamics of the even eigenmode $\ _e$ reflect the relative distance to the saddle-node bifurcation where bumps are marginally stable to expanding/contracting perturbations. When $\ < 0$, there are two fixed points of equation (31b) at $A_e = \pm w(0)\sqrt{| \ |/w'(2a_c)|}$, corresponding to the pair of emerging stationary bump solutions which are wider (+) and narrower (−) than the critical bump U_c. As expected from our analysis in section 2.1, the wide bump is linearly stable since a linearization of (31b) yields $\ _+ = -\sqrt{| \ w'(2a_c)|}$=w0 Td [(j)]TJETq1 0is linearly s9]TJ/F7 6.9738 Tfstance to 5279 1.494 Td [(<.35

$$\frac{\mathrm{d}A_o}{\mathrm{d}t} = \frac{h\,'_o; w \quad f^{00}(U_c)\ {}^2_e\ i}{2h\,'_o;\ {}_o i} A_e(\ )^2; \tag{34a}$$

$$\frac{\mathrm{d}A_e}{\mathrm{d}} = \quad \frac{h\,'_e; w \quad f^0(U_c) i}{h\,'_e;\ {}_e i} + \frac{h\,'_e; w \quad f^{00}(U_c)\ {}^2_e\ i}{2h\,'_e;\ {}_e i} A_e(\ )^2: \tag{34b}$$

We can derive the coe cients in the system (34) by computing the inner products therein. To do so, we must choose a speci c nonlinearity, such as the sigmoid (2), and a weight kernel. For illustration, we consider the cosine kernel $w(x) = \cos(x)$ on the ring $x\ 2 \quad = [\quad ; \quad]$ with periodic boundaries. As shown in previous studies, the bump solution $U_c(x) = A_c \cos x$ while the eigenmodes $\ _o(x) = \sin(x)$ and $\ _e(x) = \cos(x)$ [26, 35, 52]. Since $L \ _j \quad 0$ for $j = o; e$, this means

$$\sin(x) = \int \cos(x \quad y) f^0(A_c \cos(y)) \sin(y) \mathrm{d}y = \sin x \int \sin^2(y) f^0(A_c \cos y) \mathrm{d}y;$$

where we have used $\cos(x \quad y) = \cos x \cos y + \sin x \sin y$, and

$$\cos(x) = \int \cos(x \quad y) f^0(A_c \cos(y)) \cos(y) \mathrm{d}y = \cos x \int \cos^2(y) f^0(A_c \cos y) \mathrm{d}y;$$

so that we can write

$$\int \sin^2(y) f^0(A_c \cos y) \mathrm{d}y \quad 1; \qquad \int \cos^2(y) f^0(A_c \cos y) \mathrm{d}y \quad 1: \tag{35}$$

The identities (35) allow us to compute

$$h\,'_o;$$

3. Stochastic neural fields near the saddle-node. We now study the impact of stochastic forcing near the saddle-node bifurcation of bumps. Our analysis focuses on the spatially extended Langevin equation with additive noise (5). Guided by our analysis of the deterministic system (1), we will utilize an expansion in the small parameter ϵ, which determines the distance of the system from the saddle-node. To formally derive stochastic amplitude equations, we must specify the scaling of the noise amplitude σ as it relates to the small parameter ϵ, as this will determine the level of the perturbation hierarchy wherein the noise term dW will appear. We opt for the scaling $\sigma = \epsilon^{5/2}$, as this introduces a nontrivial interaction between the nonlinear amplitude equation for A_e and the noise.

It is important to note that our derivations are only carried up to $O(\epsilon^2)$ in the hierarchy of the regular perturbation expansion in ϵ. Were we to continue this expansion further, we would likely find that the $\sigma = \epsilon^{5/2}$ noise term does indeed shift the location of the bifurcation at higher order as in [2, 30]. Thus, as the

$$\mathrm{d}A_o(t) = \frac{\langle \varphi_o, w \quad H''(U_c \quad _c) \quad ^2_e \rangle}{2\langle \varphi_o, \quad _o\rangle} A_e(\ )^2 \mathrm{d}t \quad \frac{\langle \varphi_o, \mathrm{d}\hat{W}\rangle}{\langle \varphi_o, \quad _o\rangle} \tag{43a}$$

$$\mathrm{d}A_e(\ ) = \quad \frac{\langle \varphi_e, w \quad [H'(U_c \quad _c)]\rangle}{\langle \varphi_e, \quad _e\rangle} + \frac{\langle \varphi_e, w \quad H''(U_c \quad _c) \quad ^2_e \rangle}{2\langle \varphi_e, \quad _e\rangle} A_e(\ )^2 \quad \frac{\langle \varphi_e, \mathrm{d}\hat{W}\rangle}{\langle \varphi_e, \quad _e\rangle}. \tag{43b}$$

Utilizing the formulas for $H'(U_c \quad _c)$ (9) and $H''(U_c \quad _c)$ (24) we derived in the previous section, we can simplify the expressions in (43). Additionally, we make use of the fact that

$$\mathrm{d}\hat{W}_o(\ ) := \quad \frac{\langle \varphi_o, \mathrm{d}\hat{W}\rangle}{\langle \varphi_o, \quad _o\rangle} = \quad \frac{1}{2}\Big[\ _o(\ a_c)\mathrm{d}\hat{W}(\ a_c, \ ) + \quad _o(a_c)\mathrm{d}\hat{W}(a_c, \ )\Big]$$

$$= \frac{\mathrm{d}\hat{W}(\ a_c, \ ) \quad \mathrm{d}\hat{W}(a_c, \ )}{2},$$

$$\mathrm{d}\hat{W}_e(\ ) := \quad \frac{\langle \varphi_e, \mathrm{d}\hat{W}\rangle}{\langle \varphi_e, \quad _e\rangle} = \quad \frac{1}{2}\Big[\ _e(\ a_c)\mathrm{d}\hat{W}(\ a_c, \ ) + \quad _e(a_c)\mathrm{d}\hat{W}(a_c, \ )\Big]$$

$$= \quad \frac{\mathrm{d}\hat{W}(a_c, \ ) + \mathrm{d}\hat{W}(\ a_c, \ )}{2}.$$

Noting that $\langle \mathrm{d}\hat{W}(x, \ )\mathrm{d}\hat{W}(y, \ ')\rangle = C(x \quad y) \ (\quad ')\mathrm{d} \ \mathrm{d} \ '$, it is straightforward to compute the variances $\langle \hat{W}_o(\ )^2\rangle = D_o \quad = (C(0) \quad C(2a_c)) \ =2$ and $\langle \hat{W}_e(\ )^2\rangle =$

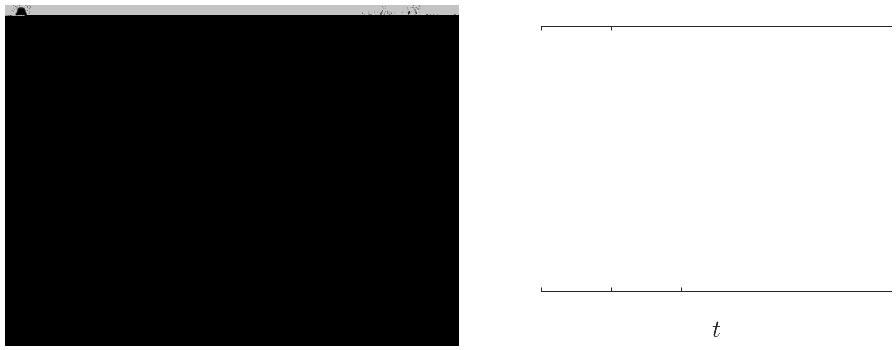

Figure 4. Noise-induced extinction of bumps in the stochastic

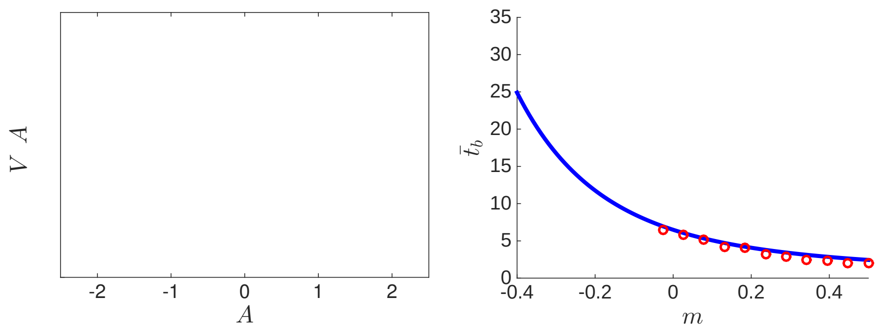

Figure 5. (A) Potential function (46) associated with the stochastic amplitude equation (45) has zero ($m > 0$); one ($m = 0$); or two ($m < 0$) extrema - associated with equilibria of $\dot{A} = -m - A^2$. When $m < 0$, crossing the saddle point requires stochastic forcing. (B) Mean time $\bar{t}_b$ until bump extinction is approximated by a mean first passage time problem of the stochastic amplitude equation (45). Numerical simulations (circles) of the full system (5) are well approximated by this theory (line) given by (51) for $\varepsilon = 0.6$.

The basin of attraction of $A = \sqrt{-m}$ is given by the interval $(-\sqrt{-m}, \infty)$. When $D > 0$, fluctuations can induce rare transitions on exponentially long timescales whereby $A(\tau)$ crosses the point $A = -\sqrt{-m}$, leaving the basin of attraction. For the non-generic case $m = 0$, the timescale of departure scales algebraically [50]. When $m > 0$, noise simply modulates the flows of the deterministic equation $\dot{A} = -m - A^2$, leading to an average speed-up in the departure from the bottleneck. In general, we consider solving the first passage time problem as an escape from the domain $(-\theta, \infty)$ where $\theta := \frac{|w'(2a_c)|}{w(0)^2}$ (equivalently where $A_e = -1$) [22]. To do so, we impose an absorbing boundary condition at $-\theta$: $p(-\theta, \tau) = 0$. Now let $T(A)$ denote the stochastic first passage time for which (45) first reaches the point $-\theta$, given it started at $A \in (-\theta, \infty)$. The first passage time distribution is related to the survival probability that the system has not yet reached $-\theta$:

$$S(\tau) \equiv \int_{-\theta}^{\infty} p(A, \tau) \mathrm{d}A,$$

which is $S(\tau) := \Pr(\tau > T(A))$, so the first passage time density is [22]

$$F(\tau) = -\frac{\mathrm{d}S}{\mathrm{d}\tau} = -\int_{-\theta}^{\infty} \frac{\partial p}{\partial \tau}(A, \tau) \mathrm{d}A.$$

Substituting for the expression for $\partial p / \partial \tau$ using the Fokker-Planck equation (47) and the formula for the flux (48) shows

$$F(\tau) = \int_{-\theta}^{\infty} \frac{\partial J(A, \tau)}{\partial A} \mathrm{d}A = -J(-\theta, \tau),$$

where we have utilized the fact that $\lim_{A \to \infty} J(A, \tau) = 0$. Thus, the first passage time density $F(\tau)$ can be interpreted as the total probability flux through the absorbing boundary at $A = -\theta$. To calculate the mean first passage time $\bar{T}(A) := \langle T(A) \rangle$, we use standard analysis to associate $\bar{T}(A)$ with the solution of the backward equation [22]:

$$(m + A^2)\frac{\mathrm{d}T}{\mathrm{d}A} + \frac{D}{2}\frac{\mathrm{d}^2T}{\mathrm{d}A^2} = -1, \tag{49}$$

with the boundary conditions $T(-\infty) = 0$ and $T'(\infty) = 0$. Solving (49) yields the closed form solution

$$T(A) = \frac{2}{D}\int_{-\infty}^{A}\int_{y}^{\infty}\frac{\Phi(z)}{\Phi(y)}\mathrm{d}z\mathrm{d}y, \tag{50}$$

where

$$\Phi(A) = \exp\left[\frac{2[V(-\infty) - V(A)]}{D}\right],$$

and $V(x)$ is the potential function (46). Explicit expressions for the integral (50) can be found in some special cases [42, 50]. For our purposes, we simply integrate (50) numerically to generate theoretical relationships between the mean first passage time and model parameters. For comparison, we focus on the case the weight function $w(x) = \cos(x)$ and the correlations $C(x) = \cos(x)$, so that $U_c(x) = \sqrt{2}\cos(x)$, $a_c = \frac{\pi}{4}$, $w(0) = 1$, $w'(2a_c) = -1$, $C(0) = 1$, and $C(2a_c) = 0$. Therefore, $\alpha = 1$, $m = \mu$, $D = 1/2$. This allows us to write the formula (50) at $A = 0$ as

$$T(0) = 4\int_{-\infty}^{0}\int_{y}^{\infty}\exp\left[4\left(\frac{z^3 - y^3}{3} + \mu(z - y)\right)\right]\mathrm{d}z\mathrm{d}y. \tag{51}$$

Lastly, note that by rescaling time $t = \varepsilon\tau$, we have that the mean first passage time in units of t will be $t_b = T(0)/\varepsilon$. We compare our theory (51) with the results of numerical simulations of the full stochastic neural field (5) in Fig. 5B. Note there is some discrepancy between our numerical simulations and theory as m is decreased. One of the primary reasons for this deviation is likely because of the moderate level of noise ($\varepsilon = 0.6$) used in comparison to the small parameter assumption ($\varepsilon \ll 1$) using in the theory we have developed. Any minor mismatch will be exacerbated by the fact that mean first passage times for escape problems depend exponentially on parameters like noise amplitude and well depth, as in (51). Nonetheless, the theory does provide a rough estimate of the mean first passage times for smaller values of the parameter m.

4. Discussion.

We have developed a weakly nonlinear analysis for saddle-node bifurcations of bumps in deterministic and stochastic neural field equations. While most of our analysis has focused upon Heaviside firing rate functions, we have also demonstrated the techniques can easily be extended to arbitrary smooth nonlinearities. In the vicinity of the saddle-node, the dynamics of bump expansion/contraction can be described by a quadratic amplitude equation. For deterministic neural fields, this low dimensional approximation can be used to approximate the trajectory and lifetime of bumps as they slowly extinguish. To do so, we focused on the initial time epoch in the bottleneck surrounding the ghost of the critical bump $U_c(x)$. In stochastic neural fields with appropriate noise scaling, a stochastic amplitude equation for the even mode of the bump can be derived. Importantly, we must choose the noise amplitude to scale as $\sigma = \varepsilon^{5/2}$, in order for the noise term to appear in the stochastic version of the quadratic amplitude equation. We then cast the lifetime of the bump in terms of a mean first passage time problem of the reduced system, which is valid for the noise scaling we have chosen.

Our work extends recent studies that have derived low-dimensional nonlinear approximations of neural field pattern dynamics in the vicinity of bifurcations [5, 7, 20, 30, 35, 36]. As in our work, most of these previous studies derived approximations where the location of the bifurcation was unaffected by noise terms. On the other hand, Hutt et al. showed that noise can in fact shift the position of Turing bifurcations in neural fields, and the amplitude of the bifurcation threshold shift was proportional to the noise variance [30]. Were we to have carried the hierarchy out to higher order, we would have found such a shift in the case we studied.

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E-mail address: zpkilpat@colorado.edu