NONLINEAR LANGEVIN EQUATIONS FOR WANDERING PATTERNS IN STOCHASTIC NEURAL FIELDS

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Abstract. We analyze the effects of additive, spatially extended noise on spatiotemporal patterns in continuum neural fields. Our main focus is how fluctuations impact patterns when they are weakly coupled to an external stimulus or another equivalent pattern. Showing the generality of our approach, we study both propagating fronts and stationary bumps. Using a separation of time scales, we represent the effects of noise in terms of a phase-shift of a pattern from its uniformly translating position at long time scales, and fluctuations in the pattern profile around its instantaneous position at short time scales. In the case of a stimulus-locked front, we show that the phase-shift satisfies a nonlinear Langevin equation (SDE) whose deterministic part has a unique stable fixed point. Using a linear-noise approximation, we thus establish that wandering of the front about the stimulus-locked state is given by an Ornstein-Uhlenbeck (OU) process. Analogous results hold for the relative phase-shift between a pair of mutually coupled fronts, provided that the coupling is excitatory. On the other hand, if the mutual coupling is given by a Mexican hat function (difference of exponentials), then the linear-noise approximation breaks down due to the co-existence of stable and unstable phase-locked states in the deterministic limit. Similarly, the stochastic motion of mutually coupled bumps can be described by a system of nonlinearly coupled SDEs, which can be linearized to yield a multivariate OU process. As in the case of fronts, large deviations can cause bumps to temporarily decouple, leading to a phase-slip in the bump positions.

Key words. neural field, traveling fronts, stochastic differential equations, spatially extended noise, phase-locking

1. Introduction. Several previous studies have explored the impact of fluctuations on spatiotemporal patterns in neural field equations by including a perturbative spatially extended noise term [5,16,18,23]. Utilizing small-noise expansions, it is then possible to develop effective equations to describe the stochastic motion of spatiotemporal patterns that emerge in the noise-free system [26]. Typically, these effective equations are linear stochastic differential equations (SDEs) [5,19], although there have been derivations of stochastic amplitude equations in the vicinity of bifurcations [16,20] or nonlinear SDEs in spatially heterogeneous networks [18]. Here we demonstrate methods for deriving nonlinear SDEs for the effective motion of patterns in stochastic neural field equations, focusing on fronts and bumps in particular.

The basic neural field equation with a noise term \( R(x,t) \) takes the form

\[
\tau \frac{du(x,t)}{dt} = -u(x,t) + \int_\Omega w(x-y)F(u(y,t))dydt + \sqrt{\epsilon}R(x,t),
\]

(1.1)

where \( u(x,t) \) represents neural population activity at position \( x \in \Omega \) and time \( t \), where \( \Omega \) is a one-dimensional domain such as \( \mathbb{R} \) or the ring \( [-\pi, \pi] \). The function \( F \) is a nonlinear firing-rate function. Synaptic connectivity in the network is represented by the function \( w(x-y) \), which describes the polarity (sign) and strength (amplitude) of connection from location \( y \) to \( x \). The stochastic forcing is assumed to be weak by taking \( 0 < \epsilon \ll 1 \). Expressing \( R(x,t) \) in terms of a spatially extended Wiener process, one can formulate the neural field equation as a stochastic integro-differential equation on a suitable function space such as \( L^2(\mathbb{R}) \). Suppose that the deterministic neural
field equation ($\epsilon = 0$) supports a wave solution $U_0(\xi)$ with $\xi = x - ct$ and $c$ the wave speed ($c \equiv 0$ for stationary waves such as bumps [18]). Motivated by perturbation methods for analyzing fronts in stochastic reaction-diffusion equations [2, 25, 26], we used a separation of time-scales to decompose the effects of noise into (i) a slow, diffusive-like displacement $\Delta(t)$ of the wave from its uniformly translating position, and (ii) fast fluctuations in the wave profile. More explicitly,

$$u(x, t) = U_0(\xi - \Delta(t)) + \sqrt{\epsilon} \Phi(\xi - \Delta(t), t).$$

Substituting this decomposition into the neural field equation and carrying out an asymptotic series expansion $\Phi = \Phi_0 + O(\epsilon^{1/2})$, one finds that boundedness of $\Phi_0$ leads to a self-consistency condition for $\Delta(t)$, which takes the form of a stochastic ODE. One thus establishes that $\Delta(t)$ undergoes Brownian motion. There have been several subsequent developments of the theory, both in terms of applications and in terms of more rigorous mathematical treatments. Bressloff and Weber have applied these methods to study the effects of noise in binocular rivalry waves, showing that wandering of the wave associated with perceptual switching is diffusive [28]. Second, Kilpatrick and Ermentrout have analyzed the wandering of stationary pulses (bumps) in stochastic neural fields [18], and Kilpatrick has shown how weak interlaminar coupling can regularize (reduce the variance) of stationary pulses and propagating waves in a multi-layered, stochastic neural field [19, 20]. Regarding rigorous treatments, Faugeras and Inglis [12] have addressed the issue of solutions and well-posedness in stochastic neural fields by adapting results from SPDEs, whereas Kruger and Stannat [22] have developed a rigorous treatment of the multi-scale decomposition of solutions.

One feature that has emerged in some applications of stochastic neural fields is that the displacement variable $\Delta(t)$ can satisfy an Ornstein-Uhlenbeck (OU) process rather than pure Brownian motion. For example, this occurs in the case of stimulus-locked fronts [5] and in the regularization of waves in multi-layer networks, where $\Delta(t)$ now represents the relative displacement of fronts in different layers [20]. However, one assumption in the derivation of the OU process is that the displacement $\Delta(t)$ is small. In this paper, we show that this assumption can break down and, in fact, $\Delta(t)$ evolves according to a nonlinear SDE. It turns out that in the aforementioned applications, the deterministic part of the SDE has a unique stable fixed point, so that one can carry out a linear-noise approximation and recover an OU process, but with modified expressions for the drift term. More significantly, the nonlinear nature of the SDE also raises the possibility of a breakdown in the linear-noise approximation due to the coexistence of multiple phase-locked states.

Our results are organized as follows. In section 2, we demonstrate how a nonlinear SDE can be derived for the stochastic motion of a stimulus-locked front driven by additive noise. The shape of the nonlinearity is determined by both the spatial profile of the stimulus as well as the front profile. We extend our methods in section 3 to derive a nonlinear system of SDEs for the motion of two reciprocally coupled fronts in two separate layers, rather than truncating to linear order as in [19]. While coupling tends to regularize the propagation of fronts by pulling their positions close together, large deviations in noise can decouple fronts leading to an instability in the case of lateral inhibitory interlaminar coupling (section 4). Lastly, we show in section 5 that our analysis can be applied to study wandering bumps in reciprocally coupled laminar neural fields. Similar to the case of fronts, the nonlinear system of SDEs we derive can be used to predict the mean waiting time until a large deviation wherein bumps become temporarily decoupled, leading to a phase-slip.
2. **Stimulus-locked fronts with additive noise.** Consider the stochastic neural field equation \[ \tau dU(x,t) = \left[ -U(x,t) + \int_{-\infty}^{\infty} w(x-y)F(U(y,t))dy \right] dt \\
+ \epsilon^{1/2}I(x-\epsilon t)dt + \epsilon^{1/2} \tau^{1/2}dW(x,t), \quad x \in \mathbb{R} \] (2.1)
where \( I(x-\epsilon t) \) represents a moving external stimulus of speed \( \epsilon \), and \( dW(x,t) \) represents an independent Wiener process such that \( \langle dW(x,t) \rangle = 0, \quad \langle dW(x,t)dW(x',t') \rangle = 2C(x-x')\delta(t-t')dtdt' \). (2.2)

Here the (stochastic) neural field \( U(x,t) \) is a measure of activity within a local population of excitatory neurons at \( x \in \mathbb{R} \) and time \( t \), \( \tau \) is a membrane time constant (of order 10 msec), \( w(x) \) denotes the spatial distribution of synaptic connections between local populations, and \( F(U) \) is a nonlinear firing rate function. \( F \) is taken to be a sigmoid function \[ F(u) = \frac{1}{1+e^{-\gamma(u-\kappa)}} \] (2.3)
with gain \( \gamma \) and threshold \( \kappa \). In the high–gain limit \( \gamma \to \infty \), this reduces to the Heaviside function \[ F(u) \to H(u-\kappa) = \begin{cases} 1 & \text{if } u > \kappa, \\ 0 & \text{if } u \leq \kappa. \end{cases} \] (2.4)

We will assume that the weight distribution is a positive, even function of \( x \), \( w(x) \geq 0 \) and \( w(-x) = w(x) \), and that \( w(x) \) is a monotonically decreasing function of \( x \) for \( x \geq 0 \). A common choice is the exponential weight distribution \[ w(x) = \frac{1}{2\sigma}e^{-|x|/\sigma}, \] (2.5)
where \( \sigma \) determines the range of synaptic connections. The latter tends to range from 100 \( \mu \)m to 1 mm. We fix the units of time by setting \( \tau = 1 \).

In the absence of any external inputs \( (\epsilon = 0) \), the resulting homogeneous neural field equation \[ \frac{\partial u(x,t)}{\partial t} = -u(x,t) + \int_{-\infty}^{\infty} w(x-y)F(u(y,t))dy \] (2.6)
supports a traveling front solution. First note that a homogeneous fixed point solution \( u^* \) of equation (2.6) satisfies \[ u^* = K_0 F(u^*), \quad K_0 = \int_{-\infty}^{\infty} w(y)dy. \] (2.7)

In the case of a sigmoid function with appropriately chosen gain and threshold, it is straightforward to show graphically that there exists a pair of stable fixed points \( u^*_{\pm} \) separated by an unstable fixed point \( u_0^* \). We define a traveling front solution to be of the form \( u(x,t) = U_0(\xi), \xi = x-ct \), where \( c \) denotes the wavespeed, such that \( \lim_{\xi \to -\infty} U_0(\xi) = u^*_+ \) and \( \lim_{\xi \to \infty} U_0(\xi) = u^*_- \). Note that \( U_0 \) satisfies the equation \[ -cU'_0(\xi) = -U_0(\xi) + \int_{-\infty}^{\infty} w(\xi-\xi')F(U_0(\xi'))d\xi'. \] (2.8)
As originally shown by Amari [1], an explicit traveling front solution can be constructed in the high gain limit \( F(u) \to H(u - \kappa) \) with \( 0 < \kappa < W_0 \). In this case \( U_0(\xi) \) is a monotonically decreasing function of \( \xi \) that crosses the threshold at a unique point. Since equation (2.6) is equivariant with respect to uniform translations, we are free to take the threshold crossing point to be at the origin, \( U_0(0) = \kappa \), so that \( U_0(\xi) < \kappa \) for \( \xi > 0 \) and \( U_0(\xi) > \kappa \) for \( \xi < 0 \). Substituting this traveling front solution into equation (2.6) with \( F(u) = H(u - \kappa) \) then gives

\[-cU'_0(\xi) + U_0(\xi) = \int_{-\infty}^{0} w(\xi - \xi')d\xi' = \int_{\xi}^{\infty} w(x)dx \equiv K(\xi), \quad (2.9)\]

where \( U'_0(\xi) = dU_0/d\xi \). Multiplying both sides of the above equation by \( e^{-\xi/c} \) and integrating with respect to \( \xi \) leads to the solution

\[ U_0(\xi) = e^{\xi/c} \left[ \kappa - \frac{1}{c} \int_{0}^{\xi} e^{-y/c} K(y)dy \right]. \quad (2.10) \]

Finally, requiring the solution to remain bounded as \( \xi \to \infty \) (\( \xi \to -\infty \)) for \( c > 0 \) (for \( c < 0 \)) implies that \( \kappa \) must satisfy the condition

\[ \kappa = \frac{1}{|c|} \int_{0}^{\infty} e^{-y/|c|} K(\text{sign}(c)y)dy, \quad (2.11) \]

and thus

\[ U_0(\xi) = \frac{1}{c} \int_{0}^{\infty} e^{-y/c} K(y + \xi)dy. \quad (2.12) \]

In the case of the exponential weight distribution (2.5), the relationship between wavespeed \( c \) and threshold \( \kappa \) is

\[ c = c_+(\kappa) \equiv \frac{\sigma}{2\kappa} \left[ 1 - 2\kappa \right] \quad \text{for} \quad \kappa < 0.5, \quad (2.13a) \]

\[ c = c_-(\kappa) \equiv \frac{\sigma}{2} \left[ 1 - \kappa \right] \quad \text{for} \quad 0.5 < \kappa < 1. \quad (2.13b) \]

Moreover, one result we will need later is the explicit form for \( U_0 \) when \( \xi > 0 \), namely

\[ U_0(\xi) = \frac{1}{2c} \left[ \frac{\sigma e^{-\xi/\sigma}}{1 + \sigma/c} \right]. \quad (2.14) \]

This establishes the existence of a unique front solution for fixed \( \kappa \), which travels to the right (\( c > 0 \)) when \( 0 < \kappa < 0.5 \) and travels to the left (\( c < 0 \)) when \( 1 > \kappa > 0.5 \). Using Evans function techniques, it can also be shown that the traveling front is stable [7,9,29]. Finally, given the existence of a traveling front solution for a Heaviside rate function, it is possible to prove the existence of a unique front in the case of a smooth sigmoid nonlinearity using a continuation method [11].

2.1. Stimulus-locking in the presence of noise. We want to determine from equation (2.1) how the combination of a weak moving stimulus and weak additive noise affects the propagation of the above traveling front solution in the small \( \epsilon \) limit. Suppose that the input is given by a positive, bounded, monotonically decreasing function of amplitude \( I_0 = I(-\infty) - I(\infty) \). From the theory of stimulus-locked fronts
in deterministic neural fields [13, 28], we expect that in the absence of noise, the resulting inhomogeneous neural field equation can support a traveling front that locks to the stimulus, provided that the stimulus speed \( v \) is sufficiently close to the natural speed \( c \) of spontaneous fronts, that is,

\[
v = c + \sqrt{v_1}.
\]

On the other hand, following recent studies of wandering fronts [5, 28] and bumps [18–20] in stochastic neural fields, we expect the additive noise term in equation (2.1) to generate two distinct phenomena that occur on different time–scales: a slow stochastic displacement of the front, and fast fluctuations in the front profile. Both stimulus-locking and stochastic wandering can thus be captured by decomposing the solution \( U(x, t) \) of equation (2.1) as a combination of a fixed wave profile \( U_0 \) that is displaced by an amount \( \Delta(t) = \Delta(t) + (v - c)t \) from its uniformly translating mean position \( \xi = x - ct \), and a time–dependent fluctuation \( \Phi \) in the front shape about the instantaneous position of the front:

\[
U(x, t) = U_0(\xi - \Delta(t)) + \epsilon^{1/2} \Phi(\xi - \Delta(t), t).
\] (2.15)

Here \( U_0 \) is the front solution in the absence of inputs moving with natural speed \( c \), see equation (2.9).

The next step is to substitute the decomposition (2.15) into equation (2.1):

\[
-\nu U_0'(\xi - \Delta(t))dt - U_0'(\xi - \Delta(t))d\Delta(t) + \epsilon^{1/2} \left[ d\Phi(\xi - \Delta(t), t) - v\Phi'(\xi - \Delta(t), t)dt \right]
-\epsilon^{1/2}\Phi'_0(\xi - \Delta(t), t)d\Delta(t)
= -U_0(\xi - \Delta(t))dt - \epsilon^{1/2}\Phi(\xi - \Delta(t), t)dt + \epsilon^{1/2}dW(\xi + ct, t) + \epsilon^{1/2}I(\xi + (v - c)t, t).
\] (2.16)

An important point to emphasize is that one cannot carry out a perturbation expansion with respect to \( \Delta(t) \), as was previously assumed in [5]. As we will show below, \( \Delta(t) \to \xi_0 \) as \( t \to \infty \) in the absence of noise with the constant \( \xi_0 \) typically of \( O(1) \). On the other hand, one can carry out a perturbation expansion in \( \Phi \) by writing \( \Phi = \Phi_0 + \sqrt{\epsilon}\Phi_1 + O(\epsilon) \). Self-consistency of this asymptotic expansion will then determine \( \Delta(t) \). Substituting the series expansion for \( \Phi \) into equation (2.16), Taylor expanding the nonlinear function \( F \), and imposing the homogeneous equation for \( U_0 \) leads to the following equation for \( \Phi_0 \):

\[
-\epsilon^{1/2}v_1U_0''(\xi)dt - U_0''(\xi - \Delta(t))d\Delta(t) + \epsilon^{1/2} \left[ d\Phi_0(\xi - \Delta(t), t) - c\Phi'_0(\xi - \Delta(t), t)dt \right]
-\epsilon^{1/2}\Phi'_0(\xi - \Delta(t), t)d\Delta(t)
= -\epsilon^{1/2}\Phi_0(\xi - \Delta(t), t)dt + \epsilon^{1/2}dW(\xi + ct, t) + \epsilon^{1/2}I(\xi + (v - c)t, t)
+\epsilon^{1/2} \int_{-\infty}^{\infty} w(\xi - \xi')F'(U_0(\xi' - \Delta(t)))\Phi_0(\xi' - \Delta(t), t)d\xi'dt.
\]

Shifting \( \xi \to \xi + \Delta(t) \) and dividing through by \( \epsilon^{1/2} \) then gives

\[
d\Phi_0(\xi, t) = \frac{\partial \Phi_0(\xi, t)dt + \epsilon^{-1/2}U_0''(\xi)d\Delta(t) + d\tilde{W}(\xi, t) + I(\xi + \Delta(t), t)dt}{\epsilon^{1/2}v_1U_0''(\xi)dt}\]
\[
(2.17)
\]
where $\tilde{W}(\xi, t) = W(\xi + \Delta(t) + vt, t)$ and $\tilde{L}$ is the non-self-adjoint linear operator

$$
\tilde{L} \circ A(\xi) = c \frac{dA(\xi)}{d\xi} - A(\xi) + \int_{-\infty}^{\infty} w(\xi - \xi') F'(U_0(\xi')) A(\xi') d\xi'
$$

(2.18)

for any function $A(\xi) \in L^2(\mathbb{R})$. It can be shown that for a sigmoid firing rate function and exponential weight distribution, the operator $\tilde{L}$ has a 1D null space spanned by $U_0'(\xi)$. The fact that $U_0'(\xi)$ belongs to the null space follows immediately from differentiating equation (2.8) with respect to $\xi$. We then have the solvability condition for the existence of a bounded solution of equation (2.17), namely, that the inhomogeneous part is orthogonal to all elements of the null space of the adjoint operator $\tilde{L}^*$. The latter is defined with respect to the inner product

$$
\int_{-\infty}^{\infty} B(\xi) \tilde{L} A(\xi) d\xi = \int_{-\infty}^{\infty} \left[ \tilde{L}^* B(\xi) \right] A(\xi) d\xi
$$

(2.19)

where $A(\xi)$ and $B(\xi)$ are arbitrary integrable functions. Hence,

$$
\tilde{L}^* B(\xi) = -c \frac{dB(\xi)}{d\xi} - B(\xi) + F'(U_0(\xi)) \int_{-\infty}^{\infty} w(\xi - \xi') B(\xi') d\xi'.
$$

(2.20)

It can be proven that $\tilde{L}^*$ also has a one-dimensional null-space [11], that is, it is spanned by some function $V(\xi)$. The solvability condition reflects the fact that the homogeneous system ($\epsilon = 0$) is marginally stable with respect to uniform translations of a front. This means that the linear operator $\tilde{L}$ has a simple zero eigenvalue whilst the remainder of the spectrum lies in the left-half complex plane. Hence, perturbations of $\Phi_0$ that lie in the null-space will not be damped and thus $\Phi_0$ will be unbounded in the large $t$ limit unless these perturbations vanish identically.

Taking the inner product of both sides of equation (2.17) with respect to $\mathcal{V}(\xi)$ leads to the solvability condition

$$
\int_{-\infty}^{\infty} \mathcal{V}(\xi) \left[ \epsilon^{-1/2} U_0'(\xi) d\Delta(t) + I(\xi + \Delta(t)) dt + v_1 U_0'(\xi) dt + d\tilde{W}(\xi, t) \right] d\xi = 0. \quad (2.21)
$$

It follows that, to leading order, $\Delta(t)$ satisfies the nonlinear SDE

$$
d\Delta(t) + \epsilon^{1/2} G(\Delta(t)) dt = \epsilon^{1/2} d\tilde{W}(t),
$$

(2.22)

where

$$
G(\Delta) = \frac{\int_{-\infty}^{\infty} \mathcal{V}(\xi) [I(\xi + \Delta) + v_1 U_0'(\xi)] d\xi}{\int_{-\infty}^{\infty} \mathcal{V}(\xi) U_0'(\xi) d\xi}.
$$

(2.23)

and

$$
\tilde{W}(t) = \frac{\int_{-\infty}^{\infty} \mathcal{V}(\xi) \tilde{W}(\xi, t) d\xi}{\int_{-\infty}^{\infty} \mathcal{V}(\xi) U_0'(\xi) d\xi}.
$$

(2.24)
Note that
\[ \langle \dot{W}(t) \rangle = 0, \quad \langle \dot{W}(t) \dot{W}(t') \rangle = 2D \delta(t - t') dt dt' \] (2.25)
with \( D \) the effective diffusivity.

\[
D = \frac{\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} V(\xi) V(\xi') \langle \dot{W}(\xi, t) \dot{W}(\xi', t) \rangle d\xi d\xi'}{\left[ \int_{-\infty}^{\infty} V(\xi) U_0'(\xi) d\xi \right]^2}
= \frac{\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} V(\xi) C(\xi - \xi') V(\xi') d\xi' d\xi}{\left[ \int_{-\infty}^{\infty} V(\xi) U_0'(\xi) d\xi \right]^2}. \tag{2.26}
\]

Suppose that there exists a unique \( \Delta = \xi_0 \) for which \( G(\xi_0) = 0 \) and \( G'(\xi_0) > 0 \). This represents a stable stimulus-locked front in the absence of noise, with \( \xi_0 \) the relative shift of the stimulus-locked front and the input. Taylor expanding about this solution by setting \( e^{1/2} Y(t) = \Delta(t) - \xi_0 \) with \( Y(t) = O(1) \) we obtain the OU process
\[
dY(t) + \frac{1}{2} A Y(t) dt = d\hat{W}(t), \tag{2.27}
\]
where
\[
A = G'(\xi_0) = \frac{\int_{-\infty}^{\infty} V(\xi) I'(\xi + \xi_0) d\xi}{\int_{-\infty}^{\infty} V(\xi) U_0'(\xi) d\xi}.
\]
(In our previous work [5], \( \xi_0 \) was assumed to be zero.) Using standard properties of an Ornstein–Uhlenbeck process
\[
\langle \Delta(t) \rangle = \xi_0 \left[ 1 - e^{-\sqrt{\tau} A t} \right] + \Delta(0) e^{-\sqrt{\tau} A t}, \tag{2.28a}
\]
\[
\langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{\sqrt{\tau} D}{A} \left[ 1 - e^{-2\sqrt{\tau} A t} \right]. \tag{2.28b}
\]

In particular, the variance approaches a constant \( \sqrt{\tau} D/A \) in the large \( t \) limit and the mean converges to the fixed point \( \xi_0 \).

In summary, it is necessary to modify the analysis of stimulus-locked fronts in [5] by noting they \( \Delta(t) \) actually evolves according to the nonlinear SDE (2.22) rather than an OU process. In order to obtain an OU process one then has to model Gaussian-like fluctuations about a stable fixed point \( \xi_0 \) of the deterministic part using a linear-noise approximation. This is reasonable provided that the deterministic equation does not exhibit multistability, which holds for stimulus-locked fronts. One additional feature of the nonlinear theory is that an explicit condition for the existence of a stimulus-locked front can be obtained in terms of the fixed point \( \xi_0 \).

2.2. Explicit results for Heaviside rate function. We now illustrate the above analysis by taking \( F(u) = H(u - \kappa) \) so that the null vector \( V \) can be calculated explicitly. That is, \( V \) satisfies the equation
\[
cV'(\xi) + V(\xi) = -\frac{\delta(\xi)}{U_0'(0)} \int_{-\infty}^{\infty} w(\xi') V(\xi') d\xi', \tag{2.29}
\]
which has the solution \[4\]

\[V(\xi) = -H(\xi) \exp(-\xi/c).\]  

(2.30)

We have used equation (2.12) for \(U_0\), which implies that

\[U_0'(\xi) = -\frac{1}{c} \int_0^\infty e^{-y/c} w(y + \xi) dy.\]  

(2.31)

For explicit calculations, we take \(w\) to be the exponential weight function, so that \(U_0\) has the explicit form (2.14). In the case that spatial noise increments are uncorrelated, we can set \(C(\xi) = C_0 \delta(\xi)\), where \(C_0\) has units of length. Then, it follows that equation (2.26) reduces to

\[D = C_0 \left[ \int_0^\infty e^{-\xi/c} \frac{d \xi}{U_0'(\xi)} \right]^2 \frac{C_0 \sigma^2}{8 \kappa^4 c}.\]  

(2.32)

On the other hand, if spatial noise is globally correlated, then \(C(\xi) \equiv C_0\), and (2.26) becomes

\[D = C_0 \left[ \int_0^\infty e^{-\xi/c} \cos \xi d \xi \right]^2 \frac{C_0 \sigma^2}{4 \kappa^4 (c^2 + 1)}.\]  

(2.33)

An example of a nontrivial correlation function is \(C(\xi) = C_0 \cos(\xi)\), in which case (2.26) is computed to be

\[D = C_0 \left[ \int_0^\infty e^{-\xi/c} \cos(\xi) d \xi \right]^2 \frac{C_0 \sigma^2}{4 \kappa^4 (c^2 + 1)}.\]  

(2.34)

In order to determine the constant shift \(\xi_0\) and the drift term \(A\), we need to specify the form of the input \(I\). For the sake of illustration, let

\[I(\xi) = I_0 H(-\xi).\]

The nonlinear function \(G(\Delta)\) becomes

\[G(\Delta) = \frac{\int_0^\infty I_0 e^{-\xi/c} [H(-\xi - \Delta) + v_1 U_0'(\xi)] d \xi}{\int_0^\infty e^{-\xi/c} U_0'(\xi) d \xi} = v_1 + I_0 H(-\Delta) \int_0^\infty e^{-\xi/c} d \xi \int_0^\Delta e^{-\xi/c} U_0'(\xi) d \xi \]

\[= v_1 - I_0 H(-\Delta) \frac{2(c + \sigma)}{\sigma} \left[1 - e^{\Delta/c}\right].\]  

(2.35)

It follows that for a given stimulus velocity there exists a unique stimulus-locked front with shift \(\xi_0\) satisfying \(G(\xi_0) = 0\), that is,

\[\xi_0 = c \ln \left[1 - \frac{\sigma v_1}{8 I_0 (c + \sigma)^2} \right] < 0,\]  

(2.36)
Fig. 2.1. Existence regions for stimulus-locked traveling fronts in the \((I_0,v)\)-plane for \(\epsilon = 1, \kappa = 0.95, \sigma = 2\) and \(c = -18\). For a given input amplitude \(I_0\), stimulus locking occurs for a finite range of \(v\) with \(c < v < v^*\). The curved boundary on the right-hand side of the existence region yields a function \(I_0 = I_0(v^*)\) whose tangent in the limit \(I_0 \to 0\) is given by the straight line \(I_0 = \sigma(v^* - c)/2(c + \sigma)^2\)

provided

\[
0 < v_1 < v_1^* = \frac{2I_0(c + \sigma)^2}{\sigma}.
\]  

Moreover,

\[
G'(\xi_0) = e^{-I_0} \frac{2(c + \sigma)^2 e^{\xi_0/c}}{\sigma} = \frac{v_1}{c} \frac{e^{\xi_0/c}}{1 - e^{\xi_0/c}} > 0,
\]

so the fixed point is stable. In Fig. 2.1 we plot an example of an existence region for stimulus-locked fronts in the \((v,I_0)\)-plane. In the limit of small inputs the tangent to the existence curve approaches the straight line obtained using perturbation theory. The stationary variance about the fixed point takes the explicit form

\[
\langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{\sqrt{\tau D}}{G'(\xi_0)}.
\]  

Hence, increasing the stimulus velocity reduces the variance. Note that the singularity in the limit \(v \to c\) reflects the fact that the stimulus-locked front becomes unstable.

3. Fronts in weakly-coupled stochastic neural fields. Another example of wandering fronts exhibiting an OU process occurs in a laminar neural field model [20]. As in the previous example of stimulus-locked fronts, we will show that the noise-induced wandering is described by a nonlinear SDE, and it is only by linearizing about a stable fixed point of the SDE that one obtains an OU process. For the sake of illustration, consider a pair of identical 1D neural fields labeled \(j = 1, 2\) that are mutually coupled via the interlaminar weight distributions \(J_1(x)\) and \(J_2(x)\):

\[
\tau dU_1(x,t) = \left[-U_1(x,t) + \int_{-\infty}^{\infty} w(x - y)F(U_1(y,t))dy \right] dt + \epsilon^{1/2} \int_{-\infty}^{\infty} J_1(x - y)F(U_2(y,t))dy dt + \epsilon^{1/2} \tau^{1/2} dW_1(x,t),
\]  

\[(3.1a)\]
As shown by Kilpatrick [20], Substituting into equations (3.1a) and (3.1b) gives

\[
\tau dU_2(x, t) = \left[ -U_2(x, t) + \int_{-\infty}^{\infty} w(x - y) F(U_2(y, t)) dy \right] dt + c^{1/2} \int_{-\infty}^{\infty} J_2(x - y) F(U_1(y, t)) dy dt + c^{1/2} \tau^{1/2} dW_2(x, t).
\]

Here \( W_1(x, t) \) and \( W_2(x, t) \) represent spatially extended Wiener processes such that

\[
\langle dW_j(x, t) \rangle = 0, \quad \langle dW_i(x, t) dW_j(x', t') \rangle = 2C_{ij} \langle x - x' \rangle \delta(t - t') dt dt'.
\]

Note that the interlaminar coupling is assumed to be weak and asymmetric (unless \( J_1 = J_2 \)). As with the intralaminar coupling, the distributions \( J_j(x) \) will be taken to be positive exponentials:

\[
J_j(x) = \alpha_j e^{-|x|/\sigma_j}.
\]

As shown by Kilpatrick [20], in the absence of noise, the interlaminar coupling phase-locks the fronts propagating in each of the two networks, resulting in a composite front with fixed relative shift \( \xi_0 \). We wish to derive conditions for such locking and determine how the presence of noise induces wandering of the composite front relative to \( \xi_0 \).

### 3.1. Interlaminar coupling of fronts in the presence of noise.

In the absence of interlaminar coupling and noise \( (\epsilon = 0) \), each neural field independently supports a traveling front solution \( U_0(\xi) \) along the lines outlined in \( \S 2 \) with \( \xi = x - ct \). Since each neural field is homogeneous the threshold crossing point of each front is arbitrary. Following our analysis of stimulus-locked fronts, we can simultaneously investigate the effects of weak coupling and noise by considering the decompositions

\[
U_j(x, t) = U_0(\xi - \Delta_j(t)) + c^{1/2} \Phi_j(\xi - \Delta_j(t), t), \quad j = 1, 2
\]

Substituting into equations (3.1a) and (3.1b) gives

\[
\begin{align*}
&-c U_0'(\xi - \Delta_j(t)) dt - U_0'(\xi - \Delta_j(t)) d\Delta_j(t) \\
&+ c^{1/2} \left[ \Phi_j(\xi - \Delta_j(t), t) - c \Phi_j'(\xi - \Delta_j(t), t) dt \right] - c^{1/2} \Phi_j'(\xi - \Delta_j(t), t) d\Delta_j(t) \\
&= -U_0(\xi - \Delta_j(t)) dt - c^{1/2} \Phi_j(\xi - \Delta_j(t), t) dt + c^{1/2} dW_j(\xi + ct, t) \quad (3.5) \\
&+ \int_{-\infty}^{\infty} w(\xi - \xi') F(U_0(\xi' - \Delta_j(t)) + c^{1/2} \Phi_k(\xi' - \Delta_j(t), t)) d\xi' dt \\
&+ c^{1/2} \int_{-\infty}^{\infty} J_j(\xi - \xi') F(U_0(\xi' - \Delta_k(t)) + c^{1/2} \Phi_k(\xi' - \Delta_k(t), t)) d\xi' dt
\end{align*}
\]

with \((j, k) = (1, 2) \) or \((2, 1) \). The next step is to carry out a perturbation expansion in \( \Phi_j \) by writing \( \Phi_j = \Phi_{j0} + c \Phi_{j1} + O(c) \). Substituting these series expansions into equation (3.5), Taylor expanding the nonlinear function \( F \), and imposing the
homogeneous equation (2.10) for $U_0$ leads to the following equations for $\Phi_j^{(0)}$:

\[-U_0'(\xi - \Delta_j(t))d\Delta_j(t) + \varepsilon^{1/2} \left[ d\Phi_j^{(0)}(\xi - \Delta_j(t), t) - c\Phi_j^{(0)}(\xi - \Delta_j(t), t)dt \right] - \varepsilon^{1/2}\Phi_j^{(0)}(\xi - \Delta_j(t), t)d\Delta_j(t) = -\varepsilon^{1/2}\Phi_j^{(0)}(\xi - \Delta_j(t), t)dt + \varepsilon^{1/2}dW_j(\xi + ct, t) + \varepsilon^{1/2}\int_{-\infty}^{\infty} w(\xi - \xi')F'(U_0(\xi' - \Delta_j(t)))\Phi_j^{(0)}(\xi' - \Delta_j(t), t)d\xi' dt + \varepsilon^{1/2}\int_{-\infty}^{\infty} J_j(\xi - \xi')F(U_0(\xi' - \Delta_k(t)))d\xi' dt \]

For $(j, k) = (1, 2)$ we perform the shift $\xi \rightarrow \xi + \Delta_1(t)$ and for $(j, k) = (2, 1)$ we perform the shift $\xi \rightarrow \xi + \Delta_2(t)$ After dividing through by $\varepsilon^{1/2}$ we obtain the pair of equations

\[d\Phi_j^{(0)}(\xi, t) = \hat{L} \circ \Phi_j^{(0)}(\xi, t)dt + \varepsilon^{-1/2}U_0'(\xi)d\Delta_j(t) + d\hat{W}_j(\xi, t) + \int_{-\infty}^{\infty} J_1(\xi - \xi')F(U_0(\xi' + \Delta_1(t) - \Delta_2(t)))d\xi' dt \quad (3.6a)\]

and

\[d\Phi_2^{(0)}(\xi, t) = \hat{L} \circ \Phi_2^{(0)}(\xi, t)dt + \varepsilon^{-1/2}U_0'(\xi)d\Delta_2(t) + d\hat{W}_2(\xi, t) + \int_{-\infty}^{\infty} J_2(\xi - \xi')F(U_0(\xi' + \Delta_2(t) - \Delta_1(t)))d\xi' dt, \quad (3.6b)\]

where

\[\hat{W}_j(\xi, t) = W_j(\xi + ct + \Delta_j(t), t),\]

and the linear operator $\hat{L}$ is given by equation (2.18).

As in the case of stimulus-locked fronts, boundedness of the fast fluctuations $\Phi_j^{(0)}$ require that the inhomogeneous terms are orthogonal to the null vector $\mathcal{V}($ of the adjoint operator $\hat{L}^*$. This leads to the following two-dimensional nonlinear SDE for $(\Delta_1(t), \Delta_2(t))$:

\[d\Delta_1(t) + \varepsilon^{1/2}G_1(\Delta_1(t) - \Delta_2(t))dt = \varepsilon^{1/2}d\hat{W}_1(t), \quad (3.7a)\]
\[d\Delta_2(t) + \varepsilon^{1/2}G_2(\Delta_2(t) - \Delta_1(t))dt = \varepsilon^{1/2}d\hat{W}_2(t) \quad (3.7b)\]

where

\[G_j(\Delta) = \frac{\int_{-\infty}^{\infty} \mathcal{V}(\xi) \left[ \int_{-\infty}^{\infty} J_j(\xi - \xi')F(U_0(\xi' + \Delta)d\xi' \right] d\xi}{\int_{-\infty}^{\infty} \mathcal{V}(\xi)U_0'(\xi) d\xi} \quad (3.8)\]

and

\[\hat{W}_j(t) = -\frac{\int_{-\infty}^{\infty} \mathcal{V}(\xi)\hat{W}_j(\xi, t)d\xi}{\int_{-\infty}^{\infty} \mathcal{V}(\xi)U_0'(\xi) d\xi} \quad (3.9)\]
Note that
\[ \langle d\hat{W}_i(t) \rangle = 0, \quad \langle d\hat{W}_j(t')d\hat{W}_k(t) \rangle = 2D_{jk}\delta(t-t')dt'dt \] (3.10)
with \( D_{jk} \) the effective diffusion matrix
\[
D_{jk} = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \frac{V(\xi)V(\xi')\langle dW_j(\xi + ct + \Delta_j(t), t)dW_k(\xi' + ct + \Delta_k(t), t) \rangle d\xi d\xi'}{\left[ \int_{-\infty}^{\infty} V(\xi)U'_0(\xi)d\xi \right]^2}.
\]
(3.11)

It is clear that if we allow correlations between the noise in different layers, then the diffusion matrix depends on the phase difference \( \Delta_1 - \Delta_2 \), and the noise terms in the SDE (3.7) are multiplicative. In order to avoid issues regarding the interpretation of the noise in terms of Ito or Stratonovich, we will simplify the correlation matrix by setting
\[ C_{ij}(\xi) = \delta_{ij}C(\xi). \]

It follows that \( D_{jk} = \delta_{jk}D \) with \( D \) given by equation (2.26).

In the original analysis of interlaminar neural fields [20], \( \Delta \equiv \Delta_1 - \Delta_2 \) was assumed to be small, and equations (3.6a) and (3.6b) were Taylor expanded to first-order in \( \Delta \), resulting in a multivariate OU process. However, as we found for stimulus-locked fronts, \( \Delta(t) \) is not necessarily small. Therefore, one should proceed by looking for a stable fixed point of the ODE
\[
\frac{d\Delta}{dt} = -\frac{1}{2}G_-(\Delta),
\]
(3.12)
which is obtained by subtracting the deterministic parts of the pair of equations (3.7) and setting \( G_+(\Delta) \equiv G_1(\Delta) \pm G_2(-\Delta) \). Suppose that there exists a \( \xi_0 \) for which \( G_-(\xi_0) = 0 \) and \( G'_-(\xi_0) > 0 \). This represents a stable phase-locked state in the absence of noise, with \( \xi_0 \) the relative shift of the fronts in the two networks. One can establish the existence of a unique phase-locked state using the properties of \( G_j(\Delta) \) given by equation (3.8). Since the interlaminar coupling is taken to be excitatory, \( J_1(\xi) > 0 \) for all \( \xi \), and \( U_0(\xi) \) is a monotonically decreasing function of \( \xi \), the following properties hold:
(i) \( G_j(\Delta) < 0 \) for all \( \Delta \)
(ii) \( G_j(\Delta) \) is a monotonically increasing function of \( \Delta \) with \( G_j(\Delta) \to 0 \) as \( \Delta \to \infty \) and \( G_j(\Delta) \to 0 \) as \( \Delta \to -\infty \)
(iii) The functions \( G_1(\Delta) \) and \( G_2(-\Delta) \) intersect at a unique point \( \Delta = \xi_0 \) with the sign of \( \xi_0 \) determined by the relative strengths of \( J_1 \) and \( J_2 \). By symmetry, if \( J_1 = J_2 \) then \( \xi_0 = 0 \).

Given the stable fixed point \( \xi_0 \), one can now apply a linear-noise approximation to the full SDE (3.7) and derive a multivariate OU process. Let
\[ \Delta(t) = \xi_0 + \epsilon^{1/2}Y(t), \quad S(t) = \Delta_1(t) + \Delta_2(t) \]
and write
\[
\Delta_1(t) = \frac{\xi_0}{2} + \frac{\epsilon^{1/2}}{2} [S(t) + Y(t)], \quad \Delta_2(t) = -\frac{\xi_0}{2} + \frac{\epsilon^{1/2}}{2} [S(t) - Y(t)].
\]
Here \(S(t)/2\) represents the “center-of-mass” coordinate. Equations (3.7) become
\[
\begin{align*}
\frac{1}{2}[dS(t) + dY(t)] + G_1(\xi_0 + \epsilon^{1/2}Y(t))dt &= d\tilde{W}_1(t), \\
\frac{1}{2}[dS(t) - dY(t)] + G_2(-\xi_0 - \epsilon^{1/2}Y(t))dt &= d\tilde{W}_2(t).
\end{align*}
\]
We can now Taylor expand the nonlinear function \(G\) with respect to \(\epsilon^{1/2}Y(t)\). Adding and subtracting the above equations then yields the linear system of SDEs
\[
\begin{align*}
dS(t) + [G_+(\xi_0) + \epsilon^{1/2}G_+'(\xi_0)Y(t)]dt &= dW_+(t), \\
dY(t) + \epsilon^{1/2}G_-'(\xi_0)Y(t)dt &= dW_-(t),
\end{align*}
\]
where
\[
W_\pm(t) = \tilde{W}_1(t) \pm \tilde{W}_2(t).
\]
\(W_\pm(t)\) are also independent Wiener processes with
\[
\langle dW_a(t) \rangle = 0, \quad \langle dW_a(t)dW_b(t) \rangle = 4D\delta_{ab}dt, \quad a, b = \pm.
\]
Under the linear-noise approximation, fluctuations in the phase difference \(\Delta(t)\) about the fixed point \(\xi_0\) satisfy a one-dimensional OU process, which in turn drives fluctuations in the center-of-mass variable \(S(t)\). If \(\xi_0 = 0\), then we recover the results of Kilpatrick [20].

It immediately follows that the mean and variance of \(Y(t)\) are given by the equations (cf. equation (2.28))
\[
\begin{align*}
\bar{Y}(t) &\equiv \langle Y(t) \rangle = Y(0)e^{-\sqrt{\epsilon}At}, \\
\Theta_Y(t) &\equiv \langle Y(t)^2 \rangle - \langle Y(t) \rangle^2 = \frac{2D}{\sqrt{\epsilon}A} \left[1 - e^{-2\sqrt{\epsilon}At}\right],
\end{align*}
\]
with \(A = G_-'(\xi_0) \equiv G_1'(\xi_0) - G_2'(\xi_0)\) and \(G_j\) defined by equation (3.8). This implies that in the limit \(t \rightarrow \infty\) the mean of the phase-shift \(\Delta(t)\) converges to the deterministic fixed point \(\xi_0\) and the variance about the fixed point converges to \(2D\sqrt{\epsilon}/A\). In the case of \(S(t)\), equation (3.14a) can be integrated explicitly to give (with \(S(0) = 0\))
\[
S(t) = -G_+(\xi_0)t - \epsilon^{1/2}G_+'(\xi_0) \int_0^t Y(s)ds + W_+(t).
\]
Taking the mean and variance of this solution yields
\[
\bar{S}(t) \equiv \langle S(t) \rangle = -G_+(\xi_0)t - \frac{G_+'(\xi_0)Y(0)}{A} \left[1 - e^{-\sqrt{\epsilon}At}\right],
\]
and
\[
\begin{align*}
\Theta_S^2 &\equiv \langle S^2 \rangle - \bar{S}^2 = \epsilon G_+'(\xi_0)^2 \int_0^t \int_0^t [(Y(s)Y(s')) - \langle Y(s) \rangle \langle Y(s') \rangle] ds' ds + 4D.
\end{align*}
\]
In the large time limit, \( Y(t) \) becomes a stationary process with zero mean and autocorrelation function

\[
(Y(s)Y(s')) = \frac{D}{\sqrt{\epsilon A}} e^{-\sqrt{\epsilon A}|s-s'|}.
\]

Moreover,

\[
\int_0^t \int_0^t e^{-\sqrt{\epsilon A}|s-s'|} ds' ds = 2 \int_0^t \int_0^t e^{-\sqrt{\epsilon A}(s-s')} ds' ds = \frac{2t}{\sqrt{\epsilon A}} - \frac{2}{\epsilon A^2} \left[ 1 - e^{-\sqrt{\epsilon A}t} \right].
\]

Hence, for large \( t \)

\[
\Theta_S^2 \approx 2Dt,
\]

where we have used the fact that \( A = G' - (\xi_0) \).

In conclusion, the mean position of each front is given by (for \( Y(0) = 0 \))

\[
\langle \Delta_1(t) \rangle = \frac{\xi_0}{2} - \frac{e^{1/2}G_+(\xi_0)}{2} t, \quad \langle \Delta_2(t) \rangle = -\frac{\xi_0}{2} - \frac{e^{1/2}G_+(\xi_0)}{2} t.
\]

Thus, as previously noted by Kilpatrick [20], one effect of the weak coupling is to induce an \( O(\sqrt{\epsilon}) \) increase in the mean speed of each front according to

\[
c \rightarrow c + \frac{e^{1/2}G_+(\xi_0)}{2} > c.
\]

Furthermore, in the presence of additive noise, fluctuations in the phase-shift are given by an OU process, whereas fluctuations in the center-of-mass are given by Brownian diffusion.

### 3.2. Explicit results for Heaviside rate function.

Since the uncoupled, deterministic neural field equations (\( \epsilon = 0 \)) are given by equation (2.6), the calculation of the null vector \( V(\xi) \) and diffusivity \( D \) for the Heaviside rate function proceeds as in §2.2. That is, \( V(\xi) = -H(\xi)e^{-\xi/c} \). Therefore, we only have to calculate the nonlinear function \( G_j(\Delta) \) of equation (3.8). First note that

\[
\int_{-\infty}^{\infty} V(\xi)U'_0(\xi) d\xi = -\int_{-\infty}^{\infty} e^{-\xi/c} U'_0(\xi) d\xi = \frac{1}{2} \frac{\sigma c}{(\sigma + c)^2},
\]

so that

\[
G_j(\Delta) = -2 \frac{(\sigma + c)^2}{\sigma c} R_j(\Delta)
\]

with

\[
R_j(\Delta) = \int_0^\infty e^{-\xi/c} \left[ \int_{-\infty}^{\Delta} J_j(\xi - \xi') d\xi' \right] d\xi.
\]

Taking \( J_j(\xi) \) to be an exponential distribution, we have for \( \Delta > 0 \)

\[
R_j(\Delta) = \alpha J \int_0^\infty e^{-\xi/c} \int_{-\infty}^{\Delta} e^{-\xi/\sigma_j} e^{\xi'/\sigma_j} d\xi' d\xi
\]

\[
= \alpha J \sigma_j e^{-\Delta/\sigma_j} \int_0^\infty e^{-\xi/c} e^{-\xi/\sigma_j} d\xi
\]

\[
= \frac{c \alpha J \sigma^2}{e^{\Delta/\sigma_j} + \sigma_j} e^{-\Delta/\sigma_j}.
\]
Fig. 3.1. Plot of $G_-(\Delta)$ as a function of phase shift $\Delta$ for different values of the relative weight $\alpha = \alpha_2/\alpha_1$ of excitatory coupling. Other parameter values are $c = 0.25$ and $\sigma = \sigma_1 = \sigma_2 = 1$. It can be seen that there exists a unique zero $\xi_0$ for which $G_-(\xi_0) = 0$ and $G'(\xi_0) > 0$. If the interlaminar weights are stronger (weaker) in the direction 2 $\rightarrow$ 1 then $\xi_0 > 0$ ($\xi_0 < 0$). In the case of symmetric inter laminar connections we have $\xi_0 = 0$.

On the other hand, for $\Delta > 0$,

$$R_j(-\Delta) = \alpha_j \int_0^\infty e^{-\xi/c} \int_{-\infty}^0 e^{-(\xi-\xi')/\sigma_j} d\xi' d\xi + \alpha_j \int_{-\infty}^\Delta e^{-\xi/c} \int_0^\Delta e^{-(\xi-\xi')/\sigma_j} d\xi' d\xi + \alpha_j \int_0^\Delta e^{-\xi/c} \int_0^\Delta e^{-(\xi-\xi')/\sigma_j} d\xi' d\xi$$

$$= \alpha_j \sigma_j \int_0^\infty e^{-\xi/c} e^{-\xi/\sigma_j} d\xi + \alpha_j \int_0^\Delta e^{-\xi/c} \left( \int_0^\xi e^{-(\xi-\xi')/\sigma_j} d\xi' + \int_\xi^\Delta e^{-(\xi-\xi')/\sigma_j} d\xi' \right) d\xi + \alpha_j \sigma_j \left[ e^{\Delta/\sigma_j} - 1 \right] \int_0^\infty e^{-\xi/c} e^{-\xi/\sigma_j} d\xi$$

$$= \frac{\alpha_j \sigma_j}{c^2 - \sigma_j^2} \left( 2(c^2 - \sigma_j^2) + \sigma_j (c + \sigma_j) e^{-\Delta/\sigma_j} - 2c e^{-\Delta/c} \right)$$

$$= \alpha_j c \sigma_j \left( 2 + \frac{\sigma_j e^{-\Delta/\sigma_j}}{c - \sigma_j} - \frac{2c e^{-\Delta/c}}{c^2 - \sigma_j^2} \right).$$

For the sake of illustration, suppose that $c = 0.25$, $\sigma = \sigma_j = 1$ and set $\alpha_2/\alpha_1 = \alpha$. In Fig. 3.1 we plot the function $G_-(\Delta)$ with respect to the phase-shift $\Delta$ for several values of $\alpha_2/\alpha_1$. As expected, $G_-(\Delta)$ is a monotonically increasing function of $\Delta$ with a unique zero $\xi_0$. In the case of symmetric weights ($\alpha = 0$) we have $\xi_0 = 0$, whereas for $0 < \alpha < 1$ ($1 < \alpha$) we find that $\xi_0 > 0$ ($\xi_0 < 0$). Recall that the stationary variance about the phase-locked state is

$$\langle (\Delta(t))^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{2\sqrt{eD}}{G'_-(\xi_0)}. \quad (3.21)$$
\[ \langle \Delta^2 \rangle \text{ saturates in the limit } t \to \infty. \]

Variance is computed as a function of time using numerical simulations (dashed line) and asymptotic theory (solid line) predicts the saturation value \((3.22)\). Interlaminar connectivity strength \(\kappa = 0\) so \(\xi_0 = 0\) and \(\langle \Delta(t) \rangle \equiv 0\); noise amplitude \(\epsilon = 0.0005\). (B) The stationary variance decreases as a function of interlaminar connectivity strength \(\kappa = 0\) in numerical simulations (circles) and theory (solid line). Threshold \(\kappa = 0.4\) and noise amplitude \(\epsilon = 0.0005\). Variances are computed using 5000 realizations each.

\[ \xi_0 \text{ is fixed by fixed the degree of asymmetry } \alpha \text{ in the inter laminar connections. However, } G_\ell'(\xi_0) \text{ scales with } \alpha_1, \text{ which establishes that increasing the strength of interlaminar coupling can reduce the variance, as previously highlighted by Kilpatrick [20].} \]

Upon considering weight spatial scale \(\sigma = \sigma_j = 1\), symmetric connectivity \(\alpha = 1\), and cosine noise correlations \(C(\xi) = \cos(\xi)\) then \(D\) is given by \((2.34)\), \(\xi_0 = 0\), \(G_\ell'(0) = 2\alpha_1/\kappa\) so \(\langle \Delta(t) \rangle \equiv 0\) and

\[ \langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{\sqrt{\epsilon}}{4\alpha_1 \kappa^3(c^2 + 1)}. \quad (3.22) \]

We compare the formula \((3.22)\) to numerical simulations in Fig. 3.2, demonstrating how the variance decreases with \(\alpha_1\) as well as the threshold \(\kappa\).

4. Breakdown of linear-noise approximation. So far we have considered examples of stochastic phase-locked fronts, in which there is a unique, stable phase-locked state in the deterministic limit. This allowed us to carry out a linear-noise approximation and thus show that fluctuations about the phase-locked state can be characterized in terms of an OU process. Here we consider an example where the linear-noise approximation breaks down due to the existence of an additional unstable phase-locked state in the deterministic limit. We again consider a pair of coupled neural fields given by equations \((3.1a)\) and \((3.1b)\), but now take the interlaminar coupling to be given by a difference of exponentials: \(J_1 = J_2 = J\) with

\[ J(x) = \alpha_1 \left[ e^{-|x|} - \beta e^{-|x|/\gamma} \right], \quad 0 < \beta < 1, \quad \gamma > 1. \quad (4.1) \]

This distribution represents short-range excitation and long-range inhibition. For the sake of illustration, we assume that the interlaminar coupling is symmetric. The analysis of stochastic phase-locking proceeds along identical lines to §3, and we obtain the nonlinear SDE \((3.7)\). In the deterministic limit, the phase-difference \(\Delta(t)\) evolves
Fig. 4.1. Plot of $G_-(\Delta)$ as a function of phase-shift $\Delta$ for different values of the inhibitory weight $\beta$. Other parameter values are $\sigma = 1$, $c = 0.25$, $\alpha_1 = 0.25$, and $\gamma = 4$. It can be seen that for intermediate values of $\beta$, a stable phase-locked state at $\Delta = 0$ coexists with a pair of unstable fixed points at $\Delta = \pm \xi_0(\beta)$.

according to equation (3.12) with $G_-(\Delta) = G(\Delta) - G(-\Delta)$ and

\[
G(\Delta) = \int_{-\infty}^{\infty} V(\xi) \left[ \int_{-\infty}^{\infty} J(\xi - \xi') F(U_0(\xi') + \Delta) d\xi' \right] d\xi
\]

(4.2)

for $J$ given by equation (4.1). In the case of a Heaviside rate function, $G(\Delta)$ may be evaluated explicitly to yield

\[
G_-(\Delta) = 4\alpha_1 \frac{(\sigma + c)^2}{\sigma} \frac{1}{c^2 - 1} \left[ c^2(1 - e^{-\Delta/c}) - (1 - e^{-\Delta}) \right] - 4\alpha_1 \beta \gamma \frac{1}{c^2 - \gamma^2} \left[ c^2(1 - e^{-\Delta/c}) - \gamma^2(1 - e^{-\Delta/\gamma}) \right]
\]

(4.3)

In Fig. 4.1, we plot $G_-(\Delta)$ for various values of $\beta$ with $\sigma = c = 1$ and $\gamma = 4$. It can be seen that for a range of $\beta$ values, there exist three fixed points, a stable fixed point at $\Delta = 0$ and a pair of unstable fixed points at $\Delta = \pm \xi_1(\beta)$. For sufficiently large $\beta$ (strong mutual inhibition), the system undergoes a pitchfork bifurcation, resulting in a single unstable phase-locked state.

Let us focus on the regime where the stable phase-locked state at zero coexists with a pair of unstable states. If we now carry out a linear-noise approximation about the stable state, then the resulting OU process will capture the Gaussian-like fluctuations within the basin of attraction of the phase-locked state on intermediate time-scales. However, on longer time-scales, large fluctuations (rare events) can lead to an escape from the basin of attraction due to $\Delta(t)$ crossing one of the unstable fixed points $\pm \xi_1$. Destabilization of the noise-free system is illustrated in Fig. 4.2. Noise-induced escape from the stable state (as in Fig. 4.3A) cannot be captured using the linear-noise approximation. The full SDE for $\Delta(t)$ is obtained by subtracting equations (3.7a) and (3.7b), which yields

\[
d\Delta(t) = -G_-(\Delta)dt + \sqrt{\mu}dW(t),
\]

(4.4)
Fig. 4.2. Decoupling of fronts in the case of laterally inhibitory connectivity in (3.1a - 3.1b) with no noise. (A) For a symmetric network, starting the front positions $\Delta_1$ and $\Delta_2$ within the basin of attraction of the coupled state ($\Delta_1(0) - \Delta_2(0) = 3$) leads to long term coupling: $\lim_{t \to \infty} |\Delta_1(t) - \Delta_2(t)| = \lim_{t \to \infty} |\Delta(t)| = 0$. (B) Starting front positions $\Delta_1$ and $\Delta_2$ outside the basin of attraction of the coupled state ($\Delta_1(0) - \Delta_2(0) = 4$) leads to long term decoupling: $\lim_{t \to \infty} |\Delta_1(t) - \Delta_2(t)| = \lim_{t \to \infty} |\Delta(t)| = \infty$. Threshold $\kappa = 0.4$ so $c = 0.25$; no noise ($W_1 = W_2 \equiv 0$); coupling parameters are $\epsilon = 0.005$, $\alpha = 1$, $\beta = 0.4$, $\gamma = 4$. This results in the unstable fixed point (separatrix) occurring at $\Delta = \Delta_1 - \Delta_2 \approx 3.78$.

where we have set $4D = 1, \mu = \sqrt{\epsilon}$ and rescaled time according to $t \to \mu t$. Here

$$\langle dW(t) \rangle = 0, \quad \langle dW(t)dW(t') \rangle = \delta(t-t')dt'dt.$$

Let $p(\Delta, t)$ be the probability density for the stochastic process $\Delta(t)$ given some initial condition $\Delta(0) = \Delta_0$. The corresponding Fokker-Planck (FP) equation is given by

$$\frac{\partial p}{\partial t} = \frac{\partial [G(T)p(\Delta, t)]}{\partial \Delta} + \frac{\mu}{2} \frac{\partial^2 p(\Delta, t)}{\partial \Delta^2} = -\frac{\partial J(\Delta, t)}{\partial \Delta}, \quad (4.5)$$

where

$$J(\Delta, t) = -\frac{\mu}{2} \frac{\partial p(\Delta, t)}{\partial \Delta} - G_-(\Delta) p(\Delta, t)$$
and \( p(\Delta, 0) = \delta(\Delta - \Delta_0) \). Suppose that the deterministic equation \( \dot{\Delta} = -G_-(\Delta) \) has a stable fixed point at \( \Delta = 0 \) and a pair of unstable fixed points at \( \Delta = \pm \xi_1 \). Thus the basin of attraction of the zero state is given by the interval \((-\xi_1, \xi_1)\). For small but finite \( \mu \), fluctuations can induce rare transitions out of the basin of attraction due to a metastable trajectory crossing one of the points \( \pm \xi_1 \). Assume that the stochastic system is initially at \( \Delta_0 = 0 \). In order to solve the first passage time problem for escape from the basin of attraction of the zero fixed point, we impose absorbing boundary conditions at \( \pm \xi_1 \), that is, we set \( p(\pm \xi_1, t) = 0 \). Let \( T(\Delta) \) denote the (stochastic) first passage time for which the system first reaches one of the points \( \pm \xi_1 \), given that it started at \( \Delta \in (-\xi_1, \xi_1) \). The distribution of first passage times is related to the survival probability that the system hasn’t yet reached \( \pm \xi_1 \):

\[
S(t) \equiv \int_{-\xi_1}^{\xi_1} p(\Delta, t) d\Delta.
\] (4.6)

That is, \( \text{Prob}\{t > T\} = S(t) \) and the first passage time density is

\[
f(t) = -\frac{dS}{dt} = -\int_{-\xi_1}^{\xi_1} \frac{\partial p}{\partial t}(\Delta, t) d\Delta.
\] (4.7)

Substituting for \( \frac{\partial p}{\partial t} \) using the FP equation (4.5) shows that

\[
f(t) = \int_{-\xi_1}^{\xi_1} \frac{\partial J(\Delta, t)}{\partial \Delta} d\Delta = J(\xi_1, t) - J(-\xi_1, t).
\] (4.8)

The first passage time density can thus be interpreted as the total probability flux leaving the basin of attraction through the absorbing boundaries.

Using standard analysis, one can show that the mean first passage time (MFPT) \( \tau(\Delta) = \langle T \rangle \) satisfies the backwards equation [15, 27]

\[- G_-(\Delta) \frac{d\tau}{d\Delta} + \frac{\mu}{2} \frac{d^2\tau}{d\Delta^2} = -1, \] (4.9)

with the boundary conditions \( \tau(\pm \xi_1) = 0 \). Solving this equation yields

\[
\tau(\Delta) = \tau_1(\Delta) - \tau_2(\Delta)
\] (4.10)

with

\[
\tau_1(\Delta) = \frac{2}{\mu} \left( \int_{-\xi_1}^{\xi_1} \frac{dy}{\psi(y)} \right)^{-1} \left( \int_{-\xi_1}^{\Delta} \frac{dy}{\psi(y)} \right) \left[ \int_{-\xi_1}^{\xi_1} \frac{dy'}{\psi(y')} \int_{-\xi_1}^{y'} \psi(z) dz \right],
\] (4.11)

\[
\tau_2(\Delta) = \frac{2}{\mu} \left( \int_{-\xi_1}^{\xi_1} \frac{dy}{\psi(y)} \right)^{-1} \left( \int_{\Delta}^{\xi_1} \frac{dy}{\psi(y)} \right) \left[ \int_{-\xi_1}^{\xi_1} \frac{dy'}{\psi(y')} \int_{-\xi_1}^{y'} \psi(z) dz \right],
\] (4.12)

and

\[
\psi(\Delta) = \exp \left[ -\frac{2}{\mu} \int_{0}^{\Delta} G_-(y) dy \right].
\] (4.13)
We can simplify the analysis considerably by exploiting the symmetry of the given problem, namely, that $G_-(\Delta) = -G_-(\Delta)$ and hence $\psi(\Delta) = \psi(-\Delta)$. It is then straightforward to show that

$$\tau(0) = \frac{2}{\mu} \int_0^{\xi_1} \frac{dy'}{\psi(y')} \int_0^{y'} \psi(z)dz. \quad (4.14)$$

This is identical to the formula for the MFPT for escape from the interval $[0, \xi_1)$ starting at $\Delta = 0$ with a reflecting boundary at $\Delta = 0$ and an absorbing boundary at $\Delta = \xi_1$. We compare our theory for the mean first passage time $\langle T \rangle = \tau(0)$ to numerical simulations for symmetric lateral inhibitory connectivity (4.1) and cosine noise correlations so $D$ satisfies (2.34), showing in Fig. 4.3 that the marginal rare
event statistic is well captured for low enough values of coupling strength $\alpha_1$. Using steepest descents, one can now derive the classical Arrhenius formula [15]

$$\tau(0) \sim \frac{2\pi}{\sqrt{|U''(\xi_1)|U''(0)}} e^{2[U(\xi_1) - U(0)]/\mu}, \quad (4.15)$$

where

$$U(\Delta) = \int_0^\Delta G_y(y) dy. \quad (4.16)$$

The above analysis provides another example where knowledge of the nonlinear nature of the phase-shift dynamics is crucial for determining the effects of noise. In §2 and §3, the nonlinearity determined the unique phase-locked state $\xi_0$ about which we could carry out a linear-noise approximation. Here, the explicit form of the nonlinearity is required in order to determine the rate of escape from a (meta)stable phase-locked state that coexists with a pair of unstable states. Note that, as expected, the mean escape time is exponentially large in the weak noise limit $\mu \to 0$, since $U(\xi_1) > U(0)$.

5. Bumps in weakly-coupled stochastic neural fields. Kilpatrick has previously shown that interlaminar coupling can reduce the long term diffusion of bumps in stochastic neural fields [19,21]. Effective equations for the stochastic motion of bumps derived in this work tended to be linear SDEs, such as OU processes. However, in [18] it was shown how the impact of spatial heterogeneities can be accounted for by a nonlinear SDE that incorporates the effective potential bestowed by the heterogeneity. Here, we extend this previous work as well as our analysis of coupled fronts by considering nonlinear contributions to the effective dynamics of bumps coupled in laminar neural fields. We focus on a pair of identical neural fields on the ring $x \in (-\pi, \pi]$, labeled $j = 1, 2$ and mutually coupled by interlaminar weight distributions $J_1(x)$ and $J_2(x)$:

$$\tau dU_1(x, t) = \left[-U_1(x, t) + \int_{-\pi}^\pi w(x-y)F(U_1(y, t)) dy \right] dt + \epsilon^{1/2} \int_{-\pi}^\pi J_1(x-y)F(U_2(y, t)) dy dt + \epsilon^{1/2} \tau^{1/2} dW_1(x, t), \quad (5.1a)$$

and

$$\tau dU_2(x, t) = \left[-U_2(x, t) + \int_{-\pi}^\pi w(x-y)F(U_2(y, t)) dy \right] dt + \epsilon^{1/2} \int_{-\pi}^\pi J_2(x-y)F(U_1(y, t)) dy dt + \epsilon^{1/2} \tau^{1/2} dW_2(x, t). \quad (5.1b)$$

The spatially extended Wiener processes $W_1(x, t)$ and $W_2(x, t)$ are defined on $x \in (-\pi, \pi]$ with

$$\langle dW_j(x, t) \rangle = 0, \quad \langle dW_1(x, t) dW_j(x', t) \rangle = 2C_{ij}(x-x') \delta(t-t') dt dt'. \quad (5.2)$$

Coupling within a layer $w(x-y)$ is assumed to be an even function of lateral inhibitory type [1,9,18]. For comparison with numerical simulations, we assume intralaminar coupling

$$w(x) = \cos(x) \quad (5.3)$$
and interlaminar coupling $J_j(x)$ may be asymmetric

$$J_j(x) = \alpha_j \cos(x),$$

(5.4)

and we will allow $\alpha_j$ to be negative or positive. We will also set the timescale $\tau = 1$. Previously, Kilpatrick has shown interlaminar coupling will phase-lock the bump positions in each of the two layers [19,21]. Noise tends to counter the effects of coupling by driving bump positions apart from one another. We will extend our analysis by considering the nonlinear contributions of this coupling as a restorative force against this noise.

### 5.1. Interlaminar coupling of bumps in the presence of noise.

In the absence of interlaminar coupling and noise ($\epsilon = 0$), each neural field independently supports a stationary bump solution satisfying

$$U_0(x) = \int_{-\pi}^{\pi} w(x - y) F(U_0(y))dy$$

(5.5)

(see [18] for details). Each neural field is translationally symmetric, so each bump $U_0(x)$ can be centered at an arbitrary location in the neural field. To explore the impact of noise and weak coupling upon the position of bumps, we consider the ansatz

$$U_j(x, t) = U_0(x - \Delta_j(t)) + \epsilon^{1/2}\Phi_j(x - \Delta_j(t), t), \quad j = 1, 2,$$

(5.6)

where $\Delta_j(t)$ describes the motion of the bump in the $j$th layer and $\Phi_j$ describes alterations to each bump’s profile. Substituting (5.6) into (5.1a) and (5.1b), we obtain equation (3.5) with $c = 0$, $\xi \to x$ and $R \to S^1$. We can now carry out a perturbation expansion in $\Phi_j$ by writing $\Phi_j = \Phi_{j0} + \sqrt{\epsilon}\Phi_{j1} + O(\epsilon)$, Taylor expanding $F$, and imposing the equation (5.5). This yields (after shifting $x$ appropriately),

$$d\Phi_{10}(x, t) = \hat{L} \circ \Phi_{10}(x, t) dt + \epsilon^{-1/2}U'_0(x)\Delta_1(t) + d\tilde{W}_1(x, t)$$

$$+ \int_{-\pi}^{\pi} J_1(x - x')F(U_0(x + \Delta_1(t) - \Delta_2(t))dx'dt$$

(5.7)

and

$$d\Phi_{20}(x, t) = \hat{L} \circ \Phi_{20}(x, t) dt + \epsilon^{-1/2}U'_0(x)\Delta_2(t) + d\tilde{W}_2(x, t)$$

$$+ \int_{-\pi}^{\pi} J_2(x - x')F(U_0(x + \Delta_2(t) - \Delta_1(t))dx'dt$$

(5.8)

where

$$\tilde{W}_j(x, t) = W_j(x + \Delta_j(t), t),$$

(5.9)

and $\hat{L}$ is the non-self-adjoint linear operator

$$\hat{L} \circ A(x) = -A(x) + \int_{-\pi}^{\pi} w(x - x')F'(U_0(x'))A(x')dx'$$

(5.10)

for any function $A(x) \in L^2(\mathbb{R})$. The nullspace of $\hat{L}$ is spanned by $U'_0(x)$, following from differentiating equation (5.5), analogous to the case of fronts. A solvability condition
for the existence of a bounded solution is given by ensuring the inhomogenous parts of (5.7) and (5.8) are orthogonal to all elements of the nullspace of the adjoint operator \( \hat{L}^* \). This is defined with respect to the inner products

\[
\int_{-\pi}^{\pi} B(x) \hat{L} A(x) dx = \int_{-\pi}^{\pi} \left[ \hat{L}^* B(x) \right] A(x) dx
\]

(5.11)

where \( A(x) \) and \( B(x) \) are arbitrary integrable functions. Thus,

\[
\hat{L}^* B(x) = -B(x) + F'(U_0(x)) \int_{-\pi}^{\pi} w(x - x') B(x') dx'.
\]

(5.12)

We can show \( \hat{L}^* \) has a one-dimensional nullspace spanned by some function \( \mathcal{V}(x) \). As in the case of fronts, the solvability condition reflects the marginal stability of the homogeneous system (\( \epsilon = 0 \)). The linear operator \( \hat{L} \) has a simple zero eigenvalue while the remainder of the spectrum lies in the left-half of the complex plane. Thus, \( \Phi_{10} \) and \( \Phi_{20} \) will be unbounded in the limit of large \( t \) unless perturbations that lie in the null-space vanish.

The solvability condition leads to the two-dimensional nonlinear SDE for the phase-shifts \( (\Delta_1(t), \Delta_2(t)) \):

\[
\begin{align*}
    d\Delta_1(t) + e^{1/2} G_1(\Delta_1(t) - \Delta_2(t)) dt &= e^{1/2} d\tilde{W}_1(t), \\
    d\Delta_2(t) + e^{1/2} G_2(\Delta_2(t) - \Delta_1(t)) dt &= e^{1/2} d\tilde{W}_2(t),
\end{align*}
\]

(5.13a, 5.13b)

where

\[
G_{ij}(\Delta) = \frac{\int_{-\pi}^{\pi} \mathcal{V}(x) \left[ \int_{-\pi}^{\pi} J_j(x - x') F(U_0(x' + \Delta)) dx' \right] dx}{\int_{-\pi}^{\pi} \mathcal{V}(x) U_0'(x) dx}
\]

(5.14)

and

\[
\tilde{W}_j(t) = -\frac{\int_{-\pi}^{\pi} \mathcal{V}(x) W_j(x, t) dx}{\int_{-\pi}^{\pi} \mathcal{V}(x) U_0'(x) dx}
\]

(5.15)

Note that

\[
\langle d\tilde{W}_i(t) \rangle = 0, \quad \langle d\tilde{W}_j(t) d\tilde{W}_k(t) \rangle = 2D_{jk} \delta(t - t') dt' dt
\]

(5.16)

with \( D_{jk} \) the effective diffusion matrix

\[
D_{jk} = \frac{\int_{-\pi}^{\pi} \int_{-\pi}^{\pi} \mathcal{V}(x) \mathcal{V}(x') \langle dW_j(x + \Delta_j(t), t) dW_k(x + \Delta_k(t), t) \rangle dx dx'}{\int_{-\pi}^{\pi} \mathcal{V}(x) U_0'(x) dx}^2
\]

\[
= \frac{\int_{-\pi}^{\pi} \mathcal{V}(x) C_{jk}(x - x' + \Delta_j(t) - \Delta_k(t)) \mathcal{V}(x') dx'}{\int_{-\pi}^{\pi} \mathcal{V}(x) U_0'(x) dx}^2.
\]

(5.17)

As in the case of fronts, correlations between noise in each layer will lead to multiplicative noise terms in the SDE (5.13), due to the dependence on phase difference.
\( \Delta_1 - \Delta_2 \). To avoid this, we assume for now there are no interlaminar noise correlations, so \( C_{ij}(x) = \delta_{ij}C(x) \), so that \( D_{jk} = \delta_{jk}D \) with

\[
D = \frac{\int_{-\pi}^{\pi} V(x) C(x-x') V(x') \, dx \, dx'}{\left[ \int_{-\pi}^{\pi} V(x) U_0'(x) \, dx \right]^2}.
\]  

(5.18)

Now, we relax the assumption that was made in [19, 21] that stated that \( \Delta \equiv \Delta_1 - \Delta_2 \) remains small. This means we cannot Taylor expand nonlinearities in (5.13) involving \( \Delta \) to first order. Thus, we proceed by looking for stable fixed points of the ODE obtained by subtracting the deterministic parts of the equations (5.13):

\[
\frac{d\Delta}{dt} = -\epsilon^{1/2}G_-(\Delta),
\]

(5.19)

where \( G_\pm(\Delta) = G_1(\Delta) \pm G_2(-\Delta) \). A stable phase locked state \( x_0 \) will satisfy \( G_+(x_0) = 0 \) and \( G'(x_0) > 0 \). Upon identifying \( x_0 \), the relative shift between the bumps in the two layers, we can apply a linear noise approximation to the full SDE (5.13) and derive a multivariate OU process. The analysis proceeds along identical lines to the case of fronts with \( \xi_0 \to x_0 \). That is, we perform the change of variables

\[
\Delta(t) = x_0 + \epsilon^{1/2}Y(t), \quad S(t) = \Delta_1(t) + \Delta_2(t)
\]

(5.20)

and Taylor expand the nonlinear functions \( G_{1,2} \) with respect to \( \epsilon^{1/2}Y(t) \). Analyzing the resulting OU process shows that the mean position of each bump is given by (for \( Y(0) = 0 \))

\[
\langle \Delta_1(t) \rangle = \frac{x_0}{2} - \frac{\epsilon^{1/2}G_+(x_0)}{2}t, \quad \langle \Delta_2(t) \rangle = -\frac{x_0}{2} - \frac{\epsilon^{1/2}G_+(x_0)}{2}t.
\]

(5.21)

Thus, the \( O(\epsilon^{1/2}) \) expansion introduces the possibility of bumps having some nonzero drift \( (\epsilon^{1/2}|G_+(x_0)|/2) \) due to interlaminar coupling. Also, noise introduces fluctuations in the phase-shift, given by an OU process. Fluctuations in the center-of-mass are given by Brownian diffusion, as was found in [19].

\textbf{5.2. Explicit results for Heaviside rate function.} The uncoupled deterministic neural field equations (\( \epsilon = 0 \)) are given by

\[
\frac{\partial u_j(x,t)}{\partial t} = -u_j(x,t) + \int_{-\pi}^{\pi} w(x-y)H(u_j(y,t) - \kappa) \, dy, \quad j = 1, 2.
\]

(5.22)

Thus, for a cosine weight function (5.3), bump solutions satisfy (5.5), so fixing their peak to be at \( x = 0 \), we have [18]

\[
U_0(x) = A \cos x, \quad U_0'(x) = -A \sin x, \quad A = \sqrt{1 + \kappa^2} - \sqrt{1 - \kappa^2},
\]

(5.23)

and

\[
U_0(\pm a) = \kappa, \quad a = \frac{\pi}{4} \pm \left( \frac{\pi}{4} - \frac{1}{2} \sin^{-1} \kappa \right),
\]

(5.24)

where the wider bump (larger \( a \)) will be stable [18]. The null-space \( V(x) \) of the adjoint operator \( \hat{L}^* \) satisfies

\[
V(x) = \frac{\delta(x + a)}{|U'(a)|} \int_{-\pi}^{\pi} \cos(a + y)V(y) \, dy + \frac{\delta(x - a)}{|U'(a)|} \int_{-\pi}^{\pi} \cos(a - y)V(y) \, dy,
\]

(5.25)
which has solution $\mathcal{V}(x) = \delta(x + a) - \delta(x - a)$. For our explicit calculations, we take $C(x) = C_0 \cos(x)$, where $C_0$ has units of length. Thus, it follows that the formula (5.18) reduces to

$$D = C_0 \left( \frac{\int_{-\pi}^{\pi} \mathcal{V}(x) \sin(x) dx}{U'_0(a) - U'_0(-a)} \right)^2 + \left( \frac{\int_{-\pi}^{\pi} \mathcal{V}(x) \cos(x) dx}{U'_0(a) - U'_0(-a)} \right)^2 = \frac{C_0}{2 + 2\sqrt{1 - \kappa^2}}. \quad (5.26)$$

Thus, we need only compute the nonlinear functions $G_j(\Delta)$ given by equation (5.14). First, we note

$$\int_{-\pi}^{\pi} \mathcal{V}(x) U'_0(x) dx = U'_0(-a) - U'_0(a) = 2A \sin a \quad (5.27)$$

so that upon taking cosine interlaminar connectivity (5.4), we have

$$G_j(\Delta) = \alpha_j \sin \Delta, \quad (5.28)$$

so that

$$G_{\pm}(\Delta) = (\alpha_1 \mp \alpha_2) \sin \Delta. \quad (5.29)$$

Note, a related result was derived in [18], demonstrating that weak nonlinear spatial heterogeneities can be inherited by the underlying dynamics of stochastically moving bumps in single layer neural fields. We thus can immediately identify the two fixed points on $\Delta \in (-\pi, \pi]$, where $G_-(\Delta) \equiv 0$ at $\Delta = 0, \pi$. Their stability is easily computed

$$\lambda_0 \equiv -G'_{-}(0) = -(\alpha_1 + \alpha_2), \quad (5.30)$$

$$\lambda_\pi \equiv -G'_{-}(\pi) = (\alpha_1 + \alpha_2), \quad (5.31)$$

so if $\alpha_1 + \alpha_2 > 0$, $x_0 = 0$ ($x_1 = \pi$) is stable (unstable), and if $\alpha_1 + \alpha_2 < 0$, $x_1 = 0$ ($x_0 = \pi$) is unstable (stable). Thus, for locally inhibitory connectivity, the bumps’ positions can be driven apart ($x_0 = \pi$) so they are anti-phase relative to one another. Either way, we can compute the stationary variance about the phase-locked state

$$\langle \Delta(t)^2 \rangle - \langle \Delta(t) \rangle^2 = \frac{2\sqrt{\epsilon}D}{G'_-(x_0)} = \frac{C_0 \sqrt{\epsilon}}{\alpha_1 + \alpha_2(1 + \sqrt{1 - \kappa^2})}. \quad (5.32)$$

Thus, we recover the result from [19], showing the strength of interlaminar coupling reduces variance in stochastic bump motion. We demonstrate in Fig. 5.1 that the variance in the phase difference is well approximated by (5.32) as compared with numerical simulations.

5.3. Noise-induced phase slips. As in the case of fronts, noise not only causes the center-of-mass of both bumps to wander diffusively, it can also lead to rare events, where the bumps temporarily become uncoupled. Typically, noise will perturb the phase-difference $\Delta(t)$, while the local dynamics of the stable fixed point will pull the phase difference back to $x_0$. However, on longer time-scales, large fluctuations can lead to $\Delta(t)$ crossing the separatrix given by the unstable fixed point $x_1$. These events cannot be captured by a linear noise approximation. Note, a similar observation was made by Kilpatrick and Ermentrout in [18] in a single layer network with periodic spatial heterogeneity in the weight function.
The nonlinear SDE describing the stochastic motion of the phase-difference $\Delta(t)$ is given by subtracting equations (5.13a) and (5.13b) to find

$$d\Delta(t) = -G_-(\Delta)dt + \sqrt{\mu}dW(t),$$

setting $4D = 1$, $\mu = \sqrt{\epsilon}$ and rescaling time so $t \to \mu t$. Then

$$\langle dW(t) \rangle = 0, \quad \langle dW(t)dW(t') \rangle = \delta(t-t')dt'dt.$$

Let $p(\Delta,t)$ be the probability density of the stochastic process $\Delta(t)$ given initial condition $\Delta(0) = \Delta_0$. The corresponding Fokker-Planck (FP) equation is given by

$$\frac{\partial p}{\partial t} = -\frac{\partial[G_-(\Delta)p(\Delta,t)]}{\partial \Delta} + \frac{\mu}{2} \frac{\partial^2 p(\Delta,t)}{\partial \Delta^2} = -\frac{\partial J(\Delta,t)}{\partial \Delta},$$

where

$$J(\Delta,t) = -\frac{\mu}{2} \frac{\partial p(\Delta,t)}{\partial \Delta} - G_-(\Delta)p(\Delta,t)$$

and $p(\Delta,0) = \delta(\Delta - \Delta_0)$. As in the case of fronts, we suppose that the deterministic equation $\dot{\Delta} = -G_-(\Delta)$ has a stable fixed point at $\Delta = 0$ and a pair of unstable fixed points at $\Delta = \pm x_1$. Thus the basin of attraction of the zero state is given by the interval $(-x_1,x_1)$. For small but finite $\mu$, fluctuations can induce rare transitions where trajectories cross through one of the unstable separatrices $\pm x_1$. To solve the first passage time problem for these phase-slips, starting with $\Delta(0) = 0$, we impose absorbing boundary conditions at $\pm x_1$, that is, we set $p(\pm x_1,t) = 0$. Let $T(\Delta)$ denote the (stochastic) first passage time for which the system first reaches one of the points $\pm x_1$, given that it started at $\Delta \in (-x_1,x_1)$. As in the case of fronts, one can show that the mean first passage time (MFPT) $\tau(0) = \langle T(0) \rangle$ is given by the formula

$$\tau(0) = \frac{2}{\mu} \int_0^{x_1} \frac{dy'}{\psi(y')} \int_0^{y'} \psi(z)dz,$$
Fig. 5.2. (A) Numerical simulation demonstrating a phase-slip (arrows) for two coupled bumps in the system (5.1a–5.1b), using the cosine coupling function (5.4) with $\alpha_1 = \alpha_2 = 0.1$. Overlaid lines represent the evolution of centers-of-mass of the bumps in time $\Delta_1(t)$ and $\Delta_2(t)$. (B) Average time $\tau(0) = \langle T \rangle$ until a phase slip increases as a function of the interlaminar coupling strength $\alpha_1 = \alpha_2$. Theory (solid line) computed using (5.40) matches numerical simulation results (circles) well. Threshold $\kappa = 0.5$, noise amplitude $\epsilon = 0.05$. Mean first passage times $\langle T \rangle$ are computed with 1000 samples.

where

$$
\psi(\Delta) = \exp \left[ -\frac{2}{\mu} \int_0^\Delta G_- (y) dy \right].
$$

(5.37)

We can obtain explicit results in the case of a Heaviside rate function, local cosine weight function (5.3), and cosine interlaminar connectivity (5.4). To begin, we employ equation (5.29) to note that

$$
\psi(\Delta) = \exp \left[ -\frac{2(\alpha_1 + \alpha_2)}{\mu} \int_0^\Delta \sin(y) dy \right] = \exp \left[ -\bar{\alpha}(1 - \cos \Delta) \right],
$$

(5.38)
where $\bar{\alpha} = 2(\alpha_1 + \alpha_2)/\mu$. Thus,

$$\tau(0) = \frac{2}{\mu} \int_0^\pi \int_0^\pi e^{\bar{\alpha} (\cos y - \cos x)} dydx,$$  \hspace{1cm} (5.39)

which is straightforward to integrate using numerical quadrature. We compare the analytically derived approximation to the mean time between phase slips (5.39) to results computed numerically simulating the full system of stochastic integrodifferential equations (5.1a-5.1b) in Fig. 5.2. The theory we compare assumes cosine noise correlations ($C(x) = C_0 \cos(x)$), so that $D$ is given by (5.26). Assuming symmetric coupling $\alpha_1 = \alpha_2 = \alpha$ and inverting the rescaling $t \rightarrow \mu^{-1} t$, we have

$$\tau(0) = \frac{1}{2\epsilon D} \int_0^\pi \int_0^\pi \frac{\alpha}{\epsilon \sqrt{D}} (\cos y - \cos x) \, dydx.$$  \hspace{1cm} (5.40)

6. Discussion. We have explored the impact of stimuli and coupling on the stochastic motion of patterns in neural field equations. Our main advance is to demonstrate nonlinear contributions to the effective stochastic equations for the position of wandering patterns. To do this, we have assumed that the stimuli or the coupling between multiple layers of a neural field are weak, namely having comparable amplitude to the spatiotemporal noise term that forces the system. Then, utilizing a small noise and small coupling expansion, we have derived nonlinear Langevin equations whose effective potentials are shaped by the spatial profile of coupling. This allows us to approximate the statistics of rare events, such as large deviations whereby waves become decoupled from one another, analogous to the well-hopping of bumps observed in spatially heterogeneous neural fields [18]. Such stochastic dynamics would not be captured by a linear system of SDEs.

There are several ways we could extend the techniques we have developed here. For instance, Figs. 4.3B and 5.2B demonstrate the power of our approach in approximating large deviation statistics of spatiotemporal patterns in stochastically-driven systems. Therefore, our approach might be utilized to study stochastic switching in neural field models of binocular rivalry [6, 17]. Since switching is brought about by a combination of adaptation as well as fluctuations, multiple timescale methods could be combined with our small noise approximation to calculate the distribution of switching times [3]. Furthermore, our nonlinear theory may be useful in describing the stochastic motion of more intricate spatiotemporal patterns in detail. Neural fields with slow adaptation are known to support spiral waves patterns [24], and the methods developed here could be employed to study how noise shapes the angular velocity and tip location of spiral waves coupled to external stimuli or other patterns.

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